THE APTIAN-CENOMANIAN MEMBERS OF THE AMMONITE GENUS TETRAGONITES

BY
MICHAEL A. MURPHY

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to

MAURICE COLLIGNON

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MICHAEL A. MURPHY

ABSTRACT

The genus *Tetragonites* is defined by the irregularly bifid or trifid character of the first lateral saddle; the possession of two or more distinctly developed saddles of the internal suture line; the strongly prorsiradiate lateral margin of the aperture and generally adorally concave sulcus of the aperture on the venter; the virtual lack of exterior shell ornamentation except on the umbilical wall.

The genus arises in the upper Aptian (Clansayesian) from *Eotetragonites* and differentiates in the Albian into three principal groups characterized by the species *T. timotheanus* (Pictet), *T. rectangularis* Wiedmann, and *T. kitchini* (Krenkel). The *T. rectangularis* group apparently gives rise to most of the Upper Cretaceous members of the subfamily Tetragonitinae and is the central morphologic theme of the genus.

The study recognizes two new taxa from Europe: *T. bournensis* n. sp. and *Tetragonites* sp.; one new taxon from Madagascar: *T. madagascarensis* n. sp.; four new taxa from North America: *T. hulenensis* n. sp., *T. lecontei* n. sp., *T. jonesi* n. sp., and *T. rectangularis* Wiedmann subsp. *alaskaensis* n. subsp.

T. epigonoides Wiedmann is suppressed in favor of Breistroffer's species *balmensis* here classified as *Eotetragonites*. *T. blaisoni* and *T. jallaberti* var. *ampakabensis* of Collignon are suppressed in favor of *T. collignoni* Breistroffer.

The study indicates that members of the genus for which good stratigraphic control is available have shorter ranges than the literature indicates and that they can be used for a general biostratigraphic subdivision of the middle Cretaceous stages.

INTRODUCTION

THIS STUDY of the genus *Tetragonites* Kossmat is necessarily incomplete, as it has not been possible to examine all the various species cited in the literature, and in some instances it has not been possible to give an adequate description or discussion because the amount or preservation of the material is inadequate. I feel, however, that these data may be useful, as I have had the advantage of investigating a large amount of material, some of which has been unavailable to other writers who have dealt with the genus. I have been helped in my research by a number of persons who have unselfishly let me study their personal collections, and by officials of many institutions who have been most cordial in making their facilities and collections available to me. Also I have profited greatly from discussions of a number of my colleagues who have contributed in one way or another to the conclusions that follow.

ACKNOWLEDGMENTS

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ABBREVIATIONS USED IN TEXT

BMNH	= British Museum (Natural History)
FD	= Faculté des Sciences, Dijon
FG	= Faculté des Sciences, Grenoble
FL	= Faculté des Sciences, Lyon
FM	= Faculté des Sciences, Marseilles
GPIT	= Geologisches—Paläontologisches Institüt, Tübingen
HU	= Harvard University, Museum of Comparative Zoology
MCC	= Maurice Collignon Collection, Moirans
MHNG	= Musée d'Histoire Naturelle, Genève
MHNP	= Muséum National d'Histoire Naturelle, Paris
OV	= Olivier de Villoutreys Collection, Monaco
S	= Sorbonne
SM	= Sedgwick Museum, Cambridge
UCB	= University of California, Berkeley
UCLA	= University of California, Los Angeles
UCR	= University of California, Riverside
USGS–M	= United States Geological Survey Mesozoic Collection
USNM	= United States National Museum, Catalogue 32.
UT	= University of Texas, Bureau of Economic Geology

The collections of the following institutions were examined during the course of this work and thanks are extended for the assistance of their respective curators: Faculé des Sciences, Institut Dolomieu, Grenoble, J.-P. Thieuloy and J. Debelmas; Faculté des Sciences, Lyon R. Busnardo; Faculté des Sciences, Dijon, P. Rat; Musée d'Histoire Naturelle de Genève, E. Lanterno; École des Mines, Paris, M. Lemoine; Sorbonne, E. Basse de Menorval; Muséum National d'Histoire Naturelle, Paris, J. Sornay; British Museum (Natural History), M. Howarth; California Academy of Sciences, L. G. Hertlein; University of California, Berkeley, J. Peck; U.S. Geological Survey, Menlo Park, D. L. Jones.

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N. J. Silberling made numerous comments and suggestions which have been incorporated in the paper.

I hope the data and interpretations given here may furnish a stimulus to future studies which will result in a more detailed and more accurate interpretation of this interesting group of ammonites.

LITERATURE AND HISTORICAL REVIEW OF STUDIES OF TETRAGONITES

Members of the genus were first described by Pictet (1847) from the late Albian of the French Alps at Mt. Saxonet (Haute Savoie) near Geneva. He described five forms which have been cited subsequently as members of the genus: *Ammonites timotheanus* and its variety *nautiloide, A. jurinianus, A. bourritianus,* and *A. jallabertianus.* The last two are now considered Gaudryceratidae. Pictet's figure of *A. timotheanus* is not very accurate (compare Pictet's figure in Pictet and Roux, 1847, pl. 3, fig. 1, with Wiedmann, 1962*a,* pl. 14, figs. 4–6) and is doubtless the source of much confusion. From the outset the two rather distinct morphologic types represented by *A. timotheanus* and *A. timotheanus* var. *nautiloide* were placed together in a single taxon.

The genus *Ammonites,* which contained most of the planospirally coiled ammonites in d'Orbigny's and Pictet's classifications, was gradually subdivided in the last half of the nineteenth century. The group Lytoceratina, now given subordinal rank, was first formally recognized by Suess in 1865 when he erected the genus *Lytoceras.* In 1894 de Grossouvre introduced *Gaudryceras* as a subgenus of *Lytoceras.* This paper was followed the next year by the introduction of another subgenus, *Tetragonites,* by Kosmat (1895).

Kossmat (1895) erected the taxon *Tetragonites* for the group of lytocerids characterized by *Ammonites timotheanus* Pictet which he designated as the type species. His concept of *Tetragonites,* however, was based on a specimen in the British Museum (Natural History) from Clars (Var) identified as *Ammonites timotheanus* and to which he compared his Indian specimens. Thus the original generic concept was not based on the genotype, but rather on *Tetragonites rectangularis* Wiedmann, 1962, which is the proper identification of the specimen in the British Museum from Clars.

In his discussion of the new subgenus he mentions the involution, rapid whorl growth, trapezoidal whorl section with high vertical umbilical wall, flattening of the flanks and venter, the configuration and depth of the constrictions, the asymmery of the first lateral saddle, the nonretracted nature of the suspensive lobe, the septal suture, and four internal saddles. For Kossmat it was the combination of characters that distinguished his new taxon from the previously described *Gaudryceras.*

A series of papers immediately following Kossmat's work introduced a number of new species of *Tetragonites* for forms found in other parts of the world. These works commenced with Anthula (1899) who described *Tetragonites heterosulcatus,* a late Aptian form from the Caucasus, and were followed by Anderson (1902), *T. jacksonense;* Yabe (1903), *T. popetense;* Jacob (1907), *T. kiliani;* Krenkel (1910), *T. kitchini.* Krenkel, however, did not recognize the generic affinity of this species. Anthula's species has recently been clarified and refigured by Drushchits (1956) and its stratigraphic position restated. Jacob's species is well illustrated and described and correctly identified in the literature, although Wiedmann (1962*a*) recently has demonstrated it is probably a synonym of *T. timotheanus.* Anderson (1958) also has supplemented our information regarding *T. jacksonensis.* Krenkel's specimen has apparently been lost and is without a nomenclatorially valid reference specimen.

After the First World War another series of papers brought the description of several more taxa: *T. brazoensis* Böse and *T. zacatecanus* Böse, two small forms from Mexico, which probably represent immature shells and which Wiedmann has synonymized with *T. jurinianus; T. simplex, T. margaritatus,* and *T. latus* Marshall based on small shells from the Upper Cretaceous of New Zealand; *T. kiliani* Jacob mut. *jacobi* Collignon (= *T. collignoni* Breistroffer) from Madagascar.

This period also saw the first effort at synthesis in Spath's (1927) review and classification of the family in which he separated the group of species characterized by *Lytoceras* (*Tetragonites*) *epigonum* Kossmat as the genotype of *Epigoniceras* Spath.

Breistroffer's series of papers ending with his synthesis of the Albian zones of France and England (1936, 1940, 1947) revised and clarified earlier work and introduced two important taxa, *T. balmensis* and *T. spathi* from the Albian and Cenomanian, respectively, of southeastern France. Also he erected the genus *Eotetragonites* for *Ammonites depressus* Raspail (= *Eotetragonites raspaili* Breistroffer) which further restricted the genus *Tetragonites* and removed such well-known species as *duvalianus* Orbigny, *jacobi* Kilian, *kossmatellaformis* Fallot, *wintunius* Anderson, and *jallabertianus* Pictet.

The next important review is by Collignon (1956) who reviewed the entire family while studying a well-preserved series of specimens from Madagascar. He described two additional taxa from the Coniacian, *T. beantalyensis* and *T. embergeri.*

Most recently Wiedmann (1962*a*) has taken a major step toward putting studies of this family on a sound nomenclatorial basis with the selection of reference specimens for Pictet's taxa. He introduced four new taxa that he felt were required by his studies: *T. subbeticus,* an Aptian form from Spain; *T. subtimotheanus,* for

Stoliczka's and Kossmat's Indian forms from the Ootatoor Group; *T. rectangularis,* for the common Albian *Tetragonites* of Europe; *T. epigonoides,* for a round-whorled form from the Balearic Islands. Wiedmann's paper is an essential reference for any future studies of the genus.

Subfamily TETRAGONITINAE Hyatt, 1900

The Subfamily Tetragonitinae is comprised of forms in which the principal lateral lobes of the suture are bifid, the major saddles irregularly bifid, and several auxiliary lobes and saddles are present. The internal suture has two or more saddles and the dorsal lobe is typically prolonged forming a septal lobe on the preceding septum. The growth rugae, lirae, and constrictions, and thus the margin of the aperture, are strongly inclined adorally on the lower flanks and generally recurved on the upper flank. In some taxa they are concave adorally on the venter. The surface of the shell is smooth or lirate. Many taxa also show a flattening of the flanks and venter that results in the quadrate or trapezoidal whorl section from which the name of the group was derived.

The genera *Tetragonites* Kossmat, 1895; *Pseudophyllites* Kossmat, 1895; *Epigoniceras* Spath, 1925; (*Saghalinites*) Wright and Matsumoto, 1954; *Gabbioceras* Hyatt, 1900; *Jauberticeras* Jacob, 1907; *Kossmatella* Jacob, 1907; *Eotetragonites* Breistroffer, 1947 (by implication as *E. duvali* is assigned to *Tetragonites*), have been assigned to the subfamily in recent general works on ammonites (Basse, 1952; Wright, 1957; Drushchits 1958, 1960).

According to Howarth (1958, p. 9) the genus *Epigoniceras* must be abandoned as the retracted suspensive lobe that has been used to separate if from *Tetragonites* is a variable character within species.

Matsumoto (1959, p. 78) arrived at the same conclusion based on his study of the suture line in various species referred to both *Tetragonites* and *Epigoniceras.* Wiedmann (1962*a,* p. 131) also supported this conclusion. Wright (letter dated Feb. 27, 1962) states, "I agree entirely with Howarth . . . that *Epigoniceras* is unnecessary."

Neither *Gabbioceras* Hyatt nor *Jauberticeras* Jacob agrees with the above list of subfamily characteristics. Both possess a different configuration of the ornamentation, a different development of the cross section of the whorl which is characterized by a strong angulation, and a different development of the elements of the suture line.

Kossmatella is excluded from the Tetragonitinae on the basis of its gaudrycerid internal suture, different style of ornamentation, and different shape of cross section.

The taxon *Saghalinites* is presently classified as a subgenus of *Tetragonites* (Wright, 1957, p. L203). I have seen only a few examples of specimens assigned to this taxon and cannot make any remarks concerning its classification from these limited observations, except that it is certainly a member of the Tetragonitinae.

I would place the two remaining genera, *Eotetragonites* and *Pseudophyllites,* in the Tetragonitinae. The last mentioned has the distinctive patterns of suture and configuration of the ornamentation which relate it to the subfamily, although in whorl shape and weight of ribbing it shows a convergence toward some members

of the Phylloceratáceae. The former represents a transitional morphology between the Tetragonitinae and Gaudryceratinae. Its position with the Tetragonitinae in the classification is demanded because the split in the family tree occurs between *Eogaudryceras* and *Eotetragonites* with each of these genera leading to a distinct and major branch of the family.

Eotetragonites Relationship to Tetragonites

A gradation exists between the genera *Tetragonites* and *Eotetragonites* in which *Eotetragonites* is demonstrably the ancestral form. Since at least some taxa usually assigned to *Eotetragonites* possess some of the basic characteristics of *Tetragonites,* such as the termination of the main saddle (see discussion of the suture under *Tetragonites*) and possession of a second internal saddle, even though incipient, the genera cannot be separated by these characters. Only the character of the constrictions, one of Breistroffer's original reasons for separating *Eotetragonites* as a separate genus, remains. In general, the difference between the constrictions in the two taxa is in their more prominent indentation of the internal mold in *Eotetragonites,* their generally more radiate course, their adorally convex configuration on the flanks, and their generally adorally convex arch on the venter. All students of the group will immediately be able to point out that some exceptions exist here as well. Some specimens of *Eotetragonites jacobi,* for example, have very lightly impressed constrictions whereas species of *Tetragonites* show adorally convex constrictions on the venter. In these instances, characters of the ornamentation, the suture, the whorl, and the biostratigraphy of the taxa indicate the classification that most nearly approximates the phylogeny of the group.

Genus *Tetragonites* Kossmat, 1895

Type species: ***Ammonites timotheanus*** **Pictet, 1847**

The genus *Tetragonites* is characterized by the following combination of characters: (1) the particular suture line, (2) the strongly prorsiradiate lateral margin, and generally adorally concave ventral margin of the aperture, and (3) the virtual lack of external shell ornamentation except on the umbilical wall.

The Suture Line

The suture line (fig. 1) is characterized by an external lobe (E) that is deeper than the first lateral lobe (L); an irregularly bifid or trifid termination of the first lateral saddle (1S); a nearly symmetrically bifid first lateral lobe which straddles the peripheral shoulder when the latter is developed; an internal suture with two or more unequally developed saddles.

The external lobe is often, especially in smaller specimens, only slightly longer than the first lateral lobe, but in the hundreds of specimens examined during this study no exception was encountered. Three principal accessory lobes are usually present on the flank on each side of the external lobe in an adult suture line.

The first lateral lobe is bifid and nearly symmetrical; the second lobe (2L) is bifid but usually not symmetrical; the configuration of the remaining lobes is quite variable although the bifid character is apparent in some specimens.

The first lateral saddle (1S) has three main, more or less symmetrical terminal

branches (trifid) or, alternatively, the two accessory lobes (AL) that divide the 1S are unequal with the inner one longer than the other (irregularly bifid). The trifid character of the 1S is shown in only a few of the published suture lines of species assigned to the genus (see, for example, text figs. 9 and 11).

The bulk of the specimens assigned to the genus shows the configuration which Breistroffer (1947, p. 72) termed "irregulierement bifides." This configuration is also found in *Eotetragonites*. The irregularly bifid saddle is intermediate between the bifid saddle found in *Eogaudryceras* and the trifid saddle. It doubtless is derived from the gaudrycerid suture by a rotation of the principal accessory lobe of the 1S. Accompanying this rotation is an increase in size of the secondary ac-

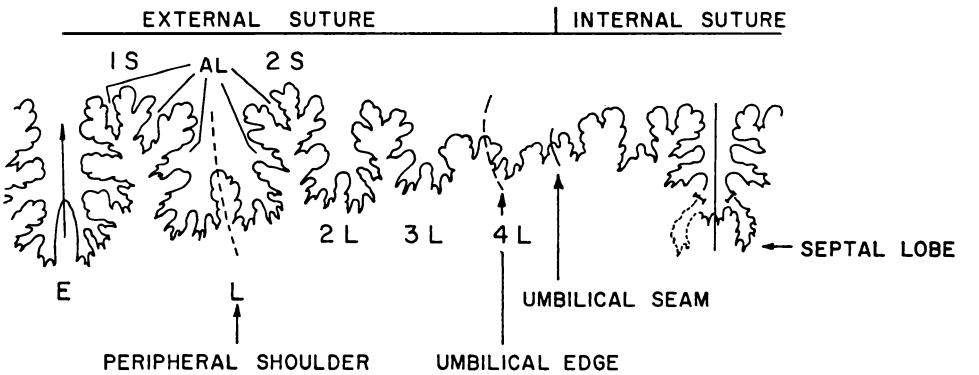


Fig. 1. Descriptive terminology of the suture line without connotation concerning its ontogenetic development or phylogeny.

cessory lobe which divides the external branch of the 1S. When the development of the two accessory lobes is equal a trifid saddle results (fig. 2).

The irregularly bifid and trifid lobes apparently have no taxonomic significance at the species level and both conditions are present in *Tetragonites*. *Eotetragonites* shows only the irregularly bifid condition and *Eogaudryceras* shows only the bifid condition.

The second lateral saddle commonly mirrors the terminations of the 1S and thus may be either trifid or irregularly bifid.

In almost all specimens examined the position of the umbilical edge and of the peripheral shoulder are constant in relation to the elements of the suture: the L invariably straddles the peripheral shoulder when the latter is present; the maximum curvature of the umbilical edge almost always is crossed obliquely by the fourth main saddle in the external suture.

The external suture seems to be a relatively stable morphologic feature within a species. The variation encountered is often as great between successive septa as between individuals. Variation between species is generally not great, but in some species the septa are consistently more extended or the individual elements broader than in others (compare *T. timotheanus* and *T. jurinianus*) so that the degree of development of the suture, in this instance may be used as a specific characteristic. Most species, however, cannot be separated by the character of the external suture.

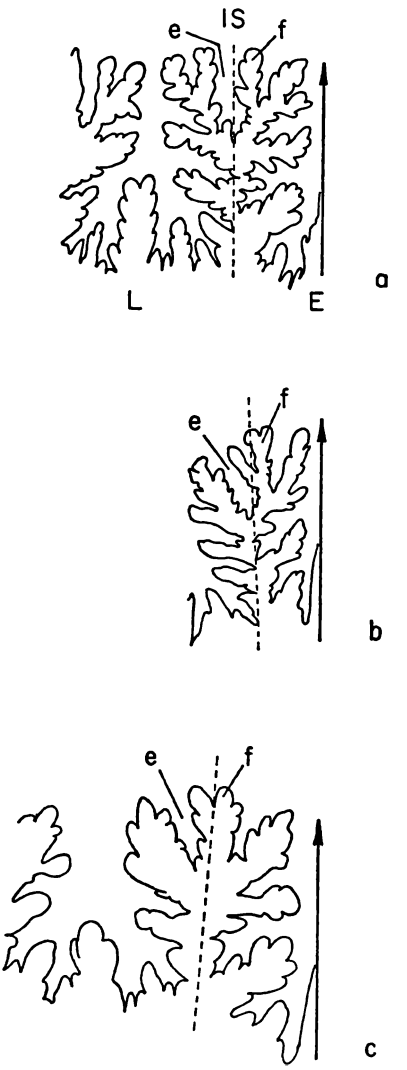


Fig. 2. *a. Eogaudryceras*—type 1S. Copied from Wiedmann (1962*a*, p. 152). 1S is symmetrically bifid, i.e., a straight line running up the trunk of the saddle bisects the principal accessory (e) without touching (f). *b. Eotetragonites*—type 1S—also present in *Tetragonites*. 1S is irregularly bifid. A line running up the trunk cuts both (e) and (f). From *Eotetragonites wintunius*. *c. Tetragonites*—type 1S. 1S is trifid. A straight line running up the trunk of the saddle bisects (f) without touching (e). From Wiedmann (1962*a*, p. 152), *T. subbeticus*.

In addition, the character of the immature suture is quite different than for large individuals. Thus, as is true of all morphologic features, sutures must be compared at equal ontogenetic stages.

The internal suture has two or more saddles and a very long dorsal lobe that terminates in a septal lobe on the preceding septum (see pl. 3, fig. 7; pl. 5, fig. 11). In some specimens the internal lateral lobes are also in part sutured to the preceding septum (see pl. 3, fig. 7).

The internal suture, like the external suture, shows little variation in number or position of the elements, but the variation that does occur seems to be an important aid in the recognition of the various evolutionary stocks. The number of internal saddles is normally two main ones and one small, poorly developed or incipient one. Most Aptian and Albian forms show this development though some have only one main and one subsidiary saddle. The relative development of the internal saddles may be observed on the septal face and may be exposed without destroying or dismounting the specimen. It seems to be associated consistently with other morphologic characters that make it a useful taxonomic criterion.

The Aperture and Associated Characteristics

The configuration of the margins of the aperture in lateral and ventral aspect is one of the most characteristic features of the subfamily and genus. Most species of *Tetragonites* show that the margin of the aperture is strongly prorsiradiate on the flanks, recurves at or near the peripheral shoulder, and is arched on the venter, usually with the concave side of the arch facing the aperture (see pl. 5, fig. 3). Exceptions to this pattern on the venter are seen on young specimens an in some species in which the margin is straight across the ventral area (e.g., *T. timotheanus*, pl. 1, fig. 18) and in a series of forms leading from the variations of *T. timotheanus* to *T. spathi* in which the margin on the venter is convex or peaked toward the aperture.

The configuration of the margin of the aperture is almost always inferred as it is rarely preserved, thus other features known to be a direct result of shell formation at the apertural margin are used. These include the growth lines, constrictions, lirae (thin raised threads ornamenting the shell surface—present only on the umbilical wall in Early Cretaceous *Tetragonites*), and growth rugae (pl. 2, fig. 7).

Growth rugae are very low, closely spaced plications of the internal mold which have a configuration similar to the constrictions and are inferred to parallel the apertural margin. They do not seem to have any taxonomic significance, as they have been noted only on a few specimens.

At some sample sites considerable variation is present in number, regularity of spacing, and degree of development of the constrictions. This seems to be the usual case. However, some are characterized by extreme regularity, and here I cite the large samples of small pyritic internal molds from the Cenomanian of Madagascar in General Collignon's collection. Specimens from two sample sites consistently show four constrictions per whorl on the smaller specimens and five on the larger specimens (max. 20 mm in diameter) with equal spacing and development (MCC localities 478, 485).

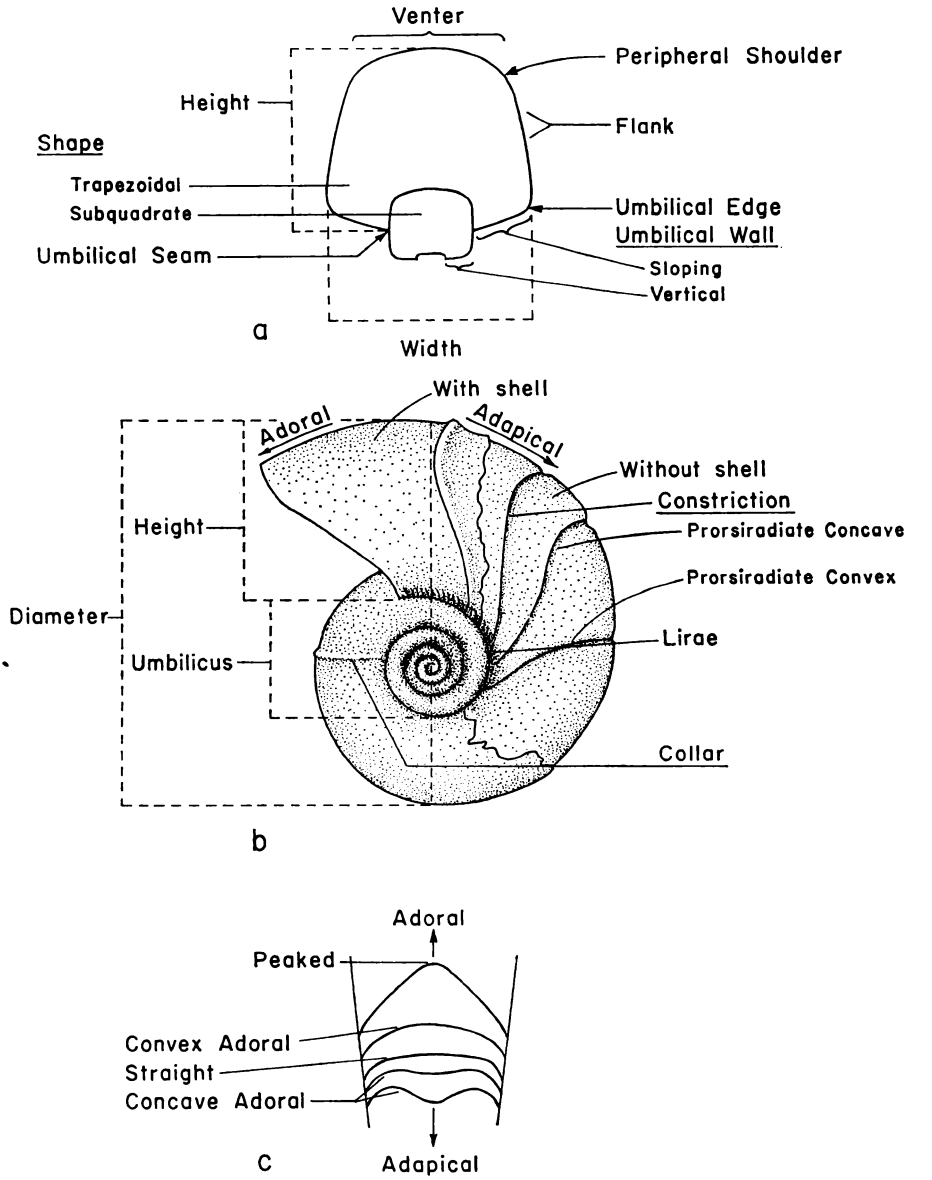


Fig. 3. Nomenclature of the tetragonitid shell. *a*. Cross section of the spire. *b*. Lateral view. *c*. Ventral view—diagrammatic showing the configuration of the margin of the aperture in different forms as reflected by the growth lines and constrictions.

Ornamentation

The genus *Tetragonites* is characterized by a smooth, polished external shell. Growth lines may or may not be discernible over the entire shell. Lirae are absent except on the umbilical wall where more or less irregularly spaced lirae are usually present. The only other ornamentation of the external shell is the collars that may be developed above the position of the constrictions.

SPECIFIC CRITERIA

Although the character of the internal suture is often used as a taxonomic criterion at the specific level, the whorl shape, ontogenetic development of the test, the relative measurements of various parameters to the size of the test, and the number, configuration, and presence or absence of constrictions have been more commonly employed as specific criteria.

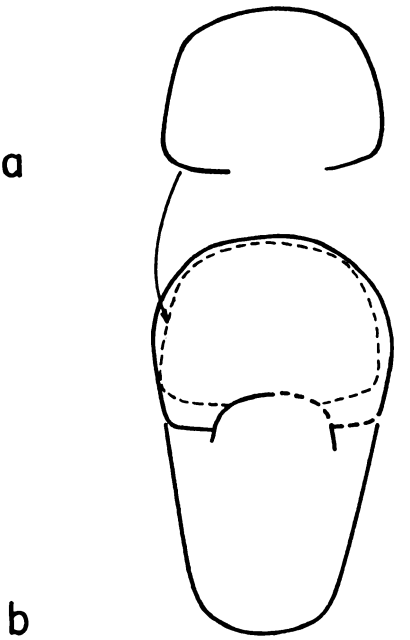


Fig. 4. *Tetragonites rectangularis* Wiedmann. *a*. Cross section of the holotype from a plaster cast. *b*. Cross section of the holotype from photograph of terminal end of the shell which shows effects of deformation. Dashed line is 4*a* superimposed.

The Shape of the Cross Section

In most of the Early Cretaceous forms both the flanks and the venter are flattened producing the characteristic trapezoidal or quadrate cross section. In later forms the venter is often rounded and the shell more compressed. Variation in cross section though not extreme within the genus is considerable. Present evaluation of ontogenetic variation after the third or fourth whorl seems to indicate it occurs in some species (*T. rectangularis*—from quadrate to trapezoidal) and not in others (*T. kitchini*—nearly square throughout).

The shape of the cross section is valuable and has been extensively used as a specific criterion for taxonomic purposes. I feel, however, that the evaluation of shape is extremely subjective (as an example, see discussion of *T. jurinianus*, p. 27) and that both studies of ontogeny and variation within samples are necessary prerequisites to its use in taxonomy.

To take some of the subjectivity out of my observations on cross-sectional shape I made plaster casts of a large number of specimens including most of the types and figured specimens I have examined. Casting is admittedly time consuming, but to avoid the effects of deformation and wear, which are most often concentrated at the terminal end of the conch, one must either break or cut the specimen or make a cast, because irregular, nonuniformly oriented, or deformed sections cannot be used (see fig. 4). The casts were then measured to guard against distortion, and cut along a plane passing through the protoconch and perpendicular to the plane of symmetry. Tracings of the cross sections may then be compared at equal or nearly equal size. The cross sections figured in this paper were done in this manner.

The method points out that some differences easily seen by the eye are in reality very slight in terms of degree of curvature, inflation, and shell shape. They may represent only morphologic variants within populations, especially when found at the same sample sites. However, some shapes and sequences of shapes are distinctive and when used in combination with other morphologic features, are useful criteria in classification.

The cross sections of the casts show that most of the specimens are not bilaterally symmetrical. In some instances this is unquestionably caused by deformation of the shell after burial. Some shells, however, show no evidence of deformation, so the asymmetry could be an original feature of the shell.

Relative Growth and Measurements

In studies of this genus mention is often made of the rapid growth of the whorl and of the relative size of the umbilicus. Like the preceding, these are relatively subjective observations, but in this instance objectivity may be increased by the measurement of the various parameters at different shell diameters.

All measurements given in this paper were made by me following the definitions given at the end of this section for height, width, umbilical diameter, and shell diameter, except as indicated in the text.

As a method of comparison of measurements within this group of ammonites I have constructed growth curves for each character measured, using as many specimens as possible from the locality of the type, and making measurements at different diameters on each specimen.

It may be seen from an examination of the growth and variation curves of the various species that the ratios of H, W, and U to the diameter have a small deviation from the mean for specimens from all localities. Also the growth curves generally confirm an expectation. The curves made from the measurements of specimens found together or at the same stratigraphic level (fig. 15) approximate a line. Those gathered over a wider stratigraphic interval show greater variation (e.g., *T. rectangularis,* fig. 18).

Table 10 presents a series of measurements which indicates that the relative size of the height, width, and umbilicus may vary systematically with growth. These measurements were made on specimens from a single bed in the *hulenense* zone of northern California and show that a tendency exists for the shell to become more

narrowly umbilicate with increase in size. This tendency is also illustrated in a general way by specimens of *Eotetragonites balmensis* from la Balme de Rencurel, Isere, France, and from Son Vida, Mallorca (table 15). This illustrates again the necessity of comparing shells at equal sizes when identifying them.

Definitions

Diameter.—The diameter is measured between two points on the venter on opposite sides of the shell which are in the plane of symmetry and in a plane perpendicular to it that also passes through the protoconch.

Height.—The height is measured along the line of intersection of the plane of symmetry and the perpendicular plane passing through the protoconch and between a line connecting the umbilical seams and a point on the venter.

Width.—The width is measured at right angles to the plane of symmetry between points of maximum inflation of the flanks.

Umbilicus.—The umbilicus is measured between points on the umbilical seam cut by a plane passing through the protoconch and normal to the plane of symmetry.

Table 16 summarizes the morphologic features that have been used in the classification of the species of *Tetragonites* and some of the better known members of *Eotetragonites.*

Evolution

Each main branch in the evolutionary scheme seems to be composed of a plexus of populations migrating from place to place through time, constantly splitting and rejoining, and occasionally becoming isolated from one another long enough for speciation to occur. Thus I have shown in figure 5 several principal branches of the family tree, each showing variation, but each retaining a general aspect that serves to distinguish the branches from one another. Each of the main branches is outlined in the above-mentioned figure.

The genus first attained its distinctive characteristics some time in the Aptian, as the earliest *Tetragonites* are recorded in the upper Aptian at three widely separated localities—in the Caucasian region of Russia, in Spain, and in California. They were almost certainly derived from some member of the genus *Eotetragonites* which is also found in these regions.

Eotetragonites is characterized by the following: (1) a suture that is transitional between the early Gaudryceratinae, represented by *Eogaudryceras numidum* Coquand as interpreted by Fallot, and the genus *Tetragonites;* (2) a quadrate cross section of the aperture; (3) irregularly developed but prominent constrictions; (4) a partly lirate shell; and (5) a small amount of overlap of the succeeding volutions.

The differences between the two genera are mostly of degree rather than of kind. With a stronger forward inclination of the margin of the aperture, slightly greater involution and concomitant stronger development of the internal saddles, and loss of lirae on the peripheral part of the shell, the transition to *Tetragonites* is complete.

Aptian Tetragonites

Three species of Aptian *Tetragonites* are now known. This is exclusive of *Ammonites duvalianus* d'Orbigny (= *Eotetragonites*). *T. heterosulcatus* Anthula is from the Crimea; *T. subbeticus* Wiedmann is from Spain; *T. lecontei* n. sp. is from northern California.

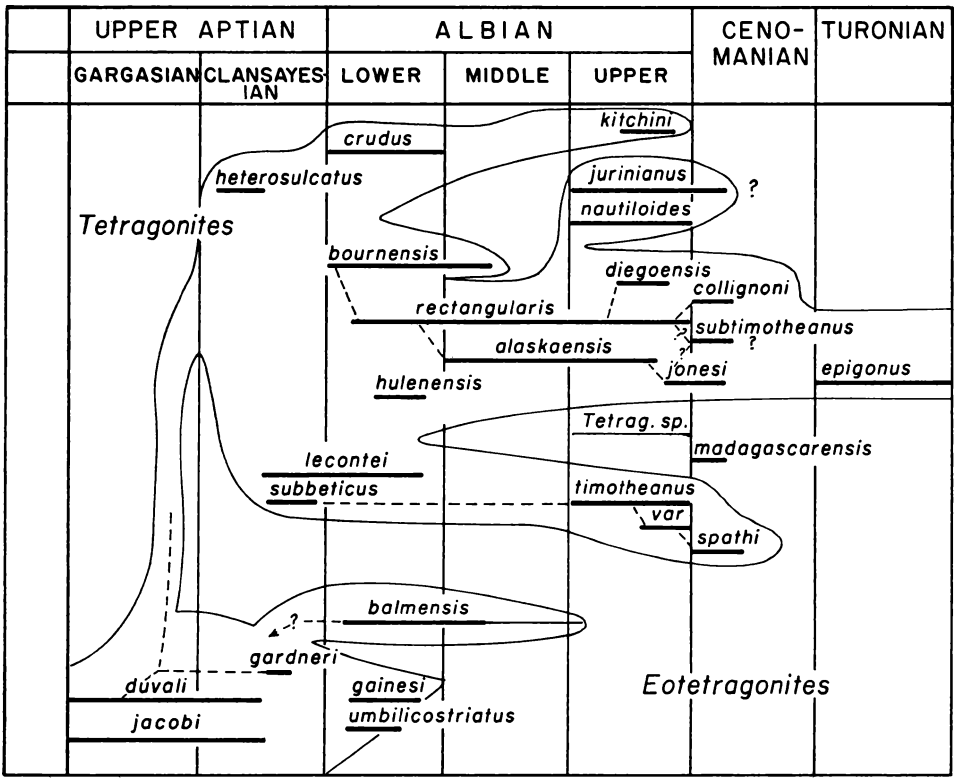


Fig. 5. Interpretation of the genetic relationship and stratigraphic ranges of middle Cretaceous *Tetragonites*. Dashed lines connect members of suggested evolutionary lineages. Light solid lines represent probable stratigraphic range—not fully confirmed. Heavy solid line represents established stratigraphic range. Breistroffer's interpretation of the ages of the French Alpine Albian sequences is accepted for purposes of this figure through certain reservations are stated in the text.

T. heterosulcatus, reported by Drushchits from the *Parahoplites melchioris* zone, seems very closely related to *Eotetragonites gardneri* n. sp. in spite of the great geographic separation. Both are apparently Clansayesian though *E. gardneri* occurs well above the zone of *Parahoplites* in California and is probably slightly younger making it ineligible as the parent stock of *T. heterosulcatus*. This close relationship between species in California and southern Europe and the Tethyan region in general is characteristic in the upper Aptian and lower Albian strata and suggests relatively easy communication between them during most of this time.

The transition of the eogaudrycerid suture with a symmetrically bifid principal saddle of the external suture and a single internal saddle to the tetragonitid suture with the development of a trifid principal saddle and two or more internal saddles is already partially completed in forms like *Eotetragonites jacobi* (pl. 1, figs. 1, 4), *E. wintunius* (fig. 6), and *E. gardneri* n. sp. The latter is very similar to *Tetragonites heterosulcatus* Anthula not just in suture pattern, but also in the peculiar cross section of the whorl.

The closest Albian descendant of *T. heterosulcatus* is inferred to be *T. crudus* Drushchits. It seems plausible that *T. heterosulcatus* or something very like it also



Fig. 6. Internal suture of *Eotetragonites wintunius* (Anderson) showing development of second internal saddle (UCR specimen).

gave rise to the principal Albian branch of the genus characterized by *T. rectangularis,* but the latter could be derived as easily from either of the other two Aptian species.

In contrast to *T. heterosulcatus, T. subbeticus* has no obvious immediate ancestor among the *Eotetragonites,* but shows a strong resemblance for the much later *T. timotheanus* and, although connecting links in the lower and middle Albian are not known, the two species seem to belong to the same lineage. *T. lecontei* n. sp., which appears in California in the same bed as *E. gardneri* n. sp., is morphologically more closely related to this branch of the genus than the others by virtue of its wide umbilicus, relatively straight constrictions and broad, low cross section. The shape of the cross section, however, is different and only two internal saddles have been seen in this species. The third smaller one present in both *T. subbeticus* and *T. timotheanus* is absent in *T. lecontei* in the internal suture.

Albian Tetragonites

Three principal morphologic groups and several isolated species of the genus are present in Albian and Cenomanian strata. The characteristics of these groups are given in table 1.

The morphologic group of the genus including *T. timotheanus* begins with the late Aptian *T. subbeticus,* which is very similar to the genotype and doubtless has

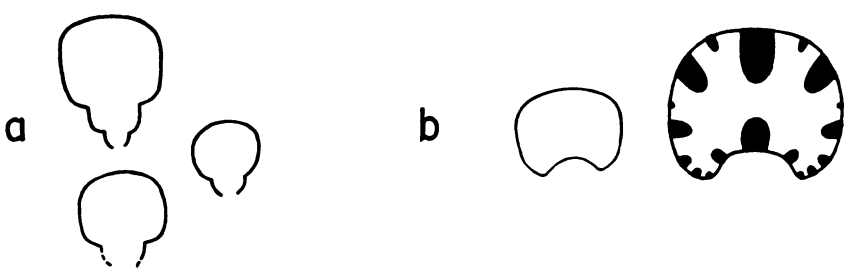


Fig. 7. Comparison of the similarity in the cross sections of *Tetragonites heterosulcatus* Anthula (after Drushchits, 1956, p. 102) and *Eotetragonites gardneri* n. sp. a. *E. gardneri n.* sp. b. *T. heterosulcatus* Anthula.

TABLE 1

ALBIAN-CENOMANIAN GROUPS OF THE GENUS TETRAGONITES

Branch	Description
T. timotheanus	Relatively small, depressed, widely umbilicate shells with weakly to moderately extended septa; internal suture with two well-developed saddles and sometimes a third incipient one; relatively straight constrictions on both flank and venter; rectangular to trapezoidal cross section.
T. rectangularis	Medium to large narrowly umbilicate shells with moderately to strongly extended septa showing subequal development of two internal saddles and weak development of a third internal saddle; constrictions, when present, are prorsiradiate concave on the flanks and show an adorally concave arch on the venter; rectangular to trapezoidal cross section.
T. kitchini	Medium-size shells with moderately extended septa; internal suture with one strongly developed saddle and one small one; constrictions prorsiradiate concave on the flanks and with an adorally concave arch on the venter; almost square cross section.

an ancestral relation to it. I know only one fragmentary specimen (possibly referable to *T. timotheanus*) of this branch of the genus from the middle Albian (La Balme de Rencurel), but several varieties, or perhaps independent taxa, of *T. timotheanus* are present in the upper Albian. Some of these (pl. 1, fig. 16) show a tendency to develop constrictions with an adorally convex arch on the venter and preview the later stronger development of this characteristic in the Cenomanian *T. spathi.*

The Californian *T. lecontei* seems to have its origin in this branch of the genus and perhaps it gave rise to the sympatric partly contemporaneous species *T. hulenensis.*

The second group of forms is much more homogeneous and consists of a single species, *T. kitchini,* and its varieties. This lineage is easily separated from the other groups of species by the almost equant and nearly square cross section of the spire and by the unequal development of only two saddles in the internal suture. These characteristics suggest derivation from *T. heterosulcatus* or a similar form rather than any member of the major Albian groups which all have a more prominent development of the internal suture line in terms of numbers of elements.

T. crudus from the lower Albian probably belongs to this branch of the genus.

The *T. rectangularis* branch of the genus is characterized by an internal suture with two strongly developed saddles. A third very small saddle is present in many of the taxa included in this group, but it has not yet been observed in all of them. The aperatural margin is prorsiradiate concave on the flanks and forms a distinct adorally concave arch on the venter. The umbilical diameter is small and the cross section of the spire is quadrate or trapezoidal.

The group apparently orignated in the earliest Albian (La Frasette) with *T. bournensis* n. sp. as its earliest representative. *T. bournensis* is a form with a

quadrate cross section and weak constrictions. With these characteristics it makes a reasonable connecting link between the Aptian forms from the Caucasus and the *T. rectangularis* branch. It is, of course, morphologically much closer to the Albian species and could have been the progenitor of any or all of the species included in this branch of the family. For example, the adult cross section in *T. bournensis* is like that of the young *T. rectangularis*. With a slight change in the shape of the adult aperture and slightly more developed constrictions, *T. rectangularis* is evolved. Equally possible by small changes in the cross section and development of a slightly more pronounced set of constrictions is the evolution to *T. hulenensis* n. sp. It is also possible to derive the nonconstricted *T. jurinianus–T. nautiloides* offshoot from *T. bournensis*, but they seem much more closely related to *T. rectangularis* in both morphology and time.

Cenomanian Tetragonites

Tetragonites rectangularis unquestionably gives rise to *T. collignoni* Breistroffer, as there is little morphologic difference between the two. It also probably gives rise to *T. subtimotheanus* Wiedmann; however, the latter may have been derived by way of *T. jonesi* n. sp. and *T. rectangularis alaskaensis* n. subsp. and has more saddles in the internal suture than the Albian members of the *T. rectangularis* group.

ECOLOGY

Little can be inferred about the ecology of smooth-shelled, normally coiled ammonites except from the fossils associated with them, the facies they are found in, and their geographic distribution with respect to these facies.

The data given below support the interpretation that members of the genus generally dwelt where the water was relatively deep over the outer slope and basin.

Most localities from which specimens have been recovered are in sandstones or argillaceous rocks, not limestones.

The *Tetragonites*-bearing sandstones almost invariably show evidence of slow deposition and reworking such as abraded shells with foreign matrix, glauconite, phosphate, and with single beds of glauconitic sandstone often yielding ammonites of several zones or subzones of the corresponding marly or argillaceous facies. Thus most of the sandstone occurrences are of little value in determining the ecology of the group.

When shells are found in place, it is generally in marl or siltstone as pyritic molds or in calcareous concretions. In these occurrences they may be accompanied by other ammonites. Other mollusks, such as *Nucula, Acila, Anchura,* and *Nerinea* common in deeper water deposits in other parts of the column, are commonly represented in this association; the abundant pelecypods and gastropods of the littoral and inner sublittoral are absent. In the occurrences from the Pacific Coast of North America fragments of the woody parts of plants are abundant in the sediments as well, but they have no special significance in determining the paleoecology of the group.

CONCLUSIONS

In general, the members of the genus *Tetragonites* represent one of the more conservative and long-ranging stocks of ammonites and do not show as much variation in shell morphology as is found in the more rapidly evolving genera. The virtual lack of shell ornamentation limits the number of characters that can be used for taxonomic purposes, especially at the species level. This has led to a dependence on the degree of development of a morphologic character as a criterion for specific distinction rather than the presence or absence of the character. In some cases this is justified; in some cases it is not.

Two major problems in the study of the genus will be difficult to solve. Probably the most important of these is the lack of precise stratigraphic control for almost all the examples coming from phosphatic greensands. The exact location and bed is known, but the evidence of reworking and transportation of at least part of these deposits leaves the biostratigraphy of many species uncertain. This problem is not materially aided by occurrences in other lithologies as these are often in isolated outcrops or poorly known sequences with few other fossils. The solution to this problem will require a great deal of patient stratigraphic work in more complete, but less fossiliferous, stratigraphic sequences such as are characteristic of the Pacific Coast of North America and the Vocontien region of France.

The second problem is our inability to assess each morphologic feature in terms of its variability at all ontogenetic stages in population samples of adequate size from single horizons. As more of these data become available, we can expect our classification of the genus to stabilize and its use in stratigraphy to become more precise.

SYSTEMATIC SECTION

Tetragonites timotheanus (Pictet), 1848

(Pl. 1, figs. 10–19)

1848 *Ammonites timotheanus* Pictet, Grès verts I, p. 295, pl. 2, fig. 6; pl. 3, fig. 1.

1908 *Lytoceras (Tetragonites) kiliani* Jacob, Amm. crétacé moyen, p. 21, pl. 1, fig. 9; text fig. 8.

1940 *Tetragonites timotheanus* Mayor in Pictet—Breistroffer, Vraconien Salazac, p. 110.

1962 *Tetragonites timotheanus* (Pictet)—Wiedmann, Vascogot. Kreide (Nordspanien), p. 172, pl. 8, fig. 10; pl. 14, fig. 4–6; text figs. 30–33.

Description

Size.—The lectotype with a nearly complete living chamber is the largest recorded specimen at slightly over 34 mm in diameter. The species seems to reach its adult stage at about the diameter of the lectotype, but there are several specimens from Entrèves-en-Bauges and Salazac which must have been 40–45 mm in diameter and possibly larger.

Measurements.—The table of measurements and the growth curves show the umbilical diameter is larger than the whorl height at shell diameters greater than 15 mm, ranges between 37 and 44 percent of the shell diameter and shows a slight tendency for the percentage to be greater at larger diameters than at smaller diameters in the same individual. The height of whorl varies between 32 and 36 percent of the shell diameter and the width of whorl is from 49 to 54 percent of the shell diameter.

Cross section.—In the early stages growth the venter is generally flattened and some specimens even have a concave ventral surface. The flanks vary from subparallel to rounded. The adult whorls show about the same range of variation with at least the upper halves of the flank being convergent and joining the venter in a rounded peripheral shoulder. In some specimens the shoulders are distinctly delimited and show as angulations bordering the venter. In others they are so rounded that they are indistinguishable.

Pictet's (pl. 3, fig. 1a; figure repeated by Wright, 1957, p. L202) representation is not accurate and probably contributed to the early misinterpretation of the species.

Suture.—The lobes and saddles of the septum are not strongly extended or complexly frilled. The first lateral lobe has a length-width ratio of about 2.5. The first and second lateral lobes are deeper than the suspensive lobe. Most specimens assigned to this species have a more distinct triphyllic termination of the first lateral saddle than the lectotype (Wiedmann, 1962*a*, p. 172, fig. 31), reproduced here as figure 9h.

Constrictions.—The number of constrictions on specimens of greater than 10 mm in diameter ranges from 4 to 8. Four specimens from Entrèves-en-Bauges (FG Coll.) identified as *T. timotheanus* have 4 or 5 constrictions per whorl at shell diameters ranging from 11 to 24 mm. A specimen in my collection from the same locality has 8 constrictions per whorl at 24 mm diameter. Six specimens from this locality (FG Coll.) identified as *T. kiliani* have 5 or 6 constrictions per whorl at shell diameters ranging from 14 to 20 mm. The holotype of *T. kiliani* (Jacob, 1908,

TABLE 2

MEASUREMENTS OF TETRAGONITES TIMOTHEANUS (PICTET)

Specimen	Catalogue number	D	H	W	U
Lectotype	MHNG Pi GV/3,1	*34.0 25.9	11.3 (33) 8.3 (32)	17.7 (52) 13.2 (51)	15.0 (44) 10.5 (41)
Hypotype	MHNG Wi VK/5	29.8	10.3 (35)	15.2± (51)	12.3 (41)
	MHNG Rochat Collection	26.5	9.5± (36)	13.8 (52)	11.0± (42)
T. timotheanus Entrèves-en-Bauges, Savoie	FG Collection No number	25.8	8.2 (32)	13.6± (53)	10.8 (42)
T. timotheanus Entrèves-en-Bauges, Savoie	FG Collection No number	24.6	8.9 (36)	12.6 (51)	9.5 (39)
T. timotheanus Entrèves-en-Bauges, Savoie	FG Collection No number	11.2	3.8 (34)	6.0 (54)	4.3 (38)
T. timotheanus Echeverri	Ce 026 IGD	15.2	5.4 (35)	8.1 (53)	5.8 (38)
Holotype *T. kiliani* Jacob	FG Collection No number	19.1	6.6 (35)	9.6 (50)	8.1 (42)
T. kiliani from St. André-de-Rosans	FG Collection larger specimen	17.6 16.5	6.3 (36) 5.8 (35)	9.4 (53) 8.8 (53)	6.8 (39) 6.5 (39)
	smaller specimen	16.2 14.1	5.4 (33) 4.6 (33)	8.1 (50) 7.2 (51)	6.9 (43) 5.9 (42)
T. kiliani Entrèves-en-Bauges	FG Collection No number	25.8	9.0 (34)	12.7 (49)	10.3 (40)
T. kiliani Entrèves-en-Bauges	FG Collection No number	21.6	7.3 (34)	10.7 (50)	8.6 (40)
T. kiliani Entrèves-en-Bauges	FG Collection No number	15.9	5.6 (35)	8.5 (53)	5.8 (37)

* Brackets indicate measurements taken at different diameters on the same specimen.

pl. 1, fig. 9), included here and by Wiedmann (1962, p. 172) in *T. timotheanus*, has 8 constrictions on the last volution preserved and 6 on the preceding volution. There are also 6 on the smaller specimen from the locality of the holotype (FG Coll.—Noyers-sur-Jabron, Basses-Alpes). Wiedmann (1962, p. 173) mentions two specimens (Ce 026, Ce 027) from Spain in the collection of R. Ciry at the Geological Institute at Dijon. These specimens have 6 or 7 constrictions per whorl.

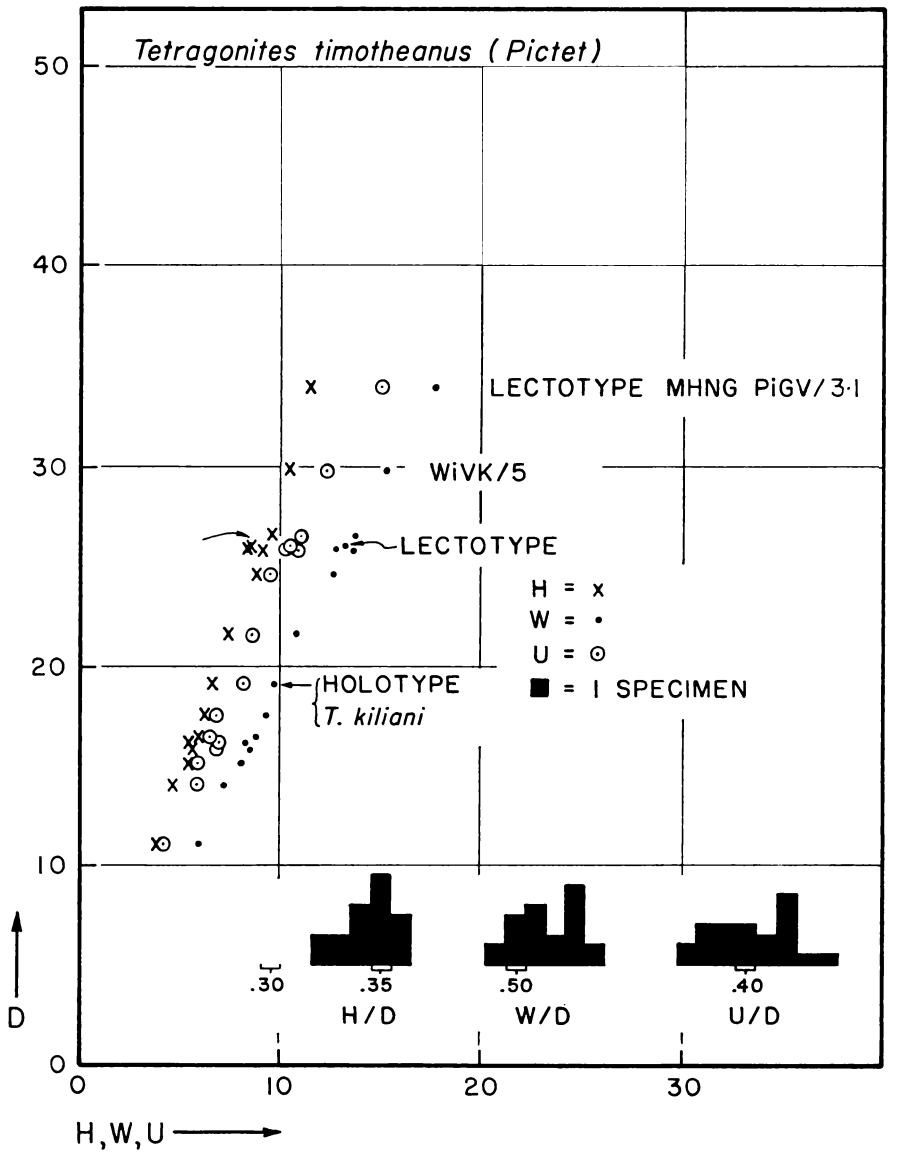


Fig. 8. Growth curves for specimens assigned to *T. timotheanus* as shown by plots of all measurements available. The bar graphs show the distribution of H/D, W/D, U/D ratios for all specimens. Half units are used where two measurements on the same specimen differed. The measurements used to construct both plots are the measurements found in table 2. The data are presented in this way throughout the text.

Constrictions may appear very early in the ontogeny as the paratype MHNG PiGV/2, 6 shows constrictions at approximately 3 mm diameter. In some specimens the internal mold becomes completely smooth at about 20 mm diameter, but others, especially those which have been assigned to *T. kiliani* by Breistroffer, have constrictions on all preserved parts of the test up to 30 mm diameter (pl. 1, figs. 10–19).

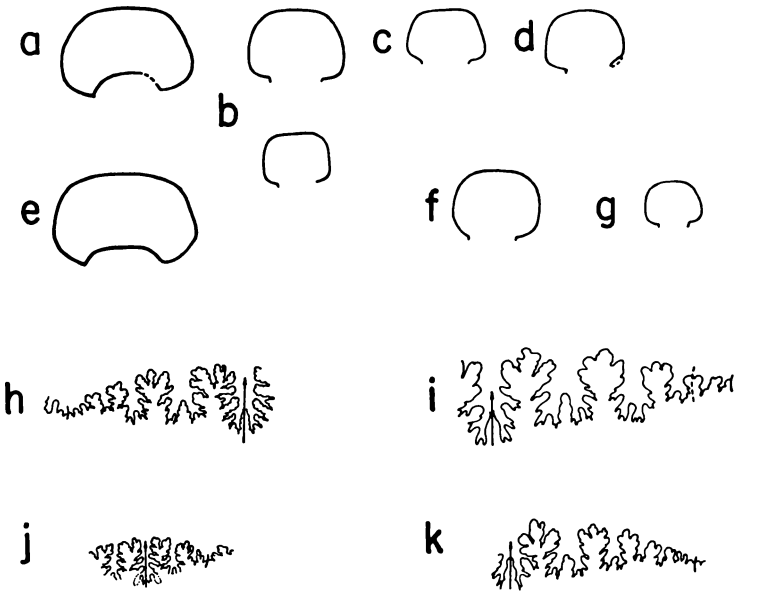


Fig. 9. Cross sections and sutures of specimens of *T. timotheanus* (Pictet) and *T. subbeticus* Wiedmann (*e.* only). *a.* Lectotype MHNG Pi GB 3/1 after Wiedmann, 1962*a*, pl. 14, fig. 4c *b.* UCR 677/1 from Entrèves-en-Bauges. *c.* FG Collection unnumbered, from Entrèves-en-Bauges identified as *T. kiliani* by Breistroffer. *d.* FG Collection unnumbered, from Salazac, identified as *T. timotheanus* mut. by Breistroffer. *e.* Holotype *T. subbeticus* for comparison, GPIT Ce 1220/21, from Alicante, Spain, after Wiedmann, 1962*b*, pl. 5, fig. 6b. *f. FG* Collection unnumbered, from Salazac, identified as *T. kiliani* by Breistroffer. *g.* FG Collection unnumbered, from Entrèves-en-Bauges, identified as *T. jurinianus* by Breistroffer. *h–k.* After Wiedmann, 1962*a*, pp. 172, 173, text figs. 31–33.

The constrictions are distinct narrow grooves on the flank and venter. They are prorsiradiate on the flanks and cross the venter in a straight line without arch or with an arch that is either convex or concave adorally (pl. 1, figs. 16–19). The specimens from Salazac (Gard), France, commonly have a convex arch on the venter at diameters greater than those at which the lectotype has become smooth.

Comparison

The very broad umbilicus (37–44 percent of the diameter easily separates *T. timotheanus* from most other described species. *T. kiliani* Jacob is regarded as a synonym. *T. subbeticus* Wiedmann is known only from small, pyritic molds, but the young whorls have a less rectangular cross section than in *T. timotheanus* of the same size.

Distribution

Upper Albian of southeastern France and Spain.

Entrèves-en-Bauges (Savoie), Noyers-sur-Jabron (Basses-Alpes), St. André de Rosans (Hautes-Alpes), Mt. Saxonet (Savoie), Salazac (Gard), France.

After Wiedmann: Echeverri, Navarra, Spain.

All specimens assigned to the species appear in upper Albian assemblages. Al-

though several of these assemblages occur in phosphatic greensands, the upper Albian age of the taxon seems relatively well established by the other occurrences.

Remarks

T. timotheanus (Pictet) has been reviewed by Breistroffer (1940, p. 110), Fabre (1940, p. 214), and Wiedmann (1962*a*, p. 172). Wiedmann refigured Pictet's original specimens and designated a lectotype thereby clarifying the nomenclature of this often misinterpreted species.

Jacob's (1908, p. 21) separation of *kiliani* apparently presumes that the type of *T. timotheanus* is a narrowly umbilicate form like *T. nautiloides* or *T. jurinianus*.

Breistroffer, however, retained the taxon as separable from *T. timotheanus* by its faster growth in width, its more elevated whorls, and less depressed section, with less flattened flanks and a less flattened ventral rgeion. His main consideration, however, was in the smaller number and less inclined constrictions.

Measurements and cross sections of the types and other specimens show almost perfect conformity in measurements and cross-sectional shape. The number of constrictions is variable as discussed above. Their inclination apparently has a wide range of variation, a single specimen from Entrèves-en-Bauges showing consecutive constrictions inclined 47 and 72 degrees, respectively.

The occurrence of *T. kiliani* Jacob with *T. timotheanus* at Entrèves-en-Bauges and St. André de Rosans, and the wide range of variability of the shell demonstrated by the collections from Entrèves showing intermediate as well as more extreme variations support Wiedmann's position in placing *T. kiliani* in synonymy with *T. timotheanus*.

Specimens from Salazac depart from the type in having constrictions at larger diameters with anteriorly convex ventral sinus and a narrower more parallel-sided whorl section suggesting an ancestral relation to *T. spathi* of the Cenomanian of Cassis. These do not, however, affect the nomenclatorial status of *T. kiliani*, as its holotype is conspecific with *T. timotheanus*. If they are separated from *T. timotheanus*, a new name will be required.

The internal suture given by Wiedmann (1962*a*, fig. 31, p. 172) shows the development of an incipient third saddle. The figure given by Matsumoto (1959, p. 78, fig. 16) is from a fragmental specimen, which is identifiable with *T. jurinianus*.

Tetragonites jurinianus (Pictet), 1848

(Pl. 2, figs. 1–4)

1848 *Ammonites jurinianus* Pictet, Grès verts Part I, p. 297, pl. 3, fig. 3.

1906 *Lytoceras* (*Tetragonites*) *epigonum* Kossmat, Boule, Lemoine, and Thevenin, Cephalopodes crétacés Diégo Suarez, p. 186, pl. III, fig. 1.

Not 1908 *Lytoceras* (*Tetragonites*) *jurinianum* Pictet, Jacob, Amm. crétacé moyen, p. 19, pl. 1, fig. 12.

?1923 *Litoceras* (*Tetragonites*) *zacatecanus* Bose, Faunas cretacicas Zacatecas, Durango, Quererro, p. 127, pl. 9, figs. 11–17.

1940 *Tetragonites jurinianus* (Pictet) Breistroffer, Vraconien, Salazac, p. 111.

1959 *Tetragonites timotheanus* (Pictet), Matsumoto, Cret. Ammonites Chitina Valley, Alaska, p. 78, fig. 16.

1962 *Tetragonites jurinianus* (Pictet) Wiedmann, Vascogot. Kreide (Nordspanien), p. 176, pl. 14, fig. 2; text figs. 37, 38.

Description

Size.—The holotype at 74 mm diameter is the largest recorded specimen. It is still septate indicating the species attained a much larger size. Most of the individuals assigned to the species are much smaller, however, and many of these have nearly complete living chambers.

Measurements.—The few data available indicate that both the umbilical diameter and the width of whorl are more variable than the height of whorl and that the umbilicus is small when compared with other members of the genus.

TABLE 3
Measurements of Tetragonites jurinianus

Specimen	D	H	W	U
Holotype MHNG	72.0 50.5	35.2 (49) 24.9 (49)	40.0 (56) 29.0 (57)	16.4± (23) 11.0 (22)
*MHNG Wi VK/8	25.0	12.0 (48)	14.5 (58)	6.5 (26)
*MHNG Wi VK/9	24.0	11.0 (46)	14.0 (58)	6.5 (27)
From Entrèves-en-Bauges, FG Coll.	34.1	16.4 (48)	....	7.4 (22)
From Entrèves-en-Bauges, FG Coll.	26.6	....	15.5 (58)	....
From Entrèves-en-Bauges, FG Coll.	26.1	11.9 (46)	16.0 (61)	6.6 (25)
From St. André de Rosans, FG Coll. slightly deformed	61.6 47.8	29.0 (47) 22.3 (47)	37.2 (60) 28.0 (59)	14.0 (23) 11.9 (25)

* After Wiedmann 1962a.

Cross section.—The cross section is rounded, but with slight development of the peripheral shoulder and flattening of the flanks and venter. The umbilical wall varies from almost vertical in the younger whorls of the holotype to a more gentle slope in the later whorls. This variation is shown in other specimens as well. The umbilical edge may be more or less abruptly rounded to angular, being more angular when the umbilical wall is more vertical in the smaller specimens.

Constrictions.—Constrictions are absent on all specimens throughout ontogeny.

Suture.—The lobes and saddles of the septum are strongly extended and complexly frilled on the holotype at 33 mm diameter. The first lateral lobe has a length/width ratio of about 6:1. The septum of the holotype shows two strong, subequal saddles are present in the internal suture. A fragmental specimen (HU 8589/1) from Mount Saxonet shows a third very small saddle. The main internal lateral lobe of this specimen is atypical for the genus in its depth and curvature.

Comparison

The complete lack of constrictions at all stages of growth, the small umbilicus, and the rounded whorl section have been cited as distinctive of this species and all set it apart from *T. timotheanus.*

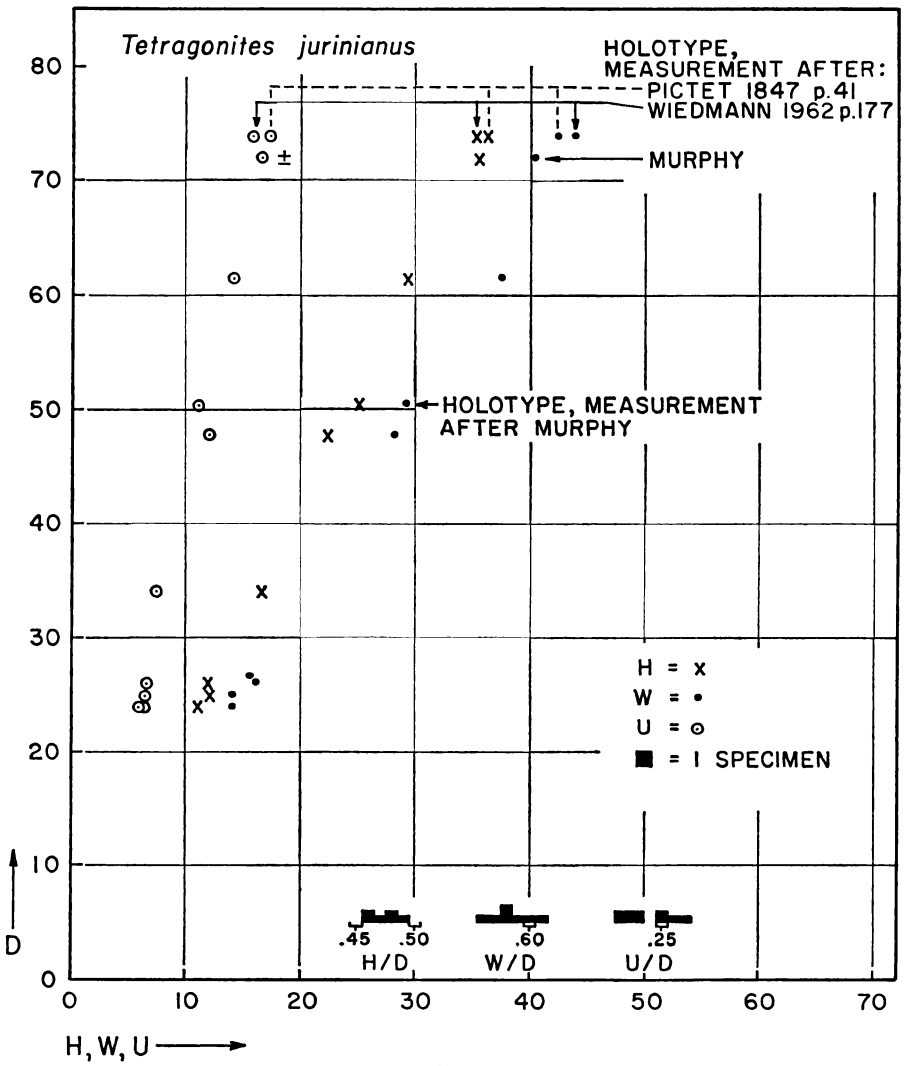


Fig. 10.

Distribution

The species has been found at a number of upper Albian localities in the French Alps: Mt. Saxonet, Entrèves-en-Bauges, St. André de Rosans. Boule and others (1906, pl. 3, fig. 1) record a specimen from the lower Cenomanian of Madagascar which seems to possess the salient features of this species.

Remarks

The holotype is about twice the diameter of the average specimen of *Tetragonites*, so we are dealing here with a much different stage in the ontogeny, though this difference in size represents at most a volution and a half. Thus this taxon is represented by a specimen that is difficult at best to compare with others.

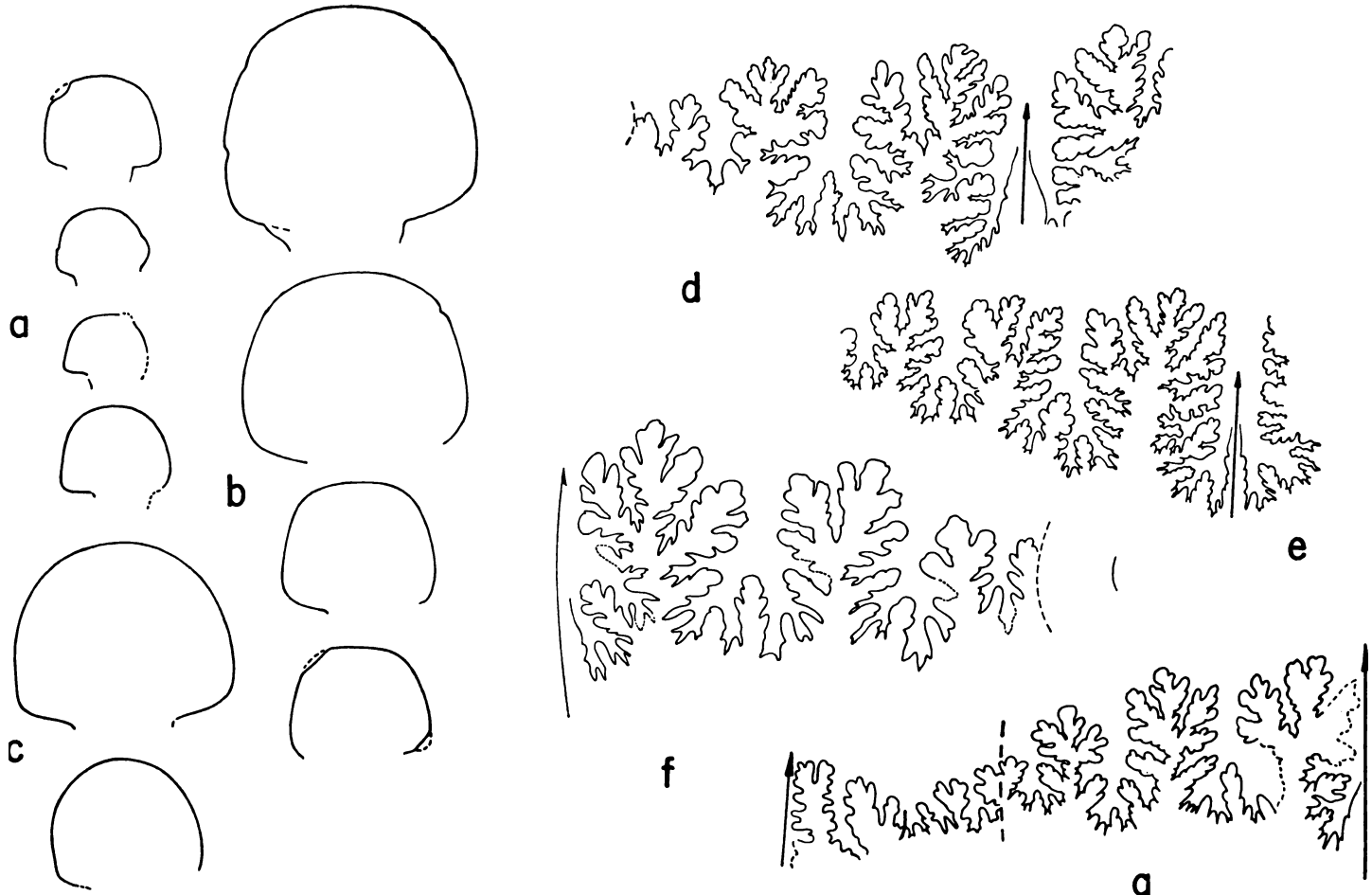


Fig. 11. Cross sections and structures of *T. jurinianus* (Pictet). *a.* FG Collection unnumbered, from Entrèves-en-Bauges. *b. Holotype* MHNG Pi GV/3,3 from Mt. Saxonet. *c.* FG Collection unnumbered, from St. André de Rosans. *d* and *e.* After Wiedmann, 1962*a*, pp. 176, 177, fig. 37 and 38. *f.* FG Collection unnumbered, from Entrèves-en-Bauges. *g.* HU8589/1 from the Albian of Ste. Croix, from original collection of Campiche.

It is worth noting that the holotype and neotype of *T. nautiloides* were collected at the same locality as the holotype of *T. jurinianus* and the neotype differs from it primarily in size. The whorl shapes as shown in sections of plaster casts of the two type specimens are not markedly different nor do the specimens themselves appear to be when held side by side and compared to one another as nearly as possible at the same diameter. Neither shows any constrictions on any part of the shell (see also p. 31 of this report; Jacob, 1908, p. 19). The relative measurements of specimens assigned to the two species are not significantly different nor are the relative measurements of the two types. The height and umbilical diameter of the neotype of *T. nautiloides* can only be approximated as the umbilicus is filled with a very hard matrix. The septum is not significantly different, but here again the comparison must employ specimens other than the types as the septal face is completely inaccessible in the neotype of *T. nautiloides*. The external suture patterns in the two show a similar degree of development and confirm the observations made on the septum of auxiliary specimens.

The only difference that I can see between these two taxa is in specimens ranging between 15 and 25 mm in diameter. These display an angular peripheral shoulder in *T. nautiloides* and a rounded peripheral shoulder in those assigned to *T. jurinianus*. This is a small difference, but one which is easily detected by the eye. Though it may not be sufficient for maintaining the separation, there is at this moment still not enough data to document the complete transition between the two forms at a single locality. The figures on plate 2 (figs. 4, 5, 8, 9, and 10), all from the upper Albian of France, suggest that there is such a transition and the taxa represent morphotypes of the same biologic species.

Wiedmann (1962*a*, p. 176) has suggested that several specimens should be included in this species, some questionably, that I have omitted from the synonymy: Pervinquière (1907, pl. 3, fig. 24) figures a juvenile specimen that has no constrictions. The dimensions of this specimen are quite different from those of *T. jurinianus*, being more similar to *T. spathi* in this and in whorl shape though lacking the constrictions. *T. brazoensis* Böse (1927, p. 203, pl. 1, figs. 2–4) has one well defined constriction near the beginning of the last volution preserved and is not, therefore, referable to *T. jurinianus*. Wiedmann has already pointed out the impossibility of using juveniles like the holotype of *T. brazoensis* as reference specimens. *T. zacatecanus* Böse is represented by two crushed juvenile specimens (1923, pl. 9, figs. 11–17). Plaster casts of these specimens graciously prepared for me by Sr. G. P. Salas show no features that would permit even generic identification.

Passendorfer (1930, p. 625) has reported this species from the Tatras in Poland, but he gives no figures and the description is insufficient to characterize the specimen.

Tetragonites nautiloides (Pictet), 1848, emended Breistroffer, 1940

(Pl. 2, figs. 5–10)

1848 *Ammonites Timotheanus* var. *nautiloide* Pictet, Grès verts I, p. 296, pl. 3, fig. 2.
1923 *Tetragonites timotheanus* (Mayor MS), Spath, Amm. Gault, pl. 1, fig. 5, p. 26.
1940 *Tetragonites nautiloidus* (Pictet), Breistroffer, Vraconien de Salazac, p. 111.
1962 *Tetragonites nautiloides* (Pictet), Wiedmann, Vascogot. Kreide, p. 174, MHNG Wi VK/6;

pl. 14, fig. 1; not p. 175, MHNG Wi VK/7; IGD Ce 027, pl. 8, fig. 7 (= *T. rectangularis* Wiedmann).

1962 *Tetragonites nautiloides* (Pictet), Wiedmann, Unterkreide Amm. Mallorca; not. pl. 5, fig. 4 (= *Tetragonites rectangularis* Wiedmann).

Description

Size.—The size of most specimens assigned to this species is small, averaging about 25 mm in diameter. The maximum size recorded is the holotype at 45 mm diameter, but a specimen in the Schlumberger Collection at the Sorbonne which is probably referable to *T. nautiloides* is completely septate at 57 mm diameter. This indicates adults attained at least 110 mm in diameter.

Measurements.—The measurements show that the umbilical diameter ranges from 24 to 32 percent of the shell diameter, but shows no tendency toward progressive change related to increasing size. The umbilical diameter and the width of whorl are slightly more variable than the height.

TABLE 4

Measurements of Tetragonites nautiloides (Pictet)

Specimen	D	H	W	U
Neotype MHNG*	30	13 (43)	19 (64)	8.0 (27)
FG Coll. Rosans: le Buisson	24.6	10.4 (42)	14.2 (58)	7.5 (30)
	19.1	7.8 (41)	10.9 (57)	5.9 (31)
FG Coll. Entrèves-en-Bauges	33.0	15.2 (46)	....	....
5 specimens	25.4	11.0 (43)	14.5 (57)	6.9 (27)
	23.8	10.9 (46)	14.0 (59)	5.7 (24)
	23.1	9.5 (41)	12.9 (56)	6.5 (28)
	11.7	5.1 (44)	6.7 (57)	....
FG Coll. Salazac	24.5	10.6 (43)	15.0 (61)	6.9 (28)
7 specimens	24.2	10.4 (43)	15.6 (64)	6.9 (28)
	22.0	9.1 (41)	12.9 (59)	6.7 (30)
	21.5	8.9 (41)	12.8 (60)	6.7 (31)
	20.5	8.7 (42)	12.2 (60)	5.9 (29)
	20.0	8.0 (40)	11.8 (59)	6.3 (32)
	17.4	7.9 (45)	10.1 (58)	4.6 (26)
FG Coll. Noyers-sur-Jabron	24.9	11.0 (44)	14.7 (59)	7.2 (29)
2 specimens	18.1	7.6 (42)	10.5 (58)	5.5 (30)
MHNG Pictet Coll. Mt. Saxonet	37.0	16.7 (45)	23.6± (64)	9.7 (26)
FL Pêrte du Rhône	34.8	15.8 (45)	21.4 (59)	8.0 (23)
S Schlumberger Coll. Clars (Var)	47.7	21.3 (45)	27.6 (58)	12.8 (27)
SM Cambridge greensand†	24	11.5 (48)	14 (58)	10.5 (23)?

* After Wiedmann, 1962*a*, p. 175.
† After Spath, 1922, p. 6.

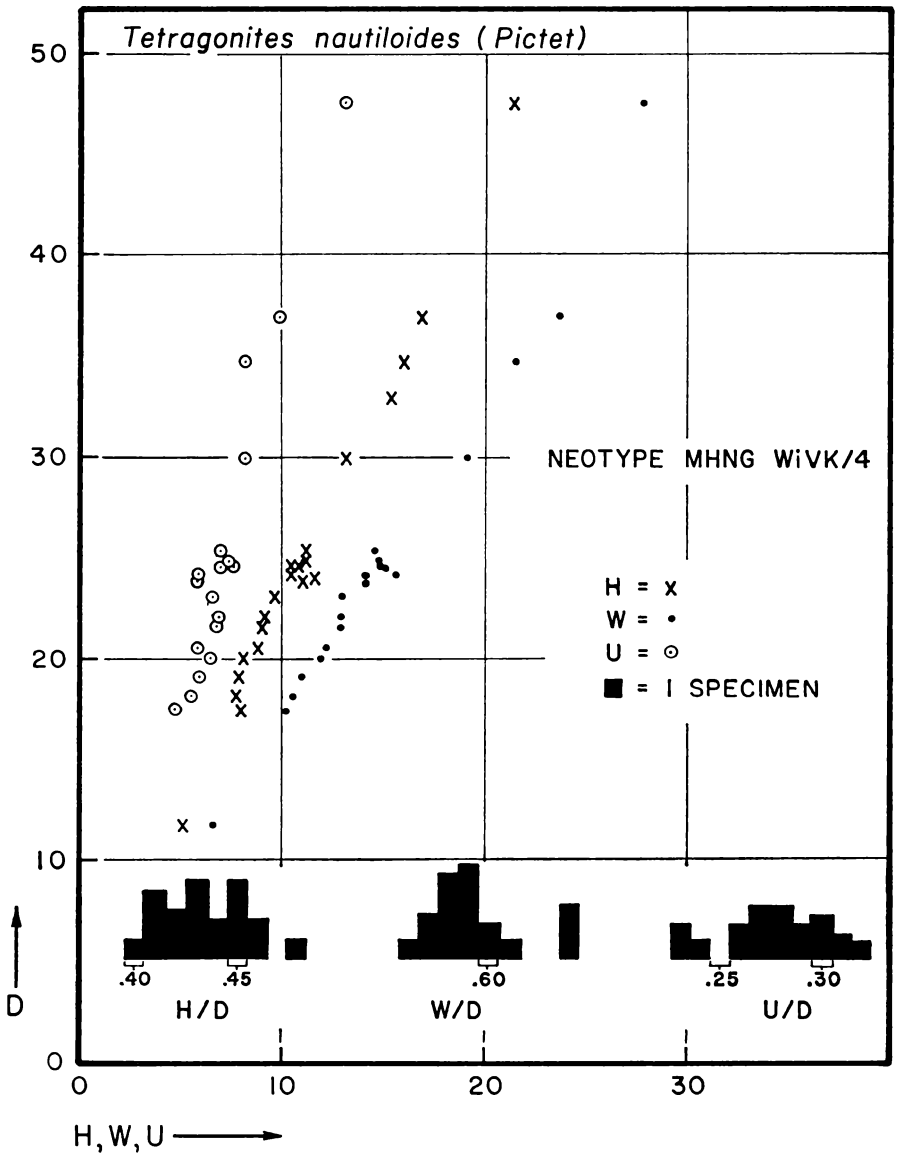


Fig. 12.

Cross section.—All specimens assigned to this species have a trapezoidal shape in cross section. The flanks and the venter are distinctly flattened and the umbilical wall is set off from the flank by an abrupt, often angular umbilical edge. The peripheral shoulder is distinct.

Constrictions.—According to Pictet (1847, p. 40) no constrictions were present on the holotype and no constrictions are present on the neotype (pl. 2, figs. 5 and 6). The neotype, however, does possess very weak, closely spaced riblike plications (growth rugae), which are especially apparent on the early part of the last pre-

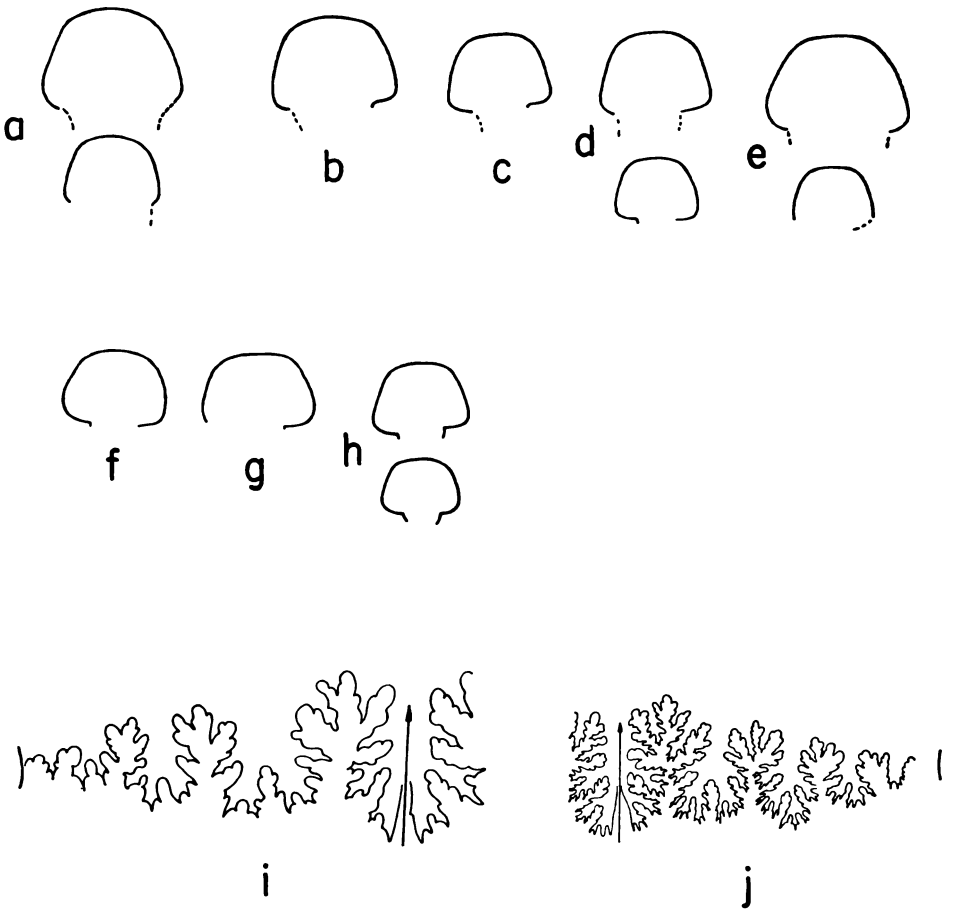


Fig. 13. Cross sections and sutures of *Tetragonites nautiloides* (Pictet). *a.* Neotype MHNG Wi VK/4, from Mt. Saxonet. *b* and *c.* FG Collection unnumbered, from Entrèves-en-Bauges. *d.* FG Collection, from Arnayon, collected by Sayn. *e.* Hypotype MHNG Wi VK/6, from Mt. Saxonet. *f* and *g.* FG Collection unnumbered, from Salazac. *h.* FG Collection unnumbered, from Rosans: le Buisson, identified by Breistroffer as *T. timotheanus* var. *i.* After Wiedmann, 1962*b*, p. 77, fig. 27, from Son Vida, Mallorca. *j.* After Wiedmann, 1962*a*, p. 175, fig. 34, neotype MHNG Wi VK/4.

served volution. These may be seen on a few other specimens, but apparently have no taxonomic significance. None of the five specimens from Entrèves in the collection at the Faculté des Sciences in Grenoble has constrictions. These shells may be observed from 3 mm to 35 mm in diameter. Twenty-two specimens from Salazac and two from Noyers-sur-Jabron show no constrictions. Those from Salazac may be observed from 3 mm to 25 mm in diameter. No constrictions are found on the specimen figured by Wiedmann from Mt. Saxonet (MHNG Wi VK/6). Other specimens assigned to the species by Wiedmann (1962*a*, 1962*b*) are discussed below under remarks.

Suture.—The lobes and saddles of the septum are variably extended. The L has a length/width ratio ranging from 2.5:1 to 4:1. The suture is not retracted, the L and 2L being longer than the suspensive lobe. The internal suture has two prominent saddles. An incipient saddle may be present, but this has not been observed.

Comparison

This species is easily distinguished from *T. timotheanus* (Pictet) by its narrow umbilicus and its cross section. It differs from *T. jurinianus* only in having more distinctly flattened flanks and venter that are sharply delimited from one another.

Remarks

The differences between *T. nautiloides* and *T. jurinianus* are minimal, as discussed above (see remarks under *T. jurinianus*), and the distinction between this species and *T. rectangularis* Wiedmann is no more easily resolved. In his redescription of *T. nautiloides* Wiedmann (1962*a*, p. 174) followed the pattern set by Breistroffer (1940, p. 111) in all but one respect. Where Breistroffer defined *T. nautiloides* as a species without constrictions, Wiedmann includes within this species forms that have constrictions early in the ontogeny, but are smooth in subsequent stages. He assigned three specimens to *T. nautiloides* on this basis. Two of these were figured (1962*a*, pl. 8, fig. 11; 1962*b*, pl. 5, fig. 4), but the third specimen was only mentioned in the text (1962*a*, p. 175, Wi VK/7). The latter is so similar to a series of forms from Son Vida, Mallorca (P. Fallot Collection, FG), that it cannot be maintained in a separate category. Constrictions are present on the specimen to at least 26 mm diameter and probably it would show them at a larger diameter if more of the shell were preserved. A specimen in the series from Son Vida shows constrictions at 36 mm diameter. Thus it seems certain that constrictions are not limited to the early whorls in *T. nautiloides* if the species includes specimens with constrictions such as Wiedmann's hypotype. This leaves the choice of suppressing *T. rectangularis* or transferring the three specimens with constrictions to *T. rectangularis* with which they agree in other characteristics including the shape of the cross section. Thus in maintaining Breistroffer's position that *T. nautiloides* has no constrictions, *T. rectangularis* is a necessary taxonomic category. I prefer Breistroffer's interpretation.

Jacob (1908, p. 19) doubtless believed the holotype of *T. timotheanus* to be the specimen recently designated by Wiedmann as the lectotype of *T. nautiloides*. When his remarks concerning the relation of this specimen with *T. jurinianus* are viewed in this perspective, they are perfectly accurate.

Spath (1923, p. 25) following Jacob identified specimens in the Sedgwick Museum at Cambridge and in the British Museum (Natural History) as *T. timotheanus* and noted (p. 26) that the Cambridge Greensand examples "are perhaps closer to the var. *nautiloide*." I examined the two specimens at the Sedgwick Museum (nos. B1472 and B1473) and agree with Spath that they should be assigned to *T. nautiloides*.

Distribution

Most strata yielding specimens of *T. nautiloides* are phosphatic greensands which have been dated by French and Swiss stratigraphers, primarily Breistroffer, as upper Albian. Apart from these it is probable that the specimens from the black marls near Rosans and near Noyers-sur-Jabron are upper Albian. The Cambridge Greensand examples are questionably referred to the *dispar* zone by Spath (1923, p. 27), again a condensed deposit of upper Albian age.

Tetragonites heterosulcatus Anthula, 1899

1899 *Tetragonites heterosulcatus* Anthula, Kreide fossilien des Kaukasus, pp. 99–100, pl. 7 (6), fig. 4; not pl. 7 (6), fig. 5.

†1907 *Tetragonites heterosulcatus* Anthula, Pervinquière, Pal. Tunisienne, p. 73.

1956 *Tetragonites heterosulcatus* Anthula, Drushchits, p. 102, fig. 44.

1960 *Tetragonites heterosulcatus* Anthula, Drushchits, p. 260, fig. 68.

Description and Relationship

Description and relationship translated from Anthula (1899, pp. 99–100):

Measurements.—Diameter = 24; height = 9(37); width = 13(54); umbilicus = 8(33).

At first sight I was inclined to call this form a variety of *Lytoceras duvalianum.* Later, however, more precise research has produced very distinctive characteristics that cannot permit the identification of this form. The exterior form corresponds almost completely to that of *Lytoceras duvalianum,* likewise it is very similar to the forms *Lytoceras timotheanum* Mayor and *Lytoceras epigonum* Kossmat. However, the whorls of *Lytoceras heterosulcatum* grow faster than those of *Lytoceras duvalianum,* but slower than those of *Lytoceras timotheanum* and *Lytoceras epigonum.* The involution covers almost two-thirds of the whorl height, and the umbilicus is considerably depressed. The whorls have a trapezoidal cross section, with flattened flanks, broad venter, and a rather high, vertically descending umbilical wall.

The sculpture of the shell consists of fine growth striation, which run obliquely forward from the umbilical seam like those in *Lytoceras duvalianum.* The swollen ribs, respectively, the constrictions are of the same nature as in *Lytoceras duvalianum.* However, the constrictions in *Lytoceras heterosulcatus* are sinused backward on the inner part of the whorl initially; not until later are they gradually bent forward, so that the outer whorl shows strongly anteriorly inclined constrictions. The number of constrictions in the last volution is eight.

The suture is distinguished by the obliquely inclined secondary lobes dividing the asymmetrical saddles as is characteristic of *Lytoceras timotheanum,* the type of the group. The external and lateral lobes are symmetrically subdivided. In the Caucasian species, as with *Lytoceras duvalianum,* the internal suture always has prominent internal lobes on both sides of the antisiphonal lobe, while *Lytoceras timotheanus* possesses several of them (up to 4).

Locality: Aptian geodes of the Akuscha Thales (Daghestan)—a small well-preserved example and two larger fragmentary individuals. *Lytoceras heterosulcatum* is distinguished very distinctly from *Lytoceras duvalianum* by the greater involution, the vertically descending umbilical wall, the deeply depressed umbilicus, and the smaller number of constrictions. *Lytoceras timotheanum* from the Gault of southern France and the lower Utatur Group of southern India, which significantly approaches *Lytoceras heterosulcatum* in its external form and trapezoidal cross section, is distinguished by the more rapid growth of whorl, fewer constrictions, and a somewhat larger number of internal lobes. [Anthula is doubtless referring here to Kossmat's figure (pl. xvii, fig. 11) which shows three, and an incipient fourth, internal saddle. Wiedmann has assigned Kossmat's specimens to a new taxon, *T. subtimotheanus.*] The relationships to *Lytoceras epigonum* from the upper Trichinopoly Group of southern India are still more distant. The Indian species posses much higher whorls and finer constrictions which are absent completely in the young examples.

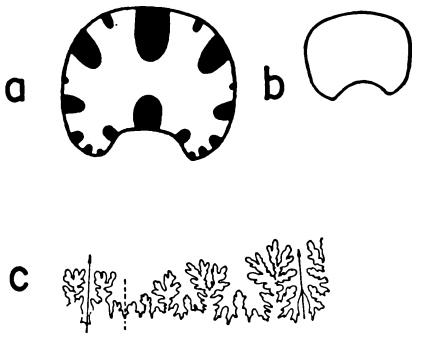


Fig. 14. Cross sections and suture line reproduced from Drushchits, 1956, p. 102.

Comparison and Remarks

I have not been able to examine any examples of this species, but from the information given by Anthula and Drushchits the species is easily separated from previously described ones by its early trapezoidal whorl cross section, which is broadest at the peripheral shoulder. In its suture it most closely resembles the similar later *T. kitchini* (Krenkel) with one strong and one weak internal saddle. In this latter respect and in cross section it is also similar to the slightly younger (?) Californian species *Eotetragonites gardneri* n. sp. When Anthula's drawing of the suture (pl. 7, fig. 5b) is compared with Drushchits,' it is seen that it is inaccurate, lacking several elements.

Distribution

The species is known only from the Caucasus where it occurs in the *Parahoplites melchioris* zone of the upper Aptian.

Tetragonites kitchini (Krenkel), 1910

(Pl. 2, figs. 11–14)

†1906 *Lytoceras* (*Tetragonites*) *timotheanus* Mayor sp., Boule, Lemoine, and Thevenin, Cephalopodes crétacés Diégo Suarez, p. 186, pl. 2, fig. 3.

1910 *Desmoceras* (*Puzosia; Latidorsella* Jacob?) *kitchini* Krenkel, Untere Kreide Deutsch Ostafrika, p. 226, pl. 22, fig. 8.

1962 *Tetragonites kitchini* (Krenkel), Wiedmann, Vascogot. Kreide, p. 171.

Introductory Remarks

Krenkel's holotype is at present not available for comparison and may have been lost during World War II. His description, however, leaves no doubt that the shell belongs to the genus *Tetragonites*. Assuming Krenkel's (1910, p. 226) description of the whorl section is accurate, the flattened parallel flanks and flattened venter may be used to separate this specimen as the type of a taxon different from those previously described. Wiedmann (1962*a*, p. 177) has assigned the specimen from Manohonda, Madagascar (MHNG), to Krenkel's species. If his interpretation is correct, and I believe it is, this specimen and several others from Madagascar in the collection of General Maurice Collignon (Collig. localities 70, 87, 435) may be used to describe this species.

Description

Size.—The largest specimen of forms assigned here is what appears to be a nearly complete living chamber, which has a maximum diameter of 46.5 mm (MCC locality 87, Madagascar). A slightly smaller specimen from Manohonda, Madagascar (MHNG no number), is still septate at 37 mm in diameter. The mature individual, therefore, probably attained a minimum shell diameter of 50 to 60 mm.

Measurements.—From the very small sample available it appears that the umbilical diameter maintains a relatively constant ratio to the shell diameter and is much less variable than the measurements of height or width.

TABLE 5
Measurements of Tetragonites kitchini Krenkel

Specimen	D	H	W	U
MHNG—Manohonda, Madagascar	37.0	15.4 (42)	18.2 (49)	11.7 (32)
	29.8	12.0 (40)	14.7 (49)	9.7 (33)
Location 87—Collignon Coll. Maniamba-Amba	45.5	19.8 (44)	21.5 (47)	15.0± (33)
Location 70—Collignon Coll. Mokaraha	18.8	7.6 (41)	9.0 (48)	6.0 (32)
Location 435—Collignon Coll. 2 specimens Vohimaranitra	27.0	10.9 (42)	14.2 (53)	8.6 (32)
	25.1	9.9 (39)	13.1 (52)	8.3 (33)
	20.8	8.3 (40)	10.6 (52)	6.9 (33)
	26.9	10.9 (41)	14.0± (52)	8.3 (31)
	21.2	8.3 (39)	11.0± (52)	6.5± (31)

Constrictions.—Constrictions number 5, 6, and possibly 7 per whorl. The variation in number does not seem to be related to increase in size because the small specimens from Vohimaranitra both have 6 per whorl at 27 mm diameter; the Manohonda and Maniamba-Amba specimens at progressively larger diameters have 5 and probably 7 (the specimen shows 5 constrictions on the two-thirds of the whorl preserved and is inferred to have had at least 7 in a complete volution).

The constrictions are of the prorsiradiate concave type, being slightly arched forward on the flank, recurving on the upper flank and showing a moderately developed, rounded adorally concave arch on the venter.

Suture.—The external suture has the standard number and position of elements for the genus. The umbilical lobe is less extended than the lateral lobes and the lateral lobe has a length/width ratio of about 3:1 at approximately 20 mm in diameter (fig. 16).

The internal suture was not observed, but the septa of most of the specimens are beautifully preserved. They show one strong and one weak internal lateral saddle, a strongly developed antisiphonal lobe, and lateral lobes that form septal sutures on the preceding septa.

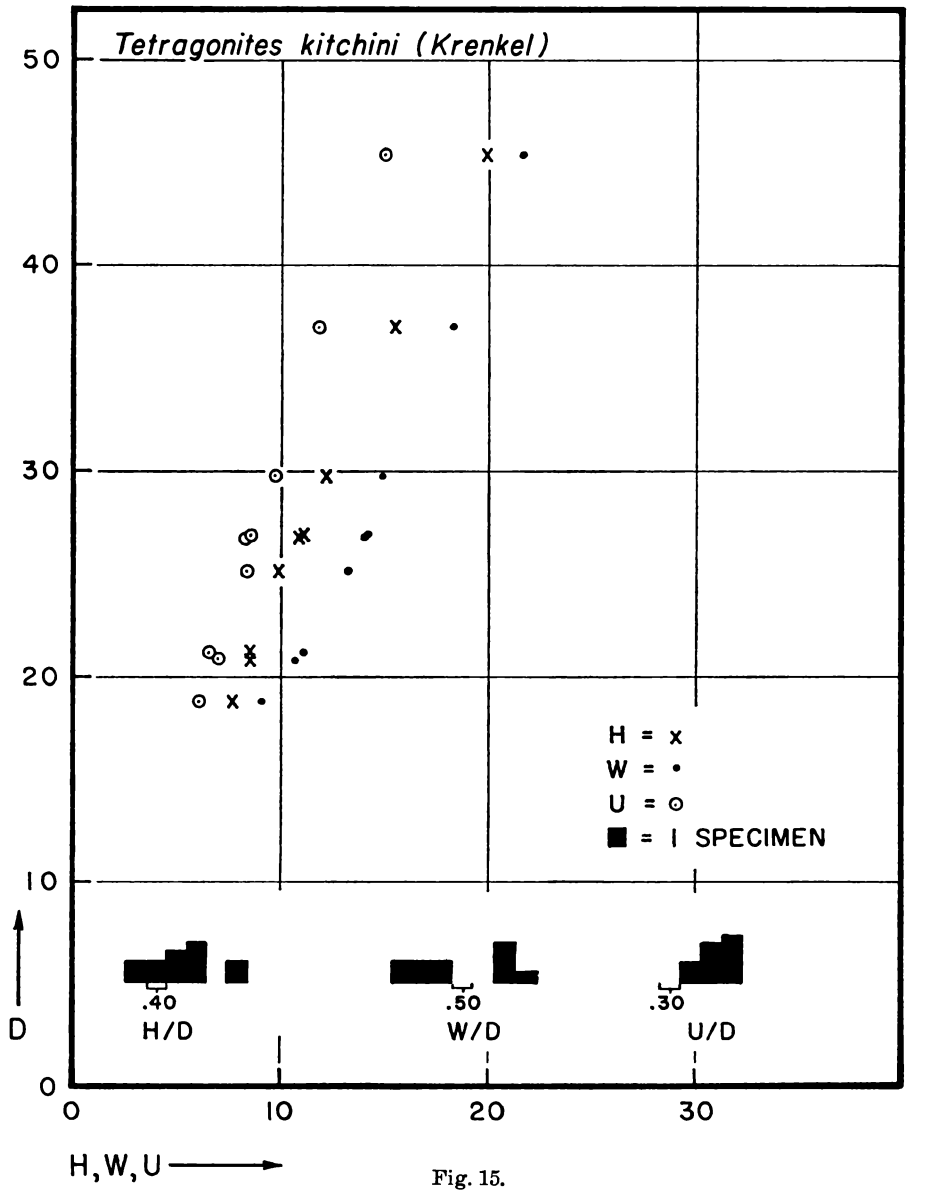


Fig. 15.

Cross section.—The cross section is nearly square with virtually parallel flanks and almost vertical umbilical wall. The venter is about as equally convex as the flanks and joins imperceptibly across a rounded peripheral shoulder. The umbilical edge is abrupt but rounded on the internal mold. It may have been almost angular on the unworn outer shell. Slight variation exists (fig. 16) among the specimens with respect to the relative inflation of the flanks and venter and of the slope of the umbilical wall.

The involution ranges from 33 to 50 percent and apparently is quite variable.

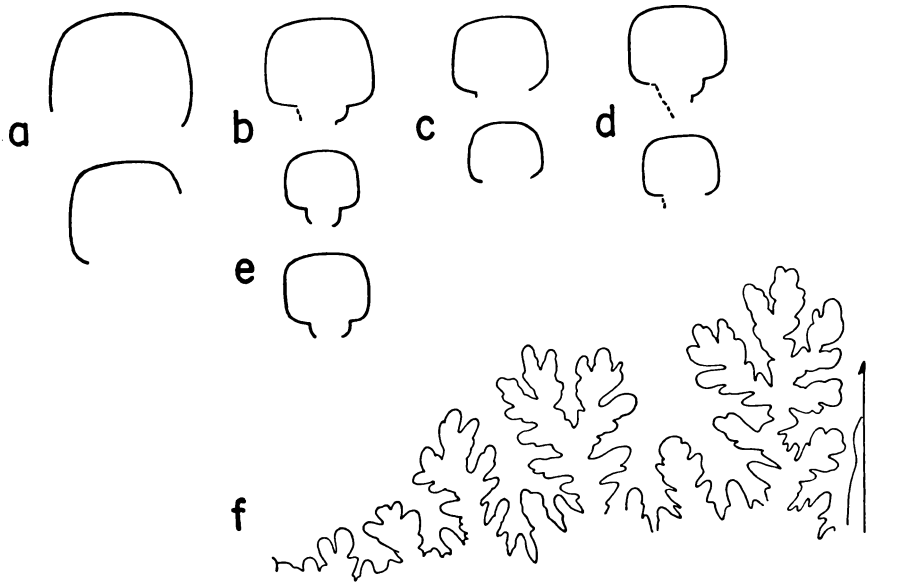


Fig. 16. Cross sections and suture of *T. kitchini* (Krenkel). *a.* MCC 87, Maniamba-Amba, Madagascar. *b* and *e.* MHNG unnumbered specimen preserved in chalcedony, Manohonda, Madagascar. *c* and *f.* MCC 435, Betioky, Madagascar.

Distribution

At present this taxon seems to be restricted to the Southern Hemisphere, African region. It is dated as upper Albian by the specimens from Collignon localities 70, 87, and 435, the other specimens having no accurate stratigraphic data recorded with them.

Comparison

T. kitchini Krenkel, based on the five specimens from Madagascar, differs from *T. timotheanus* in whorl section; it has a smaller umbilicus (31–33 percent compared to 37–42 percent in *timotheanus*), and it retains constrictions throughout growth.

From *T. jurinianus* it differs in whorl section; it has a larger umbilicus (31–33 percent vs. 23–27 percent in *jurinianus*) and has constrictions.

From *T. nautiloides* it differs in whorl section; the whorl width is much narrower at equivalent diameters, and has constrictions.

From *T. jacksonensis* it differs in whorl section; the whorl height is much less at equivalent diameters.

Remarks

The juvenile specimen of Boule and others (1906, p. 186, pl. 2, fig. 3) is tentatively assigned here, as its whorl shape and measurements agree with the Manohonda specimen, and it has 5 constrictions, but they are not so prorsiradiate concave as those in the specimens already mentioned.

I also assign to this species another small undescribed pyritic internal mold from the upper Albian of Mt. Raynaud, Madagascar (MCC locality 70). This specimen agrees in cross section, measurements, and degree of involution with the other specimens assigned here. It has 6 well-marked constrictions on the last volution.

Tetragonites crudus Drushchits, 1956

1956 *Tetragonites crudus* Drushchits, Lower Cret. Amm. Crimea and No. Caucasus, p. 105, pl. 8, fig. 29.

Description (after Drushchits)

The cross section of the spire is trapezoidal with a rounded umbilical edge and sloping umbilical wall. Prorsiradiate concave constrictions are feebly marked on the flanks and have an adorally concave arch on the venter, though they are hardly visible. Nine constrictions were counted on the outer volution.

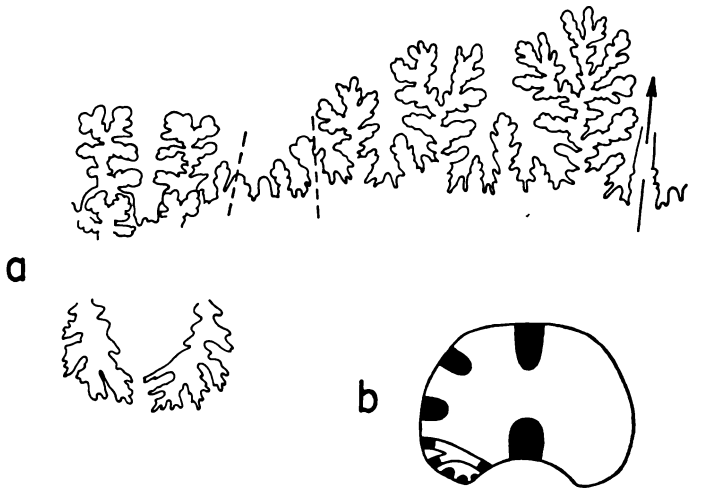


Fig. 17. Suture and cross section of *T. crudus* reproduced from V. V. Drushchits, 1956, p. 106.

The external suture shows the usual number and position of elements. 1S is irregularly bifid. The internal suture shows one prominent saddle and one incipient saddle. The internal lobe shows a strong development of the septal lobe.

The measurements given by Drushchits indicate a moderate-sized umbilicus, .32–.35 of the diameter.

Distribution

Known only from the lower Albian strata of Daghestan in the northern Caucasus.

Remarks

Though I have not examined any members of this taxon, I am confident from Drushchits' description that it is different from the other lower Albian taxa in having only a single well-developed internal saddle and one smaller saddle. According to Drushchits, the constrictions are very weak but numerous and have the adorally concave arch on the venter characteristic of most members of the genus, though these do not show on his plates.

T. crudus seems to be a close relative of the sympatric *T. heterosulcatus* and also of *T. kitchini*. It differs from these species in cross section and in the relative prominence of the constrictions. It is placed in the *T. kitchini* branch of the genus

because it has the general constriction pattern, internal suture, and relatively broad umbilicus shown by *T. kitchini*. Members of the other branches of the genus all show a strongly developed second internal saddle in the lower Albian, thus it seems this species forms part of the plexus leading to the upper Albian *T. kitchini*.

Tetragonites rectangularis Wiedmann, 1962

(Pl. 4, figs. 1–7; pl. 5, fig. 1)

1962 *Tetragonites rectangularis* Wiedmann, Vascogot. Kreide, p. 178, pl. 14, fig. 3; text fig. 39; not p. 178, MHNG Wi VK/11, MHNG Wi VK/12.
Tetragonites nautiloides (Pictet), Wiedmann, Vascogot. Kreide, p. 175, MHNG Wi VK/7.
Tetragonites rectangularis Wiedmann, Wiedmann, Unterkreide Ammon. von Mallorca, p. 78, pl. 6, figs. 1, 2, 7, 8; ? pl. 5, fig. 4.
?1963 *Tetragonites rectangularis* Wiedmann, Collignon, Albien Atlas Madagascar, pl. 249, fig. 1069; not fig. 1070.

Description

Size.—The holotype with part of the living chamber preserved, but somewhat deformed, measures about 50 mm in diameter. A still larger example from Escragnolles (Villoutreys Collection #546) measures 63 mm with partial body chamber. Other specimens range up to 40 mm in diameter. The species, therefore, was probably of moderate size with adults attaining shell diameters between 60 and 100 mm.

Measurements.—Measurements are possible on the holotype only at smaller diameters because of the deformation of the living chamber, but even at smaller diameters the shell is deformed and this may be why the measurements of whorl width deviate from the average of other specimens assigned to the species.

The umbilical diameter ranges from 25 to 32 percent of the shell diameter; the width of whorl ranges from 55 to 62 percent, or 63 percent if the holotype is included; the height of whorl ranges from 40 to 47 percent. The height of whorl, as usual, maintains a more constant relation to the diameter than the other measurements.

Suture.—The lobes and saddles of the septum are moderately extended and show the standard development for the genus in position and number. The septum is not exposed in the holotype, but other specimens assigned to the species uniformly show a moderately strong development of the second lateral internal saddle and a suspensive lobe less extended than the first lateral lobe (not retracted).

Cross section.—The cross section of the holotype is slightly trapezoidal with flattened flanks and venter, which join at a rounded peripheral shoulder. The umbilical edge is sharp, the umbilical wall is high, slightly convex, and nearly vertical. The broad, slightly trapezoidal section is typical of most of the larger shells, but smaller ones tend to have a rectangular section with the flanks almost parallel. Thus considerable variation exists which is partly the result of difference in ontogenetic stage.

Constrictions.—The last volution of the holotype shows 4 constrictions. Two of these are in the last one-quarter volution and 2 are in the first one-quarter volution. In the next-to-last volution the constrictions are evenly spaced and seven

TABLE 6

MEASUREMENTS OF TETRAGONITES RECTANGULARIS WIEDMANN

Specimen	D	H	W	U
FG—Fallot Coll. Son Vida SV 3	38.0	16.9 (45)	22.8 (60)	9.9 (26)
	29.9	13.3 (45)	17.9 (60)	7.8 (26)
FG—Fallot Coll. Son Vida SV 4	31.7	13.9 (44)	18.3 (58)	8.3 (26)
FG—Fallot Coll. Son Vida SV 5	31.0	14.0 (45)	19.3 (62)	8.3 (27)
FG—Fallot Coll. Son Vida SV 9	26.2	11.2 (43)	15.5 (59)	7.5 (29)
Unnumbered specimen FG	22.5	9.9 (44)	12.4 (55)	5.8 (26)
Unnumbered specimen FG	22.4	9.8 (44)	12.7 (57)	6.4 (29)
Unnumbered specimen FG	20.2	8.7 (43)	12.2 (60)	5.7 (28)
Unnumbered specimen FG	17.5	7.3 (42)	9.7 (55)	5.0 (29)
FG—Notre Dame d'Ongles	16.3	7.1 (44)	9.3 (57)	4.9 (30)
FG—St. André de Rosans	27.5	11.1 (40)	15.1 (55)	8.7 (32)
FG—Salazac	27.6	11.6 (42)	15.0±(54)	8.7 (32)
?FG—Arnayon	25.3	11.8 (47)	16.8 (66)	6.0±(24)
FG—Prés de Rencurel	20.2	8.2 (41)	11.6 (57)	6.5 (32)
UCR—Prés de Rencurel	26.0	10.5 (40)	14.5 (56)	8.4 (32)
MHNG—Grand Bornand 346/86	20.2	8.6 (43)	12.2 (60)	6.1 (30)
MHNG—Pêrte du Rhône 3 specimens	32.2	13.4 (42)	18.7 (58)	10.1 (31)
	26.5	11.3±(43)	16.1±(61)	7.7±(29)
	26.3	12.0 (46)	15.7 (60)	6.6 (25)
OV—Escragnolles 546	59.7	28.9±(48)	36.0 (60)	12.8 (21)
	35.7	16.0 (45)	22.1 (62)	9.1 (25)
OV—Clars 606*a*	31.4	14.2 (45)	19.0 (61)	7.9 (25)
OV—Clars 606*b*	24.6	10.8 (44)	14.4 (59)	7.1 (29)
BMNH Escragnolles—73697*b*	31.6	14.1 (45)	19.0 (60)	8.2 (26)
BMNH Escragnolles—73697*c*	18.0	7.8 (43)	11.4 (63)	4.9 (27)

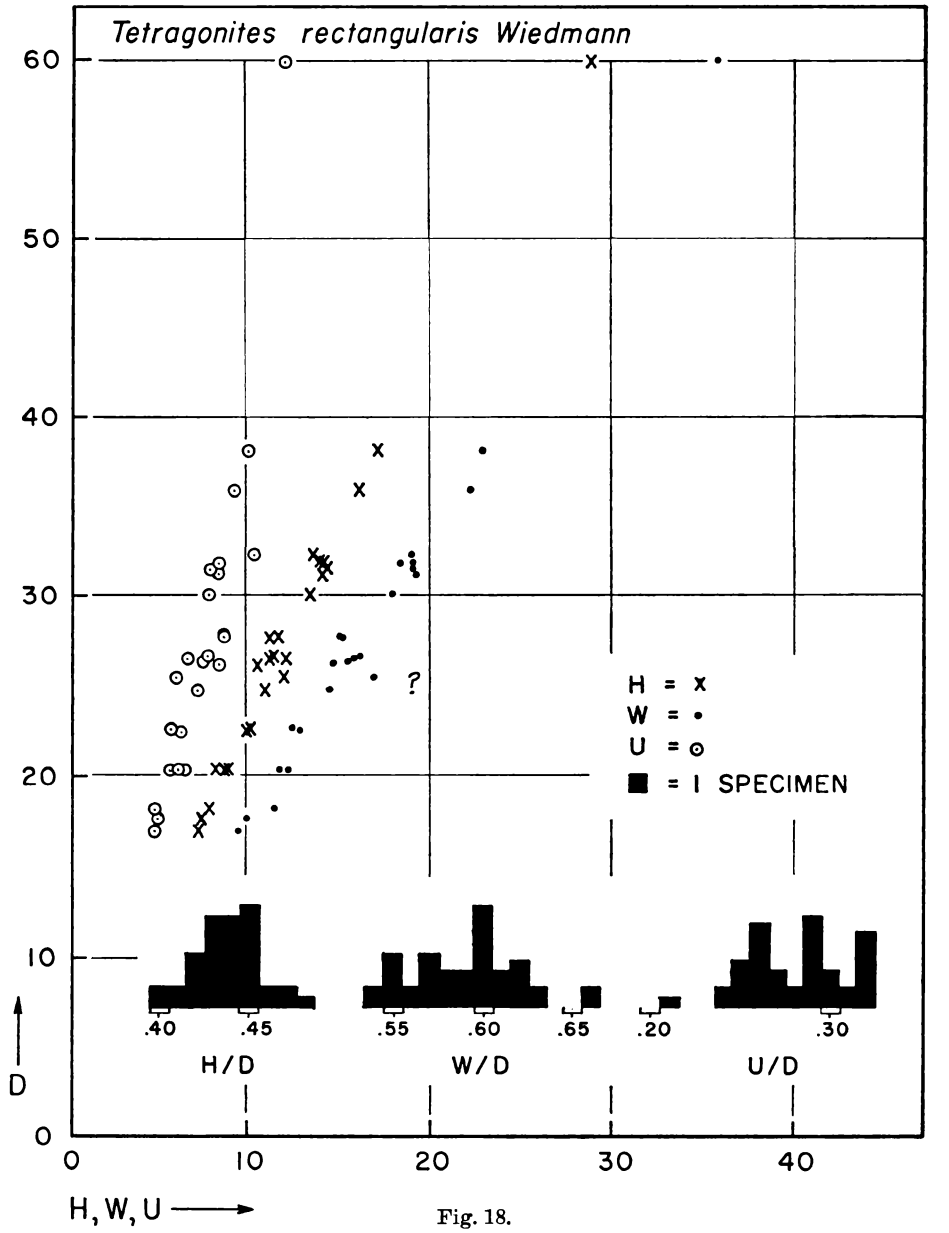


Fig. 18.

in number. The parts of the earlier whorls preserved and observable also show constrictions. Other large specimens (e.g., OV 546) show similar irregularity of development of the constrictions.

Constrictions number 4 to 7 in specimens assigned to the species in the earlier whorls. They arch concavely forward on the flank and have a strongly adorally concave sulcus on the venter. They may be irregularly developed with respect to both spacing and distinctness.

COMPARISON

T. rectangularis differs from the members of the *T. timotheanus* group in having a much smaller umbilicus and greater height of cross section at equivalent diameters, in having generally more extended lobes and saddles in the suture, and in having prorsiradiate concave constrictions on the flank and marked adorally concave constrictions on the venter; it differs from *T. heterosulcatus, T. crudus,* and *T. kitchini* in having more prominent internal saddles and three instead of two of them. It has more internal saddles and a different configuration of the constrictions than *E. balmensis;* it differs from the Late Cretaceous species *T. beantaly-*

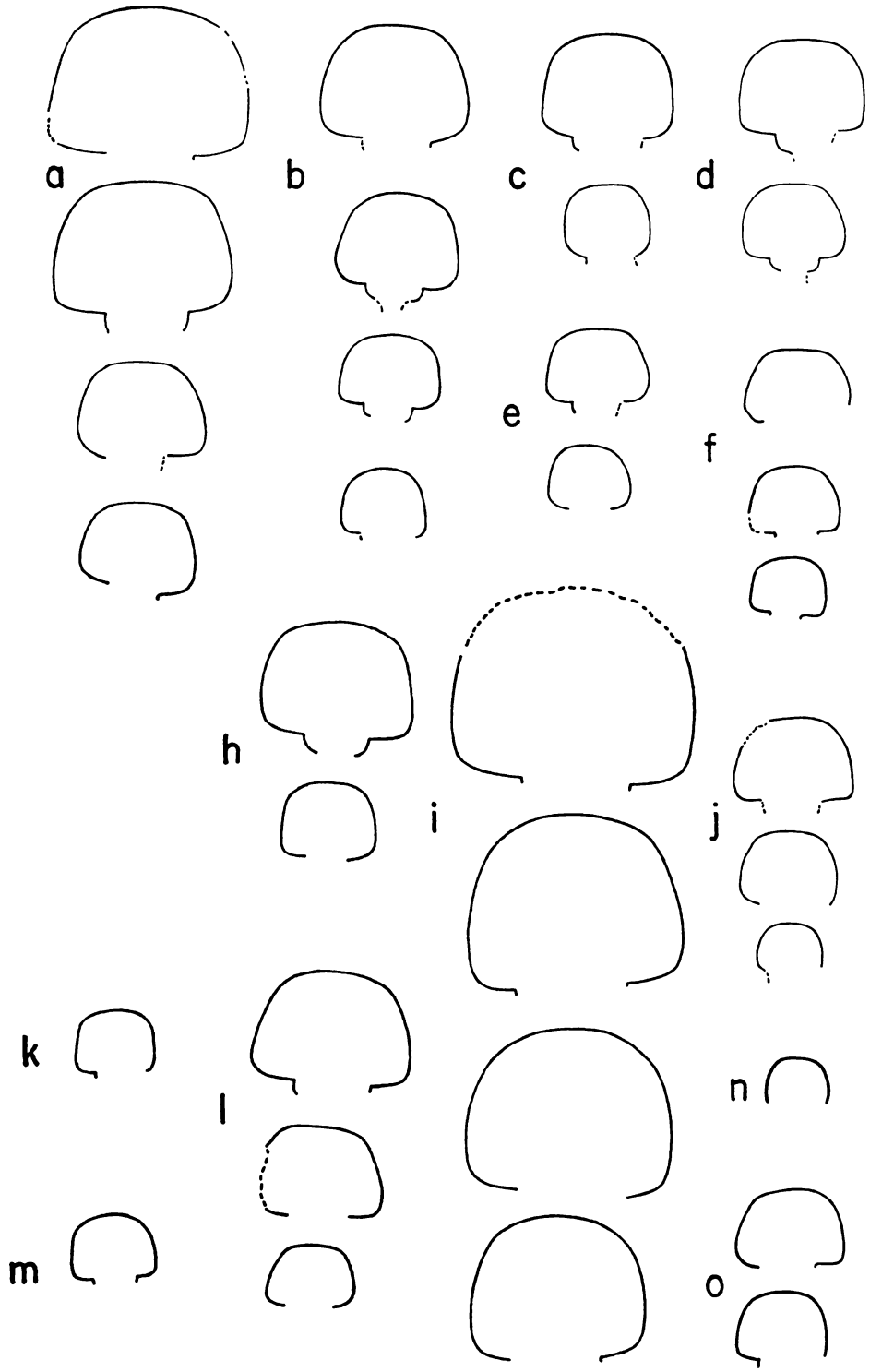


Fig. 19. Sutures of *T. rectangularis. a.* GPIT Ce 1220/23 after Wiedmann, 1962*b*, p. 79, fig. 28, from Son Vida, Mallorca. *b.* FD Ce 027 after Wiedmann, 1962*a*, p. 175, fig. 35, from Echeverri, Spain.

ensis, T. embergeri, T. popetensis, T. epigonus, T. jacksonensis, T. mitraikyensis, T. simplex, T. superestes, T. garudus, and *T. glabrus* in having a flattened rather than a rounded venter; it has a trapezoidal cross section whereas *T. margaritatus* has an oval cross section; *T. rectangularis* has constrictions whereas *T. jurinianus, T. nautiloides,* and *T. latus* have none; if Kossmat's drawing of the internal suture of *T. subtimotheanus* is correct (1895, pl. 3, fig. 11), *T. rectangularis* has fewer internal saddles than *T. subtimotheanus.*

T. collignoni Breistroffer from the Cenomanian of Madagascar is very close to this species and is doubtless a direct descendant of it. The internal suture in *T. collignoni* is not shown in the holotype, but there exist a large number of juvenile shells preserved as pyritic internal molds (Collignon, 1964, p. 5, figs. 1356, 1357) in the Cenomanian of Madagascar which may be identified with *T. collignoni.* These small shells show a third small saddle in the internal suture as in *T. rectangularis.* The only difference remaining is that, according to Wiedmann's diagnosis, the small shells of *T. rectangularis* have a quadrate cross section and the ones from Madagascar have a distinctly trapezoidal cross section. Also the constrictions in *T. collignoni* are more regularly developed than in *T. rectangularis.*

The specimen referred to by Spath (1923, p. 27; BMNH 73697a) from Clars (Var) exhibiting a peripheral groove on the internal mold above the siphonal line is assigned to *T. rectangularis.* The only difference in this specimen and others from


a
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the same locality is the peripheral groove. At present I regard the groove as a morphologic character without taxonomic importance, as it is present in several other species apparently as an aberration.

Distribution

The species is apparently confined to Switzerland, southeastern France, Mallorca, and probably England. Wiedmann (1962*a*, p. 179) also lists Japan and North America. No North American forms known to me may be identified with *T. rectangularis* ss., although I have classified one taxon, *T. rectangularis* subsp. *alaskaensis* n. subsp., as a subspecies. I have not examined any specimens from Japan.

The French examples are mostly from phosphatic greensands, which contain predominantly upper Albian faunas. Although these deposits may contain heterochronous faunas, the occurrence of this species at a number of these localities seems to verify the upper Albian association. The pyritic specimens from the Vocontien region (FG Collection) also are listed as upper Albian and further verify a late Albian age.

If Fallot's Mallorca material at the Faculté des Sciences, Grenoble, is from the horizon Wiedmann has dated as early Albian, the range also includes early Albian. The Prés de Rencurel examples in my collection all show evidence of rounding due to transportation after they were fossilized. Though this deposit contains predominantly lower Albian species, a few obviously transported fragments of much later age are found here as well. Thus the age of these specimens is not fixed and neither confirms nor denies a lower Albian occurrence.

Remarks

T. rectangularis, like *T. timotheanus,* is now endangered as there is a tendency to assign many similar isolated specimens to it. The type specimen is unfortunately somewhat deformed, but numerous other specimens from the greensands of Var and the pyritic specimens from Mallorca demonstrate the distinctive nature of this taxon.

Wiedmann has tentatively assigned here a number of other forms that, although not exactly the same, show strong affinities for *T. rectangularis*. One of these occurs at Balme de Rencurel and Frasette, Isère, France. These shells, assigned by Breistroffer to *T. kitchini,* are similar to the early growth stages of *T. rectangularis* ss., but have a cross-sectional shape that remains more or less quadrate instead of becoming trapezoidal with growth. The constrictions are much weaker and barely, if at all, perceptible on the outer flank and venter at 25 mm in diameter. For this group I propose the name *T. bournensis* n. sp., discussed below.

A second group of forms is that of the west coast of North America. These speci-

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Fig. 20. Cross sections of *T. rectangularis* Wiedmann. *a.* Holotype MHNG Wi VK/10, la Goudinière. *b–e.* FG Fallot Collection. Specimens SV3, SV4, SV5, and SV9, respectively, from Son Vida Mallorca. *f.* Paratype MHNG Wi VK/11, la Goudinière. *h.* OV 546/1, Escragnolles. *i.* OV 546/2, Escragnolles. *j.* and *o.* MHNG Wi VK/7, la Goudinière, identified by Wiedmann as a hypotype of *T. nautiloides* (1962*a*, p. 175). *k* and *m.* FG Collection unnumbered, Son Vida, Mallorca, identified by Breistroffer as *T. kitchini* (Krenkel), 2 specimens. *l.* OV 686/1, Gourdon. *n.* Paratype MHNG Wi VK/12, Mt. Saxonet.

mens probably represent several different taxa. They are much more variable in cross section, but only rarely showing the shape of *T. rectangularis*. Three of these taxa are described below as *T. lecontei, T. hulenensis,* and *T. jonesi.*

The Madagascar specimen (pl. 3, figs. 6 and 7) tentatively assigned to this species is similar to *T. rectangularis* in suture and constriction pattern, but differs in having a rounded cross section. It was originally assigned by Collignon to this taxon (1963, p. 21), but probably represents a quite different group of forms, perhaps related to *Tetragonites* sp., described below.

Passendorfer (1930, p. 624) describes a form from the Tatras of Poland which he characterizes as var. *nautiloide* and states that it has constrictions with a concave curvature on the flank and venter. It seems probable that his specimens would be identified with *T. rectangularis* if they were available.

Tetragonites rectangularis Wiedmann subsp. *diegoensis* (Collignon), 1963

(Pl. 4, fig. 8)

1963 *Tetragonites jallaberti* Pictet var. *diegoensis* Collignon, Albian Atlas Madagascar, p. 24, pl. CCL, fig. 1073.

Cross section.—The cross section of the whorl is rounded trapezoidal with distinctly flattened flanks at 66 mm diameter and tends to maintain this shape throughout the part of the shell accessible to observation. The umbilical wall is steep, almost vertical in the earlier part of the volution, but becomes more inclined with growth. The umbilical edge is acutely rounded at all stages.

Description

Size.—The only known specimen measures 62 mm in diameter. It is a completely septate internal mold indicating adult shells probably attained a much larger total diameter, a minimum size of 100 mm.

Measurements.—Holotype:

	D	H	W	U
Collignon Collection	66*	31.9(48)*	37.1(56)*	15.5(23)*
Albian Atlas #1073	61.6	29.4(48)	35.3(57)	14.6(24)

Constrictions.—The constrictions are numerous. Seven may be observed in the two-thirds volution preserved. They are strongly prorsiradiate concave on the flank and deeply arched adorally concave on the venter. They seem to be more prominent on the umbilical wall and lower flank, but the specimen is slightly weathered.

Suture.—The lobes and saddles are strongly extended and complexly frilled on the holotype at 40 mm diameter. The 1L has a length/width ratio of 6:1. The internal suture is not accessible, but the septal face shows at least two strong internal saddles are present.

Comparison

The strongly arched and numerous constrictions and narrow umbilicus ally this shell with *T. rectangularis* branch of the genus and differentiate it from *E. balmensis, T. timotheanus, T. subbeticus, T. lecontei, T. kitchini, T. heterosulcatus, T. latus, T. nautiloides, T. jurinianus, T. brazoensis, T. bournensis, T. simplex, T.*

* After Collignon, 1963.

spathi, T. embergi, T. beantalyensis, T. involutior, T. margaritatus, and *T. hulenensis* n. sp.

It is, however, closely similar to *T. rectangularis, T. collignoni,* and *T. subtimotheanus.* It has many more constrictions than is common for *T. rectangularis* and *T. collignoni* and a whorl height that is high or at the upper limit in these species, whereas the width is low or at the lower limit, respectively.

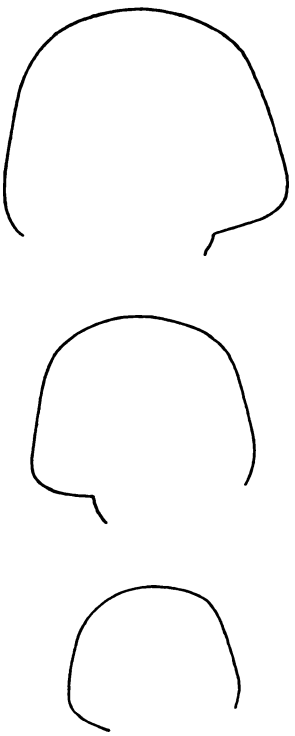


Fig. 21. Cross sections of holotype of *T. rectangularis* subsp. *diegoensis* Collignon, Atlas des Fossiles Caracteristiques de Madagascar, specimen number 1073, Albian, Mont Raynaud, Madagascar.

Remarks

This shell seems ideally classified as a subspecies as it is morphologically slightly different and contemporaneous with *T. rectangularis* ss. No other specimens of the true *T. rectangularis* are known from Madagascar. The specimens identified as *T. rectangularis* by Collignon (1963, p. 22) have a much rounder whorl than *T. rectangularis.*

Collignon (1963) identified this species with Pictet's *Ammonites jallabertianus* (= *Eotetragonites jallaberti*), but the types in the Natural History Museum in Geneva are much different from true *Tetragonites* and from *T. diegoensis* in both shape of whorl and configuration and development of the constrictions.

Tetragonites rectangularis alaskaensis n. subsp.

(Pl. 6, figs. 9, 10, 14; pl. 7, figs. 1, 2)

Description

The holotype has a maximum diameter of 47 mm, but other specimens assigned to the species are very large. The largest specimen is from Alaska (USGS M2081). It measures over 120 mm in diameter with a partial body chamber preserved, so the species attains a large size for the genus.

TABLE 7

Measurements of Tetragonites rectangularis alaskaensis n. subsp.

Specimen	D	H	W	U
USNM 155473 holotype	45.1 36.7	20.4 (45) 16.2 (44)	24.3 (54) 20.4 (56)	12.0 (27) 10.2 (28)
USGS M1333/1	27.8 24.7	11.2 (40) 9.8 (40)	15.6 (56) 13.8 (56)	8.6 (31) 7.7 (31)
USGS M1333/2	37.3	17.1 (46)	....	9.7 (26)
USGS M1333/3	21.2	8.9 (42)	11.0 (52)	6.0 (28)
USGS M1333/4	41.5± 33.6 27.8	18.0 (43) 14.5 (43) 12.3 (44)	 .... 14.9 (54)	10.9 (26) 8.9 (26) 7.2 (26)
USGS M1370/1	25.8	10.5 (41)	13.5 (52)	7.6 (29)

Cross section.—The cross section is trapezoidal with acutely rounded umbilical edge and distinct peripheral shoulder. The flanks and venter are distinctly flat-tended in the young and intermediate stages, but tend to become more inflated in the large shells resulting in a less distinct peripheral shouder and a less distinctly trapezoidal cross section. The umbilicus retains its character throughout all stages. The umbilical wall is flat, nearly vertical and only faintly ornamented by growth lines.

Suture.—The elements of the external suture are standard in position and number for the genus. 1S is trifid. 1L is broad in the younger stages with a length/width ratio from 2.5:1 to 1.5:1. In the largest specimen the 1L is strongly extended and frilled with a length/width ratio of 8:1. The internal suture shows only two saddles in very small specimens (4 to 9 mm in diameter), but larger specimens show a third small saddle.

Constrictions.—Constrictions number 6 to 8 on small and medium-sized specimens, but large specimens may have more. They are irregularly developed in both strength and spacing, but are present at all stages in the ontogeny. In the younger stages they tend to be straight on both flank and venter and weaker on the venter than on the flank. With growth their configuration on both flank and venter be-

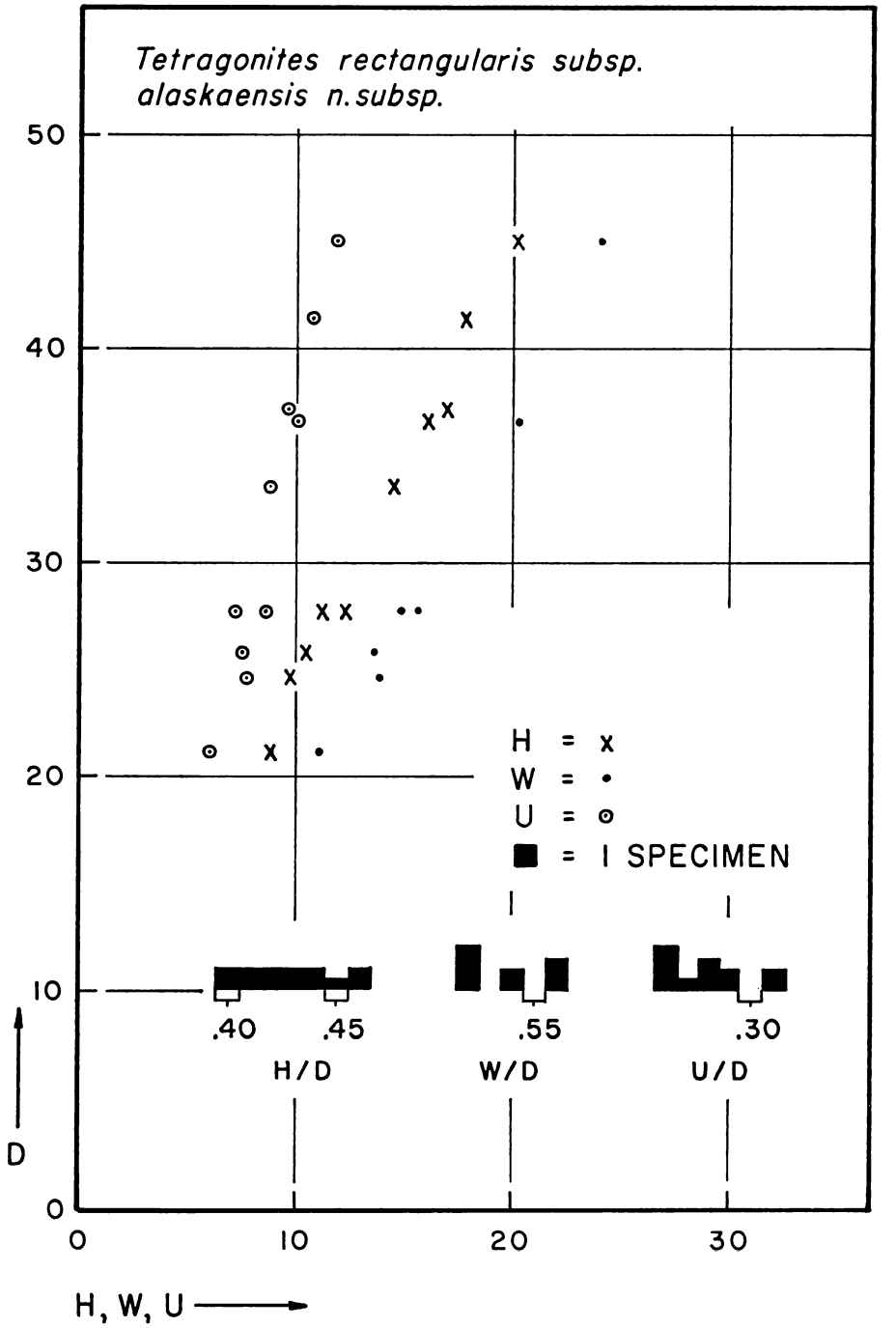

Tetragonites rectangularis subsp.
alaskaensis n.subsp.
50
40
30
20
10
0
D
H = x
W = •
U = ⊙
■ = 1 SPECIMEN
.40
.45
H/D
.55
W/D
.30
U/D
0
10
20
30
H, W, U

Fig. 22.

comes more flexed so that the flank shows moderately prorsiradiate concave configuration and the venter shows a moderate adorally concave arch.

Distribution

The species is fairly common in deposits of middle and upper Albian age in the Queen Charlotte Islands and Alaska. It is also represented in the upper Albian deposits of Oregon.



Fig. 23. *a.* USGS M1333/1, upper Albian, Alaska. *b.* Holotype USGS M1819/1, middle Albian, Queen Charlotte Islands, Canada. *c.* USGS M1333/2, upper Albian, Alaska.

Comparison

This subspecies is very close to *T. rectangularis* ss., but differs in having a generally wider umbilicus, and narrower cross section; it generally has more and better-developed constrictions; 1S is consistently trifid; the umbilical wall virtually lacks liration. Though it is close to *T. rectangularis diegoensis* in most other respects, it shows no overlap in measurements. *T. bournensis* has a broader more rectangular cross section and apparently loses its constrictions in the later ontogeny.

This taxon differs from *T. hulenensis* n. sp. by its nearly angular umbilical edge and virtual lack of lirae on the umbilical wall. It has fewer elements in the external and internal sutures than *T. jonesi* n. sp. Its measurements and constriction pattern distinguish it from *T. lecontei* n. sp.

Tetragonites bournensis n. sp.

(Pl. 6, figs. 11–13)

Description

Size.—The species is based on a small number of specimens all of which are completely septate. Thus no indication of the adult size can be given. The largest shell diameter so far recorded is 40 mm.

Cross section.—The cross section of the whorl is subquadrate with a broad flattened venter joining slightly inflated subparallel flanks at a rounded peripheral shoulder. The umbilical edge is abruptly rounded. The umbilical wall is slightly arched and essentially vertical.

Constrictions.—The constrictions are lacking or very weak and difficult to see on the larger parts of the molds (25 mm or larger), especially on the upper flanks and periphery.

In the earlier whorls 5 distinct prorsiradiate concave constrictions are present on the flank. They cross the venter with no reduction in prominence and with a

TABLE 8

MEASUREMENTS OF TETRAGONITES BOURNENSIS N. SP.

Specimen	D	H	W	U
FG Coll. Balme de Rencurel	17.1	7.3± (43)	9.7 (57)	5.3 (31)
	21.3	8.7 (41)	12.2 (57)	6.8 (32)
	24.9	10.4 (42)	13.8± (55)	7.9 (32)
	28.9	13.5 (47)	17.3 (60)	7.1 (25)
	40.0±	18.0± (45)	23.5± (58)	....
UCR—Frasette holotype	31.7	14.5 (46)	18.9 (60)	8.0 (22)

distinct adorally concave arch except in the youngest whorls exposed where they are convex.

They probably range up to 7 in number, as 3 are present in the one-half whorl bearing constrictions in specimen UCR 676/1 from Frasette.

Suture.—The external suture is moderately extended and frilled and has the standard number and position of elements. 1L has a length/width ratio of 3:1 to 4:1. 1S is trifid showing only slight asymmetry. The internal suture has two well-developed saddles and an incipient one. The suspensive lobe is not retracted.

COMPARISON

The concave arch of the constrictions on the flank and venter, the number and development of the elements of the suture ally this species to the *T. rectangularis* branch of the genus and differentiate it from the members of the *T. timotheanus* and *T. kitchini branches* and from the nonconstricted members of the *T. rectangularis* branch. The quadrate cross section and loss of constrictions in the later whorls serves to set it apart from the remaining members of the *T. rectangularis* branch.

It is more depressed in cross section than *T. hulenensis* and has more elements in the internal suture than *T. heterosulcatus* or *T. crudus*. The Upper Cretaceous forms have different cross sections.

This species is most apt to be confused with *T. rectangularis,* which it strongly resembles in the young stages (up to 25 mm). The combination of no constrictions and its quadrate shape distinguish it from *T. rectangularis* at larger diameters. *T. rectangularis* is quite variable in cross section, however, and in some instances the shape of the cross section may not be distinctive.

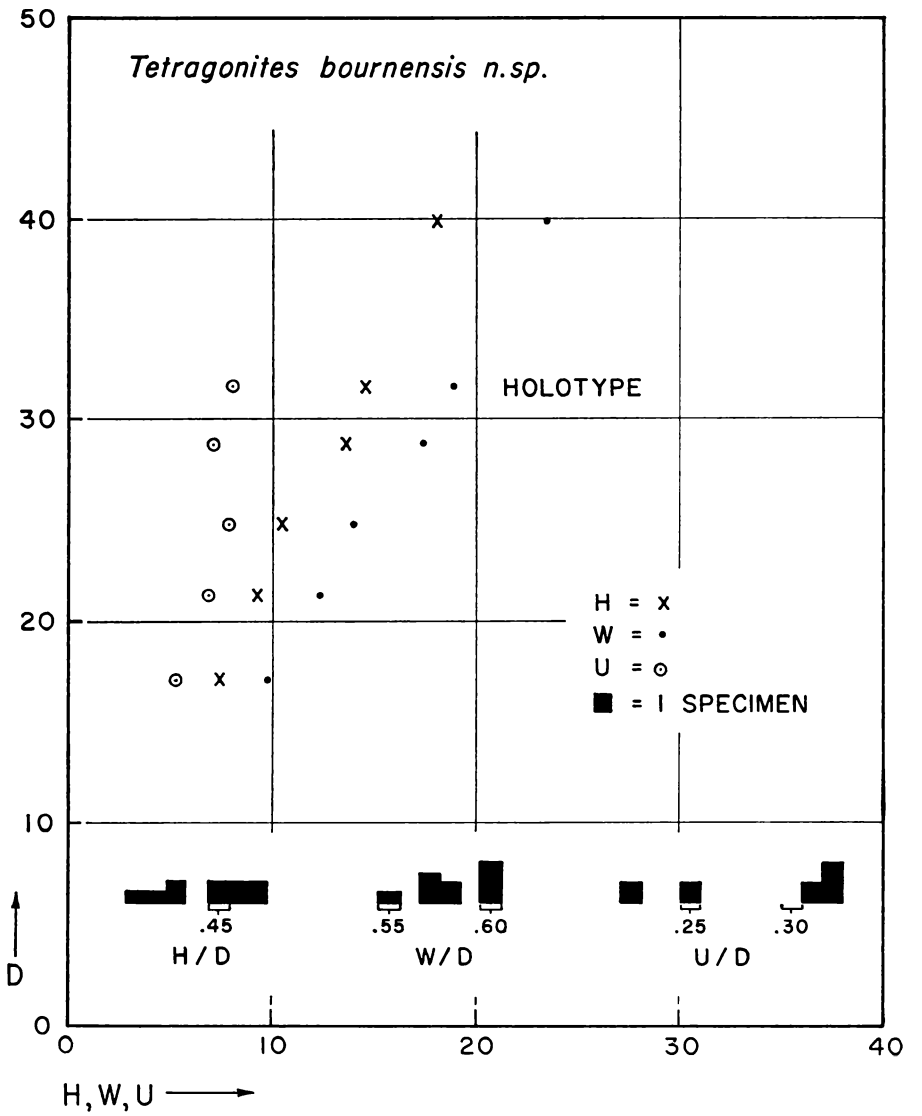


Fig. 24.

Remarks

This species was identified as *T. kitchini* by Breistroffer, but, if Wiedmann's interpretation of *T. kitchini* is correct, this identification is wrong. At present no transition can be demonstrated to *T. rectangularis,* but I believe the two species are closely related. They have not yet been found at the same locality, though they may be contemporaneous if the *T. rectangularis* from the condensed deposits of the Prés de Rencurel locality are lower Albian.

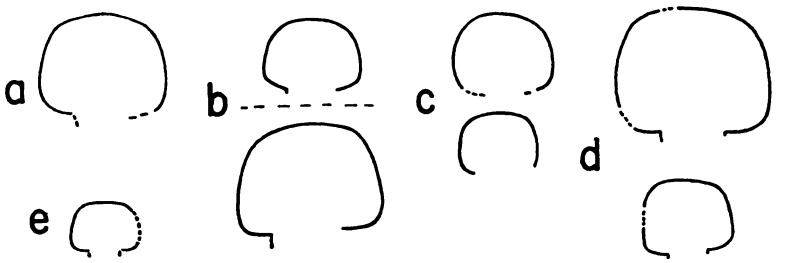


Fig. 25. Cross sections of *T. bournensis* n. sp. *a–c* and *f*. FG Collection unnumbered, Balme de Rencurel, identified by Breistroffer as *T. kitchini*. *d*. UCR 676/1, Frasette, the holotype. *e*. FG Collection, figured in Jacob, 1908, pl. 1, fig. 10, Balme de Rencurel.

Tetragonites lecontei n. sp.

(Pl. 7, figs. 11, 12, 13)

Description

Size.—The maximum diameter recorded for this species is 37 mm with the entire living chamber preserved. Many smaller specimens also have their living chambers at least partly preserved so it seems that the species remained relatively small with adults probably ranging from 35 to 50 mm in diameter.

Measurements.—The measurements show a combination of very broad cross section with very wide umbilicus, an unusual feature in the genus.

Cross section.—The cross section of the whorl is subquadrate with slight convergence of moderately inflated flanks. The venter is broadly rounded; the umbilical edge is abruptly rounded. This pattern is maintained throughout the ontogeny with slight changes in the inflation of the flanks and venter and small variations in the H/W ratio accounting for small differences in cross-sectional shape.

TABLE 9

Measurements of Tetragonites lecontei n. sp.

Specimen	D	H	W	U
UCR 109/1	27.0	10.7 (40)	14.4±(53)	9.1 (34)
holotype	29.5	11.9 (40)	15.9 (54)	9.4 (32)
UCR 104/2	25.3	10.1 (40)	13.9 (55)	8.9 (35)
UCR 411/1	24.3	9.6±(40)	14.4±(59)	8.5 (35)
UCR 20/1	24.3	9.5 (39)	13.8 (57)	9.5 (39)
UCR 143/1	23.5	9.0 (38)	13.2 (57)	8.5 (40)
UCR 16/1	19.6	7.9 (40)	10.7 (55)	6.6 (34)
UCR 117/1	14.6	4.8 (33)	7.7±(53)	6.0 (41)

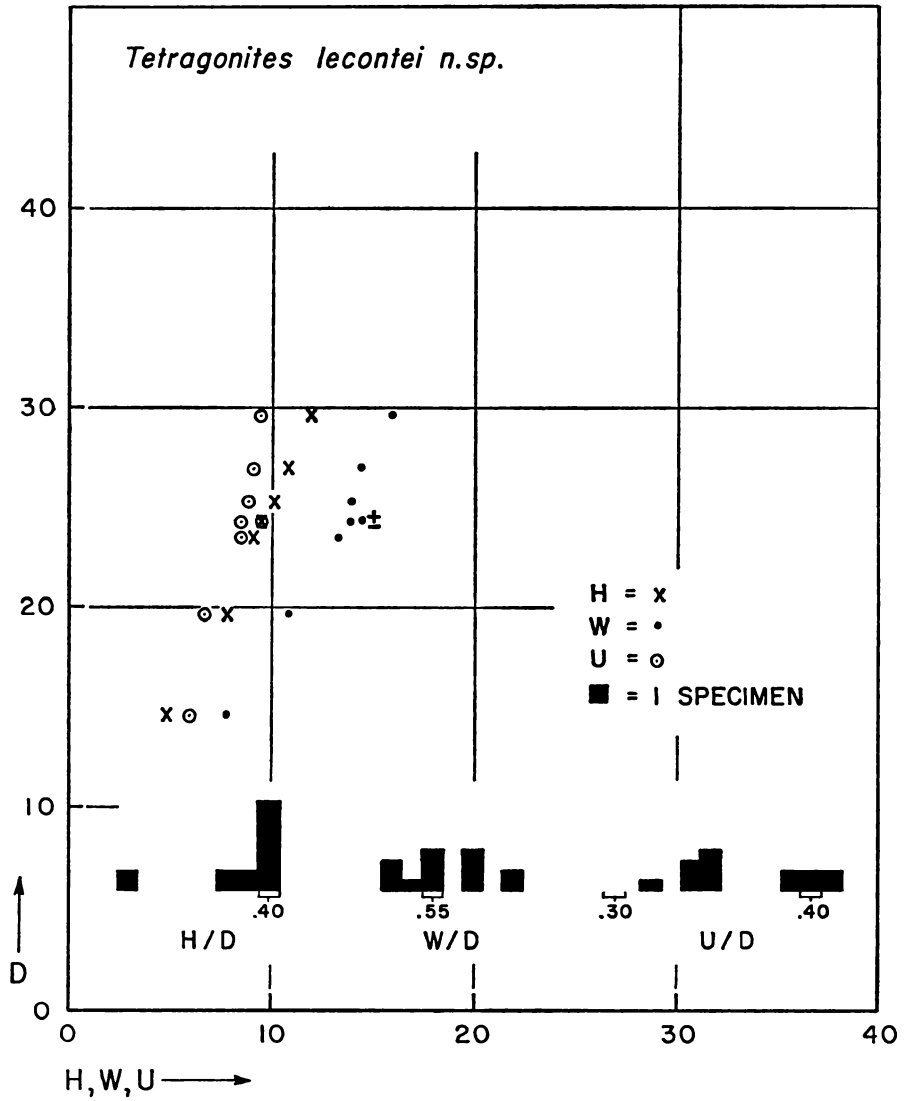


Fig. 26.

Constrictions.—Constrictions number 5 to 8 per volution with a tendency to ha more constrictions in the later growth stages than in the earlier ones. They a prominent on the flank of the internal mold, but more subdued on the venter. C the external shell they show as a slight groove preceded by a slight ridge. They ter to be straight or prorsiradiate convex on the flank, curving adapically on t peripheral shoulder and forming a slight to moderate adorally concave arch on t venter.

Suture.—Since the average shell size is small, the suture is not deeply incised, l having a length/width ratio of about 3:1 at 25 mm diameter. The septa of sever

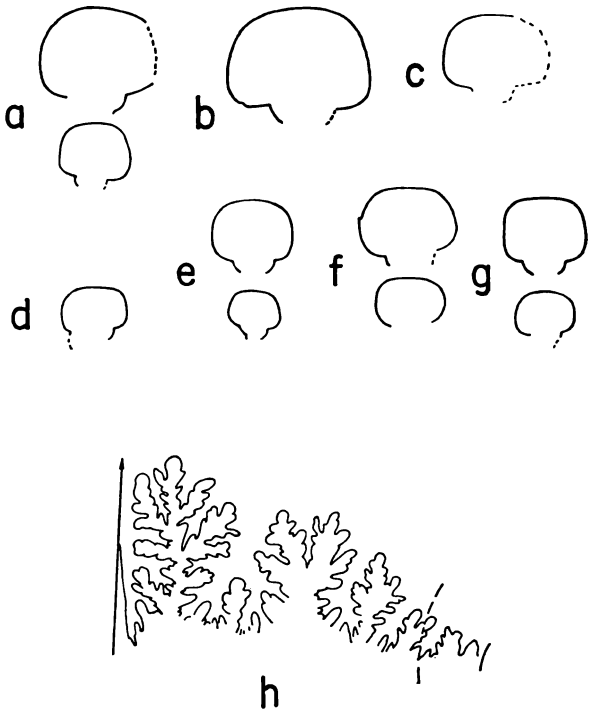


Fig. 27. *a–g.* UCR specimens 109/1, 104/3, 20/1, 117/1, 16/1, 143/1, and 411/1, respectively, all from the *lecontei* zone, lower Albian, near Ono, California. *h.* UCR 109/1 holotype, locality as above.

specimens indicate only two moderately strong internal saddles are developed. The septa and the sutures do not show any bending back or retraction of the suspensive lobe.

Comparison

T. lecontei n. sp. is similar to the genotype and to *T. subbeticus* in many respects. It may be distinguished from *T. timotheanus* by its generally higher and wider cross section and narrower umbilicus. The constrictions are straighter in the genotype and do not show the ventral adorally concave arch of *T. lecontei.* In most specimens the whorl shape of *T. timotheanus* is more trapezoidal with a more inclined umbilical wall.

The relationship to *T. subbeticus* is probably even closer. As in *T. timotheanus* the configuration of the constrictions in *T. subbeticus* is straight on the venter and nearly so on the flanks, and the section has a rounded trapezoidal appearance with steeply sloping umbilical wall. The suture shows incipient development of a third internal saddle in small shells. Thus the more quadrate section with generally greater whorl height, the arch of the constrictions on the venter, a generally steeper umbilical wall, and fewer elements in the internal suture of larger specimens separate *T. lecontei* n. sp. from *T. subbeticus.*

The whorls are much more inflated than in *T. kitchini* or *T. heterosulcatus;* much

more quadrate than *E. balmensis or T. margaritatus; T. latus, T. jurinianus,* and *T. nautiloides* have no constrictions and different cross sections; *T. simplex* and *T. spathi* have a much more compressed cross section and have adorally convex constrictions on the venter; members of the *T. rectangularis* group have more elements in the internal suture and a different configuration of the constrictions. The remaining Upper Cretaceous species have rounded venters and much more equant cross sections.

Tetragonites hulenensis n. sp.

(Pl. 6, figs. 16–19; pl. 7, figs. 3, 6, 7, 9, 10)

Description

Size.—The holotype completely septate measures 41 mm in diameter, indicating a total shell diameter of at least 70 mm. Many specimens are 40 mm or larger, so the species was probably of medium to large size for the genus. The largest specimen (USGS M1302/1), though deformed, measures 76 mm.

Measurements.—The measurements indicate a relatively equant cross section and moderate-sized umbilicus, which shows considerable variation in whorl width.

Cross section.—The cross section is subrectangular, slightly wider than high. The venter is flattened in the young (up to 25 mm) with an abruptly rounded peripheral shoulder. With growth the venter becomes more rounded and the peripheral shoulder more broadly rounded. The umbilical edge is rounded and merges gradually with the convex to flat umbilical wall, which is nearly vertical next to the umbilical seam.

TABLE 10

Measurements of Tetragonites hulenensis n. sp.

Specimen	D	H	W	U
UCR 422/2*	23.2	9.4 (40)	11.6 (50)	7.6 (33)
	21.0	8.6 (41)	10.7 (51)	7.0 (33)
UCR 98/4*	28.7	12.1 (42)	15.3 (53)	8.9 (31)
	23.3	10.0 (43)	11.7 (50)	7.8 (33)
UCR 98/5*	40.1	17.4 (43)	20.9 (52)	11.6 (29)
UCR 111/1	35.2	15.0 (43)	17.1± (49)	11.1 (32)
UCR 1000/20*	30.0±	13.0± (43)	....	9.0 (30)
UCR 1000/19*	28.7	11.9 (41)	14.5 (51)	8.6 (30)
UCR 402/22*	46.5	20.5 (45)	22.7 (49)	12.8 (28)
UCB 14853	45.0	19.6 (44)	24.1 (53)	13.4 (30)
	36.6	15.6 (43)	19.9 (54)	11.1 (30)
USNM 155481a holotype	39.6	17.7 (45)	22.0 (56)	11.5 (29)
	34.6	15.2 (44)	19.3 (56)	10.4 (30)
USGS M1337/2	25.9	10.0 (39)	13.7 (53)	9.0 (35)
USGS M1339/1	27.4	11.6 (42)	14.9 (54)	8.6 (31)

* Specimens from the same bed in the *Brewericeras hulenense* zone.

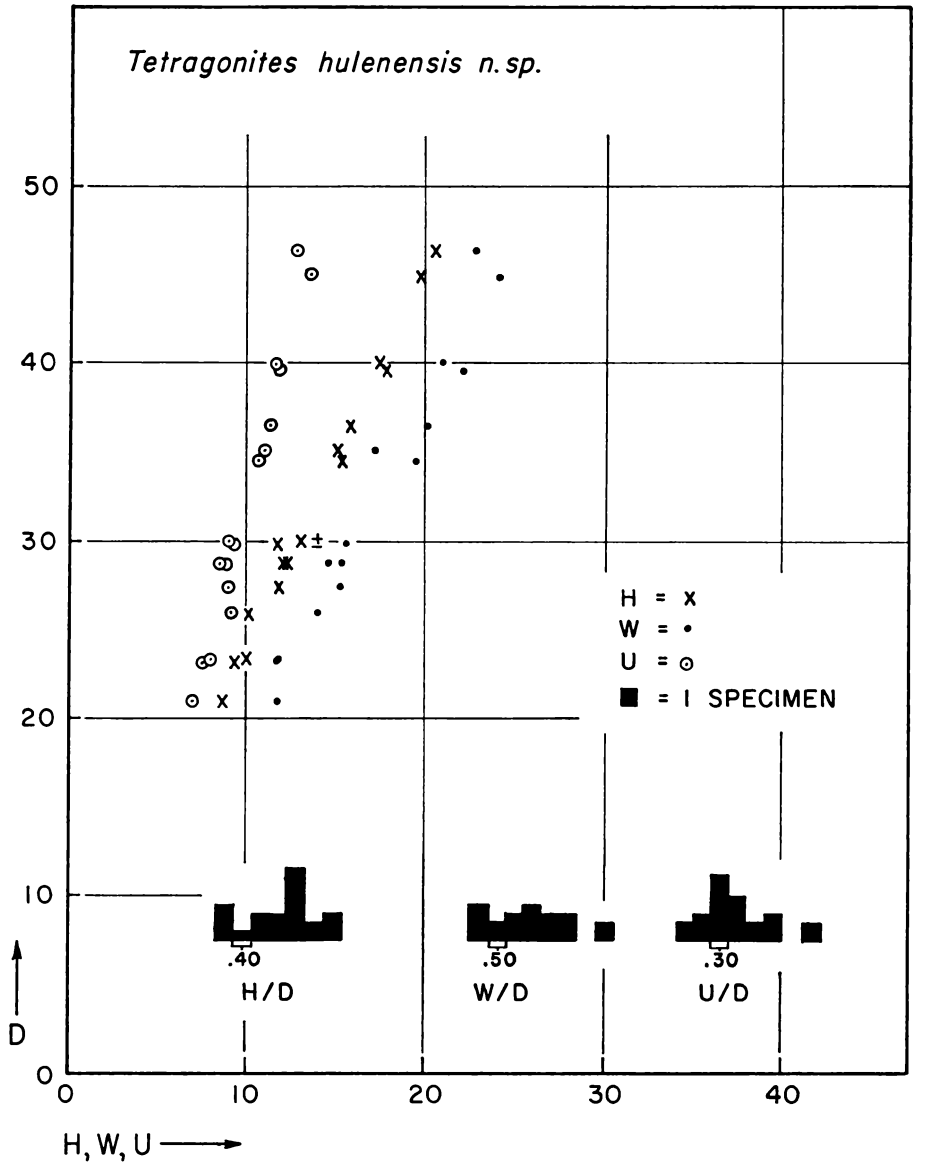


Fig. 28.

Constrictions.—The constrictions number 6 to 8. They are deep and straight on the flanks and slightly concave adorally on the venter. They are marked on the venter to about 15 mm diameter, weakening to smooth at various stages thereafter, and weakening to smooth on the flanks at various stages after 25 mm diameter. From about 40 to 50 mm diameter the shells have no constrictions or very weak constrictions. At larger diameters prominent widely spaced constrictions are present on most shells.

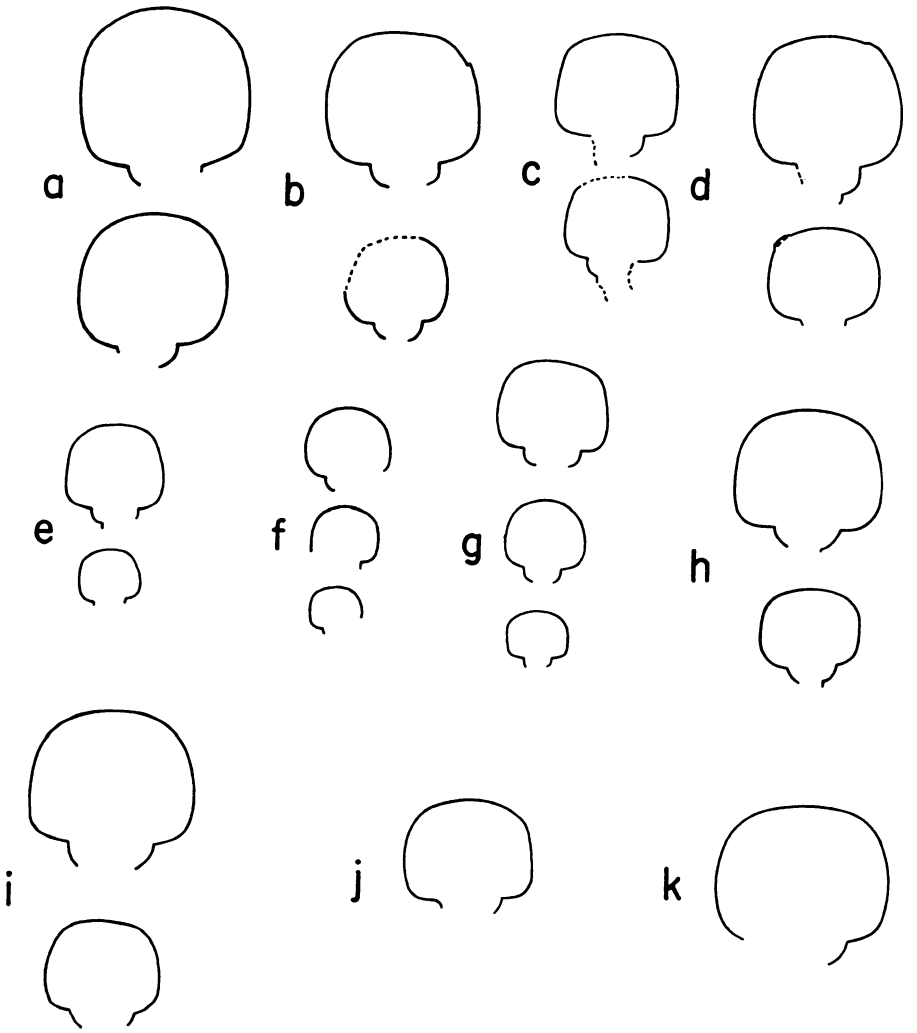


Fig. 29. Cross sections of *T. hulenensis* n. sp. *a, b, e, f,* and *g.* UCR specimens 402/22, 98/5, 1000/19, 422/2, and 98/4, respectively, from the *Brewericeras hullenense* zone, near Ono, California. *c.* UCR 111/1, *Leconteites lecontei* zone, near Ono, California. *d.* USNM 155480, *Brewericeras hulenense* zone, Alaska. *h.* USNM 155481a, the holotype, *Brewericeras hulenense* zone, Alaska. *i.* UCB 14853, near Horsetown, Shasta County, California. *j.* UCB 14854, near Jackass Flat, Shasta County, California. *k.* USGS M2920/1, *Brewericeras hulenense* zone, Alaska.

Suture.—The elements of the external suture are standard in position and number for the genus, and the septum is moderately extended and frilled. The 1L has a length/width ratio of about 3 to 1 at 30 mm diameter. 1S is trifid on most specimens examined but irregularly bifid on USGS M2920/1. The internal suture has two major saddles and an incipient one like the other species included in the *T. rectangularis* branch. This observation is based on the holotype and specimen UCB 14854 (Anderson, 1902, pl. vii fig. 145, his specimen number 28).

Comparison

This taxon probably shows the strongest affinity for the *Tetrogonites rectangularis* group when compared to the earlier members of the genus, but some specimens also resemble some later species in the shape of its cross section, e.g., *T. beantalyensis* Collignon from the Coniacian of Madagascar. The venter of *T. beantalyensis* is more arched; the devlopment of the constrictions is much less prominent and lacks the ventral sulcus. It is allied to the *T. rectangularis* group through the possession of strongly prorsiradiate concave constrictions with a pronounced ventral sulcus, but differs from other members of the group in having a more rectangular cross section and having a generally broader umbilicus.

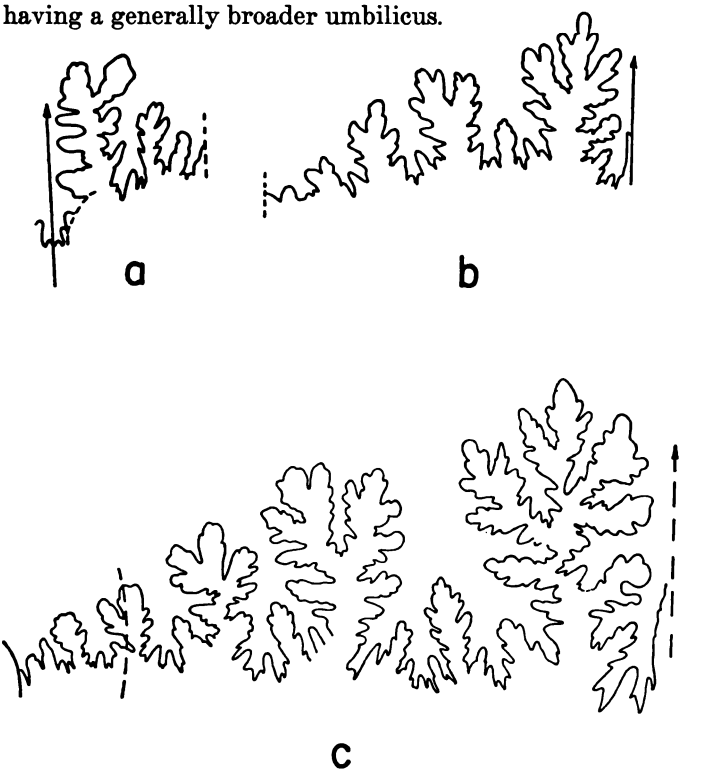


Fig. 30. Suture lines of *Tetragonites hulensis*, n. sp. *a* and *b*. Specimen UCR 1000/20, *Brewericeras hulenense* zone, near Ono, California. *c*. Specimen UCB 14854, near Jackass Flat, Shasta County, California.

It differs from *T. heterosulcatus, T. crudus, E. balmensis,* and *T. kitchini* in having a larger number of elements in the internal suture. It differs from members of the *T. timotheanus* group in having a more equant cross section, a smaller umbilicus, and in the configuration of the constrictions.

Distribution

The species is known from the upper *Leconteites lecontei* zone and the *Brewericeras hulenense* zone in northern California and from the *Moffitites robustus* fauna (Imlay, 1960, p. 91) and the *Brewericeras hulenense* zone in Alaska (Jones and Berg, 1964, p. A9). These occurrences suggest it is limited to the lower Albian.

Tetragonites jonesi n.sp.

(Pl. 6, figs. 1–4)

Description

Size.—The shell is small for the genus, all specimens studied having at least part of the living chamber preserved at 35 mm or less diameter. The maximum diameter was probably not more than 50 mm.

Measurements.—The measurements indicate a small umbilicus with more or less normal height and width measurements for the genus. Consequently the involution is much greater than usual.

TABLE 11

Measurements of Tetragonites jonesi n. sp.

Specimen	D	H	W	U
USNM 155479	28.0	12.2 (46)	....	6.9 (25)
japonicum zone	22.8	10.0 (44)	12.1 (53)	5.7 (25)
USMN 155478	26.6	12.1 (45)	15.2 (57)	5.9 (22)
	23.2	10.5 (45)	13.9 (60)	5.1 (22)
USNM 155477	25.5	12.1 (48)	15.5 (61)	5.8 (23)
holotype	22.6	10.7 (47)	13.3 (59)	5.0 (22)
USGS M1641/1 weathered specimen	35+	14.3+(41)	....	9.3 (26)
japonicum zone	31.4	12.9 (41)	....	8.2 (26)

Cross section.—The cross section is trapezoidal with acutely rounded umbilical edge and peripheral shoulder and with flattened venter and flanks. The umbilical wall is slightly inflated on the upper flank, but excavate on the lower flank next to the umbilical seam so that the umbilicus is narrower at midflank than at the umbilical seam.

Suture.—The external suture is different from other members of the genus in that there are four lobes on the flank instead of three and the fifth saddle underlies the umbilical edge. 1S is trifid. 1L is very broad in comparison to its length.

None of the specimens assigned with certainty to the taxon gives any indication of the number or position of the internal elements of the suture, but a larger specimen questionably assigned here (USGS M1816) has three strong internal saddles.

Constrictions.—Six or seven constrictions are present. They are prorsiradiate slightly concave on the flanks and straight to slightly concave on the venter. Their position is reflected on the external shell by a slight groove preceded by a slight ridge. The ridge is best developed on the peripheral shoulder and venter.

The liration of the umbilical wall, present on other members of the genus, is feeble in this species.

Comparison

This species is very similar in external appearance to small specimens of *Tetragonities rectangularis* from the upper Albian of the Maritime Alps, but is distinguished from it and all other members of the genus included in this study by the presence of an additional element of the external suture on the flank. Also it differs from

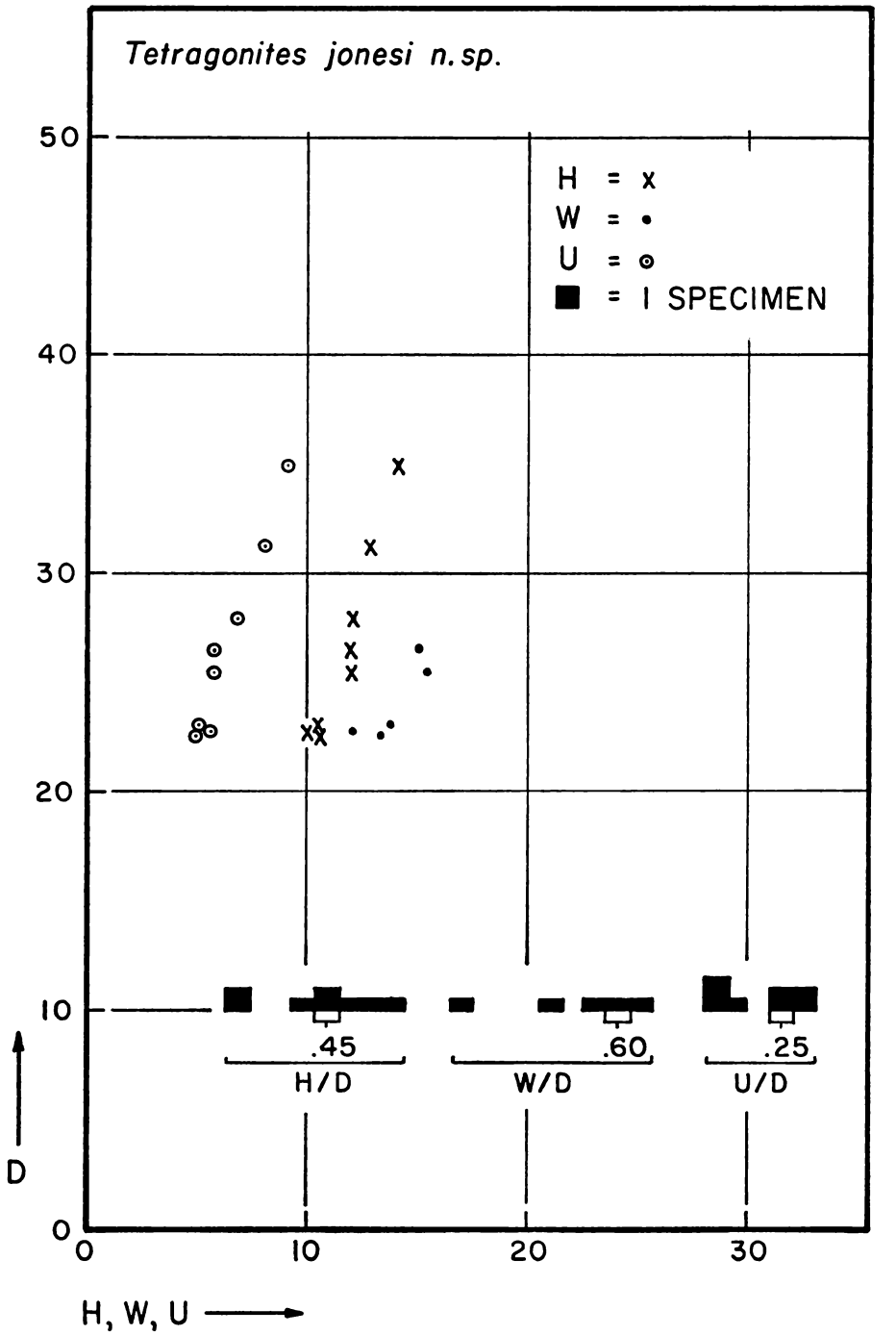

Tetragonites jonesi n.sp.
H = x
W = •
U = ⊙
■ = 1 SPECIMEN
50
40
30
20
10
0
D
0
10
20
30
H, W, U
.45
H/D
.60
W/D
.25
U/D

Fig. 31.

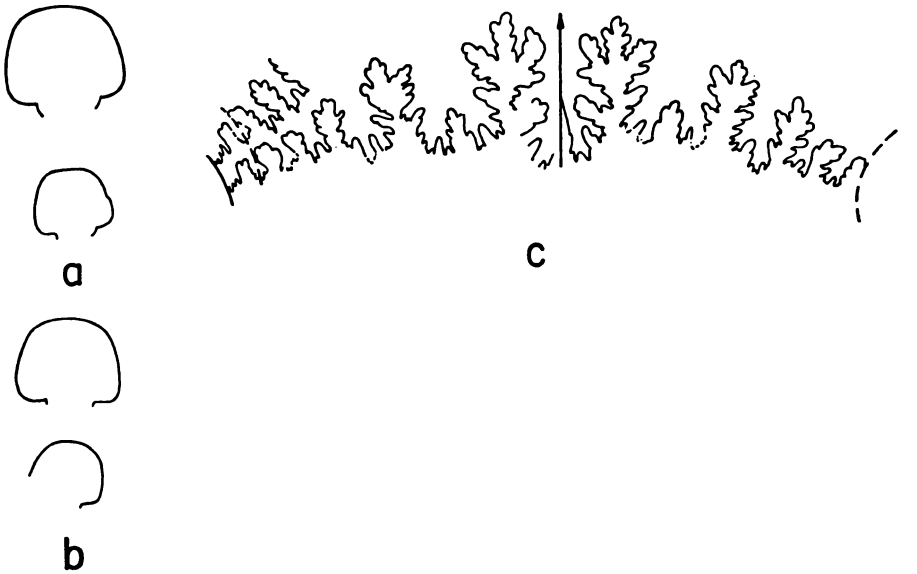


Fig. 32. Cross sections and external suture line of *Tetragonites jonesi* n. sp. from the range zone of *Pseudouhligella dawsoni*, upper Albian, Alaska. *a* and *c*. USNM 155477, the holotype. *b*. USNM 155478.

other members of the genus except *T. rectangularis alaskaensis* n. sp. in lacking prominent liration of the umbilical wall. *T. subtimotheanus*, another close relative, has a sloping umbilical wall as opposed to the overhanging one found in this species.

Distribution

The species is known only from Alaska where it is found in the *dawsoni* and *japonicum* zones (Jones and Berg, 1964). In terms of European stages this range is probably equivalent to uppermost Albian and lower Cenomanian.

Remarks

The two specimens from the *japonicum* zone have a slightly larger umbilicus than those from the *dawsoni* zone, but these specimens are slightly deformed and weathered, respectively, and the difference may be the result of these postburial changes.

A specimen from USGS M1816 is tentatively referred to this species, though its umbilical measurement seems larger than for the type, but the specimen is fragmentary and much larger than the others. The apparent difference then may be accounted for by preservation or because the larger shells have a relatively greater umbilical diameter. This specimen has 3 well-developed internal saddles and space for a very small fourth saddle, though the latter was not observed. If this identification is correct, the hypothesis of derivation of *T. subtimotheanus* from *T. jonesi* would be greatly strengthened. However, the position of the 4L on the flank in *T. jonesi* is unique and the species may represent the end of its lineage.

Cenomanian Tetragonites

Several species of Cenomanian *Tetragonites* have been described recently by Collignon and Wiedmann. Unquestionably identification of these forms will be difficult because of their very similar morphologic aspect, the lack of large samples, and the presence of considerable ontogenetic variation. These forms are also similar to *Tetragonites rectangularis* from the upper Albian and probably were derived from it. The species are: *T. subtimotheanus* Wiedmann, for Stoliczka's southern Indian specimens from the Ootatoor Group; *T. blaisoni* Collignon, from West Berakata, Madagascar; *T. jallaberti* var. *ampakabensis* Collignon, from Betioky, Madagascar.

I have undertaken a discussion of these taxa and *T. spathi* Breistroffer in the following paragraphs in order to point out their similarities to Albian taxa and because they are incompletely described or discussed in the literature.

Tetragonites spathi Breistroffer (in Fabre, 1940)

(Pl. 5, figs. 6–10)

†1907 *Lytoceras* (*Tetragonites*) *timotheanum* Mayor in Pictet, Pervinquière (in part) pl. 3, fig. 25.

1923 *Tetragonites* n. sp. Spath, Amm. Gault, pp. 26, 27.

1940 *Tetragonites spathi* Breistroffer, Fabre, pp. 214, 215.

Description

Size.—The largest reported specimen is the holotype at 43 mm in diameter with most, if not all, of the living chamber preserved.

Although quite a number of specimens are known from the locality of the holotype, few of them are well enough preserved to provide good measurements. Specimens from other localities are also abundant, but very small and thus difficult to measure accurately.

	D	H	W	U
Holotype FM	39.3	15.5 (39)	17.8 (45)	12.0 (30)
	31.5	12.8 (41)	14.4 (46)	9.5 (30)
BMNH C5896	26.5	...	...	7.6 (28)

Cross section.—The cross section is compressed with flattened flanks and rounded venter which joins the flanks in a broadly rounded curve. The umbilical edge and wall are rounded, curving to vertical at the umbilical seam. The venter has a slight rise above the siphonal line which is distinct on well-preserved specimens.

Suture.—The external suture shows the standard number and configuration of lobes and saddles for members of the genus. The septal face and the internal suture have not been observed.

Constrictions.—Constrictions are numerous and apparently are more numerous on larger shells than on smaller ones. The holotype shows 6 evenly spaced constrictions on the last half volution preceded with a larger intervening space by a less strongly developed one. Smaller specimens show up to 6 constrictions per volution. Constrictions are masked by the shell, their position being marked by low collars on the exterior shell surface.



Fig. 33. Holotype of *Tetragonites spathi* Breistroffer in Fabre. *a.* Shape of the cross section of the internal mold. Note the slight asymmetry of the venter of the larger section caused by a small patch of shell and the indentation of the right flank caused by constriction. *b.* The external suture of the specimen illustrated on pl. 5, figs. 8 and 9 (FG Collection).

Constrictions are strongly prorsiradiate concave on the flank. They cross the venter in a moderate to strong chevron, peaked adorally, but interrupted by the incipient keel that lies just above the siphonal line.

Comparison

The strongly adorally peaked pattern of the constrictions and the incipient median keel on the venter easily distinguish this taxon from all others described.

Distribution

This taxon seems to be a good marker for Cenomanian strata in France where it occurs near Cassis associated with *Phylloceras serisitense, Puzosia mayoriana, Forbesiceras largilliertianum, Acanthoceras hippocastaneum, Desmoceras* cf. *D. japonicum.* Thomel reports it also from the lower Cenomanian of Rigaud (Alpes-Maritimes) and the middle Cenomanian of Saint-Lions, Moriez, and La Mure (Basses-Alpes). He has kindly given me this information in advance of his own publication on the Cenomanian of southeastern France (letter, November, 1965).

Remarks

The specimen described by Pervinquière (1907, pl. 3, fig. 25) suggests the lateral aspect and whorl shape of *T. spathi,* but does not agree in the relative dimensions of the whorl height, width, and umbilicus. This disagreement may be the result of the very small size of Pervinquière's specimen as compared with the type. The specimen in question is reported from the upper Albian of Tunisia.

Tetragonites subtimotheanus Wiedmann, 1962

(Pl. 5, figs. 11, 13; pl. 6, figs. 5–8)

1865 *Ammonites timotheanus* Mayor, Stoliczka, Cephalopods Cretaceous Southern India, p. 146, pl. 73, figs. 3, 4, 6; not pl. 73, fig. 5.

1895 *Lytoceras* (*Tetragonites*) *timotheanus* Mayor, Kossmat, Sudind. Kreideformation, p. 133, pl. 17(3), figs. 11, 13.

Description

Size.—The largest example I have seen measures 51 mm in diameter with the last half-volution forming the living chamber. If this specimen represents a full-grown shell the species probably attained a shell diameter of 70 to 80 mm. The specimen figured by Stoliczka was 60 mm in diameter (1865, pl. 73, fig. 4), and Kossmat gives 80 mm for his largest specimen (1895, p. 134).

Measurements.—The measurements indicate a diminution of relative umbilical diameter as the shell grows, especially if Kossmat's measurement of the large specimen is used.

Cross section.—The cross section is trapezoidal with a rounded peripheral shoulder and an abrupt but rounded umbilical edge. The flanks and venter are distinctly flattened and the umbilical wall is steep to vertical.

Constrictions.—Constrictions are strongly developed on the umbilical wall and lower flank and moderately developed on the upper flank and venter throughout growth. They are strongly prorsiradiate concave on the flank and have a moderately developed adorally concave arch on the venter. There are 5 per volution at 25 mm diameter and possibly as many as 8 in larger shells. Their position on the external shell is marked by a steplike diminution of the aperture.

TABLE 12

MEASUREMENTS OF TETRAGONITES SUBTIMOTHEANUS WIEDMANN

Specimen	D	H	W	U
MHNG large specimen	51.7+	21.5+(40)	31.1 (60)	14.6*(28)
MHNG intermediate-sized specimen	32.4	13.1 (40)	18.5 (57)	10.1 (31)
MHNG small specimen	20.3	8.3 (41)	11.3 (56)	6.4 (32)
Odium large specimen*	80	41 (50)	45.0 (56)	16 (20)
Odium small specimen*	27	10.5 (39)	14.5 (54)	8 (30)
BMNH C18142 *Tetragonites* aff. *T. subtimotheanus*	24.1	10.4 (43)	13.5±(56)	7.0 (29)

* After Kossmat.

Suture.—The external suture shows a standard number and position of elements for the genus. L has a length/width ratio of 2.5:1 to 4:1. I have not seen specimens in which the septum is exposed or in which the internal suture is available. However, both Stoliczka and Kossmat figure suture lines showing at least three distinctively developed internal saddles.

COMPARISON

T. subtimotheanus possesses the group characteristics of *T. rectangularis* and thus is differentiated from members of the *T. timotheanus* group by the smaller size of the umbilicus and the configuration of the constrictions. The whorl cross section and the larger number of elements in the internal suture distinguish it from *T. heterosulcatus, T. crudus, E. balmensis,* and *T. kitchini. T. hulenensis, T. margaritatus,* and *T. bournensis* have different cross sections. *T. bournensis* also lacks the strong constrictions in the later growth stages. *T. epigonus, T. latus, T. embergeri, T. jacksonensis, T. mitraikyensis, T. popetensis,* and *T. simplex* have distinctly different measurements. *T. rectangularis* subsp. *diegoensis* has a higher cross section with a more strongly arched venter. *T. rectangularis alaskaensis* differs in the number of elements in the internal suture and in its less strongly developed and straighter constrictions on both flanks and venter.

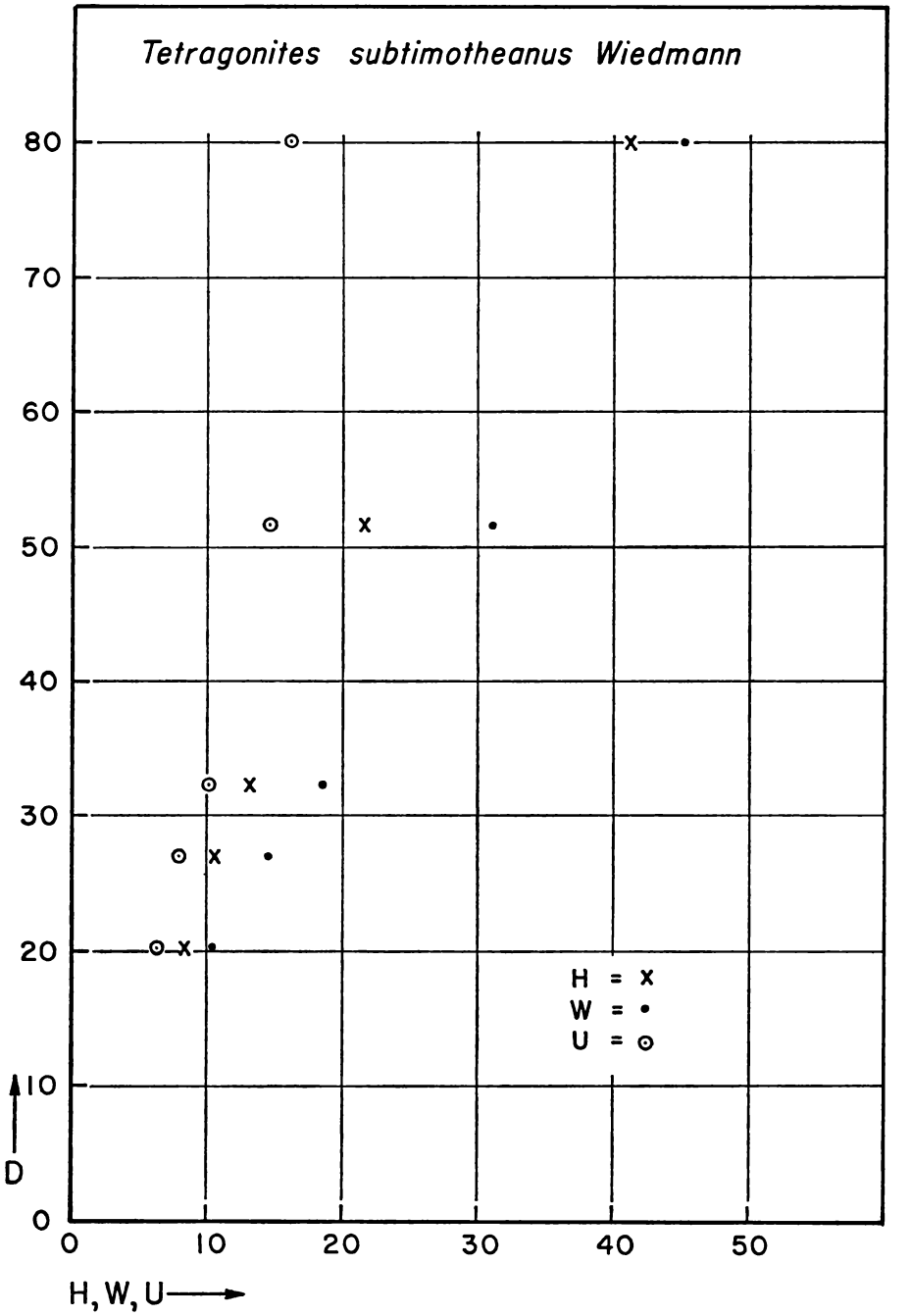

Tetragonites subtimotheanus Wiedmann
80
70
60
50
40
30
20
10
0
D
0
10
20
30
40
50
H, W, U
H = X
W = •
U = ⊙

Fig. 34.

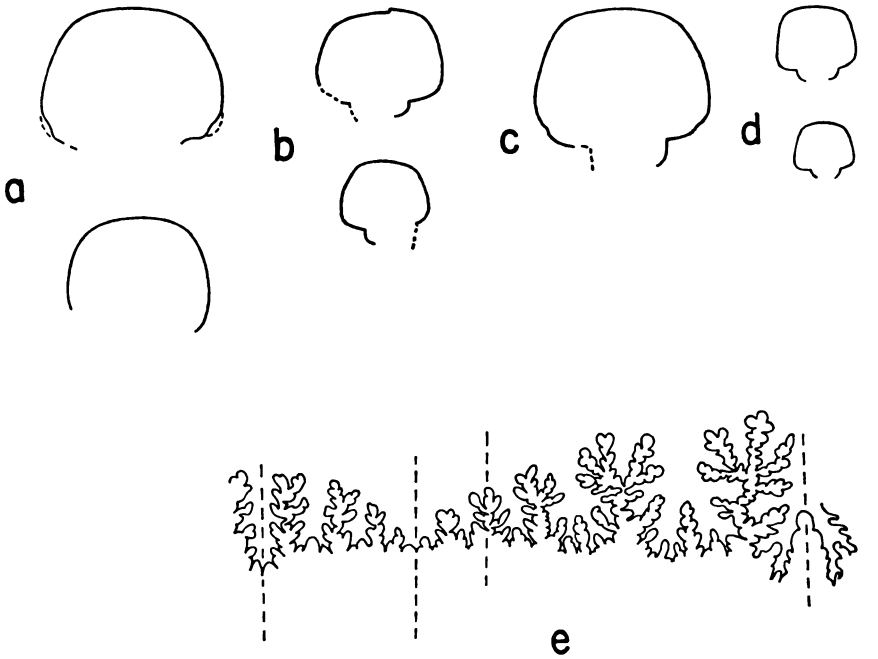


Fig. 35. Cross sections and suture line of *T. subtimotheanus* Wiedmann. *a–d.* Cross sections of three unnumbered specimens collected by Stoliczka from the Ootatoor Group, India, and donated to the Musée d'Histoire Naturelle de Genève. *e.* Suture line redrawn from Kossmat, 1894.

Remarks

This species is close to *T. rectangularis* and to *T. collignoni,* but possesses an additional internal saddle and more persistent and prominent constrictions in the later whorls.

The measurements given by Kossmat (1895, p. 134) for his larger specimen seem to be in error, as they do not fall near the growth curves based on the other specimens. If his measurements are correct, and if the large specimen is truly conspecific, there is a marked involution accompanied by exceptional broadening of the cross section in the adult volutions.

Crick's specimen (BM C18142; 1907, p. 172, pl. 10, fig. 15) from False Bay, Zululand, differs from the Indian specimens in the absence of strong, deep constrictions, especially across the umbilical edge, and a total of only three internal saddles. The other shell characters seem well within the range of variation of the Indian species and this specimen is certainly a close relative of *T. subtimotheanus.* With the data at hand I hesitate to do more than suggest that it may constitute a taxon distinct from *T. subtimotheanus.* Its measurements are included in the table of measurements of *T. subtimotheanus* for comparison.

Specimen C 2609a in the British Museum should be identified with *T. subtimotheanus.*

Tetragonites collignoni Breistroffer, 1940

(Pl. 5, fig. 2–5)

1928 *Lytoceras* (*Tetragonites*) *kiliani* mut. Jacobi Collignon, Annales Paléont., vol. 17, p. 18, pl. 1, figs. 19, 19a.

1940 *Tetragonites collignoni* nov. nom = *T. kiliani* mut. Jacobi Coll. 1928 and 1931; Breistroffer, Vraconien, Salazac, p. 111.

1962 *T. collignoni* Breistroffer, Wiedmann, Vascogot. Kreide, p. 171.

1964 *Tetragonites blaisoni* Collignon, Atlas Foss. Caracter, Madagascar, Cenomanian, pl. cccxxiv, fig. 1448; *Tetragonites jallaberti* Pictet var. *ampakabensis* Collignon, *ibid.*, pl. cccxxv, fig. 1449.

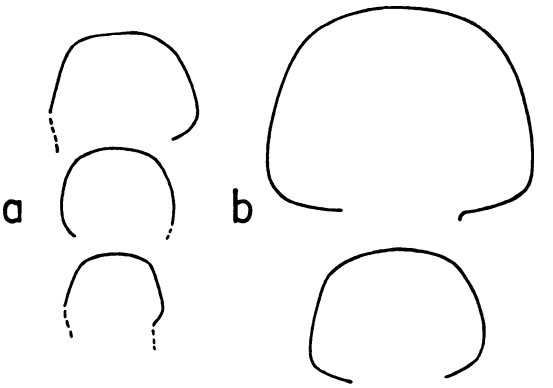


Fig. 36. Cross sections of *T. collignoni* Breistroffer. *a.* MCC 1448, from Atlas des Fossiles Caracter. de Madagascar. *b.* MCC 1449, same publication as above.

Description

The species probably reaches at least a moderate size for the genus, judging from the two calcareous specimens recently described by Collignon (1964). The larger specimen probably has a part of the living chamber preserved at 54 mm diameter, though this cannot be ascertained for sure without destroying part of the specimen. The cross section is markedly trapezoidal in the holotype and in these two specimens and also in a series of about 160 juvenile pyritic internal molds also from the lower Cenomanian of Madagascar (MCC localities 478, 485).

The measurements show a progressive change in their ratios with an increase in size. With growth, the umbilical diameter becomes smaller while the height and width of the whorl become larger when compared against the shell diameter.

The constrictions are prominent throughout all stages represented, though their position is somewhat masked by the external shell in the large specimen described above (Cenomanian Atlas #1449). Constrictions seem to appear in the first volution. At about 10 mm diameter the average shell has 4 constrictions; at about 15 mm diameter the average is 5 constrictions on the last volution. The larger two shells probably have 6 and 7, respectively, though neither is well enough preserved to show all parts of the last volution. Even the small specimens show the strong prorsiradiate concave arch on the flank. The adorally concave arch of the constrictions on the venter is present only in the larger specimens, in the smaller shells the constrictions cross the venter in a straight line.

The elements of the external suture are practically invariable in number, position, and configuration. No. 1448 shows a greater extension of the septum than the small pyritic shells, but this is a normal result of growth. The 1S is invariably trifid, 1L has a length/width ratio that varies from slightly greater than 2:1 in the small specimens to approximately 4.5:1 in No. 1448. The internal suture is not accessible in the larger specimens, but in the pyritic molds the septum clearly shows two large internal saddles and a third small one.

Comparison

This species differs from the group of forms in the *T. kitchini* branch of the genus in having more internal elements in the suture and in the characteristic trapezoidal cross section. From the members of the *T. timotheanus* branch of the genus this species differs in its relatively small umbilicus, the strongly concave arch of the constrictions on the flanks and venter, and the trapezoidal cross section. Within the *T. rectangularis* branch it is closely similar to *T. rectangularis,* and *T. subtimotheanus.* From the former it differs in the development of the cross section, and the more regular development of the constrictions. (See also discussion under *T. rectangularis.*) *T. subtimotheanus* Wiedmann, according to the drawings of Kossmat, has four saddles in the internal suture compared to the three in *T. collignoni* (pyritic molds).

TABLE 13

Measurements of Tetragonites collignoni Breistroffer

Specimen	D	H	W	U
Cenomanian Atlas #1449	54.0	26.6 (49)	35.4 (66)	10.8 (20)
Cenomanian Atlas #1448	36.2	16.6 (46)	22.0± (61)	9.8 (27)
	31.6	13.7 (43)	19.8± (63)	8.8± (28)
Specimen from MCC 478	18.0	7.5 (42)	10.2 (57)	5.5 (30)

Distribution

All specimens come from the lower Cenomanian of Madagascar.

Remarks

The small pyritic specimens (MCC 478, 485) discussed in several places above, show a strong resemblance to *T. collignoni* Breistroffer from Diégo Suarez, Madagascar, in all details. The constrictions are the same in number and configuration, the suture is similar, the cross section is the same. I have, therefore, identified them with this species.

The two calcareous specimens recently described by Collignon as *T. blaisoni* and *T. jallaberti* var. *ampakabensis* seem to be the logical adult manifestations of the small pyritic forms. Geographic, stratigraphic and morphologic relations suggest this synonymy, but intermediate growth stages will have to be found before it can be documented.

Tetragonites madagascarensis n. sp.

1928 *Lytoceras* (*Tetragonites*) *timotheanus* Mayor. Collignon, Annales Paléont., vol. 17, pl. 1, figs. 18, 18a.

A small pyritic internal mold from Diégo Suarez, Madagascar, in the collections at the University of Lyon represents a taxon near *T. spathi.* This specimen shows 5 well-developed constrictions at 14 mm diameter; the partly visible septal face shows a moderately strong second internal saddle; the cross section is more or less equant with flattened venter and flanks and rounded umbilical edge; a slight but distinct ridge is present above the siphonal line and the constrictions have a slight adorally convex arch.

A second similar specimen from this locality has been figured by Collignon (1928, pl. 1, fig. 18). This specimen is designated here as holotype of *Tetragonites madagascarensis* n. sp. Collignon's specimen is in the Muséum National d'Histoire Naturelle, Paris. The septal face of the holotype shows four lobes on the flank in the external suture and a third relatively strong and a fourth weak internal saddle in the internal suture. This latter does not show in Collignon's photograph as the plate is blurred at that point. The fourth lobe on the flank, however, is easily recognized in the photograph. There is also a slight rise on the venter, which is difficult to see without proper lighting. Like the specimen at Lyon this specimen suggests *T. spathi,* but both lack the strong adorally peaked constrictions on the venter, and Collignon's specimen shows a larger than normal number of elements in the suture.

Measurements.—Holotype:

D	H	W	U
15	6.4 (43)	7.9 (53)	3.8 (25)

Tetragonites sp.
(Pl. 7, figs. 4, 5)

A single specimen of *Tetragonites* in the collections at the Sorbonne is similar in most respects to the *T. rectangularis* group, but has a rounded cross section and a larger umbilicus than most members of that group. The specimen was collected by Petitclerc from a phosphatic greensand at Palud des Moustiers. It was associated with *Desmoceras latidorsatum.*

The specimen has 6 constrictions per volution at 44 mm diameter and 5 at 26 mm diameter. The constrictions are strongly arched concave adorally on the flanks and venter. The external suture has the standard number and position of the elements. The internal suture shows on two moderately well-developed saddles and a very small third saddle.

The measurements given in table 14 show a marked decrease in the size of the umbilicus with growth.

TABLE 14
MEASUREMENTS OF TETRAGONITES SP.

Specimen	D	H	W	U
S—Petitclerk Coll. La Palud des Moustiers	52.8	23.0 (44)	27.5 (52)	15.2 (29)
	38.2	16.4 (43)	21.0 (55)	11.5 (30)
	33.9	14.6 (43)	18.4 (54)	10.3 (30)
	24.9	10.2 (41)	14.1 (57)	7.9 (31)
	18.6	7.3 (39)	10.5± (56)	6.4 (34)

The specimen is obviously different from other taxa described above, but until more data concerning it are established, I prefer not to try to place it in the classification.

Genus *Eotetragonites* Breistroffer, 1947

Type species: *Ammonites depressus* Raspail, 1866 as figured in Kilian (1913, pl. xi, fig. 3) = *Eotetragonites raspaili* Breistroffer, 1947.

The *Eotetragonites* is characterized by the following: (1) a suture like *Eogaudryceras,* but with an irregularly bifid 1S and in some species a small second internal saddle; (2) adorally convex constrictions on the flank and venter; (3) ornamentation of growth lines, lirae, and constrictions; (4) relatively evolute shells with flattened or rounded flanks and venters.

Eotetragonites balmensis Breistroffer, 1936

(Pl. 3, figs. 1–5, 8–11; pl. 4, figs. 9–11)

1908 *Lytoceras* (*Tetragonites*) *jurinianus* (Pictet), Jacob, Ammonites crétacé moyen, pl. i, figs. 10, 12.

1910 *Tetragonites timotheanum* Mayor sp., Fallot, Gault des Baléares, p. 8, pl. iii, fig. 7.

1936 *Tetragonites balmensis* Breistroffer, Subdivisions Vraconien, p. 64.

1962 *Tetragonites epigonoides* Wiedmann, Unterkreide—Ammoniten Mallorca, p. 80, pl. 6, figs. 3, 4.

1963 *Tetragonites rectangularis* Wiedmann, Collignon, Albien Atlas Madagascar, pl. ccxlix, fig. 1070.

Tetragonites subtimotheanus Wiedmann, Collignon, Albien Atlas Madagascar, pl. ccxlix, fig. 1071.

Tetragonites aff. *timotheanus* Collignon, Albien Atlas Madagascar, pl. ccxlix, fig. 1067.

Tetragonites aff. *timotheanus* Collignon, Albien Atlas Madagascar, pl. ccxlix, fig. 1068. (Strongly weathered).

Description

The largest specimen from Balme de Rencurel is 111 mm in diameter and still septate indicating a much larger size for the complete shell. Fortunately there exists a complete series of growth stages in the University Grenoble collections from Balme de Rencurel so the ontogeny may be described and the smaller individuals, those usually encountered may be identified.

Measurements.—The umbilical diameter shows a very large range of variation (20 to 32 percent of shell D) and also shows a definite trend from larger to smaller percentage of the shell diameter as the shell grows.

Constrictions.—Constrictions are distinctly, but irregularly, developed and numerous up to a diameter of 30–40 mm after which stage they are, when present, weak, partly developed (showing only on the flank) and irregularly spaced. The constrictions are arched convexly forward (prorsiradiate convex) on the flank and cross the venter in a straight line or with a very slight posterior sulcus.

Cross section.—The holotype shows a rounded cross section with rounded venter and flanks. The peripheral shoulder is not developed and the umbilical edge is rounded. The maximum width is just below the midflank. In other specimens, however, the maximum width is at the umbilical edge, especially in the younger stages.

Suture.—Lobes and saddles of the septum are fairly strongly extended, the length/width ratio of the 1L ranging from about 2.5 to 1 at 10 mm diameter to

TABLE 15

MEASUREMENTS OF EOTETRAGONITES BALMENSIS (BREISTROFFER)

Specimen	D	H	W	U
FG Balme de Rencurel, Jacob Pl. V, fig. 1. Largest specimen	111.0	51.8 (47)	52.0± (47)	22 (20)
Jacob Pl. I, fig.12 holotype	68.4 48.6	32.8 (48) 22.5 (46)	36.3 (53) 25.8 (53)	17.2 (25) 13.2 (27)
Jacob 2 smaller specimens	50.0 41.1	23.2 (46) 17.9 (44)	28.2 (56) 23.0 (56)	14.1 (28) 12.4 (30)
	34.5 26.3	15.0 (43) 11.1 (42)	18.4 (53) 14.5 (55)	10.6 (31) 8.3 (32)
Sorbonne Reboul Coll. Balme de Rencurel 4 specimens	35.8 25.6	15.8 10.3	.... 15.5	10.6 8.4
	27.1 25.5 20.8	11.1 10.9 8.7	.... 14.6 12.2	9.2 8.5 6.7
FG Son Vida—Fallot Coll. SV 8	38.7 32.3	16.8 (43) 13.7 (42)	21.5 (56) 18.1 (56)	12.0 (31) 10.6 (33)
SV 6	33.7	14.4 (43)	18.6 (55)	11.0 (33)
SV 2	28.5 23.0	12.2 (43) 9.3 (40)	15.8 (55) 12.7 (55)	8.9 (31) 7.5 (33)
SV 1	26.4	10.9 (41)	14.6± (55)	8.6 (33)
SV 7	18.1	7.0 (39)	10.2 (56)	6.6 (36)
MSHNB A94*	44	18 (42)	23 (53)	14 (32)
MSHNB A63a*	22	9 (41)	13 (59)	7 (32)
Collignon Coll.	45.0 32.2	21.6 (48) 13.8 (43)	25.9 (58) 19.3 (60)	11.9 (26) 9.5 (30)
Collignon Coll. Spec. 1070	41.0 30.6	17.6 (43) 12.6 (41)	22.8 (56) 17.3 (56)	12.3 (30) 9.0 (29)
Collignon Coll. Spec. 1071	46.0 43.9 34.3	20. (43) 19.6 (45) 14.7 (43)	24.5 (53) 24.5 (56) 19.5 (57)	12.9 (28) 12.8 (29) 10.9 (32)
Collignon Coll. Spec. loc. 421 Collignon Coll. Spec. loc. 435	37.3 22.8	16.3 (44) 9.0 (39)	20.0 (54) 12.5 (55)	12.0 (32) 7.9 (35)
FG Gevrey Coll. Prés de Rencurel	37.3 31.1	16.5 (44) 13.6 (44)	22.0± (59) 18.4± (59)	10.2± (27) 9.1± (29)

* After Wiedmann.

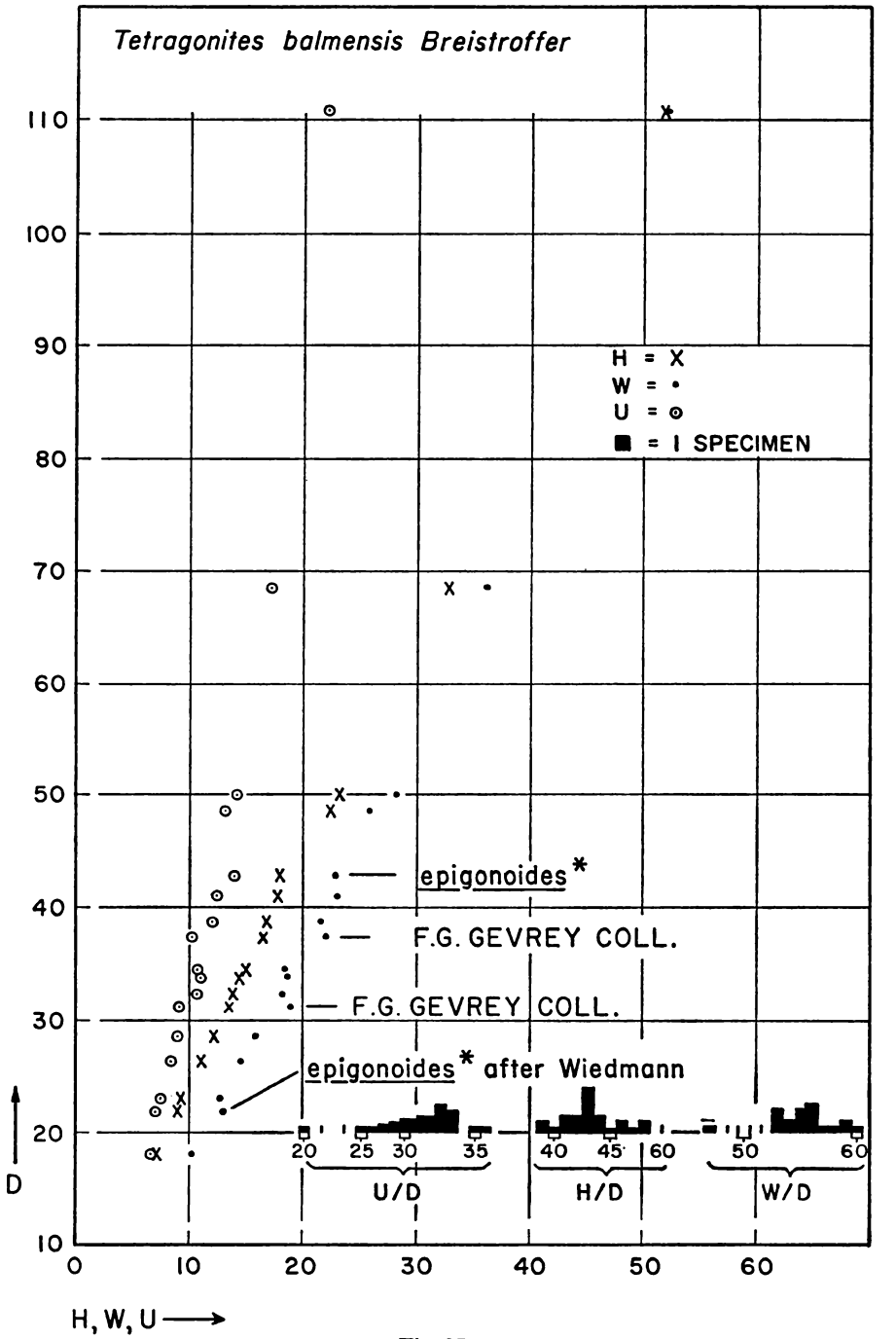

Tetragonites balmensis Breistroffer
H = X
W = •
U = ⊙
■ = 1 SPECIMEN
epigonoides*
F.G. GEVREY COLL.
F.G. GEVREY COLL.
epigonoides* after Wiedmann
U/D
H/D
W/D
D
H, W, U

Fig. 37.

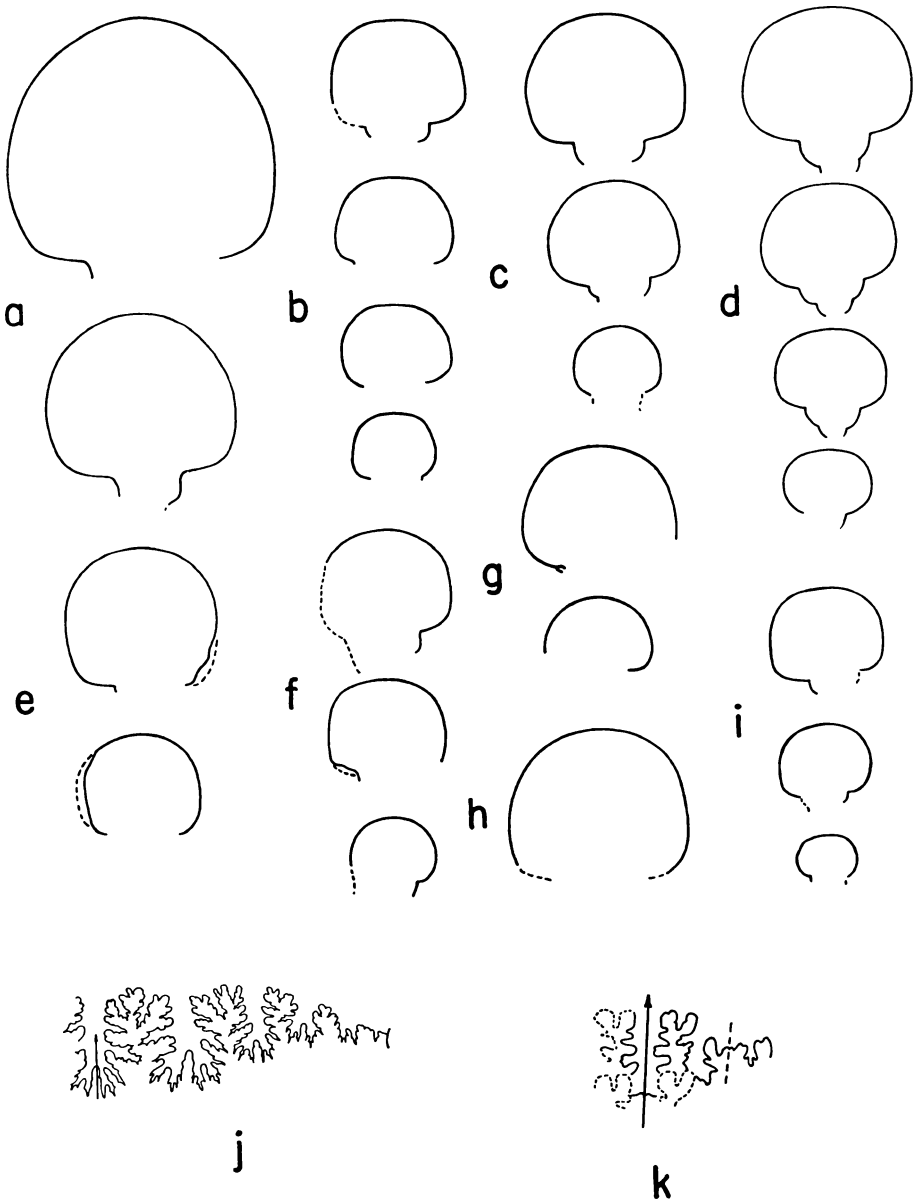


Fig. 38. Cross sections and suture of *Eotetragonites balmensis* (Breistroffer). *a* and *e*. Holotype FG Collection, Balme de Rencurel, middle Albian. *b*, *c*, and *i*. FG Fallot Collection SV6, SV8, SV2, respectively, Son Vida, Mallorca. *d*. MCC, figured 1963, Albian Atlas des fossiles caracter. de Madagascar, specimen 1070, Betioky, Madagascar. *f*. FG Collection unnumbered, Balme de Rencurel. *g*. FG Gevrey Collection unumbered, Prés de Rencurel, lower Albian. *h*. Holotype *T. epigonoides*, after Wiedmann 1962*b*, pl. 6, fig. 4b, Son Surdeta, Mallorca. *j*. Holotype *T. epigonoides*, after Wiedmann 1962*b*, fig. 29. *k*. Internal suture of fragmentary specimen from Balme de Rencurel, BMNH C54394.

6 or 7 to 1 at 65 mm diameter. The septal face is bent about at the position of maximum inflation so that the lower third is inclined to a rectiradial line and the upper two-thirds is not. The septum shows one very strong and one weak internal saddle. A large septal lobe is present on the face of the preceding septum. On some examples the internal lateral lobe also is sutured to the preceding septum.

Distribution

This species is one of the most widespread in the family being represented both in Africa and Europe. It is relatively abundant at the Balme de Rencurel locality in the Vercors Range and also in Mallorca. Only the specimens from Mallorca occur in a stratigraphic situation where reworking is improbable. Wiedmann (1962*b*, p. 81) has given a lower Albian age to these localities. It is probable that the range includes all lower Albian strata and lower middle Albian strata as well, considering the common occurrence at Balme de Rencurel.

The specimens from Madagascar were collected from a condensed deposit of upper Albian age, so it is possible that the range of the species may include some upper Albian strata as well (Collignon, 1963, p. 2).

Remarks

The holotype of Wiedmann's species, *T. epigonoides* from Son Surdeta, Mallorca, differs from the type specimen from Balme de Rencurel in having a few more constrictions (9 vs. 7 in *E. balmensis*) and slight differences in whorl shape. Both these characters are variable at Balme de Rencurel. After examining 6 specimens from Son Vida, Mallorca (Fallot Collection, FG) showing a similar range of variability, I do not believe it is possible to separate the two samples taxonomically and, therefore, I suppress *T. epigonoides* as a junior synonym of *E. balmensis*.

A single specimen from Prés de Rencurel (Gevrey Coll., FG) also falls within the range of variability of the topotype material. The locality of this specimen is lower Albian according to Breistroffer (1931, p. 193), but fragments of upper and middle Albian and even Cenomanian genera have also been collected here. The preservation of this specimen is similar to other lower Albian species and it probably lived with them.

Several specimens in General Maurice Collignon's collection from Betioky, Madagascar (localities 421 and 435) are very close to *E. balmensis* in configuration of the constrictions, development of the internal saddles, and similarity of whorl shape. Differences between individuals are apparent, but the group characteristics are the same and I have identified them with *E. balmensis*.

Comparison

E. balmensis differs from most other members of the genus in its rounded cross section. The only previously described taxon with a rounded cross section is the poorly known *E. jallabertianus* (Pictet) which has much stronger and deeper constrictions.

TABLE 16

COMPARISON OF SPECIES OF TETRAGONITES AND EOTETRAGONITES.

SPECIES	AGE			CONSTRICTIONS								ORNAMENT		I S		NO. INTERNAL SADDLES**					H/D	W/D	U/D	CROSS SECTION					
				FLANK			VENTER			← DEEP	NUMBER	W/ ON p.s.*	W/O ON p.s.*	trifid	irreg. bifid	1 1	2	2 1	3	3+	30 35 40 45 50	40 45 50 55 60	20 25 30 35 40						
	Apt	Alb	C	→	→	→	)	)	)	SHALLOW →																			
E. duvali	—			X			X	X		-	1 - 12				X	X													
jacobi	—			X			X			—	irregular	X			X	X													
wintunius	—			X			X			—	up to 13	X			X	X													
shoupi				X			X			—	up to 17	X			X														
kossmatelliformis	—			X			X			—	up to 12																		
raspaili	—			X			X			—																			
umbilicostriatus		-		X			X			—	13		X																
gardneri	—			X			X	X		—	6	X			X	X												X	
gainesi		—		X			X			—	up to 18		X		X														
balmensis		—		X			X	X		—	up to 9		X		X	X													
T. heterosulcatus	—			X					X	—	5 to many		X		X	X												X	
crudus		—				X			X	---	9		X		X	X													
subbeticus	---				X			X		—	5		X	X			X													
lecontei		—			X			X	X	—	5 - 8		X	X			X													
bournensis		—				X				—	7? or 0		X	X				X											
hulenensis		—			X	X			X	—	6-8 or 0		X	X	X			X											X	
kitchini		—				X			X	—	5-7		X		X	X														
rectangularis		—				X			X	—	4-7		X		X			X												
rect. diegoensis		-				X			X	—	7+			X				?												
rect. alaskaensis		—			X	X		X	X	—	6+		X	X			X	X												
nautiloides		-									0		X		X		X	?												
jurinianus		—									0		X	X	X			X												
timotheanus		-			X		X	X		—	4-8 or 0		X	X	X			X												
spathi		-				X	X			—	6-7		X																	
subtimotheanus		-				X			X	—	5-8?		X		X					X										
collignoni		-				X			X	—	5		X	X																
jonesi		-				X			X	—	6-7		X	X					?											
madagascarensis		-					X			-	5									X										

p.s.* = PERIPHERAL SHOULDER

** = UPPER NUMBERS REFER TO MAJOR SADDLES
LOWER NUMBERS TO INCIPIENT DEVELOPMENT ONLY

▨ RANGE EXCLUDING LARGE ODIUM SPECIMEN

The assignment of this species to *Eotetragonites* is made on the following basis: (1) The cross section, the constriction pattern, and the number and position of the elements of the internal suture are different than the two main groups of *Tetragonites,* the *T. rectangularis* and *T. timotheanus* branches; (2) though the internal suture is similar to the *T. kitchini* branch of the genus, the cross section and especially the configuration of the constrictions is different from other species placed in this branch though there is variation in the latter feature; (3) the species occurs too high in the sequence to be a transitional form between *Eotetragonites* and *Tetragonites,* though it shows a range of variation and morphologic features that would qualify it for such a position. Thus it seems that classified as *Tetragonites* it is an evolutionary anomaly, whereas classified as *Eotetragonits* it makes a logical descendant of an undescribed California *Eotetragonites* with a circular cross section.

Eotetragonites gardneri n. sp.

(Pl. 1, figs. 6–9)

DESCRIPTION

Size.—The only known specimen measures 32 mm in diameter and is completely septate. Thus the shell probably reached a minimum adult size of 50 mm.

Measurements.—Holotype UCR 412/1:

D	H	W	U
32.4	12.0 (37)	14.2 (43)	12.3 (38)
26.5	9.4 (35)	12.0 (45)	10.5 (40)

Cross section (fig. 7a).—The cross section shows flattened, slightly convergent flanks and flattened venter with the widest part of the shell being at the peripheral shoulder. Both the peripheral shoulder and the umbilical edge are abruptly rounded giving the cross section a distinctly trapezoidal shape.

Constrictions.—The constrictions number 6 per volution on the holotype at 32 mm diameter. They are prorsiradiate convex on the flanks and straight to slightly convex adorally on the venter. On the later preserved parts of the shell a faint development of lirae is present on the venter and peripheral shoulder and on the umbilical wall.

Suture.—The external suture shows the standard number and position of elements for the genus except for the variable asymmetry of the first saddle. The right side shows the first saddle to be more bifid in its character than the left side, which exhibits the normal irregularly bifid termination characteristic of the genus.

The septum shows one strong and one weak internal saddle are present in the internal suture.

DISTRIBUTION

The species is known from a single shell from the *Acanthohoplites gardneri* zone near Huling Creek, Shasta County, California (UCR locality 412). It was associated with *Tetragonites lecontei* n. sp., *Acanthohoplites gardneri* Anderson, *Ptychoceras* sp., *Phylloceras velladae* (Michelin) var. and another phyllocerid tentatively referred to *Salfeldiella.* It occurs above beds containing *Epicheloniceras* sp. and *Acanthohoplites* and below beds containing *Diadochoceras* sp. Its age seems fairly well established as upper Aptian.

Comparison

Eotetragonites gardneri n. sp. differs from other members of the genus in the shape of its cross section, which is slightly trapezoidal with the widest part of the whorl at the peripheral shoulder. It resembles *Tetragonites heterosulcatus* Anthula in this respect, but the configuration of the constrictions in Anthula's species is prorsiradiate concave on the flanks rather than prorsiradiate convex.

Remarks

The septum is not perfectly shown in the specimen. For this reason it cannot be determined whether the second internal saddle is of the *Eotetragonites* type (pl. 1, figs. 1 and 5), showing a saddle fold of the septum straddling the umbilical seam, or of the *T. kitchini* type where an independent but small saddle is developed.

The faint ornamentation of the venter and peripheral shoulder recalls that seen in the slightly earlier *Eotetragonites wintunius* and suggests a close relationship with that species.

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PLATES

PLATE 1

Figs. 1, 4. *Eotetragonites jacobi* (Kilian). MC Collection, upper Aptian, near Blieux (Basses-Alpes), France. Note the ventral ornamentation, incipient development of the second internal saddle from elements of the umbilical lobe, and the weak constrictions and high height-width ratio.

Figs. 2, 3. *Eotetragonites duvali* (d'Orbigny). Gerard Thomel Collection, upper Aptian, near Hyèges (Basses-Alpes), France. Note the marked convex flank and ventral constrictions.

Fig. 5. *Eotetragonites jacobi* (Kilian). Gerard Thomel Collection, upper Aptian, near Hyèges, France. Note the incipient development of a second internal saddle.

Figs. 6–9. *Eotetragonites gardneri* n. sp. Holotype, UCR 412/2, from the *Acanthohoplites gardneri* zone, near Huling Creek, Shasta County, California. Fig. 9, arrow, shows a little stronger development of the internal second saddle than in *E. jacobi*.

Figs. 10–19. *Tetragonites timothcanus* (Pictet). Figs. 10, 11, 12, 17 from Entrèves-en-Bauges (Savoie), France. Figs. 14, 15, the holotype of *T. kiliani* Jacob. Figs. 13, 16, 18, 19 from Salazac (Gard), France. All specimens from FG Collection except fig. 11 = UCR 677/1. Note the variation in the configuration of the constrictions on the venter on specimens from Salazac.

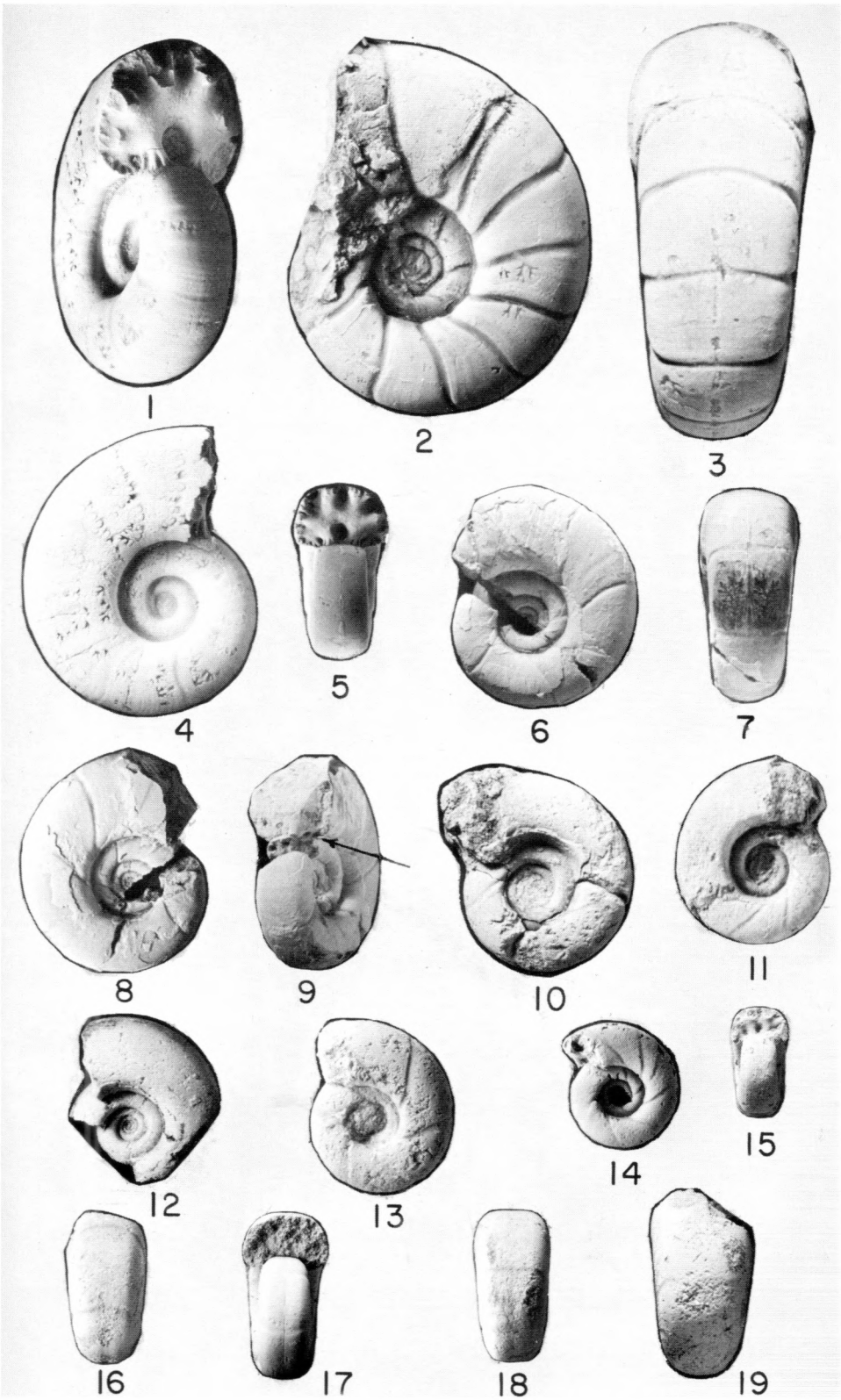

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PLATE 2

Figs. 1–4. *Tetragonites jurinianus* (Pictet). Figs. 1, 2, holotype, MHNG Collection, Mt. Saxonet (Savoie), France. Figs. 3, 4. Small specimens from Entrèves-en-Bauges (Savoie) showing rounded venter and angular umbilical edge.

Figs. 5–10. *Tetragonites nautiloides* (Pictet). Figs. 5, 6, neotype, MHNG Collection, Mt. Saxonet (Savoie), France. Figs. 7, 8, FG Collection from Rosans: le Buisson (Hautes-Alpes), France. Figs. 6 and 7 show growth rugae on the shell and on the internal mold. Fig. 8 indicates only two strong saddles are present in the internal suture in *T. nautiloides* at this size. Figs. 8, 9, 10, and 5 show a gradation in the roundness of the venter. Fig. 9, FG Collection, Arnayon (Drôme), France. Fig. 10, FG Collection from Salazac (Gard), France.

Figs. 11–14. *Tetragonites kitchini* (Krenkel). Figs. 11, 13, MC Collection, localities 87 and 435 from Madagascar. Figs. 12, 14, MHNG Collection from Manohonda, Madagascar. Note the small, but well developed second internal saddle as shown on the septal face.

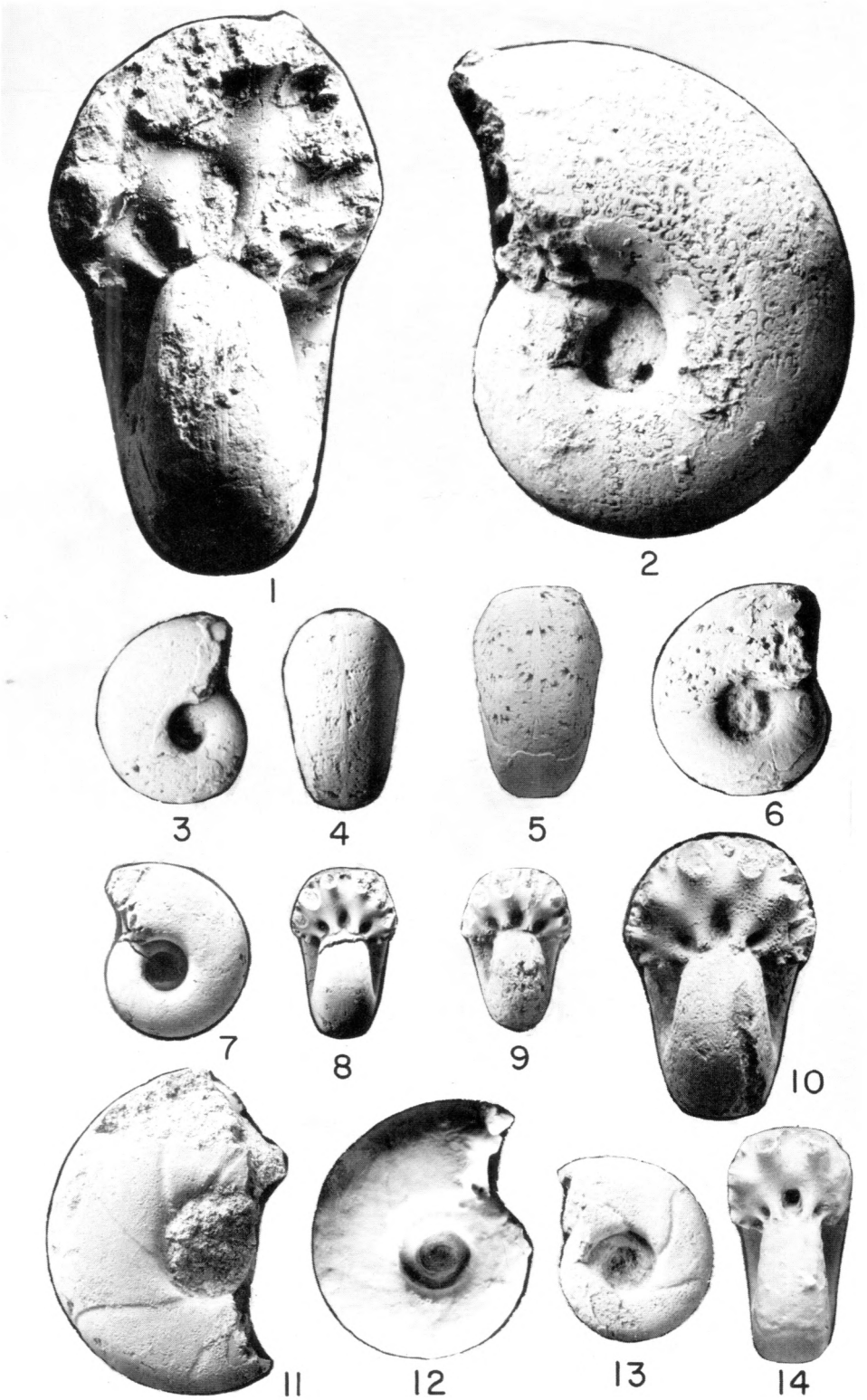

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PLATE 3

Figs. 1–5, 8–11. *Eotetragonites balmensis* (Breistroffer). Figs. 1, 2, FG Collection, SV 1 SV 2 from Son Vida, Mallorca; fig. 2 slightly enlarged. Figs. 3, 10, 11, FG Collection, Balme de Rencurel, middle Albian. Figs. 10 and 11, the holotype; note the convex flank and almost straight ventral constriction pattern and, as shown on the septal face, the development of a second small saddle in the internal suture. Figs. 4, 5, FG Gevrey Collection, Prés de Rencurel (Isère), France, lower Albian. Figs. 8, 9, MC Collection specimens 1070, 1071, respectively, from Loc. 435, a polyzonal deposit of Albian age, Betioky, Madagascar. Note the development of the second internal saddle in fig. 8 as compared with the holotype; the septal lobe in fig. 9.

Figs. 6, 7. *Tetragonites "rectangularis"* Wiedmann, Collignon. MC Collection, Loc. 435, Betioky, Madagascar. Lateral and apertural views of specimen 1069. The impression of the septal lobe and of the internal suture show on the septal face and venter of the preceding volution. Also a remnant of the preceding internal lateral lobe can be seen sutured to the septal face on the left side in the photograph.

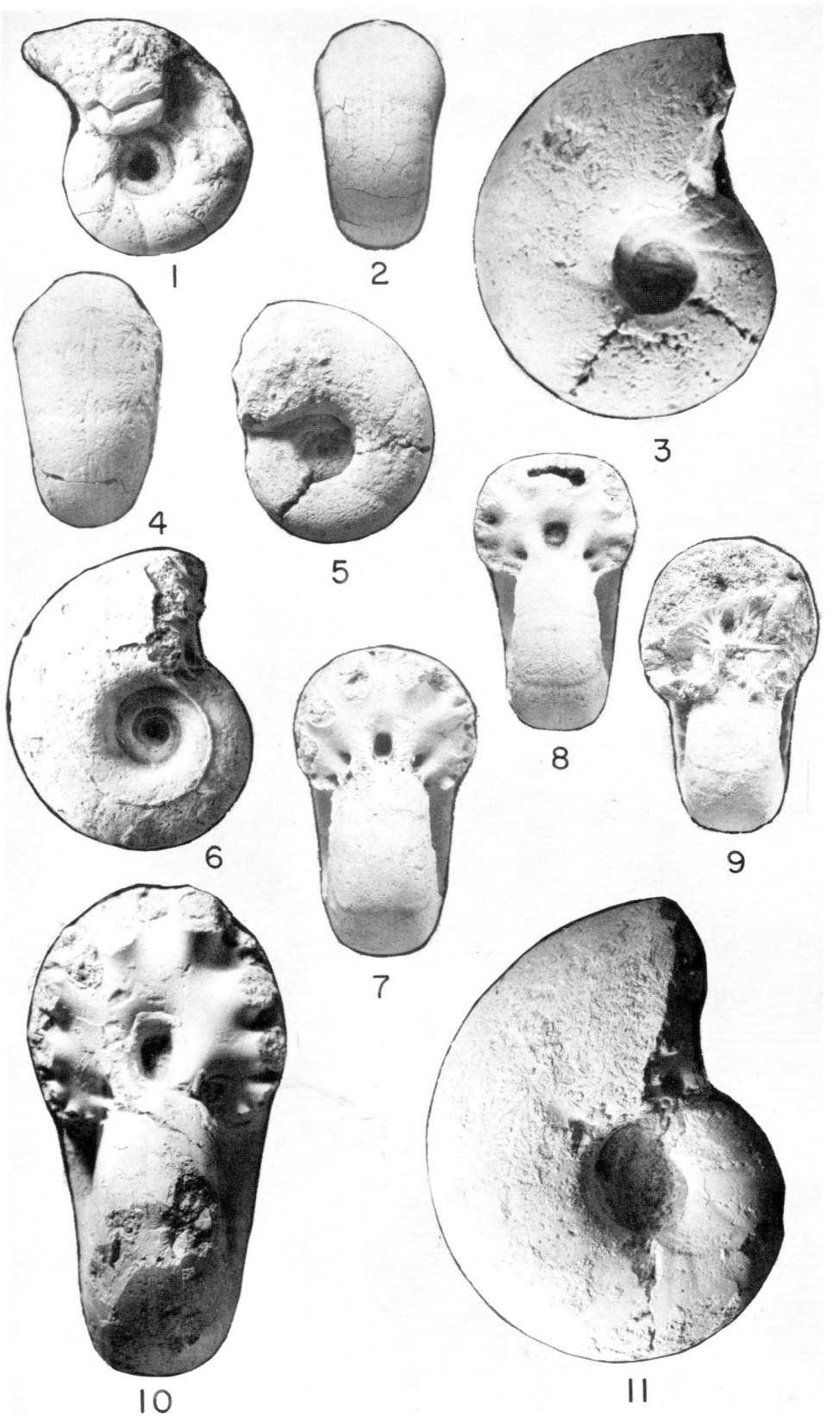

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PLATE 4

Figs. 1–7. *Tetragonites rectangularis* Wiedmann. Figs. 1, 4, 6, FG Fallot Collection, SV 9, SV 3, and SV 5, respectively, showing constriction pattern, cross section and septal face, Son Vida, Mallorca, slightly enlarged. Fig. 2, OV Collection, specimen 546/2, Escragnolles (Alpes-Maritimes), France. Note the irregular development of the constrictions on this specimen and on the holotype, fig. 7. Fig. 3, MHNG Wi VK/7, La Goudinière (Savoie), France, upper Albian. Fig. 5, FG Fallot Collection, Son Vida, Mallorca. Small specimen showing the more quadrate cross section. Fig. 7, the holotype, MHNG Wi VK/10, La Goudinière, upper Albian. Note the slightly oblate form resulting from distortion of the specimen.

Fig. 8. *Tetragonites rectangularis* subsp. *diegoensis* (Collignon). Holotype, specimen 1073, MC Collection, upper Albian, Mont Raynaud, Madagascar. Note the closely spaced strongly concave constrictions.

Figs. 9–11. *Eotetragonites balmensis* (Breistroffer). Figs. 9, 10, MC Collection specimens 1070, 1071, respectively, Betioky, Madagascar. Fig. 11, FG Collection, Balme de Rencurel (Isère), France. Note the similarity of constriction pattern in the three specimens. Fig. 10 slightly enlarged.

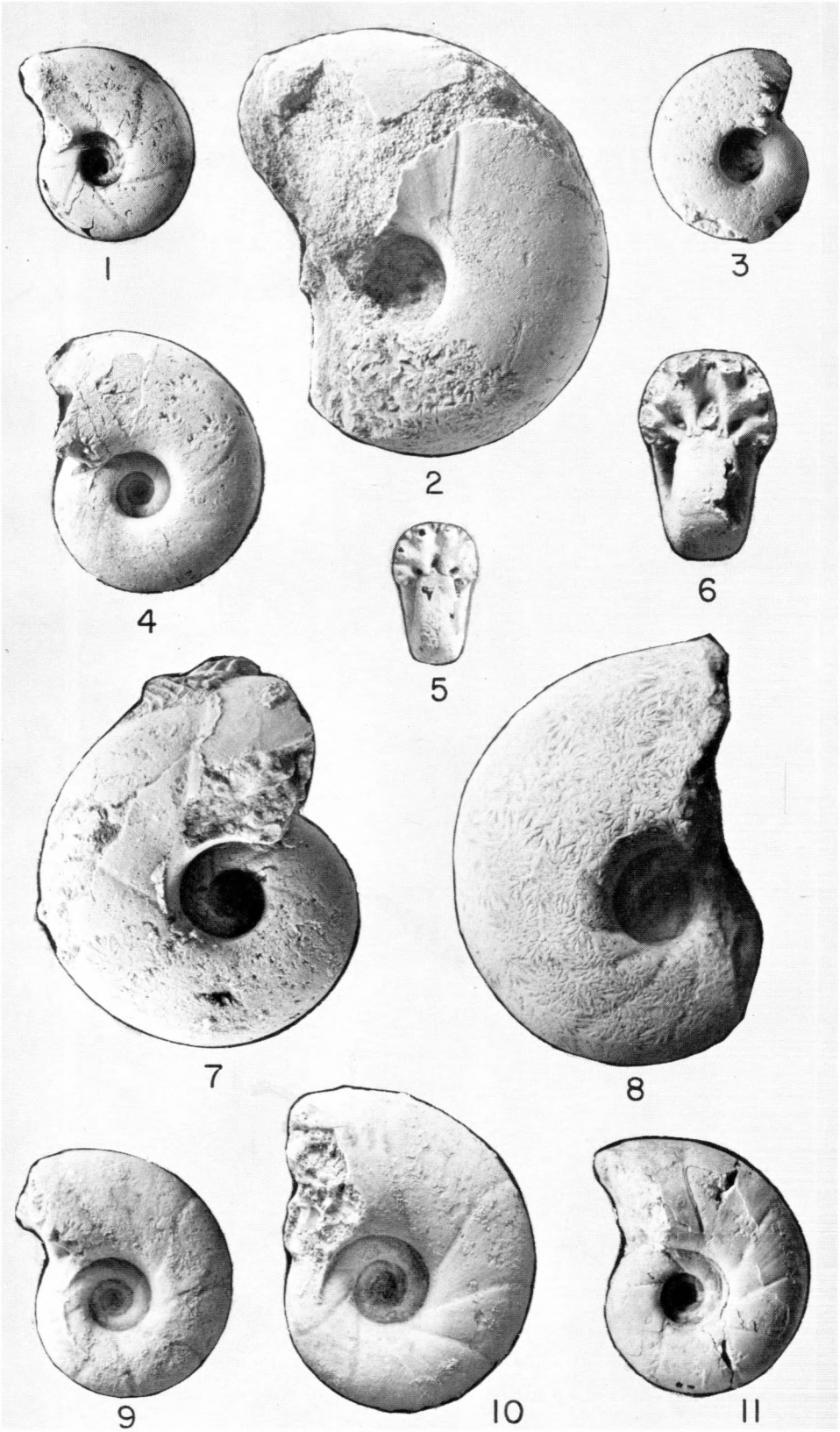

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PLATE 5

Fig. 1. *Tetragonites rectangularis* Wiedmann. OV Collection 546/1, Escragnolles (Alpes-Maritimes), France. Oblique view of the septal face showing two principal saddles and an incipient third internal saddle developing near the umbilical seam.

Figs. 2–5. *Tetragonites collignoni* Breistroffer. Lateral and ventral views MC Collection specimens 1448, 1449, respectively, lower Cenomanian, Madagascar. Note the strongly arched constrictions.

Figs. 6–10, 12. *Tetragonites spathi* Breistroffer. Figs. 6, 10, holotype, FM Collection. Note the incipient keel on the venter and the strongly anteriorly peaked constrictions. Figs. 7–9, 12, FG Collection speicmens showing weaker development of the constrictions in smaller specimens and weaker development of the incipient keel. All specimens from Banc des Lombards near Cassis (Bouches-du-Rhône), France, lower Cenomanian.

Figs. 11, 13. *Tetragonites subtimothcanus* Wiedmann. MHNG Collection unnumbered specimen from Ootatoor Group, India. Fig. 11 shows the septal lobe in a ventral view.

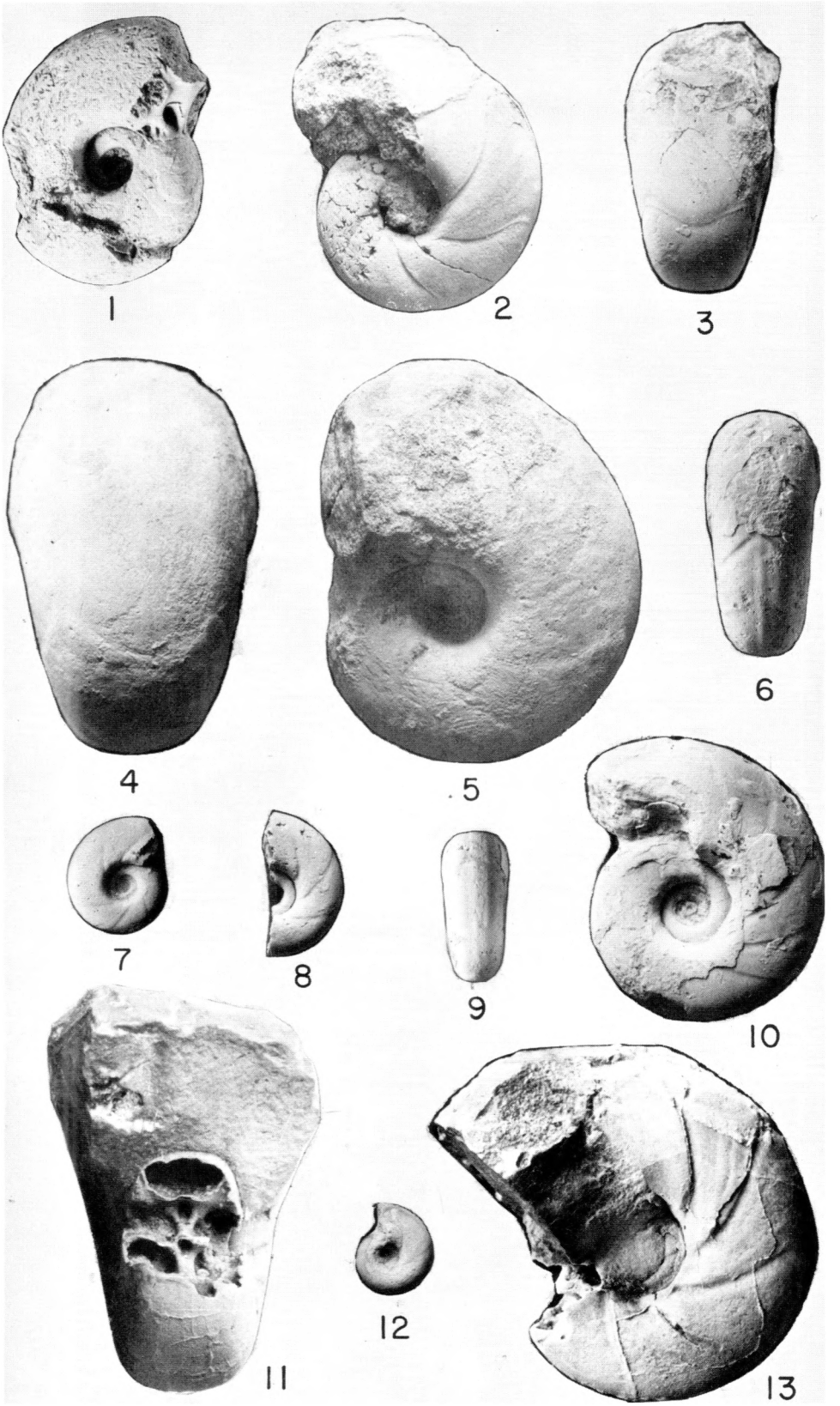

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PLATE 6

Figs. 1–4. *Tetragonites jonesi* n. sp. USNM Collection, Alaska, 155478, 155477 (the holotype), and 155479. Fig. 3, the holotype, note the very small umbilicus.

Figs. 5–8. *Tetragonites subtimothcanus* Wiedmann. MHNG Unnumbered specimens from the Ootatoor Group, India

Figs. 9, 10, 14. *Tetragonites rectangularis* subsp. *alaskaensis* n. subsp. USNM Collection specimens 155474 and 155475, respectively, Alaska.

Figs. 11–13, 15. *Tetragonites bournensis* n. sp. Figs. 11, 12, FG Collection, Balme de Rencurel (Isère), France, middle Albian, showing very faint constrictions and the cross section. Figs. 13, 15, the holotype, UCR Collection 676/1. The incipient third internal saddle can be seen along the direction of the arrow.

Figs. 16–19. *Tetragonites hulenensis* n. sp. Fig. 16, UCR Collection 98/4. Figs. 17, 19, USNM Collection 155480, *Brewericeras* zone, Alaska. Notice the reduction in strength of constrictions in the larger stages of this specimen. Fig. 18, UCR Collection 402/21, East Fork of Huling Creek, Shasta County, California.

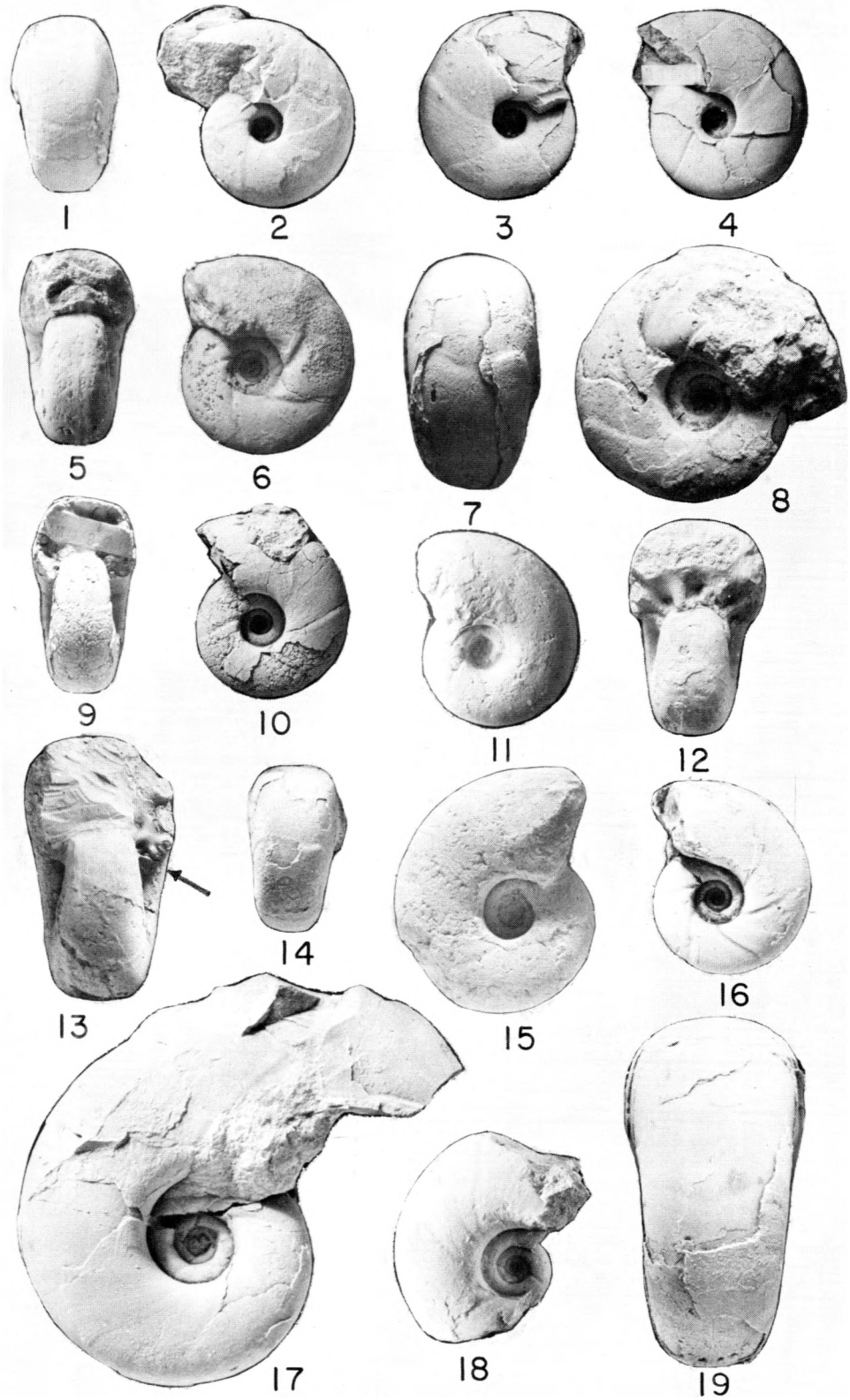
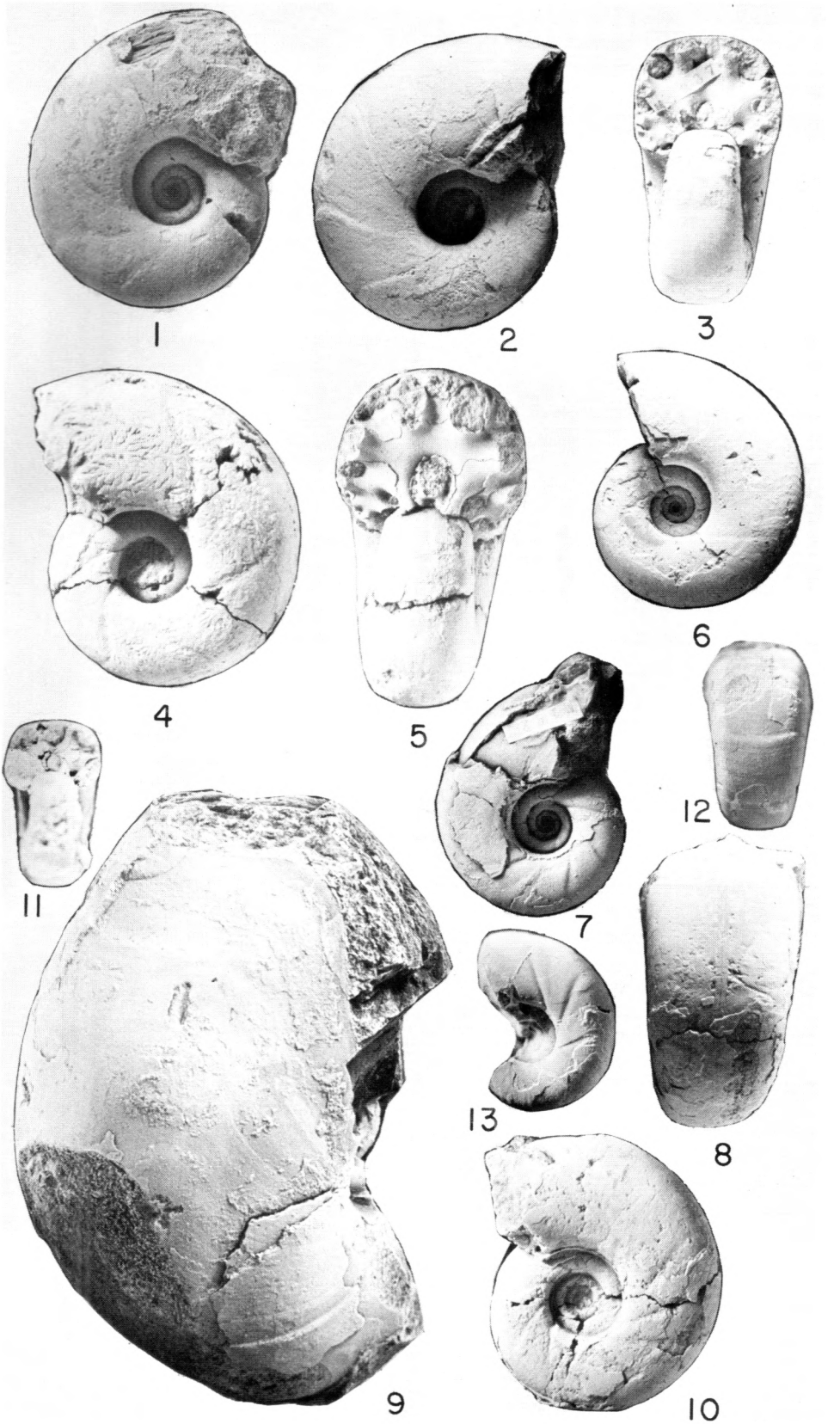

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PLATE 7

Figs. 1, 3, 6, 7, 8, 10. *Tetragonites hulenensis* n. sp. Figs. 1, 8, 10, UCB 14853 and 14854, respectively, previously figured by Anderson, 1902. Figs. 3, 6, holotype, USNM Collection 155481a, Alaska, *Brewericeras* zone. Fig. 7, smaller specimen from locallity of the holotype, USNM 155481b. Note the closely spaced, weak constrictions.

Figs. 2, 9. *Tetragonites rectangularis* subsp. *alaskaensis* n. subsp. Fig. 2, the holotype, USNM Collection 155473, middle Albian, *Cleoniceras* zone, Queen Charlotte Islands, Canada. Fig. 9, large specimen showing the margin of the aperture, USNM Collection 155476, middle Albian, Queen Charlotte Islands.

Figs. 4, 5. Tetragonites sp. S-Petitclerc Collection, Palud des Moustiers (Basses-Alpes), France. Note the *E. balmensis* type cross section and septal face combined with the *T. rectangularis* type constrictions.


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