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GEOGRAPHIC VARIATION IN *ANOLIS DISTICHUS* COPE (LACERTILIA, IGUANIDAE) IN THE BAHAMA ISLANDS AND HISPANIOLA

ALBERT SCHWARTZ[1]

ABSTRACT

Anolis distichus is widely distributed in the Bahama Islands and Hispaniola, including the Hispaniolan satellite islands of Ile-à-Vache, Grande and Petite Cayemite, Isla Catalina, and Isla Saona. Analysis of variation in head scutellation, body color and chromatic repertory, and dewlap pigmentation shows that *A. distichus* is divisible into the following subspecies: *A. d. distichus*—Bahama Islands: New Providence, Exuma Cays, Long Island, Ragged Islands; *A. d. distichoides*—Bahama Islands: Andros; *A. d. biminiensis*—Bahama Islands: South Bimini; *A. d. dapsilis* new subsp.—Bahama Islands: Eleuthera; *A. d. ocior* new subsp.—Bahama Islands: Rum Cay and San Salvador. The status of the Cat Island populations is questionable. On Hispaniola, *A. distichus* has been divided into the following subspecies: *A. d. dominicensis*—most of Haiti and the northern half of the República Dominicana; *A. d. ignigularis*—central southeastern República Dominicana; *A. d. properus* new subsp.—extreme eastern República Dominicana; *A. d. sejunctus* new subsp.—Isla Saona; *A. d. tostus* new subsp.—Isla Catalina; *A. d. ravitergum* new subsp.—south central República Dominicana; *A. d. favillarum* new subsp.—Sierra de Baoruco in southwestern República Dominicana; *A. d. aurifer* new subsp.—central portion of Tiburon Peninsula in southwestern Haiti; *A. d. vinosus* new subsp.—southwestern portion of Tiburon Peninsula; *A. d. suppar* new subsp.—extreme tip of Tiburon Peninsula; *A. d. patruelis* new subsp.—Ile Grande Cayemite. *A. d. floridanus* has been re-established as a valid name for the continental Florida populations which do not agree with their Bahaman relatives; it is suggested that *floridanus* is in actuality a Bahaman form from the western portion of Andros Island. An extensive history of *A. distichus* is presented to account for the distribution and variation in the species.

INTRODUCTION AND ACKNOWLEDGMENTS

Anolis distichus Cope is a rather small and stocky anoline lizard which occurs throughout the islands of the Great Bahama Bank, Rum Cay and San Salvador, on Hispaniola and some of its satellite islands, and in Florida. The species was first described in 1861 from New Providence Island in the Bahamas. In 1863, Reinhardt and Lütken named *Anolis dominicensis* from Hispaniola and, although recognizing the similarities between the two species, considered *dominicensis* specifically distinct from *distichus*. Barbour (1937) apparently first combined the two species (as *A. d. distichus* and *A. d. dominicensis*). This

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combination was followed by Mertens (1939) and Cochran (1941); Mertens gave a thorough review of the subspecies of *A. distichus* which had been described in the 76 years between the naming of *A. dominicensis* and 1939. These subspecies include *altavelensis* Noble and Hassler (Isla Alto Velo off Cabo Beata, República Dominicana), *caudalis* Cochran (Ile de la Gonâve, Haiti), *juliae* Cochran (Ile-à-Vache, Haiti), and *wetmorei* Cochran (Isla Beata, República Dominicana), as well as *distichoides* Rosén (Andros Island, Bahama Islands). Mertens himself named two new subspecies from the República Dominicana (*ignigularis* and *albidogularis*) and resurrected *brevirostris* Bocourt as applicable to specimens from the vicinity of Barahona in the southwestern República Dominicana. Finally, Oliver (1948) described *A. d. biminiensis* from South Bimini Island in the western Bahamas and Smith and McCauley (1948) named *A. d. floridanus* from southern Florida. Thus, as presently understood, there are 12 subspecies of *A. distichus* recognized, of which three are Bahaman, eight occur on Hispaniola and its associated islets, and one is on the North American continent.

The present paper is a result of collections made by myself and parties in both the Bahama Islands and Hispaniola and of specimens and information gathered by Dr. Ernest E. Williams at the Museum of Comparative Zoology at Harvard University under grants from the National Science Foundation, B-16066 and GB-2444, and from the American Philosophical Society. Dr. Williams, who has for some time been involved with Hispaniolan anoles, recognized that some of the forms associated with *A. distichus* in actuality pertain to another (and similar) species, *A. brevirostris*. He suggested that he and I jointly work out the variation in *A. distichus* on Hispaniola as part of a rather extensive paper dealing with new data which have accumulated concerning these lizards on that island. But because of other duties, Dr. Williams has agreed to a partition of the larger work and has also suggested that I summarize the new information on *A. distichus* by myself. His collections of anoles made in Haiti and my own collections from the República Dominicana supplement one another very nicely, so that a more or less complete picture of the situation of *A. distichus* on the entire island of Hispaniola is now much more possible than heretofore. There are still certain gaps in our knowledge, and these will be pointed out in their proper places.

Most specimens which I have examined are in the Albert Schwartz Field Series (ASFS); a more limited amount of material has been borrowed from the American Museum of Natural History (AMNH), Carnegie Museum (CM), Field Museum of Natural History (FMNH), Museum of Comparative Zoology (MCZ), Richard Thomas (RT), University of Florida, Florida State Museum (UF/FSM), Museum of Zoology, University of Michigan (UMMZ), and United States National Museum (USNM). I am grateful to the following curators and their assistants for the loan of this supplemental material: Charles M. Bogert and George W. Foley, Neil D. Richmond, Robert W. Inger and Hymen Marx, Ernest E. Williams, Wayne King, Charles F. Walker, Doris M. Cochran and James A. Peters. Paratypes of new subspecies have also been deposited in the Academy of Natural Sciences of Philadelphia (ANSP), Museum of Natural History, University of Kansas (KU), and the University of Illinois Museum of Natural History (UIMNH). Since coloration and pattern play such a major role in differentiating the various subspecies of *A. distichus*, I have not considered it worthwhile to borrow all the available specimens of the species which exist in collections. Many of these older specimens are long preserved and now much faded. I have attempted to examine all material which might be assignable to new taxa proposed herein, and have examined all specimens which are designated as paratypes. Lists of referred specimens in several cases include localities and museum numbers (MCZ) which I assign to certain taxa on the basis of provenance; specimens so listed have not been examined by myself. ASFS specimens have of course been studied in detail. The probability is high that almost all lizards listed as referred specimens are correctly designated subspecifically, since they have come from areas whose borders are delimited by fresh material which I have examined. Exceptional instances or uncertain allocations are noted in the text.

In the field I have had the capable assistance of Patricia A. Heinlein, Ronald F. Klinikowski, David C. Leber, Dennis R. Paulson, and Richard Thomas. Mr. Thomas succeeded in securing two distinctive subspecies of *A. distichus* on Isla Saona and Ile Grande Cayemite for me, and Messrs. Paulson and C. Rhea Warren made especial efforts to secure these lizards when they visited Cat Island, San Salvador, and Long Island on my behalf. Mr. Warren has also donated specimens collected by himself on South Bimini Island and in southern Florida. Carefully taken color notes from living specimens have been indispensable, and frankly, without them, the variational picture of *A. distichus* throughout its range would be impossible to interpret; I therefore wish to commend the efforts of others in this particular matter of information on fresh material, without which parts of the present paper would be in doubt.

I am particularly in the debt of David C. Leber, whose water color portraits of the various subspecies of *Anolis distichus* aid greatly in the visualization of the color differences in these lizards. Plates I and II are the result of Mr. Leber's work.[2] Of the 16 portraits, ten were executed in the field, often under trying circumstances; the remaining six were rendered from freshly preserved specimens and extensive color notes, at times additionally accompanied by Kodachrome transparencies. These latter portraits, completed under the critical eyes of myself and Richard Thomas (whose field notes are herewith gratefully acknowledged), are as accurate as those done in the field.

HISTORICAL SUMMARY

As noted in the introduction, there are 12 subspecies of *A. distichus*. However, these subspecies in actuality represent two species, whose prior names are *A. distichus* Cope and *A. brevirostris* Bocourt. Variation in the latter species, as well as its ecological interrelationships with *A. distichus*, are presently under study by Dr. Williams and need not concern us further here. In general, the two species are allotopic but broadly sympatric, although *A. distichus* is much more widely spread on Hispaniola than is *A. brevirostris*. In certain regions, however, the two species are precisely syntopic; in the most general terms, *A. brevirostris* inhabits xeric regions and *A. distichus* more mesic situations, but there are obvious and bold exceptions to this statement (for example, *A. distichus* on extremely hot and dry Isla Catalina off the southern Dominican coast).

The named forms which are correctly associated with *A. brevirostris* are *caudalis* Cochran and *wetmorei* Cochran, whereas the balance of the subspecies (*dominicensis, ignigularis, albidogularis, juliae, distichoides, biminiensis, floridanus*) are correctly associated with *A. distichus*. The most trenchant scale difference between the two species is the absence of a "preoccipital" scale in *A. brevirostris* and its presence in *A. distichus*. Even this character is not constant in either species, since most specimens of *A. distichus* from South Bimini and many from Andros lack the "preoccipital" (primarily by fusion with the interparietal), and occasional specimens from other Bahaman Islands (most commonly from Eleuthera) lack the "preoccipital" either by fusion with the interparietal or by frag-

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[2] Publication of these plates has been made possible by N.S.F. grant GB-6944 to Ernest E. Williams.

mentation. Twenty-three *A. distichus* of a total of 1001 examined from Hispaniola and its satellites lack the "preoccipital," primarily by fragmentation (thus the area usually occupied by the "preoccipital" is crowded by a number of small scales) or by fusion with the interparietal—the latter being the less common condition. Of these 23 aberrant Hispaniolan *A. distichus*, none is from regions where *A. distichus* and *A. brevirostris* are sympatric, but three are from areas where *A. brevirostris* might be expected to occur (Llanos de Azua).

I have made no attempt to examine large series of *A. brevirostris* but have studied 46 specimens of this species from the Département de l'Ouest in Haiti (localities include the northern shore of the Golfe de la Gonâve, the Cul de Sac Plain and the southern coast in the Jacmel area) and the vicinities of Barahona and San Juan in the República Dominicana. In this lot of material, I find that the "preoccipital" is very variable in occurrence and shows an amount of variation equal to that in *A. distichus*. The scale is most often absent (fused or fragmented) in lizards from the Barahona area in the República Dominicana, but in Haitian material it is more often present, although at times tiny or small in size. The amount of overlap in size of the "preoccipital" in *A. distichus* and *A. brevirostris* is fairly broad, and there are many specimens of the latter that have a "preoccipital" as large as that of many specimens of the former. I do not interpret this condition as intergradation or hybridization, but as part of the variation of each species. There are pattern differences between the two species, since *A. brevirostris* has a pair of black nuchal spots, which is absent in *A. distichus*; no *A. brevirostris* ever assumes a green color, as do many subspecies of Hispaniolan *A. distichus*. As far as my observations are concerned, *A. brevirostris* is the smaller lizard, reaching a maximum snout-vent length in males of 47 mm, whereas *A. distichus* is generally larger, with the largest males of all races represented by large numbers having snout-vent lengths between 48 and 58 mm.

One name, *altavelensis*, has not been associated with either *A. distichus* or *A. brevirostris*. This form resembles *A. distichus* in having a "preoccipital," but, because of other differences, Dr. Williams suggests that it not be associated with this species and that it be considered as a species distinct from either *A. distichus* or *A. brevirostris*. The fauna of Isla Alto Velo presents consistent peculiarities when compared with that of adjacent Isla Beata and the Península de Barahona, and specific status for *A. altavelensis* is no exception, since both Isla Beata and the Península de Barahona south of the Sierra de Baoruco are inhabited solely by *A. brevirostris*. Thus *altavelensis*, with its "preoccipital," is unexpectedly like *A. distichus* (which occurs in this region exclusively in the Sierra de Baoruco and the eastern Massif de la Selle, and not in the lowlands or along the coast) rather than like *A. brevirostris*. Doubtless *A. altavelensis* has had a long independent history from the balance of *A. distichus*; a similar situation occurs in the Alto Velo *Leiocephalus* (which I have regarded as a peculiarly disjunct subspecies of the geographically removed *L. vinculum*; Schwartz, 1967).

The material on which the name *A. dominicensis* was based had as its provenance merely "Haiti"; Dr. Williams has examined the syntypes and assures me that they are indeed identical with those lizards which are currently called *A. d. dominicensis*, and not with *A. brevirostris*. With the description of several new mainland Hispaniolan subspecies of *A. distichus*, it is appropriate to restrict the type locality of *A. d. dominicensis* in order to clarify my concepts of that subspecies. I hereby designate Port-au-Prince, Département de l'Ouest, Haiti, as the type locality of *A. d. dominicensis*. It is not unlikely that the original specimens, collected by A. H. Riise, did indeed come from the vicinity of the capital of Haiti; Port-au-Prince has long

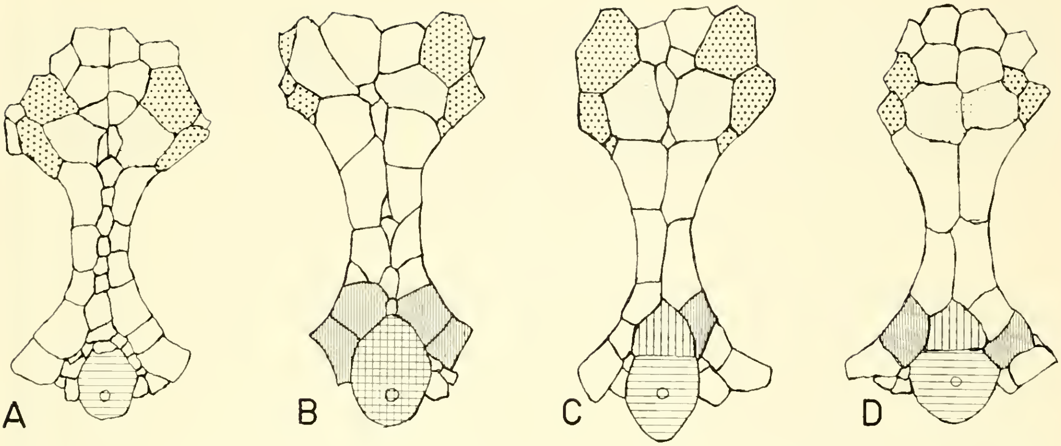

Figure 1. Partial dorsal views of heads of *Anolis distichus* showing modifications of head scales. Symbols: interparietal, widely spaced horizontal lines; "preoccipital," widely spaced vertical lines; supraorbitals in contact with interparietal, narrow vertical lines; median azygous head scales, dense stipple; postfrontals, open stipple; scales in lateral contact with postfrontals, heavy stipple.

A) ASFS 10283, Andros Island, Bahama Islands; 2/2 scales in lateral contact with postfrontals; supraorbital semicircles completely separated by a series of 10 median azygous head scales; "preoccipital" absent by fragmentation; 0/0 supraorbitals in contact with interparietal.

B) ASFS X4709, South Bimini Island, Bahama Islands; 3 scales in lateral contact with postfrontal on right side, left side abnormal; supraorbital semicircles in contact; 6 median azygous head scales; "preoccipital" absent by fusion with interparietal (denoted by overlap of symbols); 2/2 supraorbitals in contact with interparietal.

C) KU 93369, Carrefour Canon, Haiti; 3/3 scales in lateral contact with postfrontals; supraorbital semicircles in contact; 4 median azygous head scales, including "preoccipital" (denoted by shading); "preoccipital" present; 0/1 supraorbitals in contact with interparietal.

D) USNM 157924, 10 km W Baní, República Dominicana; 2/2 scales in lateral contact with postfrontals; supraorbital semicircles in contact; one (the "preoccipital," denoted by shading) median azygous head scale; "preoccipital" present; 1/1 supraorbitals in contact with interparietal.

been a prominent Caribbean seaport. Another possibility might be Cap-Haïtien, and assumption of this city as the source of the original *dominicensis* material would not alter my taxonomic conclusions, since I regard the populations of *A. distichus* at Cap-Haïtien as identical with those at Port-au-Prince. In favor of Port-au-Prince as the type locality of *dominicensis* is the (admittedly oblique) association of Riise with the type specimen of *Sphaerodactylus copei* Steindachner, a lizard which does occur in the environs of Port-au-Prince but not at Cap-Haïtien (see Schwartz and Thomas, 1965:317, for discussion of *S. copei*).

METHODS

When he described *A. d. biminiensis*, Oliver (1948) analyzed some Bahaman populations of *A. distichus* on the basis of various scale counts and relationships. Hoping that an application of his counts to non-Bahaman *A. distichus* might reveal differences other than coloration and pattern between various subspecies, I have followed his techniques and applied them to the material I have examined. Representations of several of the variant conditions are shown in Figure 1. The scale counts employed are:

1) Number of scales across the snout at the level of the second canthal scale. I follow Williams (1962:2) in making this count, in that the second canthal is reckoned from the anterior border of the orbit.

2) Number of loreal rows.

3) Scales between the supraorbital semicircles.

TABLE 1. SIXTEEN SUBSPECIES OF *Anolis distichus*, SHOWING STATISTICALLY SIGNIFICANT DIFFERENCES IN MEANS OF NUMBER OF MEDIAN AZYGOUS HEAD SCALES. SIZE OF SAMPLE IN FIRST COLUMN, MEANS AND TWO STANDARD ERRORS OF MEANS IN SECOND COLUMN. A PLUS IN TABLES INDICATES THAT THE TWO SUBSPECIES INVOLVED DIFFER SIGNIFICANTLY (NON-OVERLAP OF TWO STANDARD ERRORS OF MEAN); A MINUS INDICATES NO STATISTICAL DIFFERENCES. TWO SUBSPECIES (*sejunctus, tostus*) ARE NOT INCLUDED BECAUSE OF VERY SMALL SAMPLE SIZE.

	N	M	*distichus*	*distichoides*	*biminiensis*	*dapsilis*	*ocior*	*dominicensis*	*ignigularis*	*properus*	*ravitergum*	*favillarum*	*aurifer*	*vinosus*	*juliae*	*suppar*	*patruelis*	*floridanus*
distichus	126	6.0 ± .23	X	+	—	—	—	+	+	+	+	+	+	+	+	+	+	+
distichoides	160	8.7 ± .16		X	+	+	+	+	+	+	+	+	+	+	+	+	+	+
biminiensis	42	5.5 ± .78			X	—	—	+	+	+	+	+	+	+	+	+	—	+
dapsilis	101	6.2 ± .36				X	—	+	+	+	+	+	+	+	+	+	+	+
ocior	55	5.8 ± .49					X	+	+	+	+	+	+	+	+	+	+	+
dominicensis	235	3.9 ± .20						X	+	+	+	—	—	+	—	+	—	+
ignigularis	106	3.5 ± .08							X	+	+	—	—	—	—	—	+	+
properus	58	2.8 ± .16								X	—	+	+	+	—	+	+	+
ravitergum	49	2.6 ± .33									X	+	+	+	+	+	+	+
favillarum	26	3.8 ± .48										X	—	—	—	—	—	+
aurifer	64	3.7 ± .32											X	—	—	—	+	+
vinosus	100	3.4 ± .26												X	—	—	+	+
juliae	27	3.4 ± .46													X	—	+	+
suppar	174	3.4 ± .19														X	+	+
patruelis	25	4.6 ± .62															X	+
floridanus	90	7.9 ± .30																X

4) Number of rows of scales between supraorbital semicircles and interparietal scale. This figure is written as a fraction (i.e., 1/1, meaning that the interparietal is separated from the semicircles by one scale on each side). A count of 0/0 means that there are no scales between the semicircles and the interparietal, and that the semicircles and interparietal are thus in contact.

5) Number of subdigital lamellae on phalanges II and III of the fourth toe.

6) Number of scales bordering the postfrontal laterally (see Oliver, 1948:16, for drawings showing these scales in *A. distichus*). In a small number of specimens of *A. distichus*, the postfrontal may abnormally extend so far laterally as to make contact with one of the canthals. In such instances, I have not included the canthal as a scale in contact with the postfrontal, since the condition is obviously anomalous.

7) Number of median (usually azygous) scales posterior to the posteriormost paramedian pair of snout scales, usually restricted to the midline from the anterior border of the prefrontals posteriorly, and including the "preoccipital" as an unpaired median scale. Thus a count of 1, for example, means that between the anterior border of the postfrontals and the interparietal, there is only one scale (usually the "preoccipital"). A count of 0 occurs when the "preoccipital" is fused with the interparietal, provided that there are no additional median azygous scales. If some or all of the scales between the postfrontals are paired, but extremely irregularly so, the count includes these irregularly paired scales as median azygous scales, since they do not present the regular conformation of the paired paramedian snout scales of *A. distichus*. Table 1 shows the statistical significance of differences between subspecies in this character.

8) Number of supraorbital semicircle scales in contact with interparietal. This count is partly correlated with (4), the

TABLE 2. SIXTEEN SUBSPECIES OF *Anolis distichus*, SHOWING STATISTICALLY SIGNIFICANT DIFFERENCES IN MEANS OF NUMBER OF POSTMENTAL SCALES. SEE TABLE 1 FOR DETAILS.

	N	M	*distichus*	*distichoides*	*biminiensis*	*dapsilis*	*ocior*	*dominicensis*	*ignigularis*	*properus*	*ravitergum*	*favillarum*	*aurifer*	*vinosus*	*juliae*	*suppar*	*patruelis*	*floridanus*
distichus	127	5.5 ± .22	X	+	+	—	+	+	+	+	—	+	+	+	+	+	+	+
distichoides	159	4.6 ± .14		X	—	+	+	+	+	+	+	+	+	+	+	+	+	—
biminiensis	42	4.8 ± .20			X	+	+	+	+	+	+	+	+	+	+	+	+	—
dapsilis	105	5.2 ± .21				X	+	+	+	+	—	+	+	+	+	+	+	+
ocior	56	6.7 ± .28					X	—	+	—	+	—	—	+	—	+	+	+
dominicensis	240	6.6 ± .13						X	+	—	+	—	+	+	+	+	+	+
ignigularis	105	6.0 ± .29							X	+	—	—	+	+	+	+	+	+
properus	58	6.7 ± .38								X	+	—	—	+	+	+	+	+
ravitergum	56	5.6 ± .34									X	—	+	+	+	+	+	+
favillarum	28	6.1 ± .41										X	+	+	+	+	+	+
aurifer	62	7.2 ± .28											X	—	—	—	—	+
vinosus	98	7.4 ± .27												X	—	—	—	+
juliae	31	7.2 ± .47													X	+	—	+
suppar	171	7.9 ± .22														X	—	+
patruelis	25	7.8 ± .48															X	+
floridanus	89	4.4 ± .23																X

number of rows of scales between the semicircles and the interparietal; for instance, if the latter count is 1/1, the number of supraorbital scales in contact with the interparietal will of necessity be 0/0. However, if the count of (4) is 0/0 (i.e., there are no scales between the semicircles and the interparietals), then (8) may have a fairly wide fluctuation.

9) Number of postmental scales. Table 2 shows the statistical significance of differences between subspecies in this character.

10) Presence or absence of a "preoccipital."

The above counts have been taken on 1588 specimens from Florida, the Bahamas, and Hispaniola. Some of them have proved to be useful, primarily on a modal rather than an absolute level, in defining the subspecies. Very small samples often show such a wide diversity in some counts that it is impossible to state with certainty what the modal condition is, but with increasingly large samples, in most cases a distinct mode can be easily determined for each of the counts. The degree of overlap between the various counts for the different samples is often great, so that it is difficult to identify a particular lizard to subspecies on the basis of any single count. Reliance must be placed on such features as dewlap pattern and coloration, and coloration and pattern of the head and body.

Of the counts taken, those of scales across the snout, number of loreal rows, and lamellae overlap so broadly between the samples and are so variable *intra se* that they serve no useful purpose insofar as diagnosing the subspecies is concerned. The data for these counts are presented in each case, but merely for the sake of completeness.

BAHAMAN VERSUS HISPANIOLAN POPULATIONS AS A WHOLE

The only statement contrasting the differences (if any) between all the Bahaman populations of *A. distichus* versus all the Hispaniolan populations is that of Cochran (1941:146) who noted that "In adult examples of *distichus* there are distinct keels on the enlarged scales of the femur, while in *dominicensis* these scales are always smooth. . . ." Examination of large numbers of *A. distichus* indicates that no such dichotomy exists, and the two major geographic subdivisions cannot be distinguished on the basis of presence or absence of keeled scales on the anterior femoral face. Additionally, no other scale character will separate the two segments of *A. distichus* absolutely, but there are a few characters which generally differentiate the two sections.

1) There is a tendency for Bahaman populations to have the supraocular semicircles completely separated by a single median row of azygous head scales. This character reaches its greatest development in the populations from South Bimini and Andros in the Bahamas, but occurs casually in all other Bahaman samples. No Hispaniolan specimen shows this character.

2) All Bahaman populations but one have 0/0 scales between the semicircles and the interparietal as the modal condition, whereas in Hispaniolan samples there are either 0/0 or 1/1 scales modally between the semicircles and the interparietal, with 1/1 having the higher incidence by population.

3) Median head scales in the Bahamas vary in mean from 5.5 to 8.7, whereas in Hispaniola the means vary from 2.6 to 5.0—the highest mean being probably higher than it is in reality, since the sample is composed of only six lizards. Table 1 shows the data on head scales.

4) The absence of the "preoccipital" scale is most frequently encountered in Bahaman populations and occurs only very rarely in Hispaniolan *A. distichus*, as previously pointed out. All Bahaman populations from which I have examined samples have at least one or a few specimens which lack the "preoccipital" scale, whereas only a very few Hispaniolan *A. distichus* lack this feature.

Although none of the above is completely diagnostic of Bahaman versus Hispaniolan *A. distichus*, it does suggest that there has been a greater divergence between the two major segments of *A. distichus* than between intra-Bahaman and intra-Hispaniolan populations.

There is also one suggestive color difference between Bahaman and Hispaniolan *A. distichus*. With one exception, all Bahaman populations are incapable of a true green phase. The general coloration of Bahaman lizards is a pale ashy gray to sandy tan, capable of becoming dark wood brown, although this latter condition is rather rarely observed. Very occasionally Bahaman lizards are observed to be a very pale ashy green, but bright or dark green lizards, such as occur in several Hispaniolan populations, are unknown from the Bahamas. The one Bahaman exception is lizards from Rum Cay and San Salvador; on these two isolated islands, *A. distichus* is distinctively colored (in reference both to other Bahaman and to Hispaniolan populations) in that it is regularly a pea-green or yellow-green. In fact, the yellow component of the dorsal pigmentation may be more striking than the green hues. The Rum Cay-San Salvador lizards are the only populations in the Bahamas where *A. distichus* is known to be greenish rather than gray or tan.

Many Hispaniolan subspecies of *A. distichus*, on the other hand, do indeed have a green phase, the greens varying from bright to a pale ashy (which is much more distinctly green than any green observed in Bahaman lizards other than those on Rum Cay and San Salvador). Even this color repertory distinction between the two segments of *A. distichus* is not absolute, since some Hispaniolan subspecies are not known to be able to assume the green phase, and thus resemble the Bahaman populations.

As far as dewlap coloration and pattern are concerned, the Bahaman *A. distichus* are very like some of their Hispaniolan relatives. Although I have no quantitative data, the dewlaps of Bahaman *A. distichus* appear smaller than do those of the Hispaniolan lizards, but this may be merely an artifact of observation or preservation techniques. The dewlap pattern and coloration of Bahaman *A. distichus* resemble those of lizards from various Hispaniolan localities; the most aberrant dewlap pattern and colors occur in specimens from the extreme southwestern portion of the Tiburon Peninsula of Haiti and on its adjacent Ile-à-Vache.

SIZE AND NATURAL HISTORY

The largest specimens of *A. distichus* are from the southeastern uplands of Haiti. On the Montagne Noire in the vicinity of Peneau and Furcy, males reach a snout-vent length of 58 mm and females 48 mm. In general, in all populations, females reach a maximum size of about one centimeter less than males. The smallest of the maximally sized males (46 mm snout-vent length) are from Isla Catalina off the southern coast of the República Dominicana, and the smallest maximally sized female (38 mm) is from Isla Saona. However, the samples from both islands are very small (five males and one female from Saona; three males from Catalina), so that these comments are equivocal.

Etheridge (1966:351) stated that the largest Bahaman *A. distichus* he had examined had snout-vent lengths of 48 mm (New Providence, Andros, Cat) to 53 mm (Eleuthera). On the other hand, he noted that Hispaniolan specimens reached a maximum snout-vent length of about 50 mm. My own Bahaman data, based on 385 specimens in contrast to Etheridge's data for 126 specimens, do not agree with his Bahaman figures, since the maximally sized Eleuthera male (of 107 Eleuthera specimens) I have measured has a snout-vent length of 50 mm, slightly smaller than Etheridge's maximum for that island. The largest Bahaman males I have seen are from San Salvador and Rum Cay, and have snout-vent lengths of 53 mm, precisely the same as the largest male (from Eleuthera) examined by Etheridge. These discrepancies have little significance, but they indicate that populations on various Bahaman Islands do differ in maximum adult size.

A. distichus has a broad distribution on Hispaniola and is rivalled in this respect only by *Anolis ricordi* Duméril and Bibron, *Anolis cybotes* Cope, and *Anolis semilineatus* Cope. It occupies situations varying from mesic oases in otherwise extremely xeric regions (Cul de Sac–Valle de Neiba plain) to rain forest at high elevations; it even occurs in only slightly more shady areas within xeric areas themselves (vicinity of Monte Cristi, República Dominicana). Typically, *A. distichus* prefers shady and mesic forested or pseudo-forested situations, such as hardwood forests, coffee and cacao groves, mango-breadfruit-royal palm associations, overgrown and shady fencerows along abandoned fields, etc. In some areas it literally swarms, whereas in other and apparently quite similar areas it is extremely uncommon. *A. distichus*, in dense forest, often prefers large trees which extend above the lower canopy, and in cacao groves (where *A. distichus* and *A. cybotes* occur syntopically on the same trees), *A. distichus* in general seems to prefer the more exposed—and thus slightly more sunny—branches, although a mature cacao grove is inherently very deeply shaded and cool and often canopied by much larger forest trees. Sleeping *A. distichus* are not easily observed, as Rand (1962:11) pointed out. I saw none in Haiti in two months' fieldwork, and encountered the first sleeping individual near Miches in the República Dominicana; this lizard was on the upper surface of an herb leaf within two feet of the ground. In northwestern República Dominicana, near Palo Verde, in an extensive patch of flood plain hardwoods along the Río Yaque del Norte, Thomas and I encountered many *A. distichus* sleeping in company with *A. cybotes* and *A. chlorocyanus* Duméril and Bibron. Here *A. distichus* customarily slept on the leaves and twigs of small herbs and shrubs, within three feet of the ground, whereas both *A. cybotes* and *A. chlorocyanus* slept on the tips of small branches of saplings or on the tips of long and slender lianas and vines.

A. chlorocyanus slept distinctly higher in the canopy than *A. cybotes*, since no *A. chlorocyanus* was encountered below eight feet above the ground and most were above ten feet and inaccessible. Considering the occurrence at this locality of the vine-inhabiting and climbing snakes *Epicrates gracilis* Fischer and *Uromacer oxyrhynchus* Duméril and Bibron, the use of the tips of branches and pendant vines by *A. cybotes* and *A. chlorocyanus* is most suggestive; the distinctly lower and non-tree or vine associated sleeping sites for *A. distichus* may well have a distinct positive survival value in an area where these two primarily arboreal snakes are abundant.

A. distichus occurs in Hispaniola at elevations from below or near sea level (Valle de Neiba) to at least 6000 feet (1830 meters), in the Sierra de Baoruco, Massif de la Selle, and Cordillera Central.

In the Bahamas, *A. distichus* occurs with some frequency in hammock woods or coppice (South Bimini, New Providence), but also occupies (as Rand, 1962:4, noted for Hispaniolan *A. distichus*) isolated large and often gray-barked trees, such as *Ficus*, with whose bark coloration the Bahaman races blend excellently, and which additionally offer sanctuary among adventitious roots and buttresses. Other trees with which *A. distichus* is customarily associated in the Bahamas are *Coccoloba*, *Lysiloma*, and *Terminalia*; all have pale bark which renders the lizards inconspicuous. In Nassau, *A. distichus* occurs commonly on crannied limestone walls and street cutbanks, and on San Salvador the species was abundant about the ruins of Sandy Point House (= Watling's Castle), both on the surrounding trees and saplings and on the building itself.

On some Bahaman islands, *A. distichus* is quite common. Thus, it is abundant on New Providence and Eleuthera, for instance, and Oliver (1948:32) noted that C. M. Breder, Jr., secured a series of 164 *A. distichus* from native boys on Andros; my own observations on Andros do not indicate such a present abundance of *A. distichus*, however. On South Bimini, *A. distichus* is only moderately common; Oliver (*op. cit.*:22) secured 20 specimens from *Ficus* and *Coccothrinax*, but recent collectors have not secured these lizards so abundantly on South Bimini. At the other extreme of abundance lies Rum Cay, where *A. distichus* is distinctly uncommon; here the lizards were observed and collected primarily on *Cocos* palms and other trees in the settlement of Port Nelson, and only occasional individuals were observed away from human habitations. Only two individuals, both on Cat Island, have been noted sleeping in the Bahama Islands. Richard Thomas observed these lizards sleeping on small limbs, between 6 and 7 feet (± 2 meters) above the ground; one sleeping lizard was in a *Sabal* grove and the other in an open group of large trees surrounded by thorn scrub. Occasional individuals have been collected diurnally beneath rocks both inland and near the strand, so it is possible that Bahaman *A. distichus* resort also to such situations for nocturnal retreats.

Rand (1962) has summarized his observations on three Hispaniolan anoles (*A. distichus, A. cybotes, A. chlorocyanus*) both in the field in the República Dominicana and in the laboratory. My observations on *A. distichus* differ somewhat from his; for instance, he regarded this species as living "primarily on isolated trees and fence posts and along the edges of woods and trails in open woods." The abundance of *A. distichus* in Dominican cacao groves (admittedly an artificial situation) and in dense mesic woods high in the Cordillera Central is in contrast to Rand's statement. Such differences may well reflect different habits in different regions, and suggest that one species of anole may occupy varying habitats in different areas, and that extreme caution should be used in generalizing about the habitat preferences of geographically widely distributed anoles. It is also pertinent in this connection that Mertens (1939:15) reported the occurrence of *A.*

distichus (along with *A. cybotes*) in pine forest at Paso Bajito in the Cordillera Central. In the higher pine woods near Constanza, at elevations between about 4000 and 6000 feet (1220 and 1830 meters), *A. distichus* is at best rather rare, preferring in this region residual stands of rainforest. It has not been taken or observed in the vicinity of Valle Nuevo (about 8000 feet; 2440 meters) where *A. shrevei* Cochran is the commonest (and perhaps only) anole of the cool and open pine-forested slopes.

SYSTEMATIC ACCOUNT

Anolis distichus distichus Cope

Anolis distichus Cope, 1861, Proc. Acad. Nat. Sci. Philadelphia:208.

Type locality: New Providence Island, Bahama Islands.

Definition: A subspecies of *A. distichus* characterized by small size (males to 49 mm, females to 44 mm snout-vent length), dorsum pale ashy gray to sandy tan and without a green phase, dewlap pale yellow, rarely with a vague basal to more extensive orange blush, modally 0/0 scales between the supraorbital semicircles and the interparietal, 0/0 supraorbitals in contact with the interparietal, 2/2 scales in contact laterally with the postfrontals, and high mean number (6.0) of median azygous head scales.

Distribution: The Bahama Islands: known definitely from New Providence, the Exuma Cays (Warderick Wells Cay, Staniel [= Stanyard] Cay, Darby Cay), Great Exuma, Little Exuma, Long Island, and Great Ragged Island (Fig. 2).

Comments: *A. d. distichus* is widely distributed on the islands to the east of the Tongue of the Ocean on the Great Bahama Bank and presumably on the Ragged Islands. Specimens from Cat Island will be discussed later.

In life, *A. d. distichus* is normally a gray lizard, but some specimens are sandy tan in life. Occasional specimens demonstrate a boldly contrasting pattern of brownish black ground color with black crossbands; in this phase the snout is smudged with sooty black and the eyeskin is also sooty. Rarely some lizards show a very pale greenish gray phase. Although I have not so recorded it, I assume that *A. d. distichus* can become rich dark brown as can several of the other Bahaman subspecies. The dorsum is at best only very weakly longitudinally striate with darker, and there may be a single vague scapular chevron, its apex pointed posteriorly. The interocular dark bar is variable, but even when best expressed, is not especially prominent; other head markings are vague and ill defined. The venter is cream to very pale yellowish, and the underside of the tail is very pale yellow also. The dewlap is regularly pale yellow (Pl. 1). Rarely is there a basal orange blush; if present, the orange is extremely faint and only barely discernible. Very occasional specimens (Long Island) have the pale orange more extensive.

The islands to which I have attributed the nominate subspecies may be conveniently divided for further discussion into four areas: 1) New Providence, 2) the Exuma Cays, including Great and Little Exuma, 3) Long Island, and 4) Great Ragged Island. The samples from these four areas are alike in dorsal coloration and pattern and presumably in dewlap color (I have not seen live Ragged Island specimens), and on these bases I group them together. In scale characters, there are some differences which may be pertinent, but I have chosen not to emphasize them. The following data are from a series of 49 New Providence specimens, 16 from the Exumas, 57 from Long Island, and 10 from Great Ragged Island. I have seen living specimens from New Providence and Long Island, and freshly preserved material from the Exumas.

Long Island and Great Ragged Island specimens modally have 0/0 scales between the semicircles and the interparietal, and 0/0 is one of two bimodes (each with 20 specimens) on New Providence. In the

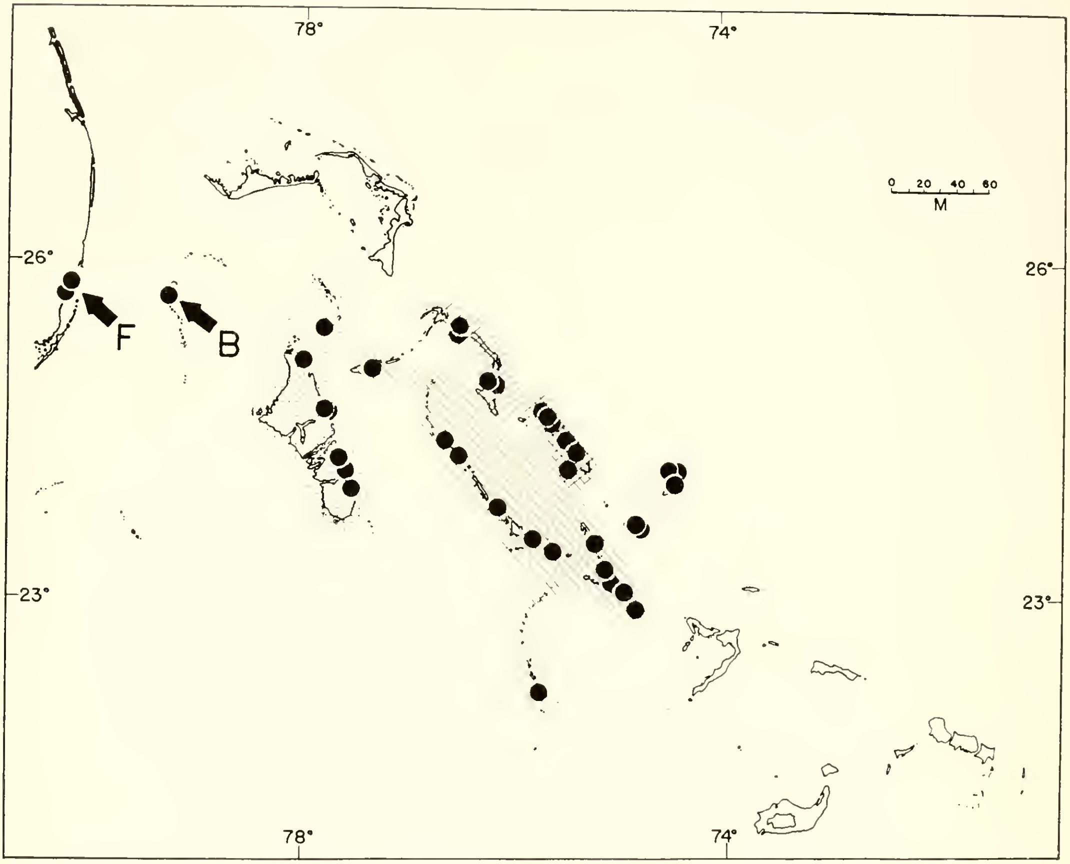

Figure 2. Map of the Bahama Islands, showing distribution of the subspecies of *Anolis distichus*; diagonal lines, upper left to lower right, *A. d. distichus*; diagonal lines, upper right to lower left, *A. d. dapsilis*; open stippling, *A. d. distichoides*; close stippling, *A. d. ocior*; F, *A. d. floridanus*; B, *A. d. biminiensis*; overlap of symbols for *A. d. distichus* and *A. d. dapsilis* suggests area of intergradation between these two subspecies.

specimens from the Exuma Cays, there are modally 1/1 scales between the semicircles and the interparietal. In number of supraorbitals in contact with the interparietal, 0/0 is the mode in all samples except that from Great Ragged, which has 1/1 modally (although 0/0 has a frequency of two lizards and 1/1 a frequency of three lizards). All samples modally have 2/2 scales in lateral contact with the postfrontals. The highest incidence of complete median separation of the supraorbital semicircles occurs on Long Island (four of 53 lizards), whereas New Providence has three of 46, the Exumas one of 16, and none occurs on Great Ragged. Scales across the snout range from 4 to 6 (New Providence), 8 (Exumas), or 7 (Long), and are either 5 or 6 on Great Ragged; modes 4 (New Providence), 5 (Great Ragged) and 6 (Exuma Cays, Long). Loreal rows vary from 3 to 5 on New Providence (mode 4), and 4 to 6 on the Exumas (mode 4) and Long (mode 5); loreal rows on Great Ragged are 4 or 5 (mode 4). Fourth toe lamellae vary from 15 to 20 (New Providence, the Exumas), 14 to 19 (Long), and 15 to 19 (Great Ragged), with modes of 18 in the former two samples and in the Great Ragged lizards, and 17 on Long Island. Median azygous head scales vary between 3 and 13 (mode 5, mean 6.2) on

New Providence, 3 and 9 (mode 5, mean 5.6) on the Exumas, 2 and 10 (mode 6, mean 5.9) on Long, and 3 and 10 (mode 6, mean 5.9) on Great Ragged. Postmentals vary from a low of 4 in all samples to 7 on New Providence, the Exumas, and Great Ragged, and 10 on Long. The mode is 4 on New Providence and the Exumas, and 6 on Long and Great Ragged. The means of postmentals are 5.0 (New Providence), 5.1 (Exumas), 5.4 (Long), and 5.3 (Great Ragged). The "preoccipital" is regularly present; one specimen from New Providence, one from the Exumas, one from Great Ragged, and four from Long lack this scale.

From the above data, it appears that a certain amount of divergence has taken place in the four areas which are inhabited by *A. d. distichus*. In general, the Exuma Cays material is closer in most counts to the lizards from New Providence (although the scales between the semicircles and the interparietal are a notable exception). The Long Island lizards, on the other hand, differ somewhat more. The sample from Great Ragged Island is too small for detailed comment. In the absence of any established chromatic or pattern differences, I place all four populations in the nominate subspecies, although I acknowledge the modal differences mentioned.

As noted above, *A. d. distichus* is common on New Providence, where it was observed abundantly in Nassau (especially on rock walls and exposed limestone street cuts), and on and about the limestone bluffs near the coast at Cave Junction. At the latter locality, the lizards occurred also on saplings and large *Ficus* about the bluffs, and on *Coccoloba* on the coast. In high coppice near Nassau East, *A. distichus* was extremely abundant, both on the trees and saplings and on an old rock wall which extended for some distance through the woods. The species is only moderately common in coppice on Great and Little Exuma.

Specimens examined: BAHAMA ISLANDS. *New Providence* (localities not mapped): Nassau, 23 (AMNH 76348–54 + 16); Cave Point, 3 (ASFS 10301–03); Cave Junction, 10 (ASFS V7206–15); 0.9 mi. (1.4 km) W Cave Junction, 2 (ASFS V7226–27); hills south of Lake Cunningham on Gladstone Road, 4 (ASFS V2092–95); Prospect Ridge, 2 (ASFS V2102–03); The Grove, 1 (ASFS V2104); Windsor Field, 1 (ASFS V2110); 0.6 mi. (1.0 km) NW Yamacraw Beach, 1 (ASFS V7242); 0.3 mi. (0.5 km) E Nassau East, 2 (ASFS V10638–39). *Exuma Cays*: Warderick Wells Cay, 3 (AMNH 76326–28); Staniel (=Stanyard) Cay, 5 (AMNH 76329–33); Darby Cay, 2 (AMNH 76334–35). *Great Exuma*: 3.2 mi. (5.1 km) NW George Town, 5 (ASFS V7033–36, ASFS V7053). *Little Exuma*: 5.7 mi. (9.1 km) SE The Ferry, 1 (ASFS V7043). *Long Island*: Simm's, 2 (MCZ 42282–83); Gray's Settlement, 5 (ASFS V8562–64, ASFS V8567–68); 2 mi. (3.2 km) E Gray's Settlement (not mapped), 3 (ASFS V8579–81); Deadman's Cay Settlement, 5 (UMMZ 115596); Clarence Town, 37 (MCZ 37986–95, MCZ 86931–53, UMMZ 80510–2 specimens, FMNH 25372–73); 3.6 mi. (5.8 km) SE Clarence Town (not mapped), 4 (ASFS V10835–38); Roses, 1 (FMNH 22750). *Great Ragged Island*: Duncan Town, 10 (UMMZ 118008–6 specimens; UMMZ 118009–4 specimens).

Anolis distichus distichoides Rosén

Anolis distichoides Rosén, 1911, Lunds Univ. Arrskr. N.F., Afd. 2, 7(5):29.

Type locality: Stanniard Creek, Andros Island, Bahama Islands.

Definition: A subspecies of *A. distichus* characterized by moderate size (males to 51 mm, females to 43 mm snout-vent length), dorsum grayish tan to gray and without a green phase, entire dewlap orange to yellowish-orange, modally 1/1 scales between the supraorbital semicircles and interparietal, 0/0 supraorbitals in contact with the interparietal, 2/2 scales in contact laterally with the postfrontals, and very high mean number (8.7) of median azygous head scales correlated with the high incidence (about 50 per cent) of complete separation of supraorbital semicircles medially.

Distribution: The Bahama Islands: known from Andros Island (including Mangrove Cay) and the Berry Islands (known definitely from Frazer's Hog Cay) (Fig. 2).

Comments: The status of *A. d. distichoides* has been disputed in the past. The main claim for its recognition has been the orange dewlap (Pl. I), in contrast to the yellow dewlap of topotypical *A. d. distichus*. Although I have collected very few *distichoides* (as pointed out previously, I have observed it rarely on Andros), those males which I have seen in life have had an orange dewlap consistently. Scale data from 161 *A. d. distichoides* show the following: snout scales 4 to 8 (mode 6), loreal rows 4 to 6 (mode 5); supraorbital semicircles in contact in 108 specimens and completely separated by median azygous head scales in 51 lizards; modally 1/1 scales between semicircles and interparietal and 0/0 supraorbitals in contact with interparietal; 2/2 scales in lateral contact with postfrontals; fourth toe lamellae 15 to 21 (mode 18); median azygous head scales 3 to 14 (mode 9, mean 8.7); "preoccipital" more often present (84 lizards) than absent (74 lizards); postmentals 2 to 8 (mode 4, mean 4.6). The almost equal incidence of presence or absence of the "preoccipital" is noteworthy, although more *distichoides* have this scale than lack it. The high mean of median head scales is correlated with the high frequency of complete separation of the semicircles. No other subspecies of *A. distichus*, either Bahaman or Hispaniolan, has so high a mean, although it is approached most closely (7.9) by the mainland populations of *A. d. floridanus*. South Bimini *A. distichus* likewise have a high incidence of complete semicircle separation, but the mean number of median head scales is much lower (5.5).

The above scale features, especially the high number of median head scales and the high incidence of absence of the "preoccipital," as well as the frequent separation of the supraorbital semicircles, all differentiate *distichoides* from the nominate subspecies. Adult male *A. d. distichus* are also slightly smaller and have a yellow rather than orange or yellow-orange dewlap. Both subspecies resemble each other in dorsal color, although I have not noted *distichoides* being tan in life. As in the nominate subspecies, head markings are suppressed or absent in *distichoides*; the interocular bar is not prominent when present and is often absent. There may be a series of four dorsal chevrons, but these are often obscure or absent, and the degree of dorsal dark striation is likewise variable, with a strong tendency for the lizards to lack striae.

A. d. distichoides is the only Bahaman subspecies which modally has 1/1 scales between the semicircles and the interparietal. Sixty-five lizards fall into this category. On the other hand, 61 lizards have 0/0 scales between the semicircles and the interparietal, so the modality is not strong. The virtually bimodal condition in this scale character is not obviously due to the samples involved; since Andros is a very large island (nearly 100 miles long and up to 40 miles wide) and is much dissected by bights and minor waterways, it was conceivable that the two modalities were due to the pooling of data from two populations which are divergent in this character. This is not the case, since most of the *distichoides* sample under study are from Mangrove Cay, and within this lot of lizards the bimodality is clearly shown.

The size of Andros and the inaccessibility of its west coast is possibly significant in another matter. There is but a single *A. distichus* available from the entire west coast of Andros. This is a female (UF/FSM 18005); its sex precludes knowledge of dewlap color and its geographic uniqueness prevents an assessment of the characters of the populations whence it was taken. The specimen is mentioned here and listed below as *A. d. distichoides*, but for several reasons I suspect that the population whence it was derived in actuality represents *A. d. floridanus*. Further comment upon this lizard will be made in the discussion of the history of the latter subspecies.

The occurrence of *A. d. distichoides* on the Berry Islands has not been previously reported. Two specimens from Frazer's Hog Cay collected by Richard Thomas are clearly referable to this subspecies; one is a male with an orange dewlap and the other a female. The male has the semicircles completely separated by a median row of 8 scales, and both lizards lack the "preoccipital." Possibly these two lizards might be better associated with the subspecies on South Bimini, but I consider them *distichoides* on the basis of provenance and the affinities of the Berry Islands fauna.

Specimens examined: BAHAMA ISLANDS. *Andros Island*: no further locality, 22 (UMMZ 80369–4 specimens, UMMZ 80377–11 specimens, 80381–6 specimens, UMMZ 80384); Morgan's Bluff (not mapped), 7 (UF/FSM 17626, UF/FSM 17628, UF/FSM 17630–32, UF/FSM 17634, UF/FSM 17637); ca. 0.5 mi. (0.8 km) N Nicholl's Town, 1 (ASFS V6972); Nicholl's Town (not mapped), 1 (UF/FSM 18013); Coakley Town, 4 (MCZ 41986–89); south side, mouth of Fresh Creek, 10 (ASFS 10280–86, UMMZ 115598–3 specimens); Mangrove Cay, 103 (MCZ 42013 + 15 untagged specimens, AMNH 63073–19 specimens, UMMZ 260210–4 specimens, UMMZ 109223–5 specimens, UMMZ 115597–34 specimens, plus 25 untagged specimens from AMNH 63067); south side, South Bight, 1 (MCZ 42001); Little Creek, 5 (UMMZ 118006); Pure Gold (not mapped), 15 (MCZ 42026–29 + 11 specimens); west coast, 2 mi. (3.2 km) at 55° from mouth of Deep Creek (not mapped), 1 (UF/FSM 18005). *Berry Islands*: Frazer's Hog Cay, 2 (ASFS V10667–68).

Anolis distichus biminiensis Oliver

Anolis distichus biminiensis Oliver, 1948, Amer. Mus. Novitates, No. 1383:16.

Type locality: Western end of South Bimini Island, Bahama Islands.

Definition: A subspecies of *A. distichus* characterized by small size (males to 50 mm, females to 44 mm snout-vent length), dorsum pale gray and without a green phase, dewlap orange, modally 0/0 scales between the supraorbital semicircles and the interparietal, 2/2 supraorbitals in contact with the interparietal, 3/3 scales in contact laterally with the postfrontals, and high mean number (5.5) of median azygous head scales.

Distribution: The Bahama Islands: known only from South Bimini (Fig. 2).

Comments: At the time of the description of *A. d. biminiensis*, Oliver had twenty specimens of this subspecies. Additional lizards taken since that time confirm his diagnosis of the race. Most striking, in comparison with all other subspecies, is the postfrontal contact with 3/3 scales laterally and the modal 2/2 supraorbitals in contact with the interparietal. Data for the series of 44 specimens are: snout scales 4 to 6 (mode 4), loreal rows 4 to 6 (mode 5); supraorbital semicircles in contact in 30 specimens and completely separated by median azygous head scales in 13 lizards; modally 0/0 scales between semicircles and interparietal and 2/2 supraorbitals in contact with interparietal; fourth toe lamellae 14 to 19 (mode 16); median azygous head scales 1 to 10 (mode 5, mean 5.5); "preocciptal" usually absent (41 of 44 lizards; see comments below); postmentals 4 to 6 (mode 5, mean 4.8). Of the three lizards which have the "preoccipital" present, in one (AMNH 68638) the scale is very tiny and in the second (AMNH 68637) the scale which I consider the "preoccipital" may in actuality be a fragment of the interparietal. Only in one lizard (CM 32552) is there an unequivocal "preoccipital" present. In having such a high percentage of absence (by fusion) of the "preoccipital," *biminiensis* stands alone among all subspecies of *A. distichus.*

Aside from the scale characters noted above, *A. d. biminiensis* differs from *A. d. distichus* in the color of the dewlap—orange in the former (Pl. 1) and yellow in the latter. In this feature *biminiensis* resembles *distichoides*; it seems very likely that the population on South Bimini is a direct derivative of *distichoides* on Andros, with resulting intensification by isolation of some of the characters of the Andros subspecies.

A. d. biminiensis usually is a gray lizard, but it is capable of turning a rich velvety brown. The shade of the orange dewlap is that of plate 9 I 10 and plate 10 L 9; all color designations are from Maerz and Paul, 1950. The venter is creamy to whitish or grayish, and the underside of the tail and hindlimbs has been noted as pale yellow (pl. 17 J 1). Head markings and dark body striae are usually obsolete, but the interocular bar is at least often indicated, and young lizards show both the interocular bar and an occipital dark V.

Oliver (1948:22) noted that *A. d. biminiensis* was encountered at low heights on light gray colored trees such as *Ficus* and *Coccothrinax.* More recently *biminiensis* has been collected on trees in hammock woods (high coppice) as well as on isolated *Ficus.* The absence of *A. distichus* from North Bimini is puzzling. Sutcliffe (1952) did not report the species from North Cat Cay south of South Bimini in the chain, but Wayne King advises me that he has collected the species in this chain but the specimens have been lost. Presumably the absence of *A. d. biminiensis* from North Bimini (paralleled by that of *Sphaerodactylus decoratus flavicaudus* Barbour, which also occurs, among the Biminis, only on South Bimini) is due to a fluke of colonization from Andros, and the lizards have been unable to cross even the narrow water gap between South and North Bimini.

Specimens examined: BAHAMA ISLANDS. *South Bimini*: no other locality, 3 (MCZ 80132–34); western end, 12 (ASFS X4709–15, ASFS X4721–24, ASFS X4932); western part, 2 (ASFS V10750–51); west end, 27 (AMNH 68637–38 + 6 specimens, AMNH 68639 + 8 specimens, MCZ 49739–40, UMMZ 118303, CM 34118–20, CM 32549–52).

Anolis distichus dapsilis[3] subsp. n.

Holotype: MCZ 81139, an adult male, from ocean side, opposite Hatchet Bay, Eleuthera Island, Bahama Islands, one of a series taken 15 June 1966 by Richard Thomas. Original number V10385.

Paratypes (all from Eleuthera Island, Bahama Islands): ASFS V10386–405, same data as holotype; ASFS 17144–49, Alicetown, 23 October 1961, native collector; ASFS 17167–74, Alicetown, 24 October 1961, native collector; ASFS 17176–82, Alicetown, 25 October 1961, native collector; AMNH 96509–15, ANSP 27163–69, CM 40623–29, KU 93380–86, MCZ 92001–08, UIMNH 61696–700, UF FSM 21526–33, USNM 160692–99, Alicetown, 26 October 1961, native collector; ASFS 17498–500, Alicetown, 30 October 1961, native collector; ASFS 17151, Hatchet Bay (not mapped), 24 October 1961, A. Schwartz; ASFS V6799–800, 4 mi. (6.4 km) N Rock Sound, 2 October 1965, R. Thomas; ASFS V6864, 4 mi. (6.4 km) NW, thence ca. 2 mi. (3.2 km) E Rock Sound, 5 October 1965, R. Thomas; ASFS V6811, Southeast Point, 4 October 1965, R. Thomas.

Definition: A subspecies of *A. distichus* characterized by small size (males to 50 mm, females to 45 mm snout-vent length), dorsum pale ashy gray with a yellowish cast and without a green phase, dewlap orange with occasionally a very narrow yellow border, modally 0/0 scales between the supraorbital semicircles and the interparietal, 0/0 and 1/2 supraorbitals in contact with interparietal, 2/2 scales in contact laterally with the postfrontals, and

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[3] From Latin, *dapsilis*, plentiful.

high mean number (6.2) of median azygous head scales.

Distribution: The Bahama Islands: known only from Eleuthera Island (Fig. 2).

Comments: The holotype has the following measurements and scale counts: snout-vent length 50 mm, tail 42 mm, distal half regenerated; 4 scales across snout, 4 loreal rows, semicircles in contact, 0/0 scales between supraorbital semicircles and interparietal, 2/2 supraorbitals in contact with interparietal, 2/2 scales in lateral contact with postfrontals, 15 fourth toe lamellae, 4 median azygous head scales, "preoccipital" present, 4 postmentals.

Scale counts for the series of 107 *A. d. dapsilis* are: snout scales 4 to 7 (mode 6), loreal rows 3 to 5 (mode 4); supraorbital semicircles in contact in 99 specimens and completely separated by median azygous head scales in six lizards; modally 0/0 scales between semicircles and interparietal and 0/0 and 1/2 (both with 24 lizards) supraorbitals in contact with interparietal; 2/2 scales in lateral contact with postfrontals; fourth toe lamellae 14 to 20 (mode 17); median azygous head scales 2 to 11 (mode 6, mean 6.2); "preoccipital" usually present (93 of 107 lizards); postmentals 4 to 9 (mode 6, mean 5.2).

The dorsum of *A. d. dapsilis* is usually pale ashy gray with a yellowish cast, and the head in adults regularly lacks any darker markings, including the interocular dark bar. In subadults and juveniles, the interocular bar and occipital V are somewhat more obvious. The dorsum lacks longitudinal dark striae but may be vaguely streaked with darker gray. The dewlap is completely orange, or orange with a very narrow yellow edge; hues noted for the dewlap are those of plate 11 C 10 and plate 10 E 12, and the yellow border has been noted as that of plate 10 H 3. The eye ring is white and the eye skin gray or tan, the latter in contrast to the gray head and dorsum. There is no evidence that *dapsilis* has a dark brown phase, but I assume that this color occurs. One lizard was recorded as being pale gray with a very faint greenish cast when caught.

A. d. dapsilis differs from *A. d. distichus* in dewlap color (orange versus pale yellow) and in reaching a very slightly larger size; in this latter context, Etheridge (1966: 351) reported 48 mm as the maximum size for New Providence specimens and 53 mm as a maximum on Eleuthera. Although none of the 107 *A. d. dapsilis* examined by me is so long as that reported by Etheridge, his data indicate that *dapsilis* is even larger than *A. d. distichus*.

The Eleuthera subspecies resembles *distichoides* and *biminiensis* in dewlap color. It differs from these two more western subspecies in several ways: the 2/2 lateral postfrontal contact separates *dapsilis* from *biminiensis* with 3/3, and the higher mean number of median head scales (8.7) in *distichoides* differentiates that form from *dapsilis* (with 6.2). *A. d. biminiensis* and *A. d. distichoides* both have the supraorbital semicircles more often separated than does *dapsilis*, and both the western subspecies more regularly lack the "preoccipital."

The holotype and paratopotypes from the ocean side of Eleuthera at Hatchet Bay were taken from saplings around the edges of an abandoned and overgrown *Cocos* grove. The specimens from Alicetown were from an edificarian situation. *A. d. dapsilis* is common on Eleuthera; I observed many at Hatchet Bay Plantation on isolated *Lysiloma* trees on the lawns and in high coppice between Hatchet Bay and The Glass Window. Considering the quantity of specimens examined by me, as well as many more in collections which I have not studied, *A. d. dapsilis* must be the commonest subspecies of *A. distichus* in the Bahamas.

Anolis distichus ocior[4] subsp. n.

Holotype: MCZ 81140, an adult male, from Port Nelson, Rum Cay, Bahama Islands, one of a series taken 20 June 1966

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[4] From Latin, *ocior*, more rapid.

by Albert Schwartz and Richard Thomas. Original number V10488.

Paratypes (all from Rum Cay, Bahama Islands): ASFS V10489–90, ASFS V10493–94, MCZ 81147–48, same data as holotype; ASFS V10418–21, Summer Point, 17 June 1966, R. Thomas; ASFS V10446, Port Nelson, 17 June 1966, R. Thomas; ASFS V10473, Summer Point, 18 June 1966, R. Thomas.

Associated specimens: BAHAMA ISLANDS. *San Salvador* (localities not mapped): no further locality, 7 (MCZ 36729–31, FMNH 222, FMNH 225–26, FMNH 263); Cockburn Town, 19 (ASFS V2277, ASFS V2279–81, ASFS V2297–302, ASFS V2355–60, ASFS V2285); 4.2 mi. (6.7 km) N Cockburn Town, 1 (ASFS V10572); 9.9 mi. (14.9 km) by road N Cockburn Town, 1 (ASFS V10539); 7.1 mi. (11.4 km) N Cockburn Town, 1 (ASFS V2292); 1.2 mi. (1.9 km) N Dixon Hill, 1 (ASFS V2278); Dixon Hill, 3 (ASFS V2286–88); Sandy Point House, 7.6 mi. S Cockburn Town, 10 (ASFS V10559–67, RT 1464); 2.3 mi. (3.7 km) E Watling's Castle (= Sandy Point House), 1 (ASFS V2339); *Green Cay*, 1 (ASFS V10625); *Man Head Cay*, 1 (ASFS V2337).

Definition: A subspecies of *A. distichus* characterized by moderate size (males to 53 mm, females to 48 mm snout-vent length), dorsum yellow-gray to brown with a prominent pale flank stripe between the fore- and hindlimbs bordered above and below by dark brown or gray and with a pea-green phase, dewlap pale yellow, modally 0/0 scales between the supraorbital semicircles and the interparietal, 1/1 supraorbitals in contact with the interparietal, 2/2 scales in contact laterally with the postfrontals, and high mean number (5.8) of median azygous head scales.

Distribution: The Bahama Islands: known from Rum Cay and San Salvador, including its satellites Green Cay and Man Head Cay (Fig. 2).

Comments: The holotype has the following measurements and scale counts: snout-vent length 53 mm, tail ca. 90 mm; 6 scales across snout, 4 loreal rows, semicircles in contact, 1/1 scales between supraorbital semicircles and interparietal, 0/0 supraorbitals in contact with interparietal, 3/3 scales in lateral contact with postfrontals, 19 fourth toe lamellae, 7 median azygous head scales, "preoccipital" present but somewhat fragmented, 7 postmentals.

Scale counts for the series of 59 *A. d. ocior* are: snout scales 4 to 8 (mode 6), loreal rows 3 or 4 (mode 4); supraorbital semicircles in contact in 49 specimens and completely separated by median azygous head scales in nine lizards; modally 0/0 scales between semicircles and interparietal and 1/1 supraorbitals in contact with interparietal; 2/2 scales in lateral contact with postfrontals; fourth toe lamellae 15 to 19 (mode 17); median azygous head scales 2 to 10 (mode 6, mean 5.8); "preoccipital" usually present (55 of 57 specimens); postmentals 5 to 9 (mode 7, mean 6.7).

Dorsally, Rum Cay *A. d. ocior* varies from unstriate gray to brown, but most specimens observed were some shade of green, from a grayish pastel green to a rich pea-green. There is a complete cream labial stripe which extends above the shoulder and continues down the flank between the fore- and hindlimbs and is bordered both above and below by dark gray (dark gray-green in the green phase) or brown. The green phase of *ocior* is fairly bright, but not so bright a green as, for example, *Anolis carolinensis*. In the green phase there are no head markings, but an occipital V is often present in the gray phase. The dewlap is yellow (Pl. 1). The venter is a rich yellowish tan in all phases, slightly brighter (more yellow) under the tail and along the lower lips.

Specimens from San Salvador differ from those from Rum Cay described above in that they do not show the green phase so consistently nor quite so brightly. The cream subocular mark is conspicuous, and the flank stripe is present but not so distinct nor so regularly bordered with darker as in

Rum Cay lizards. The dewlap is yellow on San Salvador. In scutellation, Rum Cay and San Salvador specimens are completely comparable in both modes and means in all counts taken; the largest female (48 mm) is from the small series from Rum Cay, whereas the largest female from the much longer San Salvador series is smaller (44 mm). I group the lizards from these two islands together, since it is apparent that they are derivative populations which together are more divergent from the balance of the Bahaman populations than they are from one another. Isolation on San Salvador and Rum Cay has resulted in some differentiation *in situ*, but not sufficient for nomenclatorial recognition.

A. d. ocior differs from all other Bahaman subspecies in having a green phase. From *biminiensis*, *distichoides* and *dapsilis*, *ocior* differs in having a yellow rather than an orange dewlap. The Rum Cay-San Salvador subspecies resembles *A. d. distichus* in dewlap color, but has 1/1 supraorbitals in contact with the interparietal in contrast to 0/0 in the nominate race, and also is larger and has a green phase, which *A. d. distichus* lacks. *A. d. ocior* is the only Bahaman subspecies with 1/1 supraorbitals in contact with the interparietal, and has the highest mean number of postmentals (6.7) of any Bahaman subspecies; the highest postmental mean other than that of *ocior* is that of *distichus* (5.5) among the Bahaman subspecies.

On Rum Cay, *A. d. ocior* is uncommon; all of our specimens were taken in edificarian situations, especially on *Cocos*, *Lysiloma*, and *Terminalia* in Port Nelson and on a *Lysiloma* near a cottage at Summer Point. Lizards were also observed on *Thrinax* palms near the beach, but not commonly. On San Salvador, *A. d. ocior* is more abundant, but is still not so common as is *A. d. distichus* on New Providence or *A. d. dapsilis* on Eleuthera, for instance. Specimens were collected on *Ficus* and *Terminalia* in Cockburn Town and were observed on exposed fence posts in company with *Anolis sagrei*; the latter species was more common in such situations. At Sandy Point House, *A. d. ocior* was extremely abundant on saplings about the ruins and on the walls of the ruins themselves. On Green Cay, *A. d. ocior* is moderately common on *Coccoloba* tangles, and the single lizard from Man Head Cay was taken under a flat rock among strand plants.

Rum Cay and San Salvador stand isolated from the Great Bahama Bank on two separate banks of their own. Rum Cay lies closest to Long Island (which is inhabited by *A. d. distichus*), whereas San Salvador is about equidistant from Long Island and Cat Island (but is closer to Rum Cay than to either of these). Aside from *Cyclura rileyi* Stejneger and *Leptotyphlops columbi* Klauber which are endemic to San Salvador, and *Sphaerodactylus corticola* Garman which occurs on both islands, the herpetofauna of Rum Cay and San Salvador is depauperate. Doubtless *A. d. ocior* has been a long resident of these two islands; it has diverged strikingly from the balance of the Bahaman subspecies.

CAT ISLAND

Cat Island, located on its own bank along with Little San Salvador, lies southeast of Eleuthera (which is inhabited by *A. d. dapsilis*), east of the Exuma Cays (which are inhabited by *A. d. distichus*) and northwest and west of Rum Cay and San Salvador (which are inhabited by *A. d. ocior*). I have examined 27 *A. distichus* from Cat Island, of which 14 were freshly taken by Dennis R. Paulson. These lizards I leave unassigned subspecifically, although I doubt that they merit nomenclatorial separation from the balance of the Bahaman subspecies.

In dorsal color and pattern, the Cat Island lizards resemble New Providence *A. d. distichus*. They do not have a green phase and thus are unlike *ocior*, but like *distichus* and *dapsilis*. The dewlap coloration is variable—more so than in any other

Bahaman race; in a single series, Paulson noted that three had pale yellow dewlaps, one had a yellow dewlap with an orange center, and the fifth had an orange dewlap with a narrow yellow edge. Thus, in dewlap color, the Cat Island lizards combine (are intermediate in?) the characters of both *distichus* and *ocior*, on the one hand, and *dapsilis*, on the other.

In the relationships between the interparietal and supraocular semicircles, the Cat Island lizards are not distinctive and resemble both *distichus* and *dapsilis* but not *ocior* (which modally has 1/1 supraorbitals in contact with the interparietal, in contrast to 0/0 or 1/2 in *distichus* and *dapsilis*). The "preoccipital" is absent in six of 24 lizards; this is a higher proportion than *dapsilis*, *distichus* or *ocior*. The mean of median head scales is 4.8, in strong contrast to 6.2 in *dapsilis*, 6.0 in *distichus*, or 5.8 in *ocior*. The postmental mean is 6.0, higher than both *distichus* and *dapsilis*, but lower than *ocior*. The postfrontal contact is bimodal, with both 2/2 and 3/3 having equal frequencies of eight lizards; there is also a strong tendency (as intimated by the bimode of 3/3) for Cat Island lizards to have 3/4 and 4/4 scales in contact laterally with the postfrontals (18 of 26 lizards have three scales in contact unilaterally), whereas counts above 2/3 are relatively uncommon in *distichus* (22 of 128 lizards), *dapsilis* (five of 102 lizards) and *ocior* (six of 59 lizards). Such high lateral postfrontal contact counts are more usually encountered in *biminiensis* (23 of 42 lizards). It should be recalled that 3/3 is the modal condition in *biminiensis*.

On the basis of dewlap color, it would seem appropriate to consider the Cat Island lizards intermediate between *distichus* and *dapsilis*, and the geographic position of Cat Island is in accord with a possibly double "invasion" of lizards from the islands to the northwest and west. I can see no *ocior* influence in the Cat Island lizards. In contrast to the situation with the dewlap color, the scale counts present a peculiar melange of characters which cannot reasonably be attributed to interaction of the two adjacent races. It is probable that Cat Island has been colonized at various times by both *distichus* and *dapsilis*, but that there has been imposed upon these two parent stocks other local differentiation on Cat Island, so that the Cat Island lizards resemble their parent stocks in some characters but have diverged considerably in others.

Specimens examined: BAHAMA ISLANDS. *Cat Island*: Orange Creek, 7 (ASFS V2145–51); Arthur's Town, 7 (MCZ 39580–83, UMMZ 79449); Bennett's Harbour, 4 (AMNH 76337–40); Tea Bay, 2 (ASFS V2159–60); The Bight, 5 (ASFS V2188–91, CM 20444); hills above The Bight, 1 (ASFS V2123); 1 mi. (1.6 km) S McQueen, 1 (AMNH 76336).

Anolis distichus dominicensis Reinhardt and Lütken

Anolis dominicensis Reinhardt and Lütken, 1863, Vid. Medd. Nat. Foren. Kjobenhavn: 261.

Anolis distichus albidogularis Mertens, 1939, Abh. Senckenberg. Naturf. Ges., 449:59.

Type locality: Haiti; restricted to Port-au-Prince, Dépt. de l'Ouest, Haiti.

Definition: A subspecies of *A. distichus* characterized by very large size (males to 58 mm, females to 48 mm snout-vent length), dorsum varying between all green and all dark brown with darker longitudinal striae in all phases, dewlap pale yellow (occasionally white or almost so) to yellow with a faint orange basal blush, modally 1/1 scales between the supraorbital semicircles and the interparietal, 0/0 supraorbitals in contact with the interparietal, 2/2 scales in contact laterally with the postfrontals and moderate mean number (3.9) of median azygous head scales.

Distribution: All of Haiti with the exception of the Tiburon Peninsula west of Miragoâne (precise limits along the southern coast of the Tiburon Peninsula at the longitude of Miragoâne unknown); the República Dominicana in extreme western

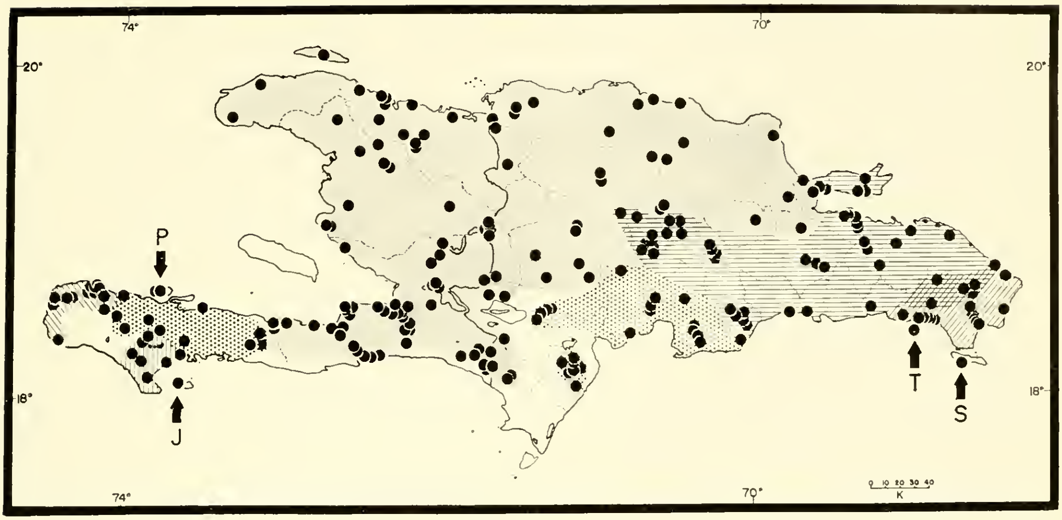

Figure 3. Map of Hispaniola, showing distribution of the subspecies of *Anolis distichus*; fine diagonal lines, *A. d. dominicensis*; horizontal lines, *A. d. ignigularis*; diagonal lines, upper right to lower left, *A. d. properus*; open stippling, *A. d. ravitergum*; crosshatching, *A. d. favillarum*; close stippling, *A. d. aurifer*; vertical lines, *A. d. vinosus*; diagonal lines, upper left to lower right, *A. d. suppar*; P, *A. d. patruelis*; J, *A. d. juliae*; T, *A. d. tostus*; S, *A. d. sejunctus*.

Pedernales Province on the south, through extreme western Independencia Province, thence east through San Juan Province to northern La Vega Province (Jarabacoa), Sánchez Ramírez Province (Cotuí), San Cristóbal Province (Gonzalo), and Samaná Province (mouth of the Río Yuna), and north to the northern coast in María Trinidad Sánchez Province (Cabrera), but excluding the Península de Samaná; possibly the Ile de la Tortue off the northern coast of Haiti (Fig. 3).

Comments: *A. d. dominicensis* has the widest distribution of any of the Hispaniolan subspecies. Throughout this wide range, it is remarkably constant in dewlap and dorsal colorations. The dewlap is most often pale yellow (Pl. I), but at times (and not segregated geographically) there is a vague and pale orange basal blush on the otherwise yellow dewlap. Occasional specimens (for example, in the Sierra de Baoruco in Pedernales Province and at Cap-Haïtien in northern Haiti) have the dewlap very pale yellow to practically white.

In the green phase, the ground color is fairly bright and marbled and/or streaked with green, brown, black, or yellow. The head is pale green, and the ventral color varies from pale green to gray or even black. The underside of the tail ranges from bright yellow to yellow-orange. In the brown phase, the back is a rich chocolate or wood brown; some specimens seem incapable of achieving a uniform brown and have a marbled or mottled pattern of darker and lighter browns. There is an intermediate color phase (greenish tan or grayish brown), which presumably is assumed between the definitive green or solid brown conditions.

Scale counts of the series of 245 *A. d. dominicensis* are: snout scales 4 to 10 (mode 4), loreal rows 3 to 7 (mode 4); supraorbital semicircles always in contact; modally 1/1 scales between the semicircles and the interparietal and 0/0 supraorbitals in contact with the interparietal; 2/2 scales in lateral contact with postfrontals; fourth toe lamellae 14 to 24 (mode 19); median azygous head scales 2 to 11 (mode 3, mean 3.9); "preoccipital" almost always present (235 of 251 lizards); postmentals

2 to 12 (modes 6 and 7, mean 6.6). The largest males are from the higher elevations in the Montagne Noire. These elevations (5000 and 5600 feet—1525 and 1708 meters) are among the very highest at which *A. distichus* has been collected. *A. d. dominicensis* also occurs at sea level in many coastal situations, and below sea level in the extreme eastern Cul de Sac Plain.

The specimens from the eastern Cul de Sac Plain are of special interest. In this region (Thomazeau, Manneville), the dorsal coloration is like that of specimens from the uplands on the northern slopes of the Morne l'Hôpital (Pétionville, Morne Calvaire, for instance), but the dewlap color is a deep orange (pl. 4 C 11, pl. 4 G 10 and pl. 4 G 11), at times with a faintly brown cast. This is one of the regions where *A. distichus* is sympatric (but not syntopic) with *A. brevirostris*, which in this same area has an orange dewlap. Of the two species in the Thomazeau-Manneville area, *A. brevirostris* is distinctly the inhabitant of the xeric scrub and *A. distichus* the inhabitant of more mesic situations, oases, and cultivated areas. In this region, *A. brevirostris* is the widespread lizard of open areas, whereas *A. distichus* is restricted to certain less rigorous habitats and is in effect surrounded by *A. brevirostris*. The orange dewlap of *A. distichus* may well be the result of partial or complete isolation of the *A. distichus* populations from the balance of the species. To the east, in the Valle de Neiba in the República Dominicana, *A. d. dominicensis* remains unknown, but is replaced to the east of Lago Enriquillo by the western extreme of another subspecies. Doubtless *A. d. dominicensis* will ultimately be collected between the Dominico-Haitian border and the western end of Lago Enriquillo in the República Dominicana.

Considering the fact that *A. d. dominicensis* occurs at a great variety of elevations, it is obvious that it also occupies a great variety of habitats, from the hot oases in the Cul de Sac Plain to upland mesic cacao groves and rain forest. Cultivated lands are quite suitable, and it is often the dominant anole of shady fence rows and the interior of humid coffee plantings and woods. Along the coast it occurs in mangroves (Trou Forban), mesic and open banana-breadfruit-royal palm associations, on large trees in open cultivated semi-arid regions, and it is common almost everywhere, at least where a minimal patch of shady woods occurs. In the hot and dry Valle de Cibao, *A. d. dominicensis* was encountered in thorn and tree-cactus scrub but in the more shady situations. In short, throughout its broad Hispaniolan range, *A. d. dominicensis* is encountered in almost any situation which offers shade and refuge.

I have noted in the introduction the sleeping habits of *A. d. dominicensis* at Miches and Palo Verde in the República Dominicana. One other observation has been made; two *A. d. dominicensis* were taken sleeping exposed on a large, wet log lying adjacent to a rushing stream, in a deep and cool montane ravine at 2200 feet (671 meters), near Puesto Grande in the Cordillera Septentrional in northern República Dominicana.

I do not regard *A. d. albidogularis* Mertens as a valid subspecies. Mertens was misled into the description of *albidogularis* by the material which he regarded as *dominicensis* from Haiti; his "*dominicensis*" were three males and a female from Gonaïves, and two males and a female from St. Marc. His comments (1939:56) on the distinguishing characters of *A. d. dominicensis* (as based upon these seven specimens) do not apply to *dominicensis*—i.e., that *dominicensis* is never green but rather is gray to gray-brown, has a bright and clear supralabial streak, a pair of dark scapular spots and a lined dorsum, and a chrome-orange-yellow dewlap with citron-yellow scales. These are precisely the characters—especially the always gray color and the pair of scapular spots and a lined dorsum—which distinguish the species *A. brevirostris* from *A. distichus*. It is apparent that Mertens, when describing *albidogularis*, did not have for comparison specimens of *A. d. dominicensis*, as he presumed, but rather *A. brevirostris*. The characters of *albidogularis* are those of *dominicensis*, and specimens from the vicinity of the type locality (Monte Cristi, República Dominicana) do not differ significantly in any feature from topotypical Port-au-Prince material. The pale dewlap coloration which is ascribed to *albidogularis* is not consistent in the Valle de Cibao population and occurs only sporadically elsewhere; specimens which I have collected near Monte Cristi and in the Valle de Cibao have the dewlap color pale yellow, as do specimens from elsewhere within the range of *A. d. dominicensis*.

A. d. dominicensis differs from all the Bahaman subspecies except *ocior* in having a green phase; the green of *ocior* is a much more yellow-green than the green of *dominicensis*. Of the Bahaman subspecies, all are smaller than *dominicensis; ocior* most closely approaches *dominicensis* in size. The median head scale mean of *dominicensis* (3.9) is lower than that of any Bahaman race (5.5 to 8.7). Only *distichoides* in the Bahamas has the 1/1 scales between the semicircles and the interparietal as does *dominicensis*. Other head scale differences (such as the regular presence of the "preoccipital" and the regular contact between the semicircles in *dominicensis*) are also significantly different in comparison with the Bahaman subspecies.

A. d. dominicensis presumably comes into contact with four other subspecies. In one of these instances (Sierra de Baoruco) no intergradient specimens are known, since there is an hiatus between the closest records of *dominicensis* and this next adjacent form to the east. In three instances, however (*ignigularis*; the subspecies to the west on the Tiburon Peninsula; and the subspecies to the east in the Valle de Neiba), there are samples which I interpret as intermediates. In the case of *ignigularis*, the material from the higher elevations in the eastern portion of the Cordillera Central (vicinity of Constanza, Paso Bajito, etc.) shows the dewlap rather intermediate between the yellow or yellow-with-orange-blush *dominicensis* condition and the solid orange dewlap with a narrow yellow border of *ignigularis*, although the dewlap in general is much closer to that of *ignigularis* than to that of *dominicensis*. I have included these Cordillera specimens with *ignigularis* for that reason.

A small series from Padre las Casas, Azua Province, República Dominicana, I interpret as intergradient between *dominicensis* and the Valle de Neiba-Llanos de Azua subspecies. This lot is closer to the latter race, and I have discussed it in detail there. Finally, lizards from the vicinity of Saint Michel du Sud on the Tiburon Peninsula are intermediate in dewlap color between *dominicensis* and the next adjacent race to the west on the Peninsula (which has a deep orange dewlap with a narrow yellow edge), but they are closer to the latter subspecies, and I have included them in the discussion of that race rather than with *dominicensis*.

I have seen no fresh material from Ile de la Tortue and only three old specimens which are distinctive in neither scutellation nor what is discernible of pattern or pigmentation. I include Tortue in the range of *A. d. dominicensis* only provisionally, since on all other satellite islands where *A. distichus* is found, it is racially distinct. Thus there is a good likelihood that fresh specimens from Tortue will demonstrate that there is a different subspecies present there.

Referred specimens: HAITI. *Dépt. du Sud*: Miragoâne, 30 (MCZ 25489–98 + 20 untagged specimens); Butête, nr. Miragoâne (not mapped), 7 (MCZ 66133–39); Etang Miragoâne, 7 (MCZ 66140–46). *Dépt. de l'Ouest*: 7.1 mi. (11.4 km) E Miragoâne, 1 (ASFS X3850); 3 mi. (4.8 km) W Grand Goâve, 300 feet (92 meters), 1 (ASFS X3856); 1.1 mi. (1.8 km) NE Fauché, 2 (ASFS X2045–46); 5 km S Dufort, 4 (MCZ

63099–102); 4 mi. (6.4 km) SE Léogâne, 4 (ASFS V8463–66); Léogâne, 2 (MCZ 13779–80); Ça Ira, 9 (MCZ 63898–906); bridge over Rivière Momance on road to Léogâne, 1 (MCZ 63103); Mariani, 7 mi. (11.2 km) E Gressier, 7 (ASFS V8446–52); Diquini, 17 (MCZ 59430–32, MCZ 8696–700, MCZ 8703, MCZ 8705, MCZ 8710, MCZ 8712, MCZ 8714–18); Port-au-Prince, 1 (MCZ 51427); Boutillier Road, S of Port-au-Prince, 17 (MCZ 59413–29); SW of Port-au-Prince (not mapped), 1 (MCZ 51258); 2.8 km S Pétionville, 1700 feet (519 meters), 2 (ASFS V8117–18); 5 mi. (8.0 km) NE Pétionville, ca. 160 meters, 3 (ASFS V9405–07); 3 km (airline) W Pétionville, Morne l'Hôpital, 920 meters, 11 (ASFS V8435–45); Morne Calvaire, 1 mi. (1.6 km) SW Pétionville, 2300 feet (702 meters), 44 (ASFS X1237–80); Kenscoff, 2 (MCZ 45745, MCZ 59401); Morne Bourette (not mapped), 2 (MCZ 47546 + one untagged specimen); Peneau, 5000 feet (1525 meters), 4 (ASFS X1350–51, ASFS X1574–75); Furcy, 5600 feet (1708 meters), 45 (ASFS X1591–95, MCZ 63535–39, MCZ 59393–97, MCZ 59433–41); Peneau and Furcy, ca. 4000–5000 feet (1220–1527 meters), 4 (ASFS V4821–44); Hatte Lathan (not mapped), 2 (MCZ 51421–22); Thomazeau, 4 (MCZ 13771–72, MCZ 37455, USNM 59191); near Thomazeau, 2 (MCZ 37495–96); Tète Source, 1.4 km NNE Thomazeau, 3 (ASFS V8173–75); Manneville, 9 (ASFS V8194, CM 38881, MCZ 59390–92, MCZ 63107–10); Ste. Philomène (not mapped), 1 (MCZ 51428); 3.9 mi. (6.2 km) NW Ganthier, 1 (ASFS X2171); Gormand, nr. Saltrou (not mapped), 2 (MCZ 68614–15); Colombier, nr. Saltrou, 4 (MCZ 68616–19); Lan Banane, nr. Saltrou, 5 (MCZ 68620–24); Tète à l'Eau, nr. Saltrou, 6 (MCZ 68625–30); Thiotte, nr. Saltrou, 9 (MCZ 69631–39); Caroye, nr. Saltrou (not mapped), 31 (MCZ 69315–45); Londry, nr. Saltrou (not mapped), 4 (MCZ 69346–49); Citadelle, nr. Saltrou (not mapped), 15 (MCZ 69350–64); Maviete, nr. Saltrou (not mapped), 15 (MCZ 69365–79); Mapou, nr. Saltrou, 7 (MCZ 69380–86); ca. 3.5 mi. (5.6 km) NE Trouin, 800 feet (244 meters), 1 (ASFS V9664); 5 mi. (8.0 km) S Trouin, 700 feet (214 meters), 3 (ASFS V9668–70); Jacmel, 1 (ASFS V9825); ca. 5.5 mi. (8.8 km) NW Jacmel, 600 feet (183 meters), 1 (ASFS V9784); 3 mi. (4.8 km) E Jacmel, 2 (ASFS V9757–58); ca. 1 mi. (1.6 km) W Cayes Jacmel, 4 (ASFS V9700–03); 10 mi. (16.0 km) NNE Marigot, 3200 feet (976 meters), 1 (ASFS V9737); Trou Forban, 1 (ASFS V8216); 1.6 km SW Trianon, 1100 feet (336 meters), 3 (ASFS V8278–80); 1.6 km NE Trianon, 6 (ASFS V8282–87); 7 mi. (11.2 km) N Mirebalais, 1 (ASFS X2234); La Tombe, nr. Mirebalais (not mapped), 21 (MCZ 68204–24); Fer-à-Cheval, nr. Mirebalais, 5 (MCZ 68225–29); Boudou, nr. Mirebalais (not mapped), 13 (MCZ 68230–42); Ledie, nr. Mirebalais (not mapped), 4 (MCZ 68243–46); Dubuison, nr. Mirebalais (not mapped), 3 (MCZ 68247–49). *Dépt. de l'Artibonite*: south end, Etang Bois Neuf, 1 (MCZ 59942); Pierre Payen, 8 (MCZ 59402–03, MCZ 59407–12); bridge over Rivière de l'Artibonite, St. Marc road, 2 (MCZ 59404–05); Passe Reine, 3 (MCZ 63055–57); 8 to 9 km W Marmelade, 3500 feet (1068 meters), 2 (ASFS V9913–14); 5 mi. (8.0 km) NW St. Michel de l'Atalaye, 4 (ASFS V10030–33); 2 mi. (3.2 km) NW St. Michel de l'Atalaye, 2 (ASFS V10034–35); Hinche, 5 (MCZ 25499–503); Gros Morne, 8 (MCZ 63075–82). *Dépt. du Nord*: 3 mi. (4.8 km) NW Terrier Rouge, 1 (ASFS V10163); Dondon, 10 (MCZ 63063–72); Dondon, southeastern outskirts, 4 (ASFS V10017–20); ca. 2 km S Dondon, 2 (ASFS V10038–39); Grande Rivière du Nord, 13 (MCZ 66655–67); Cap-Haïtien, 94 (MCZ 37483–92 + 69 untagged specimens, MCZ 63058–62, ASFS V10194–204); Ti Guinin, near Cap-Haïtien (not mapped), 8 (MCZ 66668–75); Citadelle Lafèrriere, 7 (MCZ 33370, MCZ 63073–74, MCZ 66651–54); nr. Citadelle Lafèrriere, 2 (MCZ 25487–88); 4 mi. (6.4 km) SSW Limbé, 200 feet (61 meters), 1 (ASFS

V9964); 4 mi. (6.4 km) N Port Margot, east side of Rivière de Port Margot, 1 (ASFS V9971); ca. 2 km inland from Anse à Margot, 1 (ASFS V10277); Chouchou, 10 mi. (16.0 km) NW Port Margot, 6 (ASFS V9978–83); 1 mi. (1.6 km) SW Le Borgne, west side Rivière du Borgne, 2 (ASFS V10001–02); *Dépt. du Nord Ouest*, Jean Rabel, 1 (MCZ 63098); Bombardopolis, 15 (MCZ 63083–97). *Ile de la Tortue*: 3 (MCZ 37493–94, USNM 95121). REPÚBLICA DOMINICANA. *Pedernales Prov.*: 19 km N Pedernales, 1000 feet (305 meters), 1 (ASFS V2702); Las Mercedes, ca. 1400 feet (427 meters), 1 (ASFS V2659); 1 km S Los Arroyos, 4100 feet (1251 meters), 1 (ASFS V2605); 27 km N Puerto de Alcoa, 1 (ASFS X9765). *Independencia Prov.*: Aguacate, 3 (MCZ 58467–69); 8 km E Aguacate, 1600 feet (488 meters), 1 (ASFS X9945); 7.6 km NW La Descubierta, ca. 2000 feet (610 meters), 2 (ASFS V4375–76); Guayabal, 6 km N Postrer Río, 4 (MCZ 58470–73). *San Rafael Prov.*: 18 km SW Hondo Valle, 6000 feet (1830 meters), 1 (ASFS V360); 9.0 mi. (14.4 km) NW Elías Piña, 1 (ASFS V330); Rancho La Guardia, 13 (MCZ 58441–53); Pedro Santana, 1 (MCZ 58440); Bánica, 1 (MCZ 58438); 3 km E Bánica, 1 (MCZ 58439); 3 km NE Bánica, 13 (MCZ 58454–66). *San Juan Prov.*: San Juan, western edge, 6 (ASFS V499–504); 15 km SE San Juan, 4 (ASFS V487–90); 3 km E Las Matas, 4 (ASFS V305–08); Río Arriba del Norte, 1950 feet (595 meters), 3 (ASFS V521–23); 7 km N Carpintero, 9 (MCZ 58500–08); 7 km NW Vallejuelo, 2600 feet (793 meters), 3 (ASFS V302, ASFS V394–95). *La Vega Prov.*: Jarabacoa, 2 (MCZ 58480–81); 3 km NE Jarabacoa, 1 (ASFS V1948). *Sánchez Ramírez Prov.*: 12.3 km E Cotuí, 5 (ASFS V611–15). *San Cristóbal Prov.*: 10 km NE Gonzalo, 600 feet (183 meters), 2 (ASFS V3131–32). *Samaná Prov.*: south side of Río Yuna, approximately 1 km upstream from mouth, 7 (ASFS V2961–67). *María Trinidad Sánchez Prov.*: 11.2 km S Cabrera, 3 (ASFS V4244–46). *Duarte Prov.*: 1 km NW Arensoso, 3 (ASFS V1841–43). *Espaillat Prov.*: 2 km N Puesto Grande, 2200 feet (671 meters), 2 (ASFS V1962–63). *Puerto Plata Prov.*: Puerto Plata, 2 (MCZ 5442, MCZ 43670); Sosúa, 8 (ASFS V1631–32, MCZ 13754–59); 6 km E Imbert, 700 feet (214 meters), 2 (ASFS V1691–92). *Santiago Prov.*: Santiago, 1 (MCZ 58482); Licey al Medio, 4 (MCZ 58317–20); Ceboruco (not mapped), 12 (MCZ 58483–94); 3 km S Pena (not mapped), 5 (MCZ 58495–99); 6 km E El Rubio, 1000 feet (305 meters), 2 (ASFS V2922–23); 7 km SE El Rubio, 2300 feet (702 meters), 1 (ASFS V2924). *Valverde Prov.*: 7 km E Valverde, 2 (ASFS V2954–55). *Monte Cristi Prov.*: 24 km E Monte Cristi, 1 (MCZ 43681); 4 km E Pepillo Salcedo, 1 (ASFS V1167); 2 km NE Palo Verde, 10 (ASFS V1303–12); 1 km S Palo Verde, 4 (ASFS V1357–60). *Dajabón Prov.*: 6 km S Copey, 1 (ASFS V1170); 1 km S Loma de Cabrera, 900 feet (275 meters), 1 (ASFS V1171).

Anolis distichus ignigularis Mertens

Anolis distichus ignigularis Mertens, 1939, Abh. Senckenberg. Naturf. Ges., 449:58.

Type locality: San Pedro de Macorís, San Pedro de Macorís Province, República Dominicana.

Definition: A subspecies of *A. distichus* characterized by moderate size (males to 55 mm, females to 44 mm snout-vent length), dorsum usually green anteriorly and rich and translucent reddish tan posteriorly (but capable of turning completely brown), dewlap vivid orange centrally with a narrow yellow margin, modally 0/0 scales between the supraorbital semicircles and the interparietal, 1/2 supraorbitals in contact with the interparietal, 2/2 scales in contact laterally with the postfrontals, and low mean number (3.5) of median azygous head scales.

Distribution: The República Dominicana from eastern San Cristóbal Province in the west, east along the coast to the type locality, thence inland to the vicinity of Higüey and to the north coast (east of Miches) in La Romana Province; along the north coast to the Bahía de San Lorenzo in El Seibo Province, south into eastern San Cristóbal Province (Bayaguana), and west into the Cordillera Central; Península de Samaná, west to the vicinity of Yayales (Fig. 3).

Comments: The dewlap and dorsal colors of *A. d. ignigularis* are very constant throughout the range of the subspecies. The vivid and extensive orange center and narrow yellow margin of the dewlap (Pl. 1) are diagnostic features of *ignigularis* in the eastern and central portions of the República Dominicana. The dorsum is usually a rather dark green anteriorly, grading rapidly into a translucent reddish tan posteriorly. The lizards can become completely brown, although this brown is of a more reddish shade (cinnamon) than that of *A. d. dominicensis*. The extent of the orange center of the dewlap is slightly variable, but the bright pigment is never restricted to a small and indistinct orange blush, as it is occasionally in *dominicensis*.

Scale data on the series of 103 *A. d. ignigularis* are: snout scales 4 to 8 (mode 4), loreal rows 3 to 6 (mode 5); supraorbital semicircles always in contact; modally 0/0 scales between the semicircles and the interparietal and 1/2 supraorbitals in contact with the interparietal; 2/2 scales in lateral contact with postfrontals; fourth toe lamellae 14 to 22 (mode 20); median azygous head scales 1 to 9 (mode 3, but 4 scales are almost equally as common, mean 3.5); "preoccipital" usually present (100 of 103 lizards); postmentals 4 to 10 (mode 5 or 6, mean 6.0). The asymmetrical mode of 1/2 supraorbitals in contact with the interparietal is peculiar, but the mode is fairly strong (34 individuals; next highest category is 0/0 with 26 lizards). Judging from the high incidence (26) of 1/1 supraorbitals in contact with the interparietal, I suspect that *ignigularis* is a population which is in the process of evolving from a mode of 1/1 to 2/2 but has not completed the transition.

The largest males have snout-vent lengths of 55 mm, and both are from the vicinity of Higüey; the status of that particular population is probably intergradient between *ignigularis* and the race next to the southeast, but these two large males are clearly much more like *ignigularis* than the drab southern form. The largest female *ignigularis* has a snout-vent length of 44 mm; this individual, from the Valle de Culata, at an elevation of 5000 feet (1525 meters) in the Cordillera Central, is from an area of extreme intergradation with *dominicensis*.

A. d. ignigularis is readily separable from all previously discussed subspecies; the combination of orange dewlap and bicolor dorsum occurs in no other form. Comparison with the three orange-dewlapped Bahaman subspecies, *biminiensis*, *distichoides*, and *dapsilis*, is easily made. Aside from these three races lacking the bicolored dorsum, all are smaller, have much higher median head scale means (5.5 to 8.7 in contrast to 3.5 in *ignigularis*), lower means of postmentals (4.6 to 5.2 in contrast to 6.0), and have a high percentage of specimens which lack the "preoccipital." Of the three Bahaman subspecies, only *dapsilis* modally has 0/0 scales between the supraorbitals and the interparietal and 1/2 supraorbitals in contact with the interparietal as does *ignigularis*. In *dapsilis*, however, 1/2 is one of two bimodes. Extended comparisons with *dominicensis* are not necessary; the dewlap and dorsal colorations are sufficient to distinguish the two races. The 1/1 scales between the semicircles and the interparietal and 0/0 supraorbitals in contact with the interparietal in *dominicensis* differ from the conditions of 0/0 and 1/2 in *ignigularis*.

The apparently disjunct range of *ignigularis* is of especial interest. Were it not for the series (seven specimens) from the mouth of the Río Yuna, I would consider that *ignigularis* has a continuous distribution about the western end of the Bahía de Samaná. However, the Río Yuna lizards are clearly *dominicensis* and have the pale yellow dewlaps of that subspecies. Although there is evidence (Cochran, 1941:2) that the Península de Samaná was in historic time an island separated from the mainland, this seems hardly likely when the isthmus is visited today, since, although it is low-lying and swampy and is bisected by the *canos de Gran Estero*, it is also heavily forested, and it seems doubtful that the Samaná has been completely severed from the mainland so recently. Doubtless the Península has been completely insular at various times in the past. It seems possible that *ignigularis* invaded the Samaná across the Bahía de Samaná from the south, while the former was cut off from the balance of Hispaniola, and became established there, rather than having reached the Península around the western end of the Bahía. Another possibility is that *dominicensis* has followed down the Río Yuna from the interior and has invaded the area at the head of the bay, thereby severing the two components of the *ignigularis* population. Larger numbers of specimens from this immediate area may demonstrate intergradation; the series at hand from the mouth of the Río Yuna, however, does not show it.

Intergradation between *ignigularis* and *dominicensis* occurs in the eastern Cordillera Central, although specimens from the foot of the eastern escarpment of the Cordillera (vicinity of Monseñor Nouel) are clearly *ignigularis*. Specimens from the area about Constanza and Paso Bajito are much like *ignigularis*, except that the dewlap orange is somewhat paler (although usually very extensive), and the dorsum is more regularly all green rather than sharply bicolor. These specimens I regard as closer to *ignigularis* and have so listed them below.

A. d. ignigularis comes into contact with two other subspecies, that to the south and east in the La Romana to Cabo Engaño region, and that to the southwest in the Llanos de Azua. No intergrades are known for the latter contact, and the break between the two subspecies must be rather sharp (see comments below). The four lots of fresh material from the vicinity of Higüey and Bejucal are much closer to *ignigularis* than to the subspecies to the south, although the series from 2 miles south of Higüey has one male with a yellow dewlap without any orange. Taken as a whole, the Higüey and Bejucal material is close to *ignigularis*. In two other areas, the intergrades between these two forms are closer to the unnamed subspecies and will be discussed below.

Like *A. d. dominicensis*, *ignigularis* has a wide altitudinal range, from sea level to elevations of at least 6000 feet (1830 meters) in the Cordillera Central. In the lowlands, it is a customary denizen of moist, shady cacao groves and other wooded situations. In the Cordillera it is encountered most frequently in heavily wooded ravines and local stands of rain forest, although at Valle de Culata it was found on a rail fence in an exposed and abandoned pasture. It does not occur commonly in the pine woods in the highlands.

Specimens examined: REPÚBLICA DOMINICANA. *San Cristóbal Prov.*: 15.5 km SE El Cacao, 1400 feet (427 meters), 1 (ASFS V2463); El Tablazo, nr. Río Nigua, 15 km NW San Cristóbal, 7 (MCZ 58714–20); La Cabirma de la Loma, northwest of San Cristóbal, 4 (MCZ 79269–72); Colonia Ramfis (= La Cabirma de la Loma), 5 (MCZ 58721–22, MCZ 58566–68); 1 km NW Colonia Ramfis (not mapped), 5 (MCZ 58561–65); 3 km SE Colonia Ramfis (not mapped), 7 (MCZ 58569–75); 6 km SE Colonia Ramfis (not mapped), 4 (MCZ 58576–79); 9 km SE Colonia Ramfis (not mapped), 5 (MCZ 58580–84); 12 km SE Colonia Ramfis, 5 (MCZ 58585–89); 15 km SE Colonia Ramfis (not mapped), 3 (MCZ 58590–92); 7 km N San Cristóbal, 6 (MCZ 58593–98); Mt. Calabozo, near San Cristóbal (not mapped), 3 (MCZ 58599–601); 2 mi.

(3.2 km) SE San Cristóbal, 2 (ASFS X7774–75); 3 km W Bayaguana, 4 (ASFS V602–06); 10 km NE Bayaguana, 1 (ASFS V3141); Comate, Municipio Bayaguana, 5 (MCZ 79286–90); Monte Plata, 1 (MCZ 16441). *Distrito Nacional*: 9.8 mi. (15.7 km) E Santo Domingo, 5 (ASFS X7735–39); Santo Domingo, 8 (MCZ 53945, MCZ 58655, MCZ 58708, MCZ 75185–86, MCZ 79266–68). *San Pedro de Macorís Prov.*: 6 km N San Pedro de Macorís, 2 (ASFS X7832–33). *La Romana Prov.*: Bejucal, 5 (MCZ 58602–06); 1 mi. (1.6 km) NE Higüey, 5 (ASFS V771–75); 2 mi. (3.2 km) S Higüey, 4 (ASFS V747–50); 6.6 km W. Higüey, 1 (ASFS V1013); 24.8 mi. (39.7 km) ESE Miches, 2 (ASFS X7891-92). *El Seibo Prov.*: 1.4 mi. (2.2 km) SE Miches, 1 (ASFS X9349); 14 km SW Miches, 8 (MCZ 75187–94); 6.6 mi. (10.6 km) NW Hato Mayor, 2 (ASFS X7871–72); San Francisco, 6 km SE Hato Mayor, 1 (MCZ 58614); 2.1 mi. (3.4 km) N El Valle, 2 (ASFS X7866–67); Sabana de la Mar, 42 (ASFS V3081–98, MCZ 58615–38); 3.5 mi. (5.6 km) S Sabana de la Mar, 7 (ASFS X7841–44, ASFS X7930–32); 20 km S Sabana de la Mar, 11 (MCZ 58639–49); Cueva de Caño Hondo, 5 (ASFS X9284–88); Bahía de San Lorenzo (small beach west of railway bed), 2 (ASFS V3150–51). *La Vega Prov.*: Paso Bajito, 1 (ASFS X8787); 7 km E Paso Bajito, Casa de los Michelenas, 3 (ASFS X8781–83); El Río, 6 (MCZ 64371–76); 7.1 mi. (11.4 km) E El Río, 3500 feet (1068 meters), 1 (ASFS X8112); Constanza, 9 (MCZ 44387, MCZ 58652–54, MCZ 58709–13); 9.1 mi. (14.6 km) N Constanza, 6000 feet (1830 meters), 3 (ASFS X8487, ASFS X8700–01); 9 km N Constanza, 1 (ASFS X8699); 5.1 mi. (8.2 km) N Constanza, Valle de Culata, 5000 feet (1525 meters), 11 (ASFS X8488–98); 6 km W Constanza, 4250 feet (1296 meters), 2 (ASFS X8832–33); Loma Vieja, 1 (MCZ 44383); Paraje La Palma, Municipio Constanza (not mapped), 41 (MCZ 75153–79, MCZ 79273–85); El Convento, Municipio Constanza (not mapped), 5 (MCZ 79291–95); El Montazo, Municipio Constanza (not mapped), 1 (MCZ 79296); Sección La Culata, Paraje La Cienaga, 1 (MCZ 75180); Municipio Jarabacoa, Sección Manabao, Paraje la Cienaga, 3 (MCZ 75181–83); between Constanza and Jarabacoa (not mapped), 5 (MCZ 64383–87); Loma Rucilla, 3 (MCZ 44384–86); Monseñor Nouel, 1 (MCZ 64370); 1.2 mi. (1.9 km) SE Monseñor Nouel, 700 feet (214 meters), 1 (ASFS X8125); Piedra Blanca, 6 (MCZ 64377–82); 2 km NW La Cumbre, 2 (MCZ 56850–51). *Samaná Prov.*: 8 km SE Yayales, 1 (ASFS V1918); 6 km E Sánchez, 2 (ASFS V1908–09); Sánchez, 11 (MCZ 37497–506 + one untagged specimen); 5 km W Samaná, 1 (ASFS V1983); Samaná, 2 (MCZ 5448, MCZ 43699); Puerto Escondido, 4 (ASFS V2974–77).

Anolis distichus properus[5] subsp. n.

Holotype: MCZ 81130, an adult male, from 0.5 mi. (0.8 km) NW Boca de Yuma, La Romana Province, República Dominicana, taken 31 August 1963 by Ronald F. Klinikowski. Original number V920.

Paratypes (all from La Romana Province, República Dominicana): ASFS V921, same data as holotype; ASFS X8235, Río Cumayasa, 17 km W La Romana, 28 June 1963, D. C. Leber; MCZ 16443–51, La Romana, 1922, E. Lieder; MCZ 75203, MCZ 75205–06, La Romana, 27 March 1963, C. E. Ray, R. Allen; MCZ 75184, MCZ 75195–97, 5 km E La Romana, 27 March 1963, C. E. Ray, R. Allen; USNM 157917, 8 km E La Romana, 19 July 1963, R. Thomas; ASFS X9316, 2 km E La Romana, 19 July 1963, R. Thomas; ASFS V1062–63, mouth of Río Chavón, west side, 4 September 1963, R. F. Klinikowski; MCZ 58607, MCZ 58609–13, Sanate, 12 km S Higüey, 26 August 1958, C. E. Ray and A. S. Rand; AMNH 96472–75, 0.3 mi. (0.5 km) NW Boca de Yuma, 29 August 1963, A. Schwartz, R. Thomas; ASFS V1135, 2.5 km NW Boca de Yuma, 4 September 1963, native collector; RT 807, 2.5 km NW Boca

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[5] From Latin, *properus*, quick.

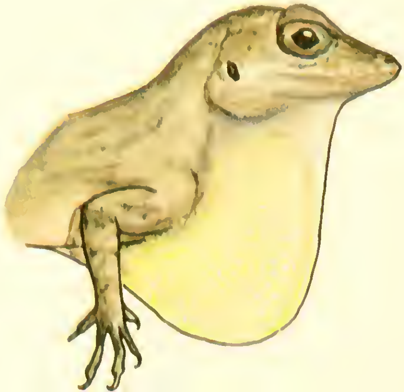


Plate I

First row: *left, A. distichus distichus* (ASFS 10301), Cave Point, New Providence Island, Bahama Islands, snout-vent length 46 mm; *right, Anolis d. distichoides* (ASFS 10280), Fresh Creek, Andros Island, Bahama Islands, snout-vent length 46 mm.

Second row: left, *A. d. biminiensis* (ASFS X4932), western end, South Bimini Island, Bahama Islands, snout-vent length 47 mm; right, *Anolis d. ocior* (MCZ 81140), Port Nelson, Rum Cay, Bahama Islands, snout-vent length 53 mm.

Third row: left, *A. d. dominicensis* (ASFS X1237), Morne Calvaire, 1 mi. SW Pétionville, 2300 feet, Dépt. de l'Ouest, Haiti, snout-vent length 54 mm; right, *A. d. ignigularis* (ASFS X7735), 9.8 mi. E Santo Domingo, Distrito Nacional, República Dominicana, snout-vent length 48 mm.

Fourth row: left, *A. d. properus* (MCZ 81130), 0.5 mi. NW Boca de Yuma, La Romana Province, República Dominicana, snout-vent length 48 mm; right, *A. d. sejunctus* (MCZ 81131), environs of Mano Juan, Isla Saona, República Dominicana, snout-vent length 50 mm.

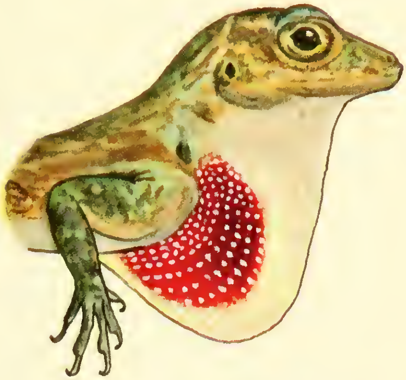
Plate II

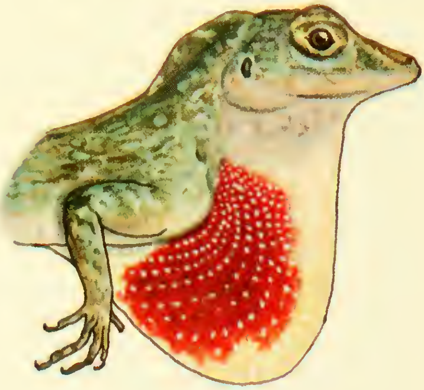
First row: left, *A. d. tostus* (MCZ 81134), western end, Isla Catalina, República Dominicana, snout-vent length 49 mm; right, *A. d. ravitergum* (MCZ 81132), 16.5 mi. S San Jose de Ocoa, Peravia Province, República Dominicana, snout-vent length 53 mm.

Second row: left, *A. d. favillarum* (MCZ 81133), 3 km NE Las Auyamas, 3300 feet, Barahona Province, República Dominicana, snout-vent length 50 mm; right, *A. d. aurifer* (MCZ 81135), 11 km N Cavaillon, 1300 feet, Dépt. du Sud, Haiti, snout-vent length 52 mm.

Third row: left, *A. d. vinosus* (MCZ 81136), Camp Perrin, Dépt. du Sud, Haiti, snout-vent length 53 mm; right, *A. d. juliae* (ASFS X3548), western end, Ile-à-Vache, Haiti, snout-vent length 48 mm.

Fourth row: left, *A. d. suppar* (MCZ 81137), Dame-Marie, south side of town along coast, Dépt. du Sud, Haiti, snout-vent length 52 mm; right, *A. d. patruelis* (MCZ 81138), vicinity of Pointe Sable, Ile Grande Cayemite, Haiti, snout-vent length 49 mm.





de Yuma, 6 August 1963, native collector; MCZ 75198–202, Boca de Yuma, 28 March 1963, C. E. Ray, R. Allen; MCZ 75207–21, Juanillo, 29 March 1963, C. E. Ray, R. Allen; UIMNH 61681–83, 16.5 km SE El Macao, 31 August 1963, R. F. Klinikowski, R. Thomas.

Intergrades between *A. d. ignigularis* and *A. d. properus* (but closer to the latter): República Dominicana, La Romana Province: 12 km NE La Romana, 2 (ASFS X9319–20); 0.7 mi. (1.1 km) SE El Macao, 3 (ASFS X7879–81).

Definition: A subspecies of *A. distichus* characterized by moderate size (males to 54 mm, females to 45 mm snout-vent length), dorsum plain ashy to very pale green (rarely) and without any distinct dark markings on the head, dewlap very pale yellow with at times a pale central orange blush, modally 0/0 scales between the supraorbital semicircles and the interparietal and 0/0 supraorbitals in contact with the interparietal, 2/2 scales in contact laterally with the postfrontals, and very low mean number (2.8) of median azygous head scales.

Distribution: La Romana Province, República Dominicana, from the Río Cumayasa on the west, east and north around Cabo Engaño to the vicinity of El Macao; intergrades with *A. d. ignigularis* northeast of La Romana, south of Higüey, and at El Macao (Fig. 3).

Comments: The pale and drab *A. d. properus* stands in strong contrast to its brightly colored relative *ignigularis* to the north and west. The two are readily separable on the basis of body color, since *properus* is always faded and pale and usually ashy gray in the field, although it is capable of a very pale green phase. No specimens were observed to become solid dark brown, one of the phases in the repertory of *ignigularis*. The pale yellow dewlap of *properus* is in harmony with the balance of its faded coloration (Pl. I); occasional specimens have a pale orange central blush on the dewlap. In dewlap color, *properus* resembles *dominicensis* (from whose range it is separated by *ignigularis* and an undescribed subspecies), but it can be differentiated from *dominicensis* by the lack of bright green and dark brown phases. The head is virtually patternless, and this character will differentiate *properus* from the unnamed subspecies to the west in the Valle de Neiba and Llanos de Azua. The hindlimb banding, which is a fairly constant feature of *dominicensis* and *ignigularis*, is much reduced or absent in *properus*.

The holotype has the following measurements and counts: snout-vent length 48 mm, tail ca. 57 mm, tail regenerated; 5 scales across snout, 4 loreal rows, semicircles in contact, 0/0 scales between supraorbital semicircles and interparietal, 1/1 supraorbitals in contact with interparietal, 3/3 scales in lateral contact with postfrontals, 19 fourth toe lamellae, 3 median azygous head scales, "preoccipital" present, 7 postmentals.

Scale counts for the series of 58 *A. d. properus* are: snout scales 4 to 9 (mode 4 but 6 scales is almost equally modal), loreal rows 4 to 6 (mode 5); supraorbital semicircles in contact in all specimens; modally 0/0 scales between supraorbital semicircles and interparietal, and 0/0 supraorbitals in contact with interparietal; 2/2 scales in lateral contact with prefrontals; fourth toe lamellae 15 to 21 (mode 17); median azygous head scales 1 to 6 (mode 3, mean 2.8); "preoccipital" usually present (55 of 58 specimens); postmentals 4 to 11 (mode 6, mean 6.7). The largest male (54 mm snout-vent length) is from La Romana, and the largest female (45 mm) is from 2.5 km NW Boca de Yuma.

Intergradient specimens between *properus* and *ignigularis* from south of Higüey and Bejucal have already been noted under the discussion of the latter subspecies. The Higüey material was collected on fence posts in a shady pasture; in life these lizards were olive to gray with more or less longitudinal dark striae (which *properus* lacks). One specimen had a dirty yellow dewlap, whereas in the remainder of the series the dewlaps had variable amounts of orange centrally and pale yellow edges. These lizards are appropriate both geographically and in characteristics as intermediates between *properus* and *ignigularis*, but as a whole they are closer to the latter. The Bejucal series, which I did not see in life, at least shows dorsal pattern features which are likewise more like those of *ignigularis* than *properus*.

The specimen from 0.7 mi. (1.1 km) SE El Macao has the dorsum tan and striated. The dewlap has a restricted patch of dull orange basally and a wide pale yellow margin. This specimen, by virtue of its striate dorsum and more prominent orange dewlap blotch, seems intermediate between *properus* and *ignigularis*, although much closer to the former. Specimens of *ignigularis* were taken about 30 kilometers northwest of El Macao.

The remaining locality for *ignigularis* × *properus* intergrades is 12 km NE La Romana. The situation at this locality is most peculiar, since the two specimens were collected in a mesic and forested ravine which presently cuts deeply through cane fields. The dewlap of the single male was dull orange centrally with a narrow dull yellow edge—an *ignigularis* character. The dorsal color was dull grayish to dull greenish; the back was not bicolor and the hues were much subdued and faded, but not so pale as those of *properus*. These specimens combine the characters of *properus* and *ignigularis*.

Comparisons of *properus* with both *dominicensis* and *ignigularis* have been made above. Of the Bahaman subspecies, *properus* most closely resembles *distichus*; from *biminiensis*, *distichoides* and *dapsilis*, *properus* differs in having a yellow rather than an orange dewlap, as well as in several scale characters, the most striking of which is the extremely low mean for median head scales (2.8 in contrast to 5.5 to 8.7 in the above listed Bahaman subspecies). *A. d. ocior* in its non-green phase is somewhat like *properus*, but the longitudinally lined flanks will distinguish the former from the latter, as will also the median head scales (5.8 in *ocior*). From the nominate race, which *properus* most closely resembles in general aspect and dewlap color, *properus* differs in lower mean median head scales (2.8 versus 5.9), greater number of postmentals (6.7 versus 5.4), larger size (54 mm versus 49 mm), and in never having the supraorbital semicircles separated by a row of scales. *A. d. distichus* and *A. d. properus* both have 0 0 scales between the semicircles and the interparietal and 0 0 supraorbitals in contact with the interparietal as the modal conditions.

The range of *A. d. properus* embraces the arid portion of extreme eastern Hispaniola. Lizards were taken on fences and in xeric woods and on rocks with which their color blends exceptionally well. Although I have no data on elevation, there are no high mountains in this southeastern region, and thus no specimens come from elevations of any consequence. The type locality lies on the forested limestone ridge which parallels the coast at Boca de Yuma. At Boca de Chavón, *A. d. properus* was collected in coastal stands of *Coccoloba*. Nowhere does the subspecies appear to be so abundant as *ignigularis* and *dominicensis*.

Anolis distichus sejunctus[6] subsp. n.

Holotype: MCZ 81131, an adult male, from environs of Mano Juan, Isla Saona, República Dominicana, taken 19 July 1964 by Richard Thomas. Original number V3064.

Paratypes: ASFS V3061–63, AMNH 96476, USNM 157918, same data as holotype.

Definition: A subspecies of *A. distichus* characterized by small size (males to 50 mm snout-vent length; only one female known, with snout-vent length of 38 mm),

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[6] From Latin, *sejungere*, to sever.

dorsum light gray with darker spots and flecks and suffused with greenish yellow, head without any distinct dark markings, dewlap uniform pale yellow, modally 1/1 scales between the supraorbital semicircles and the interparietal and 0/0 supraorbitals in contact with the interparietal, 2/2 scales in contact laterally with the postfrontals, and moderate mean number (4.3) of median azygous head scales.

Distribution: Isla Saona, República Dominicana (Fig. 3).

Comments: The five males and one female taken on Isla Saona are the only specimens of *A. distichus* known from that island. The dorsum is light gray and (in large males) is suffused with greenish yellow. Thus, *sejunctus* seems to have both a gray and a greenish color phase in its repertory. In both phases, the dorsum is marked with a scattering of dark spots and flecks, although the head lacks any definitive pattern. The dewlap is regularly faint yellow (Pl. I). The holotype has the following measurements and scale counts: snout-vent length 50 mm, tail 37 mm, two thirds regenerated; 7 scales across snout, 5 loreal rows, semicircles in contact, 0/0 scales between semicircles and interparietal, 1/1 supraorbitals in contact with interparietal, 2/3 scales in lateral contact with postfrontals, 18 fourth toe lamellae, 3 median azygous head scales, "preoccipital" present, 5 postmentals. The series of six *A. d. sejunctus* has the following scale counts: snout scales 5 to 7 (mode 5), loreal rows 4 to 6 (mode 5); supraorbital semicircles in contact in all specimens; modally 1/1 scales between supraorbital semicircles and interparietal and 0/0 supraorbitals in contact with interparietal; 2/2 and 3/3 (each with two specimens) scales in lateral contact with postfrontals; fourth toe lamellae 15 to 18 (mode 18); median azygous head scales 3 to 6 (mode 3 or 5, both with two lizards, mean 4.3); "preoccipital" always present; postmentals 5 to 7 (mode 5, mean 5.7).

A. d. sejunctus resembles *A. d. properus* on the adjacent mainland. Two features distinguish them: the absence in *properus* of any dorsal markings, with a consequently plain back, and the greenish tints which *sejunctus* is apparently able to assume regularly. *A. d. properus* only very rarely has any green hues in its repertory. The two races resemble each other in lacking any dark head pattern, and in having a uniform pale yellow dewlap (although *properus* may have a pale basal orange blush). Scalewise, *properus* modally has 0/0 scales between the semicircles and the interparietal, whereas *sejunctus* has a formula of 1/1. In mean of median head scales, *properus* (2.8) is lower than *sejunctus* (4.3).

From the balance of the subspecies, *sejunctus* differs from *distichoides, biminiensis, dapsilis,* and *ignigularis* in having a yellow rather than an orange dewlap. From the yellow-dewlapped forms *distichus* and *ocior, sejunctus* differs in having 1/1 scales between the semicircles and the interparietal (0/0 in the two Bahaman subspecies) and 0/0 supraorbitals in contact with the interparietal (0/0 in *distichus,* 1/1 in *ocior*). *A. d. distichus* is incapable of a green phase, and the lineate sides and unpatterned back of *ocior* contrast with the patterned back and plain sides of *sejunctus.* The usual differences in presence of the "preoccipital" and higher frequency of complete separation of semicircles in Bahaman versus Hispaniolan races apply as well. Compared with the yellow dewlapped *A. d. dominicensis* to the west, *sejunctus* differs in smaller size, flecked and spotted in contrast to striate dorsum, and lower mean number of postmentals (5.7 versus 6.6). The aspect of these two subspecies is quite different.

The area about Mano Juan is generally shady woody scrub, and the lizards were taken in this habitat as well as in the settlement of Mano Juan.

The fauna of Isla Saona is becoming increasingly well known, and all species which occur there which have been studied (*Leiocephalus lunatus, Ameiva chrysolaema, Ameiva taeniura, Dromicus parvifrons*) are represented by distinctive subspecies, which show expected affinities with their relatives on the adjacent mainland or in extreme eastern Hispaniola. *A. distichus* follows this pattern. Presumably *A. d. sejunctus* is widespread on Saona, despite the fact that it is known only from the area about Mano Juan.

Anolis distichus tostus[7] subsp. n.

Holotype: MCZ 81134, an adult male, from Isla Catalina, western end, República Dominicana, taken 20 August 1963 by Richard Thomas. Original number V558.

Paratypes: ASFS V559–60, same data as holotype.

Definition: A subspecies of *A. distichus* characterized by (presumably) small size (males to 46 mm snout-vent length; females unknown), dorsum yellow-tan with little or no flecking or striations and no head pattern, dewlap deep orange centrally with a yellow border, modally 0/0 scales between the supraorbital semicircles and the interparietal, and moderate mean number (5.0) of median azygous head scales.

Distribution: Isla Catalina, República Dominicana (Fig. 3).

Comments: The three male specimens of *A. d. tostus* are so distinctive that I have no hesitancy in describing them as a subspecies which differs both from *properus* on the adjacent coast and *sejunctus* on Isla Saona to the east. The yellow-tan dorsum (pl. 12 J 3) is like that of no other subspecies of *A. distichus*; the patternless head resembles that of both *sejunctus* and *properus*, but the extensively orange-centered dewlap (Pl. H) is more like that of *ignigularis* (which usually has the orange center larger and the yellow edge much narrower) than the pale yellow dewlaps of both *properus* and *sejunctus*. There is no evidence (but the number of specimens both collected and observed was few) that *tostus* has a green phase or has green pigment in its repertory.

The holotype has the following measurements and counts: snout-vent length 46 mm, tail broken; 5 scales across snout, 5 loreal rows, semicircles in contact, 0/0 scales between semicircles and interparietal, 2/2 supraorbitals in contact with interparietal, 2/2 scales in lateral contact with postfrontals, 16 fourth toe lamellae, 5 median azygous head scales, "preoccipital" present but tiny, 4 postmentals. The series of three *A. d. tostus* has the following scale counts: snout scales 5 and 6 (mode 6), loreal rows 4 and 5 (mode 4); supraorbital semicircles in contact in all specimens; modally 0/0 scales between supraorbital semicircles and interparietal; no mode for number of supraorbitals in contact with interparietal—counts of 1/1, 2/0, 2/2; no mode for number of scales in lateral contact with postfrontals—counts of 2/2, 2/3, 3/3; fourth toe lamellae 16 to 19 (mode 16); median azygous head scales 4 to 6 (no mode; mean 5.0); "preoccipital" always present; postmentals 3 and 4 (mode 4, mean 3.7). The mean of median head scales is the highest for any Hispaniolan population; the small sample of *tostus* renders the significance of this high figure dubious.

From the subspecies *distichus, ocior, dominicensis, properus*, and *sejunctus, A. d. tostus* differs in having a yellow-tan dorsum and a dewlap with a deep orange center and a broad yellow edge. It resembles the races *biminiensis, distichoides, dapsilis*, and *ignigularis* in having an orange dewlap, but differs from these races in dorsal color and pattern. Scale counts are not profitably compared.

On Isla Catalina, *A. d. tostus* was collected exclusively in dry hammock woods (= low coppice), and even there was uncommon. Since Isla Catalina is very dry and much of it is sun-baked scrub and grassland, presumably *tostus* is restricted to the shadier situations in xeric woods.

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[7] From Latin, *torrere*, to parch.

Anolis distichus ravitergum[8] subsp. n.

Holotype: MCZ 81132, an adult male, from 16.5 mi. (26.4 km) S San José de Ocoa, 500 feet (122 meters), Peravia Province, República Dominicana, one of a series taken 24 August 1963 by Ronald F. Klinikowski, Albert Schwartz, and Richard Thomas. Original number V728.

Paratypes (all from the República Dominicana): ASFS V729–35, same data as holotype; ASFS X7988, 1.8 mi. (2.9 km) W, thence 1.1 mi. (1.8 km) N Azua, Azua Province, 24 June 1963, R. Thomas; AMNH 96477–80, CM 40604–08, 1.8 mi. (2.9 km) W, thence 2.7 mi. (4.3 km) N Azua, Azua Province, 24 June 1963, R. F. Klinikowski, D. C. Leber; MCZ 58422–23, 12 km N Azua, Azua Province, 11 August 1958, C. E. Ray, A. S. Rand; ASFS V3169–77, 2 km W Puerto Viejo, Azua Province, 27 July 1964, D. C. Leber, R. Thomas; UIMNH 61684–85, 15.2 mi. (24.3 km) S San José de Ocoa, Peravia Province, 24 August 1963, A. Schwartz; UF/FSM 21514–15, 1.8 mi. (2.9 km) S San José de Ocoa, 1300 feet (397 meters), Peravia Province, 24 August 1963, R. F. Klinikowski, R. Thomas; USNM 157919–25, 10 km W Baní, Peravia Province, 27 July 1964, D. C. Leber, R. Thomas; MCZ 58421, 13 km NW Baní, Peravia Province, 6 August 1958, C. E. Ray, A. S. Rand; KU 93359–64, 4.2 mi. (6.7 km) NE Sabana Grande de Palenque, San Cristóbal Province, 27 June 1963, A. Schwartz.

Referred specimens: REPÚBLICA DOMINICANA. *Independencia Prov.*: 6.3 mi. (10.1 km) SW Neiba, 3 (ASFS V269–71). *Baoruco Prov.*: 3.9 mi. (6.2 km) ENE Neiba, 4 (ASFS V221–24); 3.4 mi. (5.4 km) ENE Neiba, 1 (ASFS V246); 0.8 mi. (1.3 km) SW Neiba, 4 (ASFS V248–50, RT 774).

Intergrades between *A. d. ravitergum* and *A. d. dominicensis*: REPÚBLICA DOMINICANA. *Azua Prov.*: Padre las Casas, 3 (MCZ 58477–79).

Definition: A subspecies of *A. distichus* characterized by large size (males to 56 mm, females to 45 mm snout-vent length), dorsum ashy gray to tan or pale greenish, head usually with a distinct interocular dark brown bar and a dark U extending from the eyes across the occiput, dewlap pale yellow, at times with a faintly orange center, modally 0/0 scales between the supraorbital semicircles and the interparietal and 1/1 supraorbitals in contact with the interparietal, 2/2 scales in contact laterally with the postfrontals, and a very low mean number (2.6) of median azygous head scales.

Distribution: The Valle de Neiba and the Llanos de Azua, from east of Lago Enriquillo east to the vicinity of Sabana Grande de Palenque in San Cristóbal Province, República Dominicana (Fig. 3).

Comments: *A. d. ravitergum* is typically an ashy gray to drab tan lizard with a fairly prominent brown head pattern. Some individuals show a greenish phase, but the green is neither bright nor vivid. The dewlap is pale yellow and occasionally has a pale orange center (Pl. II). Specimens with orange-centered dewlaps are commoner in the Valle de Neiba and may be demonstrating in this area the residual genetic influence of the subspecies in the uplands of the adjacent Sierra de Baoruco. The back is usually moderately marked with vague longitudinal striae, but some specimens are plain above. A few lizards (as preserved) lack the head markings described for the subspecies, but in general the markings are a consistent feature of the entire series. The venters are whitish and the undersides of the tails vary from pale yellow to orange or yellowish green. In general, the entire coloration is faded and subdued.

The holotype has the following measurements and counts: snout-vent length 53 mm, tail 56 mm, incomplete; 4 scales across snout, 5 loreal rows, semicircles in contact, 0/0 scales between supraorbital semicircles and interparietal, 1/2 supraorbitals in contact with interparietal, 2/2 scales in lateral

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[8] From Latin, *ravum*, gray, and *tergum*, back.

contact with postfrontals, 19 fourth toe lamellae, 2 median head scales, "preoccipital" present but divided longitudinally, 6 postmentals.

Scale counts for the series of 57 *ravitergum* are: snout scales 4 to 8 (mode 6), loreal rows 3 to 6 (mode 4); supraorbital semicircles in contact in all specimens; modally 0/0 scales between supraorbital semicircles and interparietal and 1/1 supraorbitals in contact with interparietal; 2/2 scales in lateral contact with postfrontals; fourth toe lamellae 14 to 23 (mode 17); median azygous head scales 0 to 5 (mode 3, mean 2.6); "preoccipital" usually present (49 of 52 specimens); postmentals 4 to 9 (mode 5, mean 5.6). The largest males (56 mm) are from 3.9 mi. (6.2 km) ENE Neiba, Baoruco Province, and the largest female (45 mm) is from 12 km E Azua, Azua Province.

In having a yellow dewlap, *ravitergum* differs from the orange-dewlapped subspecies *biminiensis*, *distichoides*, *dapsilis*, *ignigularis* and *tostus*. *A. d. ravitergum* in its drab coloration is most like *properus* and *sejunctus*. The presence of a head pattern and of at least vague striae on the dorsum will distinguish *ravitergum* from these races. From *dominicensis*, *ravitergum* differs in dorsal coloration (lacking either a bright green or a dark brown phase), in having 0/0 scales between the semicircles and the interparietals and 1/1 supraorbitals in contact with the interparietal (1/1 and 0/0, respectively, in *dominicensis*), and lower mean number of median head scales (2.6 versus 3.9). *A. d. ravitergum* resembles *A. d. ocior* in general dorsal color, but the latter race has a prominent lateral pale streak, a brighter green phase, and much higher mean of median head scales (2.6 versus 5.8). *A. d. ravitergum* is the second largest subspecies, being exceeded in snout-vent length only by *A. d. dominicensis*. It is most closely approached by *ignigularis* and *properus* in size.

Presumably *A. d. ravitergum* comes into contact with three other subspecies of *A. distichus*. To the west in the Valle de Neiba it must meet *dominicensis* somewhere between Neiba, on the one hand, and Aguacate and the mountains above La Descubierta, on the other. No specimens are available from this hiatus, and it is interesting that the lizards from both the latter localities are from the ascending slopes of the Sierra de Neiba (2000 feet—610 meters) and the Sierra de Baoruco (1600 feet—488 meters). Since *ravitergum* is in essence an inhabitant of the floor of the Valle de Neiba in the western portion of its range, the zone of intergradation may well be narrow and restricted to the lower slopes of the ranges. The nearest localities in the valley floor whence I have seen *A. d. dominicensis* to the west in Haiti are Manneville and Thomazeau; comment on the orange-dewlapped populations of *dominicensis* in the Thomazeau-Manneville region has already been made. It is pertinent to note again that the highest frequency of orange dewlap centers in *ravitergum* is in the Valle de Neiba east of the Thomazeau-Manneville area.

A short series of three specimens is from Padre las Casas, Azua Province, on the southern dry slopes of the Cordillera Central. These lizards, even though preserved for some time, still are noticeably green, especially about the head; the larger female has a snout-vent length of 47 mm, which is near the upper extreme of female *dominicensis* but below that of *ravitergum*. The general area about Padre las Casas is transitional between the lower arid Llanos de Azua and the more mesic interior uplands, but its aspect and fauna (i.e., *Ameiva lineolata*) are closer to those of the hot lowlands. I would expect on ecological grounds that the *A. distichus* at Padre las Casas would be *ravitergum*; geographically, however, it is an almost ideal situation for intergradation between a lowland and (in this area) highland subspecies.

A. d. ravitergum comes into contact in the east with *A. d. ignigularis*, in southwestern San Cristóbal Province. Here, the line of demarcation between the two subspecies is extremely sharp, since *ravitergum* is known from 4.2 mi. (6.7 km) NE Sabana Grande de Palenque and *ignigularis* from 2 mi. (3.2 km) SE San Cristóbal and 15.5 km SE El Cacao at 1400 feet, as well as from a series of specimens from various measured localities along the road from San Cristóbal to El Cacao. The *ignigularis* localities are distinctly upland and mesic, although the locality southeast of San Cristóbal is in the mesic lowlands. The distance between the San Cristóbal and Sabana Grande localities is about 16 kilometers airline, but the situation near San Cristóbal (a shaded fence row adjacent to pasture in a generally mesic region) is in contrast to the drier coastal region near Sabana Grande. In general, this area in the vicinity of Baní is becoming increasingly well known as either a place where there is fairly rapid shift in subspecies or as the extreme limit of distribution of species, since on the west are the xeric Llanos de Azua and on the east the more mesic regions which extend toward Santo Domingo. The specimens which I have examined from this general region are referable to either *ravitergum* or *ignigularis*, and I do not regard any of them as intergradient.

There is presumably also a zone of contact between *ravitergum* and the undescribed subspecies in the Sierra de Baoruco, but there are no specimens from lower intermediate elevations, and all material at hand from the eastern Baoruco is clearly the race indigenous to that massif and shows no tendencies toward *ravitergum* (see however the discussion below concerning the material from southwest of Barahona in the Sierra de Baoruco).

Although *A. d. ravitergum* is essentially a lowland subspecies in the Valle de Neiba and the Llanos de Azua, it does ascend the southern rolling piedmont of the Cordillera Central in the vicinity of San José de Ocoa and also occurs in the Sierra de Ocoa. But in both these regions, conditions are xeric and merely continuations of the same habitat in the lower plains. The highest elevation for *A. d. ravitergum* is 1300 feet (397 meters); presumably it also occurs below sea level at the eastern end of Lago Enriquillo.

The relationships of *A. d. ravitergum* and *A. brevirostris* in the Valle de Neiba will be discussed later in detail by Dr. Williams. It is pertinent at this time to point out that in this low and arid valley, *A. d. ravitergum* is more or less confined to shady palm oases and other less rigorous situations, whereas *A. brevirostris* is the lizard of the open scrub. On the ascending slopes of the Sierra de Baoruco, *A. distichus* and *A. brevirostris* are precisely syntopic; in this area of syntopy, the vegetational cover is intermediate between that of the rain forest above and the arid plains below.

Anolis distichus favillarum[9] subsp. n.

Holotype: MCZ 81133, an adult male, from 3 km N Las Auyamas, 3300 feet (1007 meters) Barahona Province, República Dominicana, taken 24 July 1963 by David C. Leber. Original number X9593.

Paratypes (all from Barahona Province, República Dominicana): ASFS X9592, same data as holotype; ASFS X9838–41, 7.0 mi. (11.2 km) S Cabral, 2300 feet (702 meters), 27 July 1963, R. Thomas; CM 40609–12, 7.1 mi. (11.4 km) S Cabral, 2300 feet (702 meters), 27 July 1963, D. C. Leber, R. Thomas; ASFS X9832–33, 8.8 mi. (14.1 km) S Cabral, 2700 feet (824 meters), 27 July 1963, D. C. Leber, R. Thomas; MCZ 58424, MCZ 58426–28, MCZ 58430–31, MCZ 58433–35, MCZ 58437, La Cueva, 11 km SW Cabral, 17 August 1963, C. E. Ray, A. S. Rand; UF/FSM 21516, 8 km NE Las Auyamas, 2600 feet (793 meters), 28 July 1963, native collector; UF/FSM 21517, 24 km SW Barahona, 3700 feet (1129 meters), 2 August 1963, D. C. Leber; AMNH 96481–83, 24 km SW Barahona, 3700 feet (1129 meters), 6 July 1964, D. C.

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[9] From Latin, *favilla*, glowing ashes.

Leber, R. Thomas; MCZ 65353, Hermann's finca, near Paraíso, 2400 feet (732 meters), 26 August 1932, W. G. Hassler.

Definition: A subspecies of *A. distichus* characterized by moderate size (males to 54 mm, females to 47 mm snout-vent length), dorsum bright dark green and heavily striate with darker green or brownish, head with rusty temples and interparietal scale yellow-green and sharply set off from remainder of green head coloration, dewlap vivid orange centrally with a narrow pale yellow edge, modally 1/1 scales between the supraorbital semicircles and the interparietal and 0/0 supraorbitals in contact with the interparietal, 2/2 scales in contact laterally with the postfrontals, and a moderate mean number (3.8) of median azygous head scales.

Distribution: Known only from intermediate and higher elevations in the eastern portion of the Sierra de Baoruco in the República Dominicana (Fig. 3).

Comments: Perhaps the most gaudy of the Hispaniolan mainland races of *A distichus* is *favillarum*. This is especially true when it is compared with its neighbors *dominicensis* in the west and *ravitergum* in the north. The latter is essentially a drab brownish lizard with a pale yellow dewlap and the former a green lizard with a pale yellow dewlap. Neither has the rusty temples and sharply distinct yellow-green interparietal scale nor the vivid orange *favillarum* dewlap (Pl. II).

The holotype of *A. d. favillarum* has the following measurements and counts: snout-vent length 50 mm, tail broken; 4 scales across snout, 4 loreal rows, semicircles in contact, 0/0 scales between supraorbital semicircles and interparietal, 2/2 supraorbitals in contact with interparietal, scales in lateral contact with postfrontals indeterminate, 21 fourth toe lamellae, 1 median head scale, "preoccipital" absent, 5 postmentals.

The series of 28 *A. d. favillarum* has the following counts: snout scales 3 to 6 (mode 4), loreal rows 4 to 6 (mode 4); supraorbital semicircles in contact in all specimens; modally 1/1 scales between supraorbital semicircles and interparietal and 0/0 supraorbitals in contact with interparietal; 2/2 scales in lateral contact with postfrontals; fourth toe lamellae 16 to 22 (mode 19); median azygous head scales 1 to 6 (mode 4, mean 3.8); "preoccipital" usually present (26 of 28 specimens); postmentals 4 to 8 (mode 7, mean 6.1).

In having an orange dewlap, *favillarum* differs from the subspecies *distichus, ocior, dominicensis, properus, sejunctus,* and *ravitergum.* Although in dewlap color *A. d. favillarum* resembles *biminiensis, distichoides, dapsilis, ignigularis,* and *tostus,* none of these races is deep bright green above with rusty temples and a distinct yellow-green parietal. Despite the dewlap similarities, for instance, it is hard to visualize two subspecies more distinct in general appearance than *favillarum* and *tostus*, or *favillarum* and *biminensis.* In having 1/1 scales between the semicircles and the interparietal and 0/0 supraorbitals in contact with the interparietal, *favillarum* resembles *distichoides, dominicensis,* and *sejunctus.* The moderate mean of median head scales (3.8) in *favillarum* is lower than those of the other orange-dewlapped races (5.0 to 8.7) with the exception of *ignigularis* (3.5).

In some ways *favillarum* most closely resembles *ignigularis,* but these two subspecies can be differentiated in that *favillarum* lacks the bicolor dorsum of *ignigularis,* and *ignigularus* lacks the rusty temples of *favillarum.* The ranges of the two are separated by some 62 kilometers at their nearest points (and the distance is longer if one considers the intervening coastal embayments and irregularities) as well as by the intervening lowland subspecies *ravitergum* in the Llanos de Azua. *A. d. favillarum* is so distinctive in color and pattern that it really requires little detailed comparison with any other subspecies.

A. d. favillarum presumably comes into contact with *ravitergum* to the north at the base of the Sierra de Baoruco and with *dominicensis* to the west in the western portion of the Sierra de Baoruco. The lack of *favillarum* × *ravitergum* intergrades has been explained in the discussion of the latter subspecies. The absence of *favillarum* × *dominicenses* intergrades is doubtless due to the fact that there is no material available from the central (and virtually inaccessible) portion of the Sierra de Baoruco. *A. distichus* from the Sierra de Baoruco along the Dominico-Haitian border are *dominicensis.* One of the paratypes of *A. d. favillarum* is of possible interest insofar as the problem of intergradation between this subspecies and *ravitergum* is concerned. This adult lizard, from 24 km SW Barahona at an elevation of 3700 feet (1129 meters), was noted as having a plain yellow dewlap. The specimen might be interpreted as showing tendencies toward the *ravitergum* dewlap condition; on the other hand, this seems unlikely, especially in view of the extreme elevation of the locality. I consider it more likely that it is simply a *favillarum* with an aberrantly colored dewlap.

A. d. favillarum is esentially a denizen of mesic woods and *cafetales* at higher elevations in the Sierra de Baoruco; the known altitudinal limits for the subspecies are from 2300 feet (702 meters) to 3700 feet (1129 meters), although the subspecies must occur at both higher and somewhat lower elevations in this mountain range. In the area of syntopy with *A. brevirostris* (the lower altitudinal limits noted above), the vegetational cover is transitional between that of the very mesic uplands and that of the Valle de Neiba below.

Anolis distichus aurifer[10] subsp. n.

Holotype: MCZ 81135, an adult male, from 11 km N Cavaillon, 1300 feet (397 meters), Dépt. du Sud, Haiti, one of a series taken 6 August 1962 by Dennis R. Paulson, David C. Leber, and native collectors. Original number X3717.

Paratypes (all from Dépt. du Sud, Haiti): ASFS X3658–63, ASFS X3680–84, ASFS X3718–23, AMNH 96484–87, KU 93365–68, CM 40613–16, UIMNH 61686–89, same data as holotype; MCZ 74838–64, Pourcine, Massif de la Hotte, 31 December 1962—2 January 1963, F. Vuilleumier; MCZ 74833–37, Trou Bois on Jérémie Road, 30 December 1962, D. Hill.

Referred specimens: HAITI. *Dépt. du Sud*: Tosia, 1 (MCZ 69756); nr. Massif de la Hotte (= Pic Macaya), 3 (MCZ 38254–56); Petit Trou de Nippes, 8 (USNM 80801–08).

Definition: A subspecies of *A. distichus* characterized by moderate size (males to 54 mm, females to 46 mm snout-vent length), dorsum heavily marbled with varying shades of greens and browns, dewlap vivid orange with a narrow yellow border, modally 1/1 scales between the supraorbital semicircles and the interparietal and 0/0 supraorbitals in contact with the interparietal, 2/2 scales in contact laterally with the postfrontals, and a moderate mean number (3.7) of median azygous head scales.

Distribution: Known definitely from only three localities (the type locality, Pourcine, and Trou Bois) on the north and south flanks of the Massif de la Hotte on the Tiburon Peninsula in southwestern Haiti; by inference and observation (see below) assumed to occur from southeast of Jérémie east to the vicinity of Saint Michel du Sud, where *aurifer* intergrades with *dominicensis* (Fig. 3).

Comments: The Tiburon Peninsula of Haiti, west of about the longitude of Miragoâne on the north coast and a presently unknown locality on the south coast, is inhabited by a complex of (at least) three subspecies of *A. distichus.* In addition to these three mainland races, there are additional subspecies on Ile-à-Vache off the south coast and Ile Grande Cayemite off the north coast. The three mainland subspecies are very different in dewlap color in life, but the dewlap colors and

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[10] From Latin, *aurifer*, gold bearing.

pattern are of course fugitive in preserved material. Consequently, the precise boundaries of the various races can be defined only in terms of freshly collected specimens, and many older specimens from this region may be placed with a particular subspecies only if there are adequate field data on color in life—which in some critical material there are not. Questionable subspecific assignments will be noted in appropriate discussions.

The series of *A. d. aurifer* from the type locality was examined by me in life. These lizards were heavily mottled and streaked above with varying shades of greens and browns, but lacked any bright colors (i.e., rusty temples) on the head or body. The dewlap was vivid orange with a narrow yellow margin (Pl. II); some males had the dewlap orange-red, a still more distinctive and vivid color. The series from Pourcine in the Museum of Comparative Zoology was noted by the collector to have the dewlaps orange "with yellow spots in the orange"—this latter a feature not seen in the topotypical series. The Trou Bois lizards were likewise noted to have "brilliant orange-red" throats. Richard Thomas collected a single male *A. distichus* about 7.5 km (airline) south-southeast of Roseaux which also had an orange dewlap, but the lizard escaped. These localities summarize the *known* distribution of orange-dewlapped *A. distichus* in this region. I have included the single lizard from Tosia, three from Pic Macaya, and eight from Petit Trou de Nippes with *aurifer* on the basis of provenance. Tosia is on the Les Cayes-Jérémie road on the north side of the Massif de la Hotte, and the lizard might be assigned to the Les Cayes-Camp Perrin subspecies described below. However, there are no known specimens of the more southern race from the north slope of the La Hotte, and it seems likely that the specimen is an *aurifer*. The same comments apply equally well to the Pic Macaya lizards. The series from Petit Trou de Nippes falls into the same category, since there are no fresh specimens from the northern coast of the Tiburon Peninsula in this region.

The measurements and counts of the holotype of *A. d. aurifer* are: snout-vent length 52 mm, tail ca. 70 mm; 6 scales across snout, 5 loreal rows, semicircles in contact, 1/1 scales between supraorbital semicircles and interparietal, 0/0 supraorbitals in contact with interparietal, 2/2 scales in lateral contact with postfrontals, 20 fourth toe lamellae, 4 median head scales, "preoccipital" present, 6 postmentals.

The series of 67 *A. d. aurifer* has the following counts: snout scales 4 to 7 (mode 4), loreal rows 3 to 6 (mode 4); supraorbital semicircles in contact in all specimens; modally 1/1 scales between supraorbital semicircles and interparietal and 0/0 supraorbitals in contact with interparietal; 2/2 scales in lateral contact with postfrontals; fourth toe lamellae 16 to 23 (mode 19, but 20 has almost the same frequency); median azygous head scales 1 to 7 (mode 3, mean 3.7); "preoccipital" always present; postmentals 4 to 10 (mode 7, mean 7.2).

The orange dewlap of *A. d. aurifer* differentiates the subspecies from the yellow-dewlapped races *distichus*, *ocior*, *dominicensis*, *properus*, *sejunctus*, and *ravitergum*. In addition to dewlap and dorsal color and pattern (none of the above subspecies has a heavily mottled green-and-brown back), *aurifer* differs in the high mean number of postmentals (7.2 in *aurifer*, 5.4 to 6.7 in the above races, with *ocior* approaching *aurifer* most closely). The other orange-dewlapped subspecies are *biminiensis*, *distichoides*, *dapsilis*, *ignigularis*, *tostus*, and *favillarum*, of which *aurifer* is closest geographically to *favillarum*, but from which it is separated by the intervening range of *dominicensis*. All these subspecies differ in dorsal pattern and color from *aurifer* (in fact, only *favillarum* has a green phase); the rusty temples of *favillarum* additionally distinguish it from *aurifer*. The mean postmentals of *aurifer*

(7.2) aid in separating it from the other orange-dewlapped subspecies (3.7 to 6.1, with *favillarum* approaching *aurifer* most closely).

A. d. aurifer is presumed to intergrade with *A. d. dominicensis* in the vicinity of Saint Michel du Sud, southwest of Miragoâne. A series of 18 specimens (ASFS X3830–47) from 3.5 mi. SW Saint Michel du Sud, 1000 feet (305 meters), was noted as having the dewlaps pale orange with a yellow edge—precisely the condition expected at the place of intergradation of an orange-dewlapped and a yellow-dewlapped race. Purely on the basis of provenance, I consider two other lots of specimens from this same region (MCZ 66113–32, Fond des Nègres, and MCZ 25504–08, 10 mi. [16.0 km] SW Miragoâne) *aurifer* × *dominicensis*. The latter lot may be assignable to *A. d. dominicensis*, but the Fond des Nègres series is close to Saint Michel du Sud, the known locality for *aurifer* × *dominicensis* intergradation. Other than these intergrades, the eastern limits of *aurifer* are unknown; specimens from the north coast in the Miragoâne region were clearly *dominicensis* in life.

In the northwest *aurifer* intergrades with the yellow-dewlapped population on the tip of the Tiburon Peninsula in the area about Roseaux, and in the south *aurifer* intergrades with another subspecies in the vicinity of Cavaillon. In both cases, these intergrades will be discussed with their respective subspecies.

The distribution herein attributed to *A. d. aurifer* is indeed most peculiar, since it is assumed to occur on both sides of at least the eastern portion of the Massif de la Hotte, and along a portion of the north coast as well. Much of the upland range assigned to *aurifer* is extremely difficult to penetrate, and it may be some time before the details of the distribution of *aurifer* are clarified. On the basis of the few annotated series presently available, there is no choice but to regard all these specimens as one subspecies.

The type locality of *A. d. aurifer* is a rocky shaded hillside on the southern slopes of the Massif de la Hotte.

Anolis distichus vinosus[11] subsp. n.

Holotype: MCZ 81136, an adult male, from Camp Perrin, Dépt. du Sud, Haiti, one of a series taken 22 July 1962 by native collectors. Original number X2711.

Paratypes (all from Dépt. du Sud, Haiti): ASFS X2533–49, ASFS X2560–70, AMNH 96488–97, UIMNH 61690–95, CM 40617–22, UF/FSM 21518–23, same data as holotype; MCZ 63125–31, Camp Perrin, 5 August 1960, A. S. Rand and J. D. Lazell, Jr.; ASFS X3361–62, Les Cayes, 2 August 1962, D. R. Paulson; MCZ 63111–17, Les Cayes, 3 August 1960, A. S. Rand and J. D. Lazell, Jr.; ASFS X3353–55, 9.9 km ENE Port-Salut, 650 feet (198 meters), 3 August 1962, D. C. Leber, D. R. Paulson; ANSP 27156–62, KU 93369–75, USNM 157926–27, Carrefour Canon, 500 feet (153 meters), 1 August 1962, R. F. Klinikowski, A. Schwartz; MCZ 63118–21, Carrefour Canon, 4–5 August 1960, A. S. Rand and J. D. Lazell, Jr.; MCZ 63122–24, Les Platons, above Carrefour Canon, 5 August 1960, A. S. Rand and J. D. Lazell, Jr.

Referred specimens: HAITI. *Dépt. du Sud*: Tombeau Cheval, 3 (MCZ 63132–34).

Definition: A subspecies of *A. distichus* characterized by moderate size (males to 54 mm, females to 45 mm snout-vent length), dorsum marbled with greens and browns of varying shades, dewlap with a rather restricted basal maroon (wine colored) blotch or spot and a broad pale yellow margin, modally 1/1 scales between the supraorbital semicircles and the interparietal and 0/0 supraorbitals in contact with interparietal, 2/2 scales in contact laterally with the postfrontals, and a low mean number (3.4) of median azygous head scales.

Distribution: The southern slopes of the Massif de la Hotte from Camp Perrin (and

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[11] From Latin, *vinosus*, full of wine.

Tombeau Cheval?) and Les Platons, south to Les Cayes, and west onto the Presqu'île du Port-Salut; intergrades with *A. d. aurifer* at Cavaillon (Fig. 3).

Comments: The holotype of *A. d. vinosus* has the following measurements and counts: snout-vent length 53 mm, tail 35 mm, broken; 5 scales across snout, 5 loreal rows, semicircles in contact, 1/1 scales between supraorbital semicircles and interparietal, 0/0 supraorbitals in contact with interparietal, 2/2 scales in lateral contact with postfrontals, 20 fourth toe lamellae, 4 median head scales, "preoccipital" present, 6 postmentals.

The series of 102 *A. d. vinosus* has the following counts: snout scales 4 to 8 (mode 4), loreal rows 4 to 6 (mode 5); supraocular semicircles in contact in all specimens; modally 1/1 scales between supraorbital semicircles and interparietal and 0/0 supraorbitals in contact with interparietal; 2/2 scales in lateral contact with postfrontals; fourth toe lamellae 16 to 24 (mode 20); median azygous head scales 2 to 8 (mode 3, mean 3.4); "preoccipital" always present; postmentals 4 to 11 (mode 7, mean 7.4).

Compared with all other subspecies of *A. distichus*, from both the Hispaniolan mainland and the Bahamas, none is so easily differentiable as *vinosus*. The combination of maroon or wine-red centered dewlap with a broad yellow margin (Pl. II) and heavily mottled brown and green dorsum will distinguish it from any other subspecies. Only *A. d. juliae* on Ile-à-Vache resembles *A. d. vinosus* in dewlap color and pattern; *juliae* will be discussed further below. The amount of maroon in the basal spot of the *vinosus* dewlap is variable, and the illustrated individual (which is the holotype) resembles the maximal condition. The range of *vinosus* is bordered on the east by the orange-dewlapped *aurifer* and on the northwest by a yellow-dewlapped subspecies. In both cases, the contrast between the *vinosus* dewlap and that of its neighbors is striking, and the races are easily separable. In dorsal coloration, *vinosus* is most like *aurifer*, with a marbled or mottled pattern of browns and greens. As far as scales are concerned, there is nothing distinctive about *vinosus*; along with the Hispaniolan subspecies *dominicensis*, *sejunctus*, *favillarum*, and *aurifer*, *vinosus* has 1/1 scales between the supraorbitals and the interparietals and 0/0 supraorbitals touching the interparietal. With a mean of 3.4 median head scales, *vinosus* ranks low among all subspecies, and with a mean of 7.4 postmentals, it ranks among the highest.

A. d. vinosus is extremely common throughout its range and especially so at Camp Perrin, where it was observed and taken on trees and hedgerows along dirt roads. At Carrefour Canon, these lizards were abundant in a *cafetal* with cacao, shaded by a high canopy. In Les Cayes, *A. d. vinosus* was abundant about walls and buildings, trees and gardens, etc.

Intergrades between *vinosus* and the race to the northwest will be discussed later. Intergrades between *vinosus* and *aurifer* are represented by a series of three specimens from Cavaillon (ASFS X3729–31). The two males in this short series had dewlaps which had the basal maroon spot paler (more reddish-orange) than in *vinosus*, and the broad margin of the dewlap distinctly more orange—a combination which I interpret as demonstrating intergradation between the two subspecies. These Cavaillon specimens were collected on the same day as the topotypical series of *aurifer*, and direct comparisons of the intensities of the dewlap colors in both lots were made directly with one another.

I have associated the three specimens from Tombeau Cheval (MCZ 63132–34) with *vinosus* rather than *aurifer* or the race to the northwest on the basis of provenance. Tombeau Cheval lies on about the high point of the road between Les Cayes and Jérémie, and just north of Camp Perrin. Since Tombeau Cheval is closer to Camp Perrin than to any other locality whence

A. distichus is known in this region, I have considered the specimens from that locality as *vinosus*, although I admit the possibility of error in such an assignment in this particular region.

Anolis distichus juliae Cochran

Anolis dominicensis juliae Cochran, 1934, Occ. Papers Boston Soc. Nat. Hist., 8:169.

Type locality: Ile-à-Vache, Haiti.

Definition: A subspecies of *A. distichus* characterized by moderate size (males to 53 mm, females to 44 mm snout-vent length), dorsum brownish-gray to green, somewhat marbled with darker browns and greens, dewlap almost completely dark wine-red with a pale yellow margin, modally 0/0 scales between the supraorbital semicircles and the interparietal and 0/0 supraorbitals in contact with the interparietal, 2/2 scales in contact laterally with the postfrontals, and a low mean number (3.4) of median azygous head scales.

Distribution: Ile-à-Vache, Haiti(Fig. 3).

Comments: *A. d. juliae* is obviously an insular derivative of the mainland *A. d. vinosus*, which it resembles in general dewlap pigmentation. Four characters separate the two subspecies: 1) the wine-red pigment in the dewlap of *juliae* is brighter (more red) than that of *vinosus*, 2) the extent of the wine-red spot is greater in *juliae* than in *vinosus* (Pl. II), 3) the dorsum of *juliae* is generally paler and less marbled and dark than that of *vinosus*, and 4) the modal condition of 0/0 scales between the semicircles and the interparietal and 0/0 supraorbitals in contact with the interparietal differ from the 1/1 and 0/0 (respectively) modes in *vinosus*. Comparisons with the remaining races are unnecessary, since no subspecies, other than *vinosus*, has the red-blotched dewlap of *juliae*.

Measurements and scale counts of the holotype (a male) of *A. d. juliae* are: snout-vent length 47 mm, tail ca. 49 mm, broken; 4 scales across snout, 5 loreal rows, semicircles in contact, 1/0 scales between supraorbital semicircles and interparietal, 0/1 supraorbitals in contact with interparietal, 3/2 scales in lateral contact with postfrontals, 21 fourth toe lamellae, 4 median azygous head scales, "preoccipital" present, 8 postmentals.

Scale counts on the series of 31 *A. d. juliae* are: snout scales 4 to 8 (mode 4), loreal rows 4 to 6 (mode 5); supraorbital semicircles always in contact; modally 0/0 scales between the semicircles and the interparietal and 0/0 supraorbitals in contact with the interparietal; fourth toe lamellae 16 to 22 (mode 20); median azygous head scales 2 to 6 (mode 4, mean 3.4); "preoccipital" usually present (29 of 30 lizards); postmentals 5 to 9 (mode 8, but 6 has almost as high a frequency, mean 7.2).

Where we collected on the western end of Ile-à-Vache, *A. d. juliae* was moderately common, occurring about houses and on trees in cultivated areas, as well as on *Cocos* trunks in old coconut plantings.

Specimens examined: HAITI. *Ile-à-Vache*: no other locality, 9 (MCZ 37517—holotype, MCZ 37518–19—paratypes, MCZ 6171, MCZ 86767–71); western end, 22 (ASFS X3516–36, ASFS X3548).

Anolis distichus suppar[12] subsp. n.

Holotype: MCZ 81137, an adult male, from Dame-Marie, south side of town along coast, Dépt. du Sud, Haiti, taken 13 March 1966 by Richard Thomas. Original number V9236.

Paratypes (all from Dépt. du Sud, Haiti): ASFS V9237, same data as holotype; ASFS V9268, ca. 5 km (airline) S Dame-Marie, 13 March 1966, R. Thomas; ASFS V9269, ca. 10 km (airline) WSW Moron, 13 March 1966, R. Thomas; ASFS V9192–94, ASFS V9213, ca. 7.5 km (airline) WSW Moron, 13 March 1966, E. Cyphale, R. Thomas; MCZ 74766, MCZ 74768–810, MCZ 74812–25, Marfranc, 26–27 December 1962, D. Hill and F. Vuillemier; USNM 160682–86,

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[12] From Latin, *suppar*, almost equal.

Jérémie, 9–10 March 1966, R. Thomas, native collectors; UF/FSM 21524–25, Jérémie, 11 March 1966, R. Thomas; AMNH 96501–04, Jérémie, 11 March 1966, R. Thomas, native collector; MCZ 63106, Jérémie, 31 July 1960, A. S. Rand and J. D. Lazell, Jr.; MCZ 3346, MCZ 86772–77, Jérémie, no date, D. F. Weinland; KU 93376–79, 2 km NW Jérémie, 14 March 1966, native collector; MCZ 69766–79, Carrefour Sanon, nr. Jérémie, December 1962, G. Whiteman; MCZ 69780-91, Place Nègre, nr. Jérémie, December 1962, G. Whiteman; CM 37811 + 10 untagged specimens, Place Nègre, nr. Jérémie, 10–11 December 1961, L. Whiteman; MCZ 69792–809, Mayette, nr. Jérémie, December 1962, G. Whiteman; MCZ 64630–37, Tiga, nr. Jérémie, 15 December 1960, G. and L. Whiteman; MCZ 69751, Lancenise, nr. Jérémie (not mapped), December 1962, G. Whiteman; MCZ 69757–65, La Source, nr. Jérémie (not mapped), December 1962, G. Whiteman; MCZ 69754–55, Perine, nr. Jérémie (not mapped), December 1962, G. Whiteman; MCZ 65627–28, nr. Jérémie, 1960, L. and G. Whiteman; MCZ 69752–53, Bozo, nr. Jérémie (not mapped), December 1962, G. Whiteman; ASFS V9359–60, ca. 8 km (airline) S Marché Leon, 3000 feet (915 meters), 15 March 1966, native collector.

Referred specimens: HAITI. *Dépt du Sud*: Tiburon, 6 (MCZ 6170, MCZ 86778–82); Paroty, nr. Jérémie (not mapped), 1 (MCZ 64638); Place Nègre, nr. Jérémie, 39 (MCZ 64675–713); nr. Jérémie, 7 (MCZ 3346).

Definition: A subspecies of *A. distichus* characterized by moderate size (males to 54 mm, females to 44 mm snout-vent length), dorsum pale green, somewhat marbled with gray and yellow, dewlap pale yellow to yellow-green or grayish yellow and at times with a dull yellow-orange basal smudge, modally 1/1 scales between the supraorbital semicircles and the interparietal and 0/0 supraorbitals in contact with the interparietal, 2/2 scales in contact laterally with the postfrontals, and a low mean number (3.4) of median azygous head scales.

Distribution: The extreme western tip of the Tiburon Peninsula in Haiti, from Dame-Marie east to Jérémie, and south on the northern slopes of the Massif de la Hotte in the vicinity of Marché Leon; occurrence at Tiburon problematical (see below) (Fig. 3).

Comments: The terminal subspecies on the western tip of the Tiburon Peninsula is remarkably different from its neighbors to the east (*aurifer*) and south (*vinosus*) and in fact resembles its relative *dominicensis* far to the east, both in dorsal color and dewlap color. In having a yellow dewlap (Pl. II), *suppar* is readily distinguishable from *aurifer* (orange dewlap) and *vinosus* (maroon-centered dewlap). The resemblances to *dominicensis* are strong, including a dorsal green color, a pale yellow dewlap, comparable means of median head scales (3.4 and 3.9), and 1/1 scales between semicircles and interparietal and 0/0 supraorbitals in contact with interparietal. The major differences are the higher mean number of postmentals (7.9 in *suppar*—the highest mean of any subspecies—and 6.6 in *dominicensis*) and the more pastel or paler green dorsum.

The measurements and counts for the holotype of *A. d. suppar* are: snout-vent length 52 mm, tail 65 mm; 5 scales across snout, 5 loreal rows, semicircles in contact, 1/1 scales between supraorbital semicircles and interparietal, 0/0 supraorbitals in contact with interparietal, 2/2 scales in lateral contact with postfrontals, 22 fourth toe lamellae, 4 median head scales, "preoccipital" present, 7 postmentals.

Scale counts for the series of 176 *A. d. suppar* are: snout scales 4 to 8 (mode 4), loreal rows 3 to 6 (mode 5); modally 1/1 scales between supraorbital semicircles and interparietal and 0/0 supraorbitals in contact with interparietal; 2/2 scales in lateral contact with postfrontals; fourth toe lamellae 16 to 25 (mode 18 and 19); median azygous head scales 1 to 7 (mode 3, mean

3.4); "preoccipital" usually present (170 of 176 lizards); postmentals 4 to 13 (mode 7, mean 7.9).

The dewlaps of *A. d. suppar* have been noted in life as pale yellow-green (Jérémie, Dame-Marie, and west-southwest of Moron) and pale yellow (Marché Leon; pl. 17 E 1, west-southwest of Moron). A male from the Moron region also has a dull yellow-orange (pl. 9 J 10) basal smudge. The dorsum is usually pale or pastel green, somewhat overlaid with grayish marbling and/or streaking, and commonly there are yellow or paler green middorsal blotches, especially on the anterior trunk and neck. Preserved specimens, regardless of freshness of preservation, very regularly show both a broad dark (black) V-shaped collar which arises from about the angle of the jaws and extends across the neck, and a large dark (black) area on the upper side of the head, separated from the collar by a narrow paler (gray) V-shaped band. Since no note of these markings was made in life, they must not be conspicuous in the living animal, but they are remarkably consistent in the preserved lizards. I do not know if *suppar* is capable of a brown phase.

Comparisons of *suppar* with the adjacent *aurifer* and *vinosus* were made above. From the orange-dewlapped subspecies *biminiensis, distichoides, dapsilis, ignigularis, tostus,* and *favillarum, suppar* differs in having a yellow dewlap. From *juliae, suppar* also differs in having a yellow dewlap instead of a dewlap with an extensive wine-colored basal blotch. From the yellow-dewlapped races (*distichus, ocior, properus, sejunctus,* and *ravitergum*; comparison with *dominicensis* was made above) *suppar* differs in being (always?) green (in contrast to *distichus, properus, sejunctus,* and *ravitergum*) and in lacking the lateral pale line of *ocior* (although many *suppar* have the flank stripe fairly well developed, it is not clearly outlined above and below by darker). Other differences from *ocior* include a much lower mean number of median head scales (3.4 versus 5.8), 1/1 scales between the semicircles and the interparietal (0/0 in *ocior*), and 0/0 supraorbitals in contact with the interparietal (1/1 in *ocior*).

The specimens from Tiburon were collected by Garman and thus are quite old and faded, and there are no color data on them. I consider them *suppar* only provisionally; Tiburon is 28 kilometers airline south of Dame-Marie, but it may be precisely in this intervening region that *suppar* intergrades with *vinosus*. The Tiburon lizards may be *vinosus*; there are no specimens from any locality between Dame-Marie and Tiburon, on the one hand, or between Tiburon and Port-Salut, on the other.

Although there is no evidence of intergradation between *suppar* and *vinosus*, there is evidence of intergradation between *suppar* and *aurifer*. A series (MCZ 74826–32) from Roseaux was noted as having the dewlap with a "deep orange rust spot at base." It may be recalled that there is a sight record of an *aurifer* from 7.5 km (airline) south-southeast of Roseaux. The zone of intergradation between *suppar* and *aurifer* appears to be very narrow, centering in the region about Roseaux.

A. d. suppar is quite common throughout most of its range, occurring from sea level to elevations of 3000 feet (915 meters) above Marché Leon on the northern slopes of the Massif de la Hotte. In habitat, it does not differ from other altitudinally wide-ranging races, in that it was taken in edificarian situations, along the southern slopes of the Monts Cartaches, and in both natural and artificial wooded situations which the species inhabits throughout its range.

Anolis distichus patruelis[13] subsp. n.

Holotype: MCZ 81138, an adult male, from vicinity of Pointe Sable, Ile Grande

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[13] From Latin, *patruelis*, relating to a cousin.

Cayemite, one of a series taken 18 March 1966 by Richard Thomas and native collectors. Original number V9409.

Paratypes: ASFS V9410–14, ASFS V9423–26, MCZ 81142–46, USNM 160687–91, AMNH 96505–08, same data as holotype; MCZ 25519, Grande Cayemite, 3 August 1927, W. J. Eyerdam.

Definition: A subspecies of *A. distichus* characterized by small size (males to 50 mm, females to 42 mm snout-vent length), dorsum green to gray, usually not prominently striate, dewlap solid dark reddish to mustard orange, modally 1/1 scales between the supraorbital semicircles and the interparietals and 0/0 supraorbitals in contact with the interparietal, 2/2 scales in contact laterally with the postfrontals, and a moderate mean number (4.6) of median azygous head scales.

Distribution: Ile Grande Cayemite, Haiti (Fig. 3).

Comments: The measurements and scale counts for the holotype of *A. d. patruelis* are: snout-vent length 49 mm, tail ca. 60 mm; 4 scales across snout, 4 loreal rows, semicircles in contact, 1/1 scales between supraorbital semicircles and interparietal, 0/0 supraorbitals in contact with interparietal, 2/2 scales in lateral contact with postfrontals, 19 fourth toe lamellae, 2 median head scales, "preoccipital" present, 8 postmentals.

The series of 25 *A. d. patruelis* has the following counts: snout scales 4 to 8 (mode 4), loreal rows 4 to 6 (mode 4); modally 1/1 scales between supraorbital semicircles and interparietal and 0/0 supraorbitals in contact with interparietal; 2/2 scales in lateral contact with postfrontals; fourth toe lamellae 16 to 22 (mode 20); median azygous head scales 2 to 7 (mode 4, mean 4.6); "preoccipital" always present; postmentals 6 to 11 (mode 8, mean 7.8).

The dorsum of *A. d. patruelis* varies between green and gray; most specimens show little or no striae, but others have a lineate dorsum. The dewlap varies in life from dark reddish to mustard orange (pl. 6 K 9, pl. 5 L 11), and has an orange (rather than pale yellow) margin (Pl. II).

Ile Grande Cayemite is adjacent to the northern section of the presumed mainland range of *A. d. aurifer*, and *A. d. patruelis* resembles the former subspecies in dewlap color. A major difference is the absence in *patruelis* of the narrow yellow dewlap margin which occurs in *aurifer*; the richer and deeper hues of the *patruelis* dewlap are likewise different than the brighter pigments of *aurifer*. The back of *aurifer* is heavily marbled and mottled with greens and browns, whereas that of *patruelis* is generally much plainer, lacking pronounced mottling, and is rarely clearly striate.

A. d. patruelis, with its deep orange dewlap, differs from the subspecies which have yellow dewlaps (*distichus, ocior, dominicensis, properus, sejunctus, ravitergum*, and *suppar*) and those which have a maroon or wine-red basal spot (*vinosus, juliae*). The other orange-dewlapped subspecies are *biminiensis, distichoides, dapsilis, ignigularis, tostus, favillarum* (and *aurifer*, with which *patruelis* was compared above). Aside from the differences in dorsal pigmentation and pattern, the deeper hue of the dewlap color, and the absence of a yellow dewlap margin in *patruelis*, the Grande Cayemite subspecies differs from all other orange-dewlapped forms in having a very high mean of postmentals (7.8 in *patruelis*, 3.7 to 7.2 in other orange-throated subspecies, with *aurifer* having the highest mean). In fact, other than *suppar, patruelis* has a higher postmental mean than all other subspecies.

Most of the paratypic series were native collected; the lizards came from dry scrubby woods growing on almost bare limestone and from about the village at Pointe Sable.

There is a short series (USNM 80814–18) of *A. distichus* from Ile Petite Cayemite, just to the west of Grande Cayemite. These specimens have long been in preservative, and consequently no details of coloration or pattern are discernible. They may be *patruelis*, although, as pointed out for *Ameiva taeniura* Cope, which is known from both the Cayemites, there is a possibility that each island has its own subspecies (Schwartz, 1967a). In this short Petite Cayemite series of five specimens, the postmentals range between 4 and 7 (two specimens have counts of 4 and 5, and are thus lower than the much longer series from Grande Cayemite). One lizard (USNM 80818) has only a single median azygous head scale, the "preoccipital," a condition not observed in the Grande Cayemite series. I consider the Petite Cayemite lizards *A. d. patruelis* only provisionally.

THE FLORIDA POPULATIONS

Anolis distichus was first reported from the continental United States by Smith and McCauley (1948), who described *A. d. floridanus* on the basis of a short series of six specimens from Brickell Park in downtown Miami, Florida. The status of the mainland lizards was later discussed by Duellman and Schwartz (1958:279–281), who regarded *floridanus* as a synonym of *A. d. distichus*. Of the four scale characters and one pigmental trait, these authors noted that "*floridanus*" (of which form they examined 77 specimens in detail) agreed with topotypical *distichus* in number of infraorbital scales, number of scales bordering the median suture (= median azygous head scales), and in having the throat unpigmented, but disagreed with the nominate subspecies in having a higher percentage (63.6 per cent versus 14.0 per cent) of specimens with the supraocular semicircles separated and in the modal number of scales separating the prefrontal from the anterior supraocular (mode 1 and 2 with almost equal frequencies in "*floridanus*," mode 2 in topotypical *distichus*). With increased knowledge of *Anolis distichus* in its insular range, it is appropriate to reassess the status not only of "*floridanus*" but also that of another mainland Floridian population.

Through the efforts of C. Rhea Warren, I have been able to examine a short series of seven lizards (RT 1478–84) from Northwest South River Drive in Miami, Florida. These lizards were green in life and capable of becoming solid brown; they represent a small sample from a large and very successful colony centering near the junction of the Miami Canal (the northwestern extension of the Miami River) and the artificial Tamiami Canal. The specimens are typical in all ways of *A. d. dominicensis*, with the possible exception of three of the seven specimens having 3/3 scales in lateral contact with the postfrontals. This high frequency is doubtless due to the small sample size; in the series of 245 *A. d. dominicensis* from Hispaniola, 32 have 3/3 scales in lateral contact with the postfrontals, whereas 162 have 2/2 scales in this position. The yellow dewlaps with occasional orange basal blush and the green dorsa agree in detail with my concepts of *A. d. dominicensis*, and I assume that these lizards have been recently introduced into this region through some fluke of international shipping. King and Krakauer (1966:146) have reported this population as *A. d. dominicensis* at my suggestion.

Anolis distichus floridanus Smith and McCauley

Anolis distichus floridanus Smith and McCauley, 1948, Proc. Biol. Soc. Washington, 61:160.

Type locality: Brickell Park, Miami, Dade County, Florida.

Definition: A subspecies of *A. distichus* characterized by small size (males to 50 mm, females to 45 mm snout-vent length), dorsum gray to dark brown and without a green phase, dewlap pale yellow (occasionally pale orange), modally 1/1 scales between the supraorbital semicircles and interparietal, 0/0 supraorbitals in contact with the interparietal, 2/3 scales in contact laterally with the postfrontal, and very high mean number (7.9) of median azygous head scales correlated with the very high incidence (about 60 per cent) of complete separation of supraocular semicircles medially.

Distribution: Known only from the extreme eastern coastal and near-coastal margin of Dade County, Florida (Fig. 2).

Comments: I have examined 90 *A. distichus* (aside from the *A. d. dominicensis* noted above) from southern Florida. Although Duellman and Schwartz (1958: 279–281) considered *A. d. floridanus* synonymous with *A. d. distichus* from New Providence, the above definition clearly shows that *floridanus* differs from *distichus* in several characters which elsewhere in the Bahamas and Hispaniola I regard as indicative of subspecifity. The use of the name *A. d. floridanus* for the continental lizards mainly involves the philosophical problem of its appropriateness if the mainland *A. distichus* have been introduced only recently by man. This question is discussed below.

The two major samples which I have studied come from two localities (Brickell Park and its vicinity in downtown Miami, and Fairchild Tropical Garden). Mr. Warren advises me that *A. distichus* occurs elsewhere in Miami and in Coral Gables, Florida, and Wayne King (*in litt.*, 28 September 1966) reported its occurrence at one additional locality in Miami, four in Coral Gables, three in Coconut Grove, and one in Kendall. I have not examined material from any of these localities. Dr. King suggests that the Brickell Park-Fairchild Garden population is continuous (the Coconut Grove localities and a locality at the junction of Brickell Avenue and the Rickenbacker Causeway in downtown Miami fill in fairly well the hiatus between the two presumed terminal stations for *A. d. floridanus*), and I concur. King and Krakauer (1966:146) stated that all other localities are the result of secondary introductions by reptile fanciers; a second method for dispersal may be that Fairchild Garden supplies plants for ornamental purposes to Dade County and to private persons for decorative planting, with resultant accidental distribution of *A. floridanus* throughout the county.

The two terminal localities are distant about 8.5 miles (13.6 km) from one another. Both are more or less coastal, and Fairchild Tropical Garden has for many years been a center to which plants from outside the United States have been introduced for purposes of culture and exhibit. The Brickell Park locality lies in downtown Miami on the coast on the south side of the Miami River. The lizards are extremely abundant at both localities. In most characters the two samples are alike, and if they represent two different "introductions," their later convergence has been along remarkably similar lines.

The largest mainland male and female are both from Brickell Park (snout-vent length 50 mm in the male, 45 mm in the female), whereas the largest of each sex from Fairchild Garden are 47 mm and 39 mm. The scale characters of the two populations are: snout scales 3 to 6 (mode 6) at Brickell Park, 3 to 7 (mode 6) at Fairchild Garden; loreal rows 4 and 5 (mode 4) at Brickell Park, 4 to 6 (mode 4) at Fairchild Garden; semicircles usually not in contact (27 of 42 lizards from Brickell Park, 25 of 48 lizards from Fairchild Garden); modally 1/1 scales between the supraorbital semicircles and the interparietal and 0/0 supraorbitals in contact with the interparietal in both samples; fourth toe lamellae 15 to 19 (both localities), modes 17 or 18 (Brickell Park) and 18 or 19 (Fairchild Garden); modally 3/3 scales in lateral contact with postfrontals at Brickell Park, but almost an equal frequency of 2/2 at this locality; modally 2/3 scales in lateral contact with postfrontals at Fairchild Garden; median azygous head scales 5 to 12 (mode 8, mean 8.0) at Brickell Park, 4 to 10 (mode 8, mean 7.8) at Fairchild Garden; "preoccipital" usually present (40 of 42 lizards from Brickell Park, 42 of 48 lizards from Fairchild Garden); postmentals 3 to 6 (mode 4, mean 4.3) at Brickell Park, 3 to 8 (mode 5 or 6, mean

4.4) at Fairchild Garden. The dewlap is pale yellow to yellow with an extensive pale orange blush; dorsally the lizards are gray, incapable of a green phase but capable of becoming dark brown.

The mainland *A. distichus* obviously are related to the Bahaman populations of the species rather than to the Hispaniolan forms. Such features as the high incidence of complete separation of the semicircles, the low number of postmentals, and the lack of a green phase all point to the Bahamas as the place of origin of *A. d. floridanus*. It has generally been assumed that the continental *A. distichus* are the result of a very recent introduction, either fortuitous or intentional, by man from the Bahamas. If such were the case, it should be a simple matter to determine from which of the five Bahaman subspecies *floridanus* has been drawn. This is not the case; *A. d. floridanus* presents a suite of characters which distinguishes it from all Bahaman, as well as Hispaniolan, populations. If the forerunners of *floridanus* were only recently introduced by man, then differentiation in Florida of *floridanus* must have been extremely rapid. If, on the other hand, *A. d. floridanus* has had a history other than that generally accepted—i.e., it has been in Florida for a longer period or *A. d. floridanus* has been introduced only recently but evolved its peculiar characteristics elsewhere—its differences from any other subspecies could be accounted for more readily. Evidence for the relationship and a suggested history of the continental populations are offered below.

Turning first to dorsal and dewlap colors, *floridanus* resembles all the Bahaman subspecies except *ocior* in the former (since *floridanus* lacks a green phase) and only *distichus* in the latter. The scale characters, on the other hand, are distinctive. The very high incidence of complete separation of the semicircles (57.8 per cent if both samples are combined; 64.2 per cent in the Brickell Park sample alone, 52.1 per cent in the Fairchild Garden sample alone) is much greater than that of any Bahaman subspecies, being approached most closely by *distichoides* (32.1 per cent) and *biminiensis* (30.2 per cent). In modally having 1/1 scales between the semicircles and the interparietal, *floridanus* differs from all Bahaman populations except *distichoides*. New Providence and Exuma Cays *A. d. distichus* do have 1/1 as the modal condition (or as a bimode in the former case), however. Although the modal condition is 2/3 scales in lateral contact with the postfrontals in *floridanus* (30 individuals), 29 lizards have 2/2 scales in lateral contact and 25 have 3/3 (of which 15 are from Brickell Park, where 3/3 is the mode). Such a high incidence of 3/3 scales in lateral contact with the postfrontals is unequalled in any Bahaman population except *biminiensis*, where 3/3 is the mode.

The mean of 7.9 median azygous head scales in *floridanus* is higher than that of any Bahaman subspecies with the exception of 8.7 in *distichoides*. In having 0/0 supraorbitals in contact with the interparietal, *floridanus* is like *distichus*, *distichoides*, and *dapsilis*, but unlike *biminiensis* and *ocior*. The regular occurrence of the "preoccipital" in *floridanus* resembles the condition in all Bahaman subspecies except *distichoides* and *biminiensis* which more often lack the "preoccipital." Finally, the mean of 4.4 postmentals in *floridanus* is lower than those of all Bahaman populations, being most closely approached by *distichoides* (4.6) and *biminiensis* (4.8).

From the above resume, it is apparent that, although *floridanus* agrees with nominate *distichus* in dorsal and dewlap colors, it differs markedly from it in scale characters. The two populations which bear the closest resemblance in scalation to *floridanus* are *distichoides* and *biminiensis*, and, not unexpectedly, these two races are those most geographically adjacent to *floridanus*. The occasional occurrence in *floridanus* of a pale orange dewlap also suggests that one or the other of these orange-dewlapped subspecies may have been the source of *floridanus.*

There are three possible histories for the continental population of *A. distichus*:

1) The populations were indeed accidentally or purposely introduced by man in the relatively recent past (shortly prior to their discovery and description in 1948) from somewhere in the Bahamas.

2) The populations are the result of a natural overseas introduction from somewhere in the Bahamas whose population as yet remains unsampled; the Bimini chain or Andros seem likely candidates, but *A. d. floridanus* does not agree with either *biminiensis* or *distichoides* in all details of color or scalation.

3) The populations reached Florida during the Pleistocene from the Bahamas but remained undetected there until 1948, by which time their precise place of origin in the Bahamas had become obscure because of *in situ* evolution to *A. d. floridanus* on the mainland.

Several facts should be taken into consideration before proceeding. 1) *A. d. floridanus* is closest in characteristics to those Bahaman lizards which are geographically most nearly adjacent to the mainland—*biminiensis* and *distichoides.* 2) The distribution of *A. d. floridanus* is primarily coastal (as one might expect of a natural invader) and is not now (and perhaps was not ever) disjunct, as previously supposed. 3) Although there is much overseas boat traffic between the Biminis and Miami, there is less between Andros and Florida; Dr. King has pointed out that "in the early nineteen hundreds there were large four-, five- and six-masted barks that sailed freight all over the Bahamas and between the Bahamas and Florida. Any of these could have been a vehicle for introducing *distichus* into Florida." 4) That *A. distichus* arrived in Florida in the Pleistocene but remained undetected until the present century may take credulity. It is not impossible that such a chain of events took place, since the Miami region has only in the present century been a large urban center, and small or restricted coastal populations of this fast-moving and inconspicuous lizard could have been easily overlooked by earlier collectors and visiting scientists, who likely were more concerned with protecting themselves from mosquitoes in the coastal regions where *A. d. floridanus* occurs. 5) Along these lines it is interesting to note that *A. d. distichus* was first described from New Providence in 1861, whereas Nassau was the home of the First Royal Governor of the Bahamas in 1718, and through the following century and a half became a veritable Bahaman metropolis, far more visited by travelers and scientists than the Miami region. No one suggests that *A. d. distichus* owes its tenancy of New Providence to the years just prior to the year it was described, yet this has always been the assumption of the status of *A. d. floridanus.*

Considering all of the above facts and suggestions, I adhere to a combined sequence of events as regards *A. d. floridanus* as noted above in postulations (1) and (2). I think it most likely that *A. d. floridanus* was introduced, either by natural overseas transport or by man long before its discovery in 1948 but in historical times. The source of this introduction remains a mystery, but one region may be mentioned. The west coast of Andros is very poorly known zoologically, and this coast is the one closest to the Florida mainland. The fragmentation of Andros by cross-island waterways and bights and its large size (Andros is as large as Puerto Rico but less physiographically diverse) suggest that intra-island differentiation in some reptiles may have taken place there. This is indeed the case with Andros *Ameiva auberi* (personal communication, Clarence J. McCoy, Jr.), and there is no reason to doubt that it occurred in other reptiles. Verification of this supposition can be had only by collection of series of specimens from this inaccessible west coast. Dr. King is the only scientist who has crossed the Big Mud to western Andros in recent times, and he secured but a single female *A. distichus* there. Western Andros remains the only extensive area in the Bahamas whose fauna is extremely poorly known.

The geographical juxtaposition of this coast to Florida makes it even more attractive as a source of introduction of *A. d. floridanus.* The assumed derivation of *A. d. floridanus* from *A. d. distichoides* is logical, considering the resemblances between the two in some scale features. Dr. King (*in litt.*, 30 September 1966) suggested that the Bahaman sponge fleet used to ply the waters of the large banks in the Bahamas (including the Big Mud west of Andros). Boats from the fleet put into Miami for sale of cargo until the Bahaman sponge industry was destroyed by the sponge blight in 1938 and 1939. Intentional or accidental transportation of *A. d. floridanus* from the west coast of Andros to the Miami area might well have been effected by ships in the sponge trade. If such is the case, then, *A. d. floridanus*, despite its name, is in reality a Bahaman subspecies from the western section of Andros which has been introduced into Florida in the relatively recent past.

Specimens examined: FLORIDA. *Dade County*: Brickell Park, 35 (UMMZ 106189–31 specimens, UMMZ 108100, UMMZ 108372–3 specimens); south of Miami River on Brickell Ave., Miami, 7 (UMMZ 109232); Fairchild Tropical Garden, Miami, 48 (RT 1485–97, UMMZ 108189–2 specimens, UMMZ 108190–6 specimens, UMMZ 108371–25 specimens, UMMZ 109231–2 specimens).

DISCUSSION

Anolis distichus is one of the most widely distributed species of amphibian or reptile in the Antillean region; its occurrence on Hispaniola, the Bahamas, and Florida is exceeded by that of another anole (*Anolis sagrei* Duméril and Bibron on the Bahama Islands north of the Crooked Island Passage, Cuba and the Isla de Pinos, Jamaica, Cayman Islands, Península de Yucatán, Swan Islands, Florida Keys), of *Typhlops lumbricalis* Linnaeus (Bahama Islands north of the Crooked Island Passage, Cuba and the Isla de Pinos, Hispaniola), and of the boa *Epicrates angulifer* (Great Bahama Bank, Sheep Cay off Great Inagua, Cuba and the Isla de Pinos, Hispaniola). Throughout its range, *A. distichus* varies in success; in more mesic situations and on some islands, it may be very abundant, but in xeric regions it is less so or absent.

As far as the Bahaman herpetofauna is concerned, *A. distichus* holds a unique position. It is generally conceded that the Bahaman herpetofauna has been derived mainly from that of Cuba, with a smaller Hispaniolan element. There are 13 Cuban forms in the Bahamas (*Hyla septentrionalis, Eleutherodactylus planirostris, Sphaerodactylus decoratus, Sphaerodactylus notatus, Tarentola americana, Anolis angusticeps, Anolis carolinensis, Anolis sagrei, Leiocephalus carinatus, Leiocephalus loxogrammus, Ameiva auberi, Typhlops biminiensis* and *Typhlops lumbricalis*). These species all have Bahaman and Cuban populations which are identical or only racially differentiated, with the exception of *L. loxogrammus* (which is endemic to the Bahamas but closely related to the Cuban *L. raviceps*) and *Typhlops lumbricalis* (in which the nominate form occurs both in the Bahamas and in part of eastern Cuba). The latter species likewise is presumed (Thomas, in press) to have originated on Hispaniola rather than Cuba, but it is included here as a Cuban element in the Bahaman fauna, since the Bahaman populations have been derived directly from Cuba rather than from Hispaniola. In general, the Cuban species are limited in the Bahamas to the islands north of the Crooked Island Passage (i.e., the Great and Little Bahama banks), although there are exceptions (*L. loxogrammus*), and some forms may not occur on both banks (*A. carolinensis*) or may occur only, but not be widespread, on the Great Bahama Bank (*T. americana*). However, compared to the Hispaniolan faunal element in the Bahamas, the species with Cuban affinities are widely distributed.

The Bahaman species with Hispaniolan affinities include eight species (*Aristelliger cochranae, Sphaerodactylus inaguae, Anolis distichus, Leiocephalus inaguae, Leiocephalus arenarius, Ameiva maynardi, Epicrates exsul*, and *Epicrates angulifer*). I include *E. angulifer* in this series rather than with the Cuban element (the species occurs on both islands), since the more widely ranging Bahaman subspecies is more closely related to the Hispaniolan than the Cuban race. Of these eight species, five are limited to the islands between the Crooked Island Passage and Hispaniola, one (*E. exsul*) to the Little Bahama Bank, and the remaining two (*A. distichus* and *E. angulifer*) occur on the Great Bahama Bank (or at least primarily on this bank). *Sphaerodactylus* "*anthracinus*" on New Providence and Andros is without doubt introduced from Hispaniola, since the Bahaman form ("*anthracinus*") is identical with one of the Hispaniolan subspecies of *S. copei.* Thus of the eight Bahaman species with Hispaniolan affinities, only two (*A. distichus* and *E. angulifer*) are widespread in the Bahamas, whereas 12 of the 13 Cuban species are widespread on the Great Bank. (There are 19 other species of reptiles—including seven nominal species of the genus *Cyclura*—in the Bahamas, but these are not readily classifiable as to origin; none is obviously or certainly related to either Hispaniolan or Cuban congeners, and need not concern us further in this context.)

From the above brief summary of the affinities of the Bahaman herpetofauna, it appears that *A. distichus* has a rather unique position therein, since it is one of the two Bahaman reptiles which are widespread in the Bahamas and have had an Hispaniolan origin. Noteworthy is the fact that *A. distichus* is absent from the Bahamas south of the Crooked Island Passage, and from the Turks and Caicos islands. This is peculiar, since these islands would seem to have been likely and handy stepping-stones from the Hispaniolan mainland to the Great Bahama Bank. Not only is *A. distichus* absent from these islands, but they have only a single anolis (*A. scriptus*), which is not closely related to *A. distichus* (*scriptus*, although associated with *distichus* as an Eastern Island Alpha anole, belongs to the *cristatellus* rather than the *bimaculatus* group; *fide* Etheridge, *in litt.*). There is no *distichus* relative in Cuba, the more logical place for invasion of the Great Bahama Bank. It seems then that *A. distichus* arrived on the Great Bahama Bank directly from Hispaniola, without using either Cuba or the southern Bahamas south of the Crooked Island Passage as way stations.

I have already commented on the general, although not absolute differences between the Bahaman and Hispaniolan segments of *A. distichus.* These differences are not especially striking, either in dewlap color and pattern or in dorsal color. The complete absence of separation of the semicircles in any Hispaniolan *A. distichus*, the higher mean numbers of median head scales in the Bahamas, and the tendency toward absence of the "preoccipital" in the Bahamas do indicate, however, that the Bahaman lizards have diverged as a unit in some scale characters. Most Bahaman subspecies have lost the ability to become green, and this phenomenon has taken place also in some Hispaniolan populations. In general, the loss of the green phase is correlated with more arid, in contrast to distinctly mesic, situations. However, the range of *A. d. ocior* in the Bahamas is not especially more mesic than that of the other Bahaman subspecies, and *ocior* retains a green phase. It is suggestive that those islands (Rum Cay and San Salvador) inhabited by *ocior* are two of the three Bahaman islands occupied by *A. distichus* which are not on the Great Bank. The other exception, Cat Island, is presently *census*) in having a yellow dewlap and

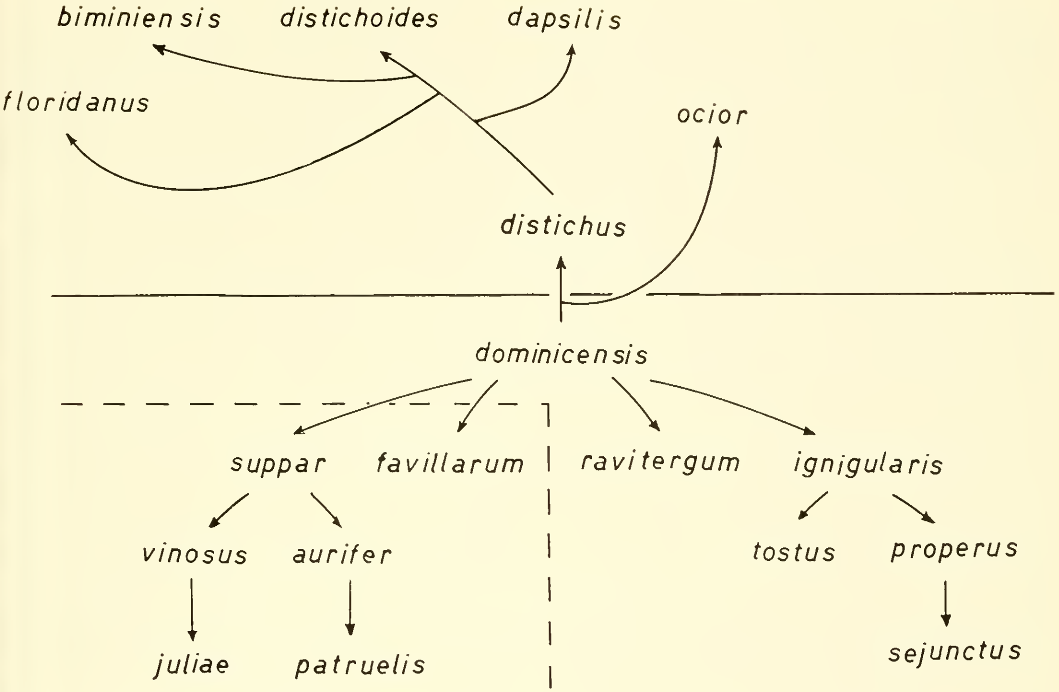

Figure 4. Dendrogram of the relationships between the subspecies of *Anolis distichus*. Bahaman subspecies above solid horizontal line, Hispaniolan subspecies below solid horizontal line; subspecies on the south island of Hispaniola and its satellite islands enclosed within dashed line in lower left of diagram.

cut off from the Great Bank, but in contrast to Rum and San Salvador, Cat is not far removed from the Great Bank and is still connected to Eleuthera by a narrow submarine strip (Clench, 1938:536). Its history has been at least partially associated with that of the Great Bank.

Not only does *A. d. distichus* have the broadest distribution of any subspecies in the Bahamas, but it also resembles the most widespread Hispaniolan race (*A. d. domini-* also is the Bahaman subspecies which occurs closest geographically to Hispaniola on the Ragged Islands and Long Island. *A. d. distichus* seems appropriate, both geographically and in dewlap color, as a direct Bahaman derivative from Hispaniola (Fig. 4). In the Bahamas, various subspecies have differentiated from *A. d. distichus* on more or less peripheral islands or island groups. Thus, *biminiensis*, *distichoides*, and *dapsilis* are all essentially orange-dewlapped *A. distichus* with head scutellation features differing from those of *A. d. distichus* but occurring in the latter subspecies as casual variants.

A. d. ocior, in contrast to the balance of the Bahaman races, retains a green phase and a yellow dewlap—characters which ally it directly with *dominicensis*. It does, however, have some "Bahaman" characteristics, such as the high number of median head scales. Possibly *ocior* reached Rum Cay and San Salvador from the Great Bahama Bank prior to the loss of the green phase by the parental stock there, but at a time when some head scale modifications were already established or becoming so. I do not consider it likely that *ocior* has had a direct and separate connection with *dominicensis*, but rather that it has had a long history independent of that of the balance of the Bahaman races.

On Hispaniola, the situation is more

complex. In essence there is a single, widespread, yellow-dewlapped subspecies (*dominicensis*) with a series of "peripheral" races on the mainland (*ignigularis, properus, ravitergum, favillarum, aurifer, vinosus, suppar*) and a series of subspecies from the satellite islands (*sejunctus, tostus, juliae, patruelis*). Of the mainland subspecies, those with plain or drab dorsa and yellow dewlaps in general inhabit the more arid regions (*properus, ravitergum*) and the orange-dewlapped and brightly colored subspecies inhabit both lowland and highland mesic areas (*ignigularis, favillarum, aurifer*). *A. d. suppar* is a distinct exception to this statement, since the extreme tip of the Tiburon Peninsula is mesic, and *suppar* is a green lizard with a yellow dewlap, much like *dominicensis*. The most strikingly different mainland subspecies in dewlap color is *vinosus*.

Of the satellite island races, all but one resemble their relatives on the immediately adjacent mainland in dewlap color and in color repertory. The major exception is *A. d. tostus* on Isla Catalina. The adjacent mainland is inhabited by *properus*, which is yellow-dewlapped, whereas *tostus* has essentially an orange dewlap, more like that of *ignigularis* to the west. The faunal history of Isla Catalina is peculiar, in that it includes an endemic and relict subspecies of *Ameiva lineolata* and a population of *A. chrysolaema*, a species which is not known from the adjacent coast. Both these lizards, as well as *tostus*, show distinctly more western than adjacent or eastern affinities. Under these circumstances it is likely that *tostus* represents an *ignigularis*, rather than a *properus*, derivative, and that through changing conditions on the adjacent mainland, there has been a shift to the westward of subspecies along the coast, with *properus* replacing *ignigularis*. As far as the balance of the satellite island races is concerned, none presents any problem. It is noteworthy that *juliae* shares with *vinosus* on the adjacent mainland the strikingly different style of dewlap pigmentation and pattern.

Although not now a satellite island, the Península de Samaná presumably was so at one time. The occurrence there of a disjunct population of *ignigularis* has been discussed in detail in the text.

There is no way of determining whether *A. distichus* was primarily and primitively an inhabitant of the historical north or south island (*sensu* Williams, 1961) of Hispaniola. The occurrence of *dominicensis* on most of the north island and on the basal half of the Tiburon Peninsula suggests in some ways that the species was primarily north island, and invaded the south island secondarily. This thesis presents the problem of the very distinct and apparently isolated *favillarum* in the Sierra de Baoruco, and the exceptionally distinctive *vinosus* and *juliae* on the distal Tiburon Peninsula and Ile-à-Vache. The three subspecies on the tip of the Tiburon Peninsula (*suppar, vinosus, aurifer*), of which two are quite different in dewlap color from *dominicensis*, may indicate that this region was colonized directly from the north island across the Golfe de la Gonâve and not serially along the peninsula itself. If so, then these terminal populations may have diverged independently and remained isolated from other *A. distichus* populations until the arrival of *dominicensis* across the much narrower inter-island strait and subsequent contact along the Tiburon Peninsula. *A. d. favillarum* in the Sierra de Baoruco may represent still another isolated derivative from a north island stock. I cannot suggest that *favillarum* was historically derived from the adjacent lowland and drab *ravitergum*, however. Another possibility is that *favillarum* is an upland offshoot from *dominicensis* (just as, to the east, *ignigularis* is an orange-dewlapped *dominicensis* derivative) in the Sierra de Baoruco, and thus has evolved rather recently. The apparent absence of *A. distichus* from the southern side of the Valle de Neiba in this particular region seems to enforce the latter suggested derivation of *favillarum*.

Although *A. distichus* is very widespread in Hispaniola, its absence in two regions is remarkable. The species is unknown from Ile de la Gonâve, which is inhabited by the *A. distichus* cognate, *A. brevirostris*. Although the coast of Gonâve is hot and arid, the interior is less hostile and more shaded. It is strange that *A. distichus* and *A. brevirostris* do not share Gonâve as they do similar portions of the mainland.

The other major region whence *A. distichus* is absent is the Península de Barahona. The lowlands of this peninsula, south of the Sierra de Baoruco, are inhabited exclusively by *A. brevirostris*, again, as on Gonâve, despite the ample availability of apparently suitable habitat for *A. distichus*. The species likewise is unknown from the coastal lowlands on the Península from the city of Barahona south (*A. brevirostris* is the exclusive species of the pair in Barahona itself and its environs), and also apparently along the southern Haitian coast between the Dominican village of Pedernales east to the area near Jacmel. (There is some doubt in this latter case because of the confused and unlocatable records for *A. distichus* labeled as coming from localities "near Saltrou." At least, all locatable stations where *A. distichus* has been taken "near Saltrou" are upland, and this is nicely correlated with the occurrence of the species on the Dominican side of the border north of Pedernales in the extreme eastern Sierra de Baoruco.)

The Península de Barahona south of the Sierra de Baoruco is emerging in Hispaniolan herpetology as a most distinctive area. The high mountain massifs of the Baoruco to the north and the La Selle to the west, coupled with the narrow and steep coastal "plain" at the eastern end of the Sierra de Baoruco, effectively trap lowland xerophiles to the south. Included in the list of such disjunct or practically disjunct forms are *Typhlops syntherus* and *Leptotyphlops pyrites* as endemic species; *Ameiva chrysolaema ficta* and *A. c. leberi*, *Ameiva lineolata privigna*, *Leiocephalus barahonensis oxygaster* and *aureus*, *Diploglossus curtissi aporus*, *Amphisbaena gonavensis hyporissor* and *A. g. leberi* as endemic subspecies. Although *A. brevirostris* is by no means restricted to this region, it is of interest that *A. distichus* has been unable to penetrate it either along the steep eastern coastal "plain," or from the uplands of the eastern Massif de la Selle or from the Sierra de Baoruco. *A. brevirostris* is the conspicuous and common member of the pair in the lowlands south of the mountains.

Although the Península de Barahona is in general arid, there seem to be ample areas which would be quite suitable for *A. distichus*; such regions are invariably inhabited by *A. brevirostris*. Correlated with the absence of *A. distichus* from the Península de Barahona is its absence from Isla Beata (which has the endemic subspecies *A. brevirostris wetmorei*). The Beata fauna is easily derivable from that on the adjacent Península de Barahona, and the lack of *A. distichus* on Beata is not noteworthy. The relationships of *Anolis altavelensis* on Isla Alto Velo have already been noted.

Although I am reluctant to attribute the absence of a species from a particular region to the catch-all phenomenon of competition, an explanation which may be glibly invoked without precise data, the situation between *A. distichus* and *A. brevirostris* suggests very strongly that competition may indeed be the reason for the absence of the former in some regions occupied by the latter. The Ile de la Gonâve and the Península de Barahona are both arid regions. In the Cul de Sac Plain, where mesic oases occur within otherwise arid scrub, *A. distichus* is confined to the former habitat, whereas the latter is occupied by *A. brevirostris*. Wherever the two species occur sympatrically in an arid situation, *A. brevirostris* is regularly the more "successful" and *A. distichus* the species whose distribution is limited to favorable pockets within the area occupied by *A. brevirostris.* Such encounters (Thomazeau-Manneville; Haitian coast in the Jacmel area; arid coast on the north shore of the Golfe de la Gonâve) invariably are "unfavorable" for *A. distichus.* If the Ile de la Gonâve and the Península de Barahona were originally colonized by *A. brevirostris*, it seems likely that *A. distichus* may simply not have been able to penetrate into these regions to reach ecologically suitable habitats (shaded woods, oases, etc.) because of the previous presence there of *A. brevirostris.* The situation on Gonâve may be less complex, since as an off-shore island, Gonâve may never have been reached by *A. distichus.* On the other hand, it seems plausible, in the light of evidence from areas of contact between *A. brevirostris* and *A. distichus* elsewhere and the absence of *A. distichus* from the Península de Barahona, that *A. distichus* may not be able to compete with *A. brevirostris* on Gonâve where the latter species is already well established.

In summary, *A. distichus* has a wide distribution in the Bahama Islands and on Hispaniola, having arrived in the Bahamas directly from Hispaniola without employing either Cuba or the southern Bahamas as way stations. These two major segments of *A. distichus* have been isolated from one another for a sufficiently long period for some differentiation to have taken place between them, but in general they are similar. In the Bahamas, *A. d. distichus* is considered the basic stock whence have been derived four peripheral subspecies, of which one (*ocior*) was isolated on Rum Cay and San Salvador prior to the separation of the remaining three Bahaman races from *A. d. distichus.* On Hispaniola, *A. d. dominicensis* is suggested as a north island parent stock (whence the Bahaman races also were derived) which has invaded the south island. Previously, the terminal portion of the Tiburon Peninsula has received *A. distichus* across the Golfe de la Gonâve, and three subspecies had differentiated there. With the invasion of *A. d. dominicensis* across the inter-island strait, this subspecies came in contact with the easternmost (*aurifer*) of the Tiburon races. The subspecies in the Sierra de Baoruco (*favillarum*) is considered a relatively recent derivative from *dominicensis. A. d. tostus* on Isla Catalina suggests that there has been a westward shift in *A. distichus* populations along the southeastern coast, with the result that *tostus* is, alone of the four satellite island subspecies, unlike its neighbor on the adjacent mainland. The absence of *A. distichus* from Ile de la Gonâve and the Península de Barahona is attributed to the inability of *A. distichus* to compete with *A. brevirostris* in arid areas where the latter is well established.

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tion of living chamber is believed to belong to this genus, which is known from only one species in the upper Scythian strata at the mouth of the Olenek River, Siberia. The adoral part of the fragment measures 19 mm high and 17.5 mm in width. The whorl section is subquadrate in outline with a broad, low arched venter, rounded ventral shoulders, lateral areas that are only slightly convex and convergent, rounded umbilical shoulders, and a steep umbilical wall. The lateral areas bear radial ribs that enlarge slightly towards the ventral shoulders. There is a faint trace of the ribs across the venter, which gives the venter an undulating appearance. The posterior end of this fragment has some traces of the last septum, enough to indicate that there is a large first lateral lobe, adjacent to large rounded saddles. The second lateral lobe is high on the lateral areas and is much smaller, and there is probably a very small auxiliary lobe on the umbilical wall.

This fragment is assigned to *Czekanowskites* on the basis of the great similarity of the whorl outline and pattern of ribs to the Siberian species of this genus. The suture, insofar as it can be observed, is also similar in basic pattern to that of the Siberian species. The major difference appears to be in the nature of the venter. The Siberian species appears to have a smooth venter, whereas the form recorded here has traces of the ribs across the venter.

Occurrence. Upper member of the Thaynes Formation, Hammond Creek, Bear River Range, southeast Idaho.

Repository. MCZ 9649.

Genus *Popovites* Tozer, 1965

Type species, *Popovites occidentalis* Tozer, 1965

"Inner whorls globose, outer whorl of approximately equal height and width, with a perpendicular umbilical wall, prominent, rounded umbilical shoulder, flat sides, and a broadly arched or slightly flattened venter. Sculpture consists of regular growth lines; radial wrinkles or faint ribs may also occur on the venter. Constrictions are absent. Body chamber about one whorl in length. The suture line comprises: a deep external lobe, with incised branches; two ceratitic lateral lobes; a suspensive lobe with one or more auxiliary incisions; and one internal lateral lobe" (Tozer, 1965a: 21).

This new genus shows marked affinities to *Prosphingites*, on the one hand, and to *Czekanowskites*, on the other. The suture of *Popovites* is quite similar to that of *Prosphingites* and at the same time not as elaborate as the suture of *Czekanowskites*. There is, however, in the fairly large size of the first lateral lobe a similarity in the suture of *Popovites* and *Czekanowskites* (Fig. 17E). The general conch form of this new group of ammonites is like that in various species of *Prosphingites* and *Czekanowskites*.

The genus is known by two species from an upper Scythian horizon in British Columbia and Ellesmere Island.

Popovites occidentalis Tozer

Text-figure 17

Popovites occidentalis Tozer, 1965a: 22, pl. 3, figs. 2–12, text-figure 5.

The type species is well illustrated and described by Tozer (1965a, Fig. 17E of this report). It differs from *P. borealis* only in being slightly more involute; however, since that species is based on a single specimen, there is no way of evaluating the significance of this difference. Among the measured specimens of *P. occidentalis* there is only a variation of 5 percent in the diameter of the umbilicus (Tozer, 1965a: p. 23). The umbilical diameter of the holotype of *P. borealis* is 31 percent at a diameter of 31 mm and 35 percent at a diameter of 43 mm. This is 5 and 10 percent, respectively, greater than the maximum diameter of the umbilicus for *P. occidentalis.*

Occurrence. Toad Formation, Halfway River area, British Columbia, associated with *Preflorianites intermedius* Tozer and *Monacanthites monoceros* Tozer.

Popovites borealis Tozer

Popovites borealis Tozer, 1965a: 24, pl. 3, figs. 1a, b, text-figure 6.

See above for discussion of this species.

Occurrence. Blaa Mountain Formation, lower shale member, Ellesmere Island.

Genus *Monacanthites* Tozer, 1965
Type species, *Monacanthites monoceros* Tozer, 1965

"Globose ammonoids with sculpture of widely spaced, unbranched ribs that are curved to form a sharp ventral sinus. On the outer whorl each rib, at the ventral mid-line, carries a single, solid spine. Body chamber one whorl in length. Suture ceratitic, with two lateral lobes, both internally and externally" (Tozer, 1965a: 27).

Monacanthites monoceros Tozer
Text-figure 17

Monacanthites monoceros Tozer, 1965a: 27, pl. 1, figs. 8–10, pl. 2, fig. 4, text-fig. 8.

A unique species, quite unlike any other ammonite of comparable age (Fig. 17F).

Occurrence. Toad Formation, Halfway River area, British Columbia, associated with *Preflorianites intermedius* Tozer and *Popovites occidentalis* Tozer.

Genus *Tunglanites* Chao, 1959
Type species, *Tunglanites lenticularis* Chao, 1959

Involute, compressed conch with narrowly rounded to acute venter; inner volutions more inflated, bearing oblique constrictions. Body chamber of one volution. Suture with single ceratitic lateral lobe, two rounded lateral saddles.

The combination of conch shape and suture of this genus is unique among late Scythian ammonoids. The group was first recognized from the *Subcolumbites* fauna of Albania by Arthaber (1911) who placed it in the genus *Styrites* of much younger age. This generic assignment for this late Scythian form has never been accepted. Diener (1915: 271) listed it with question in the genus *Styrites*, and Spath (1934: 197) clearly recognized the independent status of this form but refrained from proposing a new generic name, most likely because data on the Albanian forms were very incomplete. Renz and Renz (1948) gave no indication that they were familiar with any literature on this form after the publication of Arthaber's paper in 1911.

The discovery of eight specimens in the *Subcolumbites* fauna of Kwangsi, China, has enabled a much clearer understanding of the group, and a new generic name is well justified.

There are at present two species of the genus *Tunglanites*, *T. lenticularis* Chao, the type species, and *T. alexi* n. sp. for the Albanian and Chios forms assigned to *Styrites lilangensis* Diener by Arthaber and Renz and Renz, respectively. Direct comparison of these two species is handicapped by the incompleteness in our knowledge of the Albanian and Chios specimens. Unfortunately, one of the specimens studied by Arthaber is lost and the Chios fauna has yielded only two specimens. These western Tethyan specimens were thought by both Arthaber and the Renzes to have a goniatitic lateral lobe. However, the preservation, in hard red limestone, makes development of the suture extremely difficult, and the smooth character of the lobe may be due to over grinding or etching. Regardless of this there can be no doubt of the close relationship, and perhaps even identity, of these two species.

In regard to the genetic relations of the group, Spath (1934: 197) suggested they represent a specialized offshoot of *Isculitoides*. The recognition of faint constrictions on the early volutions of the Kwangsi specimens, the compression of the conch, and nature of the suture make this suggestion perfectly reasonable.

In the three localities where *Tunglanites* has been recorded, Albania, Chios, and

Kwangsi, China, the associated fauna includes such typical upper Scythian genera as *Subcolumbites, Proptychitoides,* and *Hemilecanites.*

Tunglanites lenticularis Chao
Text-figure 21

Tunglanites lenticularis Chao, 1959: 120, 294, pl. 27, figs. 25–32, pl. 28, figs. 23–25.

Involute, compressed, small conch with rounded venter on early volutions becoming acute on last volution. Living chamber one volution or more in length. Surface may bear fine striae of growth which curve backward along flanks; constrictions may be present on early volutions. Suture with broad ventral lobe, two rounded lateral saddles and single lateral lobe; occasionally a second lateral lobe is present on the umbilical shoulder and wall.

Chao established his new genus and species on the basis of eight specimens of which three were illustrated. It appears that the umbilicus is completely closed on the earlier volution and gradually opens slightly on the more adoral volutions. The only other recorded occurrence of this genus is that of specimens from Albania and Chios which are very similar in over-all appearance to this Kwangsi species. The western Tethyan specimens have a more open umbilicus at a smaller diameter; however, the significance of this difference is questionable. More material is needed to evaluate the ontogenetic changes in growth. Another distinctive feature is the suture (Fig. 21A). The Chios and Albanian specimens are reported to have smooth lobes. However, the preservation of these specimens in hard red limestone requires grinding and acid to observe the suture in most cases. It is not at all certain that the lobes are really goniatitic. The Albanian specimen described by Arthaber (1911: 260, pl. 23(7), fig. 12) as *Styrites lilangensis* Diener does not show a suture; just where Arthaber obtained the suture of his figure 12c is a puzzle (Fig. 21B). The specimen from Chios described by Renz and Renz (1948: 31, pl. 12, fig. 4) does not show the suture clearly enough to establish whether it is really goniatitic. I strongly suspect that the lateral lobe is indeed denticulated.

Occurrence. From a black, thin bedded limestone 0.6 meters thick and 14 meters above the lower Permian Maokou Limestone (Chao collection 542b); the Chashanao section of Chao (1959: 162) at the border of Hochich and Tunglan districts (Chao collection 610), western Kwangsi, China. The Scythian strata at this locality comprise only about 16 meters of shale and limestone. The only fossils present are from this 0.6 meter bed, which in addition to *Tunglanites* contains *Subcolumbites, Proptychitoides* and *Hemilecanites.*

Tunglanites alexi n. sp.
Plate 20, figures 1, 2; Text-figure 21

Styrites lilangensis,—Arthaber (non Diener), 1911: 260, pl. 23(7), figs. 11a, b, 12a, b, c; Renz and Renz, 1947: 60; Renz and Renz, 1948: 31, pl. 12, figs. 4–4a.

Styrites (?) cf. *lilangensis* Diener, 1915: 271.

Gen. nov. "*Styrites*" *lilangensis*,—Spath, 1934: 189, 197.

This species is established for the specimens Arthaber (1911) and Renz and Renz (1948) described as *Styrites lilangensis* Diener from the *Subcolumbites* faunas of Albania and Chios. Arthaber had two specimens from Albania both of which he illustrated; the smaller of his two specimens (Arthaber, 1911: pl. 23(7), fig. 11) is lost, but the larger specimen (Arthaber, 1911: pl. 23(7), fig. 12) is available and is selected as the type specimen. The diameter of this specimen is approximately 30 mm, the width of the adoral whorl 8.5 mm, the height 12.5 and the diameter of the umbilicus 6.7 mm. A portion of the phragmocone is broken off and missing. The whorls are compressed and convergent, forming an acute venter. The umbilical shoulders are very low but rounded; the umbilicus is excentrumbilicate. Arthaber (1911: pl. 23(7), fig. 12c) shows a suture (Fig. 21B of this report) which presum-

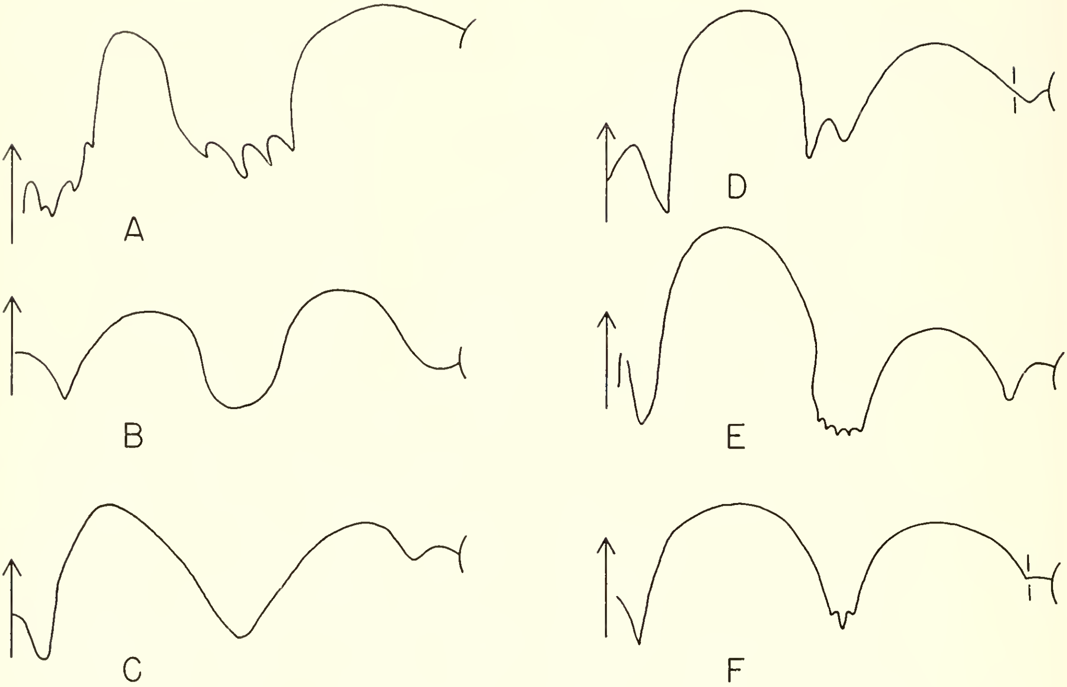


Figure 21. Diagrammatic representation of the suture of: A, *Tunglanites lenticularis* Chao from an upper Scythian horizon in Kwangsi, China (1959: pl. 27, fig. 32), at a diameter of approximately 15 mm; B, *Tunglanites alexi* n. sp. (= *Styrites lilangensis*,—Arthaber, 1911: pl. 23(7), fig. 12c) from *Subcolumbites* fauna of Albania, suture presumably from paratype of Arthaber (1911: pl. 23(7), fig. 11) which is apparently lost; C, *Paradinarites suni* Chao (1950: fig. 4), holotype, at a diameter of approximately 30 mm; D, *Pseudoceltites constrictilis* (Astakhova, 1960: fig. 8) from *Columbites* Zone of Astakhova (1960) on the Mangyshlak Peninsula, at a diameter of approximately 15 mm; E, *Pseudoceltites nevadi* n. sp., from Upper Thaynes Formation, Confusion Range, Utah, un-numbered paratype at whorl height of approximately 10 mm; F, *Pseudoceltites nevadi* n. sp., from Upper Thaynes Formation, Confusion Range, Utah, un-numbered paratype at whorl height of approximately 10 mm.

ably was taken off the other type specimen. Careful examination of this specimen has failed to show any trace of a suture.

The specimen from the *Subcolumbites* fauna of Chios illustrated by Renz and Renz (1948: pl. 12, fig. 4) measures 17.1 mm in diameter, 5.2? mm for the width of the adoral whorl, 7.0 mm for the height of the adoral whorl and 3.5 mm for the diameter of the umbilicus. Renz and Renz state that their Chios specimen had a goniatitic suture; however, my examination of the specimen reveals that the suture is not well preserved and it cannot be established whether it is goniatitic or not. I strongly suspect that the lateral lobe is indeed denticulated.

The general shape of the conch is very much like that of *T. lenticularis* except for an apparently slightly larger umbilicus.

Occurrence. Subcolumbites fauna of Albania and Chios.

Repository. Holotype (Pl. 20, figs. 1, 2), Paleontological Institute, University of Vienna; specimens from Chios NHMB J13582 (Renz and Renz, 1948: pl. 12, fig. 4), unfigured specimen NHMB J13583.

Genus *Columbites* Hyatt and Smith, 1905

Type species, *Columbites parisianus* Hyatt and Smith, 1905

Columbites parisianus Hyatt and Smith

Plate 39, figures 1–10; Plate 40, figures 1–11; Plate 41, figures 1–7;

Plate 42, figures 1–9; Plate 43, figures 4, 5; Text-figures 22, 23.

Columbites parisianus Hyatt and Smith, 1905: 51, pl. 1, figs. 9–14, pl. 61, figs. 1–21, pl. 72, figs. 1–24; Frech, 1908: pl. 42, fig. 2; Diener, 1915: 112; Diener, 1925: 69, pl. 24, fig. 2; Smith, 1932: 107, pl. 1, figs. 9–14, pl. 61, figs. 1–21, pl. 72, figs. 1–24; Spath, 1934: 201, pl. 13, fig. 3, text-fig. 61; Kummel, *in* Arkell, et al., 1957: L140, fig. 172, 2.

Columbites spencei Smith, 1914: 36, pl. 70, figs. 1–16, pl. 71, figs. 1–16; Smith, 1932: 108, pl. 77, figs. 1–21, pl. 78, figs. 1–16; Kutassy, 1933: 490.

Columbites consanguineus Smith, 1932: 106, pl. 46, figs. 1–13.

Columbites minimus Smith, 1932: 106, pl. 47, figs. 9, 10.

Columbites ligatus Smith, 1932: 106, pl. 47, figs. 1–8.

Columbites ornatus Smith, 1932: 107, pl. 46, figs. 14–21.

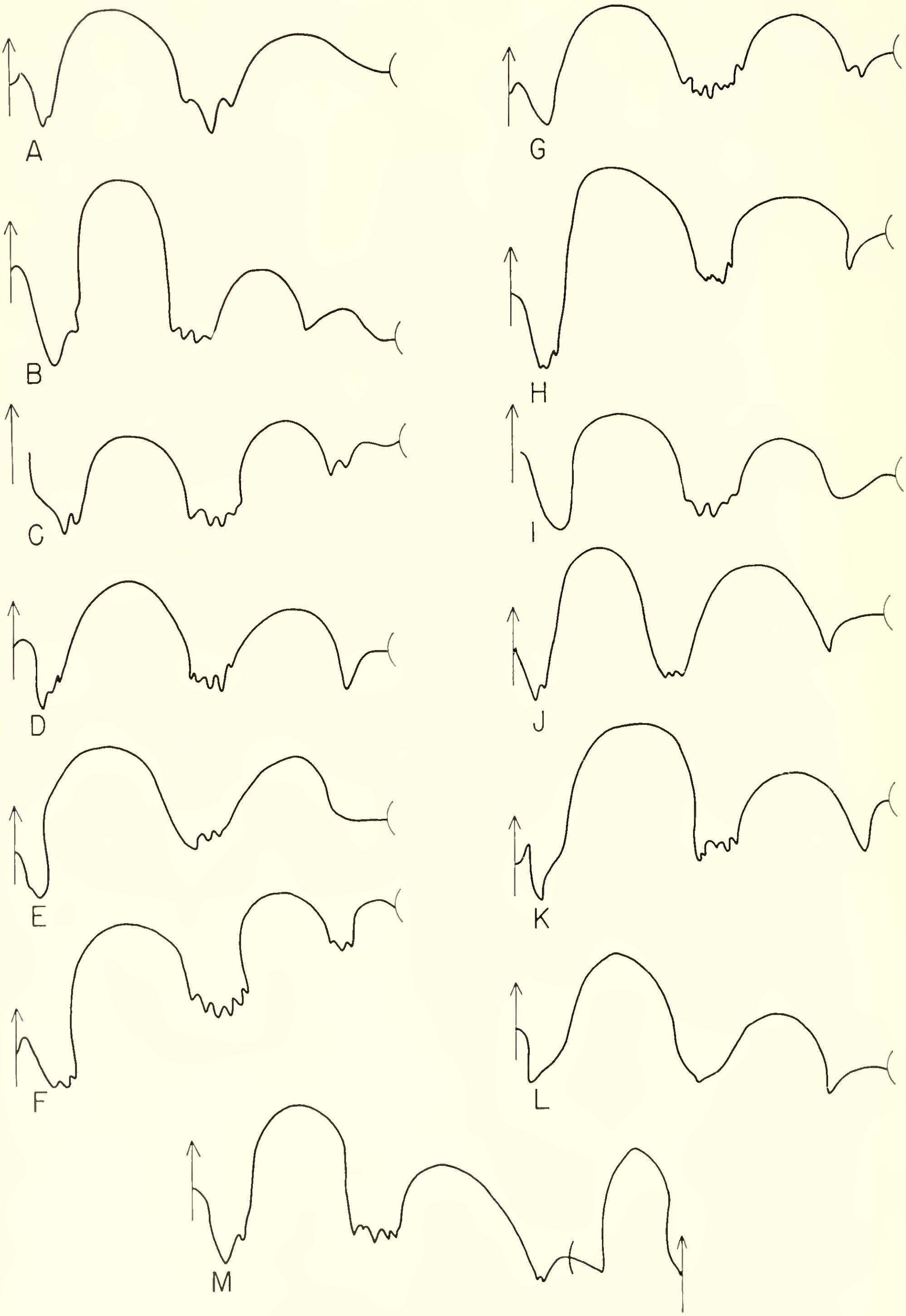
All the specimens assigned to the six species of *Columbites* by J. P. Smith came from outcrops of the middle shale member of the Thaynes Formation (*Columbites* fauna) in Paris Canyon, southeast Idaho. The original description of the type species by Hyatt and Smith (1905), later slightly enlarged by Smith (1932), is quite adequate. The five additional "species" introduced by Smith in 1932 were distinguished on differences in whorl dimensions and on ornamentation. On Table 33 are given the measurements of 107 specimens of *Columbites* from the same horizon, at three localities around the north end of Bear Lake (including Paris Canyon), southeast Idaho. These data are plotted on Figure 23. It can readily be seen from this large sample that slight differences in conch dimensions are meaningless. The differences in ornamentation are more difficult to quantify. But here again, as with most ornamented ammonites, there is complete gradation from very weak ribs to strong ribs; within this species there is also an ontogenetic variable, that is, successive patterns of ribs appear in differing orders. All of these features, however, are completely gradational. Close study of the specimens figured here will bring this fact out.

Smith (1932) did not make particular note of the suture of his six species but this feature is also quite variable. On Figure 22 are 13 sutures of *Columbites*. As can be seen, the variation is expressed in the shape and size of the first and second lateral lobe and thus also in the saddles.

There are no other well authenticated species of *Columbites* recorded to date. *Columbites* sp. described by Kiparisova (1961:119) from an uncertain horizon (*Columbites* Zone?) in the Scythian of the Primorye Region is based on a single poorly preserved specimen. It is possible this is a species of *Columbites*, but it is much more involute than *C. parisianus*. At the same time it could well be a species of *Pseudoceltites*. From northern Siberia, Popov (1961) has described two species of *Columbites*, *Columbites* (?) aff. *ornatus* Smith and *Columbites morpheos* Popov. The first of these records is based on two poorly preserved casts showing no suture; I believe these to be unidentifiable. The second, *C. morpheos*, is a species of *Tirolites* and is discussed under that genus in this paper. Finally, there are *Columbites dolnapaensis* Kiparisova (1947: 143) and *Columbites constrictilis* Astakhova (1960: pl. 140) from the Mangyshlak Peninsula of southern Russia. These two species belong in *Pseudoceltites* and are discussed under that genus. *Columbites parisianus* is thus far only known from southeast Idaho.

Occurrence. Middle shale member, Thaynes Formation, *Columbites* fauna at Paris Canyon, Montpelier Canyon, and Hot Springs, all around north end of Bear Lake, southeast Idaho, and same horizon along Draney Creek, Stewart Flat Quadrangle, southeast Idaho (USGS locality M98).

Repository. Holotype (Pl. 39, figs. 3, 4) USNM 75246a; paratypes (Pl. 39, figs. 8, 9) USNM 75246b, (Pl. 41, fig. 7) USNM 75286a, (Pl. 39, figs. 1, 2) USNM 75286b, (Pl. 39, figs. 5–7) USNM 75286c, (Smith,


A
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1932, pl. 61, figs. 8, 9) USNM 75286d, (Pl. 39, fig. 10) USNM 75286e; all the remaining small juvenile specimens of this species studied by Hyatt and Smith (1905) and Smith (1932) are in the U.S. National Museum but are not formally numbered; suture specimens of Figure 22, MCZ 9532–9538; specimens from Montpelier Canyon MCZ 9633, from Hot Springs 9634; from Draney Creek, Stewart Flat Quadrangle, southeast Idaho, USGS; holotype *C. consanquineus* Smith, (Pl. 41, figs. 1, 2) USNM 74983a; paratypes (Pl. 41, figs. 3, 4) USNM 74983b, (Pl. 41, figs. 5, 6) USNM 74983c, (Smith, 1932: pl. 46, figs. 7–9) USNM 74983d, (Smith, 1932: pl. 46, figs. 10–13) USNM 74983e; holotype *C. ligatus* Smith, (Pl. 43, figs. 4, 5) USNM 74985a; paratypes (Pl. 42, fig. 7) USNM 74985b, (Pl. 40, figs. 7–9) USNM 74985c; holotype *C. minimus* (Smith, 1932: pl. 47, figs. 9, 10) USNM 74986; holotype *C. ornatus* Smith, (Pl. 40, figs. 1, 2) USNM 74984a; paratypes (Pl. 40, figs. 10, 11) USNM 74984b, (Smith, 1932: pl. 46, figs. 19–21) USNM 74984c; holotype *C. spencei* Smith (Pl. 42, figs. 1, 2) USNM 75309; paratypes (Smith, 1932: pl. 78, fig. 3) USNM 75309b, (Pl. 42, figs. 3, 4) USNM 75309c, (Pl. 42, figs. 8, 9) USNM 75309d, (Pl. 42, figs. 5, 6) USNM 75309e, (Pl. 40, figs. 5, 6) USNM 75309f, (Pl. 40, figs. 3, 4) USNM 75309g, specimens of Smith (1932: pl. 77, figs. 1–21) USNM 75309h–i.

Genus *Subcolumbites* Spath, 1930
Type species, *Columbites perrinismithi* Arthaber, 1908

The most common elements in many late Scythian faunas are species of *Subcolumbites.* The five species of this genus recognized to date can be separated into three distinct groups. The first group contains only the type species, which is known from Albania, Chios, China, and Japan, and is characterized by carination of the venter. The second group contains only *S. dusmani*, and is characterized by a more marked development of reticulate ornamentation. The third group contains *S. robustus* from China, *S. multiformis* from the Primorye Region, and *S. americanus* from Nevada. This third group is characterized by a more depressed whorl section.

Subcolumbites perrinismithi (Arthaber)

Plate 1, figures 1–9; Plate 2, figures 5–8; Plate 3, figures 1–9; Plate 4, figures 1–4; Text-figure 24

Columbites perrini-smithi Arthaber, 1908: 277, pl. 12, fig. 1; Arthaber, 1911: 262, pl. 23(7), figs. 19, 20; Diener, 1915: 112; C. Renz, 1928: 155; Renz and Renz, 1947: 59; Renz and Renz, 1948: 20, pl. 11, figs. 7–7a.

Subcolumbites perrini-smithi,—Spath, 1930: 77; Spath, 1934: 203, pl. 12, figs. 5a, b; Kummel, *in* Arkell et al., 1957: L140, figs. 172, 15a, b; Kummel, 1968b: 495, pl. 1, figs. 1–3.

Columbites europaeus Arthaber, 1908: 278, pl. 12, fig. 2; Arthaber, 1911: 261, pl. 23(7),

←

Figure 22. Diagrammatic representation of the sutures of *Columbites parisianus* Hyatt and Smith. A, suture of holotype at a diameter of 35 mm (USNM 75246a), from Smith (1932: pl. 1, fig. 11); B, at a diameter of 35 mm (USNM 75286b), from Smith (1932: pl. 61, fig. 4); C, suture of holotype of *C. ligatus* Smith (1932: pl. 47, fig. 3), at a diameter of 40 mm (USNM 74985a); D, at a diameter of 46.7 mm (MCZ 9532); E, at a diameter of 22.3 mm (MCZ 9533); F, paratype of *C. spencei* Smith (1932: pl. 78, fig. 4), at an approximate diameter of 35 mm (USNM 75309b); G, paratype of *C. consanguineus* Smith (1932: pl. 46, fig. 4), at a diameter of approximately 40 mm (USNM 74983b); H, at a diameter of 42.0 mm (MCZ 9534); I, paratype of *C. ornatus* Smith (1937: pl. 46, fig. 18), at a diameter of 25 mm (USNM 74984b); J, at a diameter of 28.6 mm (MCZ 9535); K, at a diameter of 33.7 mm (MCZ 9536); L, at a diameter of 23.0 mm (MCZ 9537); M, at a whorl height of 10 mm (MCZ 9538). All specimens from *Columbites* fauna, Thaynes Formation, southeast Idaho; A, B, C, F, G, I, are from Paris Canyon, the remaining specimens from Hot Springs.

Table 33. Measurements of *Columbites parisianus* Hyatt and Smith from *Columbites* fauna from three localities around north end of Bear Lake, southeast Idaho.

	D	W	H	U	W/D	H/D	U/D		D	W	H	U	W/D	H/D	U/D
1.	67.9	17.3	18.4	34.8	25.5	27.1	51.4	41.	40.3	?	10.8	20.4	?	27.0	50.5
2.	66.2	16.0	19.5	32.2	24.2	29.4	49.4	42.	39.4	12.0	10.5	20.8	30.5	26.7	52.8
3.	65.0	16.5	18.8	31.8	24.4	39.0	49.0	43.	39.0	11.4	11.9	17.7	29.2	30.5	45.5
4.	63.0	16.0	19.4	27.4	25.4	30.8	43.5	44.	38.7	11.0	12.5	16.5	28.4	32.3	42.7
5.	62.5	16.9	16.7	30.4?	27.1	26.7	54.4?	45.	38.3	11.0	11.7	18.6	28.7	30.6	48.6
6.	61.7	15.3	20.6	25.9	24.8	33.4	42.0	46.	37.8	11.9	12.0	17.8	31.5	31.7	47.1
7.	59.7	15.0	19.1	25.0	25.1	32.0	41.9	47.	37.6	11.9	11.3	17.8	31.6	30.1	47.4
8.	59.0	15.4	16.1	29.5	25.8	26.9	49.3	48.	37.3	11.9	10.0	18.5	31.9	26.8	49.6
9.	58.7	15.8	15.0	32.7	27.1	25.5	55.6	49.	36.7	11.8	9.4	18.7	32.2	25.1	51.0
10.	58.5	16.6	16.4	30.2	28.4	28.1	51.6	50.	36.4	12.0	10.3	17.8	33.0	27.5	48.9
11.	58.3	16.7	18.4	28.3	28.6	31.6	48.6	51.	35.8	10.6	10.1	17.5	30.5	28.2	48.9
12.	56.5	17.3?	15.6	29.0	30.6?	27.6	51.3	52.	35.7	11.4	10.1	18.0	31.9	28.3	50.5
13.	54.5	14.2	17.1	24.2	26.1	31.4	44.4	53.	35.6	11.2	10.3	18.4	31.3	28.9	50.6
14.	54.0	15.5?	17.2	23.7	28.7?	31.9	43.9	54.	35.3	13.3	9.3	18.5	37.7	26.3	52.4
15.	54.0	14.4	17.4	25.3	26.7	32.3	46.9	55.	35.0	10.5	9.8	16.4	30.0	28.0	46.9
16.	53.5	15.4	15.0	27.8	28.8	28.0	52.0	56.	33.8	12.7	8.8	17.8	37.6	26.0	52.7
17.	52.4	15.7	14.3	26.1	30.0	27.3	49.8	57.	33.4	10.5	9.2	17.3	31.5	27.5	51.8
18.	50.7	14.4	14.0	25.8	28.4	27.8	50.8	58.	33.2	9.7	11.1	14.5	29.2	33.4	43.7
19.	50.5	14.0	15.0	24.3	27.7	29.7	48.1	59.	32.1	10.5	10.0	15.0	32.7	31.2	46.7
20.	50.5	14.7	13.5	27.3	29.2	26.7	54.1	60.	31.4	11.7	8.9	16.1	37.3	28.3	51.3
21.	49.8	12.8	15.5	23.4	25.7	31.2	47.0	61.	31.4	11.0	11.2	12.5	35.0	35.7	39.9
22.	49.7	?	14.8	24.7	?	29.7	49.5	62.	30.9	13.9	8.4	16.2	45.0	27.2	52.5
23.	49.4	15.8	13.8	25.2	32.0	28.0	50.6	63.	30.8	11.3	10.5	13.0	36.9	34.1	42.3
24.	49.0	13.7	15.0	20.8	27.9	30.6	42.4	64.	30.5	10.8	7.5	16.2	34.8	24.6	53.2
25.	48.7	15.0	12.5	27.8	30.7	25.6	56.9	65.	30.3	11.5	10.2	13.2	38.0	33.6	43.6
26.	48.4	13.4	16.3	21.1	27.7	33.7	43.6	66.	29.0	10.0	8.7	13.7	34.5	30.0	47.3
27.	48.2	9.4	12.9	24.4	19.5	26.7	50.6	67.	29.0	10.0	7.7	15.0	34.5	26.5	51.7
28.	48.2	13.7	13.7	23.1	28.4	28.4	48.0	68.	28.8	11.1	8.7	9.1	38.6	30.2	39.1
29.	48.0	14.3	12.5	24.8	29.8	26.1	51.6	69.	28.7	10.6	8.2	15.0	36.9	28.6	52.3
30.	47.8	14.7	13.7	24.7	30.8	28.7	51.6	70.	28.5	10.8	8.0	14.4	37.8	28.1	50.6
31.	47.7	14.0	12.7	25.4	29.4	26.6	53.3	71.	28.0	11.7	9.1	13.0	42.3	32.5	46.4
32.	46.6	15.0	14.4	23.4	32.2	30.9	50.2	72.	27.0	9.6	7.3	12.5	35.5	27.0	46.3
33.	44.2	13.3	13.5	21.0	30.1	30.6	47.6	73.	26.4	10.0	7.0	14.0	37.9	26.5	53.0
34.	43.7	11.9	13.4	20.0	27.3	30.7	45.8	74.	26.1	11.0	7.2	13.8	42.2	38.7	55.0
35.	43.0	12.3	12.0	22.8	28.6	27.9	53.0	75.	26.0	9.7	9.4	11.8	37.2	36.2	45.4
36.	42.7	13.5	11.7	22.1	31.6	27.4	51.8	76.	25.3	9.4	7.3	13.3	37.1	28.8	52.5
37.	42.3	11.1	13.5	18.2	26.2	31.9	43.0	77.	25.0	10.7	7.0	12.8	42.8	28.0	51.3
38.	41.5	11.5	11.4	19.6	27.7	27.5	47.2	78.	24.6	9.5	8.4	10.9	38.8	34.1	44.3
39.	41.5	12.3	12.4	21.3	29.6	29.9	51.4	79.	24.5	10.5	7.0	13.0	42.9	28.5	53.1
40.	41.0	10.9	12.8	18.7	26.6	31.2	45.6	80.	24.3	11.5	9.2	10.3	47.3	27.9	42.4

2. Plesiotype, Smith (1932: pl. 61, fig. 1), USNM 75286a.
3. Holotype, *C. ligatus* Smith (1932: pl. 47, figs. 1–3), USNM 74985a.
6. Paratype, *C. consanguineus* Smith (1932: pl. 46, fig. 3), USNM 74983b.
7. Holotype, *C. consanguineus* Smith (1932: pl. 46, figs. 1, 2), USNM 74983a.
11. Holotype, *C. spencei* Smith (1932: pl. 78, figs. 1, 2), USNM 75309a.
13. Holotype, *C. ornatus* Smith (1932: pl. 46, figs. 14, 15), USNM 74984a.
15. Plesiotype, Smith (1932: pl. 61, figs. 2–4), USNM 75286b.
26. Plesiotype, Smith (1932: pl. 61, figs. 5–7), USNM 55286c.
40. Holotype, Smith (1932: pl. 1, figs. 9–11), USNM 75246a.
45. Paratype, *C. ligatus* Smith (1932: pl. 47, figs. 4, 5), USNM 74985b.
46. Paratype, *C. spencei* Smith (1932: pl. 78, figs. 5, 6), USNM 75309c.
59. Paratype, *C. ligatus* Smith (1932: pl. 47, figs. 6–8), USNM 74985c.
61. Plesiotype, Smith (1932: pl. 61, figs. 8, 9), USNM 75286d.
63. Paratype, Smith (1932: pl. 1, figs. 12–14), USNM 75246b.
65. Paratype, *C. spencei* Smith (1932: pl. 78, figs. 7, 8), USNM 75309d.
78. Paratype, *C. ornatus* Smith (1932: pl. 46, figs. 16–18), USNM 74984b.
80. Paratype, *C. spencei* Smith (1932: pl. 78, figs. 9, 10), USNM 75309e.

Table 33. *Continued.*

	D	W	H	U	W/D	H/D	U/D
81.	23.7	10.0	7.2	10.3	42.2	30.1	43.5
82.	23.0	10.0	8.0	9.4	43.5	34.8	40.7
83.	22.8	9.4	6.5	11.1	41.2	28.5	48.7
84.	22.7	9.8	6.5	10.7	43.2	28.6	47.2
85.	22.7	9.3	6.5	11.2	40.9	28.6	49.3
86.	22.2	11.8	6.7	10.2	53.3	30.2	46.0
87.	21.9	9.4	8.3	8.5	42.9	37.8	38.8
88.	21.8	10.4	6.2	10.0	47.7	28.4	45.9
89.	20.5	9.8	6.0	10.8	47.8	29.3	52.7
90.	19.3	9.2	5.8	9.3	47.6	30.1	48.2
91.	18.7	9.5	7.2	8.2	50.8	38.4	43.8
92.	17.0	8.8	4.7	8.4	51.7	27.6	49.4
93.	15.8	7.3	4.3	7.3	46.2	27.2	46.2
94.	15.3	7.5	5.2	6.7	49.0	34.0	33.8
95.	14.3	7.0	4.6	5.7	48.9	32.2	39.8
96.	14.3	7.8	5.1	6.4	54.5	35.6	44.7
97.	13.8	8.0	4.7	6.5	58.0	34.0	47.1
98.	13.5	7.0	5.0	5.2	56.0	37.0	38.5
99.	13.0	4.0	4.0	6.7	30.8	30.8	51.5
100.	11.4	4.9	3.8	4.5	43.0	33.3	39.4
101.	10.6	6.6	3.7	4.8	62.2	34.9	45.3
102.	9.7	5.5	3.5	3.7	56.7	36.1	37.8
103.	9.5	5.5	3.5	4.1	58.0	36.9	43.2
104.	8.8	6.1	3.2	3.5	69.2	36.4	39.8
105.	8.4	5.1	3.0	2.8	60.7	35.7	33.3
106.	8.0	4.5	2.8	3.6	56.3	35.1	45.0
107.	7.2	4.4	2.5	2.3	61.1	34.7	32.0

81. Paratype, Smith (1932: pl. 61, figs. 11–13), USNM 75286t.
82. Paratype, *C. spcncei* Smith (1932: pl. 78, figs. 13–16), USNM 75309g.
87. Paratype, *C. consanguineus* Smith (1932: pl. 46, figs. 5, 6), USNM 74983c.
91. Paratype, *C. spencei* Smith (1932: pl. 78, figs. 11, 12), USNM 75309f.
94. Paratype, Smith (1932: pl. 61, figs. 14, 15), USNM 75286g.
96. Paratype, Smith (1932: pl. 72, figs. 22–24), USNM 75286q.
97. Paratype, *C. spencei* Smith (1932: pl. 77, figs. 1–4), USNM 75309h.
98. Paratype, *C. consanguineus* Smith (1932: pl. 46, figs. 7–9), USNM 74983d.
99. Holotype, *C. minimus* Smith (1932: pl. 47, figs. 9, 10), USNM 74986.
100. Paratype, *C. ornatus* Smith (1932: pl. 46, figs. 19, 20), USNM 74984c.
101. Paratype, *C. spencei* Smith (1932: pl. 77, figs. 5–8), USNM 75309i.
102. Paratype, Smith (1932: pl. 61, figs. 16–18), USNM 75286h.
103. Paratype, Smith (1932: pl. 72, figs. 19–21), USNM 75286p.
104. Paratype, *C. spcncei* Smith (1932: pl. 77, figs. 9012), USNM 75309k.
105. Paratype, *C. consanguincus* Smith (1932: pl. 46, figs. 10–13), USNM 74983e.
106. Paratype, Smith (1932: pl. 72, figs. 16–18), USNM 75309o.
107. Paratype, *C. spencei* Smith (1932: pl. 77, figs. 13–15), USNM 75309l.

All other specimens are from the *Columbitcs* fauna of Paris Canyon, Montpelier Canyon, and Hot Springs, around north end of Bear Lake, southeast Idaho.

figs. 13–18; Diener, 1915: 112; C. Renz, 1928: 155; Renz and Renz, 1947: 59; Renz and Renz, 1948: 19, pl. 11, figs. 3–3a, 4–4a, 5–5a, 6–6a.

Subcolumbites europaeus,—Spath, 1934: 204, pl. 12, figs. 6a, b, text-fig. 62c.

Columbites europaeus-perrini-smithi Renz and Renz, 1947: 59; Renz and Renz, 1948: 20, pl. 11, figs. 1–1b, 2–2b.

Columbites mirditensis Arthaber, 1911: 263, pl. 24(8), figs. 2, 3, 4; Diener, 1915: 112; C. Renz, 1928: 155; Renz and Renz, 1947: 59; Renz and Renz, 1948: 21.

Subcolumbites mirditensis,—Spath, 1934: 205.

Subcolumbites kwangsianus Chao, 1959: 128, 304, pl. 30, figs. 14–17, text-fig. 41c.

Columbites asymmetricus Chao, 1959: 127, 303, pl. 30, figs. 10–13.

Subcolumbites cf. *perrinismithi*,—Bando, 1964a: 99, pl. 3, figs. 18, 19, pl. 4, fig. 3.

Arthaber (1908, 1911) had 70 specimens from the Kčira, Albania, fauna that he assigned to four species of *Columbites*. Of this original collection there are available today only 16 specimens, most of which were illustrated by Arthaber. The unretouched photographs reproduced here clearly demonstrate the poor preservation of these Albanian specimens, and that Arthaber's illustrations are highly retouched.

Both Arthaber (1911) and Spath (1934) recognized the gradational nature of the "species" established for these Albanian forms. Three of these so-called species (*S. europaeus*, *S. perrinismithi*, and *S. mirditensis*) vary mainly in the degree of compression of the whorls. As the whorls become more compressed the umbilical shoulder is more rounded, as the whorls become more depressed the umbilical shoulder becomes more acutely rounded. *Subcolumbites perrinismithi* is the more compressed form, *S. mirditensis* the more

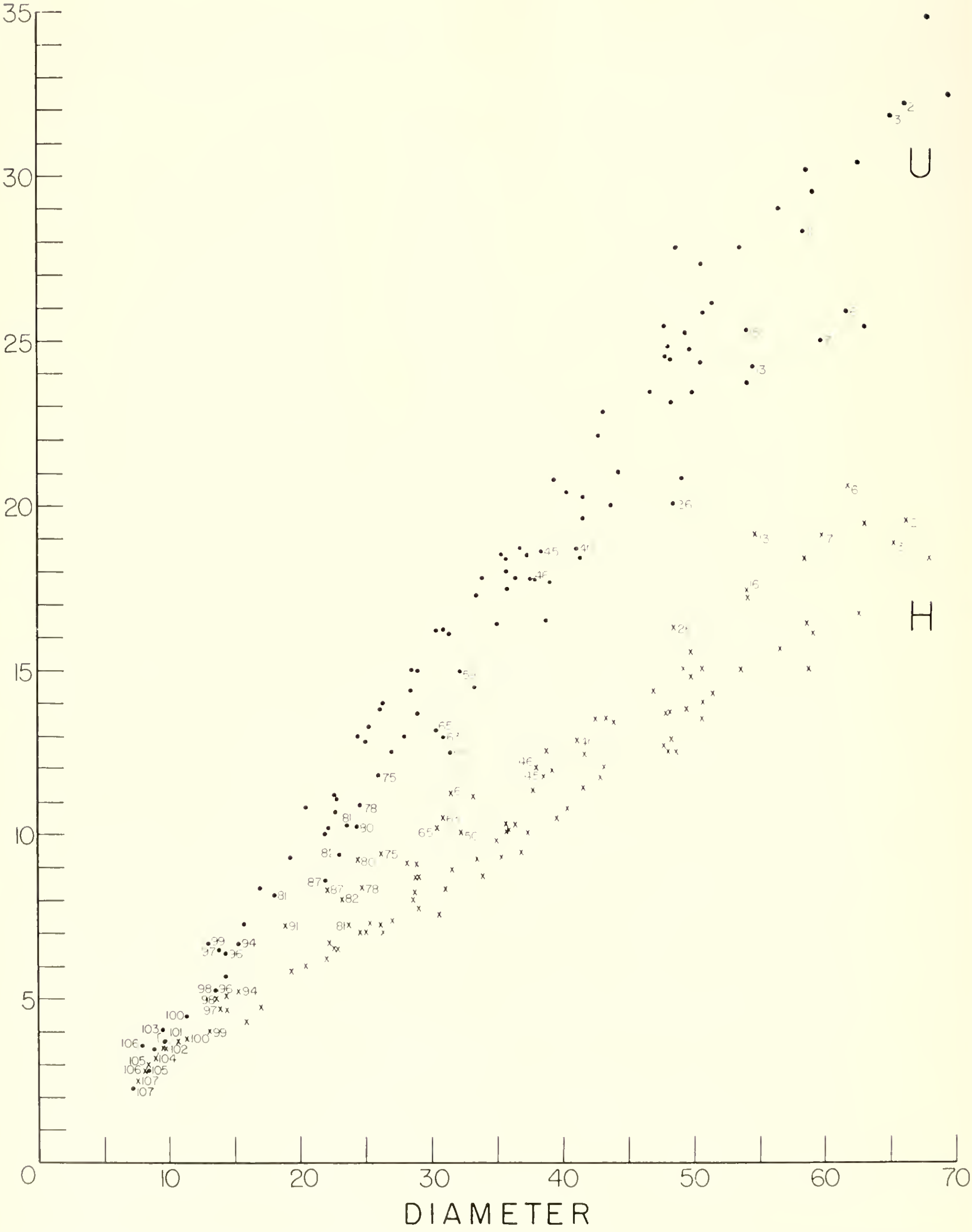


Figure 23. Variation in whorl height (H) and umbilical diameter (U) in *Columbites parisianus* Hyatt and Smith from *Columbites* Zone, Thaynes Formation, southeast Idaho. The data on this graph are from Table 33.

depressed form. Restudy of the available specimens from Kčira, conspecific forms from Chios, and topotypes of the Kčira forms in the British Museum (Natural History) clearly show that there is complete gradation in the degree of compression of the whorls. The measurements of the types available from Kčira and Chios are given on Table 34. The sutures of *S. mirditensis* and *S. europaeus* are illustrated on Figures 24A, B.

The pattern and intensity of ornamentation is also quite variable. In terms of the forward projecting ribs, they range from the fine, regular pattern, as illustrated by *S. perrinismithi* (Pl. 3, figs. 6, 7), to one where in the adoral volutions the ribs are bunched, especially on the venter, forming chevrons (Pl. 1, figs. 7, 8).

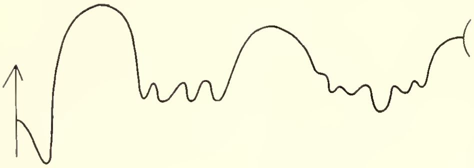
Among the four species established by Arthaber (1908, 1911), there is one (*S. dusmani*) which is quite distinct from the other three. Arthaber had only two specimens, both of small size and poor preservation. This species differs from *S. perrinismithi*, as interpreted here, in lack of a tendency toward carination of the venter and in the more conspicuous reticulate ornamentation. I cannot agree at all that this form is "scarcely more than a variety of *S. europaeus*" (Spath, 1934: 205). This conclusion is strengthened by the discovery of better preserved conspecific forms on Chios and other species of this general ornamentational pattern from Kwangsi, China, and Nevada.

Subcolumbites kwangsianus Chao (1959) was established for two poorly preserved specimens from Kwangsi, China. Though very poorly preserved, the whorl shape, carination of the venter, and ornamentation are like those features in *S. perrinismithi* of Albania and Chios. Chao (1959: 304) recognized the affinities of his species to the Albanian forms but concluded that the elliptical coiling of his species served to distinguish it. The so-called elliptical coiling is no more than that apparent in some of the poorly preserved Albanian specimens of *S. perrinismithi* (Pl. 1, figs. 3, 9). *Subcolumbites kwangsianus* is considered to be a synonym of *S. perrinismithi*. The two specimens from Japan recorded by Bando (1964a: 99) as *Subcolumbites* cf. *perrinismithi*, though poorly preserved, are surely conspecific with this species. The

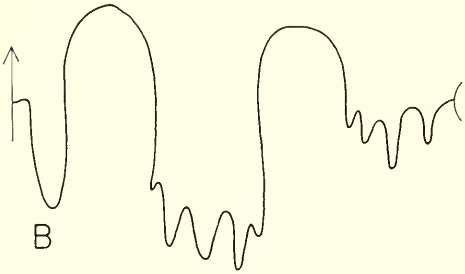
Table 34. Measurements of *Subcolumbites perrinismithi* (Arthaber) from Albania and Chios.

	D	W	H	U	W/D	H/D	U/D
1.	60.4	17.5	19.0	28.7	28.9	31.5	47.5
2.	58.0	16.8	17.5	27.5	28.9	30.2	47.4
3.	55.0	17.7	17.2	23.1	32.2	31.3	42.0
4.	54.4	18.1	20.0	24.6	33.3	36.8	45.2
5.	53.7	13.0	17.4	23.8	24.2	32.4	44.3
6.	52.3	17.2?	16.6	24.2	32.9?	31.7	46.3
7.	49.3	?	14.4	22.8	?	29.2	46.2
8.	48.8	?	13.6	23.9	?	27.9	48.9
9.	47.5	?	16.0	22.0	?	33.7	46.3
10.	46.0	?	15.0	21.3	?	32.6	46.3
11.	43.5	?	14.7	20.0	?	33.8	45.9
12.	40.7	15.4	14.1	18.3	37.8	34.6	44.9
13.	37.0	?	13.0	16.3	?	35.1	44.1
14.	34.4	?	11.8	15.7	?	34.3	45.6
15.	34.3	15.1?	11.2	14.8	44.0?	32.7	43.1
16.	28.3	11.7	10.3	12.0	41.3	36.4	42.4
17.	27.3	14.1	10.1	9.7	51.6	36.9	35.5

1. Plesiotype, *Columbites europaeus* Arthaber (1911: pl. 23(7), figs. 18a, b), PIUV.
2. Plesiotype, *Columbites europaeus-perrini-smithi* Renz and Renz (1948: pl. 11, figs. 1, 1a), NHMB J13538.
3. Plesiotype, *Columbites europaeus-perrini-smithi* Renz and Renz (1948: pl. 11, figs. 2, 2a), NHMB J13539.
4. Plesiotype, *Columbites europaeus* Arthaber (1911: pl. 23(7), figs. 15a, b), PIUV.
5. Plesiotype (Arthaber, 1911: pl. 23(7), figs. 20a, b), PIUV.
6. Plesiotype, *Columbites europaeus*,—Renz and Renz (1948: pl. 11, figs. 3–3a), NHMB J13533.
7. Plesiotype, *Columbites perrini-smithi*,—Renz and Renz (1948: pl. 11, figs. 7, 7a), NHMB J13537.
8. Plesiotype, *Columbites europaeus*,—Renz and Renz (1948: pl. 11, figs. 4, 4a), NHMB J13534.
9. Paratype, *Columbites mirditensis* Arthaber (1911: pl. 24(8), figs. 3a, b), PIUV.
10. Holotype (Arthaber, 1908: pl. 12, figs. 1a–c), PIUV.
11. Plesiotype (Arthaber, 1911: pl. 23(7), figs. 19a, b), PIUV.
12. Plesiotype, *Columbites europaeus* Arthaber (1911: pl. 23(7), figs. 16a, b), PIUV.
13. Holotype, *Columbites mirditensis* Arthaber (1911: pl. 24(8), figs. 2a, b), PIUV.
14. Paratype, *Columbites mirditensis* Arthaber (1911: pl. 24(8), figs. 4a, b), PIUV.
15. Plesiotype, *Columbites europaeus*,—Renz and Renz (1948: pl. 11, figs. 5, 5a), NHMB J13535.
16. Plesiotype, *Columbites europaeus* Arthaber (1911: pl. 23(7), figs. 13a–c), PIUV.
17. Plesiotype, *Columbites europaeus*,—Renz and Renz (1948: pl. 11, figs. 6, 6a), NHMB J13536.



A



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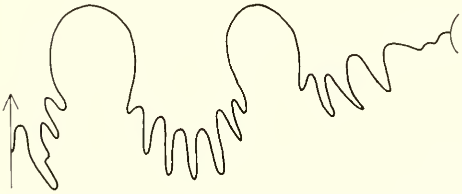

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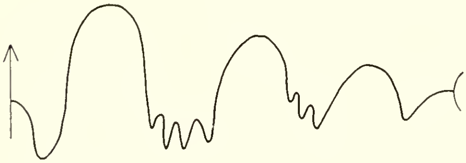

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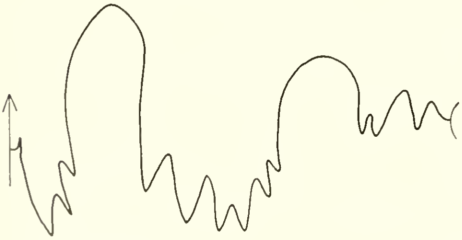

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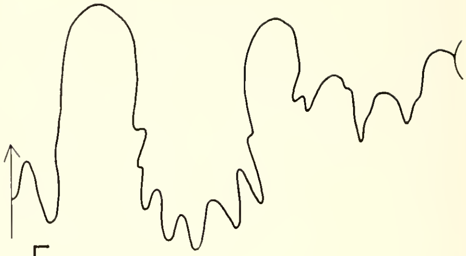

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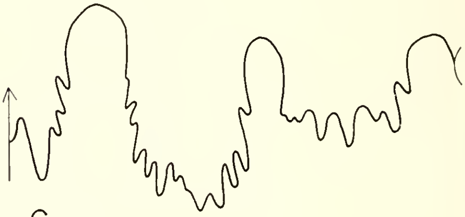

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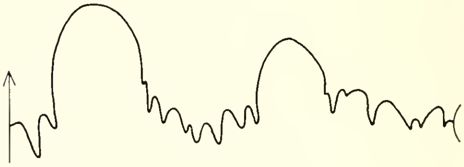

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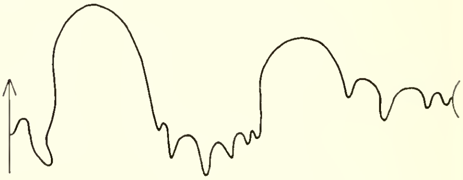

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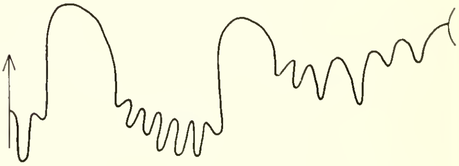


J

sutures of these species are shown on Figures 24A, B, E, J.

Occurrence. Subcolumbites faunas of Albania, Chios, Afghanistan, China, and Japan.

Repository. The following specimens are in the Paleontological Institute, Vienna: holotype *Columbites perrini-smithi* Arthaber, 1908: pl. 12(2), figs. 1a–c (Pl. 4, figs. 1, 2 of this report); topotype, *Columbites perrini-smithi* Arthaber, 1911: pl. 23(7), figs. 19a, b (Pl. 3, figs. 1–3 of this report); topotype *Columbites perrini-smithi* Arthaber, 1911: pl. 23(7), figs. 20a, b (Pl. 3, figs. 6, 7 of this report); holotype, *Columbites europaeus* Arthaber, 1908: pl. 12 (2), figs. 2a–d (Pl. 4, fig. 3 of this report); topotypes, *Columbites europaeus* Arthaber, 1911: pl. 23(7), figs. 13–18 (Pl. 1, figs. 1–9, Pl. 2, figs. 5–6 of this report); syntype, *Columbites mirditensis* Arthaber, 1911: pl. 24(8), fig. 2 (Pl. 3, figs. 8, 9 of this report); syntype, *Columbites mirditensis* Arthaber, 1911: pl. 24(8), fig. 3 (Pl. 2, figs. 7, 8 of this report); type specimen *Columbites mirditensis* var. Arthaber, 1911: pl. 24(8), fig. 4 (Pl. 3, figs. 4, 5 of this report).

The following specimens are in the Natural History Museum, Basel: plesiotype *Columbites perrini-smithi*,—Renz and Renz (1948: pl. 11, fig. 7) NHMB J13537; plesiotypes *Columbites europaeus*,—Renz and Renz (1948: pl. 11, fig. 3) NHMB J13533, (pl. 11, fig. 4) NHMB J13534, (pl. 11, fig. 5) NHMB J13535, (pl. 11, fig. 6) NHMB J13536; unfigured specimens from Maradovuno NHMB J13543, from Kephalovuno NHMB J13544; syntypes *Columbites europaeus-perrini-smithi* Renz and Renz (1948: pl. 11, fig. 1) NHMB J13538, (pl. 11, fig. 2) NHMB J13539; unfigured specimens from Maradovuno NHMB J13547, from Kephalovuno J13548; recorded specimen of *Columbites mirditensis*,—Renz and Renz (1948: 21) NHMB J13550.

The British Museum (Natural History) contains the following topotype specimens from the *Subcolumbites* fauna of Albania: *S. perrini-smithi*, C911–15, C22916–23, C22924–6; *S. europaeus*, C22890–900, C22901–10; *S. mirditensis*, C22883–6, C22887–9. Paratype from Albania MCZ 6723, from Chios MCZ 10026, specimens from Afghanistan MCZ 10138, 10146.

Subcolumbites dusmani (Arthaber)

Plate 2, figures 1–4; Text-figure 24

Columbites dusmani Arthaber, 1911: 263, pl. 24(8), figs. 1a–d; Diener, 1915: 112; Renz and Renz, 1947: 73.

Subcolumbites dusmani,—Spath, 1934: 204.

Columbites dianae Renz and Renz, 1947: 59, 73; Renz and Renz, 1948: 21, pl. 10, figs. 6–6b, 7–7b.

Columbites dianae var. *involuta* Renz and Renz, 1947: 59.

Columbites dianae var. *evoluta* Renz and Renz, 1948: 22.

Columbites graeco-americanus Renz and Renz, 1947: 59, 73; C. Renz, 1947: 176; Renz and Renz, 1948: 27, pl. 10, figs. 4–4b.

←

Figure 24. Diagrammatic representation of the sutures of species of *Subcolumbites*. A, syntype of *Columbites mirditensis* Arthaber (1911: pl. 24(8), figs. 2a–c; Pl. 3, figs. 8, 9 of this report), at a diameter of 25 mm; B, *Columbites europaeus* Arthaber (1911: pl. 23(7), figs. 15a–c; Pl. 1, figs. 1, 2 of this report), at a diameter of 35 mm; C, paratype of *Columbites dianae* Renz and Renz (1948: pl. 10, fig. 7b), at a diameter of 25 mm; D, paratype of *Fengshanites robustus* Chao (1959: 129, fig. 42a), at a diameter of approximately 30 mm; E, holotype of *Subcolumbites kwangsianus* Chao (1959: 128, fig. 41c), at a diameter of approximately 40 mm; F, *Subcolumbites multiformis* Kiparisova (1947: 144, fig. 32), at a diameter of 31 mm; G, *Subcolumbites multiformis* Kiparisova (1947: 144, fig. 31), at a diameter of approximately 15 mm; H, paratype of *Subcolumbites americanus* n. sp. (MCZ 9435, Pl. 30, fig. 8), at a diameter of 31 mm; I, paratype of *Subcolumbites americanus* n. sp. (MCZ 9438, Pl. 30 figs. 13, 14), at a diameter of 14 mm; J, syntype of *Columbites europaeus-perrini-smithi* Renz and Renz (1948: pl. 11, fig. 2b), at a diameter of approximately 40 mm.

Specimens of figures A, B from *Subcolumbites* fauna of Albania; C, J from same horizon on Chios; D, E from same horizon in Kwangsi, China; F, G from same horizon in the Primorye Region, eastern Siberia; H, I from same horizon in Tobin Formation, Nevada.

Columbites aithaliae Renz and Renz, 1947: 59, 74; Renz and Renz, 1948: 28, pl. 10, figs. 3–3b, 5–5b.

Columbites parisianus,—C. Renz, 1945: 301; C. Renz, 1947: 176; Renz and Renz, 1947: 59; Renz and Renz, 1948: 22, pl. 11, figs. 8–8b.

Columbites spencei Smith var. *chiotica* Renz and Renz, 1947: 59, 73; Renz and Renz, 1948: 22, pl. 3, figs. 7–7b.

The two syntypes of this species are relatively small specimens preserved only on one side and that only modestly well. These two specimens differ from *S. perrinismithi* in the strong reticulate ornamentation and the lack of any tendency toward carination. The reticulate ornamentation is more conspicuous on one syntype (Pl. 2, figs. 1, 2) than on the other (Pl. 2, figs. 3, 4) where it is only faintly visible.

The *Subcolumbites* fauna of Chios has yielded a number of what are believed to be conspecific forms. Renz and Renz (1948) had nine specimens of the morphological type of *S. dusmani* which they placed in five different species. Three of these species were based on one specimen each, one species was based on two specimens, and one species on four specimens. The large number of species introduced by Renz and Renz for this group reflects pronounced morphological differences from one specimen to the other. Whereas the sample comprising all these species from Chios is extremely small, a case can be made that the patterns of morphological differences are most likely gradational and that we are dealing with a single variable species. Likewise, study of large populations of other species of a similar morphological type, *Columbites parisianus* for instance, offers an insight into the potential variability that is possible in some of these Scythian ammonoids.

The holotype of *Columbites dianae* Renz and Renz is a large well preserved specimen clearly conspecific with *S. dusmani*. Renz and Renz (1948: 21) did not consider Arthaber's two syntypes of *S. dusmani* to be conspecific. On this basis they designated one of the specimens (Arthaber, 1911: pl. 24(8), figs. 1a, b; Pl. 2, figs. 3, 4 of this report) as the type (lectotype) of *S. dusmani* and considered the other specimen as conspecific with their *C. dianae* from Chios. The separation of Arthaber's two syntypes of *S. dusmani* cannot be accepted. The principal difference in these two specimens is in the expression of the reticulate ornamentation which is most pronounced on the ventral region. The specimen which Renz and Renz (1948: 21) designated as the type of *S. dusmani* is very badly weathered over most of the the venter; however, small traces of the shell are present and these clearly show a nice reticulate pattern. There is no justification for separating these two specimens into different species.

In addition to the well developed reticulate pattern on the holotype of *Columbites dianae*, there is on the adoral quarter volution a bundling of the prosiradiate ribs and a decrease in the strigations. In *Columbites aithaliae* there is a very pronounced bundling of the ribs producing strong prosiradiate folds over the ventral regions and extending half way up the flanks on the last quarter volutions. This change in ornamentational patterns takes place at an approximate diameter of 28.0 mm, whereas in *Columbites dianae* this change takes place at approximately 70 mm in diameter.

Columbites graecoamericanus Renz and Renz has the coarse bundled ribs developed on the whole adoral volution. *Columbites spencei* var. *chiotica* Renz and Renz is nothing more than a sparsely ribbed *graecoamericanus*. Each species was established on a single specimen. Finally, the *Columbites parisianus* of Renz and Renz is based on a small inner whorl of *C. dianae*. The sutures of these species are all of the same basic pattern and vary only in details (Fig. 24C).

The few specimens that are available suggest that the differences in ornament pattern are most probably a reflection of differences in ontogenetic growth, that is,

TABLE 35. MEASUREMENTS OF *SUBCOLUMBITES DUSMANI* (ARTHABER) FROM ALBANIA AND CHIOS.

	D	W	H	U	W/D	H/D	U/D
1.	74.2	25.5	31.5	21.7	34.4	42.5	29.2
2.	54.8	22.5	19.3	21.5	41.1	35.2	39.2
3.	51.3	17.8	17.7	20.7	34.7	34.5	40.4
4.	38.8	?	14.5	15.3	?	37.4	39.4
5.	37.7	?	14.5	14.9	?	38.5	39.5
6.	35.7?	?	15.3	10.4	?	59.5?	29.1?
7.	33.0	25.4	12.7	10.8	76.9	38.5	32.7
8.	26.6	14.8	15.2	10.0	55.6	57.1	37.6
9.	23.7	11.6	7.6	11.7	48.9	32.1	49.4

1. Holotype, *Columbites dianae* Renz and Renz (1948: pl. 10, fig. 6), NHMB J13540.
2. Holotype, *Columbites graeco-americanus* Renz and Renz (1948: pl. 10, figs. 4–4b), NHMB J13564.
3. Plesiotype, *Columbites spencei* var. *chiotica* Renz and Renz (1948: pl. 3, figs. 7–7b), NHMB J13553.
4. Syntype (Arthaber, 1911: pl. 24(8), figs. 1a, b), PIUV.
5. Syntype (Arthaber, 1911: pl. 24(8), figs. 1c, d), PIUV.
6. Holotype, *Columbites aithaliae* Renz and Renz (1948: pl. 10, figs. 5–5b), NHMB J13568.
7. Paratype, *Columbites aithaliae* Renz and Renz (1948: pl. 10, figs. 3–3b), NHMB J13570.
8. Paratype, *Columbites dianae* Renz and Renz (1948: pl. 10, fig. 7), NHMB J13541.
9. Plesiotype, *Columbites parisianus*,—Renz and Renz (1948: pl. 11, figs. 8–8b), NHMB J13542.

different rates of appearance of the successive stages. This type of variability in growth patterns is well illustrated in *Columbites parisianus* where we have a large population to work with and can document all of the transitional forms convincingly. It is largely on the basis of my studies of *Columbites parisianus* that I have come to the conclusion that these five species from Chios of Renz and Renz are all conspecific. Measurements of these species and of Arthaber's are given on Table 35. This interpretation, of course, needs confirmation, which can only be done when additional collections of these species are assembled.

Subcolumbites dusmani can be easily distinguished from *S. perrinismithi* in the lack of any tendency toward carination of the venter and in the general greater development of the reticulate ornamentation. *Subcolumbites robustus* Chao has a much more depressed whorl and low, broad, radial folds on the flanks, as does *S. americanus* from Nevada. *Subcolumbites multiformis* is also a species with a depressed whorl section but has no lateral nodes or folds.

Occurrence. Subcolumbites fauna of Albania and Chios.

Repository. Arthaber's two syntypes are in the Paleontological Institute, University of Vienna. The Chios fauna studied by Renz and Renz (1948) is in the Natural History Museum, Basel—holotype, *Columbites dianae* Renz and Renz (1948: pl. 10, fig. 6) NHMB J13540; paratype (pl. 10, fig. 7) NHMB J13541; unfigured paratypes NHMB J13551; holotype, *Columbites graecoamericanus* Renz and Renz (1948: pl. 10, fig. 4) NHMB J13564; unfigured paratypes J13565; holotype, *Columbites aithaliae* Renz and Renz (1948: pl. 10, fig. 5) NHMB J13568; paratype (pl. 10, fig. 3) NHMB J13570; unfigured paratypes from Maradovuno NHMB J13571, from Kephalovuno NHMB J13572; plesiotype, *Columbites parisianus*,—Renz and Renz (1948: pl. 11, fig. 8) NHMB J13542; unfigured specimens NHMB J13552; type specimen, *Columbites spencei* var. *chiotica* Renz and Renz (1948: pl. 3, fig. 7) NHMB J13553.

Subcolumbites robustus (Chao)

Text-figure 24

Fengshanites robustus Chao, 1950: 4, pl. 1, figs. 2, 3; Chao, 1959: 129, 305, pl. 8, figs. 1, 2, pl. 29, figs. 21–22, text-fig. 42a.

This species is of the same general morphological type as *S. americanus* from Nevada. Although the species is based on only two specimens, its distinctness is readily apparent. The whorls are more inflated and depressed than in *S. dusmani*. In addition, there are low irregular folds on the flanks. The suture is illustrated on Figure 24D.

Occurrence. 1.5 km north of Yali, Fengshan district, associated with *Dagnoceras* and *Hellenites* (Chao collection 546), Kwangsi, China.

Subcolumbites multiformis Kiparisova
Text-figure 24

Subcolumbites multiformis Kiparisova, 1947: 144, pl. 32, figs. 8–11, text-figs. 31–34; Kiparisova and Krishtofovich, 1954: 22, pl. 13, figs. 1–3; Kiparisova, 1961: 121, pl. 27, figs. 1–7, text-fig. 82–88.

Subcolumbites solitus Kiparisova, 1961: 123, pl. 26, figs. 4, 5, text-fig. 89, 90.

Subcolumbites anomalus Kiparisova, 1961: 123, pl. 26, figs. 6, 7, text-fig. 91.

Kiparisova (1961) had 35 specimens from what I judge to be the same horizon and locality at Cape Zhitkov, Primorye Region, eastern Siberia. Of these specimens, she placed 25 in *S. multiformis*, first described by her in 1947; seven specimens were placed in a second species, *S. solitus;* and three specimens were placed in another new species, *S. anomalus.* The latter two species were distinguished on the basis of slightly greater whorl depression and minor differences in the nature of the ornamentations. The suture, however, in all three species is essentially the same (Fig. 24F, G).

Unfortunately, Kiparisova supplied measurements for only 10 specimens of her three species of *Subcolumbites*; these data are tabulated on Table 36. On the basis of these data, there does not appear to be any real difference in relative whorl proportions. Kiparisova recognized that her *S. multiformis* was a highly variable form and that nearly all her specimens of *Subcolumbites* were juvenile specimens. This does not appear to be any justification for recognizing any more than one species of *Subcolumbites* within this faunal group.

Subcolumbites multiformis does not show any particularly close relationship to the group of *S. perrinismithi* or *S. dusmani*, but is very similar to *S. robustus* from Kwangsi, China, and *S. americanus* from western United States. The similarity to the latter two species is expressed in the depressed whorl section, reticulate ornamentation, and in the suture. It differs from these two species, however, in the lack of any lateral folds or nodes.

TABLE 36. MEASUREMENTS OF *SUBCOLUMBITES MULTIFORMIS*, *S. SOLITUS*, AND *S. ANOMALUS* FROM UPPER SCYTHIAN BEDS, PRIMORYE REGION, EASTERN SIBERIA.

	D	W	H	U	W/D	H/D	U/D
1.	45.0	24.8	15.3	18.9	55.0	34.0	42.0
2.	32.0	22.7	10.9	11.8	71.0	34.0	37.0
3.	29.0	18.9	9.9	11.3	65.0	34.0	39.0
4.	24.5	14.5	9.2	8.3	59.0	38.0	34.0
5.	17.0	11.9	5.4	6.5	70.0	32.0	38.0
6.	16.5	14.9	5.0	5.0	90.0	30.0	30.0
7.	16.0	13.4	3.5	5.9	84.0	22.0	37.0
8.	16.0	10.1	5.0	5.9	63.0	31.0	37.0
9.	11.5	10.4	3.0	4.5	90.0	26.0	39.0
10.	8.0	8.6	2.6	2.6	108.0	33.0	33.0

1–3, 5, 7, 9. *Subcolumbites multiformis*, data from Kiparisova, 1961: 121.

4, 8. *Subcolumbites solitus*, data from Kiparisova, 1961: 123.

6, 10. *Subcolumbites anomalus*, data from Kiparisova, 1961: 124.

Occurrence. Subcolumbites fauna at Cape Zhitkov, Primorye Region, eastern Siberia.

Subcolumbites americanus n. sp.
Plate 30, figures 1–14; Text-figure 24

This is one of the common ammonites in the Tobin Formation fauna from Nevada. The collections contain a large number of well preserved but mainly fragmentary specimens. However, ten specimens are sufficiently complete to yield measurements (Table 37).

The conch is evolute, robust, and with a characteristic pattern of ornamentation. The venter is arched and grades imperceptibly onto convex lateral areas. The umbilical shoulders are sharply rounded and the umbilical wall steep but not vertical. The conch bears low nodes situated just on the ventral side of the umbilical shoulder. In addition, there are prominent striae of growth, often bundled, which are rectiradiate on the umbilical wall and prosiradiate on the lateral areas, completely crossing the venter. There are also periodic constrictions and fine strigation.

The suture is shown on Figures 24H, I.

Clearly, this species is closely allied to *S. multiformis* from the Primorye Region and *S. robustus* from Kwangsi, China.

TABLE 37. MEASUREMENTS OF *SUBCOLUMBITES AMERICANUS* N. SP. FROM THE TOBIN FORMATION OF NEVADA.

	D	W	H	U	W/D	H/D	U/D
1.	47.3	25.0?	19.3	16.3	52.9?	40.8	34.5
2.	47.0	?	17.1	16.4	?	36.4	34.8
3.	42.2	20.8?	16.8	15.6	49.3?	39.8	36.9
4.	35.2	?	12.0	13.2	?	34.1	37.5
5.	31.8	16.1	12.6	9.7	50.6	39.6	30.5
6.	31.1	16.7	11.4	10.2	53.7	36.7	22.5?
7.	20.4	11.8?	7.3	7.0?	57.8	35.8	34.3?
8.	20.1	11.2	7.6	6.6	55.7	37.8	32.8
9.	20.1	10.3	7.8	5.7	51.2	38.8	28.4
10.	17.0	10.8	6.5	5.5	63.5	38.2	32.4

1. Holotype, MCZ 9430 (Pl. 30, figs. 1, 2).
2. Paratype, MCZ 9431 (Pl. 30, fig. 3).
3. Paratype, MCZ 9492.
4. Paratype, MCZ 9433 (Pl. 30, fig. 5).
5. Paratype, MCZ 9434 (Pl. 30, figs. 6, 7).
6. Paratype, MCZ 9435 (Pl. 30, fig. 8).
7. Paratype, MCZ 9436 (Pl. 30, figs. 9, 10).
8. Paratype, MCZ 9432 (Pl. 30, fig. 4).
9. Paratype, MCZ 9437 (Pl. 30, figs. 11, 12).
10. Paratype, MCZ 9438 (Pl. 30, figs. 13, 14).

Occurrence. Basal part of Tobin Formation, USGS locality M2562, Pershing County, Nevada; south tip of Tobin Range, Cain Mountain 1:62,500 quad., center NW ¼ sec. 9, T. 26N, R. 39E, 5,500 ft. S, 27.5 ft. W of elevation point 5088 on range crest.

Repository. Holotype (Pl. 30, figs. 1, 2) MCZ 9430; figured paratypes (Pl. 30, fig. 3) MCZ 9431, (Pl. 30, fig. 4) MCZ 9432, (Pl. 30, fig. 5) MCZ 9433, (Pl. 30, figs. 6, 7) MCZ 9434, (Pl. 30, fig. 8) MCZ 9435, (Pl. 30, figs. 9, 10) MCZ 9436, (Pl. 30, figs. 11, 12) MCZ 9437, (Pl. 30, figs. 13, 14) MCZ 9438; unfigured paratypes MCZ 9492.

Genus *Paradinarites* Chao, 1950
Type species, *Paradinarites suni* Chao, 1950
Paradinarites suni Chao
Text-figure 21

Paradinarites suni Chao, 1950: 6, pl. 1, figs, 7a, b, text-fig. 4; Chao, 1959: 98, 330, pl. 41, figs. 9–12.

Chao (1959: 331) recognized that this new genus and species was quite similar to "*Columbites*" in conch form and gross aspect of the suture but considered the goniatitic character of the lobes to indicate affinity with the dinaritids. The general shape of the conch is that of a *Subcolumbites* but lacks strigations. The suture (Fig. 21C), also, with its large first lateral lobe is columbitid in plan and, in fact, quite like the suture of *Procolumbites karataucikus* Astakhova (1960a, b) from the upper Scythian Formation of the Mangyshlak Peninsula. The species is known from only two not very well preserved specimens but on the basis of the data available it clearly appears to be a columbitid.

Occurrence. Subcolumbites fauna (Chao collection 610), Kwangsi, China.

Genus *Pseudoceltites* Hyatt, 1900
Type species, *Celtites multiplicatus* Waagen, 1895

Evolute, ribbed ammonites of rather simple design are very common in mid-Scythian formations. This has led to a proliferation of specific and generic names, the relationships of which are seldom understood or appreciated. The type specimen of *Celtites multiplicatus* is a poorly preserved specimen from the Upper Ceratite Limestone of the Salt Range (Pl. 27, figs. 5, 6). *Celtites armatus* Waagen (1895: 75, pl. 7, figs. 1, 7), the type species of *Kashmirites* Diener (1913) is clearly a synonym of *Celtites multiplicatus* Waagen (Pl. 27, figs. 7–10). Spath (1930: 35) introduced the name *Anakashmirites* (type species *Danubites nivalis* Diener, 1897: 51, pl. 15, figs. 17–19) for ammonoids not too different in appearance from *Celtites multiplicatus*. Examination of the Salt Range, Himalayan, and Timor specimens that have been assigned to one or more of these three genera by Waagen (1895), Diener (1897, 1909, 1913), Welter (1922), and Spath (1930, 1934) show that the ornamentational pattern is highly variable. It is in the suture pattern that one can readily separate *Pseudoceltites* and *Anakashmirites*. The former genus has a very reduced second lateral lobe that rests on or near the umbilical shoulder, whereas in

Anakashmirites there is a "normal" second lateral lobe and generally an auxiliary lobe at or near the umbilical shoulder.

As mentioned above, the type species is from the Upper Ceratite Limestone of the Salt Range, West Pakistan. In the upper part of the Scythian, three species are recognized: one (*cheneyi*) from the *Columbites* fauna of southeastern Idaho, the second (*nevadi*) from the Upper Thaynes Formation, western Utah, and the third (*dolnapaensis*) from the upper Scythian formation of the Mangyshlak Peninsula.

This genus is grouped here with the columbitids on the basis of the gross aspect of the conch and especially the basic pattern of the suture. In these aspects this genus shows similarities to such columbitids as *Columbites* and *Procolumbites*.

Pseudoceltites cheneyi n. sp.
Plate 44, figures 4–10; Text-figure 25

A number of exposures of the *Columbites* fauna of the Thaynes Formation in southeastern Idaho have yielded approximately 50 generally well-preserved specimens of this distinctive species. The conch is evolute and compressed. Measurements on 15 well-preserved specimens from one horizon and locality are given on Table 38. As can be readily seen, there is very little variation in relative thickness and height of the whorls or in umbilical diameter. The lateral areas of the whorls are flattened and slightly convergent; the venter is broad and arched. The ventral shoulder is broadly rounded, and the umbilical shoulder is more abruptly rounded with a short, steep umbilical wall. The umbilicus is broad and shallow.

Table 38. Measurements of *Pseudoceltites cheneyi* n. sp. from the *Columbites* fauna of Draney Creek, southeastern Idaho. The width dimension includes the lateral ribs.

	D	W	H	U	W/D	H/D	U/D
1.	29.2	8.4	9.6	12.0	28.8	32.9	41.1
2.	29.0	?	10.0	12.1	?	47.8	57.9
3.	27.8	8.6	9.8	12.1	30.9	35.3	43.5
4.	27.5	7.6?	10.0	10.0	27.6?	36.4	36.4
5.	26.5	7.8	7.6	11.6	29.4	28.7	43.8
6.	26.0	8.0	9.6	9.2	30.8	36.9	35.4
7.	25.7	7.8	9.4	9.1	30.4	36.6	35.4
8.	22.7	7.4	7.8	9.0	32.6	34.4	39.6
9.	21.7	7.3	7.5	9.6	33.6	34.6	44.2
10.	21.4	7.0	6.9	8.3	32.7	32.2	38.8
11.	20.1	7.4	6.9	8.5	36.8	34.3	42.3
12.	20.1	7.5	6.5	9.2	37.3	32.3	45.8
13.	16.6	6.5	5.7	6.8	39.2	34.3	40.9
14.	14.0	6.4	4.5	5.3	45.7	32.1	37.9
15.	13.0	5.1	4.6	4.9	39.2	35.4	37.7

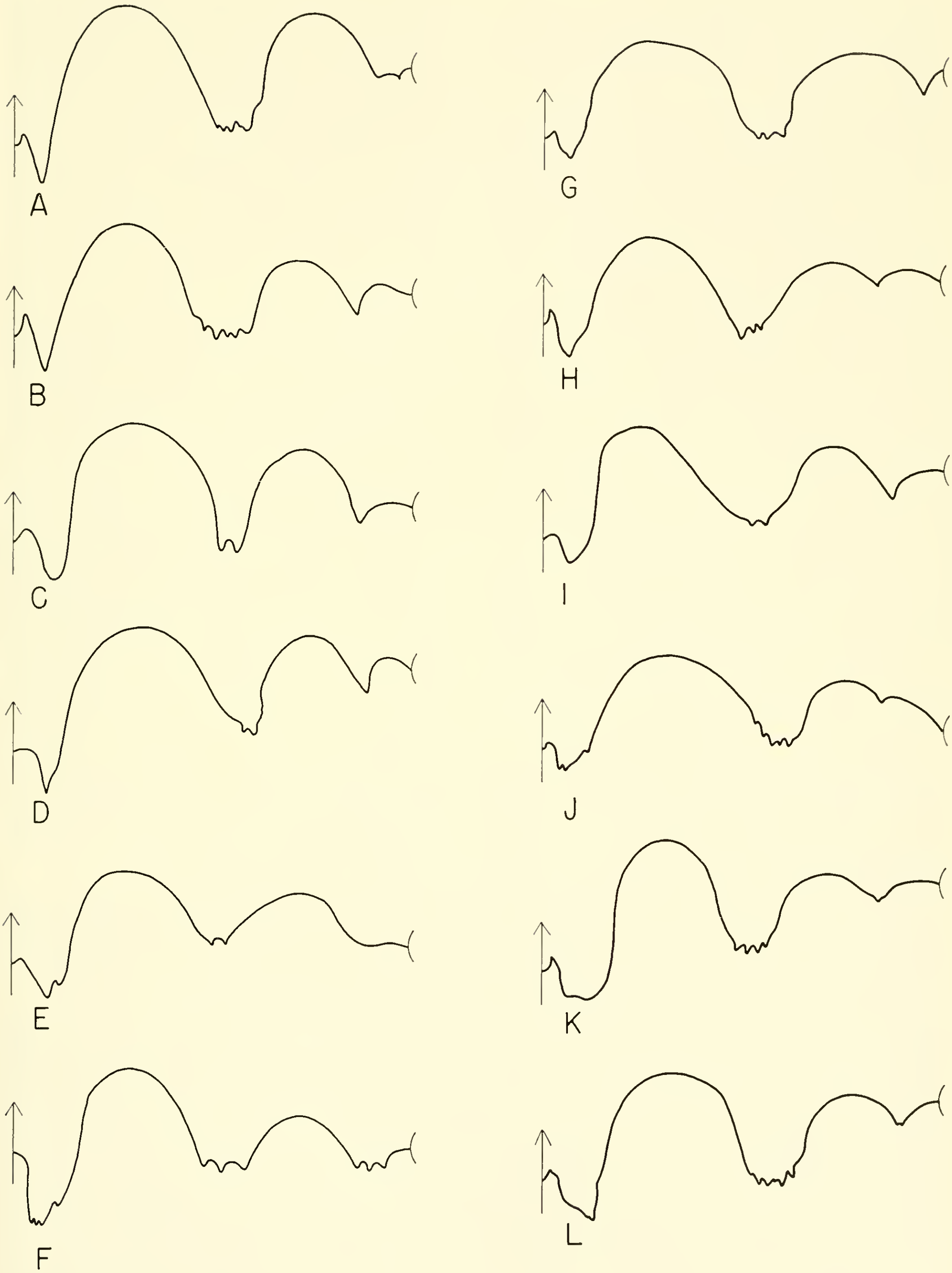
The lateral areas bear straight prosiradiate ribs that expand slightly toward the ventral shoulder where they project slightly forward. The ribs do not extend on to the venter, which is smooth except for growth lines and occasional constrictions which join the interrib areas from the opposite flanks. There are approximately 20 such ribs on the outer volution. There is some variation in the spacing of the ribs and in the relative strength or prominence of the ribs, but this variation is very slight and appears to be of no significance.

The suture consists of two rounded lateral saddles, a prominent first lateral lobe, with some denticulations, and a small, generally pointed second lateral lobe on the umbilical shoulder. The variation in the shape and proportions of the sutural elements is quite spectacular (Fig. 25).

→

Figure 25. Diagrammatic representation of the sutures of *Pseudoceltites cheneyi* n. sp. A, at a diameter of 13 mm (MCZ 9507); B, at a diameter of 17 mm (MCZ 9508); C, at a diameter of 20 mm (USNM 153074); D, at a diameter of 17 mm (MCZ 9503, Pl. 44, fig. 4); E, at a diameter of 20 mm (USNM 153075); F, at a diameter of 17 mm (USNM 153076); G, at a diameter of 16 mm (WSU); H, at a diameter of 15 mm (MCZ 9509); I, at a diameter of 14 mm (MCZ 9506); J, at a diameter of 17 mm (USNM 153077); K, at a diameter of 20 mm (USNM 153073, Pl. 44, figs. 8, 9), holotype; L, at a diameter of 17 mm (MCZ 9574).

All specimens from *Columbites* fauna, Thaynes Formation, southeastern Idaho; specimens A, B, D, H, I, J, and L are from Hot Springs; C, E, F, G, and K from Draney Creek.


A
B
C
D
E
F
G
H
I
J
K
L

The variation as illustrated by these 12 sutures should be sobering to those who tend to erect species on minor differences in the suture.

The type specimen of *Celtites multiplicatus* Waagen is a weathered specimen, in which only the outer volution is present; the inner whorls are completely weathered out (Pl. 27, figs. 5, 6). Waagen's illustration (1895: pl. 7, fig. 2) is highly restored and actually misleading. Even though the preservation of the Salt Range specimen leaves much to be desired, it is morphologically very similar to *Pseudoceltites cheneyi.* The Idaho species differs in its prosiradiate ribs rather than the radial ribs of *P. multiplicatus.* Waagen mentions slight nodes on the umbilical and ventral shoulders associated with the ribs; these nodes, however, are not present on the type specimen. The basic pattern of the suture of these two species is the same (Fig. 25). *Celtites multiplicatus* came from the Upper Ceratite Limestone of the Salt Range, which is mid-Scythian in age. The present species is from the *Columbites* Zone.

Occurrence. Middle shale member of Thaynes Formation, *Columbites* fauna, along Draney Creek, Stewart Flat, Quadrangle (USGS locality M98); and in Montpelier Canyon, Hot Springs, and Paris Canyon, all in the Bear Lake region of southeastern Idaho.

Repository. Holotype USNM 153073 (Pl. 44, figs. 8, 9); figured paratypes, MCZ 9503 (Pl. 44, fig. 4), MCZ 9504 (Pl. 44, fig. 5), MCZ 9505 (Pl. 44, figs. 6, 7), MCZ 9506 (Pl. 44, fig. 10); suture specimens MCZ 9507 (Fig. 25A), MCZ 9508 (Fig. 25B), USNM 153074 (Fig. 25C), MCZ 9503 (Fig. 25D), USNM 153075 (Fig. 25E), USNM 153076 (Fig. 25F), Department of Geology, Washington State University (Fig. 25G), MCZ 9509 (Fig. 25H), MCZ 9506 (Fig. 25I), USNM 153077 (Fig. 25J), USNM 153073 (Fig. 25K), MCZ 9574 (Fig. 25L); unfigured specimens from Hot Springs, southeast Idaho MCZ 9510; unfigured specimens from Montpelier Canyon, southeast Idaho MCZ 9511.

Pseudoceltites dolnapaensis Kiparisova
Text-figure 21

Columbites dolnapaensis Kiparisova, 1947: 143, pl. 30, fig. 3, text-fig. 30.

Columbites constrictilis Astakhova, 1960a: 140, pl. 33, fig. 6, text-fig. 8.

This species is remarkably similar to *Pseudoceltites cheneyi* n. sp. from the *Columbites* fauna of southeastern Idaho in its conch shape, ornament, and suture. The differences are primarily centered on the pattern of forward projecting constrictions on the adoral part of the conch. This species cannot be assigned to *Columbites* as the patterns of ribs and constrictions are very different. Astakhova (1960a) distinguished her species *constrictilis* from *Columbites dolnapaensis* Kiparisova partly on the basis that *constrictilis* had two denticulations on the first lateral lobe, and *dolnapaensis* had three. Examination of Figure 25, with 12 sutures of *P. cheneyi*, will give some indication of the variations possible within the basic pattern of the suture.

Occurrence. Mangyshlak Peninsula, *Columbites* Zone of Astakhova (1960a), associated with *Albanites, Epiceltites* and *Olenekites.*

Pseudoceltites nevadi n. sp.
Plate 34, figures 1–5; Text-figure 21

Xenoceltites cf. *X. spitsbergensis,*—Silberling, *in* Hose and Repenning, 1959: 2189, 2194.

The collections contain a large number of fragmentary, poorly preserved specimens. The basic form of the conch, whorl cross-section, pattern of ribs, and suture is very much like that of *Pseudoceltites cheneyi* from the *Columbites* fauna of southeastern Idaho. The suture (Figs. 21 and 25) likewise is very similar. It is possible that these two species are conspecific, but *nevadi* attains a much greater size than *cheneyi*, and on this basis it is thought best to keep the forms separate.

One fragment must be from a specimen of a diameter of approximately 65 mm.

Occurrence. USGS fauna M111, from upper part of Thaynes Formation, in section 15 of Hose and Repenning (1959: 2187), Confusion Range, western Utah.

Repository. Holotype USNM 153078 (Pl. 34, fig. 1); paratypes USNM 153079 (Pl. 34, figs. 2, 3), USNM 153080 (Pl. 34, figs. 4, 5).

Genus *Procolumbites* Astakhova, 1960
Type species, *Procolumbites karataucikus* Astakhova, 1960

Procolumbites karataucikus Astakhova
Text-figure 26

Procolumbites karataucikus Astakhova, 1960a: 142, pl. 34, figs. 1a–c, text-fig. 9 (*nomen nudum* Bajarunas, 1936: 547).

A columbitid with low ventral keel on phragmocone, venter on body chamber rounded. Ornamented with radial ribs and constrictions that cross the venter. Suture (Fig. 26G) with single, pointed, lateral lobe.

Occurrence. This genus and species is only known from the upper Scythian formation of the Mangyshlak Peninsula in beds associated with *Pseudoceltites dolnapaensis, Olenekites mangyshlakensis,* and *Albanites triadicus.*

Genus *Prenkites* Arthaber, 1911
Type species, *Prenkites malsorensis* Arthaber, 1911

There are only three species of this genus. One of these (*timorensis*) is known from Chios, Timor, and China. The type species is represented in the *Subcolumbites* fauna of Albania and Chios, whereas the third species (*helenae*) is only known from the Chios fauna.

Prenkites malsorensis Arthaber
Plate 7, figures 7–10; Text-figure 26

Prenkites malsorensis Arthaber, 1911: 258, pl. 22(6), figs. 17–19; Diener, 1915: 226; C. Renz, 1931: 344; Spath, 1934: 208, pl. 12, figs. 7a–c, text-figs. 111f–h; Renz and Renz, 1947: 59; Renz and Renz, 1948: 29, pl. 12, figs. 11–11a, 12.

Arthaber (1911: 258) stated he had 29 specimens of this species, but of these only 6 are still preserved in the Paleontological Institute, Vienna. In contrast to this fair representation, the *Subcolumbites* fauna of Chios has yielded only two specimens. The general character of the conch and the suture (Fig. 26A, B) is quite similar to that of *P. timorensis* which is distinguished on the basis of its ornamentation. *Prenkites helenae* Renz and Renz (1948) is a more broadly evolute form with rounded umbilical shoulders and lacking the small nodes on the umbilical shoulder.

Occurrence. Subcolumbites fauna of Albania and Chios.

Repository. Six specimens, including the two figured by Arthaber (1911: pl. 22(6), figs. 17, 19; Pl. 7, figs. 7–10 of this report) are in the Paleontological Institute, Vienna. The two plesiotypes from Chios, NHMB J13574, J13575.

Prenkites helenae Renz and Renz
Text-figure 26

Prenkites helenae Renz and Renz, 1947: 60, 74; Renz and Renz, 1948: 30, pl. 12, figs. 2–2a, 5–5a.

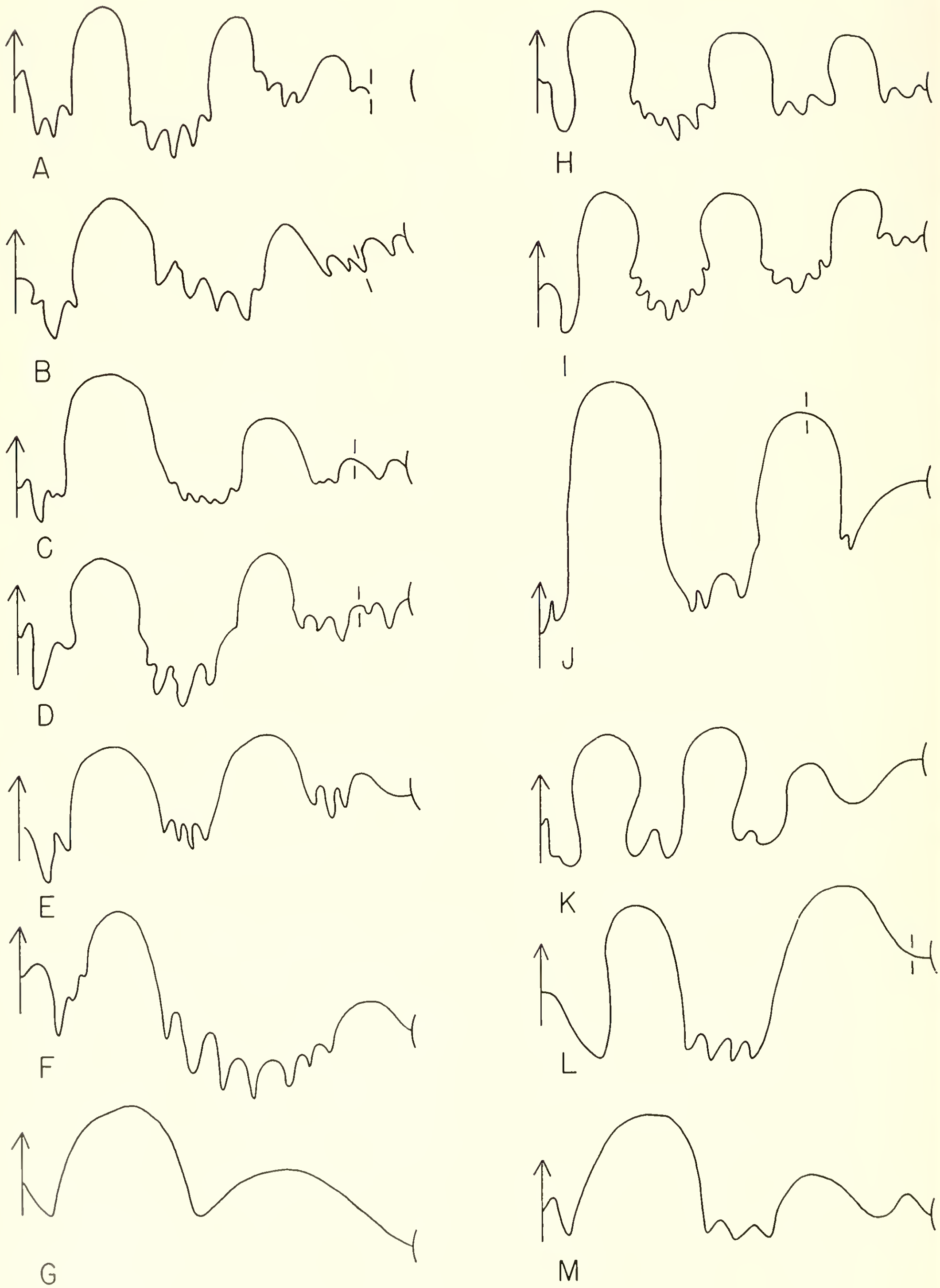
This species is an evolute *malsorensis* with rounded umbilical shoulders that lack the small nodes. The species is based on only two specimens; the measurements of the holotype are Diameter 49.3 mm, Width 18.5 mm, Height 18.3, Umbilicus 17.5, the same for the paratype are Diameter 35.8, Width 17.8, Height 12.1, Umbilicus 14.6. The suture is shown on Figure 26C.

Occurrence. Subcolumbites fauna, Chios.

Repository. Holotype NHMB J13577; paratype NHMB J13578; unfigured paratypes from Maradovuno J13579, 13580.

Prenkites timorensis Spath
Text-figures 17, 26

Columbites nov. sp. indet. Welter, 1922: 150, pl. 168(14), figs. 12, 13.


A
H
B
I
C
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F
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G
M

Prenkites timorensis Spath, 1930: 77; Spath, 1934: 208, fig. 62d, e.
Columbites malayanus C. Renz, 1945: 301; C. Renz, 1947: 176; Renz and Renz, 1947: 59, 73; Renz and Renz, 1948: 24, pl. 9, figs. 5, 6–6c, 8–8b, 9–9d, 10.
Columbites malayanus var. *crassa* Renz and Renz, 1947: 59, 73; Renz and Renz, 1948: 26, pl. 9, figs. 4–4b.
Columbites bubulinae Renz and Renz, 1947: 59, 73; Renz and Renz, 1948: 26, pl. 9, figs. 7–7a, pl. 10, figs. 1–1b.
Columbites levantinus Renz and Renz, 1947: 59, 74; Renz and Renz, 1948: 27, pl. 10, figs. 2–2b.
Columbites hellenicus Renz and Renz, 1947: 59, 74; Renz and Renz, 1948: 28, pl. 11, figs. 9–9c.
Columbites ex aff. *plicatuli* Smith,—Renz and Renz, 1948: 23.
Prenkites kwangsianus Chao, 1959: 130, 307, pl. 29, figs. 15–20, text-fig. 42b.
Columbites huangi Chao, 1959: 126, 301, pl. 29, figs. 6–11, text-fig. 41a.
Columbites costatus Chao, 1959: 126, 302, pl. 29, figs. 1–3, text-fig. 41b.
Columbites yaliensis Chao, 1959: 126, 302, pl. 29, figs. 12–14.

TABLE 39. MEASUREMENTS OF *PRENKITES TIMORENSIS* SPATH.

	D	W	H	U	W/D	H/D	U/D
1.	45.2	22.8	23.0	15.5	50.4	50.9	34.3
2.	45.2	?	17.4	16.0	?	38.5	35.4
3.	42.0±	24.4	15.6	15.7	58.1±	37.1±	47.4±
4.	38.5	22.7	15.3	13.5	59.0	39.7	35.1
5.	36.5	21.7?	14.4	12.3	59.5?	39.5	33.7
6.	34.8?	24.7?	13.0	14.7	71.0?	37.4?	42.2?
7.	32.0	15.1	13.2	10.0	47.2	41.3	31.3
8.	29.1	20.5	12.8	8.2	70.4	44.0	28.2

1. Holotype, *Columbites bubulinae* Renz and Renz (1948: pl. 10, fig. 1), NHMB J13561.
2. Paratype, *Columbites bubulinae* Renz and Renz (1948: pl. 9, fig. 7), NHMB J13562.
3. Paratype, *Columbites malayanus*,—Renz and Renz (1948: pl. 9, fig. 9), J13558.
4. Holotype, *Columbites malayanus*,—Renz and Renz (1948: pl. 9, fig. 6), J13555.
5. Paratype, *Columbites malayanus*,—Renz and Renz (1948: pl. 9, fig. 8), J13557.
6. Type specimen, *Columbites malayanus* var. *crassa* Renz and Renz (1948: pl. 9, fig. 4), J13549.
7. Holotype, *Columbites hellenicus* Renz and Renz (1948: pl. 11, fig. 9), J13573.
8. Paratype, *Columbites malayanus*,—Renz and Renz (1948: pl. 9, fig. 5), J13556.

This is the "ornamented" species of *Prenkites*. It has a conch essentially like that of *P. malsorensis* except for constrictions and associated ribs which extend over the flanks and project adorally as they cross the venter. Welter (1922) had only one specimen of this species and this is the type; a second specimen is in the British Museum (Natural History). The *Subcolumbites* fauna from Chios has yielded eight specimens which I believe are conspecific with the Timor form originally described by Welter (1922). Their measurements are given on Table 39. Renz and Renz (1948: 24) were not familiar with Spath's publications (1930, 1934) in which he introduced the name *Prenkites timorensis* for *Columbites* sp. indet. Welter (1922: 150, pl. 168(14), figs. 12, 13). *Columbites malayanus* Renz and Renz was introduced for a series of Chios forms that were believed to be conspecific with the Timor *Columbites* sp. indet. of Welter. A second species, *Columbites bubulinae* Renz and

←

Figure 26. Diagrammatic representation of the suture of: A, *Prenkites malsorensis* Arthaber (1911: pl. 22(6), fig. 17c), at a diameter of 20 mm; B, *Prenkites malsarensis*,—Renz and Renz (1948: pl. 12, fig. 12), at a diameter of approximately 15 mm; C, *Prenkites helenae* Renz and Renz (1948: pl. 12, fig. 5b), at a diameter of approximately 25 mm; D, *Prenkites timorensis*,—Renz and Renz (1948: pl. 9, fig. 9d), at a diameter of approximately 27 mm; E, *Prenkites timorensis*,—Chao (1959: fig. 42b), at a diameter of approximately 20 mm; F, *Protropites hilmi* Arthaber (1911: pl. 22(6), fig. 16), at an unknown diameter; G, *Procolumbites karataucikus* Astakhova (1960a: fig. 9), at a diameter of approximately 20 mm; H, *Chiaceras mitzopoulai* Renz and Renz (1948: pl. 12, fig. 13), at a diameter of approximately 30 mm; I, *Chiaceras nodosum* Renz and Renz (1948: pl. 12, fig. 7c), at a diameter of approximately 20 mm; J, *Arianites musacchi* Arthaber, new suture from holotype (Pl. 2, figs. 9, 10), at a diameter of 20 mm; K, *Merapella plejanae* Renz and Renz (1948, pl. 3, fig. 4b); L, *Epiceltites gentii* Arthaber (1911: pl. 24(8), fig. 8d), at a diameter of 20 mm; M, *Epiceltites subgracilis* (Astakhova, 1960a: fig. 132), at a diameter of approximately 15 mm.

Specimens of figures A, F, J, L from *Subcolumbites* fauna of Albania; specimens of figures B, C, D, H, I, K from *Subcolumbites* fauna of Chios; specimen of figure E from *Subcolumbites* fauna of Kwangsi, China; G, M from upper Scythian horizon on the Mangyshlak Peninsula.

Renz was introduced for slightly more compressed forms. A third species, *Columbites hellenicus* Renz and Renz is a slightly aberrant form, compressed, with more rounded umbilical shoulders and with a more subdued pattern of ornamentation. This species is based on a single specimen and is considered here as falling within the pattern of variation of *P. timorensis.*

Columbites ex aff. *plicatuli,* Renz and Renz (1948: 23) is based on two fragmentary specimens that have nothing in common with *Columbites plicatulus* Smith (1914: 37). They are actually more like the forms Renz and Renz assigned to *Columbites bubulinae.*

Prenkites kwangsianus Chao (1959) was established on three specimens from *Subcolumbites* horizons in Kwangsi, China. The descriptions and illustrations of this species leave much to be desired. In spite of this, I believe this species to be conspecific with the forms from Timor and Chios assigned to *P. timorensis.* The insight one can get on the variation within this species from a study of the Chios fauna lends support to the conclusion that the differences in the ribbing used by Chao to distinguish his species are not of specific importance. The Kwangsi species of *Columbites—huangi, costatus,* and *yaliensis* —described by Chao (1959) occur together at least in some outcrops and with *Prenkites kwangsianus* at the Yali section. These three species are clearly conspecific; they differ only in the degree of ribbing. These three forms are remarkably similar to *Columbites levantinus* Renz and Renz (1948: pl. 10, fig. 2) from the *Subcolumbites* fauna of Chios. Analysis of the whole Chios fauna suggests that *Prenkites timorensis* is a highly variable species that can and should include *Columbites levantinus.* These Kwangsi species (*C. huangi, costatus,* and *yaliensis*) are here considered to be a variant similar to *C. levantinus* which belongs within the scope of *P. timorensis.*

The suture of *Columbites huangi* Chao is shown on Figure 17C; *Prenkites timorensis* Spath is illustrated on Figures 26D, E.

Occurrence. Subcolumbites fauna of Chios; from block E, Nifoekoko, Timor; from *Subcolumbites* fauna in the Linglo and Fengshan districts of Kwangsi, China (Chao collections 542a, 546, 610); *Prenkites* aff. *timorensis* is present in the *Subcolumbites* fauna of the Primorye Region.

Repository. Holotype, Paleontological Institute, Bonn; topotype BMNH C33714; holotype, *Columbites malayanus* Renz and Renz (1948: pl. 9, fig. 6) NHMB J13555; paratypes (pl. 9, fig. 9) NHMB J13558, (pl. 9, fig. 8) NHMB J13557, (pl. 9, fig. 5) NHMB J13556; var. *crassa* (pl. 9, fig. 4) NHMB J13549, (pl. 9, fig. 10) NHMB J13559; unfigured paratypes NHMB J13546; holotype *Columbites bubulinae* Renz and Renz (1948: pl. 10, fig. 1) NHMB J13561; paratype (pl. 9, fig. 7) NHMB J13562; unfigured paratypes from Maradovuno NHMB J13563, from Kephalovuno NHMB J13569; holotype *Columbites hellenicus* Renz and Renz (1948: pl. 11, fig. 9) NHMB J13573.

Genus *Protropites* Arthaber, 1911

Type species, *Protropites hilmi* Arthaber, 1911 (lectotype selected by Spath, 1934)

Involute, inflated forms with cadicone inner whorls and carinate outer whorls. With strongly prosiradiate growth lines, occasionally enlarged on crossing the keel. Suture with single wide lateral lobe.

The type species is the only one known for this genus and has been recognized only in the *Subcolumbites* fauna of Kčira, Albania. Spath (1934: 206) considered *Protropites* to be an extreme development of *Subcolumbites mirditensis.* In this conclusion I concur. The rather poor preservation of the available material does not permit analysis of the ontogeny of the only known species; however, in its gross morphological features and the suture it does appear to be a columbitid though its exact relationships remain uncertain.

Protropites hilmi Arthaber

Plate 14, figures 1–8; Text-figure 26

Protropites hilmi Arthaber, 1911: 256, pl. 22(6), figs. 9–16; Diener, 1915: 235; Renz, 1928: 155; Spath, 1934: 206, pl. 13, figs. 4a–c.

Arthaber's illustrations of the *Subcolumbites* fauna of Albania are retouched photographs which on the whole are successful. Arthaber illustrated six specimens plus a suture (Fig. 26F) from an unspecified specimen. Two of these specimens plus the specimen which yielded the suture are missing in the collection and presumed lost. These are the specimens of figures 10, 11, and 16 of plate 22(6) in Arthaber (1911). The collections of the Paleontological Institute at the University of Vienna contain approximately 20 specimens of the species with no label as to origin, collector, etc. It is presumed that these are part of the original collection from Kčira, studied by Arthaber. Unfortunately, the preservation of these specimens is uniformly bad, none yielded any sutures, and none could yield any useful measurements.

None of the four surviving primary types studied by Arthaber are particularly well preserved. The measurements of these specimens are as follows:

	D	W	H	U	W/D	H/D	U/D
1.	33.2	?	12.1	12.6	?	36.4	38.0
2.	32.2	10.5?	11.9	12.8	32.6?	37.0	39.8
3.	29.2	10.2	11.4	10.8	34.9	39.0	37.0
4.	25.5	11.2	10.5	10.6	43.9	41.2	41.6

1. Lectotype, Arthaber (1911: pl. 22(6), fig. 15a, b).
2. Paralectotype, Arthaber (1911: pl. 22(6), fig. 13a, b).
3. Paralectotype, Arthaber (1911: pl. 22(6), fig. 12a, b).
4. Paralectotype, Arthaber (1911: pl. 22(6), fig. 14a, b).

The lectotype (Pl. 14, figs. 3, 4) was selected by Spath (1934: 206). Only the venter and one side of the specimen are preserved. The keel is very well developed and present on the whole adoral volution. Because of poor preservation, surface features of the shell are obscure. Faint patches of growth lines are present and on the most adoral part of the last volution there are two broad radial folds. The umbilical shoulder of the inner volutions appears to bear small nodes, but these are obscured by the poor preservation.

The largest of Arthaber's figured paralectotypes (Pl. 14, figs. 1, 2) is a more compressed form with less inflated whorls. Likewise only one side and the venter of the specimen is preserved. The next paralectotype (Pl. 14, figs. 5, 6) is of the same preservation and is an even more compressed form. The inner whorls are not as depressed and cadicone as in the lectotype. The growth lines are in places well preserved and show the strong forward projection on the keel. Some of the growth lines on crossing the keel are enlarged. The specimen figured by Spath (1934: pl. 8, fig. 4a) is comparable to this compressed form. The fourth specimen (Pl. 14, figs. 7, 8) is the most inflated, with strongly depressed cadicone inner whorls. It shows the gradual contraction of the body chamber very well. The conch is smooth except for very faint and indistinct growth lines.

Occurrence. Subcolumbites fauna, Kčira, Albania.

Repository. Lectotype, three figured paralectotypes, and approximately 20 topotype specimens are in the Paleontological Institute, University of Vienna. There are eight topotype specimens in the British Museum (Natural History) (C22838–45).

Genus *Chioceras* Renz and Renz, 1947

Type species, *Chioceras mitzopouloi* Renz and Renz, 1947

Smooth, evolute conchs, inner whorls rounded, slightly depressed, showing progressive expansion; outer whorls with conspicuous, smooth rounded keel; body chamber slightly more than one volution in length; suture with two denticulated lateral lobes, third lobe on umbilical shoulder, saddles rounded. One species bears large lateral nodes.

This genus is known only from two

species from the *Subcolumbites* fauna of Chios. It is, however, fairly well represented in numbers of individuals in the Chios fauna, as preserved in the Natural History Museum in Basel.

The rounded keel immediately reminds one of *Protropites* and at first these forms were thought to belong to that genus. However, the cadicone inner whorls of *Protropites* and the completely different suture preclude any genetic relationship. It is interesting to note that whereas *Protropites hilmi* is fairly well represented in the *Subcolumbites* fauna of Albania, it is not present in the fauna from Chios.

The character of the suture appears to be the best indication of genetic relations and this suggests *Prosphingites.* The conch can be looked upon as an evolute form of *Prosphingites* with the marked addition of the rounded keel.

Chioceras mitzopouloi Renz and Renz

Text-figure 26

Chioceras mitzopouloi Renz and Renz, 1947: 60, 74; Renz and Renz 1948: 37, pl. 12, figs. 3–3b, 6–6a (holotype), 9–9a, 13; Kummel, *in* Arkell et al., 1957: L140, figs. 172, 10a–c.

Chioceras mitzopouloi var. *meridionalis* Renz and Renz, 1947: 10; Renz and Renz, 1948: 38, pl. 12, figs. 8–8b.

This is the smooth species of *Chioceras.* The measurements of the holotype and figured paratypes are as follows:

	D	W	H	U	W/D	H/D	U/D
1.	49.0	?	16.6	19.7	?	33.9	40.2
2.	44.3	14.8	15.9	16.7	33.4	35.9	37.7
3.	43.5	13.7	13.1	18.4	31.5	30.1	42.3
4.	33.9	13.8	10.5	15.5	40.7	31.0	45.7
5.	30.6	10.8	10.7	13.0	35.3	35.0	42.5

1. Holotype, Renz and Renz (1948: pl. 12, fig. 6) NHMB J13626.
2. Paratype, Renz and Renz (1948: pl. 12, fig. 13) NHMB J13627.
3. var. *meridionalis* Renz and Renz (1948: pl. 12, fig. 8) NHMB J13632.
4. Paratype, Renz and Renz (1948: pl. 12, fig. 9) NHMB J13628.
5. Paratype, Renz and Renz (1948: pl. 12, fig. 3) NHMB J13629.

There are numerous unfigured paratypes in the Chios collection in Basel that are too poorly preserved or prepared to yield useful measurements. The suture is shown on Figure 26H.

Occurrence. Subcolumbites fauna, Maradovuno, Kephalovuno, and Marmarotrapeza, Chios.

Repository. The figured specimens are listed in the table of measurements; in addition there are unfigured paratypes from Maradovuno NHMB J13630, and from Kephalovuno NHMB J13631.

Chioceras nodosum Renz and Renz

Text-figure 26

Chioceras nodosum Renz and Renz, 1947: 60, 74; Renz and Renz, 1948: 38, pl. 12, figs. 7–7c.

This species was established for a single species that is like *C. mitzopouloi* except for the presence of large, rounded nodes on the lateral areas. The measurements of the holotype are:

D	W	H	U	W/D	H/D	U/D
30.5	12.1	10.7	12.5	39.7	35.1	41.0

The suture is illustrated on Figure 26I.

Occurrence. Subcolumbites fauna, Maradovuno, Chios.

Repository. Holotype NHMB J13633; unfigured paratype NHMB J13634.

Genus *Arianites* Arthaber, 1911

Type species, *Arianites musacchi* Arthaber, 1911

This genus and species are based on a single poorly preserved specimen from the *Subcolumbites* fauna of Albania. I agree with Spath (1934: 209) that it is most probably a columbitid.

Arianites musacchi Arthaber

Plate 2, figures 9, 10; Text-figure 26

Arianites musacchi Arthaber, 1911: 264, pl. 24(8), fig. 5; Diener, 1915: 53; Spath, 1934: 209; Kummel, *in* Arkell et al., 1957: L140, fig. 172, 14.

The type, and only specimen, of this species is incomplete and generally poorly preserved. The last half volution is body chamber; the inner whorls are for the most part buried in matrix. The outer volution is completely smooth except for vague traces of growth lines. A small portion of the penultimate volution is visible, and this shows sharp radial ribs on the flanks and umbilical shoulder. A new drawing of the suture is reproduced here on Figure 26J. Arthaber's drawing of the suture is inaccurate, especially in his treatment of the first lateral lobe.

Occurrence. Subcolumbites fauna, Kčira, Albania.

Repository. Paleontological Institute, Vienna.

Genus *Meropella* Renz and Renz, 1947
Type species, *Arianites (Meropella) plejanae* Renz and Renz, 1947

Evolute conchs with rounded whorl section of approximately equal width and height dimensions. Ventral and umbilical shoulders rounded. Early volutions bear slight umbilical nodes.

The suture consists of two bifid lateral lobes and a smooth, small auxiliary lobe on the umbilical shoulder.

This genus and species is known only from the *Subcolumbites* fauna of Chios. A fragmentary specimen from the *Subcolumbites* fauna of Kotal-e-Tera, Afganistan, has been described by Kummel (1968b) as *Meropella* cf. *plejanae.*

Meropella plejanae Renz and Renz
Plate 20, figures 14, 15; Text-figure 26

Arianites (*Meropella*) *plejanae* Renz and Renz, 1947: 67, 79; Renz and Renz, 1948: 95, pl. 3, figs. 3–3b, 11–11b.

Meropella plejanae,—Kummel, *in* Arkell et al., 1957: L140, fig. 172, 12.

There are only four specimens of this species known. The measurements of these are:

	D	W	H	U	W/D	H/D	U/D
1.	22.5	5.7	5.8	11.8	25.3	25.8	52.4
2.	20.0	4.6	5.7	9.8	23.0	28.5	49.0
3.	14.6	4.0	4.0	7.3	27.5	27.5	50.0
4.	12.5	3.2	3.6	5.6	25.6	28.8	44.8

1. Figured paratype, Renz and Renz (1948: pl. 3, fig. 11) NHMB J13826.
2. Holotype, Renz and Renz (1948: pl. 3, fig. 4) NHMB J13825.

3, 4. Unfigured paratypes, NHMB J13827.

One of the unfigured paratypes of the Renz and Renz monograph is figured here on Plate 20, figures 14, 15. Neither of these small paratype specimens shows the umbilical nodes as present in the holotype, nor is the suture preserved. However, aside from the lack of nodes, the remaining features of the conch are identical to those of the holotype. The drawing of the suture (Renz and Renz, 1948: pl. 3, fig. 4b) is accurate and is reproduced here as Figure 26K.

Occurrence. Subcolumbites fauna, Maradovuno, Chios.

Repository. Holotype NHMB J13825; figured paratypes NHMB J13826 (Renz and Renz, 1948: pl. 3, fig. 11), NHMB J19550 (Pl. 20, figs. 14, 15); unfigured paratypes NHMB J13827.

Genus *Epiceltites* Arthaber, 1911
Type species, *Epiceltites gentii* Arthaber, 1911

Epiceltites gentii Arthaber
Plate 3, figures 10, 11; Plate 35, figures 6, 7; Text-figure 26

Epiceltites gentii Arthaber, 1911: 268, pl. 24(8), fig. 8; Diener, 1915: 131; C. Renz, 1928: 155; Kutassy, 1933: 510; Spath, 1934: 210, pl. 13, figs. 5a–d; Renz and Renz, 1947: 60; Renz and Renz, 1948: 43, pl. 1, figs. 9a–d.

Epiceltites n. sp. cf. *E. gentii,*—Kummel, 1954: 187.

Arthaber (1911) had five specimens of this unique species of which only the holotype (Pl. 3, figs. 10, 11) is still preserved in the Paleontological Institute, Vienna. The evolute, compressed conch with periodic flares or constrictions that are strongly projected forward on the venter makes identification of this species easier than with most species of Scythian ammonoids. The holotype measures 36.3 mm in diameter, 9.3 mm for the width of the last whorl, 12.8 mm for the height of the last whorl, and 14 mm for the diameter of the umbilicus.

The *Subcolumbites* fauna of Chios also contains this species. The specimen figured by Renz and Renz (1948: pl. 1, fig. 9) measures 31 mm in diameter, 7.3 mm for the width of the last whorl, 10.3 mm for the height of the last whorl and 12.6 mm for the diameter of the umbilicus.

The Thaynes Formation of southeastern Idaho has yielded two incomplete and poorly preserved specimens. One specimen (Pl. 35, fig. 6) consists of only a portion of one side of the conch, thoroughly embedded in matrix; the other specimen (Pl. 35, fig. 7) shows only the venter and part of the lateral area of one-half volution. As no suture is preserved on either of the specimens, there has been some hesitation as to their specific identity. However, with due consideration of the preservation and incompleteness of the specimens, I feel that the shape and involution of the conch and the pattern of ornamentation are so similar to the specimens of this species from Albania and Chios that one must assign these specimens to Arthaber's species. Arthaber's suture is reproduced on Figure 26L.

Occurrence. The holotype is from the *Subcolumbites* fauna of Albania. The species is also known from that same fauna from Chios, and from the uppermost member of the Thaynes Formation, Hammond Creek, Bear River Range, southeastern Idaho.

Repository. Holotype, Paleontological Institute, Vienna; topotypes BMNH C-22867–74. Specimens from Chios, NHMB J13657 (Renz and Renz, 1948: pl. 1, fig. 9); unfigured specimens NHMB J13658, J13659. Specimens from southeastern Idaho MCZ 9470 (Pl. 35, fig. 6), MCZ 9471 (Pl. 35, fig. 7).

Epiceltites subgracilis (Astakhova)
Text-figure 26

Anasibirites subgracilis Astakhova, 1960a: 147, pl. 34, fig. 8, text-fig. 13.

The general shape etc. of the conch and the suture (Fig. 26M) is very much like that of the type species. The pattern of ornamentations is sufficiently different to warrant separation.

Occurrence. From *Columbites* Zone of Astakhova (1960a), Mangyshlak Peninsula.

Family USSURIIDAE Spath, 1930
Genus *Parussuria* Spath, 1934
Type species, *Ussuria compressa* Hyatt and Smith, 1905
Parussuria latilobata Chao

Parussuria latilobata Chao, 1959: 94, p. 260, pl. 31, figs. 14, 15, text-fig. 31.

The few species that previously have been assigned to this genus are of mid-Scythian age; this is the first species from a late Scythian horizon, and it is known from only a single specimen. Chao (1959: 261) concluded that his species was most closely related to *Parussuria iwanovi* (Diener, 1895) from the Primorye Region. In this I am in complete agreement; in fact, these two specimens could well be conspecific. Unfortunately, precise data on the stratigraphic position of *P. iwanovi* are lacking. This species was not in the faunas described by Kiparisova (1961) from the Primorye Region.

Occurrence. Limestone block in Lolou village, Kwangsi, China (Chao collection 542b).

Family HEDENSTROEMIIDAE Waagen, 1895
Genus *Metahedenstroemia* Spath, 1934
Type species, *Hedenstroemia kastriotae* Arthaber, 1911

This is a very unsatisfactorily defined genus because the type specimen is most probably an immature form of only modest preservation. Spath (1934) considered the suture to be the most unique aspect of his new genus. The suture as illustrated by Arthaber (1911) is highly idealized. As with practically all the specimens from the *Subcolumbites* fauna of Albania and Chios,

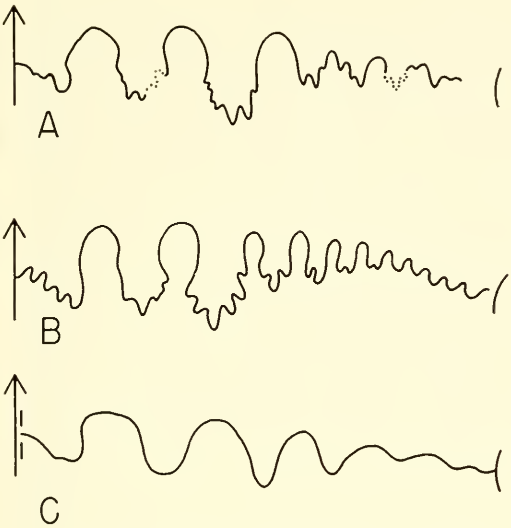

Figure 27. Diagrammatic representation of the suture of: A, holotype of *Metahedenstroemia kastriotae* (Arthaber), from the *Subcolumbites* fauna of Albania, at a diameter of 36 mm; B, holotype *Hedenstroemia pityoussae* Renz and Renz (1948: pl. 16, fig. 8b), from the *Subcolumbites* fauna of Chios, at a diameter of approximately 20 mm; C, holotype *Beatites berthae* Arthaber (1911), from *Subcolumbites* fauna of Albania, new drawing at a diameter of 32 mm.

the suture can be exposed only by grinding. In the case of the type specimen of this genus the grinding has been excessive. A new drawing of the suture, as exposed, is shown on Figure 27A. The Chios species, *Hedenstroemia pityoussae* Renz and Renz (1948), differs from the type species of *Metahedenstroemia* in details of the suture. However, as I believe the differences are due mainly to the results of specimen preparation and are more apparent than real, I consider the two species conspecific. This genus and species is known only from the *Subcolumbites* fauna of Albania and Chios.

Metahedenstroemia kastriotae (Arthaber)
Plate 14, figures 9, 10; Text-figure 27

Hedenstroemia kastriotae Arthaber, 1911: 208, p. 17(1), figs. 14a–c; Diener, 1915: 148.

Metahedenstroemia kastriotae.—Spath, 1934: 223, fig. 72; Kummel, *in* Arkell et al., 1957: L140, fig. 173, 10.

Hedenstroemia pityoussae Renz and Renz, 1947: 61, 78; Renz and Renz, 1948: 83, pl. 16, figs. 8–8b.

Arthaber (1911: 208) had two specimens of this species but only the specimen Spath (1934: 223) selected as the type of his genus *Metahedenstroemia* is still preserved in the Paleontological Institute, University of Vienna. This specimen is all phragmocone and measures 36.4 mm in diameter, 22.0 mm for the height of the last whorl, and 4.7 mm for the width of the last whorl. It is illustrated here on Plate 14, figures 9, 10 and the suture on Figures 27A, B.

The species *Hedenstroemia pityoussae* described by Renz and Renz (1948: 83) from the *Subcolumbites* fauna of Chios is based on three small fragmentary specimens. These authors differentiated their species on the basis of the suture; these differences are, however, partly due to preservation and preparation of the specimen.

Occurrence. *Subcolumbites* fauna of Albania and Chios.

Repository. Holotype is in the Paleontological Institute, Vienna; specimens from Chios, holotype, NHMB J13791; unfigured paratypes NHMB J13792.

Genus *Beatites* Arthaber, 1911
Type species, *Beatites berthae* Arthaber, 1911

Highly compressed, involute form with oxynote venter; sinuous growth lines. Suture long with low goniatitic lobes and saddles.

Beatites berthae Arthaber
Plate 21, figures 3, 4; Text-figure 27

Beatites berthae Arthaber, 1911: 210, pl. 17(1), fig. 15; Diener, 1915: 66; Diener, 1917: 169; Welter, 1922: 98; Kummel, *in* Arkell et al., 1957: L142, fig. 173, 4.

The dimensions of the holotype (and only specimen of this genus and species) are: Diameter 32.3 mm, Width 3.7 mm, Height 16.0 mm, Umbilicus 5.8 mm. The specimen is essentially all phragmocone. The flanks of the penultimate half volution have the wrinkle layer well preserved. The suture has been exposed by grinding; whether this has affected the details of the lobes is not known. Arthaber's suture drawing is not as accurate as it should be and a new drawing is reproduced here on Figure 27C.

Occurrence. Subcolumbites fauna, Kčira, Albania.

Repository. Paleontological Institute, University of Vienna.

Genus *Lanceolites* Hyatt and Smith, 1905
Type species, *Lanceolites compactus* Hyatt and Smith, 1905

Until recently this genus has been known only from the *Meekoceras* limestone of Idaho, Nevada, and California. In addition to the type species, Smith (1932: 90) has described one other (*L. bicarinatus*) which is clearly closely related to the type species and may be conspecific with it. Neither of these species are very common in the *Meekoceras* limestone of western United States. Recently Ganev (1966) has described *L. discoidalis* on four specimens from the Campil Member of the Werfen Formation of eastern Bulgaria. As these forms are associated with a typical Werfen tirolitid fauna, they are considered to be of *Prohungarites* Zone age. This new record considerably extends the range of the genus.

Lanceolites discoidalis Ganev

Lanceolites discoidalis Ganev, 1966: 23, pl. 1, figs. 1, 2, 4.

The conch shape of this species is nearly identical to that of the species from the *Meekoceras* limestone of western United States. In this respect the Bulgarian species is more similar to *L. bicarinatus* than to *L. compactus*, which appears to have a slightly more inflated conch. However, so few specimens of any of these species are known that there are no data available on the amount of variability possible in conch inflation. The suture of *L. discoidalis* has the same basic pattern as that of the American species but details are quite different. Through the kindness of Dr. Ganev I have plastotypes of his specimens. I suspect, from studying these, that the lack of fine denticulations in the suture is the result of poor preservation and weathering. At the same time, the suture is not too unlike that of *L. bicarinatus* reproduced by Smith (1932: pl. 55, figs. 3, 5, 7, 10), or that of weathered specimens of *L. compactus* reproduced by Smith (1932: pl. 5, fig. 9).

Occurrence. Campil Member, Werfen Formation, perhaps as exotic blocks, Luda-Kamčija region of eastern Bulgaria.

Repository. Primary types in Geological Institute of the Bulgarian Academy of Science; plaster casts are in the MCZ.

Family MEEKOCERATIDAE Waagen, 1895

Genus *Svalbardiceras* Frebold, 1930
Type species, *Lecanites* (?) *spitzbergensis* Frebold, 1929

Svalbardiceras spitzbergensis (Frebold)
Plate 26, figures 1–4; Text-figure 28

Lecanites (?) *spitzbergensis* Frebold, 1929b: 299, pl. 1, fig. 1; Kutassy, 1933: 577.

Ammonites sp. indet. Frebold, 1929a: 14, pl. 1, fig. 12.

Ammonites sp. indet. Frebold, 1929a: 15, pl. 1, fig. 13.

Svalbardiceras spitzbergensis (Frebold), 1930: 24, pl. 6, figs. 1–3; Spath, 1934: 251, fig. 85; Kummel, *in* Arkell et al., 1957: L142.

Interpretation of this species has been in doubt amongst several authors, mainly due to the uncertainty as to the nature of the suture. The holotype is the specimen described by Frebold in 1929 (1929b: pl. 1, fig. 1) and not that figured by Frebold in 1930 (pl. 6, fig. 1–1a), as indicated by Spath (1934: 251). The holotype specimens came from Agardhberge on Storfjord, Spitsbergen. The specimens described by Frebold (1929a) as *Ammonites*

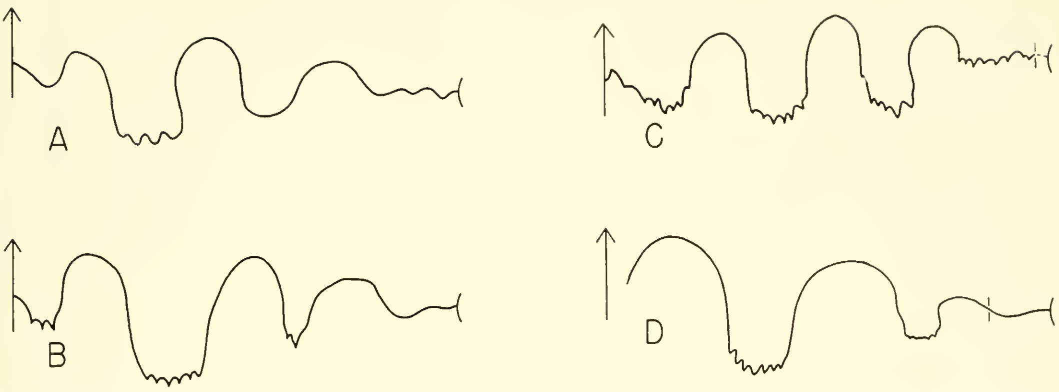

Figure 28. Diagrammatic representation of the sutures of several species of *Svalbardiceras*. A, topotype of *Svalbardiceras schmidti* (Mojsisovics), from *Olenekites* Zone, Olenek region, Siberia, at a whorl height of 13 mm (Popov, 1961: 39, fig. 6b); B, *Svalbardiceras* sp. indet., from Upper Thaynes Formation, Hammond Creek, southeastern Idaho, at a whorl height of 15 mm (MCZ 9488); C, holotype of *Svalbardiceras sheldoni* n. sp., from *Columbites* fauna, Thaynes Formation, Draney Creek, southeastern Idaho, at a diameter of 38 mm (MCZ 9493); D, *Svalbardiceras spitzbergensis* (Frebold, 1929a: pl. 1, fig. 13; Pl. 26, figs. 3, 4 of this report), from upper Scythian beds, Cape Thordsen, Spitsbergen, at a diameter of 37 mm.

sp. indet., which I believe to be conspecific with the holotype, came from Cape Thordsen. The specimens described in 1930 by Frebold came from Agardh Bay, Milne Edwardsberg, and Botneheia (Corrie Down). All these specimens came from what is interpreted as a late Scythian horizon. The specimens from Cape Thordsen were associated with a *Keyserlingites*.

All of the known specimens of this species show it to be an evolute form with compressed whorls, higher than wide, and with a flattened venter. The inner whorls bear slight radial ribs which are strongest near the umbilical shoulder and decrease down the flank; the weak ribs can be observed throughout the phragmocone. On the living chamber, the pattern of ornamentation is more irregular and is more like irregular bundled growth lines. The full details of the suture were not available to Frebold, but on one of his specimens—*Ammonites* sp. indet. (Frebold, 1929a: pl. I, fig. 13; Pl. 26, figs. 3, 4 of this report)—it has been possible to develop the suture (Fig. 28D). The suture bears two lateral lobes that are clearly denticulated, and a smooth auxiliary lobe on the umbilical wall. The highly crystalline nature of the phragmocone on many of the Spitsbergen ammonites makes development of the suture generally very difficult.

This Spitsbergen species of *Svalbardiceras* is quite similar to the other species of the genus but tends to be more involute and with more development of an ornamentational pattern than the Siberian *S. schmidti*. The Idaho *S. sheldoni* has very different whorl dimensions and a more elaborate suture.

Occurrence. From presumably the uppermost Scythian horizon at Agardh Bay, Milne Edwardsberg, Botneheia (Corrie Down), and Cape Thordsen, Spitsbergen.

Repository. The holotype was in the Mineralogisch-Geologischen Staatsinstitut, Hamburg, but was destroyed in the great fire of 1943; the specimens described by Frebold (1929a) are in the Paleontologisk Museum, Oslo; the specimens described by Frebold (1930) are in the Geologisk Institut, Uppsala.

Svalbardiceras schmidti (Mojsisovics)
Plate 26, figure 5; Text-figure 28

Xenodiscus schmidti Mojsisovics, 1886: 77, pl. 11, figs. 8–11.

Gyronites mojsisovicsi Waagen, 1895: 297 (=

Xenodiscus schmidti Mojsisovics, 1886: pl. 11, figs. 11a–c); Spath, 1934: 90, 251.

Prionolobus schmidti,—Noetling, *in* Frech, 1905: pl. 28, figs. 6a, b.

Meekoceras (*Gyronites*) *schmidti*,—Diener, 1915: 197.

Meekoceras sp. indet. Frebold, 1929a: 13, pl. 1, fig. 11.

Svalbardiceras spitzbergensis (Frebold) 1930: 24, pl. 6, fig. 2.

Gyronites (?) *schmidti*,—Kiparisova, 1947: 134, pl. 30, figs. 4, 5, text-fig. 16.

Svalbardiceras schmidti,—Tozer, 1961a: 32.

Nordophiceras schmidti,—Popov, 1961: 39, pl. 12, fig. 3.

Popov (1961: 39) recognized that his Siberian species was very similar to *Svalbardiceras spitzbergensis* (Frebold) but on the argument that the suture of this latter species was "unsatisfactorily defined" and that the suture was unknown he felt a comparison was not possible. It is true that no drawing of a suture was presented with the original description of *Lecanites* (?) *spitzbergensis* Frebold (1929b: 299, pl. 1, fig. 1), but they are visible on the photograph of the specimen. Frebold, however, interpreted the lobes as being goniatitic. The two specimens Frebold (1929a: 14, 15, pl. 1, figs 12, 13) described as *Ammonites* sp. indet. were considered by their author as most probably closely related to *Lecanites*(?) *spitzbergensis*; I believe them to be conspecific to that species. One of these specimens does preserve the suture (Fig. 28D) and this clearly shows denticulated lobes; the general pattern of the suture is identical to that shown on the photograph of the holotype (Frebold, 1929b: pl. 1(36), fig. 1). It does not, on this basis, seem justified to disregard *Svalbardiceras* as a valid generic name.

Acceptance of *Svalbardiceras* can and does clarify the genus *Nordophiceras* Popov (1961) from the Olenek region, Siberia. Within this new genus, Popov (1961) included a variety of species described by Mojsisovics (1886) as *Xenodiscus schmidti*, *Xenodiscus dentosus*, *Xenodiscus enomphalus* and the holotype, *Xenodiscus karpinskii*; in addition, Popov (1961) described one new species, *Nordophiceras alexeevae*. Thus within his genus *Nordophiceras*, Popov (1961) combined what I consider to be a heterogeneous assemblage of species. The group includes round ventered forms as illustrated by *Xenodiscus karpinskii*, the holotype of *Nordophiceras*, and forms with truncate venters as illustrated by *Xenodiscus schmidti* and *X. dentosus*. It is this latter group which is more properly allied to the Spitsbergen species of *Svalbardiceras*.

Mojsisovics (1886) illustrated three specimens of his *Xenodiscus schmidti*; the principal variation observable is in the sharpness of the ventral shoulders. Waagen (1895: 297) renamed the form shown on Mojsisovics' plate 11, figure 11a, b, as *Gyronites mojsisovicsi*. This additional name did not add clarity to the understanding of the group. Spath (1934: 251) lists the specimen of Mojsisovics (1886: pl. 11, fig. 8a, b) as lectotype.

Of the species of *Nordophiceras* described by Popov (1961), his specimen of *Nordophiceras schmidti* (Fig. 28A) is like that of Mojsisovics (1886: pl. 11, fig 9) in which the venter is slightly rounded but the ventral shoulders still quite distinct. I would, however, also include in this species *Meekoceras* sp. indet. Frebold (1929a: pl. 1, fig. 11; Pl. 26, fig. 5 of this report). This specimen has the very flat venter with angular ventral shoulders shown by Mojsisovics' specimen of *schmidti* on his plate 11, figure 11. Likewise the abrupt umbilical shoulder and the nature of the growth lines are nearly identical. The suture is unfortunately not preserved. In addition, the specimen of *Svalbardiceras spitzbergensis* (Frebold, 1930: pl. 6, fig. 2) should be included. Both of these specimens differ from the other Spitsbergen specimens assigned to *S. spitzbergensis* in being more involute and having a higher height-width relationship in the whorl dimensions. This is the primary difference between *S. schmidti* and *S. spitzbergensis*. The general conch form of S. *sheldoni* is like that of S. *schmidti*, but in this species there are conspicuous transverse ribs on the venter and differences in the spacing of the suture elements.

Occurrence. Mojsisovics' species are only listed as coming from the region of the mouth of the Olenek River. Popov (1961) lists his specimens as from his *Olenekites* Zone. Frebold's specimen of *Meekoceras* sp. indet. is from Cape Thordsen, associated with *Keyserlingites;* his specimen of *Svalbardiceras spitzbergensis* (Frebold, 1930: pl. 6, fig. 2) is from Milne Edward Mountain.

Repository. The only specimen of this species personally handled is Frebold's *Meekoceras* sp. indet., and this is in the Paleontological Museum, Oslo, Norway.

Svalbardiceras sibiricum (Mojsisovics)

Meekoceras sibiricum Mojsisovics, 1886: 85, pl. 11, figs. 1–6; Spath, 1934: 224, 246, 254, 274, 341.
Aspidites sibiricus,—Frech, 1905: pl. 28, fig. 11.
Meekoceras (*Koninckites*) *sibiricum*,—Diener, 1915: 198.
Meekoceras ? *sibiricum*,—Kiparisova, 1947: 150, pl. 35, fig. 2.
Hemiprionites sibiricus,—Popov, 1962a: 176, 187, pl. 2, fig. 3.

This species has been a puzzle to most students of Triassic ammonoids. Tozer (1965a: 37) suggested assignment of this species to *Svalbardiceras* and I believe there is much merit in this suggestion. The umbilical width of slightly less than 10 percent the diameter of the conch makes this the most involute species of the genus. As already pointed out by Tozer (1965a: 37), Popov's (1962a) assignment of this species to *Hemiprionites* cannot stand for many reasons.

Occurrence. Olenek fauna, mouth of Olenek River, northern Siberia.

Svalbardiceras dentosus (Mojsisovics)

Xenodiscus dentosus Mojsisovics, 1886: 78, pl. 11, figs. 12a, b.
Goniodiscus dentosus,—Diener, 1915: 135; Spath, 1934: 330.

This species is like S. *schmidti* except for long, low clavi along the sharp ventral shoulders. It is based on a single specimen.

Occurrence. From near the mouth of the Olenek River.

Svalbardiceras freboldi Tozer

Svalbardiceras freboldi Tozer, 1965a: 36, pl. 4, figs. 12, 13, pl. 5, fig. 2, text-fig. 11.

With an umbilical width approximately 20 percent the diameter of the conch, this is one of the more involute species of *Svalbardiceras*. Aside from the slightly greater involution, it is very similar to *schmidti* and *spitzbergensis*.

Occurrence. Uppermost Scythian, Blaa Mountain Formation, lower shale member, northern Ellesmere Island.

Svalbardiceras chowadei Tozer

Svalbardiceras chowadei Tozer, 1965a: 37, pl. 4, figs. 9–11.

This species could very well be conspecific with S. *spitzbergensis*. The differences are mainly in a slight difference in the degree of involution. However, with both species the number of specimens known is so small that really no data are available on the range of variability of any of the morphological features.

Occurrence. Toad Formation, Halfway River area, British Columbia.

Svalbardiceras sheldoni n. sp.

Plate 43, figure 1; Text-figure 28

The *Columbites* fauna of southeastern Idaho has yielded three specimens which form the basis for this new species. The two larger specimens are embedded in matrix with only one side completely exposed and a portion of the venter on the phragmocone, and the body chamber exposed. The body chamber is crushed. The holotype specimen measures 70 mm in diameter; the height of the adoral volution is 30 mm and the umbilicus has a diameter of 22.7 mm. The conch is evolute, compressed, and essentially smooth. The venter is flat, and aligned by angular ventral shoulders. The lateral areas are broadly convex with the maximum breadth at about mid-way between the ventral and umbilical shoulders. The umbilical shoulders are likewise sharply rounded and the umbilical wall is vertical. The body chamber occupies approximately two-thirds of a volution. The shell bears fine growth lines that are slightly prosiradiate. On the phragmocone the venter has narrow, shallow, transverse grooves that extend from one ventral shoulder to the other.

The suture is shown on Figure 28C. It consists of a wide ventral lobe, highly denticulated, two lateral lobes, and a serrated shallow lobe adjacent to the umbilical shoulder. The large paratype has an inner core of 59 mm in diameter of excellent preservation. Attached to it is a portion of body chamber with a whorl height of 39 mm. The specimen must have had a diameter of at least 100 mm. The small paratype has a diameter of 25.2 mm, and the whorl shape of the large specimens. At a diameter of 4 mm the venter is rounded; it appears that in the following volutions the venter begins to become flattened.

This species has a remarkable similarity to *Svalbardiceras schmidti* (Mojsisovics, 1886: 77, pl. 11, figs. 11a, b), that is, in the identity of the greatly compressed, evolute conch, and the flattened venter. *Svalbardiceras schmidti* appears to have a smooth venter, lacking transverse furrows. The essential plan of the suture is the same except that the ventral lobe lies within the venter and does not spread out on the lateral areas as in *S. sheldoni.* Mojsisovics noted a fair degree of variability in the nature of the venter of his species, some forms having rounded venters and ventral shoulders. This observation has been confirmed by Popov (1961).

The Spitsbergen species, *S. spitzbergensis* (Frebold, 1930: 24, pl. 6, figs. 1–3) tends to be slightly more inflated than the species described here. Likewise, the lateral area bears weak radial ribs, widely spaced on the inner whorls, but becoming more bunched and sinuous on the body chamber. The venter bears weak transverse furrows.

Occurrence. From middle shale member of Thaynes Formation (*Columbites* fauna), on hillside north of Sage Creek, Stewart Flat Quadrangle, and at Hot Springs, southeast Idaho.

Repository. Holotype MCZ 9493; paratypes MCZ 9643, 9644.

Svalbardiceras sp. indet. (S.E. Idaho)
Text-figure 28

Svalbardiceras sp. Kummel, 1954: 187.

This specimen is recognized on the basis of a fragment of phragmocone consisting of only five camerae. The whorl height is 14 mm, and the width is 7.3 mm. The cross section of the whorl is compressed, the lateral areas broadly convex. The venter is slightly concave, measuring about 2 mm in breadth, and lined by angular ventral shoulders. The umbilical shoulder is broadly rounded. The suture is shown on Figure 28B. The specimen recorded here is much too fragmentary to compare in a detailed fashion with the Spitsbergen and Olenek species, but in its whorl shape and suture it agrees well with the basic conch pattern for the genus.

Occurrence. Upper member Thaynes Formation, Hammond Creek, Bear River Range, southeast Idaho.

Repository. MCZ 9488.

Svalbardiceras sp. indet. (Pakistan)

Svalbardiceras sp. indet., Kummel, 1966: 394, pl. 2, figs. 6–9.

This identification was based on a complete phragmocone and a fragment of another. The specimens are complete enough to confidently assign them to the genus *Svalbardiceras* but are not sufficiently complete to make any meaningful comparisons with other species of the genus.

Occurrence. Narmia Member of Mianwali Formation, Nammal Gorge, Salt Range, West Pakistan.

Repository. MCZ 9587, 9588.

Genus *Stacheites* Kittl, 1903
Type species, *Stacheites prionoides* Kittl, 1903

Compressed, involute forms with tabulate, often sulcate venter. Suture with prominent first lateral lobe and shallow, broad, second lateral lobe; first lateral saddle narrow, second lateral saddle broadly rounded.

The type specimens came from the Werfen Formation in Dalmatia. The type species, S. *prionoides,* is also stated to occur in the Mangyshlak Peninsula in the Caspian region, but unfortunately no specimens from there have been described or illustrated (Astakhova, 1960b). A second species, S. *floweri,* from the *Subcolumbites* fauna of the Tobin Formation of Nevada is described here. An indeterminate species is known from the Narmia Member of the Mianwali Formation in the Salt Range of West Pakistan (Kummel, 1966); likewise, two specifically indeterminate forms are recorded from the Thaynes Formation of southeastern Idaho.

Stacheites dionysi (Renz and Renz, 1948: 50) is here considered to be a synonym of *Metadagnoceras terbunicum* (Arthaber). I agree with Spath (1934: 267) that *Stacheites webbianus* Diener (1907) from the Himalayan Anisian is a completely unrelated stock to the Scythian species discussed here.

Stacheites prionoides Kittl
Plate 56, figures 9, 10; Text-figure 29

Stacheites prionoides Kittl, 1903: 27, pl. 4, fig. 8; Diener, 1915: 266; Spath, 1934: 267, fig. 92.

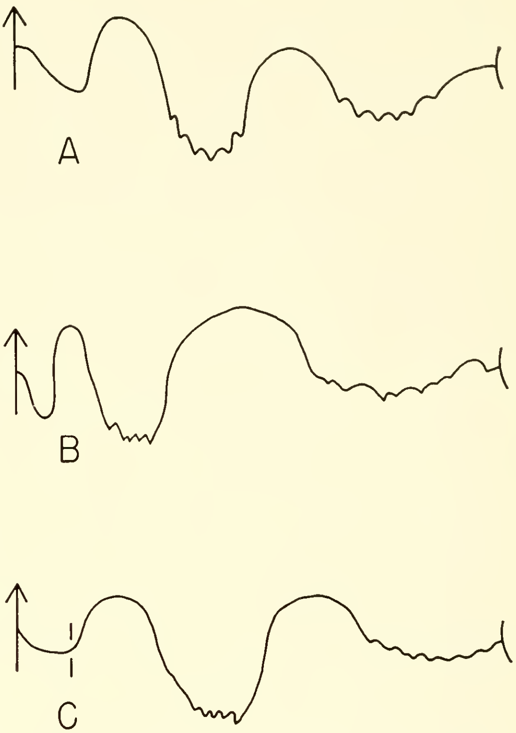

Figure 29. Diagrammatic representation of the suture of: A, *Stacheites prionoides* Kittl (1903: pl. 4, fig. 8), at a diameter of 33 mm, from Werfen Formation, Dalmatia; B, *S. floweri* n. sp., composite suture from specimens MCZ 9439 and 9491, at a diameter of approximately 35 mm, from *Subcolumbites* fauna, Tobin Formation, Nevada; C, S. sp. indet. II, at a diameter of 21 mm, from uppermost Thaynes Formation, Sublette Ridge, western Wyoming (MCZ 9501).

Kittl's original figure was a highly reconstructed drawing with no view of the venter. The type specimen is illustrated here for the first time. It can be seen that the specimen is a compressed form but obviously crushed. The opposite side of the conch is completely missing. The venter is narrow, flattened and sulcate, bordered by acute ventral shoulders. The measurements of Kittl's type are as follows:

D	W	H	U	W/D	H/D	U/D
45.8	?	24.2	5.0	?	52.8	10.9

The suture is slightly weathered and the ventral lobe could well be denticulated, but is too weathered to preserve such features. I consider Kittl's illustrations a fairly good representation of this specimen.

Stacheites prionoides is morphologically quite similar to the only other species of the genus, S. *floweri,* from the Tobin Formation of Nevada. The sutures especially are similar (Fig. 29). The shape

TABLE 40. MEASUREMENTS OF *STACHEITES FLOWERI* N. SP. FROM TOBIN FORMATION, NEVADA.

	D	W	H	U	W/D	H/D	U/D
1.	48.5	?	25.7	5.2?	?	52.9	10.6?
2.	40.5	?	20.8	5.5	?	50.2	13.2
3.	39.7	10.5	22.0	3.9	26.45	54.0	9.9
4.	31.7	8.2?	17.1	3.0	25.9?	53.9	9.48
5.	28.5	8.2?	16.7	2.6	28.75?	58.6	9.1

1. Paratype, MCZ 9440 (Pl. 28, fig. 2).
2. Paratype, MCZ 9444 (Pl. 28, fig. 8).
3. Holotype, MCZ 9441 (Pl. 28, figs. 3, 4).
4. Paratype, MCZ 9445 (Pl. 28, fig. 9).
5. Paratype, MCZ 9443 (Pl. 28, figs. 6, 7).

of the conch, degree of inflation and involution are also strikingly similar. The Nevada species, however, does bear faint sigmoidal ribs on the flanks whereas *S. prionoides*, as far as can be told, is smooth. Astakhova (1960b) records this species from the Mangyshlak Peninsula; in fact she used this as the name species of her highest local zone. Unfortunately, no descriptions or illustrations of these Mangyshlak specimens are available.

Occurrence. Werfen Formation, Mué, Dalmatia.

Repository. The holotype and only specimen of this species is in the Natural History Museum, Vienna.

Stacheites floweri n. sp.
Plate 28, figures 1–10; Text-figure 29

This is the second species of the genus *Stacheites* to be recorded. The species is represented by a fairly large number of specimens, mainly fragmentary. The measurements of five of the most complete specimens are given on Table 40.

The conch is very involute and discoidal. The venter is narrow, typically slightly concave, and bordered by a fairly sharp ridge. In some forms (e.g. Pl. 28, figs. 6, 7) the venter loses its concavity, and the adjoining ventral shoulders are rounded and not angular; on the earlier volutions, however, the former condition prevails. The material available does not allow an evaluation as to the nature and extent of variations in the character of the venter.

The flanks are slightly arched, with the maximum width in the dorsal third of the flank. The umbilical shoulders are abruptly rounded, and the umbilical wall vertical. The flanks bear interesting low falciform ribs. These commence above the umbilical shoulders as very low, narrow, radial ribs. At about the mid part of the flanks, the ribs broaden greatly, and inscribe a concave arc. Where the venter is concave, it is perfectly smooth; on the specimen (Pl. 28, figs. 6, 7) where the venter is not concave, there are faint ridges crossing the venter. In some specimens the falciform ribs are extremely faint.

The suture consists of a fairly broad first lateral lobe, a second lateral saddle occupying about one-third of the width of the flank, and a second lateral lobe that is low, and with a characteristic pattern of denticulation (Fig. 29B).

The basic features of the conch and suture place this species morphologically very close to *S. prionoides*. The falciform ribs are the most obvious distinguishing features.

Occurrence. Tobin Formation, Pershing County, Nevada; south tip of Tobin Range, Cain Mountain 1:62,500 quad., center NW ¼ sec. 9, T. 26N, R. 39E, 5,500 ft. S, 27.5 ft. W from elevation point 5088 on range crest.

Repository. Holotype, MCZ 9441 (Pl. 28, figs. 3, 4); paratypes MCZ 9442 (Pl. 28, fig. 5), MCZ 9443 (Pl. 28, figs. 6, 7), MCZ 9444 (Pl. 28, fig. 8), MCZ 9445 (Pl. 28, fig. 9), MCZ 9446 (Pl. 28, fig. 10), MCZ 9439 (Pl. 28, fig. 1), MCZ 9440 (Pl. 28, fig. 2); suture specimen MCZ 9491; unfigured paratypes MCZ 9500.

Stacheites sp. indet. (S.E. Idaho)
Plate 37, figs. 7–10; Text-figure 29

Two specimens from the Thaynes Formation of southeastern Idaho can be assigned to *Stacheites*. The first of these specimens (Pl. 37, figs. 7, 8) is a weathered individual of only a quarter volution. The narrow concave venter, angular ventral shoulder, slender compressed conch and distinctive suture are characteristic of the genus. The specimen is too incomplete to allow a specific determination or comparison.

The second specimen (Pl. 37, figs. 9, 10) is a small weathered individual of 33.6 mm in diameter that could well be conspecific with *Stacheites floweri* of the Tobin Formation of Nevada. The venter is flat with angular ventral shoulders. The lateral areas are broadly convex and smooth. The adoral half of the specimen is body chamber. The suture is shown on Figure 29C. The suture is quite similar to that of *S. floweri* except in the ventral lobe, but the differences here could well be the result of weathering.

Occurrence. The first specimen (Pl. 37, figs. 7, 8) came from the Upper Thaynes Formation, Hammond Creek, Bear River Range, southeast Idaho. The second specimen (Pl. 37, figs. 9, 10) came from a float 150–200 feet from top of upper calcareous siltstone member of Thaynes Formation (Kummel, 1954), Spring Canyon, Sublette Ridge, western Wyoming.

Repository. MCZ 9487 (Pl. 37, figs. 7, 8), MCZ 9501 (Pl. 37, figs. 9, 10).

Stacheites sp. indet. (West Pakistan)

Stacheites sp. indet., Kummel, 1966: 396, pl. 3, fig. 13.

This record is based on a single, poorly preserved specimen. The basic conch outline and pattern of suture generically identify the specimen.

Occurrence. The single specimen came from a five-foot limestone bed 38 feet above the base of the Narmia Member of the Mianwali Formation, Narmia Nala, Surghar Range, West Pakistan.

Repository. MCZ 9609.

Genus *Dagnoceras* Arthaber, 1911
Type species, *Dagnoceras nopcsanum* Arthaber, 1911

When Arthaber established this genus he included within it a varied group of species which are as follows:

Dagnoceras nopcsanum Arthaber
Dagnoceras zappanense Arthaber
Dagnoceras terbunicum Arthaber
Dagnoceras komanum Arthaber
Dagnoceras lejanum Arthaber

As Arthaber (1911) did not select a type species, Diener (1915: 115) selected *D. nopcsanum.* This selection was apparently overlooked by Smith (1932: 65) who selected *D. komanum* as type on the principle that this was the first mentioned species; this is, of course, an invalid selection.

Interpretation of the genus then rests first on a consideration of *D. nopcsanum.* The principal features are a moderately involute conch, with rounded flanks, a rounded umbilicus, and a suture with a large first lateral lobe and small second lateral lobe on or near the umbilical shoulder. Arthaber's (1911) sutures of this group were not accurately reproduced, and new drawings of his type specimens are offered here (Fig. 30). The sutures of all these specimens are to a greater or lesser extent altered by excessive grinding and polishing. *Dagnoceras nopcsanum* and *D. zappanense* are congeneric and actually quite similar. These two species differ mainly in the width of the first lateral lobe. *Dagnoceras lejanum* is a synonym of *D. zappanense. Dagnoceras komanum* is completely different in the aspect of the conch morphology and suture and is considered here to be a representative of *Albanites triadicus.* The specimen Arthaber (1911: 254, pl. 22(6), fig. 8) assigned to *Pseudosibirites* cf. *dichotomus* Waagen is also considered to be *Albanites triadicus.* Finally, there is *D. terbunicum,* a species with a narrow truncate venter and with a more elaborate suture. This species is assigned to *Metadagnoceras.* This genus is characterized by elaborate denticulation of the first lateral saddle and first lateral lobe. The conch is not too unlike that of a species

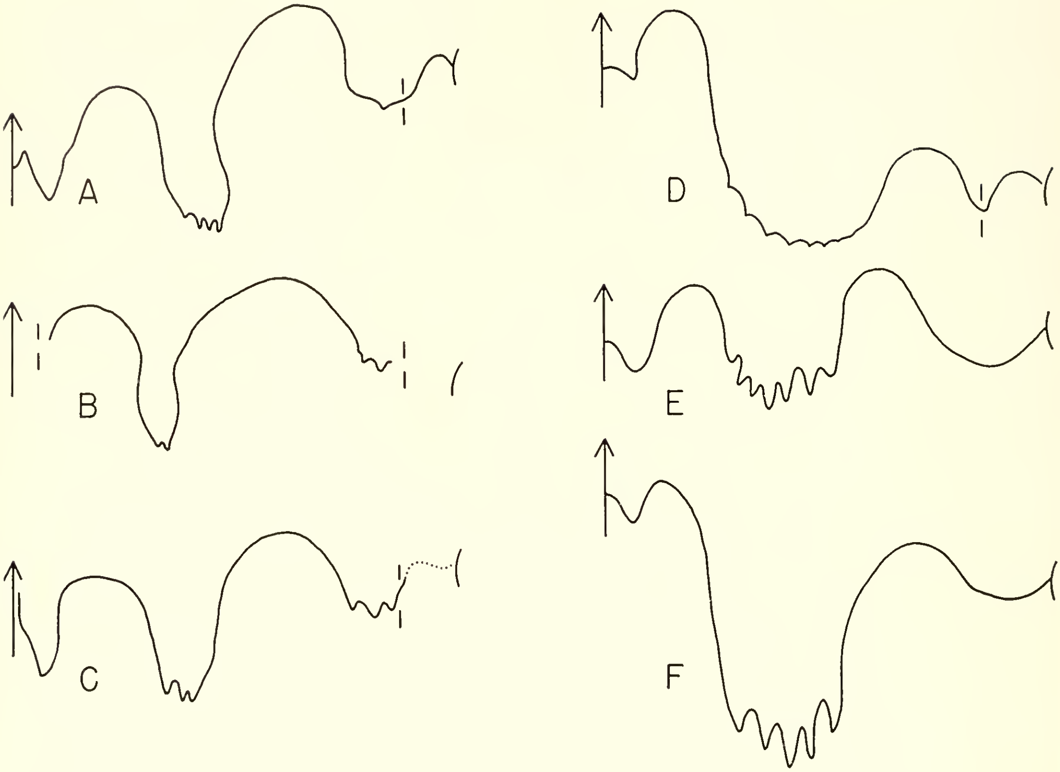

Figure 30. Diagrammatic representation of the sutures of species of *Dagnoceras*. A, syntype of *D. zappanense* Arthaber (1911: pl. 21(5), fig. 8; Pl. 15, figs. 3, 4 of this report), original drawing at a whorl height of 8 mm; B, syntype of *D. zappanense* Arthaber (1911: pl. 21(5), fig. 9; Pl. 15, figs. 5, 6 of this report), original drawing at a whorl height of 11.5 mm; C, syntype of *D. lejanum* Arthaber (1911: pl. 21(5), fig. 13; Pl. 15, figs. 7, 8 of this report), original drawing at a whorl height of 11 mm; D, holotype of *D. nopcsanum* Arthaber (1911: pl. 21(5), fig. 6; Pl. 15, figs. 1, 2 of this report), original drawing at a whorl height of 9 mm; E, *D. ellipticum* Chao (1959: fig. 47a), at a whorl height of 10 mm; F, *D. latilobatum* Chao (1959: fig. 47b), at a whorl height of 8 mm.

Specimens of figures A–D from *Subcolumbites* fauna of Albania; specimen of figure E from isolated block containing typical upper Scythian fauna in Kwangsi, China; specimen of figure F from a *Subcolumbites* fauna in Fengshan District of Kwangsi, China.

of *Dagnoceras*, but some species do have truncate venters, at least during a part of their ontogeny. *Metadagnoceras* appears to be a valid genus, distinct from *Dagnoceras*. However, it needs to be emphasized that the sutures of the two type specimens of *D. nopcsanum* are affected by grinding and polishing, and one cannot be sure as to how much these factors have given the suture its apparent simple pattern. None of the specimens of *D. nopcsanum* in the British Museum (Natural History) show the suture.

In addition to Albania, *Dagnoceras* is known from a single specimen (*D. zappanense*) from the *Prohungarites* fauna of Timor. The genus is known also from two species from late Scythian faunas in Kwangsi, China. A fragmentary specimen assigned to *D.* cf. *zappanense* has been recorded from the Narmia Member of the Mianwali Formation in the Surghar Range of West Pakistan (Kummel, 1966). It is of interest to note that no species of this genus has been recorded from the *Subcolumbites* fauna of Chios. *Dagnoceras*

(?) *unicum* Kiparisova from the Primorye Region is here assigned to *Metadagnoceras*. The three species from the *Meekoceras* fauna of southeastern Idaho that Smith (1932) assigned to *Dagnoceras* (*D. bonnevillense, D. bridgesi,* and *D. haydeni*) are completely unlike the type species and are excluded from this genus.

Dagnoceras nopcsanum Arthaber

Plate 15, figures 1, 2; Plate 16, figures 1, 2; Text-figure 30

Dagnoceras nopcsanum Arthaber, 1911: 241, pl. 21(5), figs. 6, 7; Diener, 1915: 115; Spath, 1934: 268–271, pl. 8, fig. 1, text-fig. 93a; Kummel, *in* Arkell, et al., 1957: L144, fig. 175, 1.

The two specimens of this species that Arthaber figured are the only specimens remaining in the original collection. They have the following measurements:

	D	W	H	U	W/D	H/D	U/D
Holotype (Arthaber, 1911: pl. 21(5), fig. 6)	28.5	9.1	11.1	10.0	49.2	38.9	35.1
Paratype (Arthaber, 1911: pl. 21(5), fig. 7)	36.3?	?	16.2	11.2	?	44.6?	30.9?

The holotype is a specimen of only fair preservation. The conch is evolute with a broad and fairly deep umbilicus. The whorls are oval in cross-section with a narrowly rounded venter, broadly convex lateral areas, an acutely rounded umbilical shoulder, and a steep umbilical wall. The greatest width of the whorls is at the umbilical shoulder. The specimen is essentially all phragmocone and devoid of any ornamentation or growth lines. The suture is shown on Figure 30D. As with all the specimens from the *Subcolumbites* fauna of Albania, the suture is revealed only by grinding and polishing, and in this case it is not possible to evaluate the full extent of the damage. The paratype has been so badly ground and polished that the suture is essentially meaningless. The holotype was prepared in slightly less damaging fashion but there is grave uncertainty as to whether the first lateral saddle and the first lateral lobe are as simple as shown on Figure 30D. The character of this part of the suture is critical for determining the relations of this species to those species assigned to *Metadagnoceras*.

Of the five species established by Arthaber from the Albanian Kčira fauna, only the type, *D. nopcsanum*, and *D. zappanense* are accepted as valid members of *Dagnoceras*. *Dagnoceras nopcsanum* differs from *D. zappanense* mainly in the suture, especially in the character of the first lateral lobe (Fig. 30B, D).

Occurrence. *Subcolumbites* fauna, Kčira, Albania.

Repository. Arthaber's two figured specimens are in the Paleontological Institute, University of Vienna.

Dagnoceras zappanense Arthaber

Plate 15, figures 3–11; Plate 24, figures 4, 5; Text-figure 30

Dagnoceras zappanense Arthaber, 1911: 241, pl. 21(5), figs. 8, 9; Diener, 1915: 115; Spath, 1934: 268–271, pl. 7, fig. 2, text-fig. 93d, e, f.

Dagnoceras cf. *zappanense*,—Kummel, 1966: 396, pl. 3, figs. 9, 10.

Dagnoceras lejanum Arthaber, 1911: 242, pl. 21(5), figs. 12, 13; Diener, 1915: 115; Spath, 1934: 269 (footnote), 271, text-fig. 93c.

The four specimens of this species figured by Arthaber are available for study. This species differs from *D. nopcsanum* mainly in the very slender first lateral lobe (Figs. 30A, B). In addition, there is some ornamentation. One specimen (Pl. 15, fig. 11) has faint umbilical nodes, and another faint sigmoidal ribs (Pl. 15, fig. 6). The other two specimens are smooth, which may be due to preservation or excessive preparation.

Arthaber distinguished between *D. zappanense* and *D. lejanum* on the basis of degree of involution and ornamentation. Both these characters are known to be highly variable in most ammonite species, and though the sample available is much too small to see "gradations," it is felt that we are dealing here with a single species complex.

The measurements of the four illustrated types are as follows:

	D	W	H	U	W/D	H/D	U/D
1.	42.7	12.1	17.5	13.3	28.3	40.9	31.1
2.	37.2	12.3	18.4	9.1	33.1	49.5	24.5
3.	33.1	11.5	16.2	7.2	34.7	48.9	21.8
4.	30.1	10.7	13.7	8.5	35.5	45.5	28.2

1. Lectotype, *D. lejanum* Arthaber (1911: pl. 21(5), fig. 13).
2. Lectotype, *D. zappanense* Arthaber (1911: pl. 21(5), fig. 9).
3. Paralectotype, *D. zappanense* Arthaber (1911: pl. 21(5), fig. 8).
4. Paralectotype, *D. lejanum* Arthaber (1911: pl. 21(5), fig. 12).

The sutures of these two species are likewise nearly identical (Figs. 30A, C). Arthaber's drawings of the sutures for these species are deceptive; his drawing of the suture of *D. zappanense* (Fig. 30B) actually terminates on the umbilical shoulder, while that for *D. lejanum* (Fig. 30C) terminates on the umbilical seam.

The specimen from Timor identified by Spath (1934: 271, 272) as inseparable from *D. lejanum* is figured here on Plate 24, figures 4, 5. I completely agree with Spath on this conclusion; the specimen, though smaller, is nearly identical to the smaller paralectotype of *D. lejanum* illustrated here on Plate 15, figures 9–11. A fragmentary specimen of a form quite similar to this species has been recorded by Kummel (1966) from the Narmia Member of the Mianwali Formation, Surghar Range, West Pakistan, in association with *Procarnites kokeni*.

Occurrence. Subcolumbites fauna, Kčira, Albania, *Albanites* fauna, Nifoekoko, Timor; Narmia Member of Mianwali Formation, Surghar Range, West Pakistan.

Repository. The four types of Arthaber's are in the Paleontological Institute, University of Vienna; the specimen from Timor is BMNH C33713; the specimen from West Pakistan is MCZ 9565.

Dagnoceras latilobatum Chao
Text-figure 30

Dagnoceras latilobatum Chao, 1959: 142, 322, pl. 18, figs. 6–8.

This species was founded on two specimens with a "narrow, subtruncate venter" and "obtusely rounded" ventral shoulders. The suture (Fig. 30F) is characterized by a very large first lateral lobe. On the basis of the data available, I believe it to be a valid species of this genus.

Occurrence. From black, thick-bedded limestone about 1.5 km north of Yali, Kwangsi, China, associated with *Subcolumbites*, *Hellenites*, etc. (Chao collection 546).

Dagnoceras ellipticum Chao
Text-figure 30

Dagnoceras ellipticum Chao, 1959: 143, 323, pl. 18, figs. 3–5, text-fig. 47a.

This species is based on a single specimen which, however, is poorly illustrated. From the data available, it is clearly a species of *Dagnoceras* of the general type of *nopcsanum*, the type species. It differs from *nopcsanum* in its suture (Fig. 30E) but not enough data are available to analyze the relationships.

Occurrence. Upper limestone bed, Naliling section near village of Lolou, Linglo District, Kwangsi, China, associated with *Hellenites*, *Prenkites*, etc. (Chao collection 542a).

Genus *Metadagnoceras* Tozer, 1965
Type species, *Metadagnoceras pulcher* Tozer, 1965

This genus is characterized by its large, highly denticulated first lateral lobe and narrow first lateral saddle, that may or may not be denticulated. This basic plan of the suture is like that of *Dagnoceras* except for the pattern of denticulation. The suture of *Dagnoceras nopcsanum* is known only from the type specimen, and this suture has been affected by grinding. Taking this into consideration, the differences between *Dagnoceras* and *Metadagnoceras* in regards to the suture are not all that great.

The genus *Metadagnoceras* includes the following species:

M. pulcher Tozer
M. tobini n. sp.
M. unicum (Kiparisova)
M. freemani Kummel
M. terbunicum (Arthaber)

Metadagnoceras pulcher occurs in the Toad Formation of British Columbia closely associated with species of *Isculitoides* and *Keyserlingites*; *Metadagnoceras tobini* is from the Tobin Formation of Nevada, associated with *Subcolumbites* etc.; *Metadagnoceras unicum* is from the Primorye Region, presumably from a late Scythian horizon (*Columbites* Zone); *Metadagnoceras freemani* is from the *Prohungarites* fauna of Timor; and *Metadagnoceras terbunicum* is from the *Subcolumbites* fauna of Albania and Chios.

This newly recognized genus is as yet incompletely known; three of the species (*unicum, freemani*, and *pulcher*) are known from only one specimen, and the other two species by a few specimens of only modest preservation.

Metadagnoceras pulcher Tozer
Text-figure 31

Metadagnoceras pulcher Tozer, 1965a: 29, pl. 1, figs. 11a–e.

This unique species was based on a single, well preserved specimen. It is readily differentiated by its suture (Fig. 31A) and its delicate strigate sculpture.

Occurrence. Toad Formation, Halfway River area, British Columbia.

Metadagnoceras tobini n. sp.
Plate 27, figures 1–4; Text-figure 31

This species is based on four fragmentary specimens of fair preservation. The conch is moderately involute with compressed whorls. The lateral areas are broadly arched, the venter low but rounded and bordered by rounded but distinct ventral shoulders. The umbilical shoulder is more abruptly rounded and the umbilical wall is nearly vertical. The flanks bear sinuous growth lines and the living chamber of one of the larger specimens has faint indications of widely separated low radial undulations. The venter on the two largest specimens is unfortunately not preserved; it is assumed that in these mature specimens the venter is like that of the smaller specimen illustrated on Plate 27, figures 1, 2.

The suture (Fig. 31B) consists of a large first lateral lobe which has denticulations extending up the ventral side to a narrow and irregular first lateral saddle. There is a second lateral lobe on the umbilical shoulder and wall. The second lateral saddle is asymmetric and rounded.

In its conch shape and dimensions, *Metadagnoceras tobini* is distinct from all the other species of this genus. However, its suture is nearly identical to the suture of *M. freemani* (Fig. 31D).

Occurrence. Lower part of Tobin Formation, USGS Locality M2562, Pershing County, Nevada; south tip of Tobin Range, Cain Mountain 1:62,500 quad., center NW ¼ sec. 9, T. 26N, R. 39E, 5,500 ft. S, 27.5 ft. W of elevation point 5088 on range crest.

Repository. Holotype (Pl. 27, fig. 3) MCZ 9637; paratypes (Pl. 27, figs. 1, 2) MCZ 9638, (Pl. 27, fig. 4) MCZ 9639; unfigured paratype MCZ 9640.

Metadagnoceras unicum
Text-figure 31

Dagnoceras (?) *unicum* Kiparisova, 1961: 74, pl. 13, fig. 6, text-fig. 35.

This species was based on a single well preserved specimen. In its general conch morphology it differs from other species of the genus in the great width of the whorl in the area of the umbilical shoulder, in the strongly converging whorl sides and

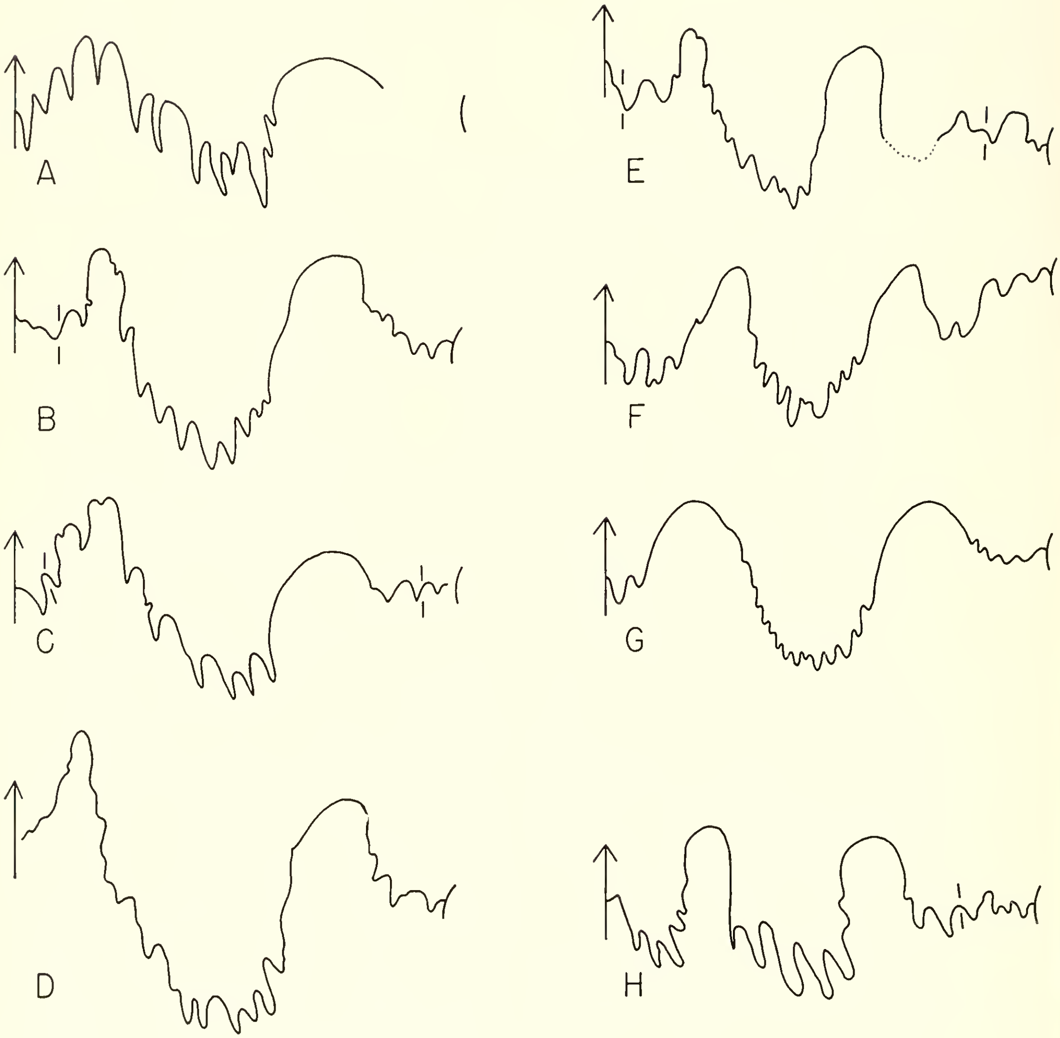

Figure 31. Diagrammatic representation of the sutures of species of *Metadagnoceras*. A, holotype of *M. pulcher* Tozer (1965a: fig. 9), from British Columbia, at a whorl height of approximately 20 mm; B, paratype of *M. tobini* n. sp., from Tobin Formation, Nevada, at a whorl height of 11 mm (MCZ 9638); C, *M.* sp., undescribed species collected by N. J. Silberling from Star Peak Formation, Nevada, at a whorl height of 22 mm; D, holotype *M. freemani* Kummel, from Nifoekoko, Timor, at a whorl height of 14 mm (BMNH C33701); E, holotype of *M. terbunicum* (Arthaber), from *Subcolumbites* fauna, Albania, at a whorl height of 18 mm; F, plesiotype *M. terbunicum*,—Renz and Renz (1948: pl. 1, fig. 7b), from *Subcolumbites* fauna of Chios at a whorl height of 14 mm (NHMB J13692); G, holotype of *Stacheites dionysi* Renz and Renz (1948: pl. 1, fig. 6b), from *Subcolumbites* fauna of Chios, at a whorl height of 17 mm (NHMB J13689); H, *M. unicum* (Kiparisova, 1961: fig. 35), from late Scythian horizon, Primorye Region, Siberia, at a whorl height of 19 mm.

the narrowly rounded venter. Its suture (Fig. 31H) is likewise quite different.

Occurrence. Russki Ostrov, Cape Schmidt, Primorye Region, from concretions in a dark siltstone together with *Columbites parisianus.* This horizon is probably equivalent to the *Columbites* Zone of southeast Idaho.

Metadagnoceras freemani Kummel
Plate 24, figures 1, 2; Text-figure 31

Metadagnoceras freemani Kummel, 1968a: 11, pl. 1, figs. 12, 13.

This species is proposed for the specimen from Timor mentioned by Spath (1934: 269, footnote) as "an isolated example of a new species from Timor . . . which is very close to *Dagnoceras terbunicum*." The specimen measures 47.8 mm in diameter, 14.7 mm for the width of the last whorl, 21.7 mm for the height of the last whorl, and 10.4 mm for the diameter of the umbilicus. The conch is compressed with a low, arched venter and rounded ventral and umbilical shoulders. The suture (Fig. 31D) has a very large first lateral lobe with denticulations extending all along the ventral side to a narrow irregular first lateral saddle. There is a small denticulated second lateral lobe on the umbilical shoulder and wall.

This species does not resemble *Dagnoceras terbunicum* in conch shape; the differences are centered mainly in the character of the venter. In the suture the first lateral saddle and the first lateral lobe of the two species are quite similar (Figs. 31D–F) but the remainder of the suture is quite different. In general conch morphology *Metadagnoceras freemani* is quite similar to the type species, *M. pulcher* Tozer. The sutures are similar in basic plan but differ in significant details. The suture of *M. tobini* n. sp. is very nearly identical to that of *M. freemani*, but in the Nevada species the whorls are of quite different proportions and the conch much more evolute.

Occurrence. Nifoekoko, Timor, from bed with manganese coated fossils, including *Albanites, Prohungarites,* etc.

Repository. BMNH C33701, holotype.

Metadagnoceras terbunicum (Arthaber)
Plate 16, figures 7, 8; Plate 18, figures 9, 10; Text-figure 31

Dagnoceras terbunicum Arthaber, 1911: 242, pl. 21(5), figs. 10a–c; Diener, 1915: 115; Spath, 1934: 269; Renz and Renz, 1947: 60; Renz and Renz, 1948: 51, pl. 1, figs. 7–7b.

Meekoceras radiosum,—Arthaber (non Waagen) 1911: 246, pl. 21(5), fig. 14; Diener, 1915: 194.

Dagnoceras aff. *terbunico*,—C. Renz, 1928: 155.

Dagnoceras nopcsanum Arthaber var. *involuta* Renz and Renz, 1947: 60; Renz and Renz, 1948: 52, pl. 1, figs. 5–5a.

Stacheites dionysi Renz and Renz, 1947: 60, 75; Renz and Renz, 1948: 50, pl. 1, figs. 6–6b, 8–8b.

When Arthaber proposed his genus *Dagnoceras*, he included within it a heterogeneous group of species. One of these was *D. terbunicum*, characterized by a flat venter and angular ventral shoulders, which is in striking contrast to the rounded venter of the more typical species. Arthaber (1911: 240) recognized the similarity of his new generic group to *Stacheites* but was uncertain of the character of the venter of Kittl's S. *prionoides*. My own examination of *S. prionoides* clearly establishes that Kittl's type specimen has a slightly sulcate venter with angular ventral shoulders. The basic morphological features of the conch of *Dagnoceras terbunicum* do suggest, at first, the possibility of this species being a more inflated representative of *Stacheites*. The basic plan of the suture, however, is more like that found in *Metadagnoceras* than that found in *Stacheites*. Arthaber's (1911: pl. 21(5), fig. 10c) representation of the suture is misleading. A new drawing of the suture from this type specimen is shown here on Figure 31E. There is a large first lateral lobe, with prominent denticulations on the base of the lobe and extending up on the ventral side of the lobe to a narrow, irregular first lateral saddle. There is a small second lateral lobe above the umbilical shoulder that apparently has a few denticulations which are, however, indistinct because of excessive grinding; this is followed over the umbilical shoulder and wall by an irregular series of large denticulations. The character of the first lateral saddle and first lateral lobe is very much like that of the suture of *M. tobini, M.*

freemani, and the specimen from Nevada collected by N. J. Silberling from the base of the Star Peak Group, Humboldt Range, Nevada (Fig. 31C). It differs from these species in the greater elaboration and length of the remainder of the suture. The measurements of the holotype of *D. terbunicum* are: Diameter 43.0?, Width 12.0?, Height 21.8, Umbilicus 7.8 mm (the second specimen of this species mentioned by Arthaber is not in the collection of the Paleontological Institute, Vienna, and is presumed lost).

With some misgivings I include in *M. terbunicum*, *Meekoceras radiosum*,—Arthaber (non Waagen). This species has the same general shell form as *M. terbunicum* (compare Pl. 16, figs. 7, 8 and Pl. 18, figs. 9, 10) except for being more involute. The dimensions of this specimen are: Diameter 45.0?, Width 13.0?, Height 24.0?, Umbilicus 3.6? mm. The suture had been exposed by grinding and the pattern reproduced by Arthaber is not at all a correct representation. One can never be absolutely sure in cases like this but it appears that the suture is actually like that of the holotype of *M. terbunicum*. Thus on the basis of conch form and probable nature of the suture, this species is considered a synonym of *M. terbunicum*.

In the fauna from Chios, the Renzes (1948: 51) record one specimen as being conspecific with *D. terbunicum* Arthaber. The measurements of this specimen (Renz and Renz, 1948: pl. 1, figs. 7–7b) are as follows:

	D	W	H	U	W/D	H/D	U/D
NHMB J13692	42.0	14.2	20.3	8.3	33.8	48.3	19.8

In addition, the Renzes assigned another specimen to *D. nopcsanum* Arthaber var. *involuta* Renz and Renz (1948: 52, pl. 1, figs. 5–5a). The measurements of this species are as follows:

	D	W	H	U	W/D	H/D	U/D
NHMB J13694	28.8	10.7	13.7?	7.2	37.2	47.6?	25.0

The Albanian specimens of *D. nopcsanum* have rounded venters, the Chios specimen has a truncate, flattened venter and is merely a smaller specimen of *terbunicum*.

The Chios collection contained two specimens which the Renzes assigned to a new species of *Stacheites*—*S. dionysi*. The measurements of these two specimens are as follows:

	D	W	H	U	W/D	H/D	U/D
NHMB J13689 (Renz and Renz, 1948: pl. 1, fig. 6)	34.8	11.4	16.4	8.1	32.8	47.1	23.3
NHMB J13690 (Renz and Renz, 1948: pl. 1, fig. 8)	45.8	?	21.2	10.4	?	46.3	22.7

The conch form of S. *dionysi* is identical to that of *Metadagnoceras terbunicum*; the only difference between these forms is in the slightly greater individualization of the second lateral lobe (Fig. 31G), a difference I can hardly consider of specific significance and surely not of generic rank. Preparation of the suture in these specimens preserved in hard red limestone is very difficult, and is generally done by acid etching or grinding. Also, with only four specimens assigned to these three different species (and two genera), it is hardly justifiable to put such importance on minor differences in the suture. All three of the species are considered to be conspecific with *Metadagnoceras terbunicum* (Arthaber).

The Albanian and Chios specimens assigned to *terbunicum* have flattened venters. Silberling (personal communication) has a specimen from the Star Peak Formation, Nevada, that also has a flattened venter. This specimen is an incomplete phragmocone of approximately 44 mm in diameter. The other species of *Metadagnoceras* have low, arched venters to more highly vaulted venters. Considering the state and nature of preservation of the Albanian and Chios specimens assigned here to *terbunicum*, I believe they are all incomplete and immature specimens. It is, of course, uncertain as to what the character of the venter is like on a mature individual. As it is now interpreted, in conch form this species is convergent to *Stacheites* but differs significantly in its suture.

Occurrence. Subcolumbites fauna of Albania and Chios.

Repository. Arthaber's (1911) figured type (pl. 21(5), fig. 10; Pl. 16, figs. 7, 8 of this report) is in the Paleontological Institute, University of Vienna. A second specimen indicated by Arthaber (1911: 242) is apparently lost. The Chios specimens are in the Natural History Museum, Basel, and are as follows: holotype *Dagnoceras nopcsanum* var. *involuta* Renz and Renz (1948: pl. 1, fig. 5) NHMB J13694; unfigured specimen NHMB J13833; holotype *Stacheites dionysi* Renz and Renz (1948: pl. 1, fig. 6) NHMB J13689; paratype (pl. 1, fig. 8) NHMB J13690; unfigured paratypes NHMB J13691; plesiotype *Dagnoceras terbunicum* (pl. 1, fig. 7) NHMB J13692; unfigured specimens NHMB J13693.

Genus *Balkanites* Ganev, 1966
Type species, *Balkanites tabulatus* Ganev, 1966

Conch compressed with flat lateral areas and broad flat venter. Ventral shoulders weakly rounded. Umbilicus small, about 20 percent the diameter of the conch. Umbilical wall nearly vertical, umbilical shoulders weakly rounded. Conch smooth with no ornamentation. Suture goniatitic consisting of a single large, smooth, lateral lobe with indication of the beginning of a second lobe at the umbilical shoulder. Ganev did not include a drawing of the suture in his report but he kindly sent me a photo of the specimen, plus a plaster cast which clearly shows the suture.

This is indeed a unique Scythian ammonoid and is an addition to the fairly large number of endemic genera which characterize the Werfen fauna. Ganev allied his new genus to *Dagnoceras* primarily on the basis of the single large lateral lobe. In this relationship I concur as being the most logical on the basis of the data available. In *Dagnoceras* the venter is rounded and the lobe denticulated.

Balkanites tabulatus Ganev

Balkanites tabulatus Ganev, 1966: 24, pl. 2, figs. 1a–d.

Discussion of this species is given above.

Occurrence. Campil Member of Werfen Formation, perhaps as exotic blocks, Luda-Kamčija region of eastern Bulgaria.

Repository. Holotype (and only specimen) in Geological Institute of the Bulgarian Academy of Science; plaster cast in MCZ.

Genus *Nordophiceras* Popov, 1961
Type species, *Ceratites euomphalus* Keyserling, 1845

Nordophiceras euomphalus (Keyserling)
Plate 47, figures 6–8; Text-figure 32

Ceratites euomphalus Keyserling, 1845: 171, pl. 3, figs. 7–9; Middendorff, 1860: 248, pl. 3, figs. 7–9; Eichwald, 1868: 1039.

Meekoceras euomphalum,—Mojsisovics, 1882: 214; Waagen, 1895: 239, 246; Diener, 1915: 191.

Xenodiscus euomphalus,—Mojsisovics, 1886: 76, pl. 11, fig. 7.

Nordophiceras euomphalus,—Popov, 1961: 39.

Xenodiscus karpinskii Mojsisovics, 1886: 75, pl. 11, fig. 13.

Meekoceras (*Gyronites*) *karpinskii*,—Diener, 1915: 196.

Nordophiceras karpinskii,—Popov, 1961: 41, pl. 25, fig. 6; Vozin and Tikhomirova, 1964: 50, pl. 27, fig. 2.

Nordophiceras contratius Popov, 1962a: 177.

Meekoceras contrarius Popov, 1962a: 185, pl. 3, fig. 7, text-fig. 8.

Meekoceras? contrarium,—Vozin and Tikhomirova, 1964: 55, pl. 30, fig. 3, text-fig. 9a.

Popov (1961) selected *Xenodiscus karpinskii* Mojsisovics (1886: 75, pl. 11, fig. 13) as the type species of his genus *Nordophiceras.* At the same time he included within that genus *Ceratites euomphalus* Keyserling (1845: 171, pl. 3, figs. 7–9). The latter species differs from *X. karpinskii* in having a slightly more inflated whorl section. The author has available four topotype specimens of *Nordophiceras*

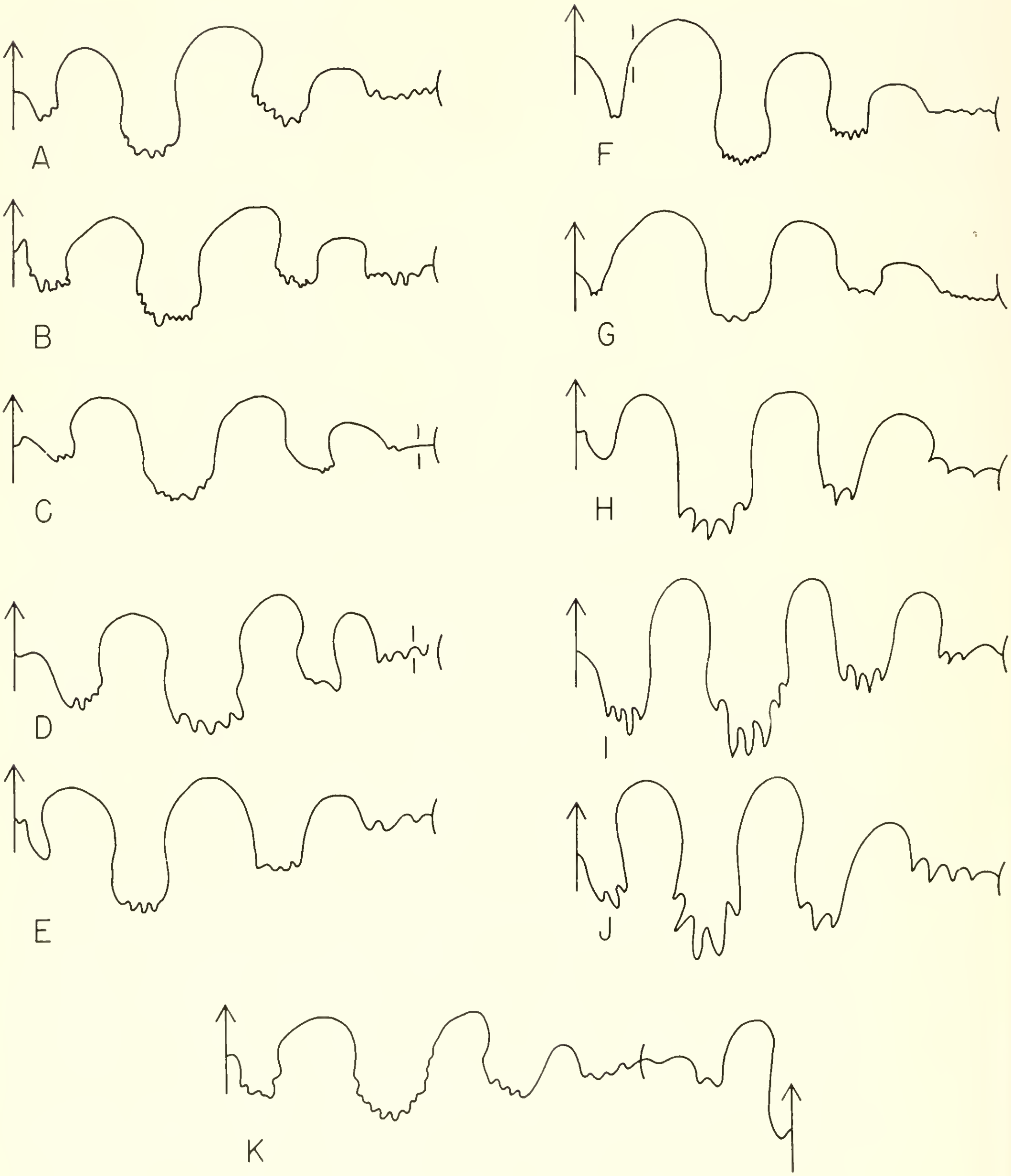

Figure 32. Diagrammatic representation of the suture of: A–C, *Nordophiceras euomphalus* (Mojsisovics), from *Dieneroceras* Zone, northern Siberia; A, topotype,—Popov (1961: 39, fig. 6e), at a whorl height of 8 mm; B, topotype (MCZ 8670a), at a diameter of 50 mm; C, topotype (MCZ 8670b), at a diameter of 26 mm; D, holotype *Nordophiceras contrarius* (Popov 1962a: fig. 8), *Dieneroceras* Zone, northern Siberia, at a whorl height of 20 mm; E, holotype *Nordophiceras alexeevae* Popov (1961: 39, fig. 6c), from *Dieneroceras* Zone, eastern Taymyr, Siberia, at a whorl height of 15 mm; F, *Nordophiceras jacksoni* (Hyatt and Smith), from *Columbites* fauna, Montpelier Canyon, southeast Idaho (MCZ 9572), at a diameter of 36 mm; G, paratype of *Prionolobus jacksoni* Hyatt and Smith (1905: pl. 62, fig. 16), from *Columbites* fauna, Paris Canyon, southeast Idaho, at a diameter of 45 mm (USNM 75292c); H, paratype *Meekoceras* (*Submeekoceras*) *compressum* Chao (1959: fig. 46a), from *Subcolumbites* fauna, Kwangsi, China, at a whorl height of 15 mm; I, holotype *Meekoceras* (*Submeekoceras*)

karpinskii identified by Dr. Popov. Examination of these specimens and of the illustrations in Mojsisovics (1886: pl. 11, fig. 7) clearly shows that these two so-called species cannot be distinguished. The combining of these two species thus makes *euomphalus* the type species of *Nordophiceras*.

Two of the Siberian topotypes in the collections of the Museum of Comparative Zoology are illustrated here on Plate 47, figures 6–8. The conch is moderately involute, compressed, with a rounded venter. The flanks are broadly convex and the umbilical shoulders rounded. The suture consists of two lateral lobes and a serrated lobe on the umbilical shoulder and wall. The sutures of two of the topotypes in the collection and that reproduced by Popov (1961: fig. 6e) are shown on Figure 32A–C. The conch is smooth except for sinuous growth lines.

Associated with this species in the Olenek fauna is a closely related species, *N. alexeevae* Popov, which differs in the presence of closely spaced fine, prosiradiate ribs on the inner whorls and more widely spaced, thin ribs on the outer whorls. In nearly all other aspects these two species are identical. A much closer relationship exists with *Nordophiceras jacksoni* (Hyatt and Smith) from the *Columbites* fauna of southeastern Idaho. The basic plan of the smooth conch and the suture is remarkably similar. The Idaho fauna has yielded a fairly large number of specimens which gives some appreciation of the variations in conch proportions (Fig. 33); this kind of data is lacking for the Siberian species described here. It is very possible that study of a large collection of the Siberian *N. euomphalus* could establish that *N. jacksoni* is a synonym; for the moment at least it seems best to keep the forms separate. It is because of this very close relationship with *N. jacksoni* that I believe *Meekoceras contrarius* is a synonym of *N. euomphalus*. The main difference in these species lies in the degree of involution. However, the difference in umbilical diameters lies well within the variation of this parameter in the populations of *N. jacksoni* from southeast Idaho. The other species of *Nordophiceras* in the *Columbites* fauna of Idaho are ornamented forms more related to *N. alexeevae*.

This species is also quite similar to *Nordophiceras planorbis* (Waagen) (Kummel, 1966: 397) from the Salt Range of West Pakistan from an upper Scythian horizon. The basic architecture of the conch is most similar; however, the Salt Range species is known from very few and generally poorly preserved specimens.

Occurrence. Mojsisovics' specimens are from the region of the mouth of the Olenek River, those described by Popov (1961) are from his *Dieneroceras* Zone in eastern Taymyr, Chernokhrebetnaya River.

Repository. Topotype specimens MCZ 9655 (Pl. 47, fig. 6), MCZ 8680 (Pl. 47, figs. 7, 8), MCZ 6107, 9656.

Nordophiceras alexeevae Popov
Text-figure 32

Nordophiceras alexeevae Popov, 1961: 39, pl. 25, fig. 7.

Nordophiceras olenekensis Popov, 1961: 40, pl. 12, fig. 8.

This species from northern Siberia is of particular interest because it is another form closely related to a species in the *Columbites* fauna of southeastern Idaho. In fact, because the Idaho fauna has yielded

←

loluense Chao (1959: fig. 45d), from *Subcolumbites* fauna, Kwangsi, China, at a whorl height of 12 mm; J, holotype *Meekoceras* (*Submeekoceras*) *longiseptatum* Chao (1959: fig. 46c), from *Subcolumbites* fauna of Kwangsi, at a whorl height of 22 mm; K, holotype *Nordophiceras olenekensis* Popov (1961:40, fig. 6d), from *Dieneroceras* Zone, northern Siberia, at a whorl height of 12 mm.

a fairly large number of specimens, the data on that species (*N. pilatum*) have aided greatly in the interpretation of this Siberian species. It should be pointed out that Popov had available only one specimen of *N. alexeevae* and six specimens of *N. olenekensis*.

This species is essentially of the same conch morphology, that is in compression, involution, etc., as the associated *N. euomphalus*, except that on the inner whorls there are fine, closely spaced prosiradiate ribs which on the outer whorls are more widely spaced. The two species of Popov differ only in the degree of this ornamentation. *Nordophiceras pilatum* from the *Columbites* fauna of southeastern Idaho has a similar pattern of ornamentation. The large number of specimens in the Idaho collection clearly show a broad range of variation in the degree of intensity of ornamentation. The suture is illustrated on Figure 32E, K.

Occurrence. Dieneroceras Zone of Popov (1961), eastern Taymyr and the delta of the Lena River, northern Siberia.

Nordophiceras pseudosimplex n. sp.

Arctoceras simplex,—Popov (non Mojsisovics), 1961: 67, pl. 18, fig. 1; Vozin and Tikhomirova, 1964: 55, pl. 29, fig. 1.

Arctoceras simplex Mojsisovics (1886) was established for specimens which are the inner, juvenile whorls of *Arctoceras blomstrandi* (Lindström), and is of mid-Scythian *Owenites* Zone age (Kummel, 1961). The specimen Popov (1961) assigned to *Arctoceras simplex* is not at all comparable. Popov's specimen is more evolute, has flattened, more or less parallel, lateral areas. Popov (1961) states his specimen has smooth inner whorls but that one specimen had widely spaced radial ribs which disappeared on the body chamber. The ribs are not apparent on Popov's illustration. The suture is said to be ceratitic but this is not borne out by the published text-figure.

Needless to say that much more data are needed, but we can be sure that this specimen is not conspecific with *Arctoceras simplex* but rather is allied to such forms as *Nordophiceras euomphalus* from the underlying *Dieneroceras* Zone of Popov. It is, likewise, quite similar to *Nordophiceras planorbis* (Waagen) from the Narmia Member of the Mianwali Formation in the Salt Range.

Occurrence. Olenekites Zone in basin of Olenek River, northern Siberia.

Nordophiceras planorbis (Waagen)

Lecanites planorbis Waagen, 1895: 278, pl. 39, fig. 3.

Meekoceras (*Gyronites*) *planorbis*,—Diener, 1915: 197.

Nordophiceras planorbis,—Kummel, 1966: 397, pl. 4, figs. 1–3.

New illustrations and descriptions of the type specimens and two topotype specimens have been published by Kummel (1966). This is the only record of *Nordophiceras* for the Tethyan region.

Occurrence. Narmia Member, Mianwali Formation, Chhidru Nala, Salt Range, West Pakistan.

Repository. Holotype GSI 7226; topotypes MCZ 9611, 9612.

Nordophiceras jacksoni (Hyatt and Smith)
Plate 47, figures 1–5; Plate 48, figures 1–4; Text-figures 32, 33

Prionolobus jacksoni Hyatt and Smith, 1905: 151, pl. 151, figs. 11–21; Krafft and Diener, 1909: 40, 41.

Meekoceras jacksoni,—Diener, 1915: 192.

Ophiceras jacksoni,—Smith, 1932: 49, pl. 62, figs. 11–21.

This species is abundantly represented in the *Columbites* beds exposed around the north end of Bear Lake, southeastern Idaho. The conch is smooth, evolute, compressed, with a rounded venter. The measurements of 48 specimens are given on Table 41 and plotted on Figure 33. These data show that there is only a moderate amount of variation in evolution

TABLE 41. MEASUREMENTS OF *NORDOPHICERAS JACKSONI* (HYATT AND SMITH) FROM *COLUMBITES* FAUNA, BEAR LAKE REGION, SOUTHEASTERN IDAHO.

	D	W	H	U	W/D	H/D	U/D		D	W	H	U	W/D	H/D	U/D
1.	62.0	14.2	20.7	25.1	22.9	33.4	40.5	25.	25.6	7.1	11.5	7.0	27.7	44.9	27.3
2.	61.0?	14.4	21.8	23.3	23.6?	35.7?	38.2?	26.	25.3	7.2	9.6	9.0	28.5	37.9	35.6
3.	55.7	12.2	21.0	20.0	21.9	37.7	35.9	27.	25.2	7.2	11.1	6.8	28.5	44.0	26.9
4.	50.4	10.8	20.4	15.3	21.4	40.5	30.4	28.	24.6	6.5	10.7	6.2	26.4	43.5	25.2
5.	47.0	11.0	18.4	15.0	23.4	39.1	31.9	29.	24.6	6.3	11.5	5.4	25.6	46.7	21.9
6.	45.3	11.4	18.3	13.5	25.1	40.4	29.8	30.	24.0	7.2	10.5	6.4	30.0	43.8	26.7
7.	44.4	11.5	16.2	16.7	25.9	36.5	37.6	31.	21.1	6.5	8.7	6.6	30.8	41.2	31.3
8.	44.2	10.6	17.5	12.5	23.9	39.6	28.3	32.	20.1	6.0	8.4	6.5	29.9	41.8	32.3
9.	43.0	9.7	18.2	11.0	22.6	42.3	25.6	33.	20.0	5.4	8.2	5.3	27.0	41.0	26.5
10.	39.1	9.6	15.4	12.5	24.6	39.4	31.9	34.	19.3	5.7	8.2	5.7	29.5	42.5	29.5
11.	36.2	8.5	14.4	11.9	23.5	39.8	32.9	35.	19.2	5.7	8.1	5.7	39.7	42.2	29.7
12.	33.8	8.2	14.7	9.0	24.3	43.5	26.6	36.	18.9	6.5	7.4	5.8	34.4	39.2	30.7
13.	32.6	?	13.0	9.9	?	39.9	30.4	37.	18.2	5.1	7.0	5.9	28.0	38.5	32.4
14.	32.5	8.4	13.7	9.3	25.8	42.2	28.6	38.	18.1	5.8	7.3	6.1	32.0	40.3	33.7
15.	31.0	8.3	13.3	8.7	26.8	42.9	28.1	39.	18.0	6.0	7.7	6.1	33.3	42.8	33.9
16.	31.0	8.5	12.4	10.2	27.4	40.0	32.9	40.	17.5	6.0	7.4	5.7	34.3	42.2	32.6
17.	29.0	7.2	10.5	10.7	24.8	36.2	36.9	41.	16.7	5.3	6.4	5.7	31.7	38.3	34.1
18.	28.4	7.6	11.2	9.1	26.7	39.4	32.0	42.	16.3	5.7	6.4	5.1	34.9	39.3	31.3
19.	28.0	7.0?	12.3	8.1	25.0?	43.9	28.9	43.	15.8	5.0	6.3	5.3	31.6	39.9	33.5
20.	27.5	7.3	11.8	7.6	26.5	42.9	27.6	44.	13.7	4.8	5.4	4.7	35.0	39.4	34.3
21.	27.2	7.0	11.2	9.3	25.7	41.2	34.2	45.	11.5	4.3	5.0	4.0	37.4	43.5	34.8
22.	26.2	7.2	11.4	7.0	27.5	43.5	26.7	46.	11.3	4.2	4.4	3.7	37.2	38.9	32.7
23.	26.0	7.5	10.8	7.8	28.8	41.5	30.0	47.	10.8	4.3	4.3	3.6	39.8	39.8	33.3
24.	26.0	6.8	9.8	9.2	26.1	37.7	35.4	48.	10.1	4.4	3.9	3.2	43.6	38.6	31.7

1. Plesiotype, MCZ 9565 (Pl. 47, fig. 2).
3. Plesiotype, MCZ 9564 (Pl. 47, fig. 1).
4. Holotype, USNM 75292a (Pl. 48, figs. 3, 4).
8. Paratype, USNM 75292c (Pl. 48, figs. 1, 2).
15. Plesiotype, MCZ 9567 (Pl. 47, fig. 4).
24. Plesiotype, MCZ 9568 (Pl. 47, fig. 5).
29. Paratype, USNM 75292d (Smith, 1932: pl. 62, figs. 17, 18).
45. Plesiotype, MCZ 9566 (Pl. 47, fig. 3).

All other specimens are from the *Columbites* fauna, Thaynes Formation at Montpelier Canyon and Hot Springs, southeastern Idaho.

or in the dimensions of the whorls. There is a tendency toward greater opening of the umbilicus with growth. Two of the largest specimens of this species are illustrated on Plate 47, figures 1, 2; both of these specimens show larger relative diameters of the umbilicus than more juvenile forms.

The suture is shown in Figure 32F, G, and consists of two denticulated lateral lobes and an auxiliary lobe on the umbilical shoulder and wall that is generally irregularly straight and denticulated. The smooth conch bears only fine growth lines.

Nordophiceras jacksoni is very similar to *Nordophiceras euomphalus* (Keyserling) from northern Siberia. The similarity is so close that I consider it possible these two species may be conspecific. The Siberian species is known from very few specimens, and no data are available on the variation within those populations. For the moment it seems best to keep the two species separate.

Nordophiceras jacksoni and *N. euomphalus* are the smooth species of this genus; in contrast to these two species there are two other described species—*N. alexeevae* and *N. pilatum*—which are very similar in general conch morphology but bear some ornamentation in the form of ribs.

Occurrence. Columbites fauna, Thaynes Formation, at Paris Canyon, Montpelier

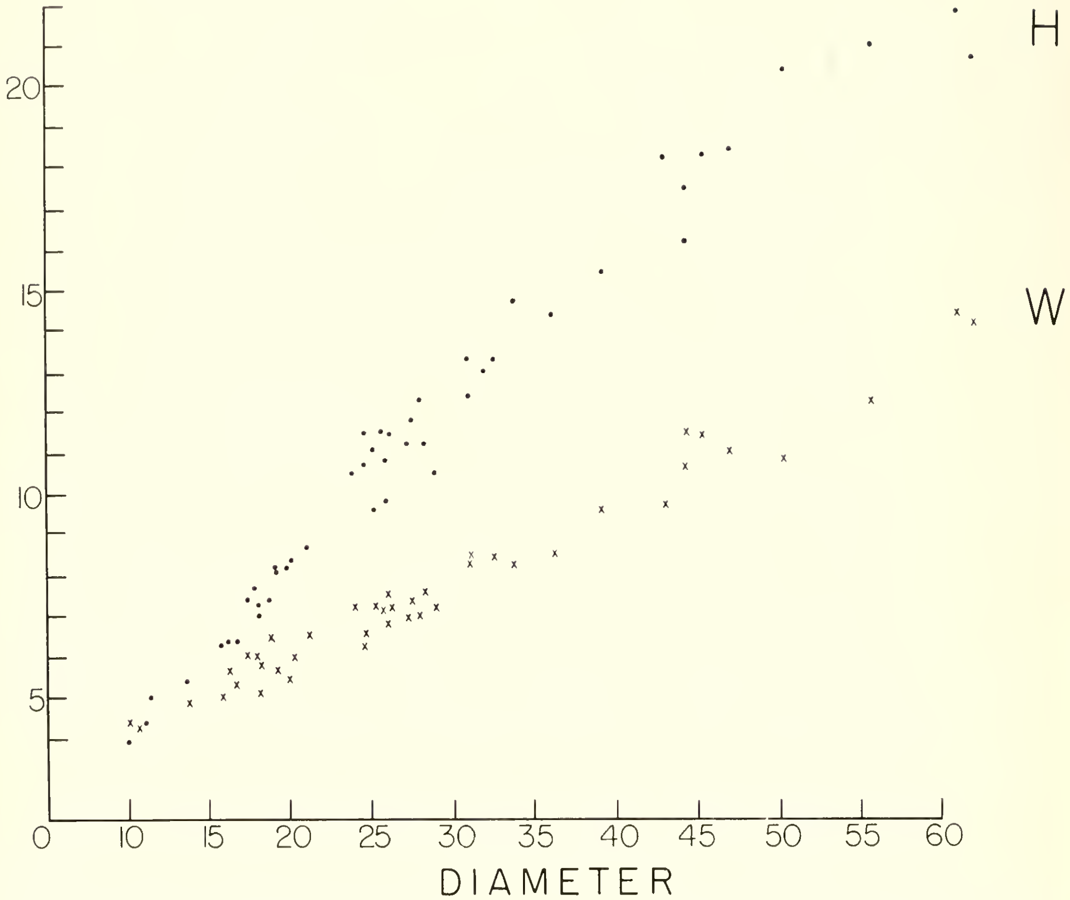

Figure 33. Variation in whorl height (H) and whorl width (W) of *Nordophiceras jacksoni* (Hyatt and Smith), from *Columbites* fauna, Bear Lake region, southeast Idaho. The data on this graph are from Table 41.

Canyon, and Hot Springs, southeastern Idaho.

Repository. Holotype, USNM 75292a (Pl. 48, figs. 3, 4); paratypes, USNM 75292b (Smith, 1932: pl. 62, fig. 14), USNM 75292c (Pl. 48, figs. 1, 2), USNM 75282d (Smith, 1932: pl. 62, figs. 17, 18), USNM 75292e (Smith, 1932: pl. 62, figs. 19–21); plesiotypes, MCZ 9564 (Pl. 47, fig. 1), MCZ 9565 (Pl. 47, fig. 2), MCZ 9566 (Pl. 47, fig. 3), MCZ 9567 (Pl. 47, fig. 4), MCZ 9568 (Pl. 47, fig. 5); suture specimen, MCZ 9572 (fig. 32F); unfigured specimens from Montpelier Canyon MCZ 9570, from Hot Springs MCZ 9571.

Nordophiceras pilatum (Hyatt and Smith)
Plate 46, figures 2, 3; Plate 49, figures 1–8; Plate 50, figures 1–11; Plate 51, figures 1–5; Text-figures 34, 35

Meekoceras pilatum Hyatt and Smith, 1905: 144, pl. 63, figs. 3–9; Diener, 1915: 193; Smith, 1932: 59, pl. 63, figs. 7–13.

Meekoceras curticostatum Smith, 1932: 56, pl. 48, figs. 21–30.

Meekoceras micromphalus Smith, 1932: 58, pl. 49, figs. 5–11.

Meekoceras sanctorum Smith, 1932: pl. 49, figs. 1–4.

This is one of the more abundant species in the *Columbites* fauna of southeastern Idaho. Basically this species has an involute, compressed conch, with a rounded venter, and bears prosiradiate ribs of varying strength. There are considerable variations in the degree of involution, inflation of the whorls, and ornamentation. The measurements of 42 specimens, including the primary types, are given on Table 42 and plotted on Figure 35.

All of Smith's (1932) collection from the *Columbites* fauna of southeastern Idaho came from one locality, namely Paris Canyon. In the description of the four species now included in *N. pilatum*, Smith (1932) made a direct comparison only between his *Meekoceras curticostatum* and *Meekoceras pilatum*; he states, "*Meekoceras curticostatum* has some resemblance to *M. pilatum*, with which it is associated, differing in the wider umbilicus, more compressed whorls, weaker and more numerous ribs." Smith considered his *Meekoceras micromphalus* to be closely related to *Meekoceras keyserlingi* Mojsisovics (now the type species of *Boreomeekoceras* Popov, 1961) from the Olenek region of Siberia. He considered his *Meekoceras sanctorum* to be closely related to *Meekoceras affine* Mojsisovics also from the Olenek region of Siberia. Even though Smith (1932) did not discuss the specific criteria upon which he separated his species of this group, it is clear that the intensity of ribbing, degree of whorl inflation, and degree of involution were important considerations. On examination of a fairly large suite of specimens it is readily apparent that the primary types of *Meekoceras sanctorum* (Pl. 49, figs. 1–3) and *Meekoceras micromphalus* (Pl. 50, figs. 7–11) are juvenile specimens. Both these specimens are characterized by rather small umbilici; examination of large mature specimens, such as the holotype of *Meekoceras curticostatum* (Pl. 50, figs. 1, 2) and the new plesiotypes (Pl. 51, figs. 1–5), clearly shows how the umbilicus increases in relative diameter with growth. This is well shown on the graph of Figure 34. The umbilical region also reflects another facet of variation and this is in the nature of the umbilical shoulder and wall. Generally, the umbilical shoulder is fairly acutely rounded with a sloping umbilical wall; at the same time, there are forms with slightly more rounded umbilical shoulders and lower, sloping umbilical walls. Among the large number of specimens before me one can recognize a continuous gradation from one type to the other.

The most conspicuous variation within this species is in the intensity of the ribbing. Typically the ribbing pattern consists of fine, prosiradiate ribs on the inner volutions that become more widely spread and more subdued with growth of the shell. In some forms the ribbing on the inner volutions is extremely faint and on the outer volutions there is nothing more than a vague bundling of the growth lines (see Pl. 49, fig. 1). On the other hand the ribbing on the inner volutions may be coarse and more widely spaced (as in the paralectotype of *N. pilatum*, Pl. 49, figs. 4–6) but on the mature volutions these become inconspicuous broad folds (as in the lectotype of *N. pilatum*, Pl. 49, figs. 7, 8). Finally, there are forms (as the specimen of Pl. 50, fig. 2) in which the ribs continue to increase in intensity throughout growth. The photographs here of the primary types and of a few additional plesiotypes illustrate the range of variation in ornamentation to be observed in the collection. Needless to say, there is complete gradation from one type to the other.

The venter is another area in which one can observe extensive variation. This may be from forms with acutely rounded venters to forms with more broadly rounded venters. Generally, the acutely rounded venters are found in the more juvenile specimens.

This species is very similar to *N. alexeevae* Popov from northern Sibera. Both these species are the ornamented nordophicerids associated in their respective faunas with smooth species, *euomphalus* in Siberia, and *jacksoni* in southeast Idaho.

The sutures are illustrated on Figure 34.

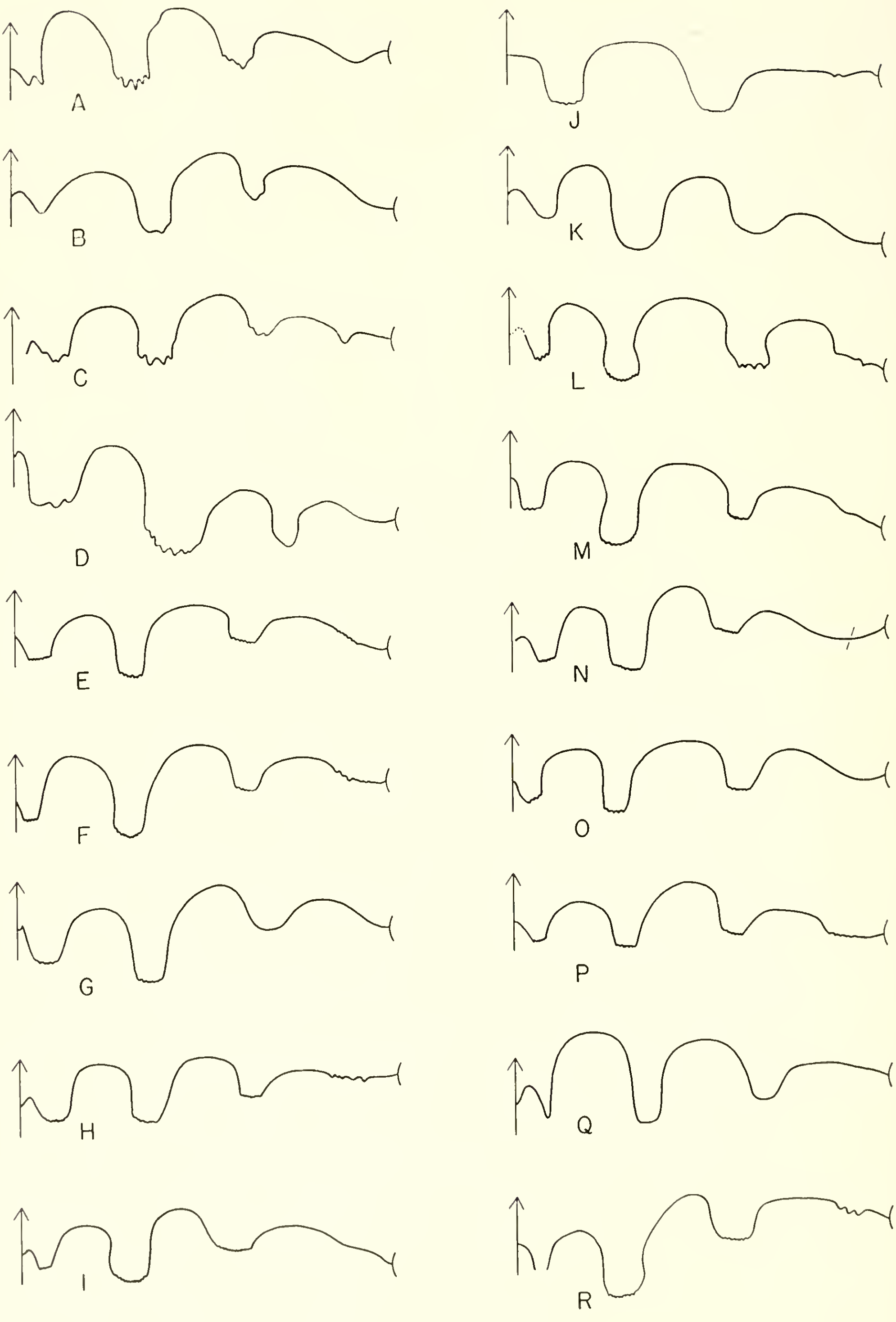
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TABLE 42. MEASUREMENTS OF *NORDOPHICERAS PILATUM* (HYATT AND SMITH) FROM THE *COLUMBITES* FAUNA AROUND BEAR LAKE, SOUTHEASTERN IDAHO.

	D	W	H	U	W/D	H/D	U/D		D	W	H	U	W/D	H/D	U/D
1.	87.0	17.8	37.2	21.4	20.5	42.8	24.6	22.	42.7	9.4	18.8	12.0	22.0	44.0	28.1
2.	78.0	15.6	33.4	18.0	20.0	42.8	23.1	23.	42.5	8.8	17.7	11.7	20.7	40.0	27.5
3.	73.7	16.0	30.5	20.6	21.7	41.4	27.9	24.	41.8	9.2	19.0	9.6	22.0	45.5	22.9
4.	72.5	13.7	29.0	21.0	18.9	40.0	28.9	25.	41.5	11.0	21.0	6.4	26.5	50.6	15.4
5.	70.2	16.0	30.2	20.0	22.8	43.0	28.5	26.	40.4	8.3	17.7	9.2	20.5	43.8	22.8
6.	68.5	13.8	28.8	19.0	20.1	42.0	27.7	27.	39.2	9.4	16.7	11.6	23.9	42.6	29.6
7.	60.0	15.8	29.0	12.3	26.3	48.3	20.5	28.	38.4	8.1	16.8	10.0	21.1	43.8	26.0
8.	57.8	12.0	22.6	16.7	20.8	39.1	28.9	29.	37.9	8.5	19.5	5.7	22.4	51.5	15.0
9.	57.4	13.2	24.8	14.2	22.9	43.2	24.7	30.	35.8	7.2	15.7	8.8	20.1	43.9	24.6
10.	57.3	11.7	26.9	11.2	20.4	46.9	19.5	31.	35.7	7.8	19.0	5.0	21.8	53.2	14.0
11.	55.0	?	22.3	16.2	?	40.5	29.5	32.	34.6	8.0	15.7	7.8	23.1	45.4	66.8
12.	54.4	9.5	23.0	15.0	17.5	42.3	27.6	33.	33.7	7.5	17.0	5.3	22.3	50.4	15.7
13.	54.4	10.8	23.7	13.0	19.9	43.6	23.9	34.	33.4	7.2	15.4	6.5	21.6	46.1	19.5
14.	53.4	10.2	21.4	16.8	19.1	40.1	31.5	35.	33.2	?	15.2	8.0	?	45.8	24.1
15.	53.1	10.8	23.5	13.7	20.3	44.2	25.8	36.	32.3	6.5	13.9	8.9	20.1	43.0	27.6
16.	52.0	11.0	22.7	13.2	21.2	22.5	25.4	37.	31.4	6.8	14.2	7.3	21.7	45.2	23.2
17.	48.7	9.2	19.8	9.0	18.9	40.7	18.5	38.	30.3	7.2	16.0	5.2	23.8	52.8	17.2
18.	48.7	10.6	21.2	13.0	21.8	43.5	26.7	39.	27.3	6.3	12.6	6.1	23.1	46.2	22.3
19.	48.6	10.2	21.4	13.7	20.9	44.0	28.2	40.	21.0	4.6	10.4	4.1	21.9	49.5	19.5
20.	46.7	9.6	21.0	10.0	20.6	44.9	21.4	41.	16.6	5.6	7.6	4.4	33.7	45.8	26.5
21.	43.3	12.1	20.7	9.4	27.9	47.8	21.7	42.	12.5	3.4	6.3	2.5	27.2	50.4	20.0

3. Holotype, *Meekoceras curticostatum* Smith (1932: pl. 48, figs. 21, 22), USNM 74990a.
5. Plesiotype, MCZ 9542 (Pl. 51, figs. 2, 3).
6. Plesiotype, MCZ 9541 (Pl. 51, fig. 5).
7. Syntype, *Meekoceras pilatum* Hyatt and Smith (1905: pl. 63, figs. 7, 8), USNM 75294a.
14. Plesiotype, MCZ 9539 (Pl. 51, fig. 1).
15. Plesiotype, MCZ 9540 (Pl. 51, fig. 4).
20. Paratype, *Meekoceras sanctorum* Smith (1932: pl. 49, figs. 3, 4), USNM 74991b.
21. Syntype, *Meekoceras pilatum* Hyatt and Smith (1932: pl. 63, figs. 10–13), USNM 75294b.
25. Holotype, *Meekoceras micromphalus* Smith (1932: pl. 49, figs. 5–8), USNM 74992a.
29. Holotype, *Meekoceras sanctorum* Smith (1932: pl. 49, figs. 1, 2), USNM 74991a.
31. Paratype, *Meekoceras curticostatum* Smith (1932: pl. 48, figs. 23, 24), USNM 74990b.
33. Plesiotype, MCZ 9544 (Pl. 46, fig. 3).
34. Plesiotype, MCZ 9543 (Pl. 46, fig. 2).
38. Paratype, *Meekoceras curticostatum* Smith (1932: pl. 48, figs. 25, 26), USNM 74990c.
40. Paratype, *Meekoceras curticostatum* Smith (1932: pl. 48, figs. 27, 28), USNM 74990d.
41. Paratype, *Meekoceras micromphalus* Smith (1932: pl. 48, figs. 9–11), USNM 74992b.
42. Paratype, *Meekoceras curticostatum* Smith (1932: pl. 48, figs. 29, 30), USNM 74990e.

All other specimens are from the *Columbites* fauna, Thaynes Formation at Hot Springs (MCZ 9546) and Montpelier Canyon (MCZ 9545), southeastern Idaho.

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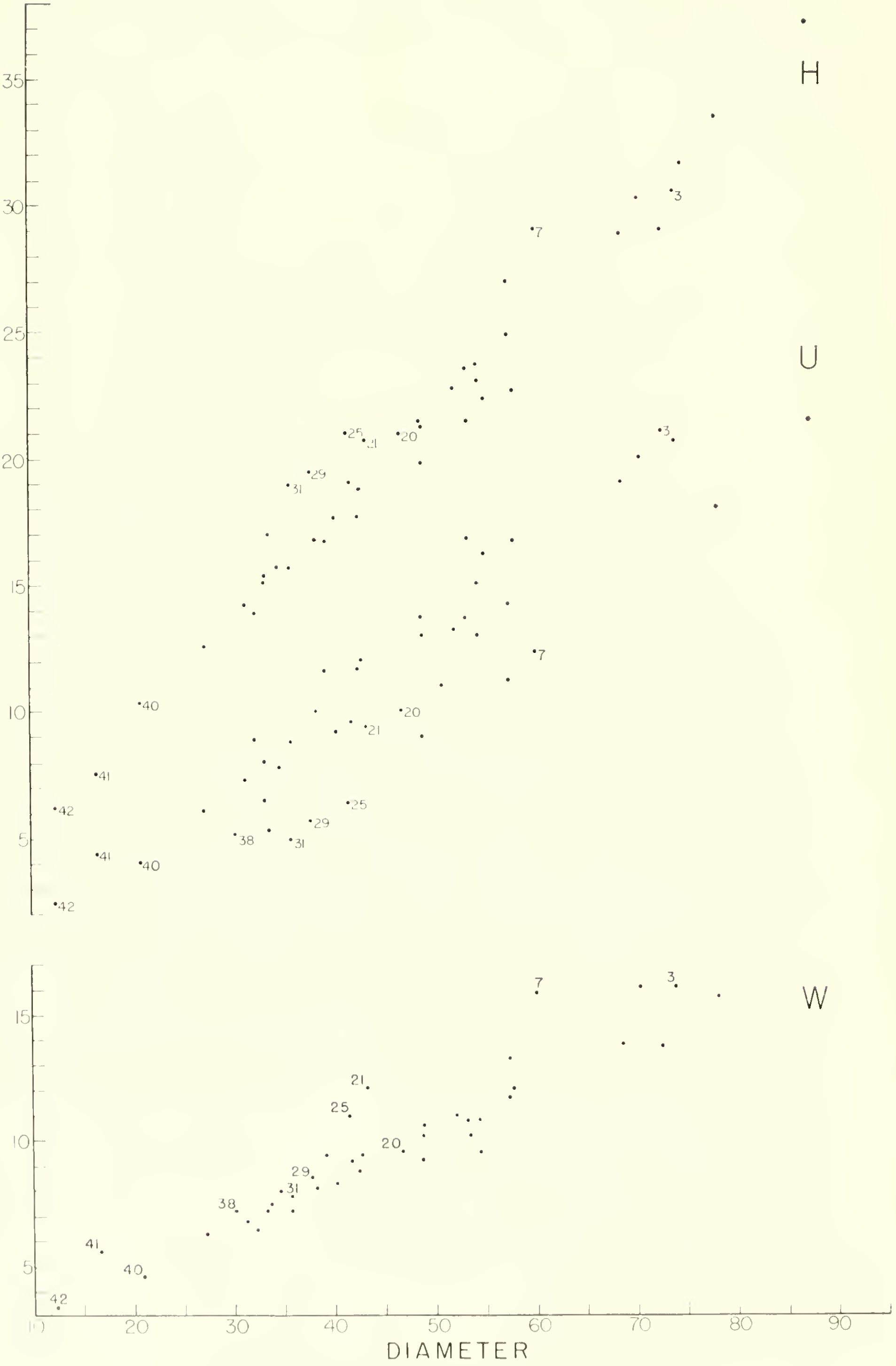
Figure 34. Diagrammatic representations of the sutures of *Nordophiceras pilatum* (Hyatt and Smith). A, from paratype of *Meekoceras micromphalus* Smith (1932: pl. 49, fig. 8), at a diameter of 17 mm (USNM 74992b); B, from paratype of *Meekoceras curticostatum* Smith (1932: pl. 48, fig. 24), at a diameter of 33 mm (USNM 74990b); C, from paratype of *Meekoceras sanctorum* Smith (1932: pl. 49, fig. 4), at a diameter of 29 mm (USNM 74991b); D, from lectotype of *Meekoceras pilatum* Hyatt and Smith (1905: pl. 63, fig. 9), at a diameter of 60 mm (USNM 75294a); E, at a diameter of 45 mm (MCZ 9573a); F, at a diameter of 31 mm (MCZ 9573b); G, at a diameter of 40 mm (MCZ 9573c); H, at a diameter of 42 mm (MCZ 9573d); I, at a diameter of 35 mm (MCZ 9573e); J, at a diameter of 45 mm (MCZ 9573f); K, at a diameter of 30 mm (MCZ 9573g); L, at a diameter of 52 mm (MCZ 9573h); M, at a diameter of 34 mm (MCZ 9573i); N, at a diameter of 40 mm (MCZ 9573j); O, at a diameter of 53 mm (MCZ 9573k); P, at a diameter of 41 mm (MCZ 9573l); Q, at a diameter of 26 mm (MCZ 9573m); R, at a diameter of 45 mm (MCZ 9573n).

All specimens from *Columbites* fauna, Thaynes Formation, southeastern Idaho; specimens A–D are from Paris Canyon, H and L from Hot Springs, the remaining specimens from Montpelier Canyon. All diameters given are approximate.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Occurrence. Columbites fauna, Thaynes Formation at Paris Canyon, Hot Springs, and Montpelier Canyon, southeastern Idaho.

Repository. Lectotype, *Meekoceras pilatum* Hyatt and Smith (1905: pl. 63, figs. 7–9) USNM 75294a; paralectotype (Hyatt and Smith, 1905: pl. 63, figs. 10–13) USNM 75294b; holotype, *M. curticostatum* Smith (1932: pl. 48, figs. 21, 22) USNM 74990a; paratypes (Smith, 1932: pl. 48, figs. 23, 24) USNM 74990b, (Smith, 1932: pl. 48, figs. 25, 26) USNM 74990c, (Smith, 1932: pl. 48, figs. 27, 28) USNM 74990d, (Smith, 1932: pl. 48, figs. 29, 30) USNM 74990e; holotype *M. sanctorum* Smith (1932: pl. 49, figs. 1, 2) USNM 74991a; paratype (Smith, 1932: pl. 49, figs. 3, 4) USNM 74991b; holotype *M. micromphalus* Smith (1932: pl. 49, figs. 5–8) USNM 74992a; paratype (Smith, 1932: pl. 49, figs. 9–11) USNM 74992b; plesiotypes MCZ 9539 (Pl. 51, fig. 1), MCZ 9542 (Pl. 51, figs. 2, 3), MCZ 9540 (Pl. 51, fig. 4), MCZ 9541 (Pl. 51, fig. 5), MCZ 9543 (Pl. 46, fig. 2), MCZ 9544 (Pl. 46, fig. 3); suture specimens MCZ 9573 a–n; unfigured specimens from Montpelier Canyon MCZ 9545; unfigured specimens from Hot Springs MCZ 9546.

Nordophiceras compressum (Chao)
Text-figure 32

Meekoceras (Submeekoceras) compressum Chao, 1959: 140, 320, pl. 44, figs. 1–6, text-fig. 46a, b.
Meekoceras (Submeekoceras) lolouense Chao, 1959: 141, p. 320, pl. 10, figs. 7, 8, text-fig. 45d.
Meekoceras (Submeekoceras) longiseptatum Chao, 1959: 141, pl. 10, figs. 5, 6, text-fig. 46c.

The three species brought together here are based on specimens that come from the same horizon and locality; two of the species were based on one specimen each, the other on five specimens. Chao (1959) made no mention of the specific criteria he used to differentiate these species. I can see no significant differences between any of these species. The sutures (Figs. 32H–J) are remarkably similar.

This is a smooth form of *Nordophiceras* of the general pattern of *euomphalus*, *pseudosimplex*, and *planorbis*. There are slight differences in conch form among these species but more than anything the suture is quite distinctive and the most useful in differentiating this species.

Occurrence. Limestone block containing a *Subcolumbites* fauna in Lolou village (Chao collection 542b) Kwangsi, China.

Genus *Pseudokymatites* Spath, 1934
Type species, *Kymatites svilajanus* Kittl, 1903

Pseudokymatites svilajanus (Kittl)
Plate 62, figure 5, Text-figure 40

Kymatites svilajanus Kittl, 1903: 69, pl. 4, fig. 3; Diener, 1915: 181.
Pseudokymatites svilajanus,—Spath, 1934: 265, fig. 91; Kummel, *in* Arkell et al., 1957: L143, fig. 175, 6.

Kittl's type and only specimen of this species is incomplete, crushed, and at best of only fair preservation. It measures 63.5 mm in diameter, 13.0? mm for the width of the adoral whorl, 29.4 mm for the height, and the umbilicus is 12.3 mm in diameter. Spath (1934: 265) created a new genus for this species in his belief that it was probably a "smooth meekoceratid" with smooth lateral lobes. The goniatitic nature of the lobes, however, is not at all certain. The specimen is weathered and the smooth nature of the lobes could well be the result of this. It is not possible to settle this question on the basis of the single specimen available. Speculations of the genetic relations of this form are pointless until the

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Figure 35. Variation in whorl height (H), whorl width (W), and umbilical diameter (U) of *Nordophiceras pilatum* (Hyatt and Smith), from *Columbites* fauna, Bear Lake region, southeast Idaho. The data on this graph are from Table 42.

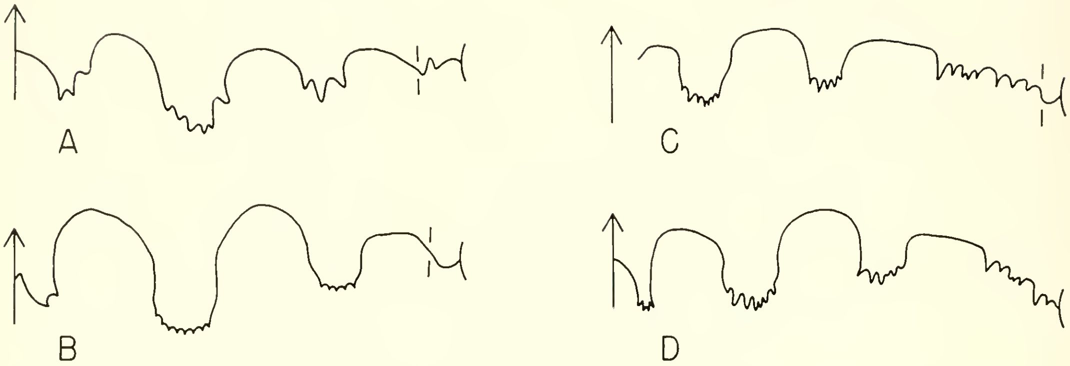

Figure 36. Diagrammatic representation of the suture of: A, *Arctomeekoceras rotundatum*,—Popov (1962a: fig. 9), from *Olenekites* Zone, northern Siberia, at a whorl height of 20 mm; B, *Arctomeekoceras* sp. indet. Kummel (1966: fig. 22E), from Narmia Member of Mianwali Formation, Surghar Range, West Pakistan, at a whorl height of 9 mm; C, D, two sutures of topotype specimen of *Boreomeekoceras keyserlingi* (Mojsisovics) from *Olenekites* Zone, northern Siberia, C, at a whorl height of 26.5 mm, D, at a whorl height of 15 mm (MCZ 8684).

basic morphological elements are better understood.

Occurrence. Werfen Formation, Muć, Dalmatia.

Repository. Natural History Museum, Vienna.

Genus *Arctomeekoceras* Popov, 1961
Type species, *Meekoceras rotundatum* Mojsisovics, 1886

Compressed, involute conchs, with narrowly rounded venters on earlier volutions tending to become more broadly rounded with age. Suture ceratitic with two lateral lobes and auxiliary series. The type and only species of the genus is known from the *Olenekites* fauna of Siberia. Indeterminate species have also been recorded from the upper part of the Lower Triassic succession in the Salt Range of West Pakistan (Kummel, 1966).

Arctomeekoceras rotundatum (Mojsisovics)
Text-figure 36

Meekoceras rotundatum Mojsisovics, 1886: 83, pl. 10, fig. 16; Diener, 1915: 194.
Boreomeekoceras rotundatum,—Popov, 1961: 42.
Arctomeekoceras rotundatum,—Popov, 1962a: 187, pl. 1, figs. 1, 5, pl. 3, fig. 4

This is as yet an incompletely known species; Mojsisovics apparently had only one specimen and Popov four specimens but the illustrations and descriptions are incomplete. The key feature of the genus and species is the broadening of the venter on the adoral whorls. The suture (Fig. 36A) has two serrated lateral lobes and a small auxiliary on the umbilical wall.

Occurrence. Olenekites Zone, Lena River delta and Olenek River, Siberia.

Arctomeekoceras sp. indet. (West Pakistan)
Text-figure 36

Arctomeekoceras sp. indet. Kummel, 1966: 398, pl. 2, figs. 1–5.

Generally incomplete and poorly preserved specimens that appear to be much like the type species of this genus, but more material is needed from both faunas before a significant comparison can be made. The suture is shown on Figure 36B.

Occurrence. Narmia Member of Mianwali Formation in Salt Range and Surghar Range of West Pakistan.

Repository. MCZ 9584–9586, 9589, 9590–9592.

Genus *Boreomeekoceras* Popov, 1961
Type species, *Meekoceras keyserlingi* Mojsisovics, 1886

Involute, compressed conch, venter narrowly rounded, flanks convergent. Suture ceratitic with two lateral lobes and extended auxiliary series. The type and only species of this genus is from the *Olenekites* fauna of the Olenek region, northern Siberia.

Boreomeekoceras keyserlingi (Mojsisovics)
Text-figure 36

Meekoceras keyserlingi Mojsisovics, 1886: 81, pl. 10, figs. 13–15; Diener, 1915: 192; Spath, 1934: 158, 254.
Boreomeekoceras keyserlingi,—Popov, 1961: 42, pl. 10, fig. 4.

This is a unique species in the known late Scythian faunas because of its tightly involute lenticular conch; the illustrations by Mojsisovics (1886: pl. 10, figs. 13–15) and Popov (1961: pl. 10, fig. 4) are quite satisfactory. The suture, however, in neither of these publications is well represented. A topotype specimen is available and two sutures from this specimen are shown on Figures 36 C, D.

Occurrence. Olenekites Zone near mouth of Olenek River, northern Siberia.

Repository. The MCZ has one topotype specimen, 8684.

Genus *Arctotirolites* Popov, 1963
Type species, *Pseudotirolites menensis* Popov, 1962

Arctotirolites menensis (Popov)

Pseudotirolites menensis Popov, 1962a: 178, pl. 2, fig. 4.
Arctotirolites menensis (Popov) 1963: 137.

This new genus and species was established on the basis of a single specimen. The illustration and description of the species leave much to be desired. The conch is moderately involute, compressed, and with an arched venter. The lateral areas bear sigmoidal folds which apparently end at the ventral shoulders in small nodes. The suture has two serrated lateral lobes and a serrated auxiliary lobe on the umbilical shoulder and wall.

On the basis of the nodes one is at first tempted to think of this form as a tirolitid of some sort. However, the greater involution of the conch and the suture does not support such a conclusion. On the basis of the very incomplete data, it seems more probable that this form is related to *Nordophiceras.* The suture of *menensis* is very much like that of a typical nordophicerid. In addition, some species of *Nordophiceras* are ornamented with ribs.

Occurrence. Olenekites Zone, Olenek River basin, Mene River, northern Siberia.

Family NORITIDAE Karpinsky, 1889

Genus *Albanites* Arthaber, 1909
Type species, *Pronorites triadicus* Arthaber, 1908

Albanites triadicus (Arthaber)
Plate 16, figures 3–6; Plate 17, figures 1–10; Plate 18, figures 7, 8; Plate 20, figures 7–9; Text-figure 37

Pronorites triadicus Arthaber, 1908: 264, pl. 11, figs. 4a-c; Arthaber, 1911: 204, pl. 17(1), figs. 8, 9; Diener, 1915: 231; C. Renz, 1928: 155; Kutassy, 1933: 624; Renz and Renz, 1947: 61; Renz and Renz, 1948: 84, pl. 14, figs. 14–14b.
Albanites triadicus,—Spath, 1934: 275, fig. 95; Kummel, 1968b: 498, pl. 2, figs. 1–9.
Pronorites osmanicus Arthaber, 1911: 205, pl. 17 (1), fig. 10; Diener, 1915: 231; C. Renz, 1928: 155.
Albanites osmanicus,—Spath, 1934: 276.
Pronorites cf. *osmanicus,*—Renz and Renz, 1947: 62; Renz and Renz, 1948: 86, pl. 15, figs. 6-6c.
Pronorites arbanus Arthaber, 1911: 205, pl. 17(1), figs. 11, 12; Diener, 1915: 230; Welter, 1922: 94, pl. 155, figs. 10–14; C. Renz, 1928: 155; Kutassy, 1933: 624; C. Renz 1945: 301; Renz and Renz, 1947: 61; Renz and Renz, 1948: 85, pl. 14, figs. 13–13b, 15–15b, pl. 15, figs. 5–5c.
Albanites arbanus,—Spath, 1934: 277.
Pronorites arbanus var. *mediterranea* Renz and Renz, 1947: 62; Renz and Renz, 1948: 85, pl. 14, figs. 12–12b.
Pronorites spec. ind. ex aff. *arbani,*—Welter, 1922: 95, pl. 155(1), fig. 9.
Anasibirites gracilis Kiparisova, 1947: 164, pl. 39, figs. 3, 4, text-figs. 60, 61.
Pronorites arbanus var. *sundaica* Renz and Renz, 1948: 85.
Albanites welteri Spath, 1934: 278.
Pronorites orientalis Renz and Renz, 1947: 62; Renz and Renz, 1948: 86, pl. 15, figs. 2–2b.

Pronorites schaubi Renz and Renz, 1947: 62, 78; Renz and Renz, 1948: 87, pl. 15, figs. 4–4a.
Pronorites schaubi var. *timorensis* Renz and Renz, 1948: 87.
Pronorites schaubi var. *kephalovunensis* Renz and Renz, 1947: 62, 78; Renz and Renz, 1948: 87, pl. 15, figs. 3–3a.
Pronorites reicheli Renz and Renz, 1947: 62, 79; Renz and Renz, 1948: 88, pl. 15, figs. 1–1c.
Albanites danispanensis (Astakhova) 1960a: 143, pl. 34, figs. 4, 5; Astakhova, 1960b: 150.
Aspidites hasserti Arthaber, 1911: 249, pl. 21(5), fig. 16; Spath, 1934: 275.
Meekoceras (Koninckites) hasserti,—Diener, 1915: 198.
Dagnoceras komanum Arthaber, 1911: 242, pl. 21(5), fig. 11; Diener, 1915: 115; Smith, 1932: 65; Spath, 1934: 269, 275.
Pseudosibirites cfr. *dichotomus* Waagen,—Arthaber, 1911: 254, pl. 22(6), fig. 8.
Anasibirites cfr. *dichotomus*,—Arthaber, 1911: 273.
Sibirites cf. *dichotomus*,—Diener, 1915: 255.

TABLE 43. MEASUREMENTS OF *ALBANITES TRIADICUS* FROM THE *SUBCOLUMBITES* FAUNAS OF ALBANIA AND TIMOR, AND FROM BLOCK "E," NIFOEKOKO, TIMOR.

	D	W	H	U	W/D	H/D	U/D
1.	55.8	26.1	22.4	15.8	46.8	40.1	28.3
2.	53.3	18.7	23.4	12.8	35.1	43.9	24.0
3.	49.2	14.2	22.3	10.1	28.9	45.3	20.5
4.	49.0	15.5	22.7	11.8	31.6	46.3	24.1
5.	40.0?	16.5	16.2?	10.1	41.3?	40.5?	25.3?
6.	38.4	13.5	16.1	11.7	35.2	41.9	30.5
7.	34.8	14.1	16.4	7.2	40.5	47.1	20.7
8.	34.7	12.8	14.4	11.4	37.1	41.5	32.9
9.	31.0	10.1	11.7	10.7	32.6	37.7	34.5
10.	28.7	8.7	11.8	9.1	30.3	41.1	31.7
11.	28.4	10.8	12.4	7.3	38.0	43.7	25.7
12.	28.2	8.4	14.4	4.4	29.8	51.1	15.6
13.	27.7	8.7	11.2	8.4	31.4	40.4	30.3
14.	25.8	9.0	12.0	6.1	34.9	46.5	23.6
15.	25.7	10.8	12.4	6.4	42.0	48.2	24.9
16.	25.0	10.5	11.1	6.4	42.0	44.4	25.6
17.	24.6	7.7	12.4	4.0	31.3	50.4	16.3
18.	?	?	?	12.8	?	?	?

1. Holotype, *Pronorites reicheli* Renz and Renz (1948: pl. 15, fig. 1), NHMB J13809.
2. Plesiotype, *Pronorites* sp. ind. ex aff. *arbani*,—Welter (1922: pl. 155(1), fig. 9), GPIBo W206.
3. Holotype, *Pronorites schaubi* Renz and Renz (1948: pl. 15, fig. 4), NHMB J13805.
4. Type specimen, *Pronorites schaubi* var. *kephalovunensis* Renz and Renz (1948: pl. 15, fig. 3), NHMB J13808.
5. Type specimen, *Pronorites osmanicus* Arthaber (1911: pl. 17(1), fig. 10), PIUV.
6. Plesiotype, *Pronorites arbanus*,—Renz and Renz (1948: pl. 14, fig. 15), NHMB J13795.
7. Syntype, *Albanites welteri* Spath (= *Pronorites arbanus*,—Welter, 1922: pl. 155, figs. 10–12), GPIBo W205b.
8. Type specimen, *Pronorites arbanus* var. *mediterranea* Renz and Renz (1948: pl. 14, fig. 12), NHMB J13800.
9. Plesiotype, *Pronorites arbanus*,—Renz and Renz (1948: pl. 14, fig. 13), NHMB J13796.
10. Holotype, *Pronorites orientalis* Renz and Renz (1948: pl. 15, fig. 2), NHMB J13801.
11. Plesiotype, *Pronorites triadicus*,—Renz and Renz (1948: pl. 14, fig. 14), NHMB J13793.
12. Syntype, *Albanites welteri* Spath (= *Pronorites arbanus*,—Welter, 1922: pl. 155, figs. 13, 14), GPIBo W205a.
13. Plesiotype, *Pronorites arbanus*,—Renz and Renz (1948: pl. 15, fig. 5), NHMB J13797.
14. Holotype, *Pronorites triadicus* Arthaber (1908: pl. 11, fig. 4), PIUV.
15. Plesiotype, *Pronorites* cf. *osmanicus*,—Renz and Renz (1948: pl. 15, fig. 6c), NHMB J13804.
16. Plesiotype, *Pronorites* cf. *osmanicus*,—Renz and Renz (1948: pl. 15, figs. 6–6b), NHMB J13803.
17. Lectotype, *Pronorites arbanus* Arthaber (1911: pl. 17 (1), figs. 11 a–d), PIUV.
18. Paralectotype, *Pronorites arbanus* Arthaber (1911: pl. 17(1), figs. 12 a, b), PIUV.

Specimens of numbers 5, 14, 17, 18 are from the *Subcolumbites* fauna of Albania; those of 2, 7, 12 are from the *Albanites* fauna of Timor; and the remaining specimens are from the *Subcolumbites* fauna of Chios.

The genus *Albanites* is a conspicuous member of the *Subcolumbites* fauna from Albania and Chios, from the Mangyshlak Peninsula, and from the *Prohungarites* fauna of Timor, but in none of these localities is the form particularly abundant. The genus is much better represented in Chios than in Albania, but the preservation of most of the specimens in these faunas often leaves much to be desired. It is factors of preservation and preparation of the Albanian specimens that have led to some of the misunderstanding about the genus. Examination of all the specimens in the Albania, Chios, and Timor collections leads me to conclude that they all represent a single species; there have been seven species and four variety names introduced for this group.

The holotype is a small specimen of only fair preservation; the lateral area and venter of the adoral quarter volution has been ground and polished to expose the suture. The smoothness of the venter commented on by Arthaber (1911: 205) and Spath (1934: 277) is the result of this grinding and polishing. The dimensions of the holotype are given on Table 43, and the suture is shown on Figure 37. At the time he introduced the species *triadicus* in 1908, Arthaber had only one specimen. In 1911 he had one additional specimen to which, however, no specific reference was made. This specimen is illustrated here on Plate 17, figures 3, 4, and the dimensions are given on Table 43. As can be seen, it is a small juvenile form with a fairly inflated whorl section. The venter is broadly arched with rounded ventral shoulders; there are numerous weak ridges across the venter which disappear just above the ventral shoulders. This specimen differs from the holotype mainly in its slightly more inflated conch.

In 1911, Arthaber introduced two additional species for this group from the Albanian *Subcolumbites* fauna. For *Pronorites osmanicus* Arthaber (1911: 205, pl. 17(1), fig. 10; Pl. 17, figs. 5, 6 of this report) the author states he had six specimens. The illustrated specimen is the only one preserved in the collections of the Paleontological Institute, University of Vienna. There are two topotypes in the British Museum (Natural History). Arthaber's illustrated specimen is selected as the lectotype; this illustration is one of the least successful in Arthaber's monograph as it is highly modified. The specimen is all phragmocone, distorted, and generally of poor preservation. Much of the lateral area of the conch has been ground and polished to expose the suture. The adoral quarter volution bears prominent cross ridges, but the remainder of the venter is too poorly preserved to show this feature. The radial ribs on the flanks of the penultimate volution are not present on the specimen. The dimensions of the specimen are given on Table 43. This species was said to differ from *A. triadicus* in the presence of cross ridges on the venter and in slight differences in the suture (Fig. 37c). The smooth venter of the holotype of *A. triadicus* is due to grinding and polishing. The ridges are clearly present on the small second specimen assigned by Arthaber to *A. triadicus* (Pl. 17, figs. 3, 4).

Pronorites arbanus (Arthaber, 1911: 205, pl. 17(1), figs. 11, 12) was based on three specimens of which two were illustrated and are still preserved. This species was said to differ from *A. osmanicus* in its more compressed conch, greater involution, and slightly different proportions of the suture. The measurements of these two specimens are given on Table 43; the smaller of the two specimens (Pl. 17, figs. 9, 10) was selected by Spath (1934: 278) as lectotype. The paralectotype (Pl. 17, figs. 1, 2) has weak falcoid folds on the adoral half volution. This species is clearly only a compressed variant and is conspecific with the remaining forms of *Albanites* from Albania.

The collections from the *Subcolumbites* fauna of Chios studied by Renz and Renz (1948) contain approximately 50 specimens of *Albanites* which they placed in six species and two varieties. One species *(arbanus)* is represented by perhaps 20 specimens, two species *(triadicus* and *schaubi)* were recognized on eight specimens each, one species *(orientalis)* on four specimens, one species (cf. *osmanicus*) on two specimens, and one species and two varieties on the basis of a single specimen each. The measurements of the prepared and more complete specimens of *Albanites* in the Renz and Renz collections from Chios are given on Table 43. The basic difference between all these species lies in the degree of compression of the conch, in degree of ornamentation, and in degree of involution of the conch. Examination of the Chios collection indicates to me that these characters are highly gradational and the numerous species names are merely labels applied to possessors of a particular morphological character within a completely gradational complex. Much of the discussion of these species by Renz and Renz (1948) is confusing and out of date due to their oversight of some of the earlier literature.

There has been some question and doubt as to whether the two specimens from Timor, described by Welter (1922) as *Pronorites arbanus*, are the inner whorls of the same species that Welter described as *Pronorites* spec. ind. ex aff. *arbani*. Exami-

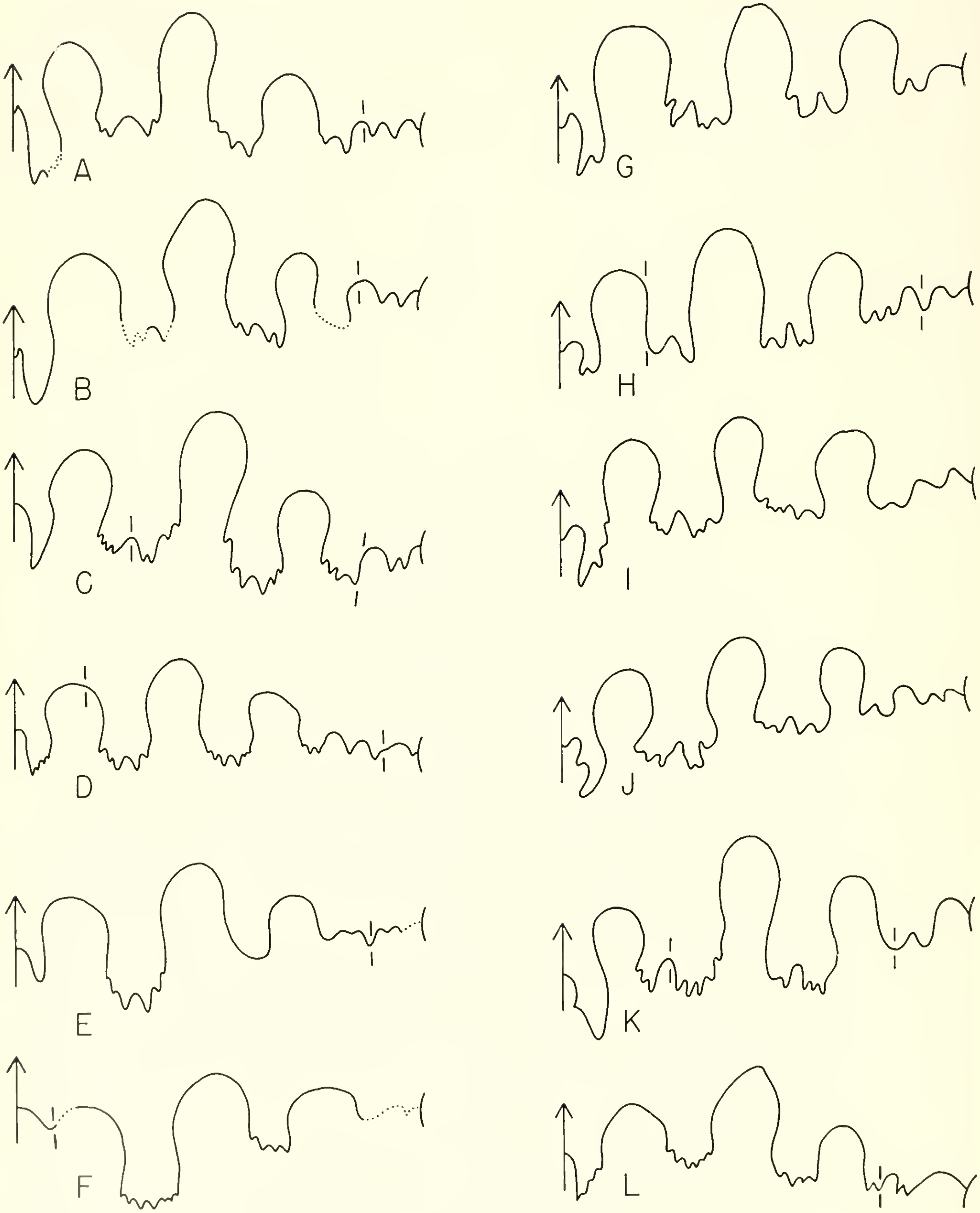

Figure 37. Diagrammatic representation of the sutures of *Albanites triadicus* (Arthaber). A, holotype (Arthaber, 1911: pl. 17(1), fig. 8), redrawn suture at diameter of 30 mm; B, paratype (Arthaber's second and smaller specimen of *triadicus*), at a diameter of 18 mm; C, figured type of *A. osmanicus* (Arthaber, 1911: pl. 17(1), fig. 10), redrawn suture at a diameter of 38 mm; D, lectotype of *A. arbanus* (Arthaber, 1911: pl. 17(1), fig. 11), redrawn suture at a diameter of 23 mm; E, holotype of *Dagnoceras komanum* Arthaber (1911: pl. 21(5), fig. 11), redrawn suture at a diameter of 18 mm; this specimen has been ground and polished so that the fine details of the sutural elements have been destroyed; F, type

nation of Welter's original specimens leaves no doubt on this question. Spath (1934: 278) came to the same conclusion on examination of a fine series of specimens in the British Museum (Natural History). Spath (1934) recognized the "external resemblance" to the Albanian *A. arbanus*, but felt because there were differences in the suture that a new name was needed, and he introduced the name *A. welteri*. The differences in the suture, however, are no more than what one can observe within the Albanian and Chios faunas.

Albanites danispanensis (Astakhova, 1960a) was stated to resemble *A. osmanicus* Arthaber and *A. arbanus* Arthaber, differing, however, in size of the umbilicus, ornamentation, and details of the suture. On the basis of the illustrations and descriptions of this species, none of these differences appear to be significant against the range of variation known to exist in the Albanian and Chios forms. This species from the Mangyshlak Peninsula can be considered as a representative of *A. triadicus*.

Finally, there is a group of species from the *Subcolumbites* fauna, based on very poorly preserved specimens; an inspection of the types suggests inclusion in this species. First, there is the specimen for which Arthaber (1911: 242, pl. 21(5), fig. 11; Pl. 18, figs. 7, 8 of this report) proposed the name *Dagnoceras komanum*. This specimen measures 27 mm in diameter, 7.2 mm for the width of the adoral whorl, 12.7 mm for the height, and 6.3 mm for the diameter of the umbilicus. The whorls are compressed, converging slightly toward a flattened venter. Both the ventral and umbilical shoulders are sharply rounded. On the adoral one-third volution the ventral shoulders bear diagonal ribs; the venter is not well enough preserved to tell just how these ribs cross the venter. In the better preserved specimen of *A. triadicus*, cross ridges on the venter are connected with weak radial ribs on the flanks. I am inclined to believe that the diagonal, projecting ribs on the ventral shoulder of the holotype of *Dagnoceras komanum* are at least partially due to the poor state of preservation of the specimen and possibly to slight crushing. Thus the difference in the rib pattern from that of the type specimen of *A. triadicus* is more apparent than real.

The specimen Arthaber (1911: pl. 22(4), figs. 8a-c; Pl. 20, figs. 7–9 of this report) assigned to *Pseudosibirites* cfr. *dichotomus* Waagen I believe to be essentially identical to the specimen he assigned to *Dagnoceras komanum*. This conclusion is made taking into account the poor and slightly different preservations of these two specimens. The lateral ribs are more conspicuous, as is the chevron aspect of the ribs across the venter. The specimen is, however, slightly crushed laterally.

The sutures of these species are shown on Figure 37E, F. First of all, it can be seen that they are essentially identical; any differences can readily be explained by excessive grinding of the specimen. Secondly, it can be seen that these two sutures are essentially identical to the sutures of the specimens of *Albanites* so far known from the Albanian *Subcolumbites* fauna.

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specimen of *Pseudosibirites* cfr. *dichotomus*,—Arthaber (1911: pl. 22(6), fig. 8), redrawn suture at a diameter of 18 mm; G, plesiotype of *A. arbanus*,—Renz and Renz (1948: pl. 14, fig. 13b), at a diameter of 20 mm (NHMB J13796); H, plesiotype of *A. arbanus*,—Renz and Renz (1948: pl. 14, fig. 15b), at a diameter of 25 mm (NHMB J13795); I, plesiotype of *A. arbanus* var. *mediterranea* (Renz and Renz, 1948: pl. 14, fig. 12b), at a diameter of 24 mm (NHMB J13800); J, plesiotype (Renz and Renz, 1948: pl. 14, fig. 14b), at a diameter of 17 mm (NHMB J13793); K, holotype of *Pronorites reicheli* Renz and Renz (1948: pl. 15, fig. 1c), at a diameter of approximately 40 mm (NHMB J13809); L, paratype of *Albanites danispanensis* (Astakhova, 1960a: fig. 10), at a diameter of 30 mm.

Specimens of figures A–F from *Subcolumbites* fauna of Albania, those of G–K from *Subcolumbites* fauna of Chios; specimen of figure L from the Mangyshlak Peninsula.

Considering all the factors available for these two "species," I believe it best to consider them as conspecific with *Albanites triadicus* of the same fauna. The differences in the rib pattern on the venter are difficult to evaluate on the basis of the sample available. No purpose is served in assigning these two forms to different genera.

Further, I suggest that the two specimens Arthaber (1911: 249, pl. 21(5), fig. 16) assigned to *Aspidites hasserti* Arthaber are poorly-preserved representations of *A. triadicus*. Arthaber's figured type (Pl. 16, figs. 3, 4) measures 44.6 mm in diameter, 14.3 mm for the width of the adoral whorl, 20.8 mm for the height, and 10.5 mm for the diameter of the umbilicus. In addition to being poorly preserved, the specimen has been ground and polished in places. The basic plan of the suture is that of *A. triadicus*. The smaller unfigured specimen referred to by Arthaber (1911: 249) is illustrated here on Plate 16, figures 5, 6. This specimen measures 22.4 mm in diameter, 6.6 mm for the width of the adoral whorl, 11.7 mm for the height and 2.5 mm for the diameter of the umbilicus. In both these specimens the basic conch form and suture show them to be close to *A. triadicus*; what differences are apparent can be readily explained as due to the state of preservation or due to grinding and polishing.

Occurrence. The species is known from the *Subcolumbites* fauna of Albania, Chios, and Afghanistan, from the *Prohungarites* fauna of Timor, and from the *Columbites* Zone of Astakhova (1960a, b) on the Mangyshlak Peninsula.

Repository. The Paleontological Institute, University of Vienna contains the holotype, and the second specimen referred to as *Pronorites triadicus* by Arthaber (1911: 204; figured here Pl. 17, figs. 3, 4), the lectotype of *Pronorites osmanicus* Arthaber, the lectotype and paralectotype of *Pronorites arbanus* Arthaber. This institution also contains the holotype of *Dagnoceras komanum* Arthaber, the figured specimen of *Pseudosibirites* cfr. *dichotomus* Waagen, and the lectotype and paralectotype of *Aspidites hasserti* Arthaber. The Natural History Museum, Basel, contains the following specimens: plesiotype *Pronorites triadicus*,—Renz and Renz (1948: pl. 14, fig. 14) NHMB J13793; unfigured specimens NHMB J13794; plesiotypes *Pronorites arbanus*,—Renz and Renz (1948: pl. 14, fig. 15) NHMB J13795, (pl. 14, fig. 13) NHMB J13796, (pl. 15, fig. 5) NHMB J13797; unfigured specimens from Maradovuno NHMB J13798, from Kephalovuno NHMB J13799; figured specimens *Pronorites arbanus* var. *mediterranea* Renz and Renz (1948: pl. 14, fig. 12) NHMB J13800; holotype *Pronorites orientalis* Renz and Renz (1948: pl. 15, fig. 2) NHMB J13801; unfigured paratypes NHMB J13802; figured specimens of *Pronorites* cf. *osmanicus* Renz and Renz (1948: pl. 15, fig. 6–6b) NHMB J13803, (pl. 15, fig. 6c) NHMB J13804; holotype *Pronorites schaubi* Renz and Renz (1948: pl. 15, fig. 4–4a) NHMB J13805; unfigured paratypes from Maradovuno NHMB J13806, from Kephalovuno NHMB J13807; figured specimen of *Pronorites schaubi* var. *kephalovunensis* Renz and Renz (1948: pl. 15, fig. 3–3a) NHMB J13808; holotype *Pronorites reicheli* Renz and Renz (1948: pl. 15, fig. 1–1c) NHMB J13809. The three specimens studied by Welter (1922) are in the Paleontological Institute, Bonn University; additional topotype specimens are in the British Museum (Natural History); specimens from Afghanistan MCZ 10136, 10145, 10152, 10153, 10156, 10168.

Family PRIONITIDAE Hyatt, 1900

Genus *Hemiprionites* Spath, 1929

Type species, *Goniodiscus typus* Waagen, 1895

Hemiprionites costatus Popov

This species is based on a single specimen which unfortunately is incompletely described and illustrated. On the basis of the data available, I can only concur in

Popov's generic assignment of this species. The genus *Hemiprionites* had previously been known only from the *Anasibirites* Subzone of the *Owenites* Zone. In this mid-Scythian horizon it is a very common and quite distinctive form. Popov (1961) states this species is associated with *Inyoites eiekitensis* Popov (here assigned to *Subvishnuites*) and *Dieneroceras nikabitensis* Popov (here considered to be a synonym of *D. demokidovi* Popov). Both these associated species are generalized forms, and it is possible all of these species belong to the *Owenites* Zone and are not equivalent to the *Columbites* Zone as are most of the faunas assigned by Popov (1961) to his *Dieneroceras* Zone.

Occurrence. Olenek River basin, northern Siberia.

Family SIBIRITIDAE Mojsisovics, 1896

Genus *Sibirites* Mojsisovics, 1886

Type species, *Ceratites eichwaldi* Keyserling, 1845

Sibirites eichwaldi (Keyserling)

Ceratites eichwaldi Keyserling, 1845: pl. 3, fig. 14; Eichwald, 1868: 1040; Mojsisovics, 1882: 41.

Sibirites eichwaldi,—Mojsisovics, 1886: 59, pl. 10, figs. 1–9; Frech, 1905: pl. 28, fig. 10; Diener, 1915: 255; Spath, 1934: 342, 344, figs. 116d, e; Kiparisova, 1947: 164; Popov, 1961: 31, pl. 14, fig. 2; Vozin and Tikhomirova, 1964: 63, pl. 38, figs. 1, 2.

Sibirites cf. *eichwaldi*,—Popov, 1961: 31, pl. 14, fig. 6.

Sibirites pretiosus Mojsisovics, 1886: 61, pl. 10, fig. 10; Diener, 1915: 256; Spath, 1934: 343, figs. 116a–c; Popov, 1961: 32, pl. 13, fig. 1a; Vozin and Tikhomirova, 1964: 64, pl. 38, fig. 3.

Sibirites ind. aff. *pretioso* Mojsisovics, 1886: 61, pl. 10, figs. 11, 12; Diener, 1915: 256.

Sibirites grambergi Popov, 1961: 31, pl. 14, fig. 1.

Parasibirites grambergi (Popov), 1962a: 181, pl. 1, fig. 3.

Sibirites grambergi var. *variaculeatus* Popov, 1961: 31, pl. 14, fig. 5.

Parasibirites variaculeatus Popov, 1962a: 182, pl. 1, fig. 2.

Sibirites grambergi var. *mixta* Popov, 1961: 31, pl. 14, fig. 7.

Parasibirites mixtus Popov, 1962a: 183, pl. 1, fig. 4.

Sibirites subpretiosus Popov, 1961: 33, pl. 14, fig. 8.

Parasibirites subpretiosus (Popov), 1962a: 181.

The large number of species brought together here reflect the usual typological treatment of trachyostracan ammonites. The "species" differ in degree of ornamentation, that is, in the relative prominence of ribs, nodes, etc. These species have now been recorded from a number of localities in northern Siberia, especially at and around the Olenek region. Neither Mojsisovics (1886) nor Popov (1961, 1962a) had particularly large collections to study nor did they present much data on the variability within their samples. I shall make the prediction that when large collections of *Sibirites* from the Olenek region become available they will show a complete gradational series from lesser to stronger ornamented forms, and that the ontogenetic development will be found to be also highly variable. I look upon *Sibirites* as having the same range of genetic variability as is seen, for instance, in *Anasibirites kingianus* or *Columbites parisianus*, both species known by large samples.

Occurrence. Olenekites Zone, northern Siberia, Olenek River, Verkhoyan region, Kolyma River basin, and eastern Taymyr.

Sibirites renzi n. sp.

Plate 24, figures 6–9

Anasibirites aff. *anguloso* (Waagen),—Renz and Renz, 1947: 60; Renz and Renz, 1948: 35, pl. 11, figs. 10, 11.

The Renzes (1948) listed only two specimens of this species, but there are in the collections four additional paratypes. The preservation of all the specimens leaves much to be desired. The shape of the conch, degree of involution, and pattern of ornamentation place this species in *Sibirites.* The ribs are slightly interrupted in their passage over the venter; in *Anasibirites* the ribs are continuous over the venter.

Occurrence. Subcolumbites fauna, Chios.

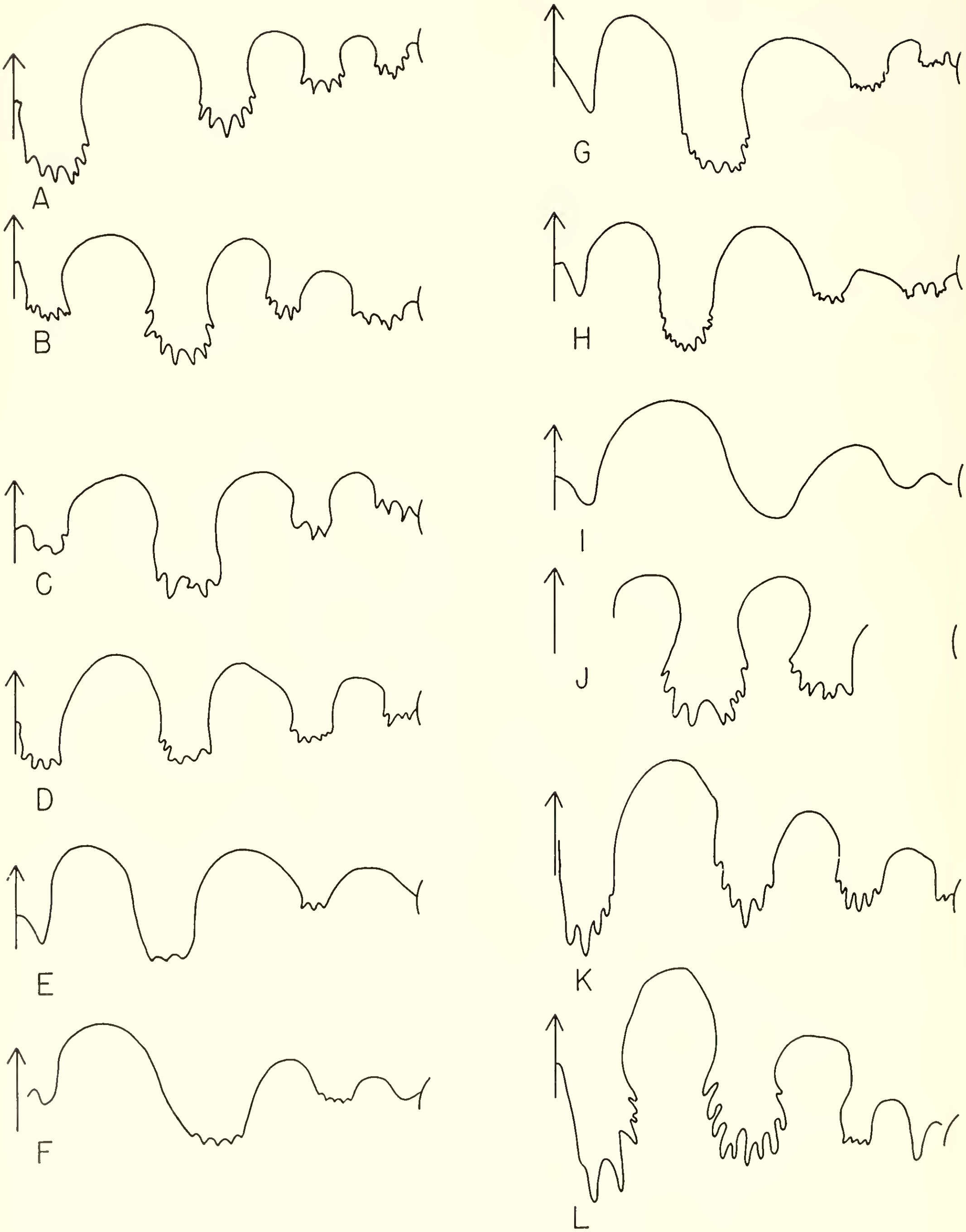

Figure 38. Diagrammatic representation of the suture of: A, *Keyserlingites subrobustus* (Mojsisovics, 1886: pl. 4, fig. 2c), at a diameter of approximately 85 mm; B, *Keyserlingites middendorffi* (Keyserling)—Mojsisovics (1886: pl. 3, fig. 1c), at a diameter of approximately 100 mm; C, *Ceratites nikitini* Mojsisovics (1888: pl. 1, fig. 13c), at a diameter of approximately 25 mm; D, *Ceratites bungei* Mojsisovics (1888: pl. 1, fig. 14c), at a diameter of approximately 50 mm; E, holotype Key-

Repository. Holotype, Renz and Renz (1948: pl. 11, fig. 10) NHMB J13623; paratype, Renz and Renz (1948: pl. 11, fig. 11) NHMB J13624; Pl. 24, figs. 6, 7 of this report, NHMB J19551; Pl. 24, figs. 8, 9 of this report, NHMB J19552; unfigured paratypes NHMB J13625.

Genus *Keyserlingites* Hyatt, 1900

Type species, *Ceratites subrobustus* Mojsisovics, 1885

There are now five late Scythian species of this genus confined to the circum-Arctic region and in western North America. Four of these species (*subrobustus, middendorffi, bearlakensis,* and *bearriverensis*) are confined to the *Prohungarites* Zone, and one species (*stephensoni*) is from the *Columbites* Zone. On the basis of studies on several well preserved specimens of *Keyserlingites subrobustus* from British Columbia and Ellesmere Island, Tozer (1965a) has been able to clarify the relations between *Keyserlingites* and *Durgaites.* Tozer's suggestion, however, that the Himalayan "*Durgaites*" *dieneri* and the Timor "*D.*" *angustecostatus* may be upper Scythian in age rather than Anisian, as concluded by Diener (1907, 1912), Spath (1934) and Welter (1915), is here rejected. This question has been fully discussed in the introductory chapter (p. 348).

Keyserlingites subrobustus (Mojsisovics)

Plate 26, figures 6, 7; Text-figure 38

Ceratites middendorffi Keyserling, 1845: pl. 2, fig. 4.

Ceratites subrobustus Mojsisovics, 1885: 155, pl. 6, fig. 3; Mojsisovics, 1886: 44, pl. 4, fig. 2, pl. 5, figs. 1a, b, pl. 6, fig. 1; Noetling, *in* Frech, 1905: 194, 200, pl. 28, fig. 5a, b.

Keyserlingites subrobustus,—Hyatt, 1900: 559; Diener, 1915: 172; Spath, 1934: 355, fig. 119a–c; Kummel, 1961: 521; Popov, 1961: 55, pl. 15, fig. 1; Tozer, 1965a: 31, pl. 5, fig. 1, pl. 6, figs. 1, 2, pl. 7, figs. 1–3, pl. 8, figs. 1, 2; Tozer, 1965b: 5.

Robustites subrobustus,—Philippi, 1901: 556.

Keyserlingites cf. *subrobustus,*—Frebold, 1929a: 12, pl. 2, figs. 8, 9; Tozer, 1962, pl. 4, figs. 6a–c.

Ceratites bungei Mojsisovics, 1888: 8, pl. 1, fig. 14; Spath, 1934: 356.

Keyserlingites bungei,—Diener, 1915: 178; Popov, 1961: 54.

This species has recently been extensively described and illustrated by Tozer (1965a) on the basis of specimens from Ellesmere Island and British Columbia which have contributed much to our knowledge of this most interesting form. *Ceratites bungei* (Fig. 38D) is believed to be based upon a juvenile specimen of *K. subrobustus.* The differences in the two Arctic species of *Keyserlingites* are largely in the nature of the whorl section. This species has a subquadrate whorl section, whereas *middendorffi* is a much more compressed form. *Keyserlingites bearlakensis* n. sp. has a suture quite similar to *subrobustus* (Fig. 38A) but a simpler pattern of ornamentation with only a single set of lateral bullae. The other species of *Keyserlingites* in the *Prohungarites* Zone of southeast Idaho, *bearriverensis,* is a compressed form like the Siberian *middendorffi.*

Occurrence. The type specimens came from the *Olenekites* Zone at the mouth of the Olenek River, Siberia. The species is also known from Spitsbergen at Cape

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serlingites bearriverensis n. sp., at a diameter of 50 mm; F, paratype *Keyserlingites bearriverensis* n. sp., at a diameter of 9.5 mm (MCZ 9521); G, holotype *Keyserlingites bearlakensis* n. sp., at a whorl height of 24 mm (MCZ 9516); H, paratype *Keyserlingites bearlakensis* n. sp., at a whorl height of 25 mm (MCZ 9523); I, paratype *Keyserlingites bearlakensis* n. sp., at a diameter of 7.3 mm (MCZ 9518); J, holotype *Keyserlingites stephensoni* n. sp. at a diameter of 190 mm; K, holotype *Ceratites subrobustus* Diener (1897: pl. 19, fig. 2) (=*Keyserlingites dieneri*), at a diameter of approximately 110 mm; L, *Keyserlingites angustecostatus* Welter (1915: 108, fig. 12).

Specimens of figures A–D from *Olenekites* Zone, Olenek River region, Siberia; of E–I from Upper Thaynes Formation, Hammond Creek, southeast Idaho; J, from Thaynes Formation, Fort Hall Indian Reservation presumably from *Columbites* Zone; K, lower Anisian, Himalayas and Tibet; L, lower Anisian, Nifoekoko, Timor.

Thordson (Frebold, 1929a), and from the *Grippia* beds, Botneheia, south of Sassanfiord (Tozer, 1962). On Ellesmere Island the species is present in the Blaa Mountain Formation and the Blind Fiord Formation, and in British Columbia in the Toad Formation in the Halfway River area (Tozer, 1965a).

Repository. The Siberian specimens are in the Central Geological Museum, Leningrad. The Spitsbergen specimen reported by Frebold (1929a) is in the Paleontological Museum, Oslo; another Spitsbergen specimen, collected by Frebold and illustrated by Tozer (1965a) is in the Geological Survey of Canada and a plastotype in the Museum of Comparative Zoology. The Ellesmere Island and British Columbia species are in the Geological Survey of Canada.

Keyserlingites middendorffi (Keyserling)

Ceratites middendorffi Keyserling, 1845: 170, pl. 1, fig. 1; pl. 2, figs. 1, 3 (non 2, 4); Mojsisovics, 1882: 11; Mojsisovics, 1885: 153, pl. 6, fig. 2; Mojsisovics, 1886: 38, pl. 2, figs. 12, 13, pl. 3, figs. 1a–c, pl. 20, fig. 10; Frech, 1905: 200; Spath, 1934: 359.

Ammonites middendorffi,—v. Buch, 1848: 15.

Ceratites (?*Stephanites*) *middendorffi*,—Frech, 1905: pl. 28, fig. 7.

Keyserlingites middendorffi,—Diener, 1907: 44; Diener, 1915: 178; Spath, 1934: 33, 353, 355, 356, 363, 432, fig. 119d; Kummel, 1961: 521; Popov, 1961: 54, pl. 15, figs. 2, 3.

Ceratites nikitini Mojsisovics, 1888: 6, pl. 1, figs. 12, 13.

Keyserlingites nikitini,—Diener, 1915: 179; Popov, 1961: 56, pl. 15, fig. 4.

Ceratites schrenki Mojsisovics, 1886: 47, pl. 4, fig. 1.

Keyserlingites schrenki,—Diener, 1915: 179.

Of the two species of Siberian keyserlingitids this is the compressed form. It differs from *subrobustus* also in ornamentation, with its prominent nodes just below the umbilical shoulder and only weak ridges crossing the venter. *Keyserlingites nikitini* (Mojsisovics) is much like *middendorffi* except for being more evolute. That species is known from only three specimens and the difference in involution of the conch from *middendorffi* is a little less than 10 percent. As these two "species" are associated in the same beds, I feel it more likely that *nikitini* is nothing more than an evolute variant of *middendorffi*. In the same vein one can look upon *Keyserlingites schrenki* (Mojsisovics) as an involute variant of *middendorffi*. In its compressed whorls *K. middendorffi* is similar to *K. bearriverensis* n. sp. from southeast Idaho, but the two species differ significantly in their ornament pattern.

The sutures of these species are illustrated on Figure 38.

Occurrence. This species is only known from northern Siberia where it occurs in the *Olenekites* Zone at the mouths of the Lena and Olenek rivers, in the Kolyma River basin of the Verkhoyan region, and in eastern Taymyr.

Repository. The Siberian specimens are in the Central Geological Museum, Leningrad. The Museum of Comparative Zoology has a specimen from the delta region of the Lena River (MCZ 6108).

Keyserlingites bearlakensis n. sp.

Plate 37, figures 5, 6; Plate 38, figures 1–3; Text-figure 38

Keyserlingites n. sp. cf. *K. subrobustus* (Mojsisovics),—Kummel, 1954: 187.

The largest ammonoids in the upper member of the Thaynes Formation at Hammond Creek, Bear River Range, southeast Idaho, are species of *Keyserlingites*. This species is represented by ten, mainly fragmentary, specimens. The conch is evolute with an umbilicus measuring approximately 30 percent of the diameter. The whorls are depressed, being wider than high, with a broadly arched venter. The lateral areas are likewise convex and merge onto a broadly rounded umbilical slope. The conch is ornamented with large, prominent bullae on the lateral areas. On the holotype (Pl. 38, figs. 1, 2), there are nine bullae on the half volution. The bullae occupy the entire lateral area. Between the bullae there may or may not be low, weak ribs extending across the venter from one ventral shoulder to the other. The suture is shown on Figures 38G–I.

The collections contain one small specimen of 7.8 mm in diameter, which is believed to be the juvenile whorls of this species (Pl. 37, figs. 5, 6). What is of special interest in this specimen is that at this diameter it already has all of the main morphological features of the large adult specimens. This includes the depressed whorl section, bullae, and suture (Fig. 38I).

The Tobin Formation of the Tobin Range, Nevada, has yielded a few poorly preserved, fragmentary specimens that are possibly conspecific with this species. In its depressed whorls this species is much like the Arctic *K. subrobustus* but differs in ornament pattern.

Occurrence. Upper member of Thaynes Formation, Hammond Creek, Bear River Range, southeast Idaho.

Repository. Holotype MCZ 9561 (Pl. 38, figs. 1, 2); figured paratypes MCZ 9517 (Pl. 38, fig. 3), MCZ 9518 (Pl. 37, figs. 5, 6); unfigured paratypes MCZ 9519.

Keyserlingites bearriverensis n. sp.
Plate 37, figures 1–4; Text-figure 38

It was pointed out above that of the two Siberian species of *Keyserlingites*, one was a form with a depressed whorl section (*K. subrobustus*) and the other was a form with a compressed whorl section (*K. middendorffi*). A similar relationship exists with two species of *Keyserlingites* that occur in the upper member of the Thaynes Formation at Hammond Creek, Bear River Range, southeast Idaho. Of the compressed species the collections contain eight poorly preserved specimens.

The venter is highly arched, grading onto convex lateral areas; the umbilical shoulder and wall are broadly convex. Prominent bullae on the lateral areas extend from the umbilical shoulder to the ventral shoulder; they are essentially radial on the phragmocone but on the living chamber become slightly prosiradiate. The suture is shown on Figure 38E, F.

The collection contains a small specimen of 9.8 mm in diameter which is believed to be a juvenile of this species. Like the juvenile specimen of *K. bearlakensis* described above, this specimen already has the essential features of the adult. That is, the compressed whorl section, high, arched venter, and bullae are clearly developed. The suture has the basic pattern of lobes and saddles, but the lobes are only slightly denticulated (Fig. 38F).

In the compressed nature of the conch this species is similar to *K. middendorffi*. It differs from that species in the nature of the bullae and of the venter.

The fact that each of the Siberian and Idaho late Scythian faunas have two species, one compressed in whorl section, the other depressed, tempts one to consider the possibility that these are dimorphs of one species in each case. However, the material available from each fauna is far too limited to explore this problem further.

Occurrence. Upper member of the Thaynes Formation, Hammond Creek, Bear River Range, southeast Idaho.

Repository. Holotype MCZ 9520 (Pl. 37, figs. 1, 2); figured paratype MCZ 9521 (Pl. 37, figs. 3, 4); unfigured paratypes MCZ 9522.

Keyserlingites stephensoni n. sp.
Plate 46, figure 1; Text-figure 38

This species is based on the largest specimen of an ammonite discovered in the Lower Triassic formations of western United States. It was discovered by Gordon R. Stephenson of the U.S. Agricultural Research Service of Boise, Idaho, in whose honor the species is named. The specimen measures 268.0 mm in diameter, 106 mm for the height of the last whorl, and 80 mm for the diameter of the umbilicus. The specimen was broken out of a large black limestone concretion, and one side is embedded in matrix. Even though a width measurement is not possible, it is clear that the whorls are higher than wide. The lateral areas are broadly convex, and slightly convergent; the venter is broadly arched. Both the ventral and umbilical shoulders are rounded.

The most striking feature of the specimen is its ornamentation. On the umbilical shoulder are large nodes. On the last volution there are seven such nodes that adorally increase in size. On the ventral shoulder there are slightly elongated nodes (clavi) which also increase in size adorally. There are approximately twice as many nodes on the ventral shoulder as on the umbilical shoulder.

The shell is preserved over much of one side of the specimen. The shell in the region of the nodes measures as much as 5 mm in thickness. On the mid-part of the venter the shell is only 2 mm thick.

The suture is only partially known, that is, the first lateral lobe, second lateral saddle, and the second lateral lobe are visible (Fig. 38J). This species is remarkably similar in its gross feature to the specimen of *Keyserlingites middendorffi* figured by Mojsisovics (1886: pl. 3) from the Olenek fauna of northern Siberia. The Idaho specimen lacks the transverse ventral ribs, and has more prominent nodes on the ventral shoulder. It differs from *Keyserlingites subrobustus*, also from the Olenek fauna, and from *Keyserlingites bearlakensis* in its compressed rather than depressed whorl section.

Occurrence. From the lower black limestone member of the Thaynes Formation, Fort Hall Indian Reservation, southeast Idaho. The specimen is presumably from a horizon equivalent to the *Columbites* fauna of the Bear Lake region.

Repository. This specimen has been presented by Mr. G. R. Stephenson to the Department of Geology, Washington State University, Pullman, Washington.

Keyserlingites sp. indet. (Afghanistan)

Keyserlingites sp. indet. Kummel, 1968b: 500, pl. 1, figs. 5–7.

A small specimen, 22 mm in diameter, is the first record of the genus *Keyserlingites* in late Scythian strata of Tethys. The specimen appears to be all phragmocone and has a whorl height of 9 mm and an umbilical diameter of 7.5 mm. The whorl sides are slightly convex and converge toward a broadly rounded venter. The umbilical shoulder is abruptly rounded and the umbilical wall nearly vertical. There are large nodes, one approximately every quarter volution, that are anchored on the umbilical shoulder and extend upward on the flanks. The most adoral node, at a diameter of 21 mm, extends half way across the lateral areas. The suture consists of a simple pronged ventral lobe, a large first lateral saddle and first lateral lobe, and much smaller second lateral saddle and lobe; a low denticulated auxiliary lobe occupies the umbilical wall. The general shape of the conch, the nodes, and the suture identifies this specimen as *Keyserlingites*. The specimen is most probably a juvenile form.

Occurrence. Subcolumbites fauna, Kotal-e-Tera, Afghanistan.

Repository. MCZ 10139.

Genus *Olenekites* Hyatt, 1900

Type species, *Dinarites spiniplicatus* Mojsisovics, 1886

Olenekites spiniplicatus (Mojsisovics)

Dinarites spiniplicatus Mojsisovics, 1886: 10, pl. 1, figs. 1–5, 8–16, 18–26, pl. 2, figs. 1–5, 7; Mojsisovics, 1888: 2, pl. 1, figs. 1–3; Frech, 1905: pl. 28, fig. 9.

Olenekites spiniplicatus,—Hyatt, 1900: 559; Spath 1934: 361, pl. 7, fig. 3; Kiparisova, 1947: 166; Kummel, *in* Arkell et al., 1957: L146, figs. 178, 5; Popov, 1961: 34, pl. 14, figs. 3, 4; Vozin and Tikhomirova, 1964: 67, figs. 4–7.

Dinarites (Olenekites) spiniplicatus,—Diener, 1915: 123.

Dinarites volutus Mojsisovics, 1886: 14, pl. 1, fig. 6, pl. 2, fig. 6; Mojsisovics, 1888: 4, pl. 1, figs. 5, 6.

Dinarites (Olenekites) volutus,—Diener, 1915: 124.

Dinarites densiplicatus Mojsisovics, 1886: 15, pl. 1, fig. 7; Mojsisovics, 1888: 4, pl. 1, fig. 4.
Dinarites (*Olenekites*) *densiplicatus*,—Diener, 1915: 123.
Dinarites altus Mojsisovics, 1886: 16, pl. 2, fig. 8.
Dinarites (*Olenekites*) *altus*,—Diener, 1915: 123.
Olenekites altus,—Popov, 1961: 35, pl. 13, fig. 1b; Vozin and Tikhomirova, 1964: 68, pl. 33, fig. 3.
Dinarites intermedius Mojsisovics, 1886: 17, pl. 2, fig. 9.
Dinarites (*Olenekites*) *intermedius*,—Diener, 1915: 123.
Dinarites glacialis Mojsisovics, 1886: 18, pl. 2, fig. 11.
Dinarites (*Olenekites*) *glacialis*,—Diener, 1915: 123.
Olenekites glacialis,—Popov, 1961: 34, pl. 13, fig. 16.

Both Mojsisovics (1886) and Spath (1934) have made particular note of the large degree of variation in nearly all morphological features in this species. Mojsisovics had 64 specimens of *spiniplicatus*, but for the remaining five species he assigned to his *Dinarites* he had only one, two, or three specimens per species. Restudy of the type specimens, topotype material, and the literature of Mojsisovics (1886, 1888) and Popov (1961) demonstrate clearly that there is but one species of *Olenekites* in this north Siberian region.

Occurrence. Northern Siberia, mainly at and around mouth of Olenek River.

Repository. The Museum of Comparative Zoology contains a number of topotype specimens (MCZ 8682, 8683). The Central Geological Museum, Leningrad, contains the types of Mojsisovics and Popov.

Olenekites mangyshlakensis Astakhova

Olenekites mangyshlakensis Astakhova, 1960a: 148, pl. 34, figs. 6, 7, text-fig. 14.

This species is obviously quite close to *O. spiniplicatus* and could possibly be conspecific. However, since data available on this species are so incomplete, it seems best to accept it as a separate and distinct species.

Occurrence. Mangyshlak Peninsula, Karatauchik Range, from *Columbites* Zone of Astakhova, 600–650 m above base of Tyur-Upa suite.

Olenekites canadensis Tozer

Olenekites canadensis Tozer, 1961a: 73, pl. 18, figs. 1–3; Tozer, 1965a: 32, pl. 4, figs. 1–8, text-fig. 10.

This is likewise a highly variable species, differing from *O. spiniplicatus* mainly in its truncate venter.

Occurrence. Blaa Mountain Formation, upper Scythian, Ellesmere Island.

Olenekites cf. *spiniplicatus* (Mojsisovics)
Plate 36, figures 4–6

Previously, the two available specimens of this species were assigned to *Olenekites*, with question, as no suture is preserved (Kummel, 1954). In recent years, I have had the opportunity of examining numerous specimens of *Olenekites* from the type locality at the mouth of the Olenek River, northern USSR, and no longer have any doubt but that these specimens represent a species of *Olenekites*. Each specimen consists of only one-half volution. The whorls are approximately as high as wide; the venter is broadly rounded, as are the ventral shoulders. The umbilical shoulders are more abruptly rounded, and the umbilical wall nearly vertical. The lateral area bears bullae that begin on the umbilical shoulder and decrease gradually toward the ventral shoulder. On one specimen (Pl. 36, figs. 4, 5) the bullae are rather robust and widely spaced, there being approximately four per half volution. On the other specimen the bullae are narrower, not as robust, and there are approximately six bullae per half volution. Both Mojsisovics (1886) and Spath (1934) have emphasized the exceedingly variable character of this species. The two specimens recorded here can be compared favorably with one or more of the specimens illustrated by Mojsisovics (1886: pl. 1). The species *O. canadensis*, described by Tozer (1961a: 73) from Ellesmere Island, is also closely related to *Olenekites spiniplicatus*, differing mainly in the subtabulate character of the venter on the later whorls.

Occurrence. Uppermost member of Thaynes Formation, Hammond Creek, Bear River Range, southeast Idaho.

Repository. MCZ 9482 (Pl. 36, figs. 3, 4), MCZ 9476 (Pl. 36, figs. 5, 6).

Genus *Eukashmirites* n. gen.

Type species, *Kashmirites acutangulatus* Welter, 1922: 125, pl. 9, figs. 9–12

The genus *Kashmirites* was introduced by Diener (1913: 33) for the "group of *Celtites subrectangularis* Waagen or *Celtites armatus* Waagen from the Ceratite Formation of the Salt Range." Diener at that time was dealing with a Scythian fauna from Kashmir. He had within his Kashmir fauna fragmentary specimens which he felt belonged to the *Celtites* of Waagen described from the Salt Range. This new generic name was introduced for these Salt Range and Himalayan species as they no longer could be accommodated in the genus *Celtites* as redefined by Mojsisovics (1893). In this revision it is quite apparent that Diener overlooked the genus *Pseudoceltites* Hyatt (1900)—type species *Celtites multiplicatus* Waagen. In the discussion of the genus *Pseudoceltites* it has already been pointed out that *Celtites armatus* (the type of *Kashmirites*, so designated by Diener, 1915: 137) is a synonym of *Celtites multiplicatus*. There is still, however, a need for separation of the group of ammonoids with subquadrate whorl sections, lateral ribs, occasional nodes which cross the venter, and a simple two lobed suture. Both Diener (1913) and Spath (1934) looked upon *Kashmirites blaschkei* Diener as a typical species. As noted by Diener (1913), the Kashmir specimens of *blaschkei* and related species are poorly preserved and fragmentary. Because of this I select Welter's Timor species *acutangulatus* as the type species of this new genus.

Eukashmirites is fairly well represented in the mid-Scythian zones of the Himalayas and Timor. In the late Scythian *Prohungarites* Zone it is represented by only two species, both from the Mangyshlak Peninsula in southern U.S.S.R.

Eukashmirites subdimorphus (Kiparisova)

Kashmirites subdimorphus Kiparisova, 1947: 148, pl. 33, figs. 3–5, text-figs. 40, 41; Astakhova, 1960a: 140.

The overall shell morphology of this species is very much like that of the type species—*E. acutangulatus*—from Timor except the whorls tend to be broader on the adoral volutions. The other species of this genus, *E. contortus* Astakhova, also known only from the Mangyshlak Peninsula, is a much more compressed form with slightly sinuous ribs on the adoral whorls.

Occurrence.—Scythian formation of Mangyshlak Peninsula but Kiparisova (1947) gives no precise horizon. Astakhova (1960b: 150) lists the species from her *Tirolites* Zone.

Eukashmirites contortus (Astakhova)

Kashmirites contortus Astakhova, 1960a: 139, pl. 33, fig. 5, text-fig. 7.

This species is also quite similar to the type species—*acutangulatus*—but much more compressed in its whorl section; the lateral ribs also are sinuous on the adoral whorls. The sample of this species available to Astakhova and to Kiparisova when she described *E. subdimorphus* was very small. It is conceivable that a large sample would show these two species to be synonyms.

Occurrence. Tirolites Zone of Astakhova, Mangyshlak Peninsula.

Genus *Anakashmirites* Spath, 1930

Type species, *Danubites nivalis* Diener, 1897

Species of this genus are known mainly from the mid-Scythian *Owenites* Zone. The only records of this genus are fragmentary and specifically indeterminate forms from the Narmia Member of the Mianwali Formation in the Surghar Range of West

Pakistan (Kummel, 1966). These specimens in conch form and ornamentation are very much like the species from the *Owenites* Zone but the suture is distinctly more advanced.

Superfamily CERATITACEAE Mojsisovics, 1879

Family TIROLITIDAE Mojsisovics, 1882

Genus *Tirolites* Mojsisovics, 1879

Type species, *Tirolites idrianus* Hauer, 1865

As with most genera of ornamented ammonites, the genus *Tirolites* includes a more than generous number of species. The great majority of these species were established for forms from the Werfen Formation of the Alps and Dalmatia. Mojsisovics in his classic monograph on "Die Cephalopoden der mediterranen Triasprovinz" (1882) recognized 14 species of *Tirolites*. The ammonites of the Werfen Formation were monographed by Kittl (1903), who recognized 40 species of *Tirolites* and three subgenera! Most subsequent authors (e.g. Smith, 1932; Spath, 1934) recognized that many (or most) of Kittl's species were very closely allied or identical, yet continued to recognize all the species—I presume as a matter of convenience.

I have had the opportunity of studying the Werfen Formation collection described by Kittl (1903), in the Natural History Museum, Vienna. All the specimens figured by Kittl (1903) were photographed, and measurements were made of all specimens sufficiently well preserved. It should be remarked here that Kittl's monograph is profusely illustrated by line drawings, and that in effect Kittl illustrated nearly every specimen of fair to good preservation. Most of the unfigured paratypes and topotypes are very poorly preserved specimens. No satisfactory photographic illustrations of the Werfen Formation *Tirolites* exist; for this reason the more important types of Kittl's study are reproduced here. Study of these illustrations first of all clearly shows the relatively poor preservation of most of the specimens, particularly since these figured forms are the very best specimens in the collection.

Tubercles on the ventro-lateral shoulder form the basic ornamentation pattern for *Tirolites*. Very often there are radial or prosiradiate ribs that extend from the tubercles dorsally along the flanks for variable distances. Study of the hundreds of specimens in the Kittl collection soon gives one the impression that they represent one continuous gradational series. Mojsisovics (1882) recognized two primary groups within the genus *Tirolites*, the Spinosi with ornamented inner whorls and the Seminudi with smooth inner whorls. Of the 14 species of *Tirolites* that Mojsisovics (1882) recognized from the Werfen Formation, 7 were assigned to the Spinosi, and 7 to the Seminudi. Kittl (1903) adopted the same two groups and recognized three additional groups as subgenera (*Hololobus*, *Svilajites*, *Bittnerites*).

Preservation of the Werfen Formation ammonites is such that retention and exposure of the inner whorls is not the usual thing. There are likewise numerous transitions between the two groups, Spinosi and Seminudi, and between these and other genera. One is tempted to consider all of the tirolitids of the Werfen Formation as a complex, variable, single species group. This could very well be the case. At the same time, in a general way, the Seminudi seldom have ribs associated with the tubercles as do the Spinosi. Clearly as a matter of convenience and not because of any real understanding of the relationships, I recognize two major species of tirolitids from the Werfen Formation—*T. idrianus* (Seminudi) and *T. cassianus* (Spinosi).

The type specimen of *Tirolites* (*Svilajites*) *cingulatus* is poorly preserved. Spath (1934) raised this group to generic rank and this was accepted by Kummel (*in* Arkell, et al., 1957). Examination of the type specimen leads me to believe that at best this can be recognized only as a distinct species of *Tirolites*.

Tirolitoides prior (Kittl, 1903) was said to have umbilical nodes and a more ceratitic suture. The so-called umbilical nodes are no more than a reflection of poor preservation and the suture is no different from that of many other specimens figured by Kittl (1903).

The comprehensive interpretation of the Werfen Formation tirolitids creates special problems in assessing the relationships to species from other horizons and localities. In no other locality or formation are the tirolitids as abundantly represented as they are in the Werfen Formation. The other species of *Tirolites* recognized here are discussed below, but in almost every case the species is known from very few specimens.

The *Subcolumbites* fauna of Albania has yielded three specimens of *Tirolites* (Arthaber, 1908, 1911) which are here considered to be *T. idrianus.* The upper Scythian formation of the Mangyshlak Peninsula has yielded *T. rossicus* Kiparisova (1947) and *T. impolitus* Astakhova (1960a). These two species were said to be associated with *T. cassianus* and *T. spinosus.* The Narmia Member of the Mianwali Formation in the Salt Range of West Pakistan has yielded a single indeterminate species of *Tirolites* (Kummel, 1966). The *Hedenstroemia* fauna of the Himalayas has yielded a single species—*T. injucundus* Krafft and Diener (1909). This is the oldest species of the genus recorded to date. A fragmentary specimen presumably from a *Subcolumbites* horizon in Kwangsi was assigned by Chao (1959) to *Tirolites* cf. *darwini.* Tirolitids are present in strata of Olenek age in the basin of the Kolyma River, Siberia (Popov, 1961).

Finally, in western North America there are several records of *Tirolites.* In fact the stratigraphic position of the *Tirolites* fauna as generally interpreted was established on the basis of the sequence of faunal zones in southeastern Idaho. In Paris Canyon, Smith (1932) discovered a small, poorly preserved fauna including three species of *Tirolites*, above his *Meekoceras* Zone and below his *Columbites* Zone. I have had several occasions to verify this sequence. These Paris Canyon species are very similar to the Spinosi of the Werfen Formation and are treated here as a single but distinct species—*T. harti* Smith. From the overlying *Columbites* Zone, Smith (1932) described a specimen as *T. illyricus.* Additional specimens of this species suggest its separation as a distinct form. The *Columbites* fauna contains two other species of *Tirolites* very different from the form Smith (1932) assigned to *T. illyricus.* Silberling (*in* Hose and Repenning, 1959: 2194) has recorded indeterminate species from the upper part of the Thaynes Formation in the Confusion Range of western Utah. These are recorded here as *T.* cf. *cassianus.*

It can be seen from this brief summary that species of *Tirolites* are now recognized throughout the upper half of the Scythian.

Tirolites idrianus (Hauer)

Plate 18, figures 1–6; Plate 66, figures 1–13; Plate 67, figures 1–9; Plate 68, figures 1–9; Plate 69, figures 1–10; Text-figure 39

Ceratites idrianus Hauer, 1865: 610, pl. 1, figs. 4, 5.

Tirolites idrianus,—Mojsisovics, 1879: 138; Mojsisovics, 1882: 67, pl. 1, fig. 1; Kittl, 1903: 36, pl. 5, figs. 8, 9; Arthaber, *in* Frech, 1906: pl. 34, fig. 14.

Tirolites seminudus Mojsisovics, 1882: 66, pl. 2, fig. 11; Kittl, 1903: 40, pl. 6, figs. 3–10, 17, 18; Arthaber, 1908: 275, pl. 11(1), fig. 9; Diener, 1915: 279; Spath, 1934: 375.

Tirolites seminudus var. *nudior* Kittl, 1903: 41, pl. 6, fig. 3; Spath, 1934: 375.

Tirolites seminudus var. *plicosus* Kittl, 1903: 41, pl. 6, figs. 5, 7; Diener, 1915: 279; Spath, 1934: 375.

Tirolites mercurii Mojsisovics, 1882: 68, pl. 1, fig. 9; Kittl, 1903: 38, pl. 5, figs. 10, 11, pl. 6, figs. 1, 2; Diener, 1915: 278; Spath, 1934: 377.

Tirolites paucispinatus Kittl, 1903: 39, pl. 6, fig. 11, pl. 7, figs. 4–6; Diener, 1915: 279.

Tirolites distans Kittl, 1903: 42, pl. 6, figs. 12–16, pl. 7, figs. 7, 8; Diener, 1915: 278; Spath, 1934: 375.

Tirolites quenstedti Mojsisovics, 1882: 66, pl. 2, fig. 12; Kittl, 1903: 42, pl. 6, figs. 19, 20; Diener, 1915: 279.

Tirolites robustus Kittl, 1903: 43, pl. 7, figs. 9–11, pl. 8, fig. 1; Diener, 1915: 279; Spath, 1934: 377.

Tirolites dimidiatus Kittl, 1903: 44, pl. 8, fig. 15; Diener, 1915: 278; Spath, 1934: 377.

Tirolites stachei Kittl, 1903: 45, pl. 7, fig. 14; Diener, 1915: 280; Spath, 1934: 377.

Tirolites dinarus Mojsisovics, 1882: 74, pl. 2, fig. 9; Kittl, 1903: 45.

Tirolites hybridus Kittl, 1903: 46, pl. 8, fig. 2; Diener, 1915: 278.

Tirolites angustus Kittl, 1903: 47, pl. 7, fig. 12; Diener, 1915: 277; Spath, 1934: 377.

Tirolites subillyricus Kittl, 1903: 47, pl. 7, figs. 15, 16; Diener, 1915: 280.

Tirolites illyricus Mojsisovics, 1882: 68, pl. 2, fig 10; Kittl, 1903: 48, pl. 8, figs. 3, 4, 6–9; Arthaber, 1911: 250, pl. 22(6), fig. 4; Diener, 1915: 278; Spath, 1934: 373.

Tirolites repulsus Kittl, 1903: 49, pl. 8, figs. 5, 10, 11, 14; Diener, 1915: 279.

Tirolites rotiformis Kittl, 1903: 50, pl. 8, figs. 12, 13; Diener, 1915: 279.

Tirolites rectangularis Mojsisovics, 1882: 69, pl. 3, fig. 5; Kittl, 1903: 50, pl. 8, figs. 16, 17; Arthaber, 1911: 251, pl. 22(6), fig. 5; Diener, 1915: 279; Spath, 1934: 374.

Tirolites undulatus Kittl, 1903: 52, pl. 7, fig. 13; Diener, 1915: 280.

Tirolites heterophanus Kittl, 1903: 38, pl. 5, fig. 7.

The species *idrianus* includes all the "species" that had been included by Mojsisovics and Kittl in the Seminudi. Measurements of 122 specimens from the Werfen Formation of Muć, studied by Kittl, are given on Table 44 and plotted on Figure 39. There is clearly considerable variation in these conch parameters. The same is true of the pattern of ornamentation, the principal criterion used to differentiate species within this group. The illustrations given here should amply show that the number, spacing, etc., of the tubercles are highly variable. The sutures in the Seminudi were claimed to be entire, that is, goniatitic. This is not at all certain, as details of fine denticulations are most often not retained in the kind of preservation which characterizes the Werfen Formation fauna. The position of the lateral lobe is likewise highly variable.

Occurrence. Werfen Formation of Alps, Dalmatia, and associated regions. The three specimens of *Tirolites* recorded by Arthaber (1908, 1911) from the *Subcolumbites* fauna of Albania are included in this species.

Repository. All of the Kittl collection is in the Natural History Museum, Vienna. The specimens from the *Subcolumbites* fauna of Albania are in the Paleontological Institute, Vienna.

Tirolites cassianus (Quenstedt)

Plate 63, figures 1–9; Plate 64, figures 1–4; Plate 65, figures 1–9; Plate 70, figures 3–6, 11, 12; Text-figures 40, 41

Ceratites cassianus Quenstedt, 1849: 231, pl. 18, fig. 11; Hauer, 1865: 606, pl. 2, figs. 1, 2; Laube, 1869: 61, pl. 37, fig. 1.

Ammonites (*Ceratites*) *cassianus*,—Hauer, 1851: 6, pl. 2, fig. 5.

Tirolites cassianus,—Mojsisovics, 1882: 70, pl. 2, fig. 48, pl. 81, fig. 3; Tommasi, 1895: 69, pl. 4, fig. 15; Kittl, 1903: 54, pl. 9, figs. 4–6; Arthaber, 1906: pl. 34, fig. 15; Wittenburg, 1908: 285, pl. 40(5), fig. 19; Diener, 1915: 278; Diener, 1925: 80, pl. 12, fig. 1; Ogilvie-Gordon, 1927: 31, pl. 3, fig. 39; Kutassy, 1933: 674; Spath, 1934: 369, fig. 126; Leonardi, 1935: 90, pl. 6, figs. 5, 6; Kollárová-Andrusovová, 1961: 56, pl. 1, figs. 1, 3, 4.

Tirolites cassianus var. *tenuis* Mojsisovics, 1882: 71, pl. 2, figs. 4–6; Kittl, 1903: 55.

Tirolites cassianus var. *alpha* Kittl, 1903: 55, pl. 9, figs. 4, 5.

Tirolites angustilobatus Kittl, 1903: 54, pl. 9, figs. 1–3; Diener, 1915: 277; Spath, 1934: 370.

Tirolites angustilobatus var. *alpha* Kittl, 1903: 54, pl. 8, fig. 19.

Tirolites spinosus Mojsisovics, 1882: 70, pl. 1, fig. 10, pl. 2, figs. 1–3; Tommasi, 1895: 70, pl. 4, fig. 16; Kittl, 1903: 56, pl. 9, fig. 7; Diener, 1915: 279; Spath, 1934: 370; Leonardi, 1935: 91, pl. 6, figs. 7–9; Kollárová-Andrusovová, 1961: 57, pl. 1, figs. 2a, b.

Tirolites haueri Mojsisovics, 1882: 71, pl. 3, figs. 2–4; Kittl, 1903: 56, pl. 9, figs. 8–13; Diener, 1915: 278; Spath, 1934: 371.

Tirolites haueri var. *minor* Kittl, 1903: 58, pl. 10, figs. 1–3; Diener, 1915: 278.

Tirolites multispinatus Kittl, 1903: 58, pl. 11, fig. 9; Diener, 1915: 279.

Tirolites percostatus Kittl, 1903: 58, pl. 10, fig. 6; Diener, 1915: 279.

Tirolites turgidus Mojsisovics, 1882: 72, pl. 3, figs. 6, 7; Kittl, 1903: 59, pl. 10, figs. 7, 8; Diener, 1915: 280; Spath, 1934: 371.

Tirolites darwini Mojsisovics, 1882: 73, pl. 2,

TABLE 44. MEASUREMENTS OF SPECIMENS OF *TIROLITES IDRIANUS* (HAUER) FROM MUĆ IN DALMATIA STUDIED BY ERNST KITTL, 1903. ALL SPECIMENS ARE DEPOSITED IN THE NATURAL HISTORY MUSEUM, VIENNA.

	D	W	H	U	W/D	H/D	U/D		D	W	H	U	W/D	H/D	U/D
1.	66.0?	18.3	19.0	22.1	27.7?	28.8?	33.5?	25.	44.9	12.8	15.5	17.7	28.5	34.5	39.4
2.	57.3	?	22.7	19.0	?	39.6	33.2	26.	44.7	12.4	18.0	16.0	27.7	40.3	35.8
3.	55.5	18.5	19.9	22.7	33.3	35.9	40.9	27.	44.5	14.4	16.0	16.3	32.4	36.0	36.6
4.	53.7	17.8	18.8?	19.7?	33.1	35.0?	36.7?	28.	44.5	13.2	16.4	16.9	29.7	36.9	38.0
5.	52.6	?	20.7	19.3	?	39.4	36.7	29.	44.5	?	18.4	15.4	?	41.3	34.6
6.	52.5?	16.1	20.0	20.7	30.7?	38.1?	39.4	30.	44.4	?	15.3	17.8	?	34.5	40.1
7.	52.4	13.1	19.9	20.0	25.0	38.0	38.2	31.	44.3	12.1	16.7	19.4	27.3	37.7	43.8
8.	51.8	16.7	18.5	21.1	32.2	35.7	40.7	32.	44.2	13.0	17.3	16.0	29.4	39.1	36.2
9.	51.7	15.5	17.0	21.0?	30.0	32.9	40.6?	33.	44.1	12.3	16.2	17.5?	27.9	36.7	39.7?
10.	51.3	17.1	19.2	18.6	33.3	37.4	36.2	34.	44.1	10.4	9.2	19.1	23.6	20.9	43.3
11.	51.2	14.7	17.4	22.0	28.7	34.0	43.0	35.	43.7	12.6	15.2	17.3	28.8	34.8	39.6
12.	51.1	16.2	20.3	18.7?	31.7	39.7	36.6?	36.	43.4	10.1	15.7	17.0	23.3	36.2	39.2
13.	50.2	10.0±	18.5	19.0	19.9±	36.9	37.8	37.	43.3	14.3	16.8	16.6	33.0	38.8	38.3
14.	50.0	12.0	16.5	19.6	24.0	33.0	39.2	38.	43.3	10.0	14.5	18.3	23.1	33.5	42.3
15.	49.7	9.9	17.3	21.1	19.9	34.8	42.5	39.	43.2	14.0	17.3	15.4	32.4	40.0	35.6
16.	49.6	15.8	17.8	19.8	38.9	35.9	39.9	40.	43.2	11.2	12.8	21.8	25.9	29.6	50.5
17.	48.4	13.2	18.0	18.1	27.3	37.2	37.4	41.	43.2	8.5?	16.7	15.7	19.7?	38.7	36.3
18.	47.5	14.3	16.0	17.5?	30.1	33.7	36.8	42.	43.0	10.4?	16.8	15.7	24.2	39.1	36.5
19.	47.2	10.8	17.2	18.4	22.9	36.4	39.0	43.	43.0	?	17.1	15.2	?	39.8	35.3
20.	47.2	?	19.2	17.1	?	40.7	36.2	44.	42.7	14.1	15.8	16.2	33.0	37.0	37.9
21.	46.3	15.5?	17.3	17.7	33.5?	37.4	38.2	45.	42.7	13.3	15.7	16.0	31.1	36.8	37.5
22.	46.2	15.0	17.2	17.5	32.5	37.2	37.9	46.	42.6	13.7	15.3	17.0	32.2	35.9	39.9
23.	45.3	16.6	16.7	16.8?	36.6	36.9	37.1?	47.	42.6	13.1	14.7	16.0	30.8	34.5	37.6
24.	45.0	13.9	16.8	18.4	30.9	37.3	40.9	48.	42.4	13.4	14.6	17.7	31.6	34.4	41.7

1. Lectotype, *T. undulatus* Kittl (1903: pl. 7, fig. 13).
2. Lectotype, *T. stachei* Kittl (1903: pl. 7, fig. 14).
3. Plesiotype, *T. mercurii,*—Kittl (1903: pl. 6, fig. 2).
4. Unfigured paratype, *T. hybridus* Kittl (1903: 46).
5. Lectotype, *T. hybridus* Kittl (1903: pl. 8, fig. 2).
6, 16, 37, 45, 46, 48, 50, 64, 92. Unfigured paratypes, *T. robustus* Kittl (1903: 43).
7, 10, 12, 39, 63, 74, 86, 88. Unfigured paratypes, *T. angustus* Kittl (1903: 47).
8, 18, 75, 77, 85, 99, 102. Unfigured paratypes, *T. mercurii,*—Kittl (1903: 38).
9. Plesiotype, *T. mercurii,*—Kittl (1903: pl. 6, fig. 1).
11, 55, 61, 67, 70, 71, 76, 89, 90, 95, 103, 104, 105, 106, 110, 111, 115, 118, 121, 122. Unfigured specimens, *T. seminudus,*—Kittl (1903: 40).
13. Plesiotype, *T. quenstedti,*—Kittl (1903: pl. 6, fig. 19).
14. Plesiotype, *T. illyricus,*—Kittl (1903: pl. 8, fig. 4).
15. Plesiotype, *T. seminudus,*—Kittl (1903: pl. 6, fig. 3).
17, 87, 98. Unfigured specimens, *T. quenstedti,*—Kittl (1903: 42).
19. Plesiotype, *T. quenstedti,*—Kittl (1903: pl. 6, fig. 20).
20. Paralectotype, *T. distans* Kittl (1903: pl. 7, fig. 8).
21. Plesiotype, *T. mercurii,*—Kittl (1903: pl. 5, fig. 11).
22. Plesiotype, *T. illyricus,*—Kittl (1903: pl. 8, fig. 3).
23. Plesiotype, *T. mercurii,*—Kittl (1903: pl. 5, fig. 10).
24. Paralectotype, *T. distans* Kittl (1903: pl. 6, fig. 12).
25. Syntype, *T. subillyricus* Kittl (1903: pl. 7, fig. 15).
26, 30. Unfigured paratypes, *T. subillyricus* Kittl (1903: p. 17).
27. Paralectotype, *T. distans* Kittl (1903: pl. 6, fig. 14).
28. Plesiotype, *T. seminudus,*—Kittl (1903: pl. 6, fig. 4).
29, 83, 113. Unfigured paratypes, *T. paucispinatus* Kittl (1903: 39).
31, 36, 60, 65, 66, 81. Unfigured specimens, *T. illyricus,*—Kittl (1903: 48).
32. Plesiotype, *T. illyricus,*—Kittl (1903: pl. 8, fig. 8).
33, 53, 69, 73, 94, 101. Unfigured paratypes, *T. distans* Kittl (1903: 42).
34. Plesiotype, *T. rectangularis,*—Kittl (1903: pl. 8, fig. 16).
35. Plesiotype, *T. seminudus,*—Kittl (1903: pl. 6, fig. 7).
38. Figured type, *T. repulsus* Kittl (1903: pl. 8, fig. 11).
40. Figured type, *T. rotiformis* Kittl (1903: pl. 8, fig. 12).
41. Plesiotype, *T. illyricus,*—Kittl (1903: pl. 8, fig. 7).
42. Plesiotype, *T. seminudus,*—Kittl (1903: pl. 6, fig. 8).
43. Plesiotype, *T. seminudus,*—Kittl (1903: pl. 6, fig. 18).
44. Figured type, *T. repulsus* Kittl (1903: pl. 8, fig. 5).
47, 108. Unfigured paratypes, *T. rotiformis* Kittl (1903: 50).

TABLE 44. *Continued.*

	D	W	H	U	W/D	H/D	U/D		D	W	H	U	W/D	H/D	U/D
49.	42.4	12.6	15.1	17.9	29.7	35.6	42.2	86.	38.0	11.7	14.4	14.6	30.8	37.9	38.4
50.	42.3	12.8	17.0	15.3	30.3	40.2	36.2	87.	38.0	8.2?	14.7	14.5?	21.6?	38.7	38.2?
51.	42.3	11.2	15.1	14.8	26.5	35.7	35.0	88.	37.8	8.4?	15.3	13.0	22.2?	40.5	34.4
52.	42.2	14.6	16.2	16.3	34.6	38.4	38.6	89.	37.5	12.0	12.8	15.4	32.0	34.1	41.1
53.	42.1	13.2	14.5	17.1	31.4	34.4	40.6	90.	37.3	10.0	13.3	16.0	26.8	35.7	42.9
54.	42.1	12.0	14.2	17.1	28.5	33.7	40.6	91.	37.0?	11.6	13.8	14.0?	31.4?	37.3?	37.8?
55.	42.0	10.2	15.0	16.1	24.3	35.7	38.3	92.	37.0	11.5	14.5	13.6	31.1	39.2	36.8
56.	41.7	13.8	16.5	14.5	33.1	39.6	34.8	93.	37.0?	11.3	12.6	12.2?	30.5?	34.1?	33.0?
57.	41.5	11.7?	16.1	15.4	28.2?	38.8	37.1	94.	37.0	10.2	13.6	13.3	27.6	36.8	35.9
58.	41.4	15.6	16.8	14.6	37.7	40.6	35.3	95.	36.3	11.5	12.7	14.7	31.7	35.0	40.5
59.	41.4	13.2	15.2	17.0	31.9	36.7	41.1	96.	36.0	8.9	14.0	14.4	24.7	38.9	40.0
60.	41.4	10.5	14.6	17.6	25.4	35.3	42.5	97.	35.7	10.7	12.3	14.8	30.0	34.5	41.5
61.	41.2	12.1?	14.1	16.1	29.4?	34.2	39.1	98.	35.7	9.8	12.0	14.4	27.5	33.6	40.3
62.	41.0	10.8	15.1	17.1	26.3	36.8	41.7	99.	35.6	12.0	14.1	11.7	33.7	39.6	32.9
63.	40.8	13.8	14.7?	15.3?	33.8	36.0?	37.5?	100.	35.6?	11.8	13.0	14.8	33.1?	36.5?	41.6
64.	40.7	13.0	14.0	15.8	31.9	34.4	38.8	101.	35.5	9.4	13.1	14.4	26.5	36.9	40.6
65.	40.5	11.6	9.2	16.1	28.6	22.7	39.8	102.	35.4	10.8?	13.6	14.0	30.5?	38.4	39.5
66.	40.5	11.3	13.8	18.2	27.9	34.1	44.9	103.	35.4	10.5	12.7	12.8	29.7	35.9	36.2
67.	40.5	8.8?	13.5	17.0	21.7	33.3	42.0	104.	35.2	11.3	13.0	13.3	32.1	36.9	37.8
68.	40.1	12.8	14.7	14.6	31.9	36.7	36.4	105.	35.2	9.3	12.6	13.8	26.4	35.8	39.2
69.	40.1	11.9	14.2	16.2	29.7	29.7	40.4	106.	35.0	8.7?	13.1	13.3	24.9?	37.4	38.0
70.	40.1	11.6	13.5	15.5	28.9	33.7	38.7	107.	34.9	8.7?	12.5	13.2	24.9?	35.8	37.8
71.	40.0	12.6	14.2	16.5	31.5	35.5	41.3	108.	34.8	9.5	11.1	15.2	27.3	31.9	43.7
72.	40.0	12.1	15.0	14.3	30.3	37.5	36.8	109.	34.6	10.7	10.5	15.5?	30.9	30.3	44.8?
73.	39.8	11.7	14.1	15.2	29.4	35.4	38.2	110.	34.1	9.6	12.5	13.4	28.2	36.7	39.3
74.	39.7	12.8	15.0	14.4	32.2	37.8	36.3	111.	34.0	10.1	12.6	13.2	29.7	37.1	38.8
75.	39.6	18.8	15.0?	14.5	47.5	37.9	36.6	112.	33.9	9.8	11.8	13.0	28.9	34.8	38.3
76.	39.4	12.3	14.5	15.7	31.2	36.8	39.8	113.	32.3	8.5	11.2	12.7	26.3	34.7	39.3
77.	39.2	14.0	15.0?	14.0?	35.7	38.3?	35.7?	114.	31.8	8.6	11.4	12.8	27.0	35.8	40.3
78.	39.0	13.8	14.1	14.7	35.4	36.2	37.7	115.	31.2	8.8	11.5	11.8	28.2	36.9	37.8
79.	38.8	?	16.1	13.6	?	41.5	35.1	116.	30.8	7.8?	9.6	8.7	25.3?	31.2	28.2
80.	38.6	10.2	13.2	16.2	26.4	34.2	42.0	117.	30.5?	7.5?	11.6	11.4	24.6?	38.0?	37.4?
81.	38.5	9.1	12.5?	17.4	23.6	32.5?	45.2	118.	30.0	7.9	11.2	11.3	26.3	37.3	37.7
82.	38.5	?	16.5	13.7	?	42.9	35.6	119.	28.7	8.9	9.3	12.3	31.0	32.4	42.9
83.	38.2	11.5	13.3	14.6	30.1	34.8	38.2	120.	28.6	7.5	9.0	12.7	26.2	31.5	44.4
84.	38.2	11.4	13.8	14.7	29.8	36.1	38.5	121.	28.4	8.5	11.1	9.9	29.9	39.1	34.9
85.	38.0	13.1	15.3	13.4	34.5	40.3	35.3	122.	21.7	6.3	7.7	7.7	29.0	35.5	35.5

49\. Unfigured paratype, *T. rectangularis*,—Kittl (1903: 50).
51\. Figured type, *T. paucispinatus* Kittl (1903: pl. 6, fig. 11).
52, 78. Unfigured paratypes, *T. undulatus* Kittl (1903: 52).
54\. Figured type, *T. paucispinatus* Kittl (1903: pl. 7, fig. 6).
56\. Holotype, *T. angustus* Kittl (1903: pl. 7, fig. 12).
57\. Figured type, *T. paucispinatus* Kittl (1903: pl. 7, fig. 4).
58\. Lectotype, *T. robustus* Kittl (1903: pl. 7, fig. 9).
59\. Plesiotype, *T. rectangularis*,—Kittl (1903: pl. 8, fig. 17).
62\. Plesiotype, *T. quenstedti*,—Kittl (1903: pl. 6, fig. 20).
68\. Paralectotype, *T. distans* Kittl (1903: pl. 6, fig. 13).
72\. Plesiotype, *T. seminudus*,—Kittl (1903: pl. 6, fig. 5).
79\. Paralectotype, *T. distans* Kittl (1903: pl. 7, fig. 7).
80\. Figured type, *T. repulsus* Kittl (1903: pl. 8, fig. 10).
82\. Figured type, *T. paucispinatus* Kittl (1903: pl. 7, fig. 5).
84\. Plesiotype, *T. illyricus*,—Kittl (1903: pl. 8, fig. 6).
91\. Lectotype, *T. distans* Kittl (1903: pl. 6, fig. 15).
93\. Paralectotype, *T. distans* Kittl (1903: pl. 6, fig. 16).
96\. Plesiotype, *T. illyricus*,—Kittl (1903: pl. 8, fig. 9).
97, 109, 119. Unfigured paratypes, *T. repulsus* Kittl (1903: 49).
100\. Paralectotype, *T. robustus* Kittl (1903: pl. 7, fig. 11).
107\. Syntype, *T. subillyricus* Kittl (1903: pl. 7, fig. 16).
112\. Plesiotype, *T. seminudus*,—Kittl (1903: pl. 6, fig. 9).
114\. Plesiotype, *T. seminudus*,—Kittl (1903: pl. 6, fig. 17).
116\. Figured type, *T. rotiformis* Kittl (1903: pl. 8, fig. 13).
117\. Plesiotype, *T. seminudus*,—Kittl (1903: pl. 6, fig. 10).
120\. Figured type, *T. repulsus* Kittl (1903: pl. 8, fig. 14).

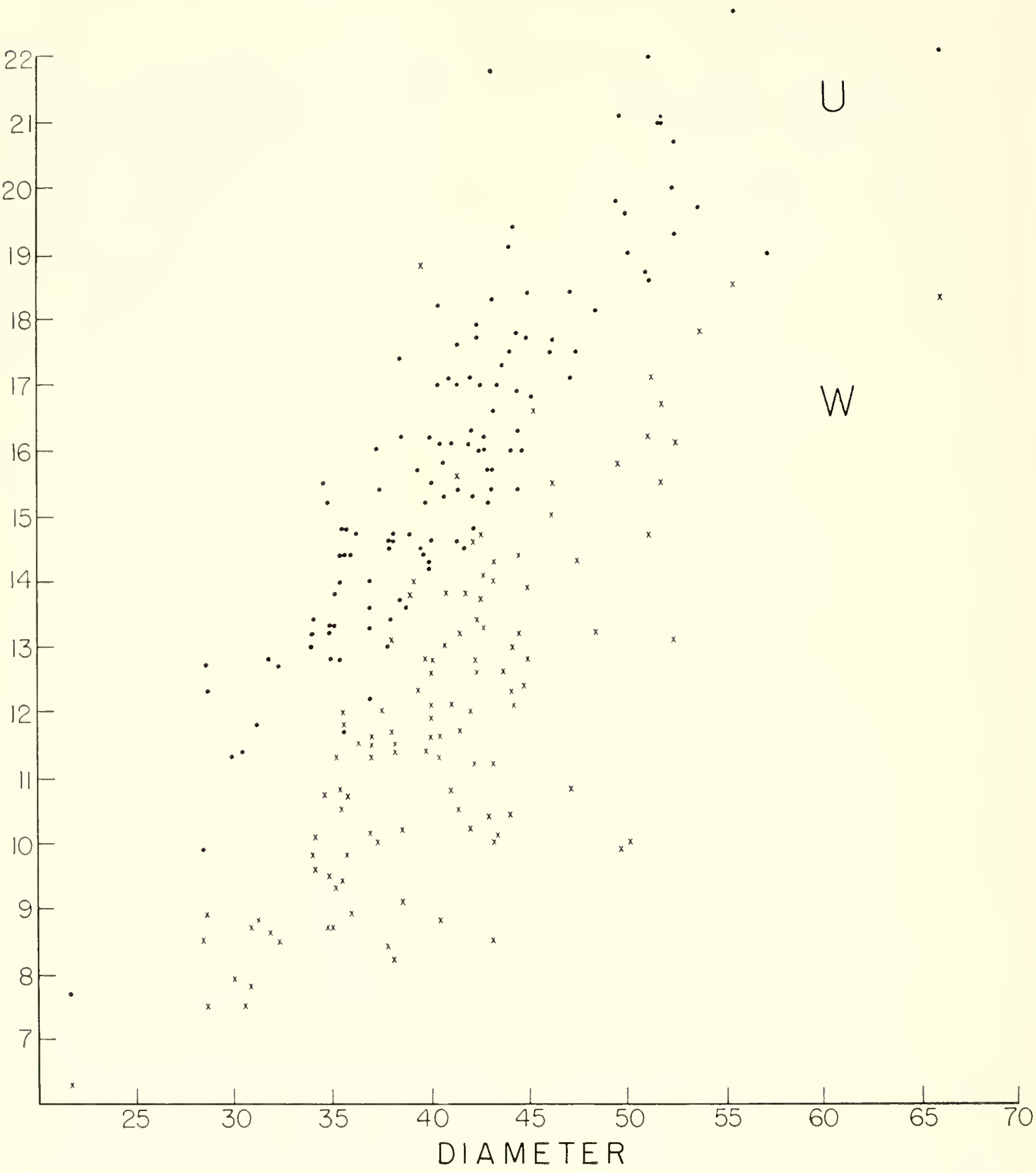

Figure 39. Variation in wharl width (W) and umbilical diameter (U) in *Tiralites idrianus*,—Mojsisovics, from Werfen Formation of Muć, Dalmatia. The data on this graph are from Table 44.

fig. 13, pl. 3, fig. 1; Kittl, 1903: 60, pl. 10, figs. 4, 5, 11, pl. 11, figs. 1–3, 7; Diener, 1915: 278; Patte, 1922: 54, pl. 3, fig. 16; Spath, 1934: 372.

Tirolites darwini var. *cinctus* Kittl, 1903: 61, pl. 10, fig. 4, pl. 11, fig. 3; Spath, 1934: 372.

Tirolites darwini var. *reminiscens* Kittl, 1903: 61, pl. 10, fig. 5; Spath, 1934: 372.

Tirolites darwini var. *modestus* Kittl, 1903: 61, pl. 11, fig. 7; Spath, 1934: 372.

Tirolites darwini var. *costatus* Kittl, 1903: 62, pl. 11, fig. 2; Spath, 1934: 372.

Tirolites darwini var. *abbrevians* Kittl, 1903: 62; Spath, 1934: 372.

Tirolites spinosior Kittl, 1903: 62, pl. 11, fig. 5; Diener, 1915: 279.

Ceratites smiriagini Auerbach, 1871: 50, pl. 4, figs. 9–11.

Tirolites smiriagini,—Mojsisovics, 1882: 73, pl. 81, figs. 1, 2; Kittl, 1903: 63, pl. 11, fig. 6;

Diener, 1915: 279; Spath, 1934: 372.
Tirolites kerneri Kittl, 1903: 64, pl. 11, fig. 8; Diener, 1915: 278; Spath, 1934: 373.
Tirolites toulai Kittl, 1903: 64, pl. 11, figs. 11, 12; Diener, 1915: 280; Spath, 1934: 358, 379.
Tirolites (*Svilajites*) *tietzei* Kittl, 1903: 66, pl. 10, fig. 9; Diener, 1915: 281.
Ceratites (*Paraceratites*) *prior* Kittl, 1903: 29, pl. 11, figs. 4, 13.
Xenodiscus prior,—Diener, 1915: 314.
Tirolitoides prior,—Spath, 1934: 378, fig. 127; Kummel, *in* Arkell, et al., 1957: L147, fig. 180, 5.
Tirolites bispinatus Ganev, 1966: 25, pl. 1, fig. 5.

The species *cassianus* includes all the species that had been included by Mojsisovics and Kittl in the Spinosi. In general the representatives of this species have ribs associated with the ventrolateral tubercles. There are, however, gradational forms to *idrianus*. Measurements of 31 specimens from the Werfen Formation of Muć, Dalmatia, are given on Table 45 and plotted on Figure 41. Very few specimens of this species in the Kittl collection that were not figured are sufficiently well preserved to yield useful measurements; this accounts for the fewer measurements of this species than of *idrianus*. The many species of this group were differentiated on differences in ornamentation and suture. There appears, however, to be complete transition among the various so-called species in these and other characters.

The types of *Tirolitoides prior* owe their umbilical tubercles to preservation. The suture likewise is no different from that of several other tirolitids (Fig. 40B).

The type specimen of *Tirolites* (*Svilajites*) *tietzei* Kittl, with its ventral cross-ribs, is no more than a typical tirolitid. Many other specimens have similar cross-ribs on the venter though generally not as well developed as in the type specimen of *tietzei*.

The binodal aspect of *Tirolites bispinatus* Ganev (1966) is apparently due to the crushed nature of the specimen. There is a plaster cast of the holotype, and only specimen, in the Museum of Comparative Zoology.

Occurrence. Werfen Formation of the Alps, Dalmatia and the associated regions. Also reported from eastern Bulgaria, from southern U.S.S.R. at Bogdo, Mangyshlak Peninsula, and Tuarkyr.

Repository. The specimens studied here are from the Kittl (1903) collection which is in the Natural History Museum, Vienna.

Tirolites cingulatus Kittl
Plate 70, figures 8–9

Tirolites (*Svilajites*) *cingulatus* Kittl, 1903: 65, pl. 8, fig. 18; Diener, 1915: 280.
Svilajites cingulatus,—Spath, 1934: 380, fig. 129; Kummel, *in* Arkell, et al., 1957: L147, fig. 180, 1.

The type species of *Svilajites* is *cingulatus*. The type specimen measures 37.3 mm in diameter, 10.3 mm for the width of the adoral whorl, 14.6 mm for the height, and the umbilicus is 13.2 mm in diameter. It is really only on the venter and one side of the last half volution that the shape and pattern of ornament are of at least fair preservation. The prior volutions and the opposite side from that shown on Plate 70, figure 9, are completely destroyed by weathering. The adoral half volution has two radial ribs extending from the umbilical shoulder to the ventral shoulder. These ribs presumably cross the venter, but on the type specimen this region of the venter is broken. An unfigured paratype in the collection of the Natural History Museum, Vienna, is weathered and poorly preserved but does show the ribs crossing the venter.

The second species that Kittl assigned to his subgenus *Svilajites* is *tietzei*, and it is illustrated here on Plate 70, figures 11, 12. The type specimen measures 41.7 mm in diameter, 12.8 mm for the width of the adoral whorl, 16.6 mm for the height, and the umbilicus is 16.9 mm in diameter. This is a typical tirolitid of much better preservation than the type specimen of *cingulatus*. There are broad folds extending across the venter from the ventro-lateral nodes. There is an indication that these cross folds decrease in prominence adorally. The general features of this species and especially the folds across the venter are to be seen

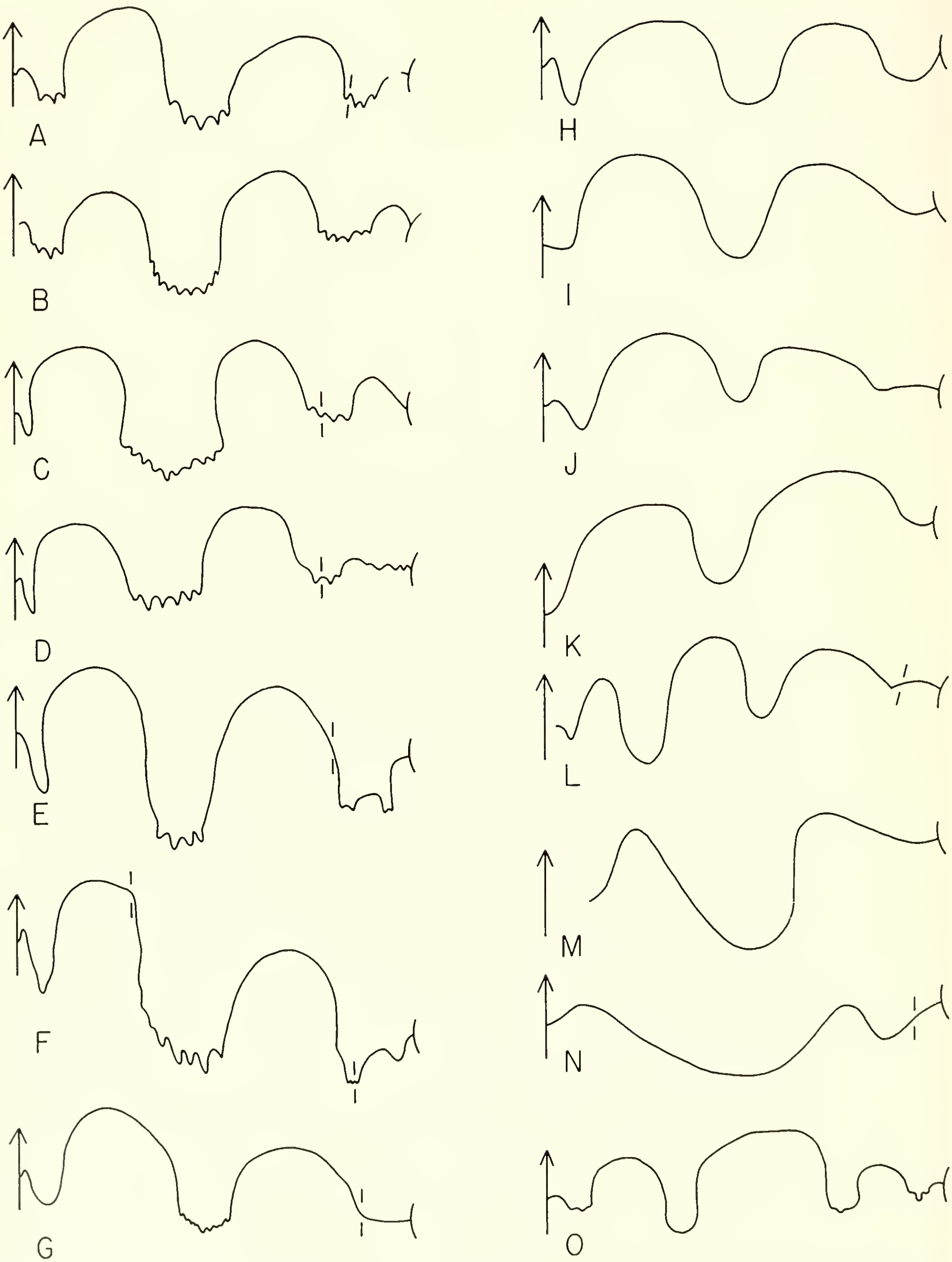

Figure 40. Diagrammatic representation of the suture of: A, *Tirolites toulai* Kittl (1903: pl. 11, fig. 11), at a diameter of 45 mm; B, paratype *Tirolitoides priar* (Kittl, 1903: pl. 11, fig. 4b), at a diameter of 35 mm; C, *Tirolites impolitus* Astakhova (1960a: fig. 16); D, *Tirolites elegans* Astakhova (1960a: fig. 15); E, *Tirolites* cf. *cassianus* (Pl. 34, figs. 9, 10), at a whorl

TABLE 45. MEASUREMENTS OF SPECIMENS OF *TIROLITES CASSIANUS* (QUENSTEDT) FROM MUĆ IN DALMATIA STUDIED BY ERNST KITTL, 1903. ALL SPECIMENS ARE DEPOSITED IN THE NATURAL HISTORY MUSEUM, VIENNA.

	D	W	H	U	W/D	H/D	U/D		D	W	H	U	W/D	H/D	U/D
1.	85.0	21.5	28.5	37.2	26.7	33.5	43.8	17.	49.8	13.1	17.7	21.0	26.3	35.5	42.2
2.	76.0	16.6	26.5	34.0	21.8	34.9	44.7	18.	49.0	15.3	15.6	21.2	31.2	31.8	43.3
3.	66.0	16.8	22.9	28.2	25.5	34.7	42.7	19.	49.0	17.0	17.3	20.7	34.7	35.3	42.2
4.	65.0	17.2?	22.5	27.2	26.5?	34.6	41.8	20.	47.7?	?	15.2	22.1	?	31.9?	46.3
5.	59.5	14.8	21.2	26.0	24.9	35.6	43.7	21.	47.1	?	16.3	20.6	?	34.6	43.7
6.	59.3	19.3	20.7	24.2	32.5	34.9	40.8	22.	46.7	15.7	17.8	17.7	33.6	38.1	37.9
7.	58.7	20.0	20.8	25.0	34.1	35.4	42.6	23.	46.6	?	9.1?	22.8	?	19.5	48.9
8.	57.0	15.5?	20.1	22.4	27.2?	35.3	39.3	24.	46.2?	13.0	15.6	20.7	28.1?	33.8?	44.8?
9.	56.6	15.3	15.4	21.7	27.0	27.2	38.3	25.	45.0	11.3	14.2	20.9	25.1	31.6	46.4
10.	56.3	17.7	19.1	24.0	31.4	33.9	42.6	26.	43.6	11.0?	15.7	19.5	25.2?	36.0	44.7
11.	55.7	14.7	19.3	23.7	26.4	34.6	42.5	27.	43.5	15.2	15.6	17.2	34.9	35.9	39.5
12.	55.0	17.0	18.6	23.2	30.9	33.8	42.2	28.	42.2	?	9.6	18.0	?	22.7	42.7
13.	51.0	17.2	17.3	22.8	33.7	33.9	44.7	29.	40.5	10.3?	13.7	18.4	25.4?	33.8	45.4
14.	50.4	16.3	17.0	20.7	32.3	33.7	41.1	30.	38.4	12.4	12.8	17.4	32.3	33.3	45.3
15.	50.4	13.5	17.2	20.7	26.8	34.1	41.1	31.	36.6	10.1	12.9	14.1	27.6	35.2	38.5
16.	50.2	10.2	17.6	21.3	20.3	35.1	42.4								

1. Plesiotype, *T. darwini*,—Kittl (1903: pl. 10, fig. 11).
2. Lectotype, *T. spinosior* Kittl (1903: pl. 11, fig. 5).
3. Plesiotype, *T. darwini*,—Kittl (1903: pl. 11, fig. 1).
4. Plesiotype, *T. darwini* var. *costatus* Kittl (1903: pl. 11, fig. 2).
5. Syntype, *T. toulai* Kittl (1903: pl. 11, fig. 11).
6. Pleisotype, *T. haueri*,—Kittl (1903: pl. 9, fig. 10).
7. Plesiotype, *T. turgidus*,—Kittl (1903: pl. 10, fig. 8).
8. Plesiotype, *T. haueri*,—Kittl (1903: pl. 9, fig. 9).
9. Lectotype, *T. percostatus* Kittl (1903: pl. 10, fig. 6).
10, 12, 14, 15. Unfigured specimens, *T. haueri*,—Kittl (1903: 56).
11. Plesiotype, *T. spinosus*,—Kittl (1903: pl. 9, fig. 7).
13. Plesiotype, *T. haueri*,—Kittl (1903: pl. 9, fig. 13).
16. Plesiotype, *T. cassianus*,—Kittl (1903: pl. 9, fig. 4).
17. Figured specimen, *T. darwini* var. *modestus* Kittl (1903: pl. 11, fig. 7).
18. Plesiotype, *T. haueri*,—Kittl (1903: pl. 9, fig. 8).
19. Plesiotype, *T. haueri*,—Kittl (1903: pl. 9, fig. 12).
20. Plesiotype, *T. smiriagini*,—Kittl (1903: pl. 11, fig. 6).
21. Lectotype, *T. angustilobatus* Kittl (1903: pl. 9, fig. 3).
22. Figured specimen, *T. haueri* var. *minor* Kittl (1903: pl. 10, fig. 1).
23. Figured specimen, *T. angustilobatus* var. *alpha* Kittl (1903: pl. 9, fig. 1).
24. Figured specimen, *T. darwini* var. *reminiscens* Kittl (1903: pl. 10, fig. 5).
25. Figured specimen, *T. darwini* var. *cinctus* Kittl (1903: pl. 10, fig. 4).
26. Plesiotype, *T. cassianus*,—Kittl (1903: pl. 9, fig. 6).
27. Figured specimen, *T. haueri* var. *minor* Kittl (1903: pl. 10, fig. 3).
28. Plesiotype, *T. cassianus*,—Kittl (1903: pl. 9, fig. 5).
29. Figured specimen, *T. angustilobatus* var. *alpha* Kittl (1903: pl. 8, fig. 19).
30. Figured specimen, *T. haueri* var. *minor* Kittl (1903: pl. 10, fig. 2).
31. Figured specimen, *T. darwini* var. *cinctus* Kittl (1903: pl. 11, fig. 3).

←

height of 19 mm; F, *Tirolites* sp. indet. II (Pl. 55, figs. 4, 5), at a whorl height of 14 mm (MCZ 9502); G, holotype *Tirolites astakhovi* n. sp. (Pl. 55, figs. 1, 2), at a diameter of 45 mm (USNM 153081); H, *Dinarites dalmatinus*,—Kittl (1903: pl. 2, fig. 4), at a diameter of approximately 40 mm; I, *Dinarites dalmatinus*,—Kittl (1903: pl. 3, fig. 3), at a diameter of approximately 30 mm; J, *Dinarites dalmatinus*,—Kittl (1903: pl. 2, fig. 2), at a diameter of approximately 26 mm; K, holotype *Hololobus monoptychus* (Kittl, 1903: pl. 4, fig. 9), at a diameter of approximately 40 mm; L, holotype *Pseudokymatites svilajanus* Kittl (1903: pl. 4, fig. 3), at a diameter of approximately 40 mm; M, *Dinarites undatus* Astakhova (1960a: fig. 17), at a diameter of approximately 25 mm; N, *Dinarites liatsikasi* Renz and Renz (1948: pl. 1, fig. 3c); O, *Doricranites bogdoanus* (Mojsisovics, 1882: pl. 80, fig. 4), at a diameter of approximately 80 mm.

Specimens of figures A, B, H, I, J, K, L from Werfen Formation, Dalmatia; of C, D, M from upper Scythian strata Mangyshlak Peninsula; of N, from *Subcolumbites* fauna of Chios; of O, from upper Scythian strata Mount Bogdo, southern Russia; E, Upper Thaynes Formation, Confusion Range, Utah; F, G, *Columbites* fauna southeastern Idaho.

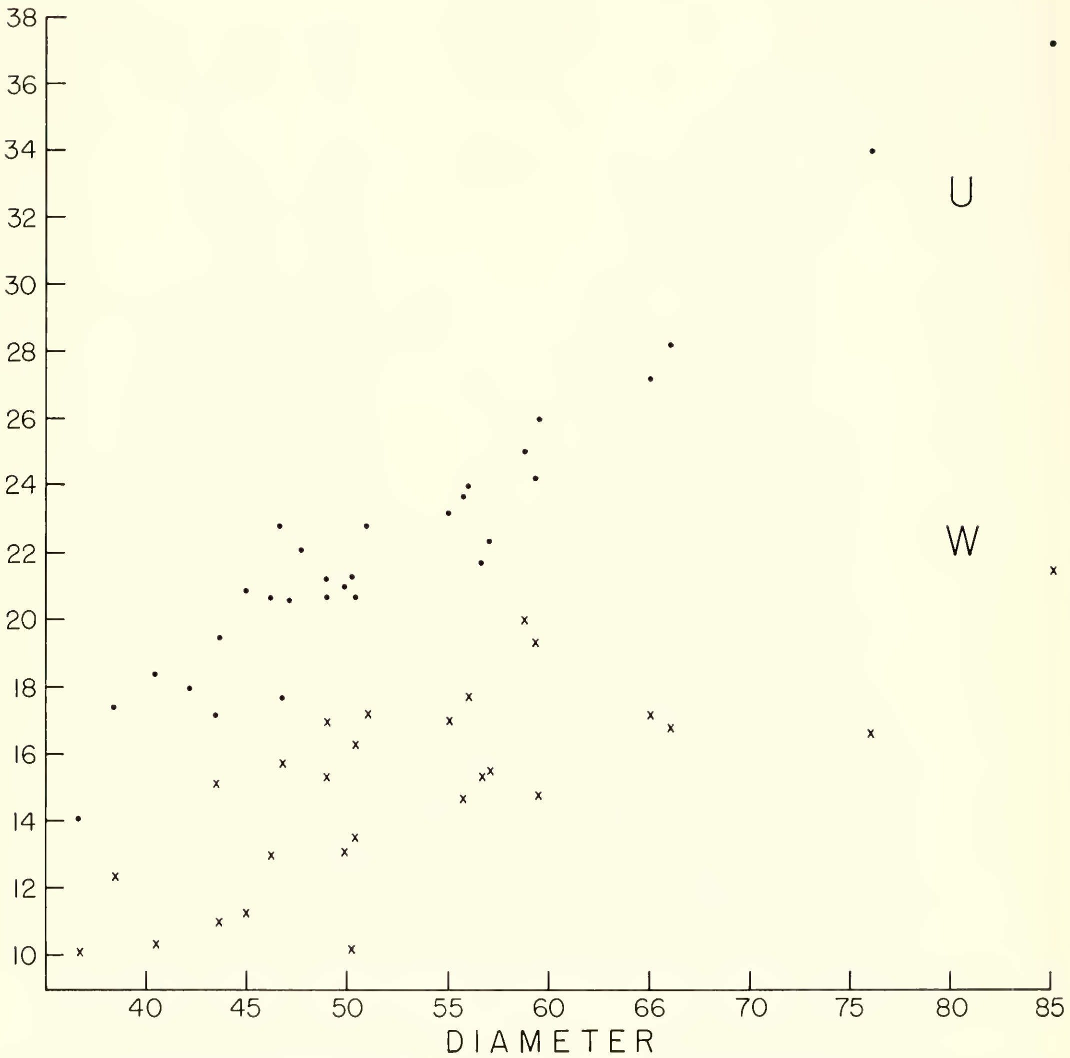

Figure 41. Variation in wharl width (W) and umbilical diameter (U) in *Tirolites cassianus* (Quenstedt), from the Werfen Formation of Muć, Dalmatia. The data on this graph are from Table 45.

in several of the so-called species of *Tirolites* of the Spinosi. The ventral ridges are related in some degree to the general prominence of the ventro-lateral nodes. The species *tietzei* belongs in the synonymy of *Tirolites cassianus.*

The species *cingulatus* is thus known from only two poorly preserved specimens. These appear to be distinct from the highly variable *Tirolites cassianus* at a specific level but not at a generic level as has been advocated.

Occurrence. Werfen Formation, Muć, Dalmatia.

Repository. Natural History Museum, Vienna.

Tirolites rossicus Kiparisova
Text-figure 40

Tirolites rossicus Kiparisova, 1947: 168, pl. 43, figs. 2, 3, pl. 44, fig. 2, text-fig. 66; Shevyrev and Shlezinger, 1960: 1418.

Tirolites elegans Astakhova, 1960a: 150, pl. 35, fig. 1; text-fig. 15.

A robust species that in its slightly

prosiradiate ribs on the inner whorls reminds one of the specimens assigned to *T.* cf. *cassianus* from the Thaynes Formation of the Confusion Range (Pl. 34, figs. 7–10). This species is clearly a member of the Spinosi and is said by Astakhova (1960a) to be associated with *T. cassianus* and *T. spinosus*. The suture of *T. elegans* Astakhova is illustrated on Figure 40D.

Occurrence. Tirolites Zone of Astakhova (1960a), Mangyshlak Peninsula.

Tirolites impolitus Astakhova
Text-figure 40

Tirolites impolitus Astakhova, 1960a: 151, pl. 35, fig. 5, text-fig. 16.

This species comes from a horizon approximately 150 m above that which yielded *T. rossicus*. It differs from that species primarily in having more prominent ribs and nodes. Too few data are available as yet on the Mangyshlak fauna. At the moment it seems best to accept this species; a great deal more collecting and study are needed of these forms. The suture is shown on Figure 40C.

Occurrence. Tirolites Zone of Astakhova (1960a), Mangyshlak Peninsula.

Tirolites morpheos (Popov)

Columbites morpheos Popov, 1961, p. 28, pl. 13, fig. 8.

Popov assigned this species (based on two specimens) to the genus *Columbites* on the strength of an apparent similarity of the suture to that of *Columbites parisianus*. Popov, however, was not aware of the tremendous variation that is present in the suture of *Columbites parisianus* (Fig. 22). This suture is quite similar to that of *Tirolites* in basic plan. A more reliable indicator of genetic affinity is the ornamentational pattern. In this respect the species *morpheos* is clearly a tirolitid.

Popov (1961) described two other tirolitids from Siberia on the basis of single fragmentary and poorly preserved specimens. Both specimens were collected from alluvium in the basin of the Kolyma River, Siberia. These two species—*T.* ex gr. *cassianus*, Popov (1961: 29, pl. 13, fig. 7) and *T. gerbaensis* Popov (1961: 29, pl. 13, fig. 5)—because of poor preservation and lack of stratigraphic data are included in the list of unrecognizable species.

Occurrence. Olenek stage, basin of Kolyma River, Siberia.

Tirolites harti Smith
Plate 71, figures 1–7

Tirolites harti Smith, 1932: 83, pl. 57, figs. 9, 10.
Tirolites knighti Smith, 1932: 84, pl. 57, figs. 1–4.
Tirolites pealei Smith, 1932: 84, pl. 57, figs. 5–8.

Smith (1932) clearly recognized that the few fragmentary specimens of *Tirolites* he had from the *Tirolites* Zone in Paris Canyon were closely related to, if not conspecific with, various species of the Spinosi of the Werfen Formation. In this conclusion I am in complete agreement. However, along with Smith, I believe it best to keep these Idaho forms under a separate species name because the fragmentary specimens known to date do not allow any kind of critical analysis.

Occurrence. Tirolites Zone, Thaynes Formation, Paris Canyon, southeast Idaho.

Repository. Holotype, USNM 75022; *T. knighti*, holotype, USNM 75020a; paratype, USNM 75020b; *T. pealei*, holotype USNM 75021a; paratype, USNM 75021; topotypes MCZ 9641.

Tirolites smithi n. sp.
Plate 54, figures 1–5

Tirolites illyricus Mojsisovics, Smith, 1932: 84, pl. 49, figs. 12–16.

Smith (1932) had a single specimen from the *Columbites* fauna of Paris Canyon, southeast Idaho, that he assigned to Mojsisovics' species—*illyricus*. There is a general resemblance to *T. illyricus* as there is to many other closely similar Werfen Formation forms. The Idaho species, however, has a very different aspect. First of all, Smith's specimen has fine radial ribs on the inner whorls, that decrease adorally; on the outer volution the ribs are gone and only sinuous growth lines are present with widely spaced tubercles at the ventral shoulders; the venter is highly vaulted. Two additional specimens have since been uncovered which are of special interest. There is first of all a small juvenile form (Pl. 54, figs. 4, 5) measuring 31.4 mm in diameter, 9.3 mm for the width of the adoral whorl, 11.2 mm for the height, and the umbilicus is 12.8 mm in diameter. The radial ribs on the inner whorls and the gradual adoral decrease in rib prominence are well displayed on this specimen. The ventral nodes are already well developed on the outer whorl of this specimen. The second specimen is a large one measuring 102 mm in diameter, 32.7 mm for the width of the adoral whorl, 39.5 mm for the height, and the umbilicus is 35.3 mm in diameter. The adoral half volution appears to be body chamber. This portion of the conch is still characterized by the prominent ventral tubercles and sinuous growth lines.

The sum total of the characters of this form set it apart from any of the Werfen Formation species of *Tirolites.* It likewise is totally different from *Tirolites astakhovi* which also occurs in the *Columbites* fauna of southeastern Idaho but at a different locality from where this species has been found.

Occurrence. The holotype (Pl. 54, figs. 2, 3) comes from the *Columbites* fauna, Thaynes Formation, Paris Canyon, southeast Idaho. The two plesiotypes recorded here (Pl. 54, figs. 1, 4, 5) come from the same horizons in Montpelier Canyon, southeast Idaho.

Repository. Holotype (Pl. 54, figs. 2, 3) USNM 74993; plesiotypes (Pl. 54, fig. 1) MCZ 9547, (Pl. 54, figs. 4, 5) MCZ 9548.

Tirolites astakhovi n. sp.

Plate 55, figures 1–3; Text-figure 40

Three excellently preserved specimens from the *Columbites* fauna of southeast Idaho are the basis for this new species. The measurements of the specimens are as follows.

	D	H	W	U
Holotype USNM 153081	51.5	14.3	?	26.0
Paratype Unfigured	82.4	22.2	?	42.2
Paratype USNM 153082	38.8	10.6	9.5	21.8

The conch is widely umbilicate with subrectangular whorl sections. The lateral areas are flattened, and the venter broadly arched. Both the ventral and umbilical shoulders are rounded. The lateral areas bear slightly prosiradiate ribs that begin on the umbilical shoulder and terminate at the ventral shoulder in a prominent node. On the smallest of the available specimens the nodes are much more prominent than on the other two specimens. Likewise on this small specimen the lateral areas are slightly divergent.

The suture of the holotype is illustrated on Figure 40G. The first lateral lobe lies just above the node on the ventral shoulder and the second lateral lobe lies on the umbilical shoulder and wall.

The morphological variations possible within species of the genus *Tirolites* were impressively illustrated by Kittl in his well-known monograph on the upper Werfen fauna from Muć. There is a strong temptation to assign these forms to one of the species described by Kittl. In fact, there is a marked morphological similarity with practically all of the thirteen species Kittl (1903: 52, 53) included in the Spinosi. The separation of this form from the Werfen species is done more as a matter of convenience than of conviction. More Idaho *Columbites* Zone material is needed, and the pattern of intraspecific variation in the Werfen species needs to be better understood before the relationships can be approached objectively.

Occurrence. From middle shale member of Thaynes Formation (*Columbites* fauna), on hillside north of Sage Creek, Stewart Flat Quadrangle, southeast Idaho.

Repository. Holotype, USNM 153081

(Pl. 55, figs. 1–2); figured paratype, USNM 153082 (Pl. 55, fig. 3); unfigured paratype USGS collections.

Tirolites cf. *cassianus* (Quenstedt)

Plate 34, figures 7–10; Text-figure 40

Tirolites cf. *spinosus* Mojsisovics,—Silberling, *in* Hose and Repenning, 1959: 2194.
Tirolites aff. *haueri* Mojsisovics,—Silberling, *in* Hose and Repenning, 1959: 2194.

The two specimens recorded here are clearly representatives of the Spinosi and could well be conspecific with the Werfen Formation species—*cassianus*. These specimens can be matched readily with several of the specimens illustrated by Kittl (1903). However, because the sample consists of only two fragmentary specimens it appears best to do no more than indicate a close affinity to the Werfen Formation species. The suture is shown on Figure 40E.

Occurrence. Thaynes Formation, Confusion Range, sample M111 in Hose and Repenning (1959, p. 2194).

Repository. USNM 153083 (Pl. 34, figs. 7, 8), USNM 153084 (Pl. 34, figs. 9, 10).

Tirolites sp. indet. II

Plate 55, figures 4, 5; Text-figure 40

A single specimen, consisting of approximately one half volution and much of the inner whorls, is clearly a tirolitid, but of uncertain specific affinities. The conch is evolute, with whorls that are about as wide as high on the earlier volutions but gradually become more compressed and higher than wide. The outer half volution of the specimen is half phragmocone and half body chamber. The lateral areas are flattened and the venter is broadly rounded. Both the ventral and umbilical shoulders are rounded. The umbilical wall slopes to the seam at an angle of approximately 45 degrees. The lateral areas bear widely spaced nodes which lie just dorsal of the ventral shoulders. There are approximately seven such nodes on the adoral half volution, and these show marked increase in size adorally. The shell bears sinuous growth lines that are slightly prosiradiate on the lateral areas and strongly projected forward in a broad arc over the venter.

The inner whorls, up to a diameter of 10 mm, are approximately as high as wide and the lateral areas bear radial ribs, some of which terminate in weak nodes at the ventral shoulder. On the next volution, that is, to a diameter of 20 mm, the whorls gradually increase in height, and the ornament consists only of widely spaced (four per half volution) conspicuous nodes at the umbilical shoulder.

The suture is shown on Figure 40F. The large first lateral lobe enclosed the ventrolateral node, and the second lateral lobe is on the umbilical wall. It is not difficult to find, among the numerous Werfen specimens illustrated by Kittl (1903), forms which are quite similar to the one mentioned here. However, because I am dealing with a single specimen, it seems best to merely document the occurrence of this form.

Occurrence. Middle shale member of Thaynes Formation (*Columbites* fauna), Montpelier Canyon, southeast Idaho.

Repository. MCZ 9502.

Genus *Diaplococeras* Hyatt

Type species, *Ceratites liccanus* Hauer, 1865

Diaplococeras liccanum (Hauer)

Ceratites liccanus Hauer, 1865: 616, pl. 3, figs. 1–3.
Dinarites liccanus,—Mojsisovics, 1882: 10, pl. 4, fig. 1; Tommasi, 1895: 69, pl. 4, fig. 14.
Diaplococeras liccanum,—Hyatt, 1900: 556; Spath, 1934: 379, fig. 128; Kummel, *in* Arkell et al., 1957: L147, fig. 180, 6.
Dinarites (*Liccaites*) *liccanus*,—Kittl, 1903: 26; Diener, 1915: 123.

Hauer (1865) based his species on one specimen. Mojsisovics apparently had three specimens for study; however, none of these specimens were available for study to the writer.

Occurrence. Werfen Formation, Muć, Dalmatia.

Diaplococeras connectens (Mojsisovics)
Plate 62, figures 1–4

Dinarites (*Ceratites*) *connectens* Mojsisovics, 1882: 9, pl. 3, fig. 10.
Dinarites (*Liccaites*) *connectens*,—Kittl, 1903: 25; Diener, 1915: 123.
Diaplococeras connectens,—Spath, 1934: 380.
Dinarites circumplicatus Mojsisovics, 1882: 8, pl. 3, figs. 8, 9.
Dinarites (*Liccaites*) *circumplicatus*,—Kittl, 1903: 24; Diener, 1915: 123.
Diaplococeras circumplicatus,—Spath, 1934: 380.
Dinarites biangulatus Kittl, 1903: 16, pl. 4, fig. 1; Diener, 1915: 120.
Dinarites (*Hercegovites*) *diocletiani* Kittl, 1903: 23, pl. 3, fig. 4; Diener, 1915: 122; Spath, 1934: 388.
Dinarites (*Liccaites*) *progressus* Kittl, 1903: 26, pl. 4, fig. 2; Diener, 1915: 123; Spath, 1934: 123.
Dinarites progressus,—Ganev, 1966: 27, pl. 2, fig. 2.

Poor preservation and misleading illustrations account for at least some of the confusion that has surrounded the species brought together here. The Werfen Formation contains a compressed form of ammonite that is modestly involute with low arched venter and conspicuous umbilical shoulder and umbilical wall. The suture is ceratitic with two lateral lobes. The flanks bear slightly prosiradiate ribs. Five species have been established for ammonites of the above general design. The major difference between these "species" is in their state of preservation. The specimens of the two species described by Mojsisovics—*connectens* and *circumplicatus*—were not personally studied. The three species established by Kittl (1903) were studied in detail.

The holotype of *Dinarites diocletiani* is shown here on Plate 62, figure 1. The specimen is crushed and the opposite side from that shown in the photograph has been destroyed by weathering. There are low, narrow, prosiradiate ribs on the flanks that are most conspicuous at and near the umbilical shoulder and decrease toward the ventral shoulder. The ribs also decrease in intensity adorally.

The holotype of *Dinarites biangulatus* is shown here on Plate 62, figures 3, 4. This specimen is highly weathered and only the body chamber approximates the original size and shape; the phragmocone is completely distorted by weathering. The basic outline of the whorls, degree of involution, and pattern of the suture (taking into account the weathering) is like that of *D. diocletiani*. The weathered body chamber has faint indications of ribs.

The holotype of *Dinarites progressus* Kittl, is shown here on Plate 62, figure 2. As can be seen, it also is a highly weathered specimen in which all surface features are obliterated or altered. In shape of whorl section, degree of involution and suture, it appears surely to be conspecific with the other forms included in this species.

The forms brought together here as *D. connectens* differ from *D. liccanum* in lacking peripheral clavi and umbilical tubercles.

Occurrence. Werfen Formation, Muć, Dalmatia, and eastern Bulgaria.

Repository. The specimens described by Kittl are in the Natural History Museum, Vienna. The specimen described by Ganev (1966) is in the Geological Institute of the Bulgarian Academy of Science; a plaster cast is in the Museum of Comparative Zoology.

Genus *Bittnerites* Kittl

Type species, *Tirolites (Bittnerites) bittneri* Kittl, 1903

Bittnerites bittneri (Kittl)
Plate 57, figures 1–6

Tirolites (*Bittnerites*) *bittneri* Kittl, 1903: 67, pl. 11, fig. 10; Diener, 1915: 280.
Bittnerites bittneri,—Spath, 1934: 381, fig. 130· Kummel, *in* Arkell, et al., 1957: L147, fig. 180, 3.
Tirolites (*Bittnerites*) *malici* Kittl, 1903: 67, pl. 3, fig. 8; Diener, 1915: 280.
Bittnerites malici,—Spath, 1934: 381, fig. 130.
Tirolites (*Bittnerites?*) *telleri* Kittl, 1903: 68, pl. 10, fig. 10; Diener, 1915: 280.

Of the three species Kittl (1903) assigned to his new genus *Bittnerites*, only the illustrated specimen of each species is still preserved. The genotype specimen—*B. bittneri*—is weathered, measuring 50.5 mm in diameter, 12.3 mm for the width of the adoral whorl, 17.7 mm for the height, and 23.1 mm for the diameter of the umbilicus. None of the inner whorls are preserved. Kittl (1903: pl. 11, fig. 10) shows the venter to be sharpened; this, however, is entirely due to weathering. The normal condition of the venter is rounded. The large specimen which represents the type of *Bittnerites malici* is of slightly better preservation in that at least the inner whorls are preserved. This specimen measures 71.1 mm in diameter, 17.2 mm for the width of the adoral whorl, 23.1 mm for the height, and the umbilicus is 30.6 mm in diameter. Kittl (1903: pl. 2, fig. 8) shows prominent prosiradiate shallow constrictions at least on the body chamber of the specimen. A photograph of the specimen reproduced here on Plate 57, figure 3, shows no such furrows. It should again be emphasized that preservation of the Werfen Formation ammonites leaves much to be desired and fine surface details are seldom preserved.

The type specimen of *Bittnerites telleri* is a very poorly preserved specimen consisting only of the outer volution. It measures 59.0 mm in diameter, 17.3 mm for the width of the adoral whorl, 18.7 mm for the height, and the umbilicus is 25.4 mm in diameter. The prosiradiate shallow furrows are visible on part of the outer volution. This specimen differs from the type specimen of *B. malici* only in having slightly more inflated whorls; there is no justification for keeping these specimens in separate species.

The genus *Bittnerites* is known only from its type species.

Occurrence. Werfen Formation, Mué, Dalmatia.

Repository. Natural History Museum, Vienna.

Genus *Doricranites* Hyatt, 1889

Type species, *Ammonites bogdoanus* v. Buch, 1831

Doricranites bogdoanus (v. Buch)
Text-figure 40

Ammonites bogdoanus v. Buch, 1831: pl. 2, fig. 1; v. Buch, 1848: 16, pl. 5, figs. 6, 7.

Goniatites bogdoanus,—de Verneuil, *in* Murchison, Verneuil and Keyserling, 1845: 366, pl. 26, fig. 1.

Ceratites bogdoanus,—Auerbach, 1871: 49, pl. 4, figs. 1–8.

Balatonites bogdoanus,—Mojsisovics, 1882: 87, pl. 80, figs. 1–4.

Dorikranites bogdoanus,—Hyatt, *in* Whiteaves, 1889: 145; Spath, 1934, p. 382, fig. 131; Kummel, *in* Arkell et al., 1957: L147, fig. 180, 2.

Doricranites bogdoanus,—Diener, 1915: 129; Kiparisova, 1947: 169, pl. 43, fig. 1; Astakhova, 1960a: 155; Astakhova, 1960b: 149; Shevyrev and Shlezinger, 1960: 1418; Astakhova, 1962: 70, 75.

Balatonites rossicus Mojsisovics, 1882: 89, pl. 80, fig. 5.

Dorikranites rossicus,—Hyatt, *in* Whiteaves, 1889: 145.

Doricranites rossicus,—Diener, 1915: 129; Kiparisova, 1947: 170, pl. 43, fig. 4; Astakhova, 1960a: 154, 157; Astakhova, 1960b: 149; Shevyrev and Shlezinger, 1960: 1418; Astakhova, 1962: 75.

Doricranites tumulosus Astakhova, 1960a: 154, pl. 35, fig. 2, text-figs. 18, 19; Astakhova, 1960b: 149; Astakhova, 1962: 75.

Doricranites lanceolatus Astakhova, 1960a: 155, pl. 36, fig. 1, text-figs. 20, 21; Astakhova, 1960b: 149.

Doricranites schairicus Astakhova, 1960a: 156, pl. 36, fig. 2, text-figs. 22, 23; Astakhova, 1960b: 149; Astakhova, 1962: 75.

Doricranites ovatus Astakhova, 1960b: 149.

Doricranites discus Astakhova, 1960b: 149.

Doricranites rarecostatus Astakhova, 1960b: 149.

The criteria used to differentiate these several species of *Doricranites* are mainly ornamentation and shape of the whorl section. Examination of the few illustrations of these species suggests that the degree of ornamentation and compression of the conch are highly variable features. One gets the impression from Astakhova's discussion of the stratigraphy of the Scythian formations of the Mangyshlak Peninsula that *Doricranites* is a common fossil and that most if not all of the species listed above occur together. On the basis of experiences with other ornamented Scythian ammonoids in which large numbers of specimens are available, it appears much more plausible that the species listed in the synonymy are part of a single species complex characteristic of a particular horizon in southern U.S.S.R. The only other species assigned to this genus is *D. acutus* which is considerably more involute. The suture of *D. bogdoanus* is illustrated on Figure 40O.

Occurrence. Scythian strata, Mount Bogdo, Mangyshlak Peninsula, and region of Tuarkyr in Turkmenia, southern U.S.S.R.

Doricranites acutus (Mojsisovics)

Balatonites acutus Mojsisovics, 1882: 89, pl. 80, fig. 6.

Dorikranites acutus,—Hyatt, *in* Whiteaves, 1889: 145.

Doricranites acutus,—Diener, 1915: 129; Astakhova, 1960a: 159; Schevyrev and Shlezinger, 1960: 1418.

Subdoricranites discoides Astakhova, 1960a: 158, pl. 35, figs. 3, 4, text-fig. 24 (*nomen nudum* of Bajarunas, 1936).

Subdoricranites orbiculatus Astakhova, 1964: 380, pl. 1, fig. 2.

This species differs from *bogdoanus* in being more compressed, more involute, and generally with a more subdued pattern of ornamentation.

Occurrence. This species along with *D. bogdoanus* is apparently quite common in the *Doricranites* Zone of Astakhova (1960a, b, 1962) at Mount Bogdo, Mangyshlak Peninsula, and the region of Tuarkyr in Turkmenia.

Family DINARITIDAE Mojsisovics, 1882

Genus *Dinarites* Mojsisovics, 1882

Type species, *Ceratites dalmatinus* Hauer, 1865

I recognize here four species of *Dinarites*, all confined to the western region of Tethys. The genus is an important member of the Werfen fauna where it is represented by two species. One of these (*carniolicus*) is the type species of *Carniolites*; this genus is considered to be a synonym of *Dinarites*. The presence of *Dinarites dalmatinus* in the *Subcolumbites* fauna of Chios is an important link in dating the Werfen fauna. The other two species of *Dinarites* (*liatsikasi* and *undatus*) are quite distinct from *dalmatinus* and *carniolicus* but closely related to each other. *Dinarites liatsikasi* is from the *Subcolumbites* fauna of Chios and *D. undatus* from the upper Scythian formations of the Mangyshlak Peninsula.

Dinarites dalmatinus (Hauer)

Plate 58, figures 1–10; Plate 59, figures 1–11; Plate 60, figures 1–8; Text-figure 40

Ceratites dalmatinus Hauer, 1865: 615, pl. 2, figs. 3, 4.

Dinarites dalmatinus,—Mojsisovics, 1882: 8, pl. 1, figs. 7, 8; Kittl, 1903: 18, pl. 2, figs. 1–11, pl. 3, figs. 1, 2; Hyatt and Smith, 1905: 162; Arthaber, *in* Frech, 1906: pl. 34, fig. 17; Diener, 1915: 120; Kummel, *in* Arkell, et al., 1957: L148, fig. 181, 1; Ganev, 1961: 182, pl. 2, figs. 4, 5, 8, pl. 4, fig. 6, pl. 6, fig. 2.

Dinarites dalmatinus var. *extensus* Kittl, 1903: 20, pl. 2, figs. 8, 9.

Dinarites dalmatinus var. *plurimcostatus* Kittl, 1903: 20, pl. 2, figs. 10, 11.

Dinarites dalmatinus var. *externeplanatus* Kittl, 1903: 20, pl. 2, figs. 1, 2.

Plococeras dalmatinum,—Hyatt, 1900: 556; Spath, 1934: 388, fig. 134.

Dinarites nudus Mojsisovics, 1882: 6, pl. 1, figs. 5, 6; Kittl, 1903: 17, pl. 1, figs. 11–13; Diener, 1915: 122; Renz and Renz, 1948: 48, pl. 1, figs. 1, 2.

Dinarites laevis Tommasi, 1902: 347, pl. 13, figs. 4, 5; Kittl, 1903: 13, pl. 1, figs. 1–3, pl. 3, figs. 10, 11; Diener, 1915: 121; Spath, 1934: 386.

Ceratites muchianus Hauer, 1865: 613, pl. 2, figs. 5, 6.

Dinarites muchianus,—Mojsisovics, 1882: 6, pl. 1, fig. 4; Kittl, 1903: 15, pl. 1, figs. 4–8; Arthaber, *in* Frech, 1906: pl. 34, fig. 16; Wittenburg, 1908: 285, pl. 40, fig. 20; Diener, 1915: 121; Spath, 1934: 386, fig. 132; Ganev, 1966: 26, pl. 1, figs. 3a–e.

Dinarites evolutior Kittl, 1903: 16, pl. 1, figs. 9, 10; Diener, 1915: 121; Spath, 1934: 384; Renz and Renz, 1948: 49, pl. 1, fig. 4; Kollárová-Andrusovová, 1961: 29, pl. 3, fig. 2.

Dinarites (?) *angulatus* Kittl, 1903: 22, pl. 3, fig. 9.

Dinarites multicostatus Kittl, 1903: 21, pl. 3, fig. 3; Diener, 1915: 122.
Dinarites tirolitoides Kittl, 1903: 21, pl. 7, figs. 1–3; Diener, 1915: 122.
Dinarites bulgaricus Berndt, 1934: 8, pl. 2, fig. 8.

Aside from *Tirolites* the most common element in the Werfen Formation fauna of the Alps and associated regions is *Dinarites*. A number of species names have been introduced for the dinaritids of this region but basically there are two main species, the first, encompassing predominantly smooth forms (*muchianus*), and the second, ornamented forms with ribs (*dalmatinus*). This second species had been set aside early (Hyatt, 1900) as the type of *Plococeras*. The latter genus had been accepted by Diener (1915) and Spath (1934). However, the selection of *dalmatinus* as the type of *Dinarites* Mojsisovics (1882), by Hyatt and Smith (1905, p. 162), makes *Plococeras* a synonym of *Dinarites*. Whereas the earlier authors wished to separate the smooth and ornamented dinaritids into distinct genera, my own studies bring me to the conclusion that we are dealing here with a single species complex rather than several species in two different genera.

The largest single collection of Werfen Formation dinaritids is that studied by Kittl (1903) and on deposit in the Natural History Museum, Vienna. The measurements of 38 specimens are listed on Table 46 and plotted on Figure 42. These 38 specimens represent the most complete and best preserved specimens available to Kittl, who illustrated most of them. Practically all of the remaining specimens that Kittl assigned to this or that species of dinaritid are very poorly preserved and of somewhat doubtful value. Kittl's illustrations are line drawings of better than average quality but yet lacking in not conveying the nature of preservation, imperfections in the conch, and at times with errors in artistry. All of the earlier illustrations for the Werfen Formation dinaritids are line drawings (e.g. Mojsisovics, 1882), and most of the more modern illustrations are impossible to decipher due to faulty printing and poor paper. Plates 58, 59, and 60 have photographic prints of the principal dinaritids studied by Kittl (1903). The smoothness of some of the specimens is clearly due to weathering and preservation. The number and intensity of the ribs is highly variable. Finally, there is a fair degree of variation in the diameter of the umbilicus (Fig. 42). Study of all of Kittl's specimens assigned to these species of dinaritids (smooth-*muchianus*; ribbed-*dalmatinus*) leads me to believe there is complete gradation from smooth to strongly ribbed forms. This observation plus the fact that all combinations of the morphological grades are found in nearly every fossiliferous locality in the Werfen Formation brings me to the conclusion we are dealing with a single, variable species.

The suture is illustrated on Figure 40H–J.

The dinaritids are a very small element in the *Subcolumbites* fauna of Chios. Renz and Renz (1948) record two specimens of *Dinarites nudus* Mojsisovics and two specimens of *Dinarites evolutior* Kittl. These specimens fall well within the range of variability recognized for *Dinarites dalmatinus* and are thus considered synonyms. The two specimens assigned to *Dinarites liatsikasi* (Renz and Renz, 1948: 49, pl. 1, fig. 3) are of special interest for the close similarity they show to *Dinarites undatus* Astakhova (1960a) from the Mangyshlak Peninsula. Each of these species is distinct from *D. dalmatinus* in ornamentation and in suture.

Occurrence. Primarily in Werfen Formation of the Alps and related regions. A few specimens are known from the *Subcolumbites* fauna of Chios.

Repository. The Werfen Formation specimens are in the Natural History Museum, Vienna; those from the *Subcolumbites* fauna of Chios are in the Natural History Museum, Basel, NHMB J13683–6; the specimens from eastern Bulgaria recorded by Ganev (1961, 1966) are in the Geological Institute of the Bulgarian Academy of

Table 46. Measurements of *Dinarites dalmatinus* (Hauer) from Werfen Formation, Muć, Dalmatia. All specimens are in Natural History Museum, Vienna; data plotted on graph of Figure 42.

	D	W	H	U	W/D	H/D	U/D		D	W	H	U	W/D	H/D	U/D
1.	63.7?	16.7	29.5	16.4	26.2	46.3	25.7	20.	45.4	14.4?	18.8	11.7	31.8	41.5	25.8
2.	59.7	?	27.1	14.4	?	45.5	24.1	21.	45.0	14.0	18.7	13.1	31.1	41.5	29.1
3.	58.7	16.8	26.0	16.4	28.6	44.3	27.9	22.	44.5	10.1	17.3	15.3	22.7	38.9	34.4
4.	56.4	?	23.9	15.7	?	42.4	27.8	23.	44.3	?	20.4	10.1	?	46.0	22.8
5.	56.2	?	25.3	13.0	?	45.0	23.1	24.	44.2	?	20.5	10.8	?	46.4	24.4
6.	55.6	16.6?	22.6	17.5	29.9	40.6	31.5	25.	44.0	8.5	20.7	8.4	19.3	47.0	19.1
7.	54.8?	?	24.8	14.7	?	45.1	26.8	26.	43.5	11.8?	17.4	11.0	27.1	40.0	25.3
8.	53.8	12.3	22.5	13.7	22.9	41.8	25.5	27.	42.8	13.3	16.8	12.8	31.1	39.3	29.9
9.	53.0	12.7	22.7	?	24.0	42.8	?	28.	41.8	?	20.1	6.4	?	48.1	15.3
10.	52.8	14.5	24.4	11.3	27.5	46.2	21.4	29.	41.7	13.0	17.2	11.9	31.2	41.2	28.4
11.	51.4	16.6	19.8	17.7	32.4	38.6	34.5	30.	41.4	9.5?	17.8	11.3	23.0	43.0	27.3
12.	51.4	11.8	23.0	11.2	22.9	44.7	21.8	31.	41.3	13.2	17.7	11.7	32.0	42.9	28.4
13.	50.6?	10.4?	20.8	9.1	20.6	41.1	18.0	32.	41.1	11.2	18.3	9.5	27.3	44.5	23.1
14.	49.0	14.1	21.1	15.0?	28.8	43.1	30.6	33.	39.5	12.3?	16.5	10.8	31.1	41.8	27.3
15.	47.8	?	21.2	12.8	?	44.4	26.8	34.	39.4	12.3	16.0	11.5	31.2	40.6	29.2
16.	47.4	?	24.6?	5.9?	?	52.0	32.3	35.	38.9	9.0	19.4	6.7	23.1	49.9	17.2
17.	47.0?	13.0	23.7	10.2	27.6	50.5	21.7	36.	37.5	6.8	16.3	10.0	18.1	43.5	26.6
18.	46.6	?	20.5	10.2	?	44.0	21.9	37.	34.7	?	15.5	9.2	?	44.7	26.5
19.	45.5	11.4	19.2	10.9	25.1	42.2	24.0	38.	26.2	6.3	13.5	3.8	24.4	51.5	14.5

1. Plesiotype,—Kittl (1903: pl. 2, fig. 5).
2. Plesiotype,—Kittl (1903: pl. 2, fig. 6).
3. Plesiotype,—Kittl (1903, pl. 2, fig. 4).
4. Plesiotype,—Kittl (1903, pl. 2, fig. 7).
5. Unfigured paratype, *Dinarites evolutior* Kittl.
6. Unfigured paratype, *Dinarites multicostatus* Kittl.
7. Plesiotype,—Kittl (1903: pl. 2, fig. 1).
8. Unfigured paratype, *Dinarites evolutior* Kittl.
9. Syntype, *Dinarites evolutior* Kittl (1903: pl. 1, fig. 10).
10. Plesiotype, *Dinarites muchianus*,—Kittl (1903: pl. 1, fig. 6).
11. Figured type, *Dinarites tirolitoides* Kittl (1903: pl. 7, fig. 2).
12. Plesiotype, *Dinarites muchianus*,—Kittl (1903: pl. 1, fig. 8).
13. Syntype, *Dinarites evolutior* Kittl (1903: pl. 1, fig. 9).
14. Unfigured paratype, *Dinarites tirolitoides* Kittl.
15. Unfigured paratype, *Dinarites evolutior* Kittl.
16. Plesiotype, *Dinarites laevis*,—Kittl (1903: pl. 1, fig. 1).
17. Plesiotype,—Kittl (1903: pl. 2, fig. 8).
18. Plesiotype, *Dinarites muchianus*,—Kittl (1903: pl. 1, fig. 7).
19. Plesiotype, *Dinarites nudus*,—Kittl (1903: pl. 1, fig. 13).
20. Figured type, *Dinarites tirolitoides* Kittl (1903: pl. 7, fig. 3).
21. Plesiotype,—Kittl (1903: pl. 2, fig. 9).
22. Figured type, *Dinarites multicostatus* Kittl (1903: pl. 3, fig. 3).
23. Unfigured paratype, *Dinarites evolutior* Kittl.
24. Plesiotype,—Kittl (1903: pl. 2, fig. 11).
25. Plesiotype, *Dinarites laevis*,—Kittl (1903: pl. 3, fig. 11).
26. Plesiotype,—Kittl (1903: pl. 2, fig. 2).
27. Unfigured paratype, *Dinarites tirolitoides* Kittl.
28. Plesiotype, *Dinarites laevis*,—Kittl (1903: pl. 1, fig. 2).
29. Plesiotype,—Kittl (1903: pl. 3, fig. 1).
30. Plesiotype,—Kittl (1903: pl. 2, fig. 10).
31. Plesiotype,—Kittl (1903: pl. 3, fig. 2).
32. Plesiotype, *Dinarites muchianus*,—Kittl (1903: pl. 1, fig. 5).
33. Plesiotype, *Dinarites nudus*,—Kittl (1903: pl. 1, fig. 11).
34. Figured type, *Dinarites tirolitoides* Kittl (1903: pl. 7, fig. 1).
35. Plesiotype, *Dinarites laevis*,—Kittl (1903: pl. 1, fig. 3).
36. Plesiotype, *Dinarites laevis*,—Kittl (1903: pl. 3, fig. 10).
37. Unfigured paratype, *Dinarites evolutior* Kittl.
38. Plesiotype, *Dinarites muchianus*,—Kittl (1903: pl. 1, fig. 4).

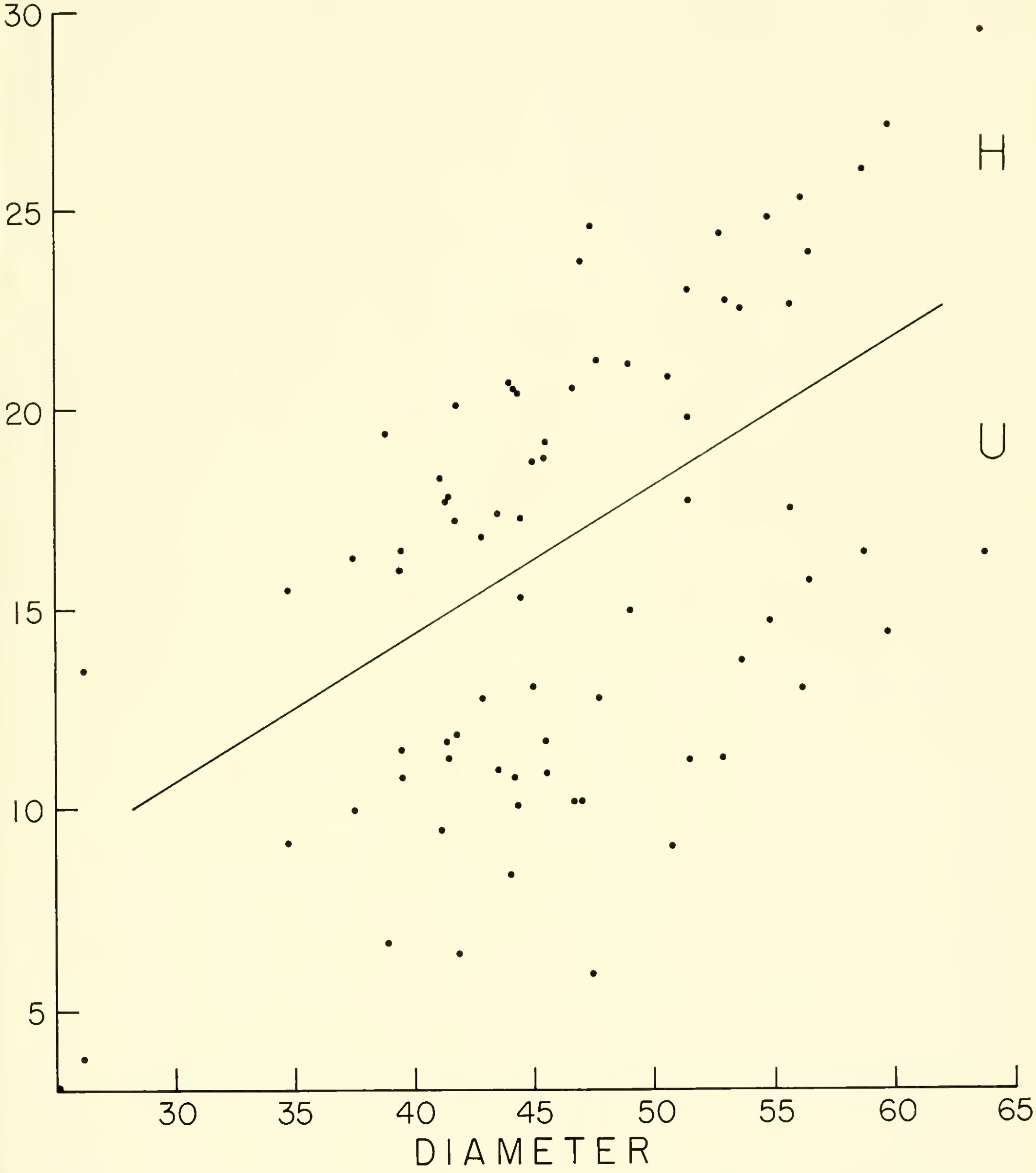

Figure 42. Variation in whorl height (H) and umbilical diameter (U) of *Dinarites dalmatinus* (Hauer), from Werfen Formation, Muć, Dalmatia. The data on this graph are from Table 46.

Science; plaster casts are in the Museum of Comparative Zoology.

TABLE 47. MEASUREMENTS OF SPECIMENS OF *DINARITES CARNIOLICUS* (MOJSISOVICS) FROM THE WERFEN FORMATION, DALMATIA, FIGURED BY KITTL (1903). ALL SPECIMENS ARE IN THE NATURAL HISTORY MUSEUM, VIENNA.

	D	W	H	U	W/D	H/D	U/D
1.	59.3	11.7	26.8	11.2	19.7	45.2	19.2
2.	58.5	?	24.6	15.5	?	42.1	26.5
3.	57.2	?	23.0	16.2	?	40.0	28.3
4.	55.2	10.0±	23.2	10.4	18.1±	42.0	18.8
5.	53.3	12.0?	24.2	12.2	22.5?	45.4	22.9
6.	52.7	10.5?	26.2	10.1	19.9	49.7	19.2
7.	52.6	12.0?	23.7?	10.3?	22.8	45.1?	19.6?

1. Plesiotype,—Kittl (1903: pl. 5, fig. 1).
2. Plesiotype,—Kittl (1903: pl. 5, fig. 2).
3. Holotype, *Tirolites heterophanus* Kittl (1903: pl. 5, fig. 7).
4. Syntype, *Tirolites serratelobatus* Kittl (1903: pl. 5, fig. 6).
5. Plesiotype,—Kittl (1903: pl. 5, fig. 3).
6. Syntype, *Tirolites serratelobatus* Kittl (1903: pl. 5, fig. 5).
7. Plesiotype,—Kittl (1903: pl. 5, fig. 4).

Dinarites carniolicus (Mojsisovics)

Plate 61, figures 1–8

Tirolites carniolicus Mojsisovics, 1882: 65, pl. 1, figs. 2, 3; Kittl, 1903: 35, pl. 5, figs. 1–4; Diener, 1915: 277.

Carniolites carniolicus,—Arthaber, 1911: 241, 250; Spath, 1934: 392, fig. 136; Kummel, *in* Arkell, et al., 1957: L148, fig. 181,3; Kollárová–Andrusovová, 1962: 31, pl. 2, figs. 6a–c, pl. 3, fig. 4.

Tirolites serratelobatus Kittl, 1903: 36, pl. 5, figs. 5, 6; Arthaber, 1911: 250; Diener, 1915: 279.

Tirolites heterophanus Kittl, 1903: 38, pl. 5, fig. 7; Arthaber, 1911: 250.

This species differs from the "smooth" class of dinaritids merely in the presence of fairly prominent tubercles near the ventral shoulder on the adoral part of the phragmocone and body chamber. I can see no justification for a separation at the generic level. Kittl's types of the species brought together here as *D. carniolicus* are illustrated here on Plate 61. The measurements of these specimens are shown on Table 47.

Occurrence. The specimens studied here are from the Werfen Formation, Muć, Dalmatia. The species is also recorded from the same formation in Czechoslovakia (Kollárová–Andrusovová, 1961, 1962).

Repository. The specimens from Muć, studied here, are in the Natural History Museum, Vienna.

Dinarites liatsikasi Renz and Renz

Text-figure 40

Dinarites liatsikasi Renz and Renz, 1947: 60, 75; Renz and Renz, 1948: 49, pl. 1, fig. 3.

Ornamentation and suture (Fig. 40N) differentiate this species from *Dinarites dalmatinus*. The ribbing consists of slightly prosiradiate folds that cross a subtruncate venter. The suture is goniatitic but with a very broad first lateral lobe. The holotype measures 35.7 mm in diameter, 11.2 mm for the width of the adoral whorl, 16.2 mm for the height, and 9.8 mm for the diameter of the umbilicus. This species is very similar to *Dinarites undatus* Astakhova from the Mangyshlak Peninsula. In that species the radial ribs are slightly sinuous and are somewhat enlarged at the umbilical shoulder. The suture, likewise, has a much narrower first lateral lobe. There is a superficial similarity in conch form to *Cucococeras* as indicated by Renz and Renz (1948) but the suture is completely different.

Occurrence. Subcolumbites fauna, Chios.

Repository. Holotype NHMB J13687, paratypes NHMB J13688.

Dinarites undatus Astakhova

Text-figure 40

Dinarites undatus Astakhova, 1960a: 152, pl. 34, fig. 9, text-fig. 17.

A species of the general design and form of *D. liatsikasi* from the *Subcolumbites* fauna of Chios. The general features are discussed under the discussion of that species. The suture is illustrated on Figure 40M.

Occurrence. Tirolites Zone of Astakhova (1960a), Mangyshlak Peninsula.

Genus *Hololobus* (Kittl)

Type species, *Tirolites (Hololobus) monoptychus* Kittl, 1903

Hololobus monoptychus (Kittl)

Plate 70, figures 1, 2; Text-figure 40

Tirolites (Hololobus) monoptychus Kittl, 1903: 33, pl. 4, fig. 9; Diener, 1915: 280.

Hololobus monoptychus,—Spath, 1934: 390, fig. 135; Kummel, *in* Arkell, et al., 1957: L148, fig. 181,5.

The type, and only specimen, of this species and genus is of only fair preservation. It measures 61.8 mm in diameter, 15.7 mm for the width of the adoral whorl, 26.7 mm for the height, and the umbilicus is 16.8 mm in diameter. The critical point of interest with this species is the nature of the ventral lobe. Examination of the type specimen clearly shows that Kittl's drawing of the suture (Fig. 40K) is accurate. Like Kittl, I could not observe any trace of a ventral siphuncle, but this I attribute more to faulty preservation than to anything else.

Occurrence. Werfen Formation, Muć, Dalmatia.

Repository. Natural History Museum, Vienna.

Genus *Pseudodinarites* Hyatt

Type species, *Dinarites mohamedanus* Mojsisovics, 1882

Pseudodinarites mohamedanus (Mojsisovics)

Plate 57, figures 7–9; Plate 62, figure 6

Dinarites mohamedanus Mojsisovics, 1882: 7, pl. 40, fig. 12.

Pseudodinarites mohamedanus,—Hyatt, 1900: 559; Spath, 1934: 387, fig. 133; Kummel, *in* Arkell et al., 1957: L148.

Dinarites (Hercegovites) mohamedanus,—Kittl, 1903: 22, pl. 3, figs. 5–7; Diener, 1915: 122.

This species is supposedly characterized by an evolute, smooth conch with rounded but slightly compressed whorls and suture with ceratitic lobes. Mojsisovics' type specimen was not studied; the specimens assigned to this species by Kittl are illustrated here. These specimens are so poorly preserved they add little to our understanding of this genus or species. The few specimens of this species have all come from the Werfen Formation of the Alps and adjacent regions. Simionescu (1908: 161) recorded a specimen as *Dinarites* cfr. *mohamedanus* from eastern Rumania. This is the only species that has been assigned to this genus. It is quite clear much more data are needed to evaluate the generic relations of the species.

Occurrence. Kittl's specimens illustrated here are from the Werfen Formation, Muć, Dalmatia.

Repository. Kittl's specimens are in the Natural History Museum, Vienna.

Family HELLENITIDAE Kummel, 1952

Genus *Hellenites* Renz and Renz, 1947

Type species, *Tropiceltites praematurus* Arthaber, 1911

Evolute forms with subquadrate whorl section. Lateral sides with rectiradiate to radial ribs which curve adorally on ventral shoulder forming an acute junction with a median ventral keel; ribs may or may not cross keel. Suture with simple pronged ventral lobe, large, denticulated lateral lobe and very simple second lateral lobe, saddles rounded.

This extremely interesting and somewhat anomalous group of late Scythian ammonoids has been the source of an evolving confusion. The group was first recognized by Arthaber (1911) on the basis of two specimens from the *Subcolumbites* fauna of Albania. Neither of these two specimens had the suture preserved, and on the basis of the conch form and ornamentation, he placed them in the genus *Tropiceltites,* a common late Triassic (Carnian) group. A more complete understanding of Arthaber's species was not possible until Renz and Renz (1948) described and illustrated a number of conspecific forms from the *Subcolumbites* fauna of Chios. The suture is well preserved on these Chios specimens and shows that it is very different from the suture of the late Triassic *Tropiceltites.* On this basis, Renz and Renz erected the genus *Hellenites.*

Neither of these authors, however, had taken note of *Pseudharpoceras spiniger* Waagen (1895: 130, pl. 21, fig. 1). This species was based on a single specimen from a horizon Waagen considered to be near the top of his Ceratite formation in the Sheik-Budin Hills of the Trans-Indus Region. Spath (1951: 8) correctly pointed out that the specimens may belong to an Upper Triassic hildoceratid or some other related form.

J. P. Smith (1932) assigned a single specimen from the *Columbites* fauna of southeastern Idaho to the genus *Pseudharpoceras.* Spath (1951: 9) made the claim, and correctly so, that since *Pseudharpoceras* was based on a poorly preserved specimen of uncertain stratigraphic position this genus should be rejected. He then introduced the genus *Pseudarniotites* with *Pseudharpoceras idahoense* Smith (1932: 81, pl. 49, figs. 17–19) as type. Spath was at this time unaware of the genus *Hellenites* Renz and Renz, 1948. *Pseudharpoceras idahoense* is clearly a species of *Hellenites.*

The specimen Waagen described and illustrated as *Pseudharpoceras spiniger* is not in the collections of the Geological Survey of India. There is, however, a partial mold of one side plus a plaster cast. These have been illustrated and discussed by Kummel (1966) and his conclusion was similar to that of Spath: that the genus and species should be rejected.

The *Subcolumbites* fauna of Chios has two species of this genus. One or both of these two species are recognized from the same horizon in Kwangsi, China, from the Primorye Region, eastern Siberia, and the Tobin Formation of Nevada. *Hellenites idahoense* occurs in the *Columbites* fauna of southeastern Idaho.

TABLE 48. MEASUREMENTS OF *HELLENITES PRAEMATURUS* (ARTHABER) FROM *SUBCOLUMBITES* FAUNAS, ALBANIA AND CHIOS.

	D	W	H	U	W/D	H/D	U/D
1.	55.2	13.2	17.7	25.5	23.9	32.1	46.2
2.	53.4	14.3	15.0	29.0	26.6	27.2	54.5
3.	52.3	15.9	16.8	26.2	30.4	32.2	50.1
4.	48.2	12.2	14.0	23.0	25.3	29.1	47.8
5.	47.0?	13.2	14.5?	22.4	28.1?	30.9?	47.6?
6.	46.2	11.7?	13.8	18.6	25.4?	29.9	41.0
7.	44.2	11.6?	14.4	20.5	27.2?	32.6	46.4
8.	43.3	13.0	13.2	21.1	30.0	30.6	48.7
9.	42.1	12.1?	12.8	20.2	28.7?	30.4	47.9?
10.	36.8	10.3	10.5	17.1	28.0	28.5	46.5
11.	36.7	10.7	10.7	17.4	29.2	29.2	47.4
12.	36.3	9.6?	11.9	16.6	26.4?	32.8	45.7
13.	36.2	9.2	10.1	19.2	25.4	27.9	53.0
14.	35.8	10.8	11.0	16.0	30.2	30.7	44.7
15.	34.1	10.7	10.4	14.6?	31.4	30.5	42.8
16.	33.4	10.1	11.1?	14.5	30.2	33.2?	43.4
17.	33.0	9.8	10.9	14.7	29.7	33.0	44.5
18.	25.7	8.0	6.8	13.0	31.1	26.5	50.6
19.	25.7	8.2?	9.1	10.2	31.9?	35.4	39.0
20.	25.5	7.5	7.5	10.8?	29.4	29.4	42.4?
21.	23.3	6.8	7.7	9.6	29.2	33.0	41.2
22.	19.1	7.8?	6.2	8.8	40.8?	32.4	46.0
23.	16.6	6.1	6.0	7.0	36.7	36.1	42.2
24.	13.8	6.3	4.8	5.6?	45.7	34.8	40.6?

1. Syntype, *H. praematurus* var. *aegaeica* Renz and Renz (1947: 60; 1948, pl. 2, fig. 6), NHMB J13664.
2. Holotype, *H. trikkalinoi* Renz and Renz (1947: 60, 75; 1948, pl. 2, fig. 2), NHMB J13668.
3, 9, 15, 18, 24. Unfigured paratypes, *H. trikkalinoi*, Maradovuno, Chios, NHMB J13672.
4, 23. Unfigured paratypes, Kephalovuno, Chios, NHMB J13673.
5. Syntype, *H. praematurus* var. *aegaeica* Renz and Renz (1947: 60; 1948, pl. 2, fig. 8), NHMB J13665.
6, 10, 14, 16, 17, 20, 21. Unfigured paratypes, Maradovuno, Chios, NHMB J13662.
7. Type specimen, *H. trikkalinoi* var. *graeca* Renz and Renz (1947: 60; 1948, pl. 2, fig. 5), NHMB J13674.
8. Plesiotype,—Renz and Renz (1948: pl. 2, fig. 7), NHMB J13660.
11. Plesiotype,—Renz and Renz (1948: pl. 2, fig. 3), NHMB J13661.
12. Syntype, *H. praematurus* var. *aegaeica* Renz and Renz (1947: 60; 1948, pl. 2, fig. 9), NHMB J13667.
13. Paratype, *H. trikkalinoi* Renz and Renz (1948: pl. 2, fig. 4), NHMB J13671.
19. Holotype, *H. praematurus* (Arthaber, 1911: pl. 24 (8), figs. 9a, b), PIUV.
22. Holotype, *H. praematurus* var. (Arthaber, 1911: pl. 24(8), figs. 10a, b), PIUV.

Hellenites praematurus (Arthaber)

Plate 7, figures 1–4; Text-figure 43

Tropiceltites praematurus Arthaber, 1911: 268, pl. 24(8), figs. 9a, b; C. Renz, 1928: 155.

Tropiceltites ? *praematurus* var. Arthaber, 1911: 269, pl. 24(8), figs. 10a, b.

Tropiceltites (?) *praematurus*,—Diener, 1915: 300.

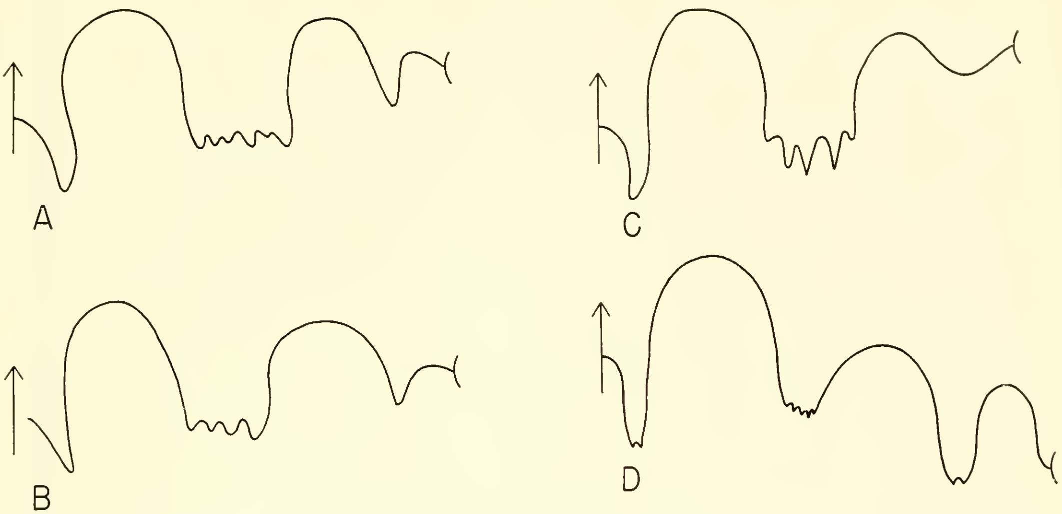

Figure 43. Diagrammatic representation of the suture of: A, *Hellenites trikkalinoi* Renz and Renz (1948: pl. 2, fig. 2b), at a diameter of 35 mm; B, *H. praematurus* (Arthaber),—Renz and Renz (1948: pl. 2, fig. 8b), at a diameter of 30 mm; C, *H. radiatus* Renz and Renz (1948: pl. 2, fig. 13b), at a diameter of 20 mm; D, *H. idahaense* (Smith) (USNM 74994), at a diameter of 13 mm.

Specimens of figures A–C from *Subcolumbites* fauna, Chios; specimen of figure D from *Columbites* fauna of southeast Idaho.

Hellenites praematurus,—Renz and Renz, 1947: 60, 75; Renz and Renz, 1948: 44, pl. 2, figs. 3–3a, 7–7a; Kummel, *in* Arkell et al., 1957: L149, figs. 181, 6a–c.
Hellenites praematurus var. *aegaeica* Renz and Renz, 1947: 60; Renz and Renz, 1948: 45, pl. 2, figs. 6–6b, 8–8b, 9–9a.
Hellenites trikkalinoi Renz and Renz, 1947: 60, 75; Renz and Renz, 1948: 46, pl. 2, figs. 1–1a, 2–2b, 4–4b.
Hellenites trikkalinoi var. *graeca* Renz and Renz, 1947: 60; Renz and Renz, 1948: 46, pl. 2, figs. 5–5b.
Hellenites cf. *praematurus*,—Chao, 1959: 145, pl. 41, figs. 1, 2 (not 3, 4).

This species was established by Arthaber on the basis of two specimens, one of which he considered to be a variety. The preservation of both of these specimens leaves much to be desired. The measurements are as follows:

D	W	H	U	W/D	H/D	U/D
25.7	8.2?	9.1	10.2	31.9?	35.4	39.7

Holotype—Arthaber, 1911: pl. 24(8), fig. 9a, b.

19.1	7.8?	6.2	8.8	40.8?	32.5	46.1

Paratype—Arthaber, 1911: pl. 24(8), fig. 10 a, b.

The suture is not preserved on either of these specimens.

This anomalous late Scythian species remained somewhat of a problem until the discovery of the contemporaneous *Subcolumbites* fauna from Chios. A number of specimens of *H. praematurus* have been well illustrated by Renz and Renz (1948). In addition to *H. praematurus,* these authors recognized a variety and another species based mainly on the relative prominence of the ribs. It is apparent on examination of the large number of specimens in the fauna studied by Renz and Renz that there is wide variation in rib prominence, and that there are gradational forms connecting the species and varieties recognized. In the other morphological features, as width, height and umbilical diameter, there is relatively little variation (see Table 48 and Figure 44). The sutures are illustrated on Figures 43 A, B.

Chao (1959) obtained two fragmentary

specimens from separate localities of the *Subcolumbites* horizon, which he described as *H.* cf. *praematurus.* One of these specimens (Chao, 1959: pl. 41, figs. 1, 2) is identical in rib pattern, conch shape, etc., to *H. praematurus.* Though a suture is not preserved on this specimen, I believe it to be a valid representative of *H. praematurus.* The second specimen is more fragmentary and of poorer preservation. The rib pattern, however, compares favorably with *H. radiatus.*

Occurrence. Subcolumbites faunas of Albania, Chios, and Kwangsi, China (Chao collections 542a, 546).

Repository. Holotype and paratype, in the Paleontological Institute, Vienna; specimens from Chios, plesiotypes, Renz and Renz (1948: pl. 2, figs. 3–3a) NHMB J13661, (1948: pl. 2, figs. 7–7a) NHMB J13660; unfigured specimens from Maradovuno NHMB J13662; unfigured specimens from Kephalovuno NHMB J13663; type specimens, *H. praematurus* var. *aegaeica* Renz and Renz (1948: pl. 2, fig. 6) NHMB J13664, (pl. 2, figs. 8–8a) NHMB J13665, (pl. 2, fig. 8b) NHMB J13666, (pl. 2, fig. 9) NHMB J13667; holotype *H. trikkalinoi* Renz and Renz (1948: pl. 2, fig. 2–2a) NHMB J13668; paratypes, Renz and Renz (1948: pl. 2, fig. 1) NHMB J13670, (pl. 2, fig. 4) NHMB J13671, (pl. 2, fig. 2b) NHMB J13669; unfigured paratypes from Maradovuno NHMB J13672, from Kephalovuno NHMB J13673; type specimen *H. trikkalinoi* var. *graeca* Renz and Renz (1948: pl. 2, fig. 5) NHMB J13674.

Hellenites radiatus Renz and Renz
Text-figure 43

Hellenites (Pallasites) radiatus Renz and Renz, 1947: 60, 75; Renz and Renz, 1948: 47, pl. 2, figs. 12–12b, 13–13b.

Hellenites (Pallasites) striatus Renz and Renz, 1947: 60, 75; Renz and Renz, 1948: 47, pl. 2, figs. 11–11a.

Hellenites (Pallasites) striatus var. *densicostata* Renz and Renz, 1947: 60, 75; Renz and Renz, 1948: 48, pl. 2, figs. 10–10b.

Hellenites cf. *praematurus* Chao, 1959: 145, pl. 41, figs. 3, 4 (not 1 and 2).

TABLE 49. MEASUREMENTS OF *HELLENITES RADIATUS* RENZ AND RENZ FROM THE *SUBCOLUMBITES* FAUNA OF CHIOS.

	D	W	H	U	W/D	H/D	U/D
1.	43.7	10.9	13.5	20.5	24.9	30.9	46.9
2.	37.1	10.5	12.7	15.7	28.3	34.2	42.3
3.	33.4?	8.5	11.7	8.2	25.4?	35.0?	24.6?
4.	31.2	8.5	10.1	14.1	27.2	32.4	45.2
5.	30.2	7.2	8.7	14.7	23.8	28.8	48.7
6.	29.5	8.5	9.8	12.6	28.8	33.2	42.7
7.	28.7	8.2	10.0	12.5	28.6	34.8	43.6
8.	27.8?	7.0	8.3	13.2	25.2?	29.9?	47.5?
9.	26.7	6.1	7.8	12.7	22.8	29.2	47.6
10.	22.8	5.4	7.4	10.3	23.7	32.5	45.2
11.	22.3	6.8	6.4	10.1	30.5	28.7	45.3
12.	17.8	5.1?	5.5	8.5	28.7?	30.9	47.8

1, 2. Unfigured paratypes, Maradovuno, Chios, NHMB J13678.
3. Holotype, *H.* (*Pallasites*) *striatus* var. *densicostata* Renz and Renz (1947: 60, 75; 1948: pl. 2, fig. 10), NHMB J13681.
4. Paratype, Renz and Renz (1947: 60, 75; 1948, pl. 2, fig. 13), NHMB J13677.
5, 6, 11, 12. Unfigured paratypes, *H.* (*Pallasites*) *striatus*, Maradovuno, Chios, NHMB J13680.
7. Holotype, Renz and Renz (1947: 60, 75; 1948: pl. 2, fig. 12), NHMB J13675.
8. Holotype, *H.* (*Pallasites*) *striatus* Renz and Renz (1947: 60, 75; 1948: pl. 2, fig. 11), NHMB J13679.
9, 10. Unfigured paratypes, *H.* (*Pallasites*) *striatus* var. *densicostata*, Maradovuno, Chios, NHMB J13682.

This species is exactly like *H. praematurus* except that the ribs are radial instead of rursiradiate. Renz and Renz (1948) distinguished within this group two species under a separate subgenus of *Hellenites.* The two species were separated on the basis of rib prominence, but again the collections have a number of transitional forms in this character. The suture (Fig. 43H) is essentially the same as in *H. praematurus.*

The only distinguishing feature between *H. praematurus* and *H. radiatus* is the character of the lateral ribs. This is presumably a valid species criterion but not one to warrant erection of a separate subgenus.

This species is not as abundant in the Chios fauna as *H. praematurus.* As in the latter species, *H. radiatus* does not exhibit any marked variability in the basic conch dimensions. On Table 49 are measurements of 12 specimens including the primary

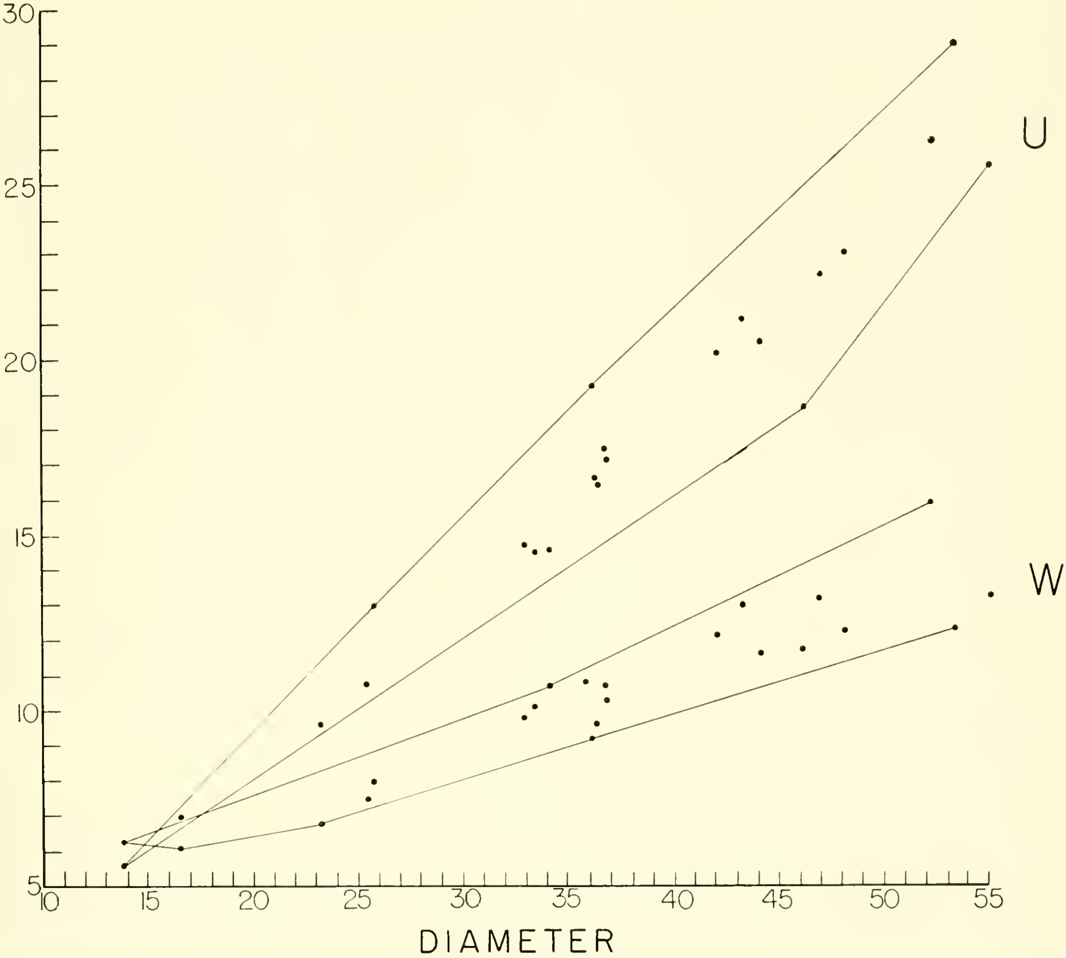

Figure 44. Variation in whorl width (W) and umbilical diameter (U) of *Hellenites praematurus* (Arthaber), from the *Subcolumbites* fauna of Albania and Chios. The data on this graph are from Table 48.

types. The measurements are plotted on Figure 44.

One of the specimens from a *Subcolumbites* horizon in Kwangsi, China, that Chao (1959: pl. 41, figs. 3, 4) assigned to *H.* cf. *praematurus* has radial ribs and should be assigned to *H. radiatus.* The specimen is poorly preserved and lacks a suture, but the pattern of ornamentation, etc., is so distinctive that this conclusion seems justified.

The Tobin Formation of Nevada has yielded one specimen, 18 mm in diameter, that appears to be identical to the other representatives of this species. No suture is preserved, but the degree of involution, ornamentation, etc., are identical.

The species of *Hellenites* from Chios and Kwangsi are from *Subcolumbites* faunas. There are two older species which need to be attached to this genus. These are *H. idahoense* (Smith, 1932: 81, pl. 49, figs. 13–19) from the *Columbites* fauna of southeastern Idaho, and *H. inopinatus* Kiparisova (1958a) from the Primorye Region at a horizon equivalent to the *Columbites* Zone of Idaho.

Occurrence. The holotype and paratype from the *Subcolumbites* fauna of Chios; from *Subcolumbites* fauna, Naliling, one kilometer northeast of Lolou, Lingolo district, Kwangsi, China; upper part of Tobin Formation, south end of Tobin Range, Nevada.

Repository. Holotype, Renz and Renz (1948: pl. 2, figs. 12–12a) NHMB J13675; paratypes, Renz and Renz (1948: pl. 2, fig. 12b) NHMB J13676, (pl. 2, figs. 13–13b) NHMB J13677; unfigured paratypes from Maradovuno NHMB J13678; holotype, *H. (Pallasites) striatus* Renz and Renz (1948: pl. 2, figs. 11–11a) NHMB J13679; unfigured paratypes NHMB J13680; type specimens *H. (Pallasites) striatus* var. *densicostata* Renz and Renz (1948: pl. 2, figs. 10–10b) NHMB J13681; unfigured paratypes NHMB J13682; specimen from Tobin Formation MCZ 9654.

Hellenites idahoense (Smith)

Plate 53, figures 13, 14; Text-figure 43

Pseudharpoceras idahoense Smith, 1932: 81, pl. 49, figs. 17–19.

Pseudarniotites idahoense,—Spath, 1951: 9.

Smith based his species on a small fragmentary specimen 19 mm in diameter, and extensive collecting from the same horizon in southeastern Idaho has not yielded any additional specimens. This species is very similar in its basic morphological features to *H. radiatus.* The differences are mainly seen in the character of the ribs on the venter, the character of the keel, and the suture (Fig. 43D).

Most other occurrences of *Hellenites* are from *Subcolumbites* faunas of latest Scythian age. This species is from the *Columbites* Zone.

Occurrence. Middle shale member, Thaynes Formation, *Columbites* Zone, Paris Canyon, southeastern Idaho.

Repository. Holotype, USNM 74994.

Hellenites inopinatus Kiparisova

Hellenites (?) *inopinatus* Kiparisova, 1958a: 13, fig. 9; Kiparisova, 1961: 169, pl. 33, fig. 4.

Kiparisova had six specimens upon which to base her species, but unfortunately none of these yielded a suture, nor was the preservation of the specimens particularly good. On the basis of the illustrations and figures of the holotype, this species is quite similar to *H. radiatus* Renz and Renz from the *Subcolumbites* fauna of Chios. Kiparisova (1961) did not give precise stratigraphic data on her species, but Zakharov (personal communication) tells me that the species is in his *Neocolumbites insignis* Subzone which is correlative with the *Columbites* fauna of southeast Idaho. Kiparisova's species is not very similar to *Hellenites idahoense* (Smith) from the *Columbites* fauna of southeast Idaho.

Occurrence. Neocolumbites insignis Subzone, Primorye Region.

Family BEYRICHITIDAE Spath, 1934

Genus *Beyrichites* Waagen, 1895

Type species, *Ammonites reuttensis* Beyrich, 1867

Beyrichites laurae Renz and Renz

Text-figure 45

Beyrichites laurae Renz and Renz, 1948: 62, pl. 8, fig. 1.

Beyrichites praematurus Renz and Renz, 1948: 61, pl. 7, fig. 5.

The authors of this species were fully cognizant that the presence of this typical Anisian genus in their Chios fauna raised serious questions. They briefly discussed the possibility of mixing and reworking versus the true existence of this genus in the late Scythian. On the basis of the data available, I have elected to accept this species as a member of the late Scythian Chios fauna. Each of the two species of this genus recognized by Renz and Renz was based on a single specimen; I can see no significant difference between these two specimens.

Occurrence. Subcolumbites fauna of Chios.

Repository. Holotype of *Beyrichites laurae*, NHMB J13712, holotype of *B. praematurus,* NHMB J13711.

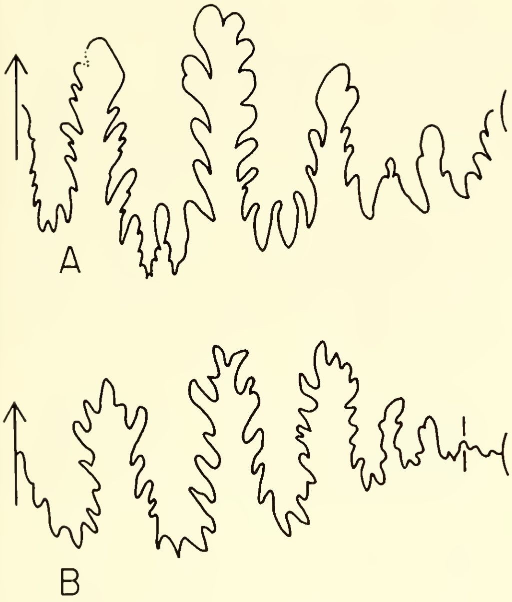

Figure 45. Diagrammatic representation of the suture of: A, *Eogymnites arthaberi* (Diener), from holotype, at a diameter of 75 mm, from *Subcolumbites* fauna of Albania; B, *Beyrichites laurae* Renz and Renz (1948: pl. 8, fig. 1b), at a diameter of 42 mm, from *Subcolumbites* fauna of Chios (NHMB J13712).

Superfamily PINACOCERATACEAE Mojsisovics, 1879

Family GYMNITIDAE Waagen, 1895

Genus *Eogymnites* Spath, 1951

Type species, *Japonites arthaberi* Diener, 1915

Eogymnites arthaberi (Diener)

Plate 21, figures 1, 2; Text-figure 45

Japonites sugriva Diener var. Arthaber, 1911: 231, pl. 20(4), fig 4.

Japonites arthaberi Diener, 1915: 158 (= *J. sugriva*,—Arthaber non Diener); Kummel, *in* Arkell et al., 1957: L185, fig. 214,4.

Japonites decipiens Spath, 1951: 172 (= *J. sugriva*,—Arthaber non Diener).

Arthaber's type and only specimen of this unusual Scythian species is only modestly well preserved, consisting mainly of phragmocone; the adoral 30 mm is body chamber. The specimen measures approximately 89 mm in diameter, 23.4 mm for the width of the adoral whorl, 29 mm for the height, and 36.4 mm for the diameter of the umbilicus. The whorls are compressed with convex whorl sides converging to a narrowly rounded venter. The maximum width is at the umbilical shoulder. The umbilical wall is low, rounded, and slopes to the umbilical seam at a steep angle. The shell is preserved only in part, and very poorly; it is apparently smooth except for slightly sinuous growth lines.

Spath (1951: 172) expressed concern over Arthaber's (1911: pl. 20(4), fig. 4c) illustration of the suture. A new drawing made from the type specimen is illustrated here on Figure 45A. As with nearly all the specimens from the *Subcolumbites* fauna from Albania and Chios, the suture can be developed only by grinding. The suture illustrated here I believe to be a fairly accurate representation and does not differ from that reproduced by Arthaber to any significant degree.

There is no other Scythian ammonoid comparable to this species.

Occurrence. *Subcolumbites* fauna, Kčira, Albania.

Repository. Paleontological Institute, University of Vienna.

Family HUNGARITIDAE Waagen, 1895

Genus *Prohungarites* Spath, 1934

Type species, *Prohungarites similis* Spath (= *Hungarites* cf. *middlemissii* Diener,—Welter, 1922)

Prohungarites crasseplicatus (Welter)

Text-figure 46

Hungarites crasseplicatus Welter, 1922: 147, pl. 168(14), figs. 1–6.

Prohungarites crasseplicatus,—Spath, 1934: 244; Spath, 1951: 20; Kummel, 1961: 525.

Hungarites cf. *middlemissii* Diener,—Welter, 1922: 146, pl. 13, figs. 6–9, 18.

Prohungarites similis Spath, 1934: 327; Spath, 1951: 19; Kummel, *in* Arkell et al., 1957: L155, fig. 186,7.

It was for this morphologic group from Timor that Spath (1934) introduced the genus *Prohungarites*. Welter (1922) had included in the genus *Hungarites* three species from the blocks with manganese coated fossils from Nifoekoko, Timor; these were cf. *middlemissii* Diener, *crasseplicatus* and *tuberculatus*. Spath (1934: 327) introduced the species name *similis* for cf. *middlemissii*,—Welter (non Diener). The first two of these species are combined here. They were originally separated merely on differences in the intensity of the ribbing. Even Welter (1922: 147) discussed the gradational aspects of the species and illustrated one specimen (Welter, 1922: pl. 167(13), figs. 10, 11) as a transitional form between *P. middlemissii* and *P. crasseplicatus*. Restudy of Welter's types show that his descriptions and illustrations are quite adequate. The measurements of Welter's types are as follows:

	D	W	H	U	W/D	H/D	U/D
1.	58.5	17.5	23.4	15.1	29.9	40.0	25.8
2.	38.7	14.2	16.5	10.6	36.7	42.6	27.4
3.	36.1	11.5	15.0	10.5	31.9	41.6	29.1
4.	35.4	11.4	16.0?	8.2?	32.2	45.2?	23.2?
5.	33.6	11.9	13.2	11.2	35.4	39.3	33.3
6.	30.0	10.1	11.9	9.5	33.7	39.7	31.7

1. Welter (1922: pl. 13, figs. 6–9) GPIBo 226a.
2. Welter (1922: pl. 14, figs. 1–3) GPIBo 228a.
3. Welter (1922: pl. 13, figs. 10–11) GPIBo 227.
4. Welter (1922: pl. 13, fig. 18) GPIBo 226b.
5. Welter (1922: pl. 14, figs. 4, 5) GPIBo 228b.
6. Welter (1922: pl. 14, fig. 6) GPIBo 228c.

The upper part of the Thaynes Formation along Hammond Creek in southeastern Idaho has yielded about 30 poorly preserved specimens which are very similar to the Timor *P. crasseplicatus*. The whorls of the Idaho species are fastigate only on the early volutions. The mature volutions have rounded venters. The slightly sinuous ribs on most of the specimens are comparable to those on Welter's transitional specimen between *P. similis* and *P. crasseplicatus* but are prosiradiate, not radial. The largest specimen, approximately 65 mm in diameter, consisting of a half volution of body chamber, has the blunt lateral ribs like Welter's *P. crasseplicatus* (Welter, 1922: pl. 14, figs. 1–3). The sutures in the Timor and Idaho specimens are likewise similar (Fig. 46).

Occurrence. The specimens from Timor came from the limestone with manganese coated fossils, Nifoekoko.

Repository. Holotype *P. similis* Spath (= *Hungarites* cf. *middlemissii*,—Welter, 1922: pl. 13, figs. 6–9) GPIBo 226a; paratype, *Hungarites* cf. *middlemissii*,—Welter (1922: pl. 13, fig. 18) GPIBo 226b; syntype *P. crasseplicatus* (Welter, 1922: pl. 14, figs. 1–3) GPIBo 228a, (pl. 14, figs. 4, 5) GPIBo 228b, (pl. 14, fig. 6) GPIBo 228c; Welter's transitional specimen (1922: pl. 13, figs. 10, 11) GPIBo 227.

Prohungarites cf. crasseplicatus (Welter)

Prohungarites cf. *crasseplicatus*,—Kummel, 1966: 400, pl. 3, figs. 11, 12.

Four small phragmocones from West Pakistan differ from the Timor *P. crasseplicatus* principally in the absence of any indication of a keel along the central part of the venter on the mature whorls. In all other conch features, such as shape of the whorl section, shape of the ventral and umbilical shoulders, and nature of the umbilical wall, it is very similar. The suture is likewise essentially the same. The other Timor species, *Prohungarites tuberculatus*, is more robust with a more highly developed ornamental pattern. There is a strong morphological similarity to *Prohungarites gutstadti* n. sp. from the Upper Thaynes Formation of southeast Idaho. Both species have acute venters only on the earliest volutions and rounded venters on the later volutions.

Occurrence. Narmia Member of the Mianwali Formation, Narmia Nala, Surghar Range, West Pakistan.

Repository. MCZ 9606, 9607.

Prohungarites tuberculatus (Welter)
Text-figure 46

Hungarites tuberculatus Welter, 1922: 148, pl. 167(13), figs. 12–17.

Prohungarites tuberculatus,—Spath, 1934: 244; Kummel, 1961: 525.

The basic form of the conch in this species is very much like *P. crasseplicatus*

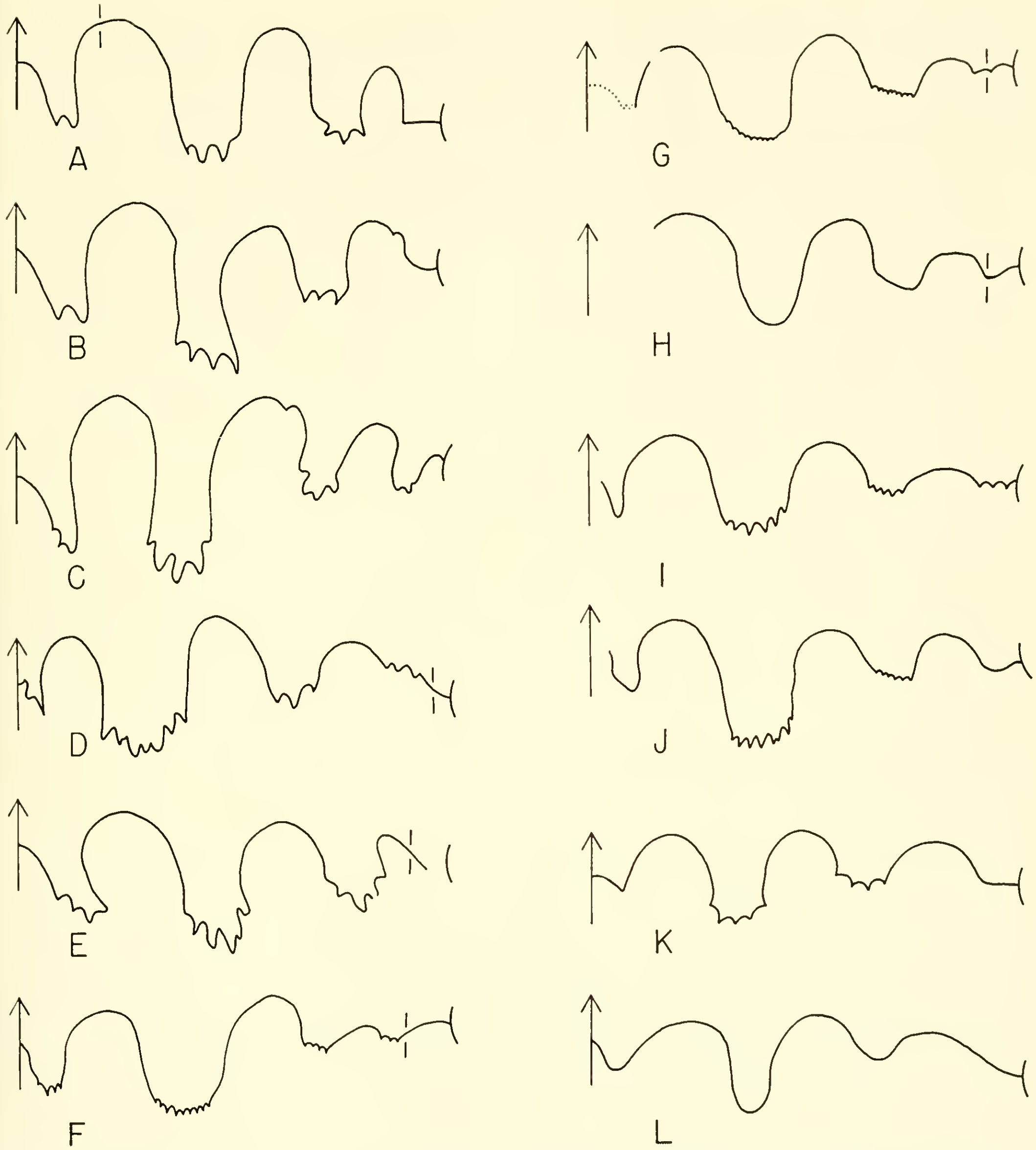

Figure 46. Diagrammatic representation of the suture of: A, *Hungarites* cf. *middlemissii* Diener,—Welter (1922: pl. 13, fig. 18), from Block E, Nifoekoko, Timor; B, *Hungarites crasseplicatus* Welter (1922: pl. 14, fig. 6), from Block E, Nifoekoko, Timor; C, *Hungarites tuberculatus* Welter (1922: pl. 13, fig. 12), from Block E, Nifoekoko, Timor; D, *Kiparisovites carinatus* Astakhova (1964: 379, fig. 1d), from *Doricranites* Zone of Astakhova, Mangyshlak Peninsula; E, *Prohungarites* (?) *popovi* Kiparisova (1961: fig. 113), from Anisian strata of the Primorye Region, at a whorl height of 13 mm; F, *Prohungarites mckelvei* n. sp. from Upper Thaynes Formation, Hammond Creek, southeast Idaho, at a whorl height of 17 mm (MCZ 9646); G, *Prohungarites gutstadti* n. sp., from Upper Thaynes Formation, Hammond Creek, southeast Idaho, at a whorl height of 13 mm (holotype MCZ 9475); H, *Prohungarites* sp. indet., from Upper Thaynes Formation, Hammond Creek, southeast Idaho, at a whorl height of 15 mm (MCZ 9648); I, *Prohungarites* sp. indet., from Upper Thaynes Formation, Hammond Creek, southeast Idaho, at a whorl height of 26 mm; J, *Dalmatites morlaccus* Kittl (1903: pl. 4, fig. 6), from Werfen Formation, Dalmatia; K, *Dalmatites kittli* n. sp., from *Columbites* Zone, Paris Canyon, southeast Idaho, at a whorl height of 10 mm (MCZ 9499).

except that it is more evolute and the whorls more inflated. The big difference in these species is in the ornamentation. This species has coarse, conspicuous ribs with a node just above the umbilical shoulder. This pattern of ornamentation commences at an early growth stage, as can be seen in the umbilical region of Welter's holotype and in the small specimen illustrated by Welter (1922: pl. 13, figs. 16, 17). The measurements of Welter's two specimens are as follows:

D	W	H	U	W/D	H/D	U/D
47.5	16.6	18.0	17.5	34.9	37.9	36.8
7.3	?	2.5	2.8	?	34.2	38.4

The first of these measurements is for the holotype and the second is for the paratype.

The suture is illustrated on Figure 46C.

Occurrence. In the limestone with black manganese coated fossils, Nifoekoko, Block E, Timor.

Repository. Holotype GPIBo 229a; paratype GPIBo 229b.

Prohungarites middlemissii (Diener)
Plate 25, figures 3–8

Hungarites middlemissii Diener, 1913: 23, pl. 3, figs. 5–7; Diener, 1915: 153; Spath, 1934: 33.
Prohungarites middlemissii,—Kummel, 1961: 525.

Diener (1913) stated he had approximately 40 specimens of this species collected from a loose block at Pastannah, Kashmir. Of these only the three figured syntypes (Diener, 1913: pl. 3, figs. 5–7) are preserved in the collection of the Geological Survey of India. The disposition of the other specimens is not known.

Even though the suture is unknown, the general conch morphology clearly indicates that this is a valid species of *Prohungarites*. In the degree of involutions and ornamentations, it is quite similar to *P. mckelvei* but is unique in the widening of the ventral part of the whorl in the mature stages and in the acquisition of nodes on the ribs. *Prohungarites crasseplicatus* has a much more robust whorl section, is more evolute, and has more pronounced ornamentation. This species strongly suggests the presence of a horizon younger than the *Hedenstroemia* beds in Kashmir. Final evaluation on the biologic affinities of this species and its stratigraphic position will have to await new field investigations and collections.

Occurrence. Loose block, Pastannah, Kashmir.

Repository. Syntype (Diener, 1913: pl. 3, fig. 5) GSI 11276, (pl. 3, fig. 6) GSI 11277, (pl. 3, fig. 7), GSI 11278.

Prohungarites carinatus (Astakhova)
Text-figure 46

Kiparisovites carinatus Astakhova, 1964: 379, pl. 1, fig. 1.

This is clearly a species of *Prohungarites* of the general form of *P. mckelvei* and *P. crasseplicatus*; just why its author introduced a new genus for her two fragmentary specimens is hard to tell. The suture is shown on Figure 46D.

Occurrence. *Doricranites* Zone (of Astakhova, 1960a, b), Mangyshlak Peninsula, Karatauchik Range.

Prohungarites mckelvei n. sp.
Plate 35, figures 1–5, 8, 9; Text-figure 46

Prohungarites n. sp. cf. *P. similis*,—Kummel, 1954: 187.

This is the most common species in the upper member of the Thaynes Formation at Hammond Creek, Bear River Range, southeast Idaho. The collection contains a couple of hundred specimens, most of which, however, are not well preserved. In addition, the Tobin Formation, Tobin Range, Nevada, has yielded 10 fragmentary and poorly preserved specimens.

The conch is involute, compressed, with a distinct knife-edged venter. A remarkable feature of this species is the high degree of constancy in basic conch proportions. The venter has a distinct fastigate appearance except that the ventral shoulders are rounded and not angular. The lateral areas are broadly convex. The umbilical shoulder is acutely rounded and the umbilical wall is vertical.

The conch is essentially smooth, except for extremely faint, moderately spaced, falcoid ribs. Within the small umbilicus only the umbilical shoulders and wall of the preceding volutions are visible. No ornamentation of any kind is visible in the umbilical area.

The suture is shown on Figure 46F.

This new Idaho species displays some morphological similarity to *Prohungarites crasseplicatus* from the manganese coated beds of Nifoekoko, Timor, but a more marked similarity to *Prohungarites middlemissii* from an unknown horizon in Kashmir. The Timor species (*P. crasseplicatus*) is more inflated, more evolute, with sharper ventral shoulders, and with a tendency towards more robust ornamentation. In spite of these differences, the morphological relationships of *P. mckelvei* and *P. crasseplicatus* are very close. The Kashmir species (*P. middlemissii*) differs mainly in that on the outer volutions the greatest width of the whorls shifts to the region of the ventral shoulders. The degree of involution, the subdued falcoid ribs, and nature of the venter are strikingly similar to *P. mckelvei.* My specimens from the Tobin Formation, though poorly preserved and fragmentary, cannot be separated from the Idaho forms. N. J. Silberling of the U.S. Geological Survey has kindly shown the author some specimens of *Prohungarites* he collected from the lower part of the Tobin Formation, Tobin Range, Nevada (U.S.G.S. locality 2565). These specimens are very much like the species described here but are slightly more inflated in whorl section; they possibly represent a new species.

Occurrence. Upper member of Thaynes Formation, Hammond Creek, Bear River Range, southeast Idaho; upper part Tobin Formation, Tobin Range, Nevada.

Repository. Specimens from Hammond Creek: Holotype MCZ 9466 (Pl. 35, figs. 1, 2); figured paratypes MCZ 9467 (Pl. 35, fig. 3, 4), MCZ 9468 (Pl. 35, fig. 5), MCZ 9469 (Pl. 35, figs. 8, 9); unfigured paratypes MCZ 9646; unfigured specimens from Tobin Formation, MCZ 9651.

Prohungarites gutstadti n. sp.

Plate 36, figures 3, 14, 15; Text-figure 46

Prohungarites cf. *crasseplicatus* Kummel, 1954: 187; Kummel, 1966: 400.

This species is represented by 30 or more specimens most of which, unfortunately, are poorly preserved. This species has the general conch form of *P. crasseplicatus.* It differs in that the venter on the mature volutions is rounded and not fastigate. A blunt sharpened venter is present up to a diameter of approximately 15 mm, as seen in the specimen of Plate 36, figures 14, 15, but at some stage after that the venter becomes rounded. The second major difference is that the ribs are prosiradiate and not radial. The range of ribbing pattern is much the same in the two species. The suture is shown on Figure 46G.

This species is remarkably similar to the specimens assigned to *Prohungarites* cf. *crasseplicatus* from the Narmia Member of the Mianwali Formation in the Surghar Range of West Pakistan (Kummel, 1966). In that species the sharpened venter likewise is confined to the earlier volutions, the more mature volutions having a rounded venter. The ribs in the Pakistan species are radial rather than prosiradiate. The restriction of the sharpened venter to the earliest volutions differentiates these two species from all others assigned to *Prohungarites.*

Occurrence. Upper Thaynes Formation, Hammond Creek, Bear River Range, southeast Idaho.

Repository. Holotype MCZ 9475 (Pl. 36, fig. 3); figured paratype MCZ 9481 (Pl. 36, figs. 14, 15); unfigured paratypes MCZ 9645.

Prohungarites sp. indet.

Plate 38, figures 4, 5; Text-figure 46

The collections from the Hammond Creek locality of the Thaynes Formation, and from the upper part of the Tobin Formation in the Tobin Range, Nevada, contain, in association with *Prohungarites mckelvei*, several poorly preserved fragments that are clearly a new and distinctive species of ammonite. However, because of the fragmentary nature of the specimens no new name is introduced. The whorls are very rapidly expanding with radial to slightly prosiradiate ribs that are greatly enlarged in the general region of the umbilical shoulder. The venter is fairly broad and fastigate. The suture is shown on Figure 46H, I.

This form is completely different from the associated *Prohungarites mckelvei* and *Prohungarites gutstadti* and is quite different from the other species of *Prohungarites* reported to date. The pattern of ribbing and the rapidly expanding whorls at first suggested a relationship to *Arctoprionites*. In that genus, however, in so far as we know, the venter is truncate and never fastigate. The suture of the form recorded here is more prohungaritid in aspect.

Occurrence. Upper Thaynes Formation, Hammond Creek, Bear River Range, southeast Idaho; upper Tobin Formation, south end Tobin Range, Nevada.

Repository. Figured specimens from southeast Idaho MCZ 9474 (Pl. 36, figs. 1, 2), MCZ 9647 (Pl. 38, figs. 4, 5); unfigured specimens from southeast Idaho MCZ 9648; specimens from Tobin Range MCZ 9652.

Genus *Dalmatites* Kittl, 1903

Type species, *Dalmatites morlaccus* Kittl, 1903

Dalmatites morlaccus Kittl

Plate 56, figures 1–8; Text-figure 46

Dalmatites morlaccus Kittl, 1903: 73, pl. 4, figs. 3–7; Diener, 1915: 115; Spath, 1951: 20; Kummel, *in* Arkell, et al., 1957: L156, fig. 187, 7.

The four specimens of this species illustrated by Kittl (1903: pl. 4, figs. 4–7) are still preserved. The photographs of these type specimens reproduced here on Plate 56 show that the preservation is no more than fair to poor. The measurements of these four specimens are as follows:

	D	W	H	U	W/D	H/D	U/D
1.	69.0	15.6	39.0	5.1	22.6	56.5	7.4
2.	53.0	10.0?	27.1	2.7	18.9?	51.1	5.1
3.	49.1	8.4	27.1	3.0	17.1	55.2	6.1
4.	43.0	9.3	23.0?	?	21.6	53.5?	?

1. Paralectotype, Kittl (1903: pl. 4, fig. 7).
2. Paralectotype, Kittl (1903: pl. 4, fig. 6).
3. Lectotype, Kittl (1903: pl. 4, fig. 4).
4. Paralectotype, Kittl (1903: pl. 4, fig. 5).

The suture is reproduced here in Figure 46J.

This species is known only from the Werfen Formation of Europe. The only other species of this genus, *D. kittli*, is known only from a single specimen from the *Columbites* fauna of southeastern Idaho. The two species are very similar.

Occurrence. Werfen Formation, Muć, Dalmatia.

Repository. Natural History Museum, Vienna.

Dalmatites kittli n. sp.

Plate 55, figures 7, 8; Text-figure 46

This species is established on a single specimen from the *Columbites* fauna of southeastern Idaho. The conch is smooth, compressed, involute, and is entirely phragmocone. It measures 33.5 mm for the width of the last whorl, and the umbilicus is 3.8 mm in diameter. The venter is acute, the lateral areas broadly convex. The broadest part of the whorl is in the mid-area of the whorl. The umbilical shoulder is rounded with a fairly steep umbilical wall. The conch is smooth except for growth lines. The pattern of the growth lines, however, is not visible due to faulty preservation of the shell.

The suture is illustrated on Figure 46K. It is of a fairly simple pattern with two lateral lobes, and an auxiliary lobe on the

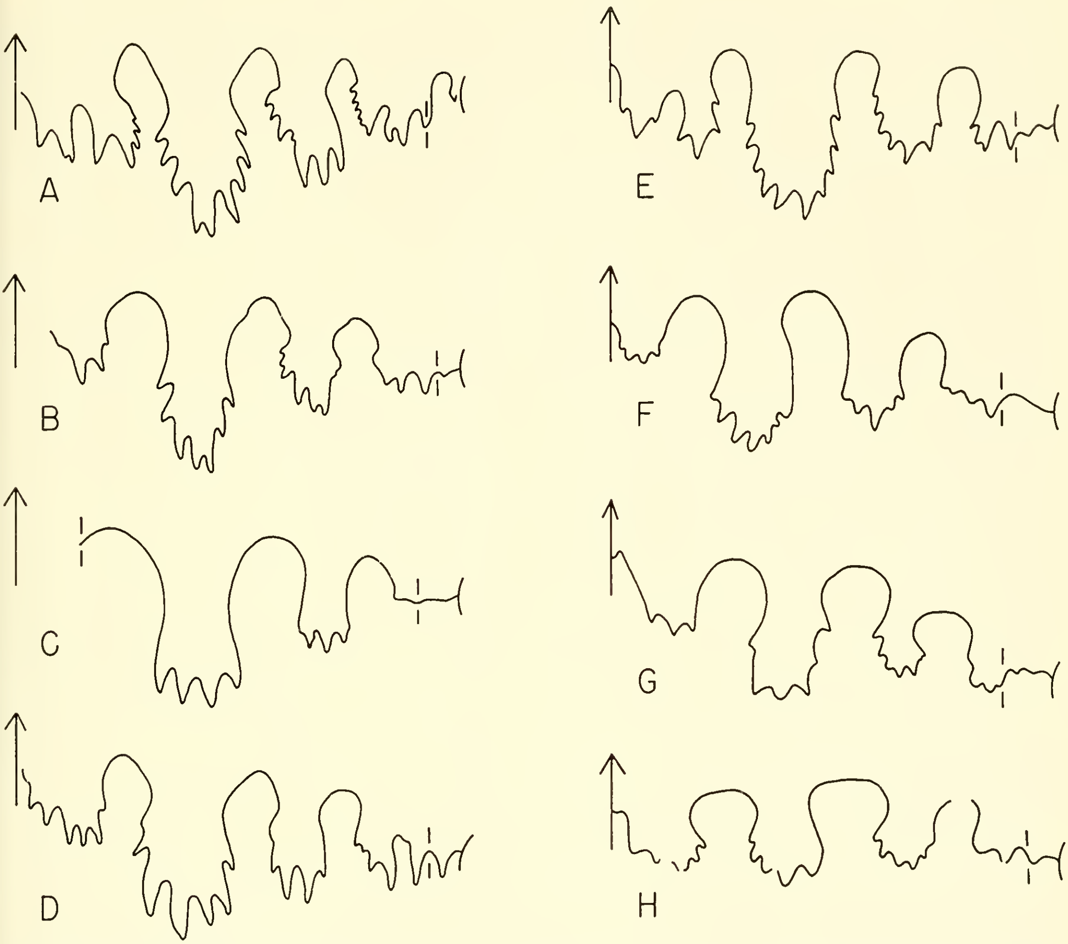

Figure 47. Diagrammatic representation of the sutures of three species of *Eophyllites*. A–F, *Eophyllites dieneri* (Arthaber); A, paralectotype (Arthaber, 1908: fig. 4), new drawing at a diameter of 42 mm; B, plesiotype (Arthaber, 1911: pl. 20(4), fig. 6), new drawing at a diameter of 47 mm; C, type specimen of *Monophyllites kingi*,—Arthaber (non Diener) = *Ussurites* (?) *decipiens* Spath (1934), at a diameter of approximately 30 mm; this suture is highly distorted due to excessive grinding of the specimen; D, holotype of *Monophyllites nopcsai* Arthaber (1908: pl. 12, fig. 5), new drawing at a diameter of 28 mm; E, holotype of *Monophyllites* (*Schizophyllites*) *betilloni* Renz and Renz (1948: pl. 4, fig. 8b), at a diameter of 47 mm; F, plesiotype (Renz and Renz, 1948: pl. 5, fig. 1b), at an unknown diameter. G, *Eophyllites orientalis* Spath,—Welter (1922: pl. 161(7), fig. 7), at an unknown diameter. H, *Eophyllites amurensis* Kiparisova (1961: text-fig. 104), at a whorl height of 10 mm.

Specimens of A–D from *Subcolumbites* fauna of Albania; E, F, from same fauna on Chios; G, from Nifoekoko, Black E, Timor; H, from *Subcolumbites* fauna, Primorye Region, Siberia.

dorsal areas of the flanks. It is difficult to be sure whether the lobes are really goniatitic as shown on Figure 46K. There are faint indications of denticulations on some of the first and second lateral lobes, and I suspect the smooth aspect is due to poor preservation.

Dalmatites morlaccus Kittl is morphologically very similar to *D. kittli.* The venter on the type species becomes rounded on the body chamber and the suture shows minor differences in proportion and shape of the elements.

Occurrence. Middle shale member of

Thaynes Formation (*Columbites* fauna), Paris Canyon, Bear River Range, Southeast Idaho.

Repository. Holotype, MCZ 9499.

Dalmatites attenuatus Smith

Plate 71, figures 8, 9;

Dalmatites attenuatus Smith, 1932: 81, pl. 57, figs. 11–13.

A highly compressed dalmatitid with a sharp venter. It is more compressed than either *D. morlaccus* or *D. kittli* and in addition more evolute. The suture is on the same basic pattern as the other species.

Occurrence. Smith's holotype came from the *Tirolites* Zone in Paris Canyon, southeast Idaho. He reports (Smith, 1932: 81) that he had only one specimen from the *Tirolites* Zone of Idaho but in addition he states the species was also found in the *Meekoceras* Zone at Phelan ranch, mouth of Cottonwood Canyon, east of the Ruby Range, Nevada; however, this latter specimen (or specimens?) is apparently no longer preserved. Smith (1932: 81) did describe a species—*D. richardsi*—from the *Meekoceras* Zone.

Repository. Holotype USNM 75023.

Order PHYLLOCERIDA Arkell, 1950

Superfamily PHYLLOCERATACEAE Zittel, 1884

Family USSURITIDAE Hyatt, 1900

Genus *Eophyllites* Spath, 1930

Type species, *Monophyllites dieneri* Arthaber, 1908

Eophyllites dieneri (Arthaber)

Plate 22, figures 1–4; Plate 23, figures 1–7; Text-figure 47

Monophyllites dieneri Arthaber, 1908: 288, pl. 13(3), figs. 3a–c, 4a–c; Arthaber, 1911: 234, pl. 20(4), figs. 5–8; Diener, 1915: 203.

Eophyllites dieneri,—Spath, 1930: 89; Spath, 1934: 293–295; Kummel, *in* Arkell et al., 1957: L186.

Monophyllites hara,—Arthaber (non Diener), 1908: 286, pl. 12(2), figs. 4a–c; Arthaber, 1911: 235.

Monophyllites (*Ussurites*) *hara* Diener, 1915: 206.

Eophyllites refractus Spath, 1934: 295, pl. 3, fig. 4.

Monophyllites kingi,—Arthaber (non Diener), 1911: 235, pl. 20(4), figs. 12a–c.

Monophyllites (*Ussurites*) *kingi* Diener, 1915: 207.

Ussurites (?) *decipiens* Spath, 1934: 302 (= *Monophyllites kingi,*—Arthaber non Diener).

Monophyllites nopcsai Arthaber, 1908: 287, pl. 12(2), figs. 5a–c; Arthaber, 1911: 235; Diener, 1915: 203.

Eophyllites nopcsai,—Spath, 1934: 302.

Monophyllites (*Leiophyllites*) *rosae* Renz and Renz, 1947: 61, 77; Renz and Renz, 1948: 74, pl. 3, figs. 8–8a.

Monophyllites (*Schizophyllites*) *betilloni* Renz and Renz, 1947: 61, 78; Renz and Renz, 1948: 76, pl. 4, figs. 8–8b.

Monophyllites (*Schizophyllites*) *betilloni* var. *evoluta* Renz and Renz, 1948: 76, pl. 4, figs. 6–6a, pl. 5, figs. 2–2a, 4–4a, 6–6a.

The lectotype of this species is not in the collections of the Paleontological Institute, University of Vienna, and is presumed lost. Two figured paralectotypes are available, but none of the unfigured specimens noted by Arthaber. The one figured paralectotype (Arthaber, 1908: pl. 13(3), figs. 4a–c; 1911: pl. 20(4), figs. 5a–c; Pl. 23, figs. 2, 3 of this report) is mainly phragmocone. The lateral area of the illustrated side has been polished to expose the sutures, but at the same time this has destroyed all surface markings. The opposite side of the conch is all matrix or highly weathered. This specimen measures 49.5 mm in diameter, 20.6 mm for the height of the last whorl and 15.7 mm for the diameter of the umbilicus. The unretouched photograph of Plate 23, figures 2, 3 shows the main features of the conch and the general state of preservation of the specimen better than the retouched illustration of Arthaber.

The second paralectotype is the specimen which yielded the suture of Arthaber's plate 20(4), figure 6 and is illustrated here on Plate 23, figures 4, 5. It is a fragmentary specimen that is nearly all phragmocone. Much of the lateral area has been ground to expose the suture (Fig. 47B).

Monophyllites hara,—Arthaber, non Diener (1908: 286, pl. 12(2), fig. 4), renamed *Eophyllites refractus* by Spath (1934: 295) is unfortunately not preserved in the collections of the Paleontological Institute, University of Vienna. There are, however, several topotypes in the British Museum (Natural History). The species was characterized mainly by its broader venter. Spath (1934: 295) also mentions differences with *Eophyllites dieneri* in the pattern of the growth lines. In regard to the width of the venter, Spath himself stated that among the topotypes he had, they could not be distinguished satisfactorily from *E. dieneri.* As yet too few specimens of *Eophyllites* from Albania have been studied, but it does not seem likely that differences in the character of the venter as used in this case are anything more than the normal type of variation one can expect and can demonstrate in many cases within ammonite species. *Eophyllites refractus* is believed to be conspecific with *E. dieneri.*

Ussurites (?) *decipiens* Spath (1934) (=*Monophyllites kingi,*—Arthaber, 1911: pl. 20(4), fig. 12) is likewise believed to be a specimen of *E. dieneri.* Proper understanding of this species (and specimens) has not been possible on the basis of Arthaber's illustrations, especially of the suture. In the first place the type specimen (Plate 23, figures 6, 7) has the same general shape, etc., as the types of *E. dieneri.* The measurements are: diameter 50.8 mm, width of last whorl 12.0? mm, height of last whorl 18.8 mm, and width of umbilicus 18.3 mm. One of the most conspicuous differences is that *decipiens* is more evolute than *dieneri*; this difference, however, amounts to only 5 percent of the conch diameter and this is hardly a criterion of specific significance. The whorls are slightly more inflated than in *decipiens* and the venter is more broadly rounded than indicated by Arthaber's (1911: pl. 20(4), fig. 12b) drawing. The whorl cross-section is intermediate between that of *E. decipiens* and *E. refractus.* The adoral quarter volution is marked by fine radial lines some of which at intervals are more conspicuous than others. The general absence of these lines on the two available specimens of *decipiens* is due to preservation plus grinding of the surface of the conch.

It is in the suture, however, that most authors recognized significant differences. As with practically all of the Albanian material, the suture can be made visible only by grinding and polishing of the surface. Arthaber's type specimen had been ground for this purpose and in this case the grinding was far too much, destroying many of the details of the lobe denticulations. Faint outlines of denticulations are visible on the lower flanks of the lobes. Arthaber's suture (1911: pl. 20(4), fig. 12c) actually ends on the umbilical shoulder and does not include anything for the umbilical wall. The suture on the umbilical wall is, however, not preserved. The relative shortness of the suture line reflects the difference in degree of involution and whorl height. The suture of *decipiens* illustrated by Arthaber came from a whorl height of 10.5 mm; the suture of *dieneri* (Arthaber, 1911: pl. 20(4), fig. 5) came from a whorl height of 17 mm. All of the above data clearly point to *Ussurites decipiens* as being part of the *dieneri* complex.

Eophyllites nopcsai (Arthaber), which is associated with *E. dieneri* in the Albanian fauna, is based on a single specimen; this is illustrated here on Plate 22, figures 1, 2. In suture (Fig. 47D) and ornamentation it is very much like *E. dieneri*, but its conch is very involute; its umbilicus is only 25 percent the diameter of the conch whereas in *dieneri* the umbilicus measures 30–36 percent the diameter of the conch. The association of this form in the same beds with *E. dieneri* and the very close similarity in all other conch features leads me to conclude that *nopcsai* represents nothing more than a variant toward involution of the conch, as *decipiens* represents a variant in the opposite direction—that is, a more evolute conch.

The *Subcolumbites* fauna of Chios contains an interesting assemblage of specimens assigned to other species which I believe are conspecific with the Albanian *E. dieneri.* The specimens which Renz and Renz (1948: 74) named *Monophyllites* (*Leiophyllites*) *rosae* I cannot separate from *E. dieneri.* The specimens assigned by Renz and Renz (1948: 76) to *Monophyllites* (*Schizophyllites*) *betilloni* were set aside into a new subgenus on the basis of a slight saddle in the ventral lobe. The suture of the subgenotype (Fig. 47E) is nearly identical to that of the suture of the paralectotype of *E. dieneri* (Fig. 47A). Spath (1934: 294) had earlier called attention to the variability in the suture of *E. dieneri* and especially to the ventral lobe. He also rightly cautioned that some of this variability is caused by preparation of the suture with acids and grinding. In all other features *betilloni* resembles *E. dieneri,* and there appears little doubt but that these two species are conspecific.

The form from Timor described by Welter (1922: 118, pl. 161(7), figs. 5–7) as *Monophyllites* nov. sp. ex aff. *dieneri* was renamed *Eophyllites orientalis* by Spath (1934: 295). This species is based on a single incomplete specimen that represents the inner whorls of what was a much larger form. It is unquestionably very close to *E. dieneri* and possibly even conspecific, but here again, since it is based on a single specimen, it is considered best for the moment to recognize it as a distinct species.

Occurrence. *Subcolumbites* fauna of Kčira, Albania, and Chios.

Repository. The Paleontological Institute, University of Vienna, contains two paralectotypes of *E. dieneri*; the lectotype is apparently lost. This collection also contains the holotype of *Ussurites* (?) *decipiens* Spath (= *Monophyllites kingi,*—Arthaber non Diener). A number of topotypes are in the British Museum (Natural History), C22939–47, C22979. The Natural History Museum, Basel, contains the following specimens from the *Subcolumbites* fauna of Chios: holotype *Monophyllites* (*Leiophyllites*) *rosae* Renz and Renz (1948: pl. 3, fig. 8) NHMB J13746; holotype *Monophyllites* (*Schizophyllites*) *betilloni* Renz and Renz (1948: pl. 4, fig. 8) NHMB J13756; var. *evoluta* Renz and Renz (1948: pl. 4, fig. 6) NHMB J13757, (pl. 5, fig. 2) NHMB J13758, (pl. 5, fig. 4) NHMB J13759, (pl. 5, fig. 6) NHMB J13760; unfigured paratypes from Maradavuno, NHMB J13761, from Kephalovuno NHMB J13762.

Eophyllites orientalis Spath
Text-figure 47

Monophyllites nov. spec. ex aff. *dieneri,*—Welter, 1922: 118, pl. 161(7), figs. 5–7; Kutassy, 1933: 595.

Eophyllites orientalis Spath, 1934: 295.

This Timor species is based on a single specimen that represents the inner whorls of what was a much larger form. The specimen measures 56.7 mm in diameter, 16.0 mm for the width of the last whorl, 23.0 mm for the height of the last whorl, and 19.1 mm for the diameter of the umbilicus. It shows a great similarity to *E. dieneri* of Albania and Chios and perhaps is conspecific with that form. However, because only one specimen is known and because there are minor differences in the suture (Fig. 47G) and conch features, it is considered best to maintain the separate identity of this species until more material becomes available.

Occurrence. Manganese coated blocks from Nifoekoko, Timor.

Repository. GPIBo-W215.

Eophyllites amurensis Kiparisova
Text-figure 47

Eophyllites amurensis Kiparisova, 1961: 137, pl. 28, figs. 7, 8, text-fig. 104.

Eophyllites cf. *refractus,*—Kiparisova, 1961: 136, pl. 28, fig. 9, text-fig. 103.

The two forms of *Eophyllites* recognized by Kiparisova from the Primorye Region represent an inflated form (cf. *refractus*) and a more compressed form (*amurensis*). The latter species was compared closely with *dieneri* from the *Subcolumbites* fauna of Albania. One of these species (cf. *refractus*) is based on a single specimen and the other (*amurensis*) was based on three poorly preserved specimens. They are in the first place considered to represent a single species complex. These specimens differ from *E. dieneri* in being slightly more involute and in the slightly simpler structure. They are clearly closely related to the *dieneri* group of Albania and could well be conspecific but much more material is needed before this relationship can be established with any degree of certainty.

Occurrence. The three specimens of *amurensis* came from the *Subcolumbites* fauna on the west coast of Amur Bay between Cape Atlasov and Cape Ugolny, Ussuri Bay, Primorye Region. The single specimen assigned by Kiparisova to cf. *refractus* came from the east coast of Ussuri Bay between Cape Kom-Pikho-Sakho and Cape Chigan from an uncertain horizon.

Genus *Palaeophyllites* Welter, 1922

Type species, *Palaeophyllites steinmanni* Welter, 1922

Palaeophyllites steinmanni Welter

Palaeophyllites steinmanni Welter, 1922: 119, pl. 162(8), figs. 5, 6, 7, pl. 163(9), figs. 3–6; Kutassy, 1933: 606; Spath, 1934: 297, fig. 103.

Monophyllites (*Palaeophyllites*) *thalmanni* Renz and Renz, 1947: 61, 78; Renz and Renz, 1948: 79, pl. 3, figs. 10–10b (= *Palaeophyllites steinmanni* Welter, 1922: pl. 163(9), figs. 3–6 (non pl. 162(8), figs. 5–7).

Monophyllites (*Palaeophyllites*) *praekieperti* Renz and Renz, 1947: 61, 78; Renz and Renz, 1948: 80, pl. 4, figs. 5–5b.

Renz and Renz (1948) established the species *thalmanni* for the specimen illustrated by Welter on his plate 163(9), figures 3–6, at the same time designating the specimen of Welter's plate 162(8), figures 5, 6, as "holotype." They were unaware that Spath (1934: 298) had previously designated this specimen as lectotype. The smaller specimens of Welter's plate 163(9), figures 3–6, are characterized by a more subdued ribbing pattern. These specimens are clearly juvenile forms; the ornamentation increases on the mature body chamber. The Chios and Timor specimens of "*thalmanni*" are immature forms but clearly conspecific. The species *praekieperti* established by Renz and Renz (1948: 80) is merely a small, juvenile specimen of *steinmanni*. Measurements for 6 specimens from Timor and Chios are given on Table 50.

TABLE 50. MEASUREMENTS OF SPECIMENS OF *PALAEOPHYLLITES STEINMANNI* FROM TIMOR AND CHIOS.

	D	W	H	U	W/D	H/D	U/D
1.	58.8	14.9	20.4	24.5	25.3	34.7	41.7
2.	48.2	12.1	16.4	20.5	25.1	34.0	42.5
3.	40.7	12.0	13.8	16.6	29.5	33.9	40.8
4.	31.5	12.2	10.7	14.3	38.7	34.0	45.4
5.	26.0	8.7	8.7	10.8	33.5	33.5	41.5
6.	23.4	7.9	10.1	7.9	33.8	43.2	33.8

1. Lectotype, Welter (1922: pl.162(8), figs. 5–7), GPIBo W216a.
2. Plesiotype, *Palaeophyllites thalmanni* Renz and Renz (1948: pl. 3, fig. 10), NHMB J13764.
3. Paralectotype, Welter (1922: pl.163(9), figs. 3–4), GPIBo W216b.
4. Holotype, *Monophyllites* (*Palaeophyllites*) *praekieperti* Renz and Renz (1948: pl. 4, fig. 5), NHMB J13766.
5. Paralectotype, Welter (1922: pl.163(9), figs. 5–6), GPIBo W216c.
6. Unfigured specimen from Chios, *Monophyllites* (*Palaeophyllites*) *thalmanni*, NHMB J13765.

Occurrence. Subcolumbites fauna of Chios and the *Prohungarites* fauna with manganese coated fossils of Timor.

Repository. Lectotype, GPIBo-W216a; paralectotypes GPIBo-W216b, c; specimens from Chios, plesiotype *Monophyllites* (*Palaeophyllites*) *thalmanni* Renz and Renz (1948: pl. 3, fig. 10) NHMB J13764; unfigured specimen from Maradovuno NHMB J13765, from Kephalovuno NHMB J13836; holotype *Monophyllites* (*Paleophyllites*) *praekieperti* Renz and Renz (1948, pl. 4, fig. 5) NHMB J13766; unfigured paratype NHMB J13767.

TABLE 51. MEASUREMENTS OF *USSURITES SIEVERI* N. SP. FROM TOBIN FORMATION, NEVADA.

	D	W	H	U	W/D	H/D	U/D
1.	62.5	20.0	25.8	17.3	32.0	41.2	27.6
2.	48.0	16.4	21.8	13.2	34.1	45.4	27.5
3.	48.0	15.3	21.4	13.7	31.8	44.5	28.5
4.	43.0	14.5?	19.5?	10.0	34.4?	45.3?	23.0
5.	38.7	?	16.5	11.5	?	42.6	29.7
6.	38.4	?	15.5	10.0	?	40.3	26.0
7.	33.5	11.4	14.4	9.3	34.0	42.9	27.7
8.	26.7	10.4	12.3	6.8	38.9	46.0	25.4
9.	25.0	?	11.1	6.4	?	44.4	25.6
10.	21.0	7.8	9.1	6.1	37.2	43.3	29.0
11.	20.6	8.4	9.0	5.7	40.7	43.6	27.6
12.	20.0	7.7	9.0	4.8	38.5	45.0	24.0

1. Holotype, MCZ 9452 (Pl. 32, figs. 1, 2).
3. Paratype, MCZ 9456 (Pl. 32, figs. 6, 7).
4. Paratype, MCZ 9455 (Pl. 32, fig. 5).
5. Paratype, MCZ 9454 (Pl. 32, fig. 4).
6. Paratype, MCZ 9472 (Pl. 35, figs. 10, 11).
10. Paratype, MCZ 9464 (Fig. 48 CD).
2, 6, 7, 9, 11, 12. Unfigured paratypes, MCZ 9484.

Genus *Ussurites* Hyatt, 1900

Type species, *Monophyllites sichoticus* Diener, 1895

Ussurites sieveri n. sp.

Plate 31, figure 8; Plate 32, figures 1–7; Plate 35, figures 10, 11; Text-figure 48

This species is well represented in the Tobin Formation fauna. There are twelve specimens sufficiently well preserved and complete to allow measurements, which are given on Table 51.

The conch is moderately involute with a rounded venter, broadly rounded lateral areas, a well rounded umbilical shoulder, and a vertical umbilical wall. The flanks bear low, narrow, slightly prosiradiate folds that cross the venter.

The sutures from a whorl height of 2.0 mm to a whorl height of 14.8 mm are shown in Figures 48A–D. The suture is typical for the genus, with the asymmetric, club-shaped saddles, the large denticulated first lateral lobe, etc.

This species differs from *Ussurites mansfieldi* n. sp. in conch form and suture. The latter species is quite distinctive in its large asymmetrical second lateral saddle; likewise the ontogenetic changes in the whorl shape are quite different. *Ussurites hosei* n. sp. is a much more robust species, with a more inflated whorl section and a suture with coarser denticulations on the lobes.

Occurrence. Tobin Formation, Pershing County, Nevada; south tip of Tobin Range, Cain Mountain 1:62,500 quad., center NW ¼ sec. 9, T. 26N, R. 39E, 5,500 ft. S, 27.5 ft. W from elevation point 5088 on range crest.

Repository. Holotype MCZ 9452 (Pl. 32, figs. 1, 2); paratypes MCZ 9464 (Pl. 31, fig. 8), MCZ 9453 (Pl. 32, fig. 3), MCZ 9454 (Pl. 32, fig. 4), MCZ 9455 (Pl. 32, fig. 5), MCZ 9456 (Pl. 32, fig. 6, 7), MCZ 9472 (Pl. 35, figs. 10, 11); unfigured paratypes MCZ 9484; suture specimen (Figures 48C, D), MCZ 9464.

Ussurites hosei n. sp.

Plate 33, figures 1–6; Text-figure 48

This new species is based on a fairly large assortment of fragmentary and partially crushed specimens that are, however, so distinctive that a description and new name is warranted. The conch is robust, and moderately involute. None of the specimens are in a state of preservation or completeness to yield any significant measurements. The whorl section is broadly oval and quite variable in relative width-height dimensions. Most of the material shows the whorl width to be approximately 75 per cent of the whorl height, thus slightly compressed. On the other hand, fragments of whorls are present in which the whorl height and width are approximately the same, and in some specimens the whorls are depressed, that is, the whorl width is greater than the whorl height.

The venter is broadly rounded grading onto broadly arched flanks. The umbilical shoulder is rounded, and merges with a broad, nearly vertical umbilical wall. The umbilicus appears to measure approximately 20–25 per cent the diameter of the conch.

None of the specimens are really sufficiently well preserved to show surface

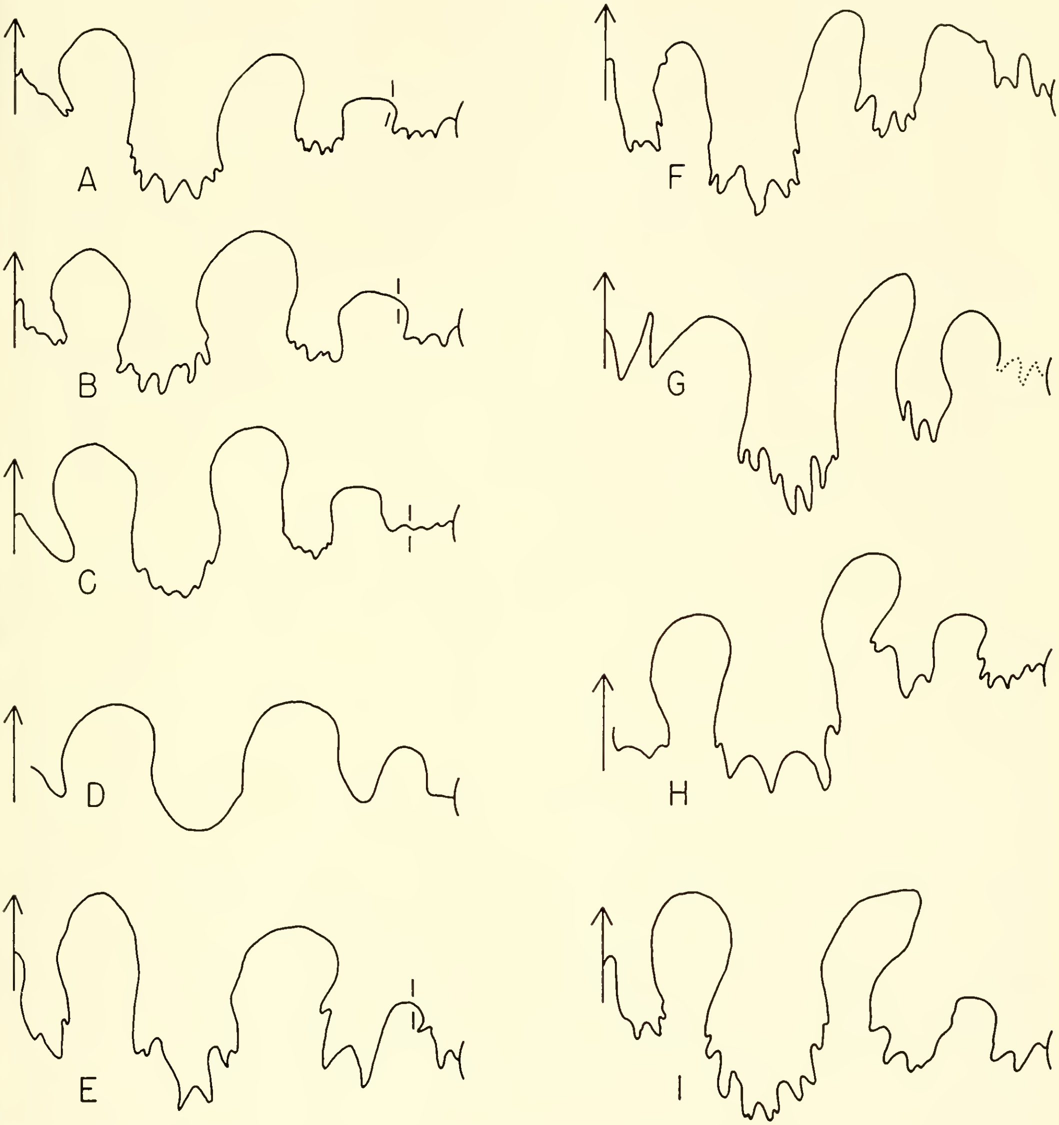

Figure 48. Diagrammatic representations of the suture of: A–D, *Ussurites sieveri* n. sp. A, holotype at a diameter of 35 mm (MCZ 9452); B, paratype at a diameter of 26 mm (MCZ 9472); C, paratype at a diameter of 21 mm; D, at a diameter of 13 mm (MCZ 9464); E, paratype of *Ussurites hoesi* n. sp. at a diameter of 53 mm (USNM 153089); F–I, *Ussurites mansfieldi* n. sp.; F, paratype (Pl. 45, figs. 2, 3), at a diameter of 110 mm; G, at a diameter of 75 mm (MCZ 9515, Pl. 44, fig. 1); H, at a diameter of 43 mm (MCZ 9513, Pl. 44, figs. 2, 3); I, at a diameter of 24 mm (USNM 153090).

Specimens of figures A–D are from Tabin Formation, Nevada, that of figure E from Thaynes Formation, Confusion Range, Nevada, and those of figures F–I, from *Columbites* fauna, Thaynes Formation, southeastern Idaho.

TABLE 52. MEASUREMENTS OF *USSURITES MANSFIELDI* N. SP. FROM THE *COLUMBITES* ZONE, SOUTHEASTERN IDAHO.

	D	W	H	U	W/D	H/D	U/D
1.	203.0	?	93.0	53.0	?	45.8	26.1
2.	126.0	39.5?	53.6	38.0	31.3?	42.5	30.2
3.	48.0	?	24.2	12.8	?	50.4	26.7
4.	43.0	?	20.6	13.6	?	47.9	31.6
5.	37.7	18.0	18.7	11.4	47.7	49.6	30.2

1. Holotype, State Historical Museum, Boise.
2. Paratype, State Historical Museum, Boise.
3. Paratype, MCZ 9513 (Pl. 44, figs. 2, 3).
4, 5. Paratypes, USGS.

marking of any kind. One of the larger phragmocones (Pl. 33, fig. 1) does appear to have broad, low, radial folds on the flanks. The suture is typical for the genus, and is illustrated on Figure 48E. It is somewhat like the suture of *U. sieveri* but has much coarser denticulation of the lobes; it differs from the suture of *U. mansfieldi* to a very marked degree.

Occurrence. Collection M111, 1,420 to 1,530 feet above the base, Thaynes Formation, Confusion Range, Utah, from section 15 of Hose and Repenning (1959).

Repository. Holotype, USNM 153085 (Pl. 33, fig. 1); paratypes USNM 153086 (Pl. 33, fig. 2), USNM 153087 (Pl. 33, figs. 3, 4), USNM 153088 (Pl. 33, figs. 5, 6); suture specimen USNM 153089 (Fig. 48E).

Ussurites mansfieldi n. sp.

Plate 44, figures 1–3; Plate 45, figures 1–3; Text-figure 48

The *Columbites* fauna of southeastern Idaho has yielded 10 specimens of this most interesting species. The available measurements of five of these specimens are listed in Table 52. There is one exceptionally large specimen, one of intermediate size, and the remaining forms of relatively small diameter. The largest specimen, and holotype, is preserved only on one side and the adoral one-half volution, which is body chamber, is crushed. The inner volutions are not crushed. These inner volutions have rounded lateral areas, rounded umbilical shoulders and a steep, rounded umbilical wall. The height of the whorl in relation to the width increases greatly during shell growth. On approximately the first two volutions, the whorl width and height are much the same; on later volutions the whorls increase rapidly in height whereas the width increases quite modestly. At all stages of growth the venter is broadly rounded.

The shell of the body chamber of the large holotype bears fine, slightly sinuous growth lines which are periodically bundled to give rise to faint broad ribs. On the inner volutions the shell bears faint strigations in addition to extremely fine growth lines.

The large paratype (Pl. 45, figs. 2, 3) is all phragmocone with much of the shell preserved. The widely spaced, low, broad radial ribs are more conspicuous on this specimen, as are the fine, sinuous growth lines.

The small specimens show the whorl width to approximate the whorl height. Likewise, the shell is smooth, except for extremely fine growth lines and strigations.

Probably the most distinguishing feature of this species is the suture (Figure 48F–I). There is a large denticulated first lateral lobe, a much smaller second lateral lobe and an auxiliary series on the umbilical shoulder and wall. The saddles, however, are unusual, especially the long asymmetrical second lateral saddle. Figure 48 compares four sutures taken from a whorl height of 12 mm (diameter of approximately 24 mm) to one taken from the paratype at a whorl height of 47 mm (diameter of approximately 110 mm). The distinctive character of the suture is already well established at a small diameter. It is interesting to note that on the late mature suture (Fig. 48F) a "degeneration" occurs, expressed in the wavy outline of the saddles and to some extent in the lobes.

The large, asymmetrical second lateral saddle sets this species apart from all other species of *Ussurites.* In addition to the suture, the general shape and configuration of the conch is distinctive. The two other American species of *Ussurites, U. sieveri* and *U. hosei,* are quite different; however, here the age factor may be significant. *Ussurites mansfieldi* is from the *Columbites* Zone. Nearly all other Scythian species of *Ussurites* are from the next higher *Subcolumbites* Zone.

Occurrence. The holotype and paratype were collected by Mr. Gordon R. Stephenson in Webster Canyon, Freedom Quadrangle, southeast Idaho (Sec. 1, T. 8S, R. 45E and Sec. 6, T. 8S, R. 46E). The paratype was found in a black limestone concretion within a 42 foot dark shale and thin limestone bed 120 feet above the *Meekoceras* limestone. The holotype was not found in place, but in a concretion at the base of a cliff with the above mentioned concretions which yielded the paratype. In addition, the species is known from the *Columbites* fauna at Hot Springs, southeast Idaho, and along Draney Creek, Stewart Flat Quadrangle, southeast Idaho (USGS Locality M98).

Repository. Holotype and large paratype (Pl. 45, figs. 1–3) are in the Department of Geology, Washington State University, Pullman, Washington; figured paratypes MCZ 9513 (Pl. 44, figs. 2, 3) and MCZ 9515 (Pl. 44, fig. 1); unfigured paratypes from Hot Springs MCZ 9514; suture specimen (Fig. 48I) USNM 153090.

Genus *Leiophyllites* Diener, 1915

Type species, *Monophyllites suessi* Mojsisovics, 1882

Leiophyllites variabilis (Spath)

Plate 22, figures 5–10; Text-figures 49, 50

Monophyllites pitamaha,—Arthaber (non Diener) 1911: 234, pl. 20(4), figs. 9–11; C. Renz, 1928: 155.

Monophyllites (*Leiophyllites*) *pitamaha* Diener, 1915: 205.

Monophyllites (*Leiophyllites*) aff. *pitamaha,*—Renz and Renz, 1947: 61; Renz and Renz, 1948: 76, pl. 3, figs. 9–9a, pl. 4, figs. 7–7b.

Eophyllites variabilis Spath, 1934: 296, pl. 2, fig. 3, pl. 6, fig. 1, pl. 7, fig. 1.

Eophyllites variabilis var. *involuta* Spath, 1934: 296 (= Arthaber, 1911: pl. 20(4), fig. 9).

Eophyllites variabilis var. *evoluta* Spath, 1934: 296, pl. 4, fig. 1.

Monophyllites (*Leiophyllites*) *praeconfucii* Renz and Renz, 1947: 61, 77; Renz and Renz, 1948: 73, pl. 4, figs. 1–1b, 2–2a.

Monophyllites (*Leiophyllites*) *georgalasi* Renz and Renz, 1947: 61, 77; Renz and Renz, 1948: 74, pl. 4, figs. 3–3a.

Monophyllites (*Leiophyllites*) *palaeotriadicus* Renz and Renz, 1947: 61, 78; Renz and Renz, 1948: 75, pl. 4, figs. 4–4a.

Leiophyllites praematurus Kiparisova, 1958b: pl. 7, fig. 13, text-fig. 17b; Kiparisova, 1961: 134, pl. 28, figs. 5, 6, text-figs. 101, 102.

The lectotype of this species (Arthaber, 1911: pl. 20(4), fig. 11) is not preserved in the collection of the Paleontological Institute, Vienna; the two figured paralectotypes (Arthaber, 1911: pl. 20(4), figs. 9, 10; Pl. 22, figs. 5–10 of this report) are fortunately still preserved and available for study. These two paralectotypes plus one additional unfigured specimen (Pl. 22, figs. 7, 8) and the many topotypes in the British Museum (Natural History) are not well preserved and the larger of the paralectotypes (Pl. 22, figs. 5, 6) has been ground and polished.

The Chios fauna contains a fair number of specimens which belong to this species but which Renz and Renz (1948) placed in four distinct species. The differences between these species are mainly in whorl dimensions and expressions of fine ornamentation. The measurements of the Chios and Albania specimens considered to belong to this species are listed on Table 53 and plotted on the graph of Figure 50. These data do not suggest that the differences in whorl dimensions are anything more than what should be expected. It is, however, possible that some of the unfigured specimens in the Chios collection placed here (e.g. the more involute forms) are really species of *Eophyllites.* In regard

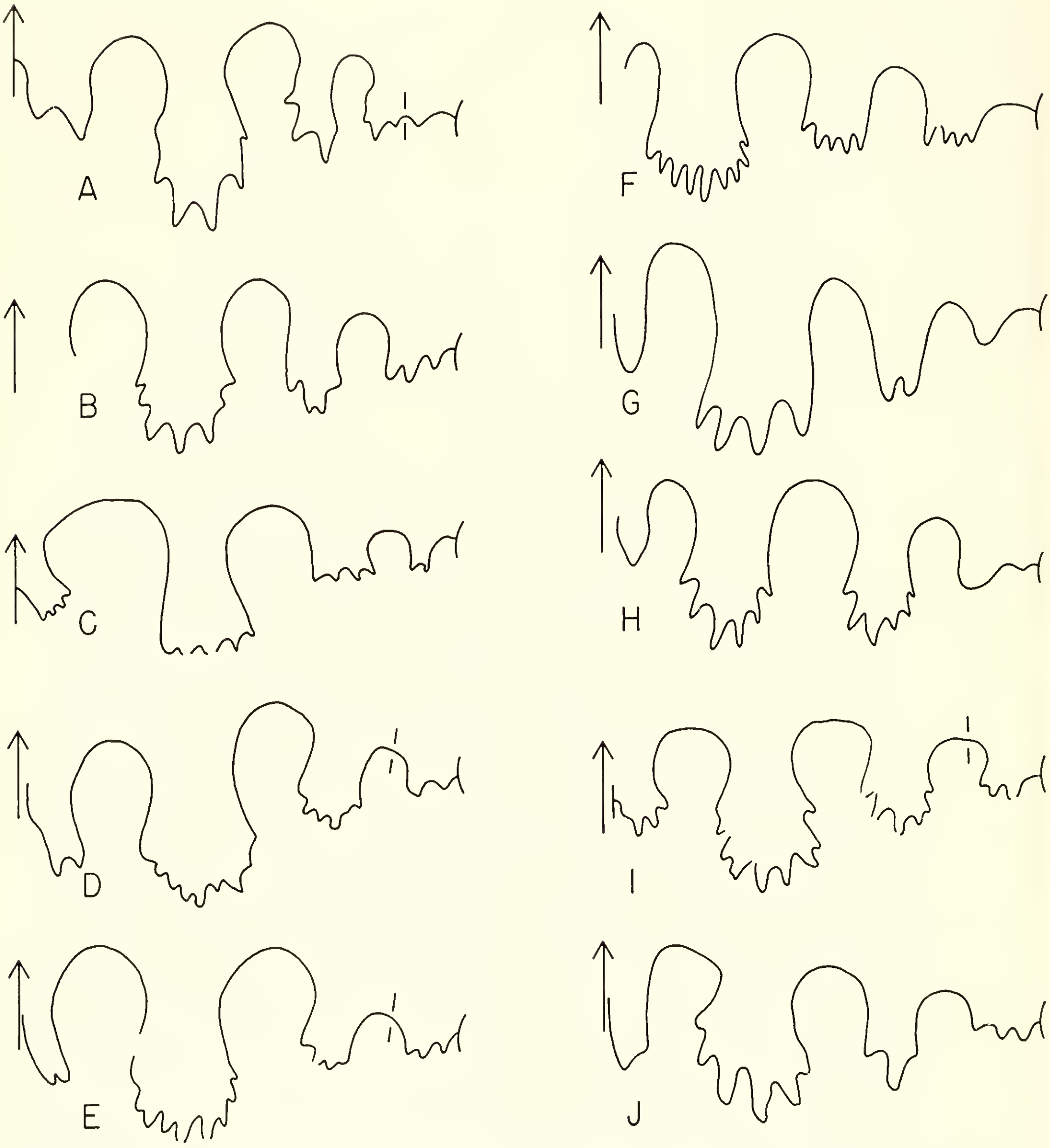

Figure 49. Diagrammatic representation of the suture of: A, paralectotype *Eophyllites variabilis* Spath (= *Monophyllites pitamaha* Arthaber [non Diener] 1911: pl. 20(4), fig. 10c; Pl. 22, figs. 5, 6 of this report), from *Subcolumbites* fauna of Albania at a diameter of 28 mm; B, paratype *Leiophyllites praematurus* Kiparisova (1961: 135, fig. 101), from *Subcolumbites* fauna, Primorye Region, Siberia; C, holotype *Leiophyllites radians* Astakhova (1960a: 146, fig. 12), from *Stacheites* Zone of Astakhova (1960a) Mangyshlak Peninsula; D, holotype *Danubites* (*Preflorianites*) *maritimus* Kiparisova (1961: 146, fig. 111), from *Subcolumbites* fauna of Primorye Region, Siberia, at a whorl height of 8 mm; E, holotype *Danubites* (*Preflorianites*) *inflatus* Kiparisova (1961: 145, fig. 110), from the *Subcolumbites* fauna of Primorye Region, Siberia, at a whorl height of 7 mm; F, holotype *Leiophyllites serpentinus* Chao (1959: 149, fig. 48a), from *Subcolumbites* fauna of Kwangsi, China, at a whorl height of 16 mm; G, holotype *Leiophyllites serpentinus* Chao (1959: 149, fig. 48c), from *Subcolumbites* fauna of Kwangsi, China, at a diameter of 23 mm; H, holotype *Leiophyllites oxynotus* Chao (1959: 150, fig. 48b), from *Subcolumbites* fauna of Kwangsi, China, at a whorl height of 10 mm; I, holotype *Danubites* (*Danubites*) *incertus* Kiparisova (1961: 143, fig. 108), from *Subcolumbites* fauna of the Primorye Region, Siberia, at a whorl height of 10 mm; J, holotype *Danubites* (*Danubites*) *admaris* Kiparisova (1961: 142, fig. 106), from *Subcolumbites* fauna of the Primorye Region, Siberia, at a whorl height of 7 mm.

to surface ornamentation, the differences noted by various authors are more a reflection of preservation than anything else. The sutures, likewise, in all these species have the same basic pattern with minor differences which I consider to be intraspecific. The suture of the paralectotype as reproduced by Arthaber (1911: pl. 20(4), fig. 10c) is idealized. The suture was exposed by grinding and a new drawing is reproduced here on Figure 49A.

Comparison with the other upper Scythian species of *Leiophyllites*, namely from the *Subcolumbites* fauna of Kwangsi, China, and *L. praematurus* from the *Subcolumbites* fauna of the Primorye Region, is difficult because of lack of information on these species. Chao (1959) described four species of *Leiophyllites* on the basis of seven specimens. These species were separated by minor morphological features that appear more understandable as reflections of the rather poor preservation. On the features of conch evolution and whorl shape and dimensions, this species cannot be separated from *L. variabilis* from Albania and Chios. However, the sutures of these Kwangsi specimens are simpler than the Albanian and Chios species (Fig. 49), and on this basis I believe they should be kept in a distinct species group.

A species which I believe to be conspecific with *L. variabilis* is *L. praematurus* Kiparisova (1958b). That author compared her species mainly with Middle Triassic species of *Leiophyllites*, merely noting the similarity of the conch to that of *L. variabilis*. In this regard she pointed to the lesser denticulation of the lobes as an important distinction. The suture pattern of *L. praematurus* as illustrated by Kiparisova falls well within the variations found within the Chios specimens of *L. variabilis* (Fig. 49).

Occurrence. *Subcolumbites* fauna of Albania, Chios, and Primorye Region.

TABLE 53. MEASUREMENTS OF *LEIOPHYLLITES VARIABILIS* (SPATH) FROM THE *SUBCOLUMBITES* FAUNAS OF ALBANIA AND CHIOS.

	D	W	H	U	W/D	H/D	U/D
1.	96.2	20.6	33.8	37.2	21.4	35.1	38.7
2.	68.8	16.7	20.0	34.3	24.3	29.1	49.9
3.	60.7	17.4	20.2	26.4	28.7	33.3	43.5
4.	52.2	13.5	15.0	27.0	25.9	28.7	51.7
5.	41.0	9.8	11.2	27.8	23.9	27.3	67.8
6.	39.5	10.5?	12.0	19.2	26.6?	30.4	48.6
7.	38.4	12.3	11.3	19.0	32.0	29.4	49.5
8.	37.4	12.5?	12.0	17.6	33.4?	32.1	47.1
9.	35.2	9.1	13.1	13.8	25.9	37.2	39.2
10.	34.5	8.2	12.0	14.5	23.8	34.8	42.0
11.	33.7	6.7	10.0	15.5	19.9	29.7	46.0
12.	30.5	8.0	9.3	13.3	26.2	30.5	43.6
13.	28.0	7.4	10.4	11.0	26.4	37.1	39.3
14.	26.5	7.7	9.1	10.6	29.1	34.3	40.0
15.	24.6	6.0	9.3	9.5	24.4	37.8	38.6
16.	21.5	6.3?	6.8	9.8	29.3?	31.6	45.6
17.	21.0	6.3	7.5	7.3	30.0	35.7	34.8
18.	19.1	5.8	7.4	7.0	30.4	38.7	36.6
19.	19.0	4.4	5.8	8.5	23.2	30.5	44.7
20.	18.0	5.3	7.0	5.6	29.4	38.9	31.1
21.	17.3	5.2	6.6	5.8	30.1	38.2	33.5

1. Plesiotype, *Monophyllites* (*Leiophyllites*) aff. *pitamaha*,—Renz and Renz (1948: pl. 3, figs. 9–9a), NHMB J13752.
2. Holotype, *Monophyllites* (*Leiophyllites*) *praeconfucii* Renz and Renz (1948: pl. 4, figs. 1–1b), NHMB J13740.
3. Plesiotype, *Monophyllites* (*Leiophyllites*) aff. *pitamaha*,—Renz and Renz (1948: pl. 4, figs. 7–7b), NHMB J13753.

4, 5. Unfigured paratypes, *Monophyllites* (*Leiophyllites*) *praeconfucii* Renz and Renz from Maradovuno, NHMB J13742.

6. Paratype, *Monophyllites* (*Leiophyllites*) *praeconfucii* Renz and Renz (1948: pl. 4, fig. 2–2a), NHMB J13741.
7. Holotype, *Monophyllites* (*Leiophyllites*) *georgalasi* Renz and Renz (1948: pl. 4, figs. 3–3a), NHMB J13744.
8. Holotype, *Monophyllites* (*Leiophyllites*) *palaeotriadicus* Renz and Renz (1948: pl. 4, figs. 4–4a), NHMB J13749.

9–11, 13–15, 17–21. Unfigured specimens of *Monophyllites* (*Leiophyllites*) aff. *pitamaha* from Maradovuno, NHMB J13754.

12. Paralectotype, *Eophyllites variabilis* Spath (=*Monophyllites pitamaha* Arthaber (non Diener), 1911: pl. 20(4), figs. 10 a–c), PIUV.

16. Paralectotype, *Eophyllites variabilis* Spath (=*Monophyllites pitamaha* Arthaber (non Diener), 1911: p. 20(4), figs. 9a, b), PIUV.

Repository. The primary types are in the Paleontological Institute, University of Vienna; the lectotype (Arthaber, 1911: pl. 20(4), fig. 11) is apparently lost, but two figured paralectotypes (Arthaber, 1911: pl. 20(4), figs. 9, 10) and one unfigured paralectotype of Arthaber are preserved in that institution. A large collection of topotypes is in the British Museum of Natural His-

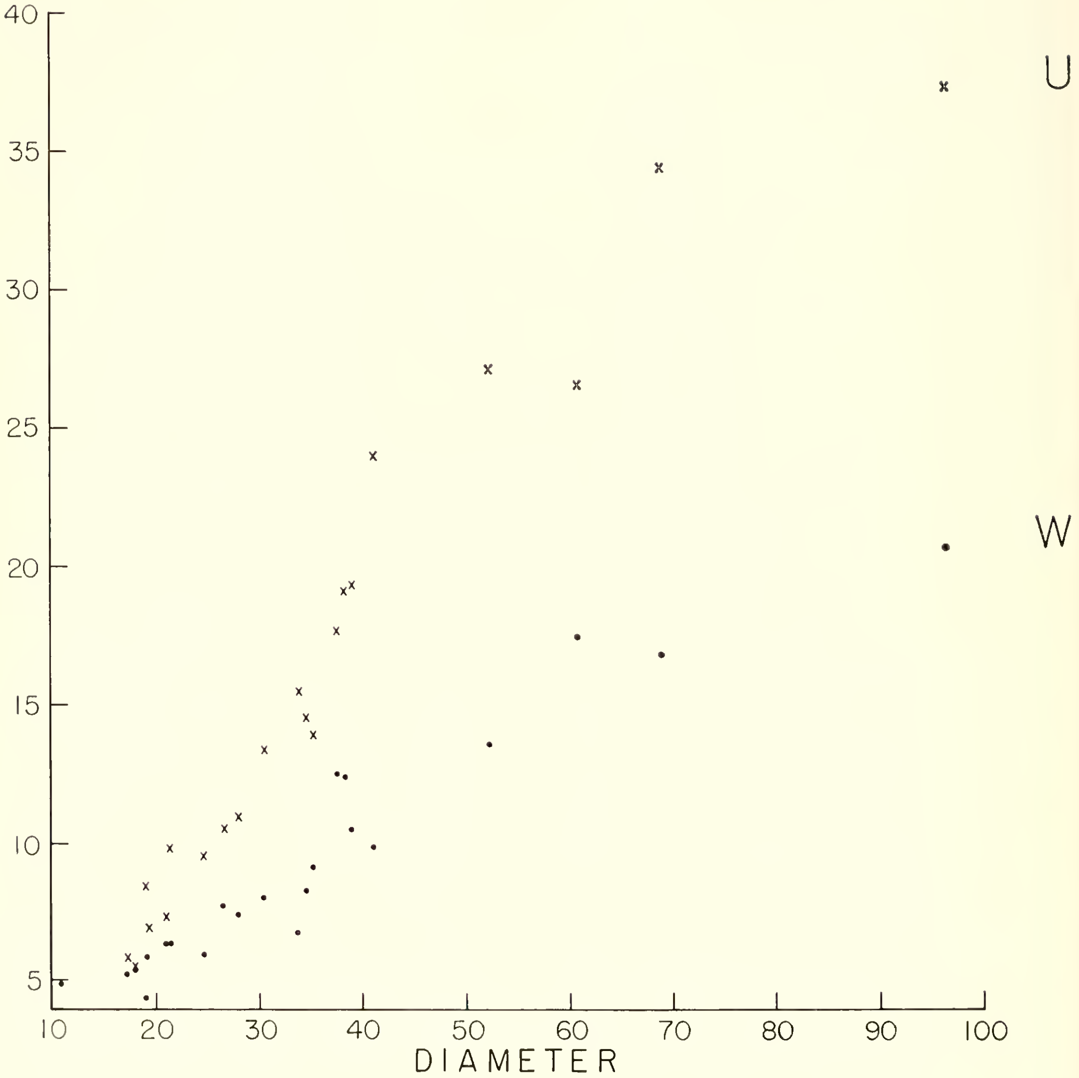

Figure 50. Variation in umbilical diameter (U) and whorl width (W) of *Leiophyllites variabilis* from *Subcolumbites* faunas of Albania and Chios. The data on this graph are from Table 53.

tory. The Natural History Museum, Basel, contains the following specimens from Chios studied by Renz and Renz (1948): plesiotype, *Monophyllites* (*Leiophyllites*) aff. *pitamaha* Renz and Renz (1948: pl. 3, fig. 9) NHMB J13752, (pl. 4, fig. 7) NHMB J13753; unfigured specimens from Maradovuno NHMB J13754, from Kephalovuno NHMB J13755; holotype, *Monophyllites (Leiophyllites) praeconfucii* Renz and Renz (1948: pl. 4, fig. 1) NHMB J13740; paratype (pl. 4, fig. 2) NHMB J13741; unfigured paratypes from Maradovuno NHMB J13742, from Kephalovuno NHMB J13743; holotype, *Monophyllites* (*Leiophyllites*) *georgalasi* Renz and Renz (1948: pl. 4, fig. 3) NHMB J13744; unfigured paratypes NHMB J13745; holotype, *Monophyllites* (*Leiophyllites*) *palaeotriadicus* Renz and Renz (1948: pl. 4, fig. 4) NHMB J13749; unfigured paratypes from Maradovuno NHMB J13750, from Kephalovuno NHMB J13751.

Leiophyllites radians Astakhova
Text-figure 49

Leiophyllites radians Astakhova, 1960a: 146, pl. 34, fig. 10, text-fig. 12.

This species has the general leiophyllitid conch form but is characterized by broadly spaced, low radial ribs that cross the venter. Adorally the ribs tend to decrease in size and eventually disappear. The suture is shown on Figure 49C. Assuming that it is accurately drawn, it is a much simpler suture than that of most other species of this genus. The only other species of *Leiophyllites* that have ornamentation consisting of ribs are the two species from the Primorye Region (*L. maritimus* and *L. admaris*). However, these two species have quite different ribbing patterns and very different sutures (Fig. 49).

Occurrence. Stacheites Zone of Astakhova (1960a) Mangyshlak Peninsula.

Leiophyllites serpentinus Chao
Text-figure 49

Leiophyllites serpentinus Chao, 1959: 149, 331, pl. 42, figs. 7, 13–15, text-fig. 48a.
Leiophyllites oxynotus Chao, 1959: 150, 332, pl. 42, figs. 11, 12, text-fig. 48b.
Leiophyllitesললlolouensis Chao, 1959: 150, 332, pl. 42, figs. 8–10, text-fig. 48c.
Leiophyllites aff. *pitamaha* Chao, 1959: 150, 332, pl. 42, fig. 1.
Leiophyllites kwangsiensis Chao, 1959: 7, 160, (*nomen nudum*).
Leiophyllites vermiformis Chao, 1959: 7, 160 (*nomen nudum*).

All the species listed above in the synonymy are based on one or very few specimens of only fair preservation, and all came from the same horizon and locality. Chao describes the venter on some of his species as fastigate but this is not apparent on the illustration of the species. On the basis of the data available, all these species have the general conch architecture of *L. variabilis* and are considered to be conspecific. They differ from *L. variabilis* in the suture (Fig. 49).

Occurrence. Limestone block (Chao collection 542b) Kwangsi, China.

Leiophyllites admaris (Kiparisova)
Text-figure 49

Danubites (*Danubites*) *admaris* Kiparisova, 1961: 142, pl. 28, fig. 11, text-fig. 106.
Danubites (*Danubites*) aff. *floriani* Mojsisovics,—Kiparisova, 1961: 141, pl. 28, fig. 10, text-fig. 105.
Danubites (*Danubites*?) *incertus* Kiparisova, 1961: 143, pl. 29, figs. 1, 2, text-figs. 107, 108.

The assignment of these species and *maritimus* to *Leiophyllites* is done entirely on the basis of the suture pattern (Fig. 49). The ornamentation of these species and especially that of *maritimus* would ally these species to *Preflorianites.* In the interpretation followed here the suture is considered the more critical sign post of genetic affinity and the ornamentation a case of homeomorphy. The different species brought together here differ mainly in the degree of ribbing.

Occurrence. Subcolumbites fauna, Primorye Region, Siberia.

Leiophyllites maritimus (Kiparisova)
Text-figure 49

Preflorianites maritimus Kiparisova, 1958b: pl. 8, fig. 3, text-fig. 22b.
Danubites (*Preflorianites*) *maritimus* Kiparisova, 1961: 146, pl. 29, figs. 8, 9, text-fig. 111.
Danubites (*Preflorianites*) *inflatus* Kiparisova, 1961: 145, pl. 29, figs. 3, 4, text-figs. 109–110.
Danubites (*Preflorianites*) aff. *maritimus* Kiparisova, 1961: 147, pl. 29, fig. 10, text-fig. 112.

This species has a suture (Fig. 49D) much like that of *L. admaris* but the rib pattern is completely preflorianitid in aspect, that is, concentrated near the umbilical shoulder. The specimen from an upper Scythian horizon in the Toad Formation of British Columbia that Tozer (1965a: 40) assigned to *Leiophyllites* sp. indet. is quite similar to *L. maritimus.*

Occurrence. Subcolumbites fauna, Primorye Region, Siberia.

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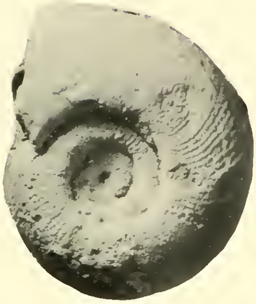
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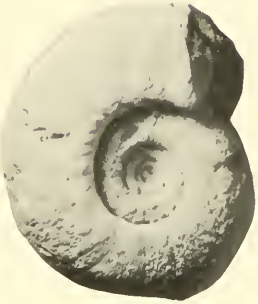
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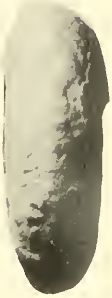
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All specimens are from the *Subcolumbites* fauna of Kčira, Albania, and are deposited in the Paleontological Institute, Vienna.


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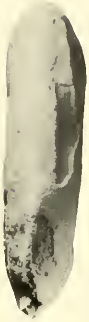
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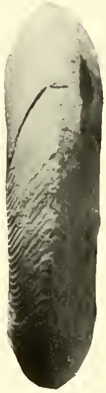
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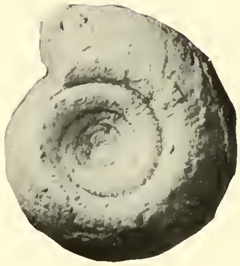
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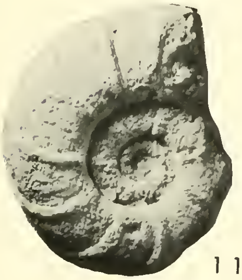
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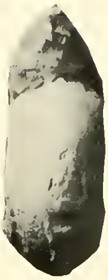
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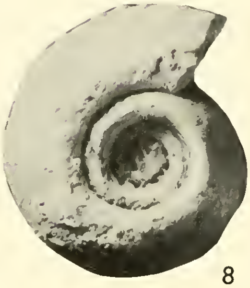
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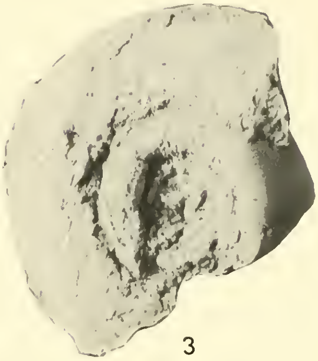
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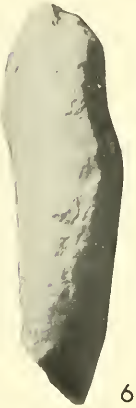
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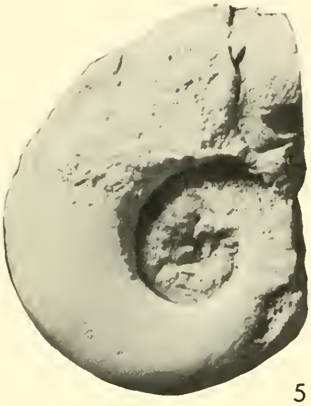
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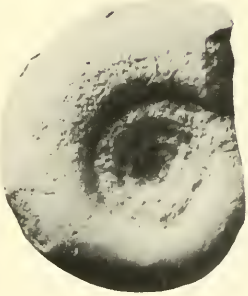
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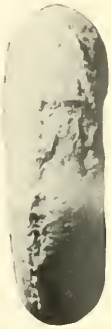
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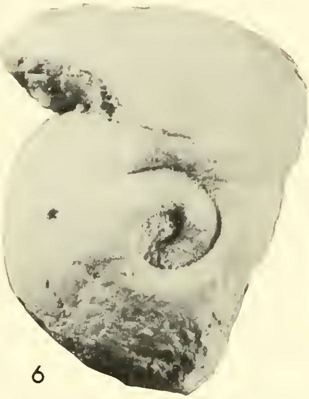
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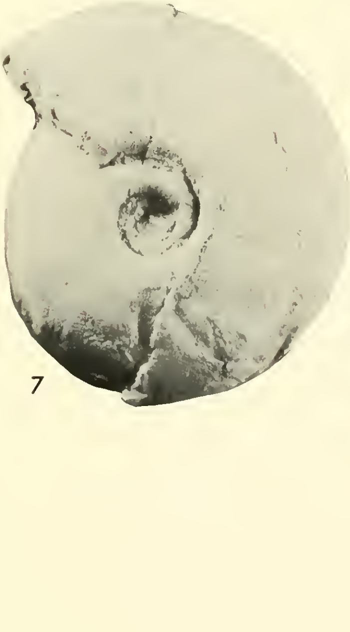
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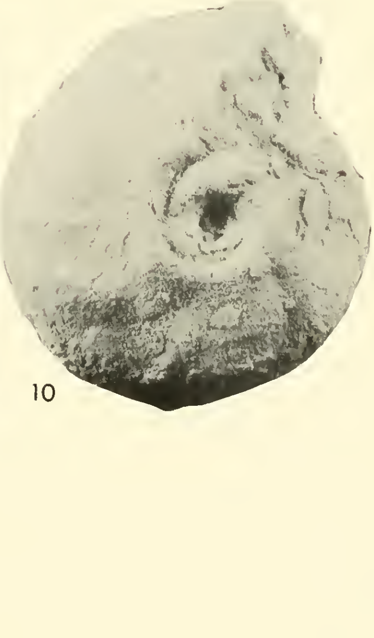
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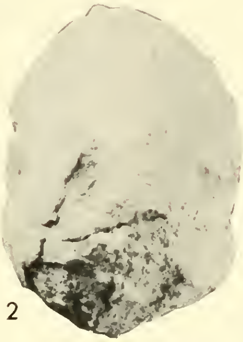
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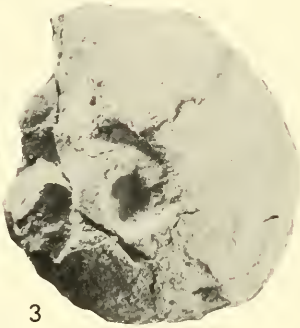
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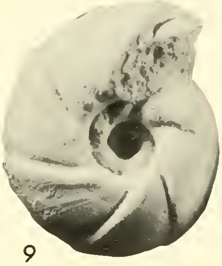
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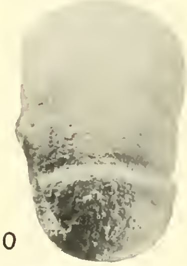
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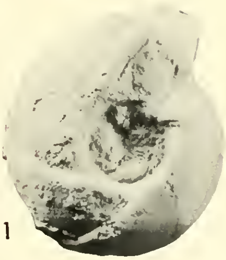
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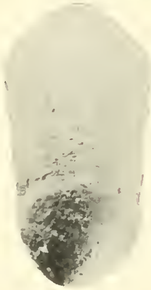
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All specimens are from the *Subcolumbites* fauna of Kčira, Albania, and are deposited in the Paleontalagical Institute, Vienna.


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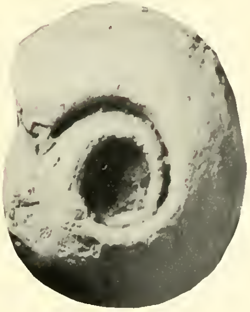
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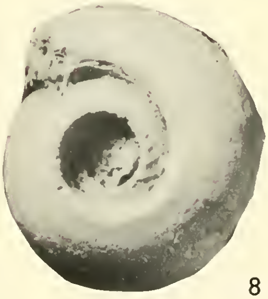
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Both specimens are from the *Subcolumbites* fauna of Kčira, Albania, and are deposited in the Paleontological Institute, Vienna.

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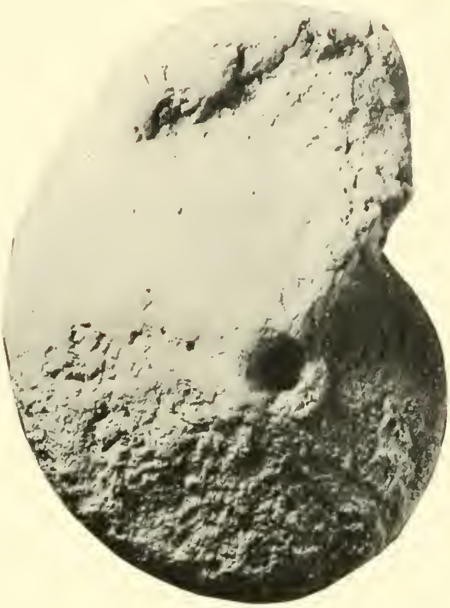

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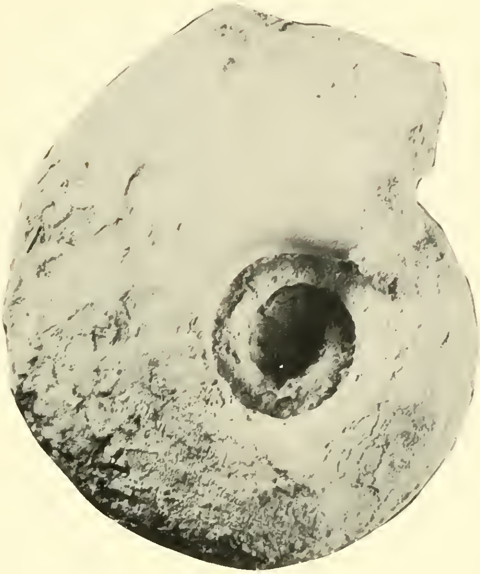
Both specimens are from the *Subcolumbites* fauna of Kčira, Albania, and are deposited in the Paleontological Institute, Vienna.



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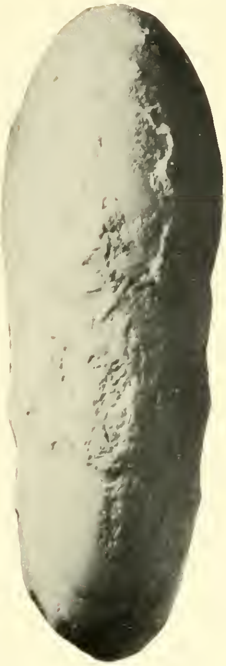

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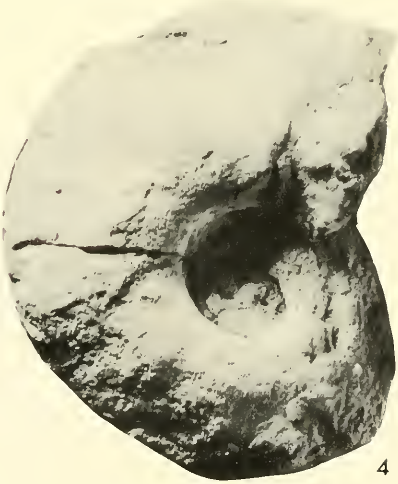

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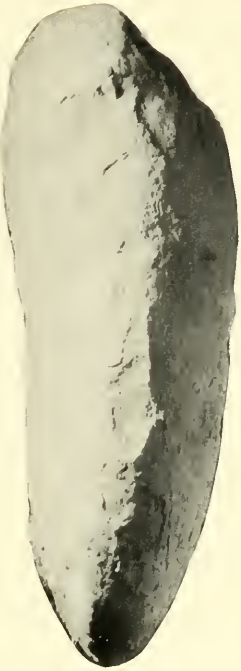
All specimens are from the *Subcolumbites* fauna of Kčira, Albania, and are deposited in the Paleontological Institute, Vienna.



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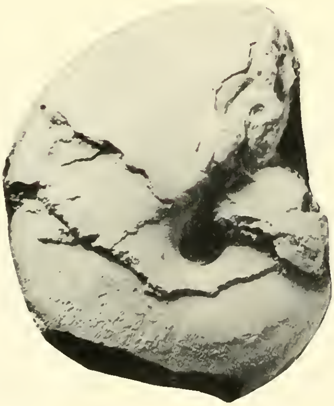

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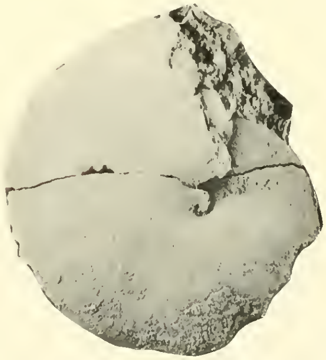

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All specimens are from the *Subcolumbites* fauna of Kčira, Albania, and are deposited in the Paleontological Institute, Vienna.


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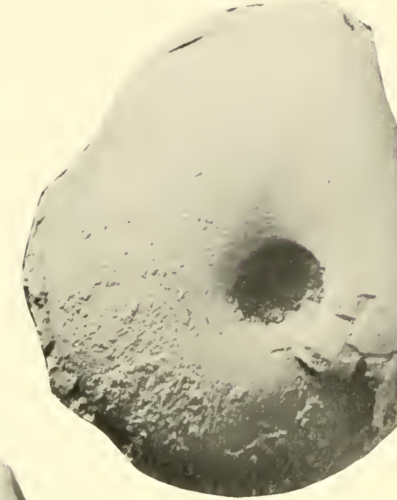
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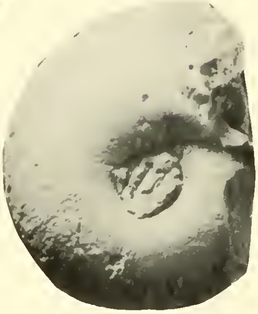


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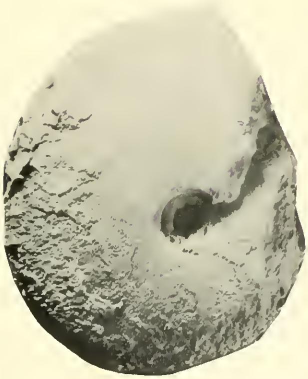
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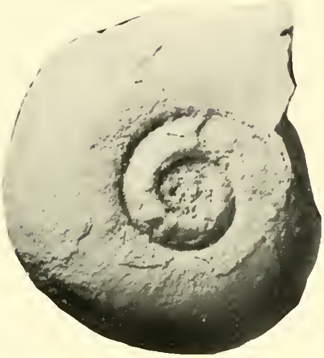
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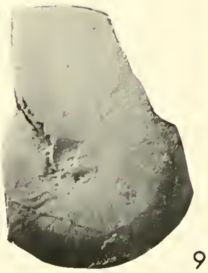
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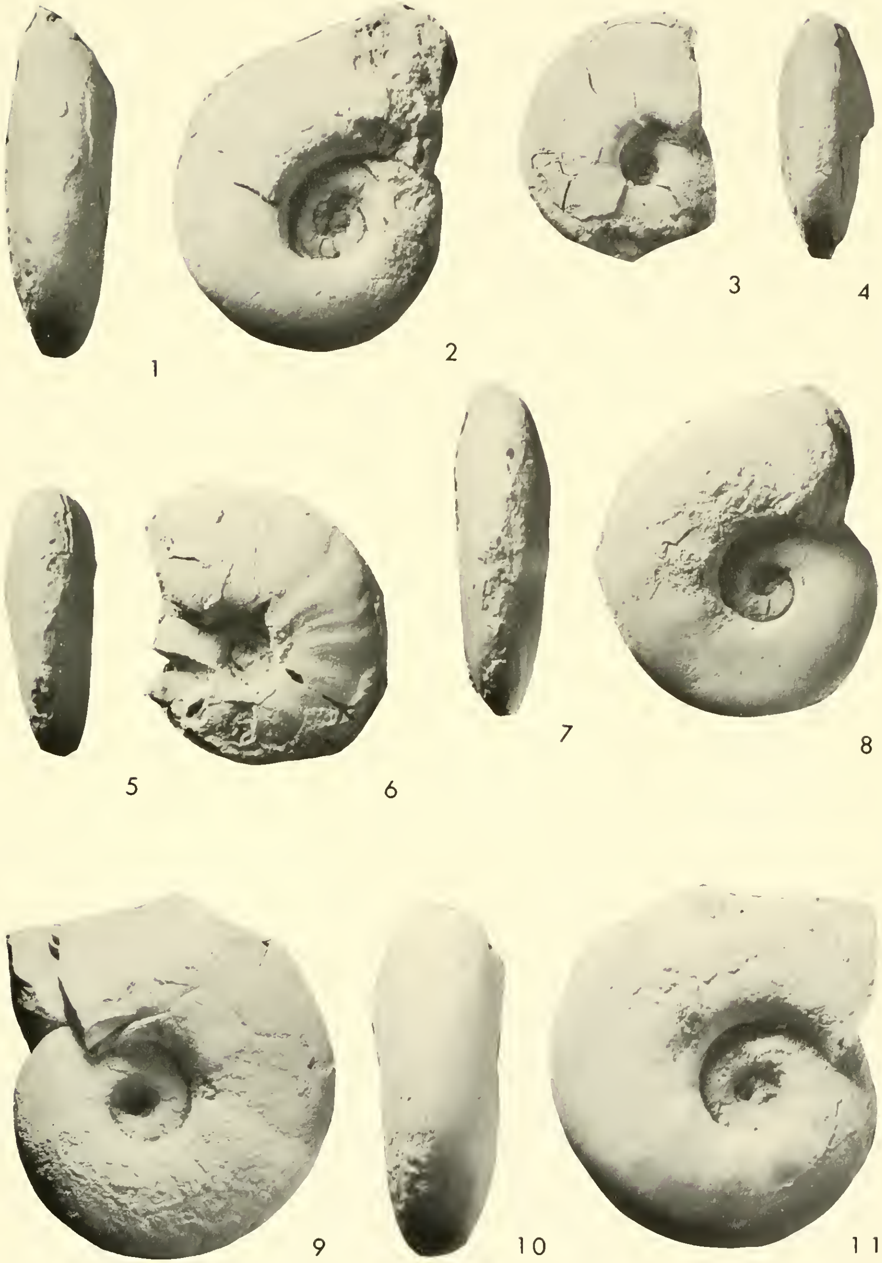

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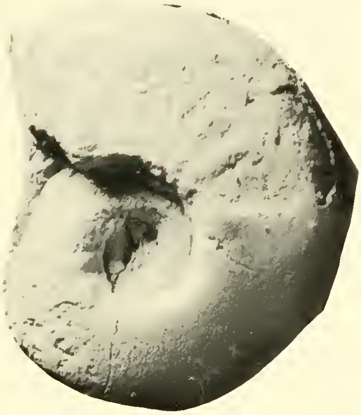
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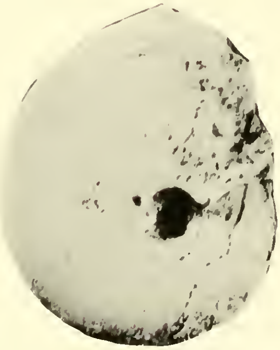
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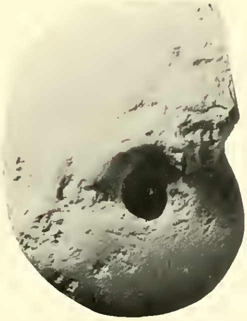
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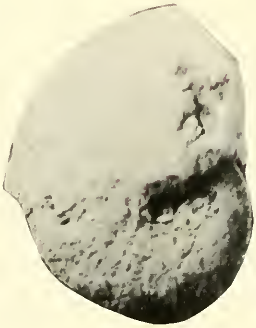
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Plate 16

PLATE 17. ALBANITES TRIADICUS

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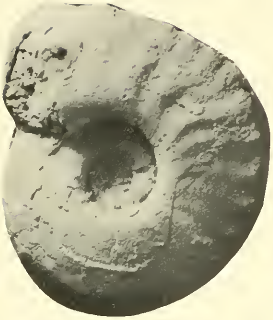
Figs. 1, 2, side and ventral view of paralectotype of *Pronorites arbanus* Arthaber (1911: pl. 17(1), figs. 12a, b), × 1. Figs. 3, 4, unfigured specimen of Arthaber (1911), × 2. Figs. 5, 6, side and ventral view of lectotype of *Pronorites osmanicus* Arthaber (1911: pl. 17(1), figs. 10a–c), × 1. Figs. 7, 8, side and ventral view of holotype of *Pronorites triadicus* Arthaber (1908: pl. 11(1), figs. 4a, c; 1911: pl. 17(1), figs. 8, 9), × 1.5. Figs. 9, 10, side and ventral view of lectotype of *Pronorites arbanus* Arthaber (1911: pl. 17(1), figs. 11 a–c), × 1.5.

All specimens are from the *Subcolumbites* fauna of Kčira, Albania, and are deposited in the Paleontological Institute, Vienna.



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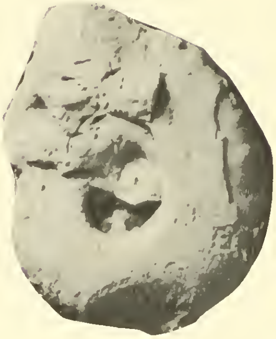

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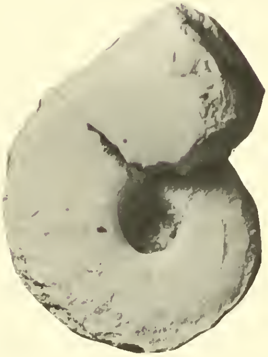

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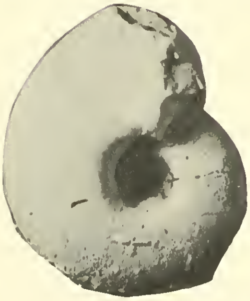

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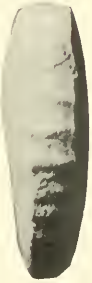

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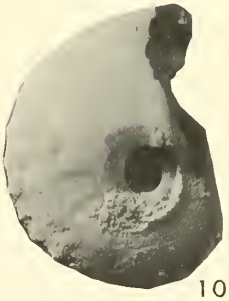

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Plate 17

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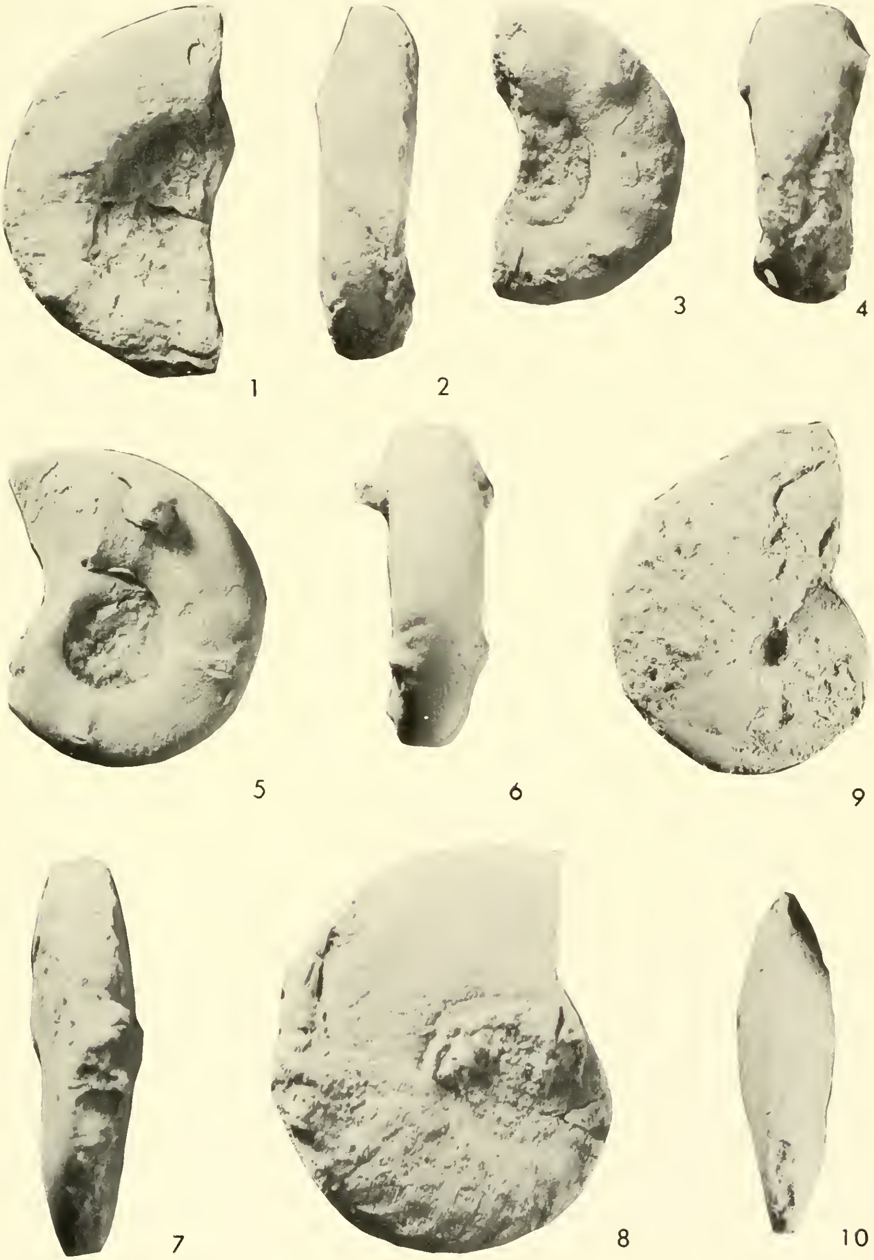

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All specimens are from the *Subcolumbites* fauna of Kčira, Albania, and are deposited in the Paleontological Institute, Vienna.


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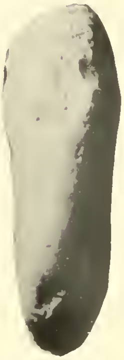
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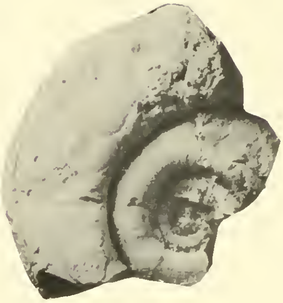
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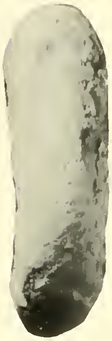
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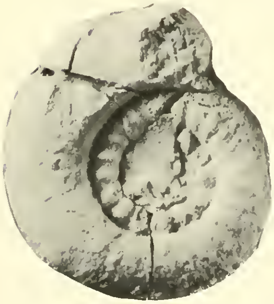
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Plate 19

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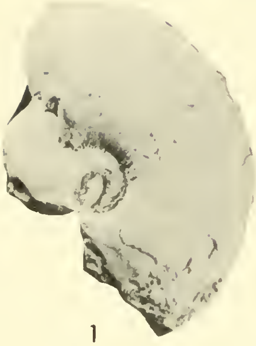
Specimens of Figures 1–9, 12, 13 are from the *Subcolumbites* fauna of Albania and are deposited in the Paleontological Institute, Vienna; specimens of Figures 10, 11, 14, 15 are from the *Subcolumbites* fauna of Chios and are deposited in the Natural History Museum, Basel.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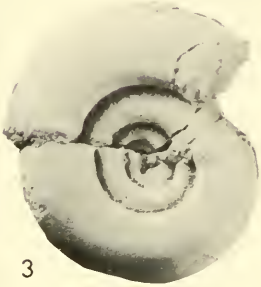
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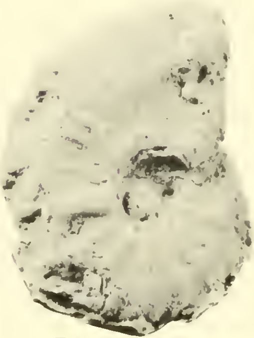
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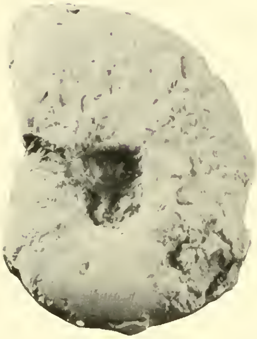
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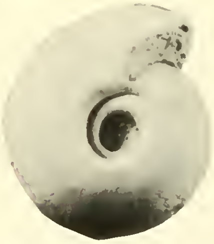
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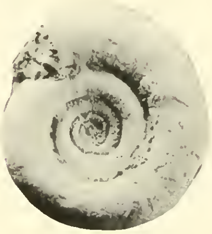
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Plate 20

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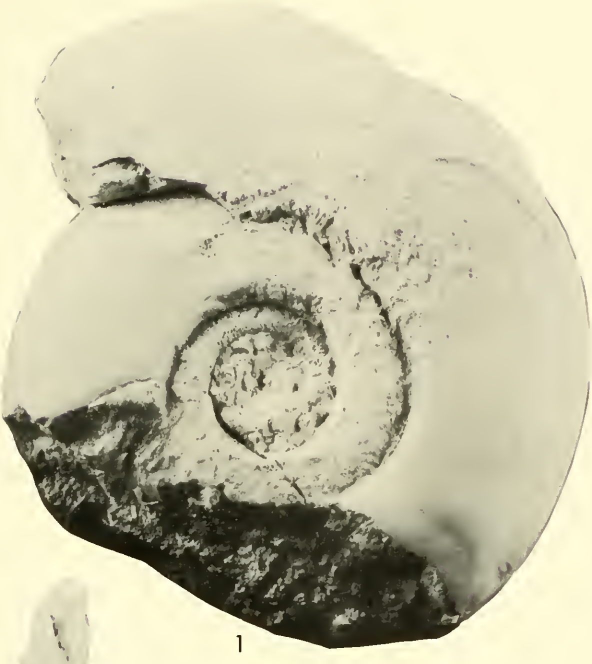
All specimens are from the *Subcolumbites* fauna of Kčira, Albania, and are deposited in the Paleontological Institute, Vienna.



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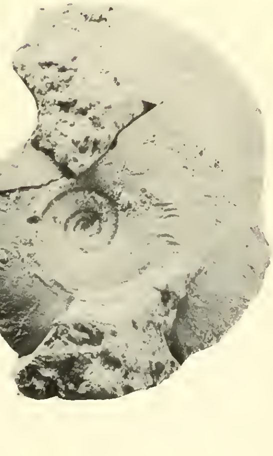

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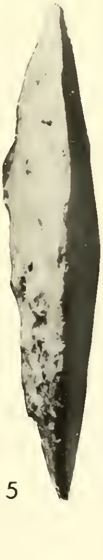

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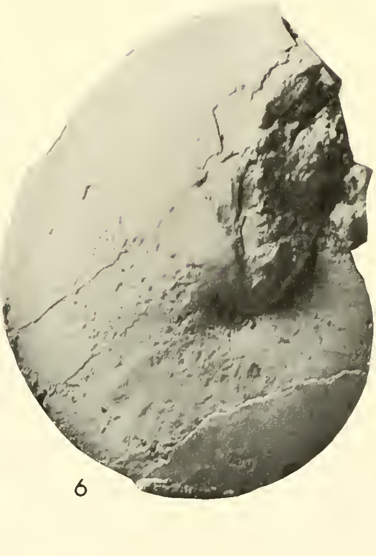

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PLATE 22. EOPHYLLITES and LEIOPHYLLITES

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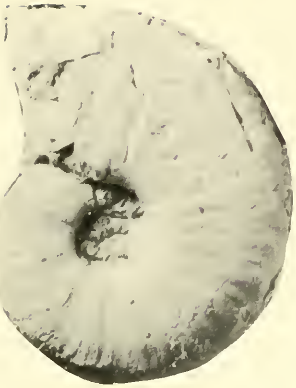
All specimens are from the *Subcolumbites* fauna of Kčira, Albania, and are deposited in the Paleontological Institute, Vienna.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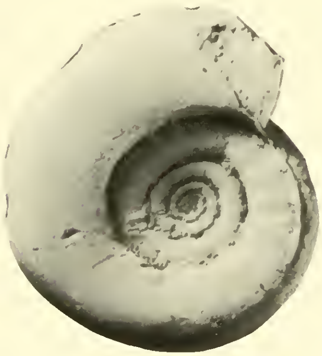
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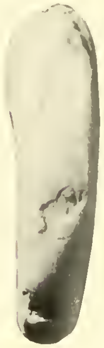
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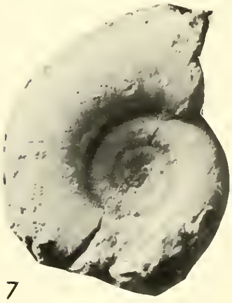
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Plate 22

PLATE 23. EOPHYLLITES

Figures		Page
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Fig. 1, suture specimen of *Monophyllites dieneri* Arthaber (1911: pl. 20(4), fig. 8), × 1. Figs. 2, 3, syntype, Arthaber (1911: pl. 20(4), figs. 5a–c), × 1. Figs. 4, 5, unfigured specimen of Arthaber, × 1. Figs. 6, 7, side and front view of *Ussurites* (?) *decipiens* Spath (= *Monophyllites kingi*,–Arthaber [non Diener], 1911: pl. 20(4), figs. 12a–c), × 1.

All specimens are from the *Subcolumbites* fauna of Kčira, Albania, and are deposited in the Paleontological Institute, Vienna.


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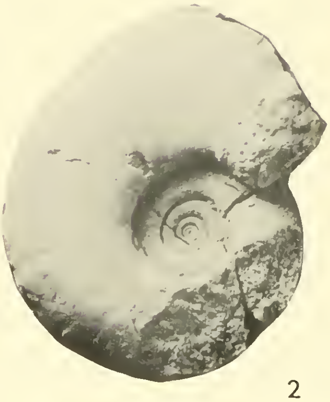
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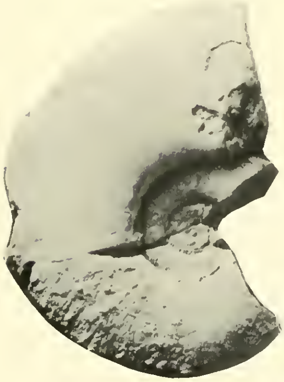
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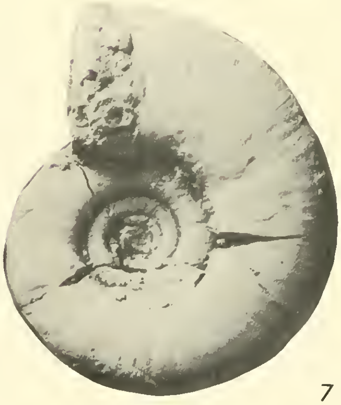
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9, 10	*Hemilecanites discus* (Arthaber)	374
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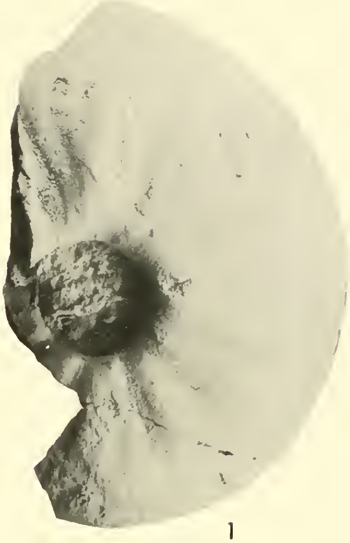
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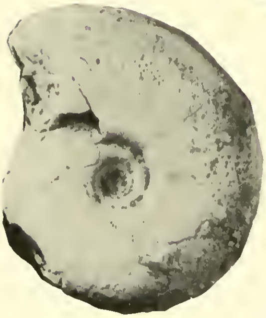
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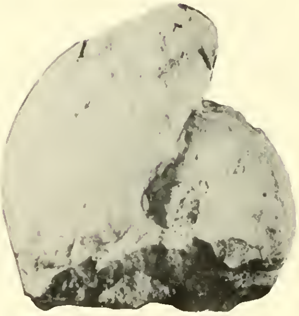
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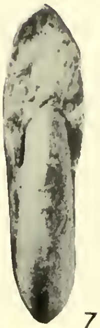
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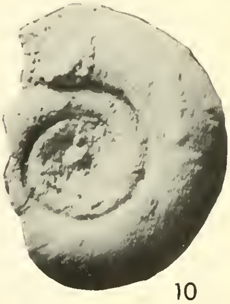
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PLATE 26. SVALBARDICERAS, KEYSERLINGITES, and PROSPHINGITES

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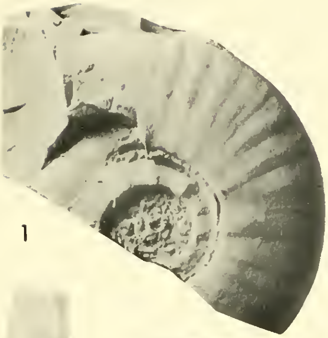
6, 7	*Keyserlingites subrobustus* (Mojsisovics) Fig. 6, side view of specimen figured by Frebold (1929b: pl. 2, fig. 9), × 1. Fig. 7, side view of specimen figured by Frebold (1929b: pl. 2, fig. 8), × 1.	485
8	*Prosphingites czekonowskii* Mojsisovics Topotype specimen, MCZ 8677, × 1.5.	405

Specimens of Figures 1–7 are from upper Scythian horizon at Cape Thorson, Isfjord, Spitsbergen; specimen of Figure 8 is from the mouth of the Olenek River, Siberia.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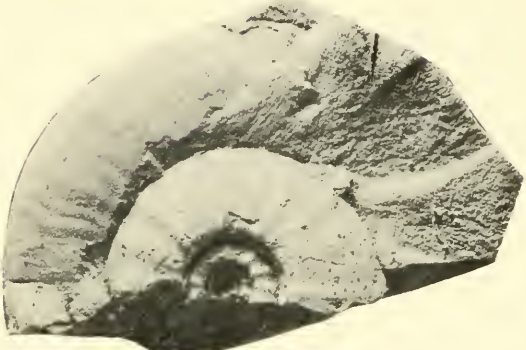
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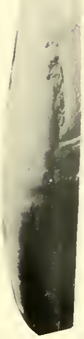
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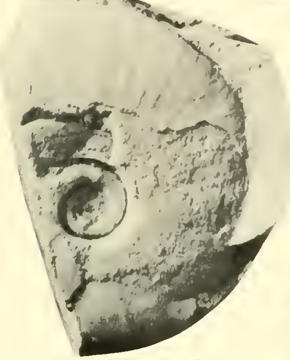
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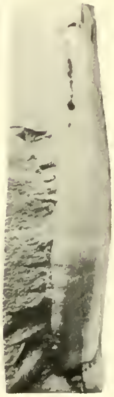
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Plate 26

PLATE 27. METADAGNOCERAS and PSEUDOCELTITES

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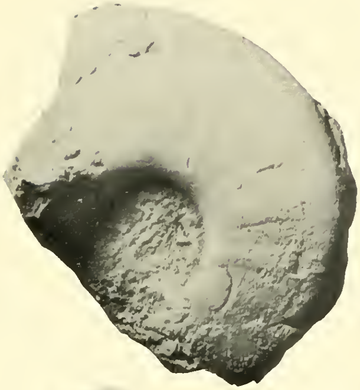
5–10	*Pseudoceltites multiplicatus* (Waagen) Figs. 5, 6, side and ventral view of holotype of *Celtites multiplicatus* Waagen (1895: pl. 7, figs. 2a–c), GSI 7062, × 1. Figs. 7, 8, side and ventral view of syntype of *Celtites armatus* Waagen (1895: pl. 7, figs. 1a–c), GSI 7061, × 1. Figs. 9, 10, side and ventral view of syntype of *Celtites armatus* Waagen (1895: pl. 7, figs. 7a–c), GSI 7067, × 1.5.	440

Specimens of Figures 1–4 are from the Tabin Formation, Tabin Range, Nevada; specimens of Figures 5–10 are from the Mianwali Formation, Salt Range, West Pakistan.



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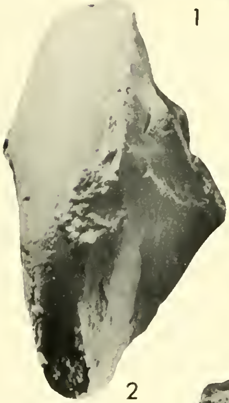

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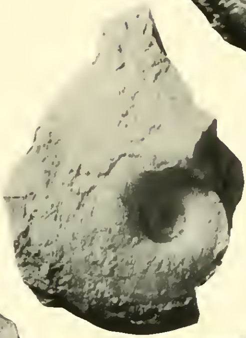

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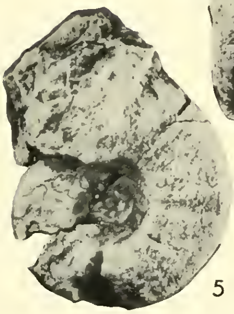

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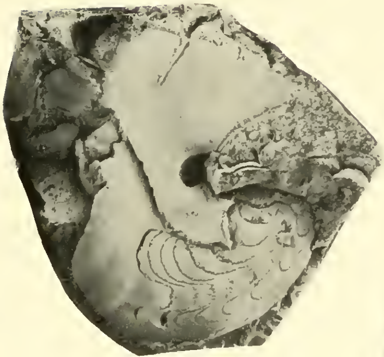
Plate 27

PLATE 28. STACHEITES FLOWERI

Figures		Page
1–10	*Stacheites floweri* n. sp.	456

Fig. 1, paratype, MCZ 9439, × 1. Fig. 2, paratype, MCZ 9440, × 1. Figs. 3, 4, holotype, MCZ 9441, × 1. Fig. 5, paratype, MCZ 9442, × 1. Figs. 6, 7, paratype, MCZ 9443, × 1.5. Fig. 8, paratype, MCZ 9444, × 1. Fig. 9, paratype, MCZ 9445, × 1. Fig. 10, paratype, MCZ 9446, × 1.

All specimens are from the Tobin Formation, Tobin Range, Nevada.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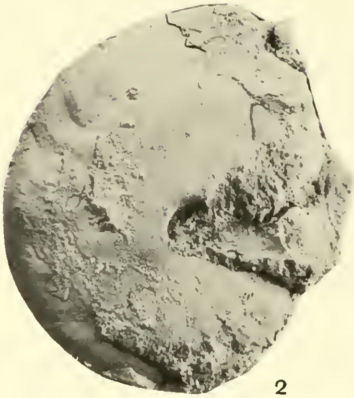
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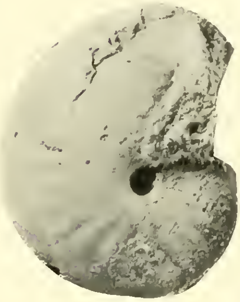
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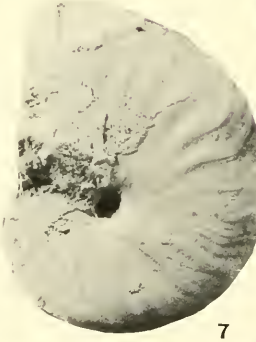
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Plate 28

PLATE 29. ISCULITOIDES and HEMILECANITES

Figures		Page
1–10	*Isculitaides wasserbergi* n. sp. Figs. 1–3, holotype, MCZ 9447, × 1.5. Figs. 4–6, paratype, MCZ 9448, × 2. Figs. 7, 8, paratype, MCZ 9449, × 2. Figs. 9, 10, paratype, MCZ 9450, × 3.	418
11, 12	*Hemilecanites paradiscus* n. sp. Paratype, MCZ 9451, × 2. All specimens are from the Tobin Formation, Tobin Range, Nevada.	375


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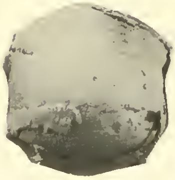
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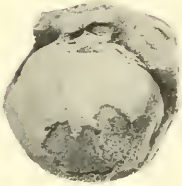
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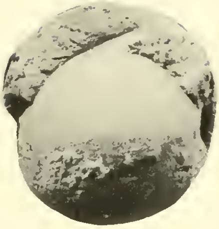
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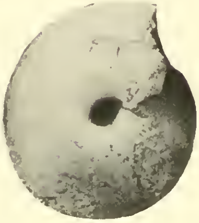
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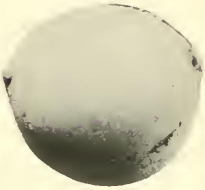
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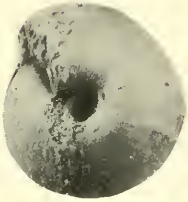
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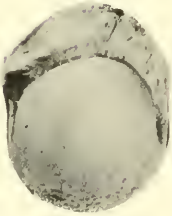
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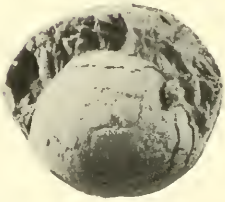
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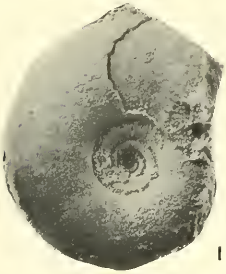
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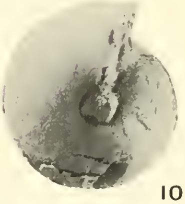
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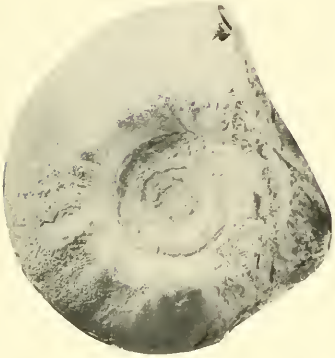
Plate 29

PLATE 30. SUBCOLUMBITES AMERICANUS

Figures		Page
1–14	*Subcolumbites americanus* n. sp. Figs. 1, 2, holotype, MCZ 9430, × 1. Fig. 3, paratype, MCZ 9431, × 1. Fig. 4, paratype, MCZ 9432, × 1.5. Fig. 5, paratype, MCZ 9433, × 1. Figs. 6, 7, paratype, MCZ 9434, × 1. Fig. 8, paratype, MCZ 9435, × 1. Figs. 9, 10, paratype, MCZ 9436, × 1.5. Figs. 11, 12, paratype, MCZ 9437, × 1.5. Figs. 13, 14, paratype, MCZ 9438, × 1.5. All specimens are from the Tobin Formation, Tobin Range, Nevada.	436



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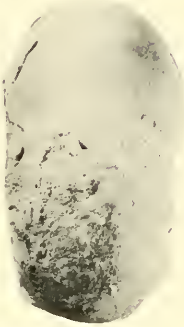

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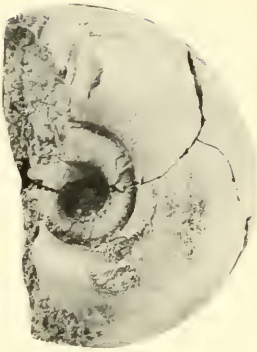

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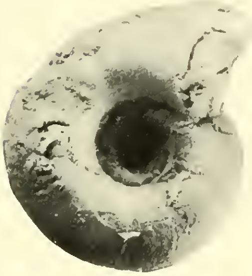

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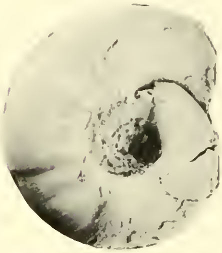

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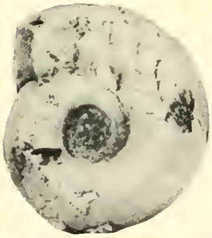

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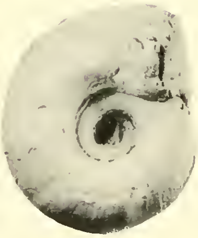

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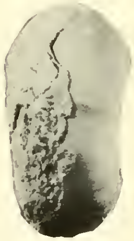

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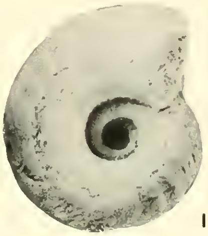

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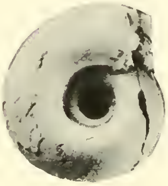

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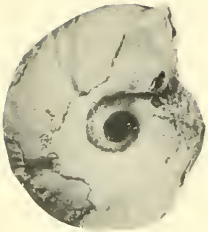
Plate 30

PLATE 31. ARNAUTOCELTITES, USSURITES, and HEMILECANITES

Figures		Page
1–7, 9, 10, 13, 14	*Arnautoceltites techerti* n. sp. Figs. 1, 2, holotype, MCZ 9457, × 1.5. Figs. 3, 4, paratype, MCZ 9458, × 1.5. Fig. 5, paratype, MCZ 9459, × 1.5. Figs. 6, 7, paratype, MCZ 9460, × 1.5. Figs. 9, 10, paratype, MCZ 9461, × 1.5. Figs. 13, 14, paratype, MCZ 9462, × 1.5.	402
8	*Ussurites sieveri* n. sp. Paratype, MCZ 9464, × 1.5.	528
11, 12	*Subcolumbites americanus* n. sp. Paratype, MCZ 9463, × 1.	436
15, 16	*Hemilecanites paradiscus* n. sp. Holotype, MCZ 9465, × 1.5.	375
	All specimens are from the Tobin Formation, Tobin Range, Nevada.	



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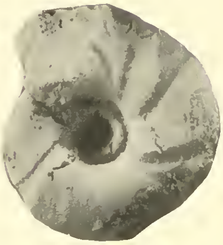

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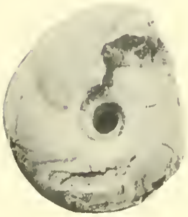

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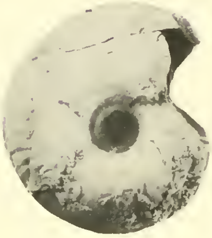

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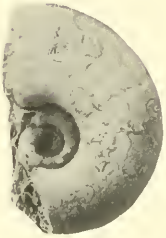

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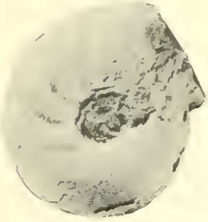

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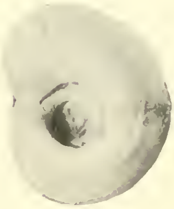

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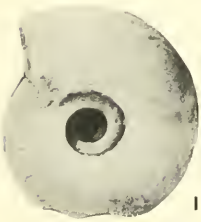

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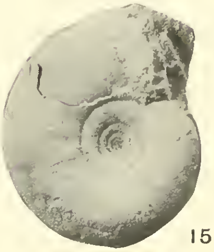

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Plate 31

PLATE 32. USSURITES SIEVERI

Figures		Page
1–7	*Ussurites sieveri* n. sp. Figs. 1, 2, holotype, MCZ 9452, × 1. Fig. 3, paratype, MCZ 9453, × 1. Fig. 4, paratype, MCZ 9454, × 1. Fig. 5, paratype, MCZ 9455, × 1. Figs. 6, 7, paratype, MCZ 9456, × 1. All specimens are from the Tobin Formation, Tobin Range, Nevada.	528


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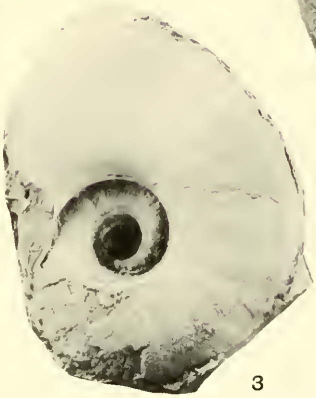
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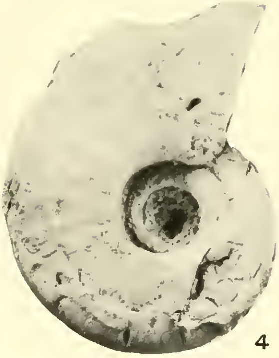
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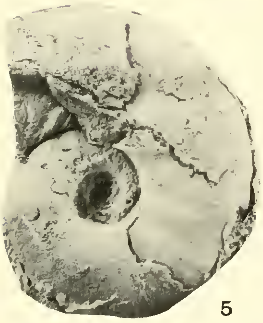
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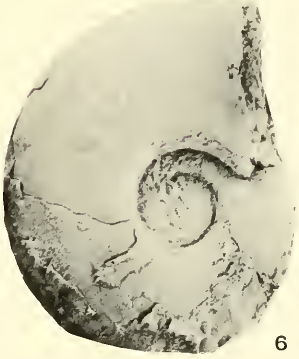
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Plate 32

PLATE 33. USSURITES HOSEI

Figures		Page
1–6	*Ussurites hosei* n. sp.	528

Fig. 1, holotype, USNM 153085, × 1. Fig. 2, paratype, USNM 153086, × 2. Figs. 3, 4, paratype, USNM 153087, × 1. Figs. 5, 6, paratype, USNM 153088, × 1.

All specimens are from the USGS collection M111, Confusion Range, Utah. From section 15 of Hose and Repenning (1959).

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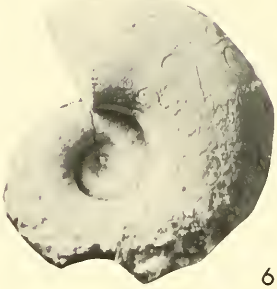

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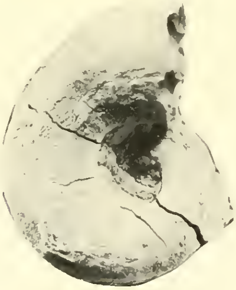

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Plate 33

PLATE 34. PSEUDOCELTITES, PSEUDOSAGECERAS, and TIROLITES

Figures		Page
1–5	*Pseudoceltites nevadi* n. sp. Fig. 1, side view of holotype, USNM 153078, × 1. Figs. 2, 3, side and ventral view of fragment of paratype, USNM 153079, × 1. Figs. 4, 5, side and ventral view of fragment of paratype, USNM 153080, × 1.	440
6	*Pseudosageceras multilobatum* Noetling Side view, USNM 153072, × 1.	361
7–10	*Tirolites* cf. *cassianus* (Quenstedt) Figs. 7, 8, side and ventral view of portion of body chamber, USNM 153083, × 1. Figs. 9, 10, side and ventral view of fragmentary specimen, USNM 153084, × 1. All specimens are from the USGS Collection M111, Thaynes Formation, Confusion Range, Utah, associated with *Ussurites hosei* n. sp.	503


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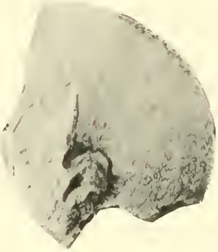
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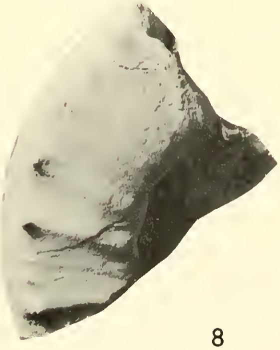
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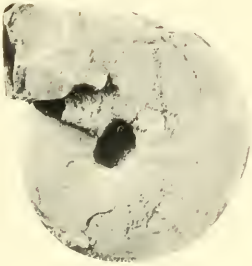
Plate 34

PLATE 35. PROHUNGARITES, EPICELTITES, USSURITES, and HEMILECANITES

Figures		Page
1–5, 8, 9	*Prohungarites mckelvei* n. sp. Figs. 1, 2, holotype, MCZ 9466, × 1. Figs. 3, 4, paratype, MCZ 9467, × 1.5. Fig. 5, paratype, MCZ 9468, × 1.5. Figs. 8, 9, paratype, MCZ 9469, × 1.	520
6, 7	*Epiceltites gentii* (Arthaber) Fig. 6, plesiotype, MCZ 9470, × 1.5. Fig. 7, plesiotype, MCZ 9471, × 1.5.	447
10, 11	*Ussurites sieveri* n. sp. Paratype, MCZ 9472, × 1.5.	528
12	*Hemilecanites paradiscus* n. sp. Paratype, MCZ 9473, × 1.5.	375

Figures 1–9 are from the upper member of Thaynes Formation, Hammond Creek, Bear River Range, southeast Idaho. Figures 10–12 are from Tobin Formation, Tobin Range, Nevada.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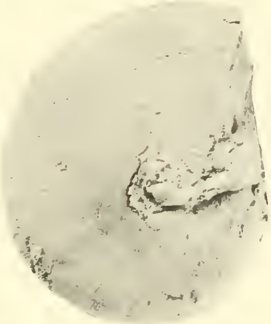
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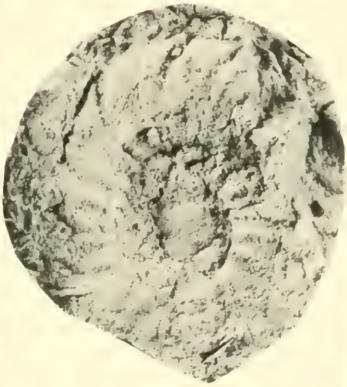
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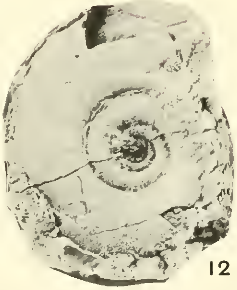
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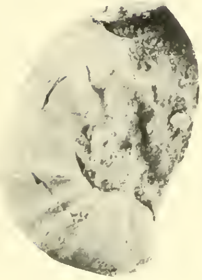
Plate 35

PLATE 36. PROHUNGARITES, OLENEKITES, and ISCULITOIDES

Figures		Page
1, 2	*Prohungarites* sp. indet. MCZ 9474, × 1.	522
3	*Prohungarites gutstadti* n. sp. Side view of holotype, MCZ 9475, × 1.	521
4–7	*Olenekites* cf. *spiniplicatus* (Majsisovics) Figs. 4, 5, plesiatype, MCZ 9482, × 1.5. Figs. 6, 7, plesiatype, MCZ 9476, × 1.5.	489
8–13	*Isculitoides hammondi* n. sp. Fig. 8, holotype, MCZ 9477, × 1.5. Figs. 9, 10, paratype, MCZ 9478, × 1.5. Fig. 11, paratype, MCZ 9479, × 1.5. Figs. 12, 13, paratype, MCZ 9480, × 1.5.	419
14, 15	*Prohungarites gutstadti* n. sp. Side and ventral view of paratype, MCZ 9481, × 2. All specimens are from the upper member of Thaynes Formation, Hammond Creek, Bear River Range, southeast Idaho.	521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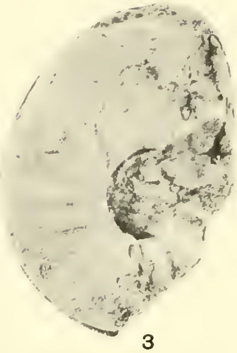
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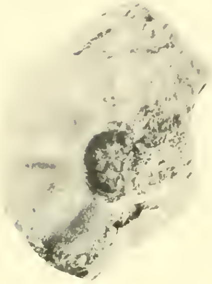
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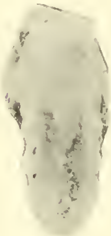
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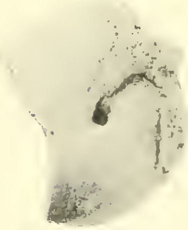
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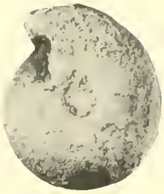
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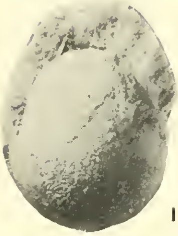
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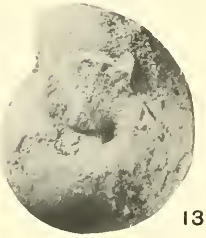
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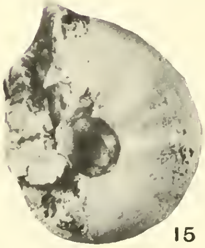
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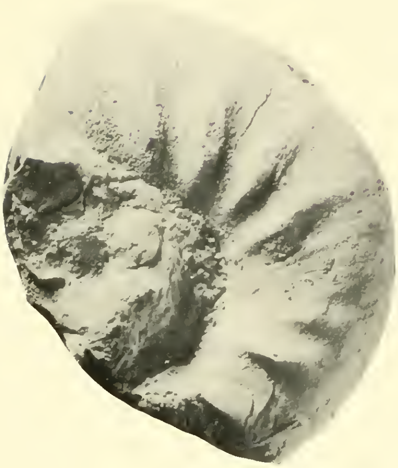
Plate 36

PLATE 37. KEYSERLINGITES and STACHEITES

Figures		Page
1–4	*Keyserlingites bearriverensis* n. sp. Figs. 1, 2, side and ventral view of holotype, MCZ 9520, × 1. Figs. 3, 4, side and ventral view of paratype, MCZ 9521, × 1.	487
5, 6	*Keyserlingites bearlakensis* n. sp. Side and ventral view of paratype, MCZ 9518, × 3.	486
7, 8	*Stacheites* sp. indet. I Side and ventral view, MCZ 9487, × 1.	456
9, 10	*Stacheites* sp. indet. II Side and ventral view, MCZ 9501, × 1.	457

Specimens of Figures 1–8 came from the upper member of Thaynes Formation, Hammond Creek, Bear River Range, southeastern Idaho; specimens of Figures 9, 10 came from the upper part of Thaynes Formation, Sublette Ridge, Wyoming.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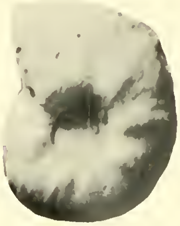
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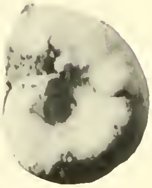
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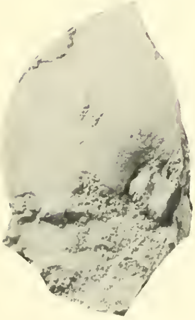
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Plate 37

PLATE 38. KEYSERLINGITES and PROHUNGARITES

Figures		Page
1–3	*Keyserlingites bearlakensis* n. sp. Figs. 1, 2, side and ventral view of holotype, MCZ 9516, × 1. Fig. 3, side view of paratype, MCZ 9517, × 1.	486
4, 5	*Prohungarites* sp. indet. Side and ventral view, MCZ 9647, × 1. All specimens are from the upper Thaynes Formation, Hammond Creek, Bear River Range, southeast Idaho.	522


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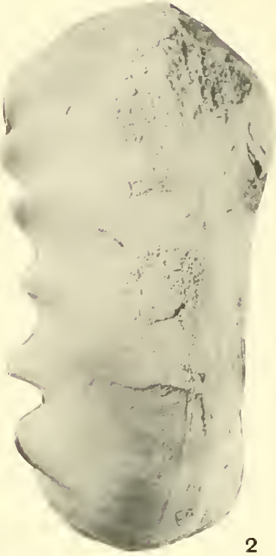
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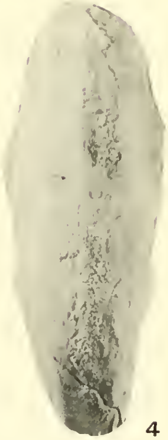
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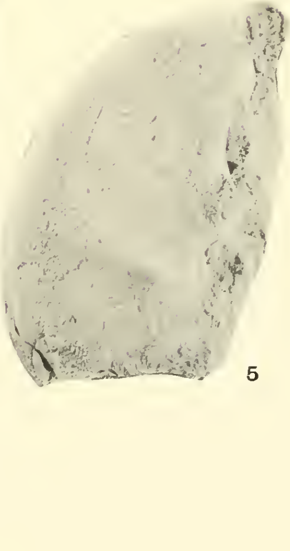
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Plate 38

PLATE 39. COLUMBITES PARISIANUS

Figures		Page
1–10	*Columbites parisianus* Hyatt and Smith	424

Figs. 1, 2, front and side view of paratype, Hyatt and Smith (1905: pl. 61, figs. 2, 3), USNM 75286b, × 1. Figs. 3, 4, front and side view of holotype, Hyatt and Smith (1905: pl. 1, figs. 9, 10), USNM 75246a, × 1. Figs. 5–7, front, ventral, and side views of paratype, Hyatt and Smith (1905: pl. 61, figs. 5–7), USNM 75286c, × 1. Figs. 8, 9, front and side view of paratype, Hyatt and Smith (1905: pl. 1, figs. 12–14), USNM 75246b, × 1. Fig. 10, front view of paratype, Hyatt and Smith (1905: pl. 61, fig. 10), USNM 75286e, × 1. All specimens are from the middle shale member of Thaynes Formation (*Columbites* fauna), Paris Canyon, Bear River Range, southeast Idaho.

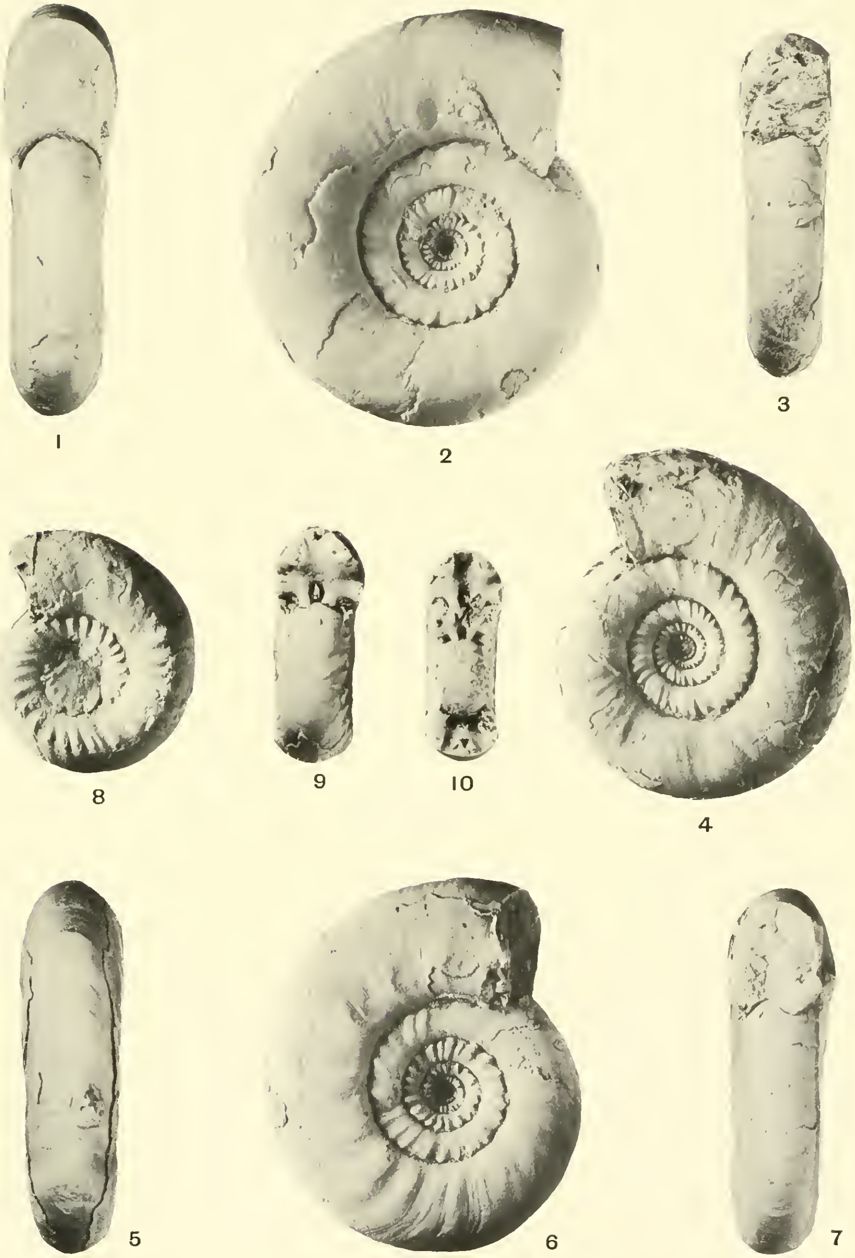

Plate 39

PLATE 40. COLUMBITES PARISIANUS

Figures		Page
1–11	*Columbites parisianus* Hyatt and Smith	424

Figs. 1, 2, front and side view of holotype of *Columbites ornatus* Smith (1932: pl. 46, figs. 14, 15), USNM 74984a, × 1. Figs. 3, 4, front and side view of paratype of *Columbites spencei* Smith (1932: pl. 78, figs. 13–15), USNM 75309g, × 2. Figs. 5, 6, front and side view of paratype of *Columbites spencei* Smith (1932: pl. 78, figs. 11, 12), USNM 75309f, × 2. Figs. 7–9, side, ventral, and front view of paratype of *Columbites ligatus* Smith (1932: pl. 47, figs. 6–8), USNM 74985c, × 1. Figs. 10, 11, side and ventral view of paratype of *Columbites ornatus* Smith (1932: pl. 46, figs. 16, 17), USNM 74984b, × 1.

All specimens are from the middle shale member of Thaynes Formation (*Columbites* fauna), Paris Canyon, Bear River Range, southeast Idaho.


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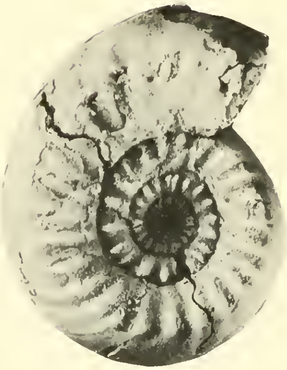
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Plate 40

PLATE 41. COLUMBITES PARISIANUS

Figures		Page
1–7	*Columbites parisianus* Hyatt and Smith	424

Figs. 1, 2, front and side view of holotype of *Columbites consanguineus* Smith (1932: pl. 46, figs. 1, 2), USNM 74983a, × 1. Figs. 3, 4, ventral and side view of paratype of *Columbites consanguineus* Smith (1932: pl. 46, figs. 3, 4), USNM 74983b, × 1. Figs. 5, 6, front and side view of paratype of *Columbites consanguineus* Smith (1932: pl. 46, figs. 5, 6), USNM 74983c, × 1. Fig. 7, side view of paratype of *Columbites parisianus* Hyatt and Smith (1904: pl. 61, fig. 1), USNM 75286a, × 1.

All specimens are from the middle shale member of Thaynes Formation (*Columbites* fauna) Paris Canyon, Bear River Range, southeast Idaho.

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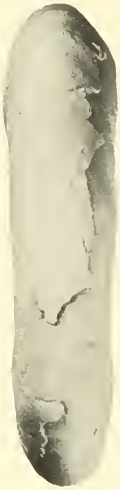

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Plate 41

PLATE 42. COLUMBITES PARISIANUS

Figures		Page
1–9	*Columbites parisianus* Hyatt and Smith	424

Figs. 1, 2, front and side view of holotype of *Columbites spencei* Smith (1932: pl. 78, figs. 1, 2), USNM 75309a, × 1. Figs. 3, 4, front and side view of paratype of *Columbites spencei* Smith (1932: pl. 78, figs. 5, 6), USNM 75309c, × 1. Figs. 5, 6, front and side view of paratype of *Columbites spencei* Smith (1932: pl. 78, figs. 9, 10), USNM 75309e, × 2. Fig. 7, side view of paratype of *Columbites ligatus* Smith (1932: pl. 47, fig. 4), USNM 74985b, × 1. Figs. 8, 9, front and side view of paratype of *Columbites spencei* Smith (1932: pl. 78, figs. 7, 8), USNM 75309d, × 1.

All specimens are from the middle shale member of Thaynes Formation (*Columbites* fauna), Paris Canyon, Bear River Range, southeast Idaho.


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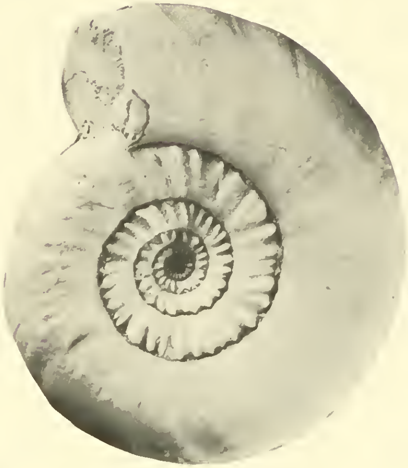
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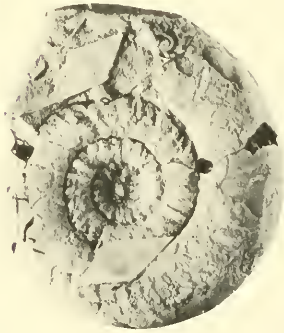
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Plate 42

PLATE 43. SVALBARDICERAS, PREFLORIANITES, and COLUMBITES

Figures		Page
1	*Svalbardiceras sheldoni* n. sp. Side view of holotype, MCZ 9493, × 1.	453
2, 3	*Preflorianites montpelierensis* n. sp. Side and ventral view of paratype, MCZ 9495, × 1.5.	382
4, 5	*Columbites parisianus* Hyatt and Smith Side and front view of holotype of *Columbites ligatus* Smith (1932: pl. 47, figs. 1–3), USNM 74985a, × 1.	425

All specimens are from the middle shale member of Thaynes Formation (*Columbites* fauna), southeast Idaho. Specimen of Figure 1 from Sage Creek, of Figures 2, 3 from Montpelier Canyon, and of Figures 4, 5 from Paris Canyon.

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Plate 43

PLATE 44. USSURITES, PSEUDOCELTITES, PREFLORIANITES, and PSEUDASPIDITES

Figures		Page
1–3	*Ussurites mansfieldi* n. sp. Fig. 1, side view of paratype, MCZ 9515, × 1. Figs. 2, 3, ventral and side view of paratype, MCZ 9513, × 1.	530
4–10	*Pseudoceltites cheneyi* n. sp. Fig. 4, paratype, MCZ 9503, × 1. Fig. 5, paratype, MCZ 9504, × 1. Figs. 6, 7, paratype, MCZ 9505, × 1. Figs. 8, 9, holotype, USNM 153073, × 1. Fig. 10, paratype, MCZ 9506, × 1.	438
11–13	*Preflorianites montpelierensis* n. sp. Fig. 11, paratype, MCZ 9635, × 1. Fig. 12, paratype, MCZ 9498, × 1. Fig. 13, holotype, MCZ 9494, × 1.	382
14–15	*Pseudaspidites popovi* n. sp. Side and ventral view of juvenile specimen, MCZ 9636, × 1.	383

All specimens come from the middle shale member of Thaynes Formation (*Columbites* fauna), southeast Idaho. Specimens of Figures 8, 9, from Draney Creek, of Figure 13 from Montpelier Canyon, all others from Hot Springs.

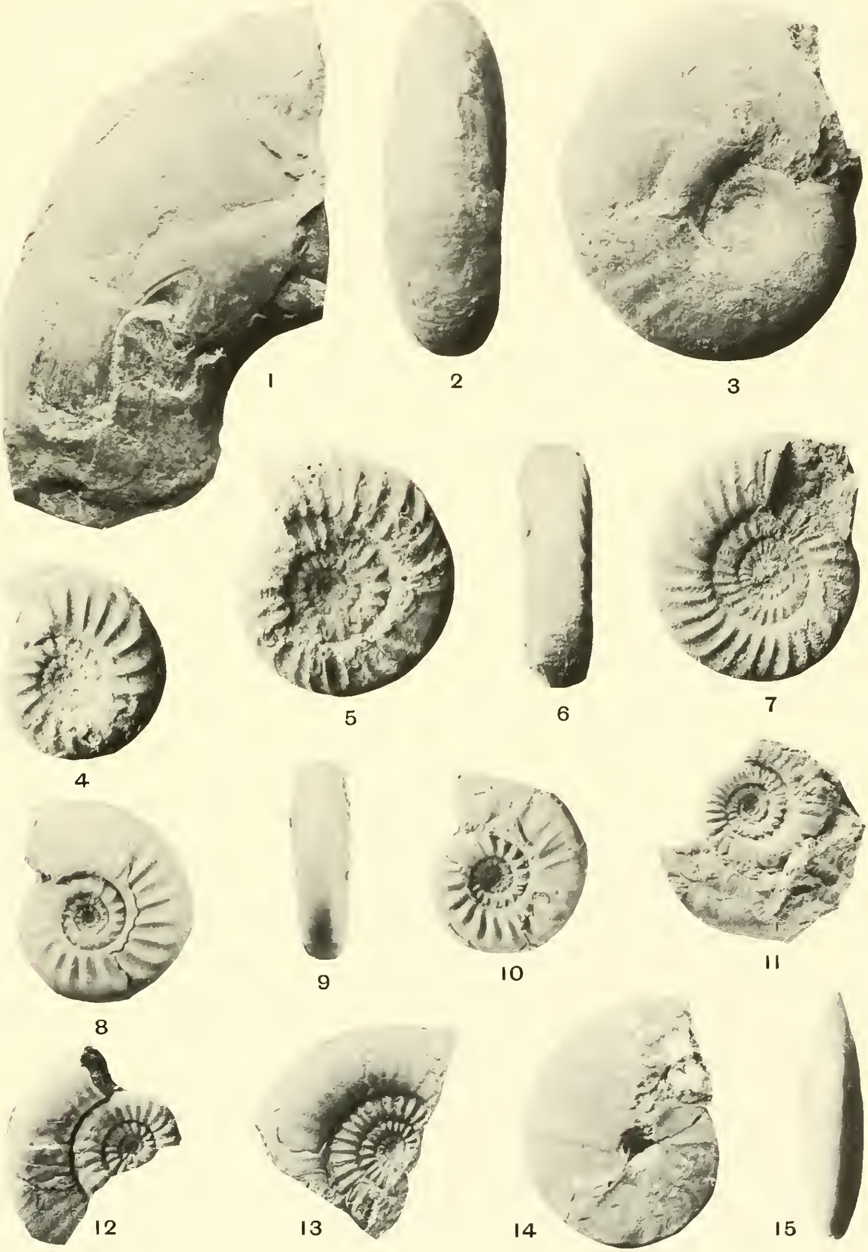


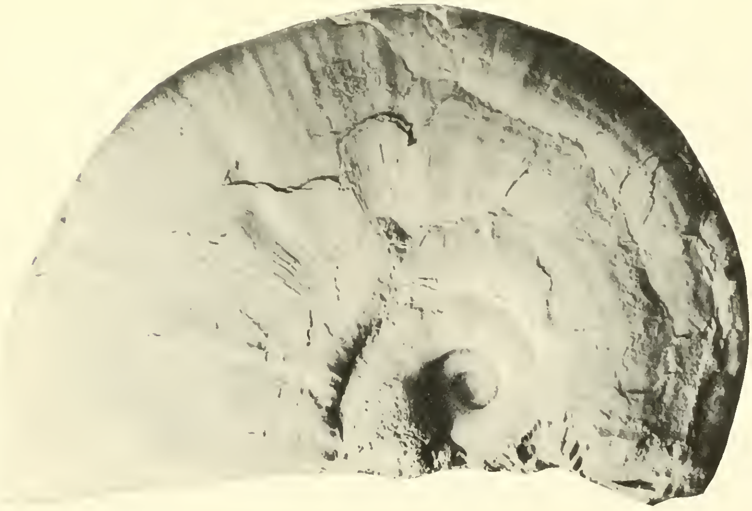
Plate 44

PLATE 45. USSURITES MANSFIELDI

Figures		Page
1–3	*Ussurites mansfieldi* n. sp.	530

Fig. 1, holotype, × 0.5. Figs. 2, 3, paratype, × 0.8.

Both specimens are from the middle shale member of Thaynes Formation (*Columbites* fauna) in Webster Canyon, southeast Idaho, and are deposited in the Department of Geology, Washington State University.



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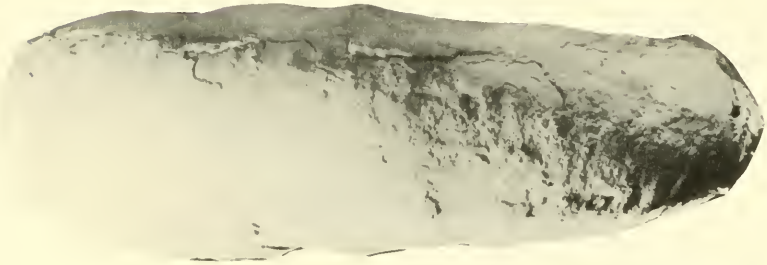

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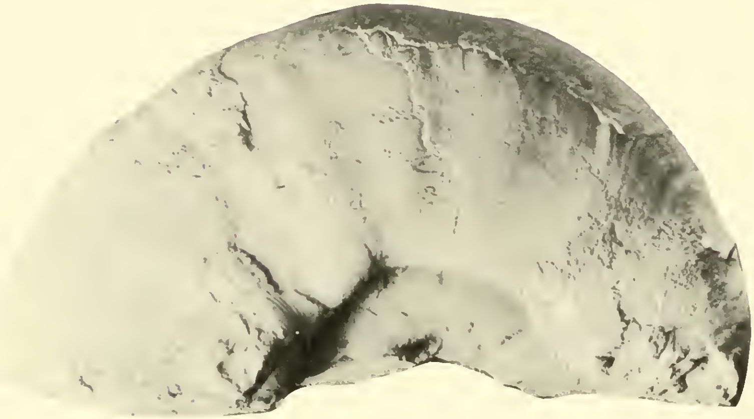

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Plate 45

PLATE 46. KEYSERLINGITES and NORDOPHICERAS

Figures		Page
1	*Keyserlingites stephensoni* n. sp. Side view of the holotype deposited in Department of Geology, Washington State University. Specimen is presumably from the *Columbites* fauna, Fort Hall Indian Reservation, southeast Idaho, × 0.3.	487
2, 3	*Nordophiceras pilatum* (Hyatt and Smith) Fig. 2, MCZ 9543, × 1.5. Fig. 3, MCZ 9544, × 1.5. Both specimens are from the middle shale member of Thaynes Formation (*Columbites* fauna) southeast Idaho, Figure 2, from Montpelier Canyon, Figure 3, from Hot Springs.	470

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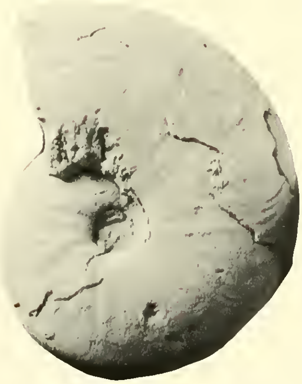

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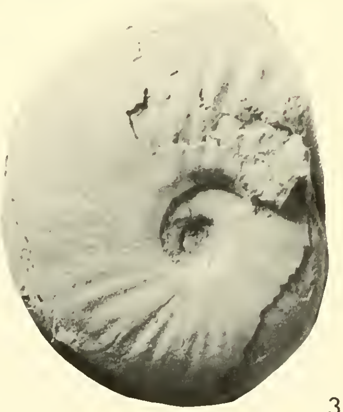

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Plate 46

PLATE 47. NORDOPHICERAS

Figures		Page
1–5	*Nordophiceras jacksoni* (Hyatt and Smith) Fig. 1, MCZ 9564, × 1. Fig. 2, MCZ 9565, × 1. Fig. 3, MCZ 9566, × 3. Fig. 4, MCZ 9567, × 1.5. Fig 5, MCZ 9568, × 1.5. All specimens are from the middle shale member of Thaynes Formation (*Columbites* fauna), southeast Idaho. Specimen of Figure 1 is from Montpelier Canyon, Figure 2 is from Paris Canyon, and the others are from Hot Springs.	468
6–8	*Nordophiceras euomphalus* (Keyserling) Fig. 6, MCZ 9655, × 1. Figs. 7, 8, MCZ 8680, × 1.5. Topotype specimens are from the Olenekian fauna, Olenek River, Siberia.	465


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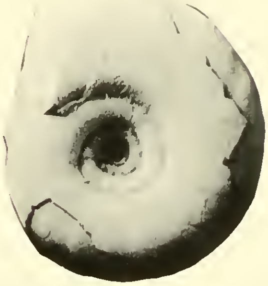
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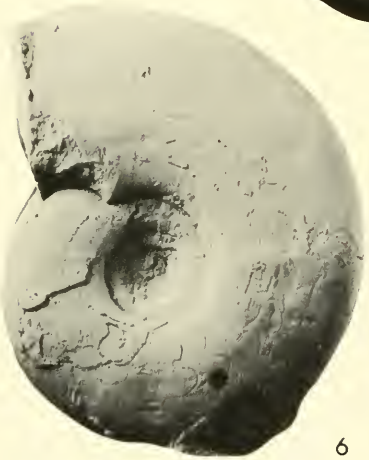
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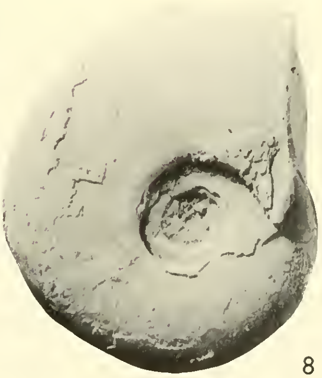
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Plate 47

PLATE 48. NORDOPHICERAS and XENOCELTITES

Figures Page

1–4 *Nordophiceras jacksoni* (Hyatt and Smith) 468

Figs. 1, 2, side and front view of paratype (Hyatt and Smith, 1905: pl. 62, figs. 15, 16), USNM 75292c, × 1.

Figs. 3, 4, side and front view of holotype (Hyatt and Smith, 1905: pl. 62, figs. 11–13), USNM 75292a, × 1.

5–9 *Xenoceltites spencei* (Hyatt and Smith) 376

Figs. 5, 6, side and front view of paralectotype (Hyatt and Smith, 1905: pl. 62, figs. 5–7), USNM 75291b, × 1.

Figs. 7–9, side, front, and ventral view of lectotype (Hyatt and Smith, 1905: pl. 62, figs. 1–3), USNM 75291a, × 1.

All specimens are from the middle shale member of Thaynes Formation (*Columbites* fauna), Paris Canyon, Bear River Range, southeast Idaho.


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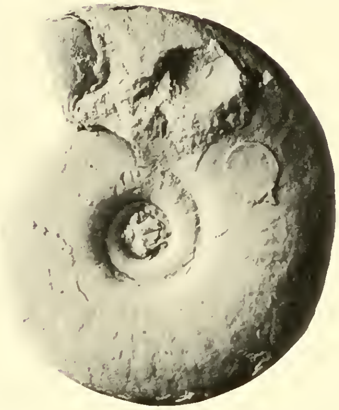
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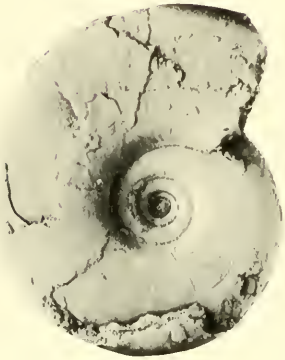
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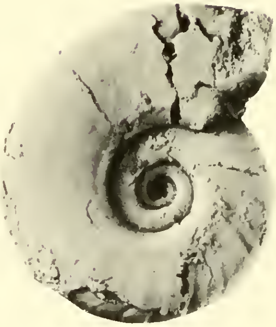
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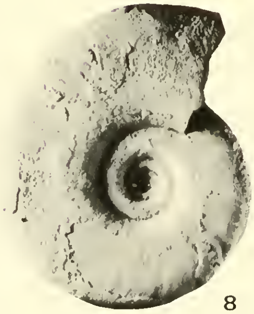
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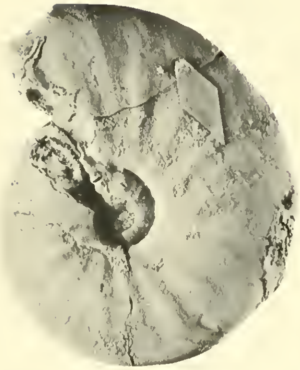
Plate 48

PLATE 49. NORDOPHICERAS PILATUM

Figures		Page
1–8	*Nordophiceras pilatum* (Hyatt and Smith)	470

Fig. 1, side view of paratype of *Meekoceras sanctorum* Smith (1932: pl. 49, fig. 3), USNM 74991b, × 1. Figs. 2, 3, side and front view of holotype of *Meekoceras sanctorum* Smith (1932: pl. 49, figs. 1, 2), USNM 74991a, × 1. Figs. 4–6, side, front, and ventral view of paralectotype of *Meekoceras pilatum* Hyatt and Smith (1905: pl. 63, figs. 10–12), USNM 75294b, × 1. Figs. 7, 8, side and ventral view of lectotype of *Meekoceras pilatum* Hyatt and Smith (1905: pl. 63, figs. 7, 8), USNM 75294a, × 1.

All specimens are from the middle shale member of Thaynes Formation (*Columbites* fauna), Paris Canyon, Bear River Range, southeast Idaho.



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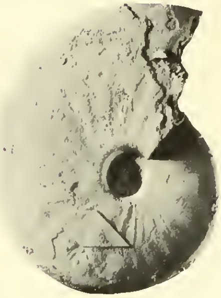

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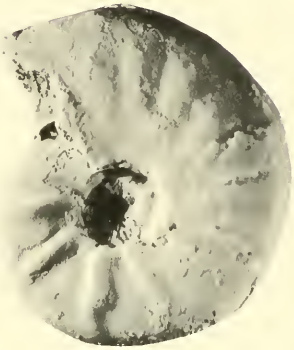

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Plate 49

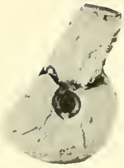
PLATE 50. NORDOPHICERAS PILATUM

Figures — Page

1–11 *Nordophiceras pilatum* (Hyatt and Smith) — 470

Figs. 1, 2, side and front view of holotype of *Meekoceras curticostatum* Smith (1932: pl. 48, figs. 21–22), USNM 74990a, × 1. Fig. 3, side view of paratype of *Meekoceras curticostatum* Smith (1932: pl. 48, figs. 27, 28), USNM 74990d, × 1. Fig. 4, side view of paratype of *Meekoceras curticostatum* Smith (1932: pl. 48, figs. 29, 30), USNM 74990e, × 2. Fig. 5, side view of paratype of *Meekoceras curticastatum* Smith (1932: pl. 48, figs. 25, 26), USNM 74990c, × 1. Fig. 6, side view of paratype of *Meekoceras curticostatum* Smith 1932: pl. 48, figs. 23, 24), USNM 74990b, × 1. Figs. 7–9, side, front, and ventral view of holotype of *Meekoceras micromphalus* Smith (1932: pl. 49, figs. 5–7), USNM 74992a, × 1. Figs. 10, 11, side and front view of paratype of *Meekoceras micromphalus* Smith (1932: pl. 49, figs. 9–11), USNM 74992b, × 2.

All specimens are from the middle shale member of Thaynes Formation (*Columbites* fauna), Paris Canyon, Bear River Range, southeast Idaho.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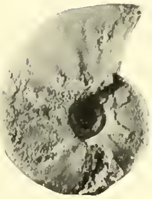
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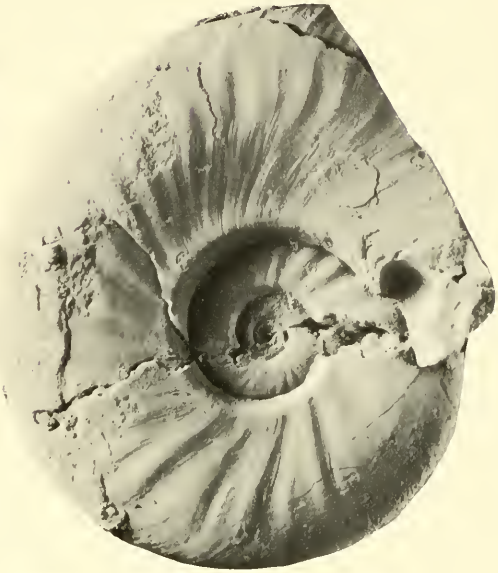
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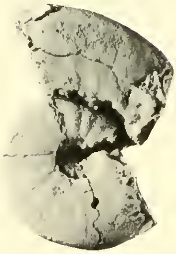
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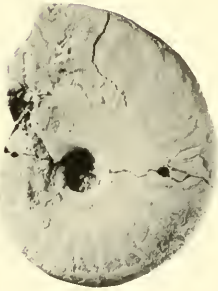
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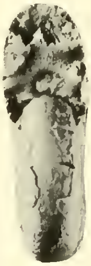
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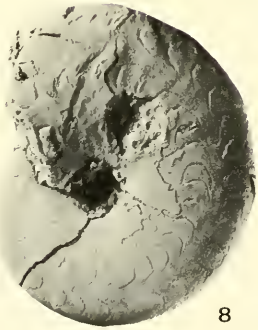
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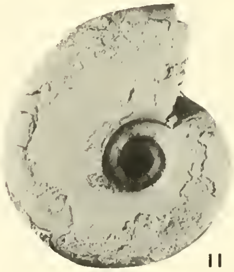
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Plate 50

PLATE 51. NORDOPHICERAS and CORDILLERITES

Figures		Page
1–5	*Nordophiceras pilatum* (Hyatt and Smith) Fig. 1, MCZ 9539, × 1. Figs. 2, 3, MCZ 9542, × 1. Fig. 4, MCZ 9540, × 1. Fig. 5, MCZ 9541, × 1.	470
6, 7	*Cordillerites angulatus* Hyatt and Smith Side and ventral view, MCZ 9569, × 1.	364

All specimens are from the middle shale member of Thaynes Formation (*Columbites* fauna), Montpelier Canyon, southeast Idaho.


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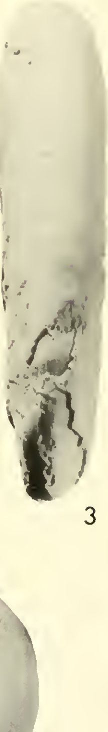
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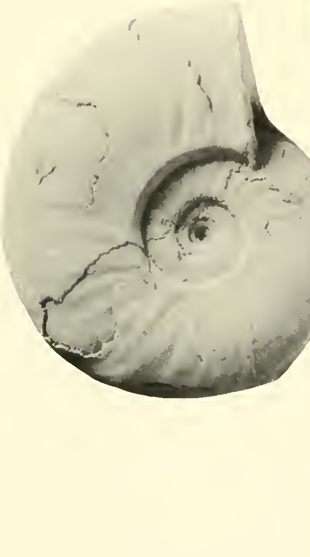
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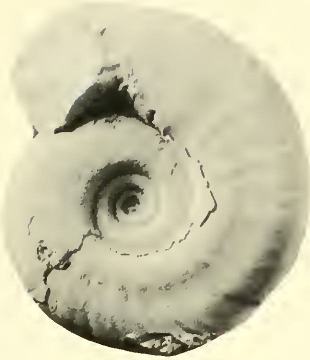
Plate 51

PLATE 52. XENOCELTITES SPENCEI

Figures		Page
1–7	*Xenoceltites spencei* (Hyatt and Smith)	376

Fig. 1, MCZ 9551, × 1. Fig. 2, MCZ 9552, × 2. Fig. 3, MCZ 9553, × 1.5. Fig. 4, MCZ 9554, × 1.5. Fig. 5, MCZ 9555, × 2. Fig. 6, MCZ 9556, × 1.5. Fig. 7, MCZ 9557, × 3.

All specimens are from the middle shale member of Thaynes Formation (*Columbites* fauna), southeast Idaho. Specimens of Figures 1, 4, 6, and 7 are from Montpelier Canyon; specimens of Figures 2, 3, and 5 are from Hot Springs.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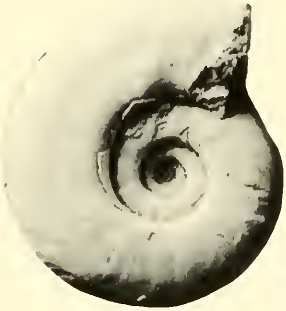
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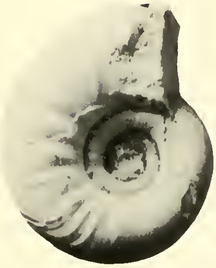
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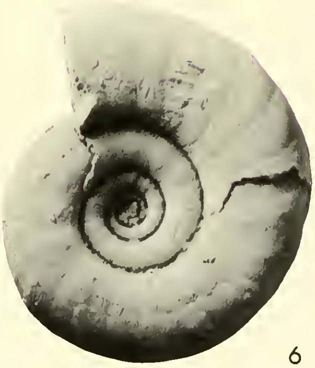
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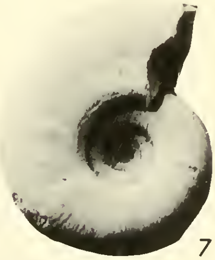
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Plate 52

PLATE 53. DIENEROCERAS, HELLENITES, and SUBVISHNUITES

Figures		Page
1–12	*Dieneroceras apostolicus* (Smith) Figs. 1, 2, side and front view of holotype of *Celtites ursensis* Smith (1932: pl. 47, figs. 11, 12), USNM 74987a, × 1. Figs. 3, 4, side and ventral view of paratype of *Celtites ursensis* Smith (1932: pl. 47, figs. 13, 14), USNM 74987b, × 1. Figs. 5, 6, side and front view of paratype of *Celtites ursensis* Smith (1932: pl. 47, figs. 15, 16), USNM 74987c, × 1. Figs. 7, 8, side and front view of holotype of *Celtites planovolvis* Smith (1932: pl. 48, figs. 11, 12), USNM 74988a, × 1. Fig. 9, side view of paratype of *Celtites planovolvis* Smith (1932: pl. 48, figs. 13, 14), USNM 74988b, × 1. Figs. 10, 11, side and front view of holotype of *Celtites apostolicus* Smith (1932: pl. 48, figs. 1, 2), USNM 74989a, × 1. Fig. 12, side view of paratype of *Celtites apostolicus* Smith (1932: pl. 48, figs. 3, 4), USNM 74989b, × 1.	369
13, 14	*Hellenites idahoense* (Smith) Side and ventral view of holotype (Smith, 1932: pl. 49, figs. 17, 18), USNM 74994, × 2.	516
15	*Subvishnuites* sp. indet. Side view, MCZ 9512, × 1.	374

All specimens are from the middle shale member of Thaynes Formation (*Columbites* fauna), Idaho. The specimens of Figures 1–14 are from Paris Canyon, and the specimen of Figure 15 is from Montpelier Canyon.

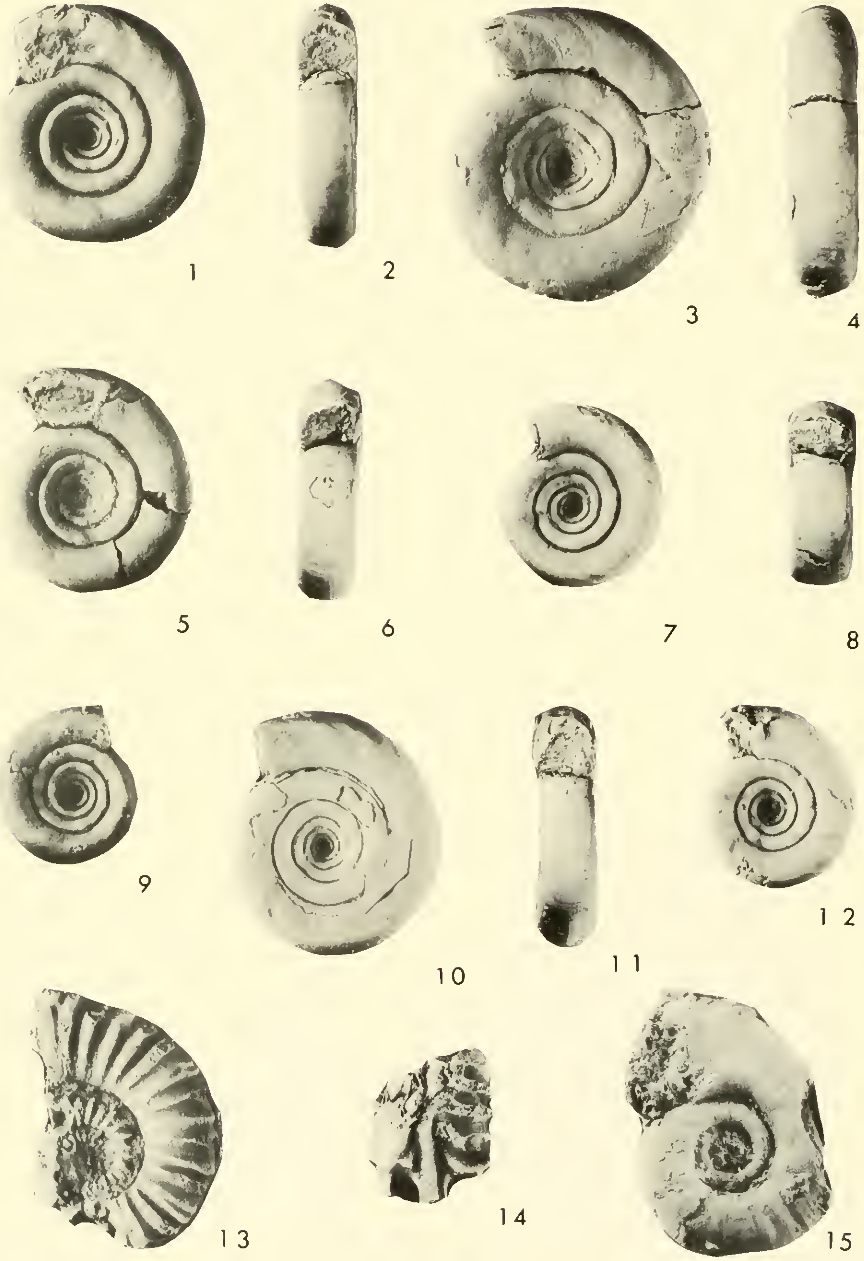

Plate 53

PLATE 54. TIROLITES SMITHI

Figures		Page
1–5	*Tirolites smithi* n. sp.	501

Fig. 1, specimen from Montpelier Canyon, MCZ 9547, × 1. Figs. 2, 3, ventral and side view of *Tirolites illyricus* Mojsisovics from Paris Canyon, figured by Smith (1932: pl. 49, figs. 12, 13), USNM 74993, × 1. Figs. 4, 5, side and ventral view of juvenile form from Montpelier Canyon, MCZ 9548, × 1.

All specimens are from the middle shale member of Thaynes Formation (*Columbites* fauna), southeast Idaho.


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Plate 54

PLATE 55. TIROLITES, DALMATITES, and PSEUDASPIDITES

Figures		Page
1–3	*Tirolites astakhovi* n. sp. Figs. 1, 2, side and ventral view of holotype, USNM 153081, × 1. Fig. 3, side view of paratype, USNM 153082, × 1.	502
4, 5	*Tirolites* sp. indet. II Side and ventral view, MCZ 9502, × 1.	503
6, 7	*Dalmatites kittli* n. sp. Side and ventral view of holotype, MCZ 9499, × 1.5.	522
8, 9	*Pseudaspidites popovi* n. sp. Side and ventral view of holotype, MCZ 9575, × 1.	383

All specimens are from the middle shale member of Thaynes Formation (*Columbites* fauna), Idaho. Specimens of Figures 1–3, from Sage Creek, of Figures 4, 5, from Montpelier Canyon, of Figures 6, 7, from Paris Canyon, of Figures 8, 9, from Hot Springs.


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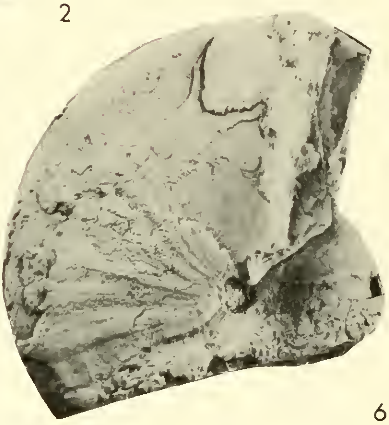
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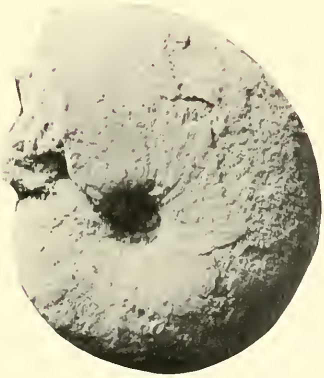
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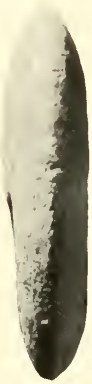
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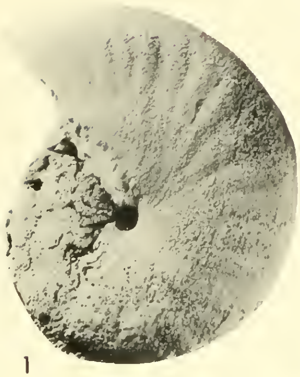
Plate 55

PLATE 56. DALMATITES and STACHEITES

Figures		Page
1–8	*Dalmatites morlaccus* Kittl	522
	Figs. 1, 2, lectotype, Kittl (1903: pl. 4, fig. 4), × 1. Figs. 3, 4, paralectotype, Kittl (1903: fig. 5), × 1. Figs. 5, 6, paralectotype, Kittl (1903: fig. 6), × 1. Figs. 7, 8, paralectotype, Kittl (1903: fig. 7), × 1.	
9, 10	*Stacheites prionoides* Kittl	455
	Holotype, Kittl (1903: pl. 4, fig. 8), × 1.	
	All specimens are from the Werfen Formation at Muć, Dalmatia, and are deposited in the Natural History Museum, Vienna.	



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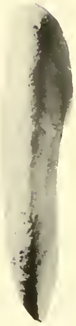

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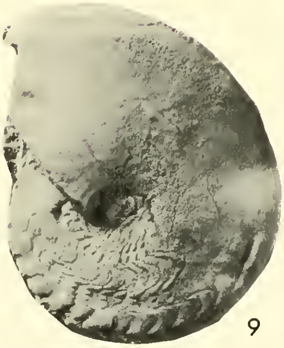

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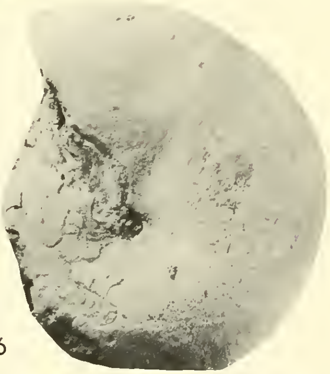

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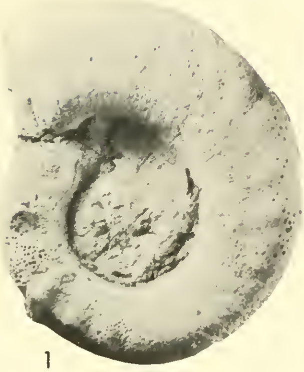
Plate 56

PLATE 57. BITTNERITES and PSEUDODINARITES

Figures		Page
1–6	*Bittnerites bittneri* Kittl Figs. 1, 2, lectotype, Kittl (1903: pl. 11, fig. 10), × 1. Figs. 3, 4, holotype, *Bittnerites malici* Kittl (1903: pl. 3, fig. 8), × 1. Figs. 5, 6, holotype, *Bittnerites telleri* Kittl (1903: pl. 10, fig. 10), × 1.	504
7–9	*Pseudodinarites mohamedanus* (Mojsisovics) Figs. 7, 8, plesiotype,–Kittl (1903: pl. 3, fig. 7), × 1; Fig. 9, plesiotype,–Kittl (1903: pl. 3, fig. 6), × 1. All specimens are from the Werfen Formation at Muć, Dalmatia, and are deposited in the Natural History Institute, Vienna.	511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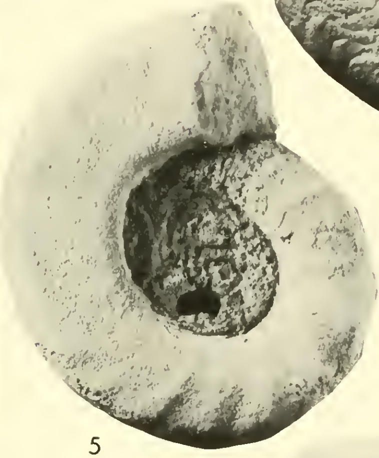
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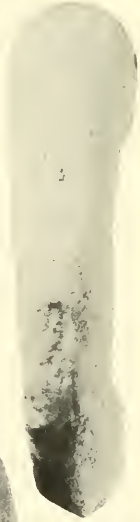
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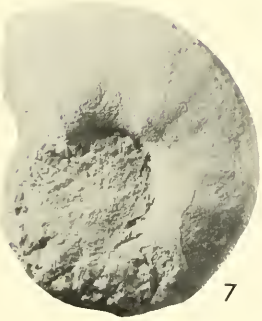
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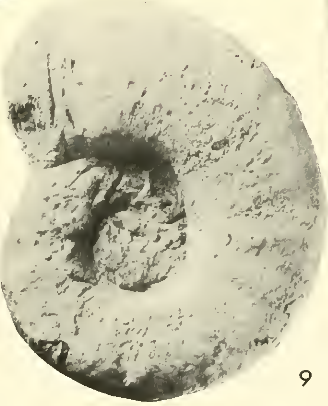
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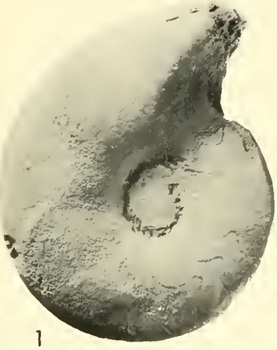
Plate 57

PLATE 58. DINARITES DALMATINUS

Figures		Page
1–10	*Dinarites dalmatinus* (Hauer)	506

Fig. 1, plesiotype, *Dinarites nudus* Tommasi,–Kittl (1903: pl. 1, fig. 13), × 1. Fig. 2, plesiotype, *Dinarites laevis* Tommasi,–Kittl (1903: pl. 3, fig. 11), × 1. Figs. 3, 4, plesiotype, *Dinarites laevis* Tommasi,–Kittl (1903: pl. 3, fig. 10), ×1. Figs. 5, 6, plesiotype, *Dinarites dalmatinus* (Hauer),–Kittl (1903: pl. 2, fig. 1), × 1. Fig. 7, plesiotype, *Dinarites dalmatinus* (Hauer),–Kittl (1903: pl. 2, fig. 5), × 1. Fig. 8, plesiotype, *Dinarites dalmatinus* (Hauer),–Kittl (1903: pl. 2, fig. 6), × 1. Figs. 9, 10, plesiotype, *Dinarites dalmatinus* (Hauer),–Kittl (1903: pl. 2, fig. 3), × 1.

All specimens are from the Werfen Formation at Muć, Dalmatia, and are deposited in the Natural History Museum, Vienna.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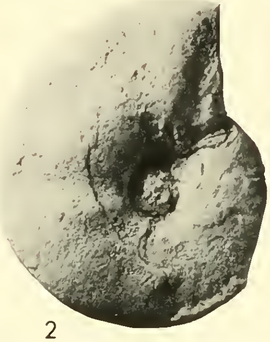
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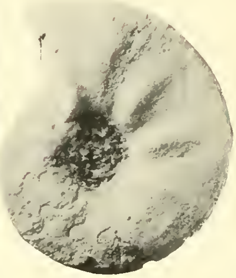
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Plate 58

PLATE 59. DINARITES DALMATINUS

Figures		Page
1–11	*Dinarites dalmatinus* (Hauer)	506

Figs. 1, 2, plesiotype, *Dinarites laevis* Tommasi,–Kittl (1903: pl. 1, fig. 1), × 1. Figs. 3, 4, plesiotype, *Dinarites laevis* Tommasi,–Kittl (1903: pl. 1, figs. 2, 3), × 1. Figs. 5, 6, plesiotype, *Dinarites muchianus* (Hauer),–Kittl (1903: pl. 1, fig. 7), × 1. Figs. 7, 8, plesiotype, *Dinarites muchianus* (Hauer),–Kittl (1903: pl. 1, fig. 5), × 1. Figs. 9, 10, syntype, *Dinarites evolutior* Kittl (1903: pl. 1, fig. 10), × 1. Fig. 11, syntype, *Dinarites evolutior* Kittl (1903: pl. 1, fig. 9), × 1.

All specimens are from the Werfen Formation at Muć, Dalmatia, and are deposited in the Natural History Museum, Vienna.


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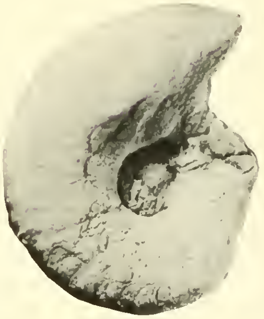
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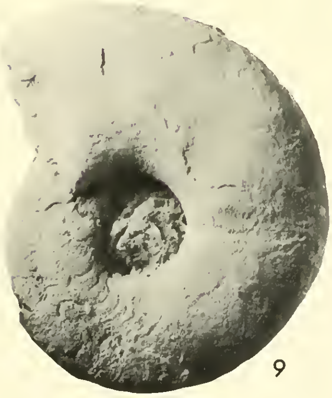
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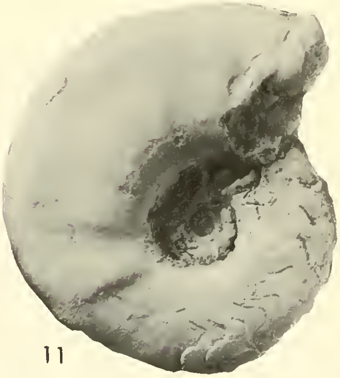
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Plate 59

PLATE 60. DINARITES DALMATINUS

Figures		Page
1–8	*Dinarites dalmatinus* (Hauer)	506

Fig. 1, plesiotype, var. *plurimcostatus* Kittl (1903: pl. 2, fig. 10), × 1. Fig. 2, plesiotype, var. *externeplanatus* Kittl (1903: pl. 3, fig. 1), × 1. Fig. 3, plesiotype, var. *externeplanatus* Kittl (1903: pl. 3, fig. 2), × 1. Fig. 4, plesiotype, var. *extensus* (Kittl: 1903, pl. 2, fig. 8), × 1. Fig. 5, holotype *Dinarites multicostatus* Kittl (1903: pl. 3, fig. 3), × 1. Fig. 6, syntype, *Dinarites tirolitoides* Kittl (1903: pl. 7, fig. 3), × 1. Fig. 7, syntype, *Dinarites tirolitoides* Kittl (1903: pl. 7, fig. 2), × 1. Fig. 8, plesiotype,–Kittl (1903: pl. 2, fig. 7), × 1.

All specimens are from the Werfen Formation at Muć, Dalmatia, and are deposited in the Natural History Museum, Vienna.


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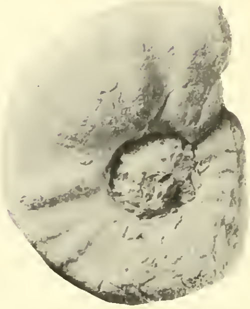
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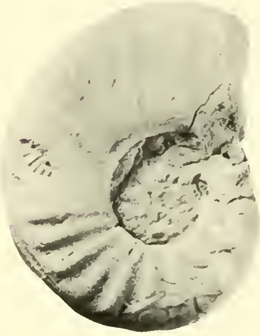
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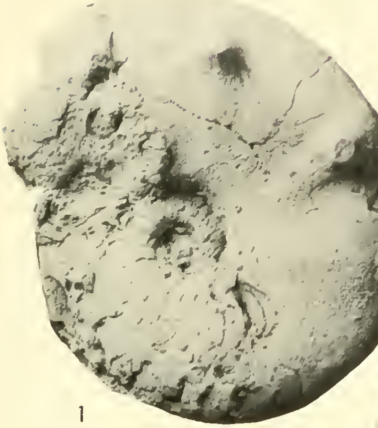
Plate 60

PLATE 61. DINARITES CARNIOLICUS

Figures		Page
1–8	*Dinarites carniolicus* (Mojsisovics)	510

Figs. 1, 2, plesiotype,–Kittl (1903: pl. 5, fig. 1), × 1. Fig. 3, plesiotype,–Kittl (1903: pl. 5, fig. 2), × 1. Fig. 4, plesiotype,–Kittl (1903: pl. 5, fig. 3), × 1. Fig. 5, plesiotype,–Kittl (1903: pl. 5, fig. 4), × 1. Figs. 6, 7, syntype, *Tirolites serratelobatus* Kittl (1903: pl. 5, fig. 4), × 1. Fig. 8, syntype, *Tirolites serratelobatus* Kittl (1903: pl. 5, fig. 6), × 1.

All specimens are from the Werfen Formation at Muć, Dalmatia, and are deposited in the Natural History Museum, Vienna.



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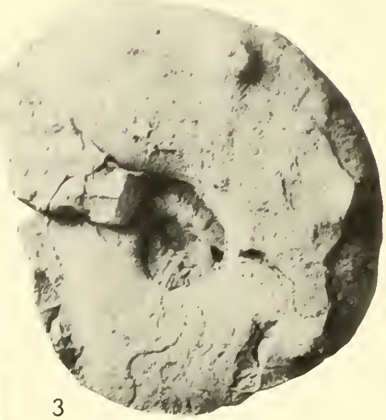

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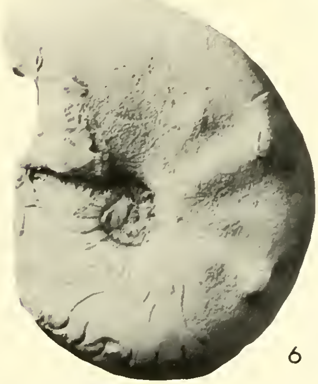

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Plate 61

PLATE 62. DIAPLOCOCERAS, PSEUDOKYMATITES, and PSEUDODINARITES

Figures		Page
1–4	*Diaplococeras connectens* (Mojsisovics) Fig. 1, holotype, *Dinarites (Hercegovites) diocletiani* Kittl (1903: pl. 3, fig. 4), × 1. Fig. 2, lectotype, *Dinarites (Liccaites) progressus* Kittl (1903: pl. 4, fig. 2), × 1. Figs. 3, 4, lectotype, *Dinarites biangulatus* Kittl (1903: pl. 4, fig. 1), × 1.	504
5	*Pseudokymatites svilajanus* (Kittl) Holotype (Kittl, 1903: pl. 4, fig. 3), × 1.	475
6	*Pseudodinarites mohamedanus* (Mojsisovics) Plesiotype,–Kittl (1903: pl. 3, fig. 5), × 0.6.	511

All specimens are from the Werfen Formation at Muć, Dalmatia, and are deposited in the Natural History Museum, Vienna.


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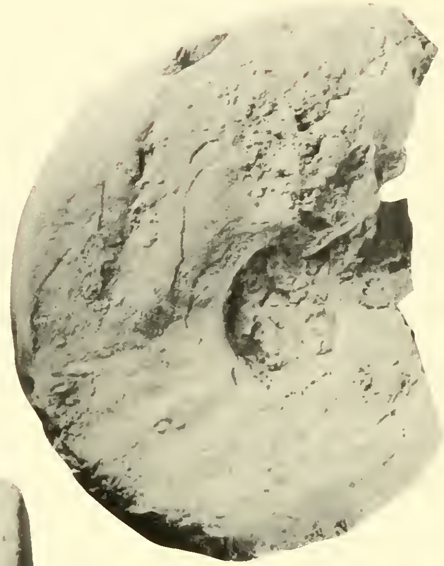
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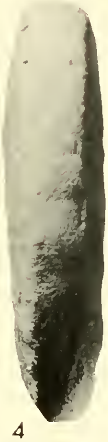
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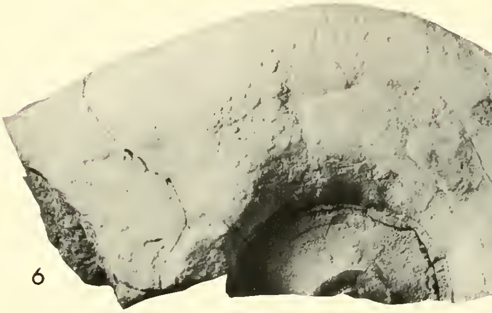
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Plate 62

PLATE 63. TIROLITES CASSIANUS

Figures		Page
1–9	*Tirolites cassianus* (Quenstedt)	493

Fig. 1, plesiotype, *Tirolites darwini*,–Kittl (1903: pl. 11, fig. 1), × 1. Figs. 2, 3, plesiotype, *Tiralites darwini*,–Kittl (1903: pl. 10, fig. 5), × 1. Fig. 4, lectotype, *Tiralites multispinatus* Kittl (1903: pl. 11, fig. 9), × 1. Figs. 5, 6, lectotype, *Tiralites percastatus* Kittl (1903: pl. 10, fig. 6), × 1. Fig. 7, plesiotype, *Tirolites turgidus*,–Kittl (1903: pl. 10, fig. 7), × 1. Fig. 8, plesiotype, *Tirolites darwini*,–Kittl (1903: pl. 11, fig. 3), × 1. Fig. 9, plesiotype, *Tirolites smiriagini*,–Kittl (1903: pl. 11, fig. 6), × 1.

All specimens are from the Werfen Formation at Muć, Dalmatia, and are deposited in the Natural History Museum, Vienna.


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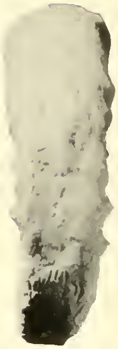
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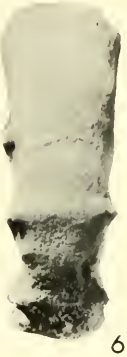
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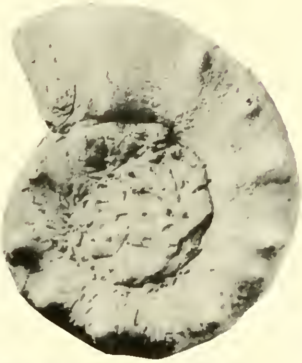
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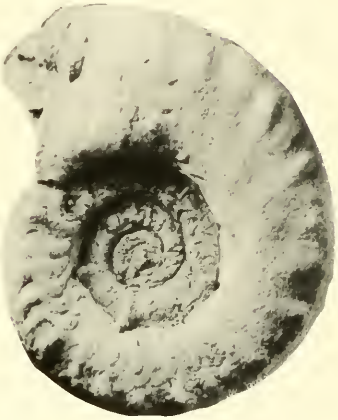
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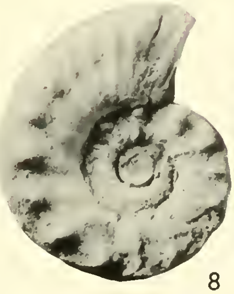
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Plate 63

PLATE 64. TIROLITES CASSIANUS

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1–4	*Tirolites cassianus* (Quenstedt)	493

Figs. 1, 2, lectotype, *Tirolites spinosior* Kittl (1903: pl. 11, fig. 5), × 1. Fig. 3, syntype, *Tirolites toulai* Kittl (1903: pl. 11, fig. 11), × 1. Fig. 4, plesiotype, *Tirolites darwini*,–Kittl (1903: pl. 10, fig. 11), × 1.

All specimens are from the Werfen Formation at Muć, Dalmatia, and are deposited in the Natural History Museum, Vienna.

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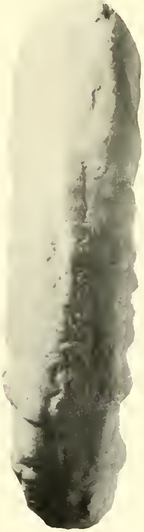

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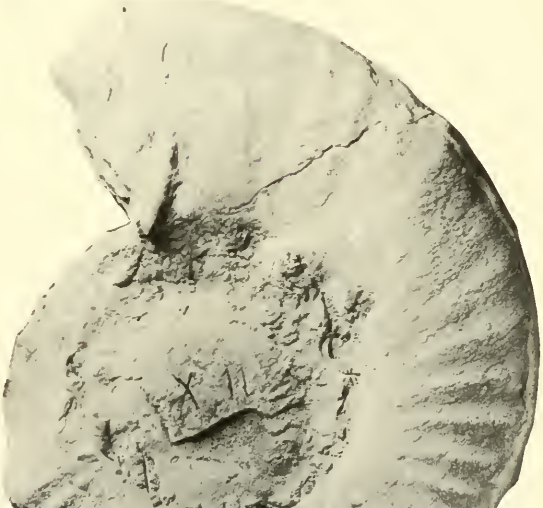

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Plate 64

PLATE 65. TIROLITES CASSIANUS

Figures		Page
1–9	*Tirolites cassianus* (Quenstedt)	493

Fig. 1, figured specimen, *Tiralites angustilobatus* var. *alpha* Kittl (1903: pl. 8, fig. 19), × 1. Fig. 2, lectotype, *Tirolites angustilobatus* Kittl (1903: pl. 9, fig. 3), × 1. Fig. 3, plesiotype,–Kittl (1903: pl. 9, fig. 5), × 1. Fig. 4, figured specimen, *Tiralites angustilabatus* var. *alpha* Kittl (1903: pl. 9, fig. 1), × 1. Fig. 5, plesiotype,–Kittl (1903: pl. 9, fig. 4), × 1. Fig. 6, plesiotype,–Kittl (1903: pl. 9, fig. 6), × 1. Figs. 7, 8, plesiatype, *Tirolites spinosus*,–Kittl (1903: pl. 9, fig. 7), × 1. Fig. 9, plesiotype *Tiralites haueri*,–Kittl (1903: pl. 9, fig. 10), × 1.

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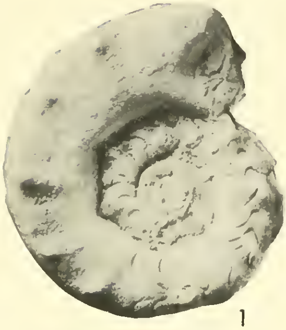

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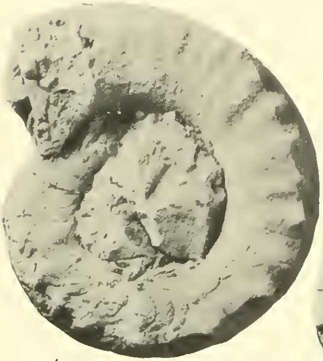

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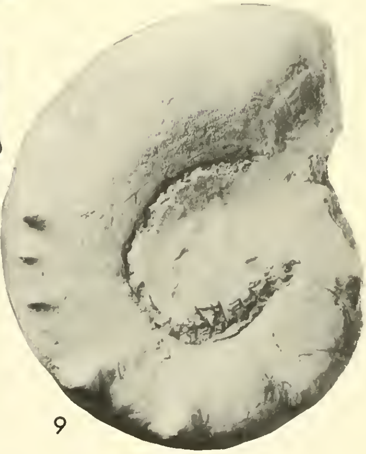

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Plate 65

PLATE 66. TIROLITES IDRIANUS

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Fig. 1, plesiotype, *Tirolites seminudus* Mojsisovics var. *nudior* Kittl (1903: pl. 6, fig. 3), × 1. Fig. 2, plesiotype, *T. seminudus* var. *plicosus* Kittl (1903: pl. 6, fig. 7), × 1. Fig. 3, plesiotype, *T. seminudus* var. *plicosus* Kittl (1903: pl. 6, fig. 5), × 1. Fig. 4, plesiotype, *T. seminudus*,–Kittl (1903: pl. 6, fig. 6), ×1. Fig. 5, plesiotype, *T. seminudus*,–Kittl (1903: pl. 6, fig. 8), × 1. Fig. 6, paralectotype, *T. distans* Kittl (1903: pl. 6, fig. 12), × 1. Fig. 7, plesiotype, *T. seminudus*,–Kittl (1903: pl. 6, fig. 4), × 1. Fig. 8, plesiotype, *T. seminudus*,–Kittl (1903: pl. 6, fig. 18), × 1. Fig. 9, lectotype, *T. distans* Kittl (1903: pl. 6, fig. 15), × 1. Figs. 10, 11, plesiotype, *T. seminudus*,–Kittl (1903: pl. 6, fig. 10), × 1. Fig. 12, plesiotype, *T. seminudus*,–Kittl (1903: pl. 6, fig. 9), × 1. Fig. 13, plesiotype, *T. seminudus*,–Kittl (1903: pl. 6, fig. 17), × 1.

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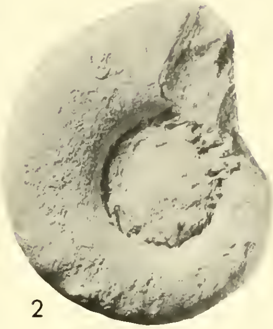
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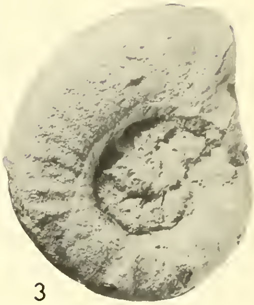
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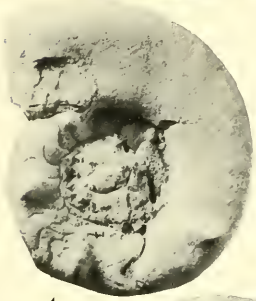
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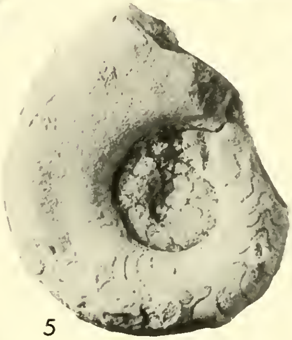
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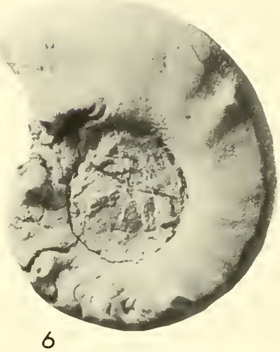
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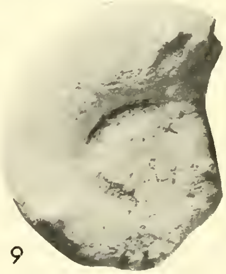
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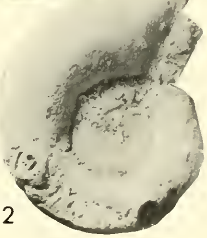
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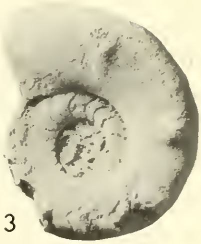
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Plate 66

PLATE 67. TIROLITES IDRIANUS

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1–9	*Tirolites idrianus* (Hauer)	492

Figs. 1, 2, plesiotype, *Tirolites mercurii*,–Kittl (1903: pl. 6, fig. 1), × 1. Fig. 3, holotype, *Tirolites heterophanus* Kittl (1903: pl. 5, fig. 7), × 1. Fig. 4, figured type, *Tiralites paucispinatus* Kittl (1903: pl. 6, fig. 11), × 1. Fig. 5, plesiotype, *Tirolites mercurii*,–Kittl (1903: pl. 6, fig. 2), × 1. Fig. 6, figured type, *Tirolites repulsus* Kittl (1903: pl. 8, fig. 10), × 1. Fig. 7, figured type, *Tiralites dimidiatus* Kittl (1903: pl. 8, fig. 15), × 1. Fig. 8, plesiotype, *Tiralites rectangularis*,–Kittl (1903: pl. 8, fig. 16), × 1. Fig. 9, figured type, *Tirolites repulsus* Kittl (1903: pl. 8, fig. 9), × 1.

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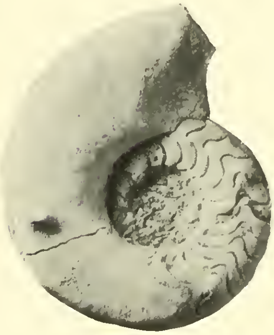
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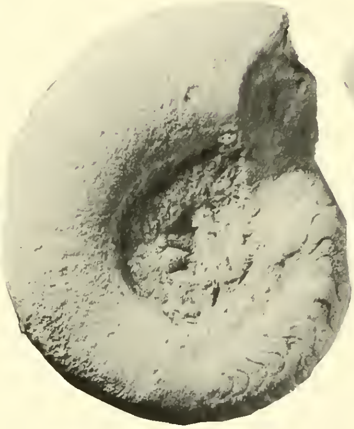
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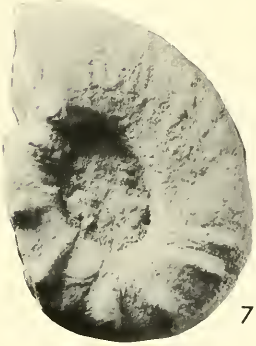
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PLATE 68. TIROLITES IDRIANUS

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1–9	*Tirolites idrianus* (Hauer)	492

Fig. 1, paralectotype, *Tirolites distans* Kittl (1903: pl. 7, fig. 8), × 1. Fig. 2, porolectotype, *Tirolites distans* Kittl (1903: pl. 7, fig. 7), × 1. Fig. 3, figured type, *Tirolites paucispinatus* Kittl (1903: pl. 7, fig. 5), × 1. Fig. 4, plesiotype, *Tirolites illyricus*,–Kittl (1903: pl. 8, fig. 3), × 1. Fig. 5, plesiotype, *Tirolites quenstedti*,–Kittl (1903: pl. 6, fig. 20), × 1. Fig. 6, plesiatype, *Tirolites quenstedti*,–Kittl (1903: pl. 6, fig. 19), × 1. Fig. 7, lectotype, *Tirolites hybridus* Kittl (1903: pl. 8, fig. 2), × 1. Fig. 8, figured type, *Tirolites rotiformis* Kittl (1903: pl. 8, fig. 12), × 1. Fig. 9, figured type, *Tirolites rotiformis* Kittl (1903: pl. 8, fig. 13), × 2.

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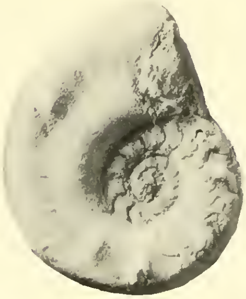

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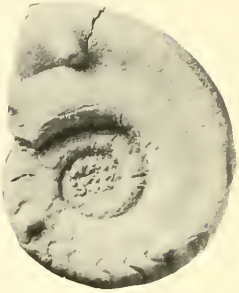

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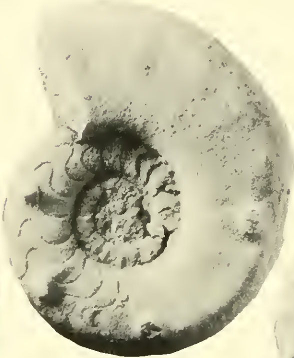

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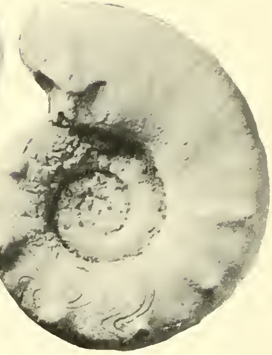

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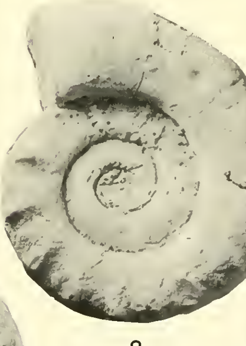

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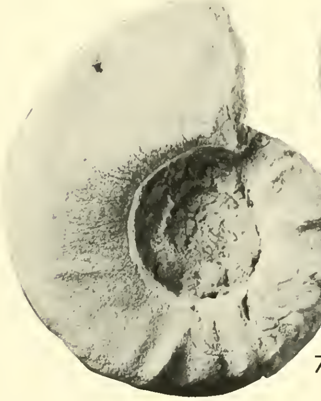

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Plate 68

PLATE 69. TIROLITES IDRIANUS

Figures		Page
1–10	*Tirolites idrianus* (Hauer)	492

Fig. 1, lectotype, *Tirolites robustus* Kittl (1903: pl. 7, fig. 9), × 1. Fig. 2, paralectotype, *Tirolites robustus* Kittl (1903: pl. 7, fig. 10), × 1. Fig. 3, paralectotype, *Tirolites robustus* Kittl (1903: pl. 7, fig. 11), × 1. Fig. 4, paralectotype, *Tirolites robustus* Kittl (1903: pl. 8, fig. 1), × 1. Fig. 5, syntype, *Tirolites subillyricus* Kittl (1903: pl. 7, fig. 15), × 1. Fig. 6, holotype, *Tirolites angustus* Kittl (1903: pl. 7, fig. 12), × 1. Fig. 7, lectotype, *Tirolites stachei* Kittl (1903: pl. 7, fig. 14), × 1. Figs. 8, 9, syntype, *Tirolites subillyricus* Kittl (1903: pl. 7, fig. 16), × 1. Fig. 10, lectotype, *Tirolites undulatus* Kittl (1903: pl. 7, fig. 13), × 1.

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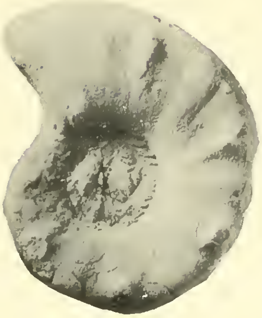
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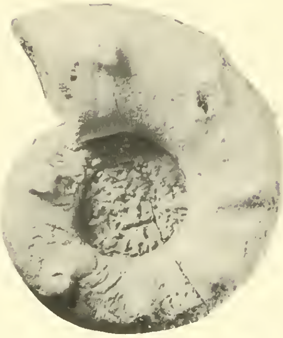
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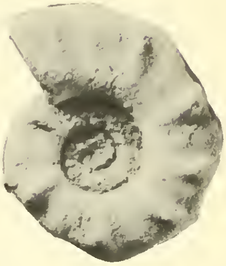
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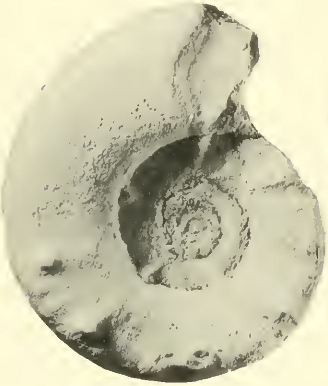
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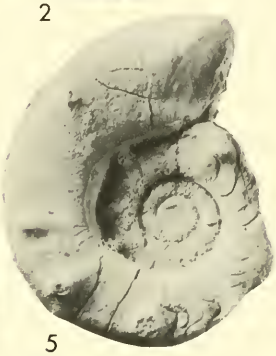
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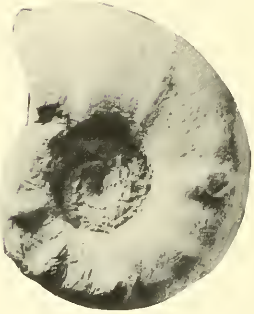
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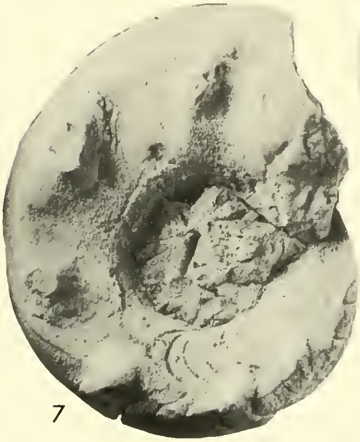
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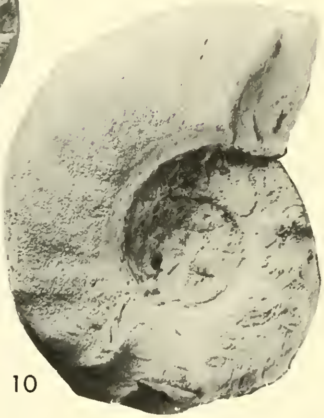
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Plate 69

PLATE 70. HOLOLOBUS, TIROLITES, and DINARITES

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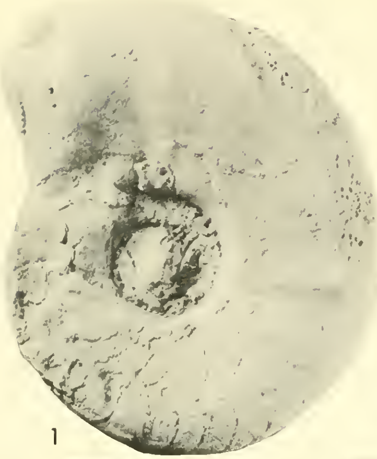
7, 8	*Dinarites dalmatinus* (Hauer) Holotype, *Dinarites* (?) *angulatus* Kittl (1903: pl. 3, fig. 9), × 1.	497
9, 10	*Tirolites cingulatus* Kittl Holotype, *Tirolites* (*Svilajites*) *cingulatus* Kittl (1903: pl. 8, fig. 18), × 1.	497
11, 12	*Tirolites cassianus* (Quenstedt) Holotype, *Tirolites* (*Svilajites*) *tietzei* Kittl (1903: pl. 10, fig. 9), × 1.	493

All specimens are from the Werfen Formation at Muć, Dalmatia, and are deposited in the Natural History Museum, Vienna.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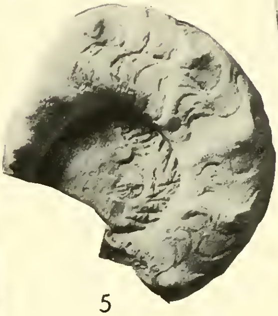
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Plate 70

PLATE 71. TIROLITES and DALMATITES

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All specimens are from the *Tirolites* Zone, Thaynes Formation, Paris Canyon, Bear River Range, southeast Idaho.

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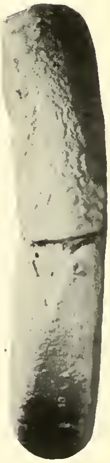

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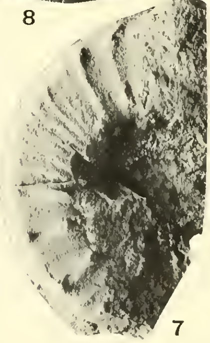

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Plate 71