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The Albian and Cenomanian Tetragonitidae (Cretaceous Ammonoidea), with Special Reference to the Circum-Indic Species

By JOST WIEDMANN[1])

ABSTRACT

The tetragonitids of Albian and Cenomanian age are discussed, and their systematics and phylogeny briefly treated. Special attention is given to the Circum-Indic species and subspecies (*T.* "*timotheanus*" auct., *T. kitchini*, *T. ampakabensis*, *T. blaisoni*, *T. subtimotheanus*, *T. nautiloides* n. ssp.?), which especially need more detailed description and refiguration. Discussion of the North American equivalents becomes necessary, since M. A. MURPHY (1967a) has proposed a number of new species. This leads to a critical review of tetragonitid paleobiogeography and the problem of faunal provinces.

Carinites n. gen. is proposed for the keeled Cenomanian *T. spathi*.

Introduction

One of the most interesting groups of derivatives of the lytoceratid main stock are the tetragonitids, for which I have (1962a) proposed superfamily rank. Decisive for this separation was the progressive development of the umbilical suture, which separates *Tetragonites* clearly from *Lytoceras* s. l. (Textfig. 1). The suture formula $ELU_2U_3=SU_1I_s$ given to this group (T. MATSUMOTO 1959, J. WIEDMANN 1962a) has been confirmed by ontogenetic suture studies (J. WIEDMANN 1963, O. H. SCHINDEWOLF 1968). SCHINDEWOLF (1968) even demonstrated that this progressive lytoceratid suture line originated ontogenetically in a sexlobate primary suture consisting of the elements $ELU_2U_3U_1I$. From this point of view, tetragonitids are the most progressive group of ammonites. (Perhaps they might have become those of the Tertiary, if ammonites would have persisted.) SCHINDEWOLF's proposal to delegate subordinary rank for tetragonitids is, however, not accepted here. There is a gradational transition to a minor extent from *Protetragonites* to *Eotetragonites*, but, especially, from *Eotetragonites* to *Tetragonites*, which becomes obvious in the difficulty in including several Aptian/Albian species either in *Eotetragonites* or *Tetragonites* (V. V. DRUCHTCHIC 1956, M. A. MURPHY 1967a, 1967b). In any case the importance of suture patterns and suture ontogeny is stressed once more as the most objective basis of

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ammonite systematics, especially if we consider those of the Cretaceous System (J. Wiedmann 1966a, 1966b).

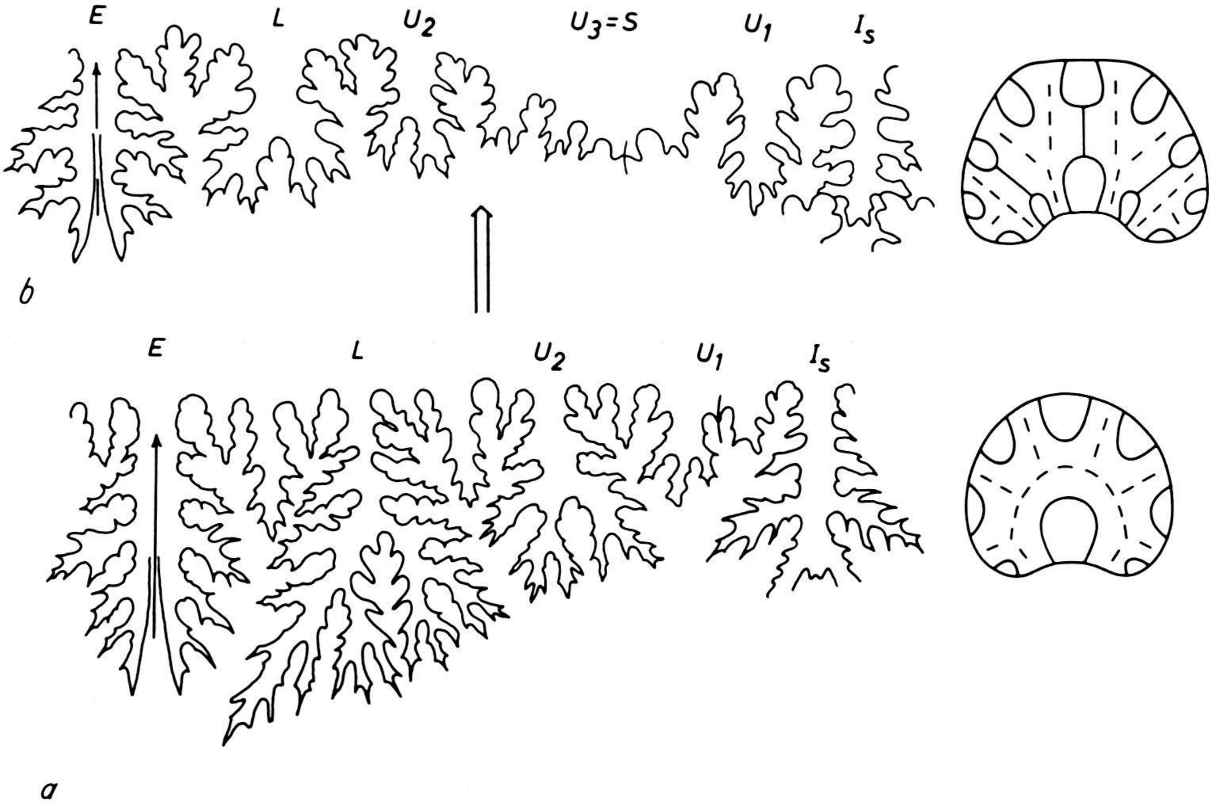

Fig. 1. Lytoceratid and tetragonitid suture lines and septa. *a Protetragonites* spp., lytoceratid precursor of Tetragonitaceae. *b Tetragonites* spp.

Tetragonites, the typical genus of this group of progressive lytoceratids, originated in the western Mediterranean region, where it can be traced back to *Eotetragonites via T. subbeticus* of uppermost Aptian age. During the Albian the genus rapidly evolves throughout the Mediterranean Tethys, while it occurs extremely rarely in the less favourable northern seas. The acme of *Tetragonites* is found in the Albian and Lower Cenomanian, where it constitutes a significant member of the Indo-Madagascan faunal associations (E. Stoliczka 1863–6, F. Kossmat 1895–7, M. Collignon 1928, 1956, 1963, 1965, and others).

From the Turonian to the Maastrichtian the development of tetragonitids is distinctly regressive and it was L. F. Spath (1925), and C. W. Wright and T. Matsumoto (1954) who separated these Upper Cretaceous forms as *Epigoniceras* and *Saghalinites* from the true Albian/Cenomanian *Tetragonites*.

On a previous occasion (1962a) I revised the European type specimens of that genus, and then came to the conclusion that a) separation of *Tetragonites* and *Epigoniceras* is unnecessary and b) none of the Circum-Indic specimens previously described as *T. timotheanus* really belongs to that highly restricted and uncommon European type species. Simultaneously, *T. subtimotheanus* was proposed as new name for the Indian specimens.

Naturally in the paper cited above (1962a) there was neither the place to give a complete description or a refiguration of that new species, nor to enter with more detail into the discussion of the remaining "*timotheanus*"-hypotypes of extra-European, especially of Indo-Madagascan origin. Moreover, in the meantime M. COLLIGNON published the Albian and Cenomanian parts (1963, 1965) of his forthcoming *Atlas des fossiles caractéristiques de Madagascar*, containing some new tetragonitid species which need brief discussion. Finally, the problem of the African *T. kitchini*, which was described as *Desmoceras* (*Puzosia*, *Latidorsella?*) by E. KRENKEL (1910), remained unsolved.

I therefore appreciated the opportunity to present these data in a paper contributed in 1966 to an envisaged Chatterjee volume. Unfortunately this volume has never been published.

In 1967, M. A. MURPHY published a parallel paper entitled *The Aptian-Cenomanian members of the ammonite genus Tetragonites*. Here I found various specimens of the PICTET collection and of my own material – erroneously attributed to the MHNG collection by the author – which I had prepared for this publication and which MURPHY had the opportunity to study during a visit to Tübingen in December 1964. Nevertheless, publication of these data is still relevant, especially, since MURPHY proposed a number of new species. Most of these are endemic to Northwest America, so that there appeared to be a pronounced geographic differentiation of "provincialism" in tetragonitids. In separating *Tetragonites* from *Eotetragonites*, MURPHY paid more attention to the nature of constrictions – which is highly variable in all these forms, as becomes obvious from Textfigure 13 – than to suture characters; this leads to some confusion in the specific classification.

The discussion of the new taxa established since 1966 and of the paleogeographic distribution of early tetragonitids thus became necessary in addition to the previous concept of this paper. Moreover, in 1971, through the kindness of Dr. J. A. JELETZKY (Ottawa), I had the opportunity to study the rich collection of tetragonitids from the Haida Formation of British Columbia. This leads to some further reflections on North American tetragonitids, additional to those in the posthumous paper of F. H. McLEARN (1972).

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Cordial thanks are due to General M. COLLIGNON (Moirans, France) for the loan of Madagascan type specimens, to Dr. E. LANTERNO (Geneva) for the kind aid during the study of PICTET's collections, to Prof. Dr. J. DEBELMAS and J. THIEULOY (Grenoble) for facilitating my study of the rich ammonite collections at their disposal, and to Dr. M. A. MURPHY (Riverside) for valuable discussions of tetragonitid systematics and phylogeny. Further thanks are due to Prof. Dr. S. TAXY-FABRE (Marseille) and to Dr. M. K. HOWARTH (London) for the loan of specimens of the Geological Institute at Marseille and the BMNH, to Dr. J. A. JELETZKY and the keeper of the Geological Survey collections at Ottawa for helpful assistance during the study of these collections, to Dr. M. WARTH (Ludwigsburg) for localizing KRENKEL's type specimens and to H. KLINGER (Pretoria, Tübingen) for linguistic advice. The photographs were made by W. WETZEL (Tübingen).

ABBREVIATIONS

AMNH American Museum of Natural History, New York
BMNH British Museum of Natural History, London
GPIT Geologisch-Paläontologisches Institut, Tübingen
GSC Geological Survey of Canada, Ottawa
IGP Istituto di Geologia, Padova
LGG Laboratoire de Géologie, Grenoble

LGM	Laboratoire de Géologie, Marseille
LGN	Laboratoire de Géologie, Nice
MHNG	Muséum d'Histoire Naturelle de Genève
MSHNB	Museo de la Sociedad de Historia Natural de los Baleares, Palma de Mallorca
SMNS	Staatliches Museum für Naturkunde, Stuttgart
UCR	University of California at Riverside
USGS	U.S. Geological Survey, Washington
D	Diameter
WH	Whorl height
WT	Whorl thickness
WU	Width of umbilicus
E	External lobe
L	Lateral lobe
U	Umbilical lobes
I_s	Internal lobe with septal lobe

Systematic part

In 1962 (1962a, p. 147–150) I gave an extensive review of the extent, subdivisions, limitations, and the origin of Tetragonitaceae. The presumed phylogenetic relationship within this superfamily was reproduced in the paper cited above on Textfigure 11 and Textplate 4, and needs no further discussion. MURPHY's (1967a) studies on tetragonitid relationships led to the conclusion that separation of *Tetragonites* from their eotetragonitid ancestors cannot be made by sutural characters ("such as the termination of the main saddle and possession of a second internal saddle") but only by the character of the constrictions. In *Eotetragonites* these constrictions are said to be more prominent on the internal mould, have a generally more radiate course, and be adorally convexly arched on the venter. But, if we regard the tetragonitid species reproduced here on Textfigure 13, there is a considerable variation of mode and even presence of constrictions so that the morphologic difference between the constricted and unconstricted *Tetragonites* is apparently more pronounced than that between *Eotetragonites* and constricted *Tetragonites*. Finally, even MURPHY (1967a, p. 5) admits that there are indeed transitions between the two genera if we consider the constrictions exclusively and especially if we consider *T. marrei* THOMEL, overseen by MURPHY. If MURPHY finally admits that "the biostratigraphy of the taxa indicate the classification that most nearly approximates the phylogeny of the group", it is hard to agree.

Consequently, MURPHY's attempt to classify *Tetragonites* leads to some confusion: The genus now would have a polyphyletic origin (1967a, Textfig. 5); previously undoubted tetragonitids (like *T. balmensis*) are now included in *Eotetragonites* and, *vice versa*, true eotetragonitids in *Tetragonites* (*E. heterosulcatus* and *E. crudus*; the latter was erroneously referred to the Lower Albian by MURPHY, in which the Russian authors generally include the Clansayesian Substage of the Aptian).

Thus MURPHY's attempt leads anew to the above stated conclusion that tetragonitid (as well as jauberticeratid) classification should be based primarily on sutural characters, especially on those of the internal suture. Mode or even absence of constrictions can be used only for lower taxa ("species groups") whereas the whorl section is regarded as the basis of the separation of species.

Superfamily Tetragonitaceae HYATT 1900

Family Tetragonitidae HYATT 1900

Previously (1962a) the family Tetragonitidae was restricted to the genera *Pseudophyllites* KOSSMAT and *Tetragonites* KOSSMAT, in which – in addition to *Epigoniceras* SPATH – *Saghalinites* WRIGHT and MATSUMOTO should also be included. In addition to these, *Carinites* n. gen. might be proposed for the keeled tetragonitids. Tetragonitidae can now be diagnosed by the acquisition of a third umbilical lobe (T. MATSUMOTO 1959, J. WIEDMANN 1963, O. H. SCHINDEWOLF 1968). The genera included may be distinguished as follows:

1. Whorl section trapezoidal, rectangular or rounded; with or without constrictions; test smooth; uppermost Aptian–Maastrichtian	*Tetragonites* KOSSMAT
2. Whorl section rounded; without constrictions; test finely striate; Campanian–Maastrichtian	*Pseudophyllites* KOSSMAT
3. Whorl section rounded; weak constrictions present; ventrally keeled; Cenomanian	*Carinites* n. gen.

Genus *Tetragonites* KOSSMAT 1895

1895 *Lytoceras (Tetragonites)* KOSSMAT, p. 131.
1925 *Epigoniceras* SPATH, p. 29.
1935 *Saghalinites* SHIMIZU, p. 181 (nom. nud.).
Neoepigoniceras SHIMIZU, p. 165 (nom. nud.).
Eoepigoniceras SHIMIZU, p. 165 (nom. nud.).
1954 *Epigoniceras (Saghalinites)* WRIGHT and MATSUMOTO, p. 110.

Type species: *Amm. timotheanus* PICTET 1848.

As indicated independently by M. K. HOWARTH (1958, p. 9), T. MATSUMOTO (1949, p. 78) and J. WIEDMANN (1962a, p. 131, 171), *Epigoniceras* is really indistinguishable from *Tetragonites*. But also the development of distinct umbilical shoulders on the outer whorls of *T. cala* and its allies cannot be regarded as an adequate basis for generic separation of "*Saghalinites*", which, moreover, contains different unrelated tetragonitid offshoots (as the Turonian(?) *T. kingianus* or the Campanian *T. cala*). *Neoepigoniceras* (type species: *T. schmidti* SHIM. = *T. timotheanus* SCHMIDT 1873, non PICTET 1848) and *Eoepigoniceras* SHIMIZU (type species: *T. kingianus* KOSSMAT) were rejected as *nomina nuda* by C. W. WRIGHT and T. MATSUMOTO (1954, p. 110). With separation of *Saghalinites*, as mentioned above, however, *Eoepigoniceras* should be maintained likewise.

Thus defined, the genus *Tetragonites* has a stratigraphical range from the uppermost Aptian to the Maastrichtian. As indicated above, only a brief treatment of the Albian-Cenomanian species, with special emphasis on those of the Circum-Indic area, will be attempted here. They can easily be classified and recognized by the following determination-key:

I. Constrictions persistent; umbilical suture straight	Group of *T. rectangularis*
A. Distinct constrictions, crowded in the adult	
a) whorl section broad-rectangular	*T. subbeticus* WIEDMANN (uppermost Aptian–Lower Albian)

b) whorl section subrectangular, evolute[2])	*T. marrei* THOMEL (Lower/Middle Albian)
c) whorl section trapezoidal at first, then	
α) periphery broadly rounded	*T. subtimotheanus subtimotheanus* WIEDMANN (Lower Albian–Lower Cenomanian)
β) oval	*T. subtimotheanus maclearnei* n. ssp. (Lower/Middle Albian)
B. Constrictions, especially in the adult, less pronounced and generally distant	
a) whorl section rectangular to subtrapezoidal at first, then with rounded periphery	
α) involute	*T. rectangularis rectangularis* WIEDMANN (Albian)
β) extremely involute	*T. rectangularis ampakabensis* COLLIGNON (Lower Cenomanian)
b) whorl section subquadrate	*T. kitchini* (KRENKEL) (upper Lower–Upper Albian)
c) whorl section semilunate to subtrapezoidal, crowed constrictions	*T. blaisoni* COLLIGNON (Lower Cenomanian)
II. Constrictions only on early stages; umbilical suture retracted	Group of *T. timotheanus*
a) whorl section rounded, numerous distinct constrictions up to a diameter of 40 mm	
α) evolute	*T. balmensis epigonoides* WIEDMANN (Lower Albian)
β) involute, inner whorls constricted	*T. balmensis balmensis* BREISTROFFER (Middle Albian)
γ) involute, inner and middle whorls constricted	*T. balmensis diegoensis* COLLIGNON (Upper Albian)
b) whorl section trapezoidal, evolute, few constrictions up to a diameter of 15 mm	
α) evolute	*T. timotheanus timotheanus* (PICTET) (Upper Albian)
β) moderately evolute	*T. timotheanus australis* WIEDMANN and DIENI (Upper Albian)
c) whorl section trapezoidal, involute, feeble constrictions up to a diameter of 10 mm	
α) involute	*T. nautiloides nautiloides* (PICTET) (Lower/Middle (?), Upper Albian)
β) extremely involute	*T. nautiloides* n. ssp.? (Upper Albian)
III. Without constrictions at any stage	Group of *T. jurinianus*
a) whorl section oval	
α) whorl section broad-oval, involute	*T. jurinianus jurinianus* (PICTET) (Middle (?)/Upper Albian–Cenomanian)
β) whorl section high-oval, extremely involute	*T. jurinianus angolanus* O. HAAS (uppermost Albian)

As becomes evident from this short key, persistence of constrictions and whorl section are the principal characteristics of tetragonitid classification. Number and course of constrictions vary with age and were therefore excluded from this brief summary. As indicated on previous occasions, the sutural differences are less important for specific separation. In some cases, where geographic separation was proved, the

[2]) The degree of involution is calibrated in the following way: the term "evolute" is used for a width of the umbilicus of more than 40% of the total diameter, "moderately evolute" for 31–40%, "involute" for 21–30%, and "extremely involute" for an umbilical width of less than 20%.

degree of involution was used for subspecific treatment of previously proposed species; but this remains open to criticism.

In addition to the key above, Table I summarizes the differences in principal measurements.

TABLE I

Measurements of Albian and Cenomanian tetragonitid species. I: Ratio whorl thickness to whorl height, Ia: of the type specimen, Ib: average ratio; II: ratio width of umbilicus to diameter; III: diameter of phragmocone, in mm.

	Ia	Ib	II	III
T. subbeticus	1.50	1.55	0.36	?
T. marrei	1.19	–	0.45	ca. 22
T. subtimotheanus subtimotheanus	1.35	1.40	0.29	up to 68
T. subtimotheanus maclearni n. ssp.	1.12	1.18	0.25	up to 55
T. rectangularis rectangularis	1.41	1.35	0.25	45
T. rectangularis ampakabensis	1.30	–	0.20	>60
T. kitchini	1.26	1.15	0.31	38
T. blaisoni	1.22	1.20	0.23	25
T. balmensis epigonoides	1.27	1.35	0.32	45
T. balmensis balmensis	1.13	1.23	0.24	100
T. balmensis diegoensis	1.13	1.30	0.32	>64
T. timotheanus timotheanus	1.60	1.50	0.43	20
T. timotheanus australis	1.43	1.40	0.36	35
T. nautiloides nautiloides	1.46	1.50	0.27	40
T. nautiloides n. ssp.?	1.25	–	0.11	50
T. jurinianus jurinianus	1.17	1.20	0.23	75
T. jurinianus angolanus	0.91	0.99	0.16	105
T. makarovensis	1.07	–	0.18	?

I. Group of *T. rectangularis*

Tetragonites subbeticus WIEDMANN

Pl. 1, Fig. 2

1962 *T. subbeticus* WIEDMANN (1962b), p. 75, Textfig. 26, Pl. 5, Fig. 6, 7.
? 1967 *T. lecontei* MURPHY (1967a), p. 51, Textfig. 26, 27, Pl. 7, Fig. 11–13.

Holotype: Specimen GPIT Ce 1220/21 from the Upper Aptian of Alcoraya, Sierra Mediana (prov. Alicante, Spain), here reproduced Plate 1, Figure 2.

Description: Moderately evolute species, with broad-rectangular to broad-trapezoidal whorl section and rounded marginal shoulders. Medium-sized(?). On the inner whorls 5 strong and prorsiradiate constrictions, which become more numerous with age (up to 10 per whorl), where they are likewise distinct. The earliest known member of *Tetragonites.*

The complete suture line of *T. subbeticus* is reproduced (Textfig. 1b) to ascertain that this species has the suture formula $ELU_2U_3 = SU_1I_s$ of *Tetragonites.* This means that the transition from *Protetragonites* (Textfig. 1a) *via Eogaudryceras–Eotetragonites* is now completed.

T. lecontei MURPHY seems almost identical with the present species in whorl section, number of constrictions (5–8, crowding with age), their persistence and conspicuousness, in suture line and, even in age, which becomes extended from the uppermost Aptian to the Lower Albian. The constrictions appear straighter in *T. lecontei;* but there is some variability in *T. subbeticus*, even in one specimen, as the refigured holotype (Pl. 1, Fig. 2) demonstrates. Whether this can be used as a criterion of subspecific value is hard to decide for the time being.

Measurements:

	D	WH	WT	WU	WT:WH
T. subbeticus, holotype GPIT Ce 1220/21	16 mm	6 mm (0.37)	9 mm (0.56)	5.8 mm (0.36)	[1.50]
T. lecontei, holotype UCR 109/1	29.5 mm	11.9 mm (0.40)	15.9 mm (0.54)	9.4 mm (0.32)	[1.34]

"*T.*" *inflatus* EGOJAN, described (1965) from the uppermost Aptian of the Caucasus, seems to be unrelated to the present species. It probably belongs to the group of *Eogaudryceras* (*Eotetragonites*) *duvalianum*.

Distribution: T. subbeticus is – as here interpreted – known from the uppermost Aptian of Southern Spain, Mallorca and California, where it persists into the Lower Albian Lecontei Zone.

Tetragonites marrei THOMEL

1964 *T. marrei* THOMEL, p. 299, Textfig.

Holotype: The specimen figured by G. THOMEL (1964, Textfig.) from the Lower/Middle Albian of Peille (Alpes-Maritimes, France), and deposited in the LGN collections.

Description: Since the holotype was not available, we can here reproduce only the original description of the cited author: Small-sized and evolute species with subrectangular whorl section; strong and projected constrictions persist throughout, about 8 per whorl. Nearly identical with the normal-sized *T. kingianus* KOSSMAT from the Indian Upper Utatur Group (?Turonian).

Measurements of the holotype:

29 mm	10.5 mm (0.36)	12.5 mm (0.43)	13 mm (0.45)	[1.19].

The species needs more adequate documentation. Suture line unknown. Occurrence as the holotype.

Tetragonites subtimotheanus WIEDMANN

Tetragonites subtimotheanus subtimotheanus WIEDMANN

Pl. 1, Fig. 5?; Pl. 2, Fig. 2; Pl. 3, Fig. 1–5; Pl. 7, Fig. 8?; Textfig. 2

1865 *Amm. Timotheanus* MAYOR. – F. STOLICZKA, p. 146, Pl. 73, Fig. 3, 4, 6.
1895 *Lytoceras (T.) Timotheanum* MAYOR. – F. KOSSMAT, p. 37, Pl. 3, Fig. 11, 13.
1902 *Lytoceras timotheanum* MAYOR. – F. M. ANDERSON, Pl. 7, Fig. 145–148.
1907 *T. Timotheanus* STOL. – G. C. CRICK, p. 172, Pl. 10, Fig. 15.
? 1928 *Lytoceras (T.) Timotheanus* MAYOR. – M. COLLIGNON, p. 18, Pl. 1, Fig. 18.
1960 *T.* aff. *T. timotheanus* (PICTET). – R. W. IMLAY, p. 100, Pl. 12, Fig. 24–28.
1962 *T. subtimotheanus* WIEDMANN (1962a), p. 131, 172.
1963 *T. subtimotheanus* WIEDM. – M. COLLIGNON, p. 22, Pl. 249, Fig. 1071.
1967 *T. rectangularis alaskaensis* MURPHY (1967a), p. 46, Textfig. 22, 23, Pl. 6, Fig. 9, 10, 14, Pl. 7, Fig. 2, 9.
pars *T. subtimotheanus* WIEDM. – M. A. MURPHY (1967a), p. 62, Textfig. 34, 35, Pl. 5, Fig. 11, 13, *non* Pl. 6, Fig. 5–8 (*sed T. blaisoni* COLL.).
? *T. madagascariensis* MURPHY (1967a), p. 68.
1972 *T. subtimotheanus haidaensis* MCLEARN, p. 24, Pl. 4, Fig. 3, 6, Pl. 34, Fig. 1.

Holotype: Lytoceras (T.) timotheanum in F. KOSSMAT 1895, Pl. 3, Fig. 13, from the Lower Utatur Group (Upper Albian) of Odium (India).

Description: Large-sized, nearly involute species with persistent constrictions. Whorl section trapezoidal at first, becoming broadly rounded (Pl. 2, Fig. 2). Number of constrictions rapidly increasing from 5 in the youth to 7 or 8, fading in the outer portion of the living-chamber (Pl. 3, Fig. 2). Constrictions strongly projected to concave on the flanks, turning back on the marginal shoulder and crossing venter with a distinct sinuosity (Pl. 3, Fig. 3b). Umbilical and marginal shoulders distinct at first, the latter vanishing at a D of 50 mm. Umbilicus much more open in the juvenile stage. Aperture deviates slightly from the logarithmic spiral.

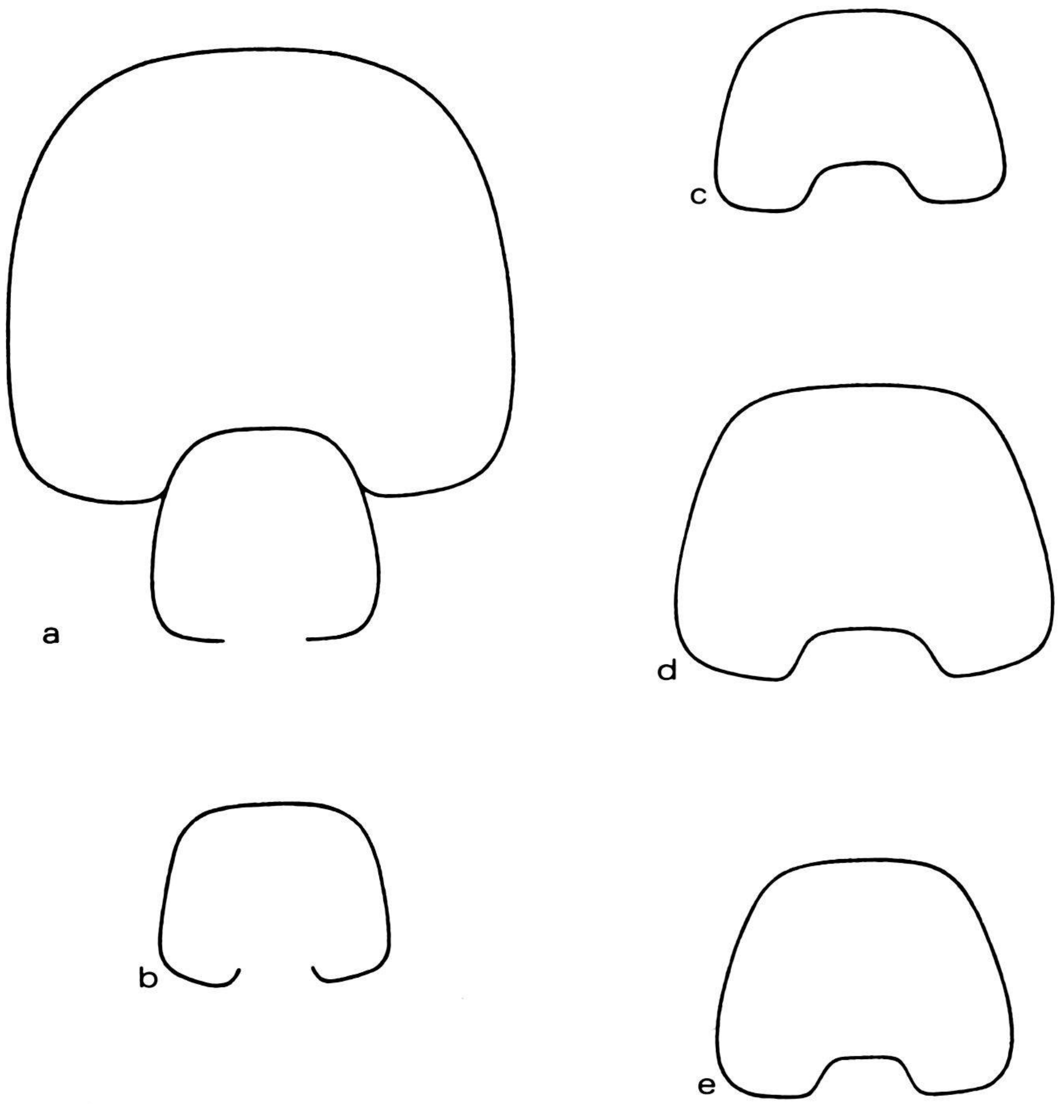

Fig. 2. Whorl sections of *T. subtimotheanus subtimotheanus* WIEDMANN. *a* GSC 21176 (Holotype of *T. subtimotheanus "haidaensis"* McLEARN). Upper Lower Albian (QH D 8), Maude Island, Q.Ch.I. (B.C., Canada). 1/1. *b* GSC 21177 (paratype of *T. subtimotheanus "haidaensis"* McLEARN). Same age (QH D 14) and locality. 2/1. *c* MHNG Wi "T"/1. Lower (?) Utatur Group (Upper Albian), Penangur (India). 1/1. *d* GSC 34665. Middle Albian (QH F 6), Lina Island, Q.Ch.I. (B.C., Canada). 1/1. *e* GSC 34678. Upper Albian (QH A 12a), Bearskin Bay, Q. Ch.I. (B.C., Canada). 1/1.

In the original description of 1962 I had provisionally included *T.* aff. *timotheanus* in IMLAY (1960) in the present species, pointing out that by its small differences in size, and in the fate of the constrictions on the body-chamber, the Alaskan form might be subspecifically separable. This subspecies has, in the meantime, been described by M. A. MURPHY (1967a) as *T. rectangularis alaskaensis* and by F. H. MCLEARN (1972) as *T. subtimotheanus haidaensis*. Both are indistinguishable. A large collection of the Alaskan form shows, however, that all these forms cannot be distinguished from *T. subtimotheanus* s. str. A high variability was found not only in final size – as can be seen from the table of measurements –, but also in the persistence of constrictions on the body-chamber. While these constrictions persist up to the mouth border in smaller individuals (Pl. 3, Fig. 1), they fade on the outer portion of the chamber in larger specimens (Pl. 3, Fig. 2).

The complete suture line, passing nearly straight over the umbilical seam, was given by F. KOSSMAT (1895, Pl. 3, Fig. 11).

Measurements:

Holotype in KOSSMAT 1895, Pl. 3, Fig. 13					
	35 mm,	14 mm (0.40),	19 mm (0.54),	10 mm (0.29),	[1.35]
T. "rectangularis alaskaensis", holotype					
USNM 155473	45.1 mm,	20.4 mm (0.45),	24.3 mm (0.54),	12 mm (0.27),	[1.19]
T. subtimotheanus "haidaensis", holotype					
GSC 21176	101 mm,	48 mm (0.47),	54 mm (0.53),	25 mm (0.25),	[1.12]
Phragmocone-D 68 mm					
ditto, paratype					
GSC 21178	72 mm,	32.8 mm (0.45),	41 mm (0.57),	18 mm (0.25),	[1.25]
ditto, paratype					
GSC 21177	23.5 mm,	9.5 mm (0.40),	12.5 mm (0.52),	8 mm (0.34),	[1.31]
MHNG Wi "T"/1	52 mm,	22.5 mm (0.43),	33 mm (0.64),	15 mm (0.29),	[1.46]
and	29 mm,	13 mm (0.45),	17 mm (0.59),	10.5 mm (0.36),	[1.21]
GSC 34669	27 mm,	11.3 mm (0.42),	14.6 mm (0.54),	8.2 mm (0.30),	[1.30]
GSC 34668	29 mm,	12 mm (0.41),	15.5 mm (0.53),	9 mm (0.31),	[1.29]
GSC 34667	39 mm,	18 mm (0.46),	21.6 mm (0.56),	8.5 mm (0.22),	[1.20]
Phragmocone-D ?22 mm					
GSC 34666	46 mm,	19 mm (0.41),	23.7 mm (0.52),	12.2 mm (0.24),	[1.25]
GSC 44668	65 mm,	30 mm (0.46),	35.5 mm (0.54),	16 mm (0.25),	[1.18]
Phragmocone-D ?35 mm					
GSC 34665	73 mm,	31 mm (0.42),	40 mm (0.55),	18 mm (0.25),	[1.29]
Phragmocone-D 45 mm					
GSC 34664	105 mm,	48 mm (0.46),	53 mm (0.50),	24 mm (0.23),	[1.10]
Phragmocone-D 60 mm					
GSC 34678	55 mm,	24.5 mm (0.45),	32 mm (0.58),	14.5 mm (0.26),	[1.30]
Phragmocone-D ?33.5 mm					
doubtful hypotypes:					
GSC 34679	48 mm,	21.5 mm (0.45),	27 mm (0.56),	12.6 mm (0.26),	[1.25]
GSC 34670	14 mm,	5.2 mm (0.37),	7.2 mm (0.52),	5.7 mm (0.41),	[1.38]

T. timotheanus has a similar juvenile shell, remaining evolute throughout, and loosing its constrictions very early in the ontogeny. *T. rectangularis* has a broad-rectangular whorl section at first, loosing its marginal shoulders at a D of 30 mm. At the same time the less crowded and straight constrictions are fading. In *T. kitchini* generally 5 constrictions and subrectangular whorl section persist to greater diameters. *T. "madagascariensis"* MURPHY, based on "*L.* (*T.*) *timotheanus*" in M. COL-

LIGNON (1928, Pl. 1, Fig. 18) may be identical with the present species. Regarding, however, the similarity of tetragonitid inner whorls, it is really too small (15 mm D) to be identified positively or used for specific separation.
Distribution: T. subtimotheanus subtimotheanus is known from the upper Lower Albian (Hulenense Zone) to Lower Cenomanian ("Turrilites" Zone) of Queen Charlotte Islands, British Columbia, and Chitina Valley, Alaska. It is known, moreover, from the Upper Albian of Oregon, Zululand, Madagascar(?) and the Lower Utatur Group of Odium, Penangur and Maravattur (India).

Tetragonites subtimotheanus maclearni n. ssp.

Pl. 4, Fig. 1; Pl. 5, Fig. 1–3; Textfig. 3

? 1967 *Tetragonites* sp. – MURPHY (1967a), p. 68, Pl. 7, Fig. 4, 5.

Holotype: Specimen GSC 34671, from the Middle Albian (Perezianum Zone) of locality A8 Bearskin Bay (see F. H. MCLEARN 1972), Skidegate Inlet, Q.C.I., B.C., Canada.
Material: 7 specimens (GSC 24526, 34672, 34673, 34674, 34575, 34676, and the holotype), of upper Lower and Middle Albian age, Skidegate Inlet.
Diagnosis: Large-sized, nearly involute form. Whorl section trapezoidal at first, but soon becoming oval with rounded marginal shoulders. 6–8 faint constrictions per whorl, persisting on the body chamber. Course of constrictions as in the typical subspecies.
Description: T. subtimotheanus maclearni n. ssp. is a large-sized form, attaining diameters of 80 mm which corresponds to a phragmocone-D of about 55 mm (Pl. 5, Fig. 3). The ontogenetic history of the whorl section is similar to that of the typical subspecies but it is more compressed throughout and becomes ventrally rounded much earlier (Pl. 5, Fig. 1b, 2b). Finally the whorl section becomes oval (Pl. 5, Fig. 1b). The umbilicus remains nearly closed. The constrictions, variable in number, have the same course as in the typical subspecies, but they are much less pronounced (Pl. 5, Fig. 3) and generally less crowded with age.

Measurements:

Holotype, GSC 34671	78 mm,	38 mm (0.49,)	42 mm (0.54),	17 mm (0.22),	[1.10]
and by asymmetry		36.5 mm (0.47),		19 mm (0.24),	[1.15]
Paratype, GSC 34672	77 mm,	37 mm (0.48),	42 mm (0.55),	20 mm (0.26),	[1.14]
Phragmocone-D 55 mm, last suture line at WH 23					
ditto, GSC 34673	80 mm,	37.5 mm (0.47),	42.5 mm (0.53),	18–19 mm (0.23),	[1.13]
Phragmocone-D 44 mm, last suture line at WH 23					
ditto, GSC 24526	74 mm,	35 mm (0.47),	37.7 mm (0.51),	19 mm (0.26),	[1.08]
Phragmocone-D 47 mm, last suture line at WH 22					
ditto, GSC 34674	50 mm,	22 mm (0.44),	27.5 mm (0.55),	12.4 mm (0.25),	[1.25]
ditto, GSC 34675	48 mm,	21 mm (0.44),	27 mm (0.56),	12.9 mm (0.27),	[1.28]
ditto, GSC 34676	40 mm,	18 mm (0.45),	21 mm (0.53),	10 mm (0.25),	[1.17]
Tetragonites sp. in MURPHY 1967a					
	52.8 mm,	23 mm (0.44),	27.5 mm (0.52),	15.2 mm (0.29),	[1.20]

The suture line is given in Textfigure 3c. It is that of the typical subspecies.

In its ontogenetic development the present subspecies has some similarity with *T. balmensis* which offers a similar whorl section in the adult age. But most of its

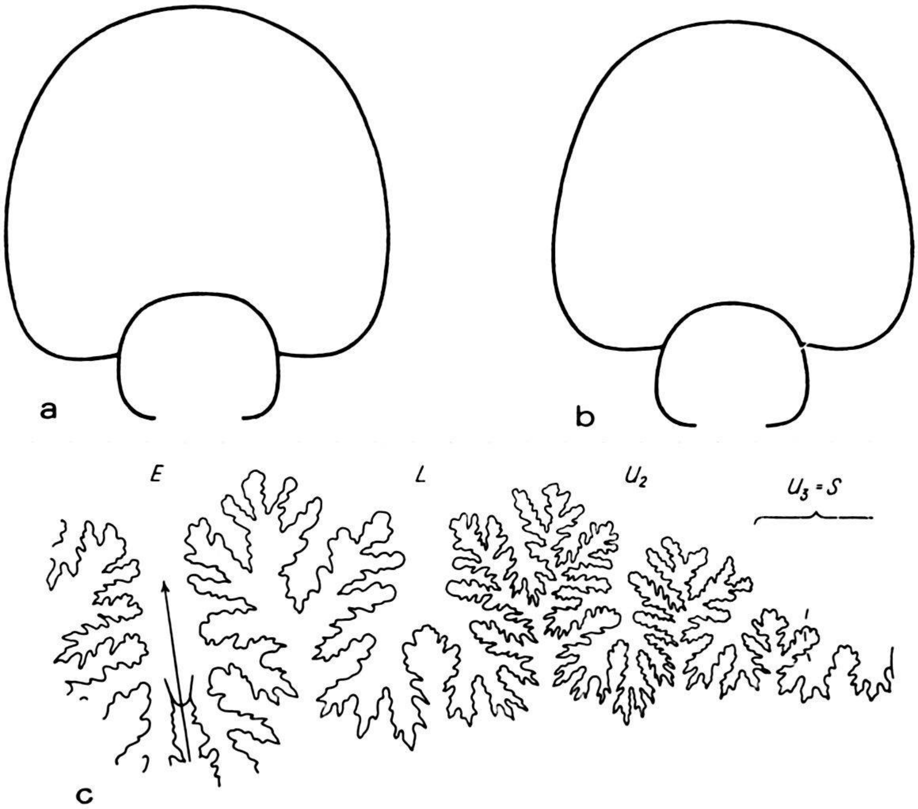

Fig. 3. Whorl sections and suture line of *T. subtimotheanus maclearni* n. ssp. *a* Paratype 34672. Upper Lower Albian (QH P 2), Alliford Bay, Q.Ch.I. (B.C., Canada). 1/1. *b* Paratype 24526. Upper Lower Albian (QH A 5), Bearskin Bay, Q.Ch.I. (B.C., Canada). 1/1. *c* External suture line of paratype 34672, at WH 22 mm. Ca. 4/1.

characters are those of *T. subtimotheanus*, in which it has to be included. There is, moreover, some similarity with MURPHY's "*Tetragonites* sp." from an unknown horizon of La Palud des Moustiers (France) with a "*balmensis* type cross section ... combined with the *rectangularis* type constrictions".

Distribution: T. subtimotheanus maclearni n. ssp. is known only from the upper Lower Albian (Hulenense Zone) and Middle Albian (Perezianum Zone) of Bearskin Bay, Maple Island, Maude Island, Alliford Bay at the Skidegate Inlet, Queen Charlotte Islands, British Columbia.

Tetragonites rectangularis WIEDMANN

Tetragonites rectangularis rectangularis WIEDMANN

Pl. 1, Fig. 1; Pl. 4, Fig. 2; Pl. 7, Fig. 1, 2

Synonomy in J. WIEDMANN 1962a, p. 178, and

1962 *T. rectangularis* WIEDM. – J. WIEDMANN (1962b), p. 78, Textfig. 28, Pl. 6, Fig. 1, 2, 7, 8.
1963 *T. rectangularis* WIEDM. – M. COLLIGNON, p. 21, Pl. 249, Fig. 1069, 1070.
non 1965 *T. rectangularis* WIEDM. – M. COLLIGNON, p. 5, Pl. 318, Fig. 1356, 1357 (*sed T. blaisoni* COLL.?).
1967 *T. rectangularis* WIEDM. – M. A. MURPHY (1967a), p. 38, Textfig. 18–20, Pl. 4, Fig. 1–7, Pl. 5,Fig. 1.
T. bournensis MURPHY (1967a), p. 48, Textfig. 24, 25, Pl. 6, Fig. 11–13.
1968 *T. rectangularis* WIEDM. – J. WIEDMANN and I. DIENI, p. 47, Pl. 4, Fig. 8.

Holotype: The MHNG specimen Wi "VK"/10 from the Upper Albian of Saxonet (Savoie, France), here reproduced Plate 4, Figure 2.
Description: Medium-sized, involute form with rectangular to subtrapezoidal whorl section at first (Pl. 1, Fig. 1b), and with broadly rounded periphery on the exterior phragmocone (Pl. 7, Fig. 1a) and the living chamber (Pl. 4, Fig. 2b). Constrictions persist throughout, but are more distinct on the inner whorls. 5–6 constrictions per whorl, quite prorsiradiate at first (Pl. 7, Fig. 2a), but more sinuously projected with age (Pl. 4, Fig. 2a) and then with a distinct sinuosity on the venter.

Suture lines were given in 1962a (Textfig. 39) and in 1962b (Textfig. 28) and run nearly straight over the umbilical seam (cf. Pl. 1, Fig. 1a).

Measurements:

Holotype, MHNG Wi "VK"/10					
	50 mm,	22 mm (0.44),	31 mm (0.62),	12.8 mm (0.25),	[1.41]
Phragmocone-D 41 mm					
COLLIGNON's Fig. 1069	45 mm,	21 mm (0.47),	27 mm (0.60),	12 mm (0.27),	[1.29]
COLLIGNON's Fig. 1070	41 mm,	19 mm (0.46),	24 mm (0.59),	12 mm (0.29),	[1.26]
LGG Ce W1	39 mm,	17 mm (0.43),	23 mm (0.59),	10 mm (0.26),	[1.35]
LGG Ce W2	34 mm,	15 mm (0.44),	19.5 mm (0.57),	9.4 mm (0.28),	[1.30]
LGG Ce W3	32 mm,	14.5 mm (0.45),	20 mm (0.62),	8 mm (0.25),	[1.38]
LGG Ce W4	27 mm,	12.4 mm (0.46),	16 mm (0.59),	7.8 mm (0.29),	[1.30]
MHNG Wi "VK"/11	21.5 mm,	9 mm (0.42),	12.5 mm (0.58),	6 mm (0.28),	[1.39]
T. "bournensis", holotype					
UCR 676/1	31.7 mm,	14.5 mm (0.46),	18.9 mm (0.60),	8 mm (0.22),	[1.30]

The characteristics ascribed to *T. "bournensis"* by MURPHY (1967a, p. 48) are completely those of *T. rectangularis* (measurements, fading of 5–7 constrictions on the periphery, which becomes rounded with age, etc.).
Distribution: As indicated in the papers cited above, *T. rectangularis* s. str. is not only the most common of the early tetragonitids, it is likewise the source of the divergent tetragonitid lineages (Textfig. 13). It is known from the Lower Albian of Mallorca and Southern Spain, the Middle and Upper Albian of Southern France, the Upper Albian of Sardinia and Madagascar, and may be represented as well in the Upper Albian of Great Britain. North American specimens previously referred to this subspecies (F. M. ANDERSON 1902, T. MATSUMOTO 1959) are now classified elsewhere.

Tetragonites rectangularis ampakabensis COLLIGNON

Pl. 2, Fig. 1; Pl. 4, Fig. 3?, 4?; Textfig. 4?

? 1959 *T.* sp. nov. (?). – T. MATSUMOTO, p. 77, Textfig. 15, Pl. 22, Fig. 1, 2.
1965 *T. Jallaberti* var *ampakabensis* COLLIGNON, p. 34, Pl. 325, Fig. 1449.
pars 1967 *T. collignoni* BREISTR. – M. A. MURPHY (1967a), p. 66, Textfig. 36b, Pl. 5, Fig. 4, 5 (*non* Textfig. 36a, Pl. 5, Fig. 2, 3, *sed T. blaisoni* COLL.).
? *T. jonesi* MURPHY (1967a), p. 58, Textfig. 31, 32, Pl. 6, Fig. 1–4.

Holotype: The specimen figured and collected by M. Collignon under No. 417, from the Lower Cenomanian of Ampakabo (Madagascar).
Description: Medium-sized and quite involute form with feeble, but persistent constrictions, about 7 per whorl, extremely projected on the sides and recurved on the marginal shoulder (Pl. 2, Fig. 1a, b). Whorl section trapezoidal at first, but with rounded periphery on the last whorl (Pl. 2, Fig. 1c), which – in the holotype – may

contain some part of the body chamber. On the venter (Pl. 2, Fig. 1a) the constrictions are likewise pronounced and bent backward.

The suture line is not visible in the type specimen, but is known from *T. jonesi* (MURPHY 1967a, Textfig. 32c).

I appreciate the opportunity to reproduce the type specimen. Thus the type of constrictions becomes visible, as does the obvious relationship to *T. rectangularis*. The only differences we can notice are a somewhat more trapezoidal whorl section and the more closed umbilicus. In view of these facts and the younger age, a subspecific separation from *T. rectangularis* s. str. seems adequate. *Amm. jallabertianus* PICTET, to which *T. ampakabensis* was attributed by Collignon, really belongs to *Eotetragonites* and has only superficial similarities with the forms described here.

T. jonesi MURPHY as well as *T.* sp. nov. (?) of MATSUMOTO agree with *T. rectangularis ampakabensis* in dimensions, number and course of weak constrictions and, especially, in the degree of involution. They probably belong to the Madagascan subspecies. Unfortunately only small specimens are known of the Alaskan species, having nearly the same age (uppermost Albian–Lower Cenomanian). This is the reason for including these forms in the present subspecies only with a mark of interrogation. The same holds true for two specimens with a similar whorl section of an unknown horizon of the Sandstone Member of the Haida Formation (Lower Albian–Lower Cenomanian) of Queen Charlotte Island, B.C. (Pl. 4, Fig. 3, 4, Textfig. 4). Their adult whorl section is slightly more rounded then in the holotype. Therefore they bear some similarity to *T. blaisoni* COLL.

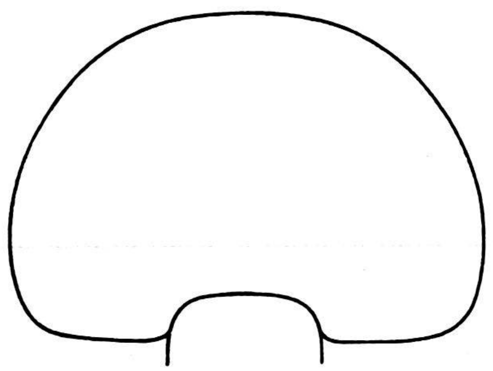

Fig. 4. Whorl section of *T. rectangularis ampakabensis* COLLIGNON (?). Doubtful hypotype 34662. Albian, Skidegate Inlet, Q.Ch.I. (B.C., Canada). 1/1.

Identification of *T. rectangularis ampakabensis* and *T. blaisoni* with *T. collignoni* BREISTROFFER, as proposed by MURPHY (1967a, p. 66) is rejected here, since the latter species is – based on a small pyritic nucleus – really indeterminable and "intermediate growth stages will have to be found before it can be documented" (M. A. MURPHY 1967a, p. 67).

Measurements:

Holotype in M. COLLIGNON coll. No. 417					
	60 mm,	31 mm (0.52),	40 mm (0.67),	12 mm (0.20),	[1.29]
Doubtful hypotypes					
CGS 34662	70 mm,	31.5 mm (0.45),	45.5 mm (0.65),	16 mm (0.23),	[1.44]
Phragmocone-D 43 mm?					

CGS 34663	58 mm,	28 mm (0.48),	37 mm (0.64),	13 mm (0.22),	[1.32]
T. jonesi, holotype					
USNM 155477	25.5 mm,	12.1 mm (0.48),	15.5 mm (0.61),	5.8 mm (0.23),	[1.28]

Distribution: This subspecies is known from the Lower Cenomanian of Madagascar. Further specimens of uppermost Albian and Lower Cenomanian age of the Upper Chitina Valley (Alaska) and of the Sandstone Member of the Haida Formation at Queen Charlotte Islands, B.C. are doubtfully referred to it.

Tetragonites kitchini (KRENKEL)

Pl. 1, Fig. 7; Pl. 6, Fig. 1, Fig. 2–4?; Textfig. 5, Textfig. 6?

? 1876 *Amm. Timotheanus* MAYOR. – J. F. WHITEAVES, p. 41, Pl. 3, Fig. 2.
1910 *Desmoceras (Puzosia; Latidorsella?) Kitchini* KRENKEL, p. 226, Textfig., Pl. 22, Fig. 8.
1962 *T. kitchini* (KRENKEL). – J. WIEDMANN (1962a), p. 171.
1967 *T. kitchini* (KRENKEL). – M. A. MURPHY (1967a), p. 33, Textfig. 15, 16, Pl. 2, Fig. 11–14.
T. hulenensis MURPHY (1967a), p. 54, Textfig. 28–30, Pl. 6, Fig. 16–19, Pl. 7, Fig. 3, 6, 7, 8, 10.
T. hulenensis MURPHY (1967b), Pl. 4, Fig. 8, 9.

Holotype: The assumption that the type specimen might have been lost (M. A. MURPHY 1967a, p. 33) has not been verified. I am indebted to Dr. Warth, keeper at the SMNS collections, for kind permission to restudy the specimen he had recently located in the named collection. It was collected with *Parasilesites africanus* at Lindi (Tanzania) and can thus be referred to the upper part of the Lower Albian.

Since the type specimen is an inner whorl, the species needs to be redefined with the aid of the GPIT specimen Ce 1311/1 from Manohonda (Madagascar), here reproduced Plate 6, Figure 1.

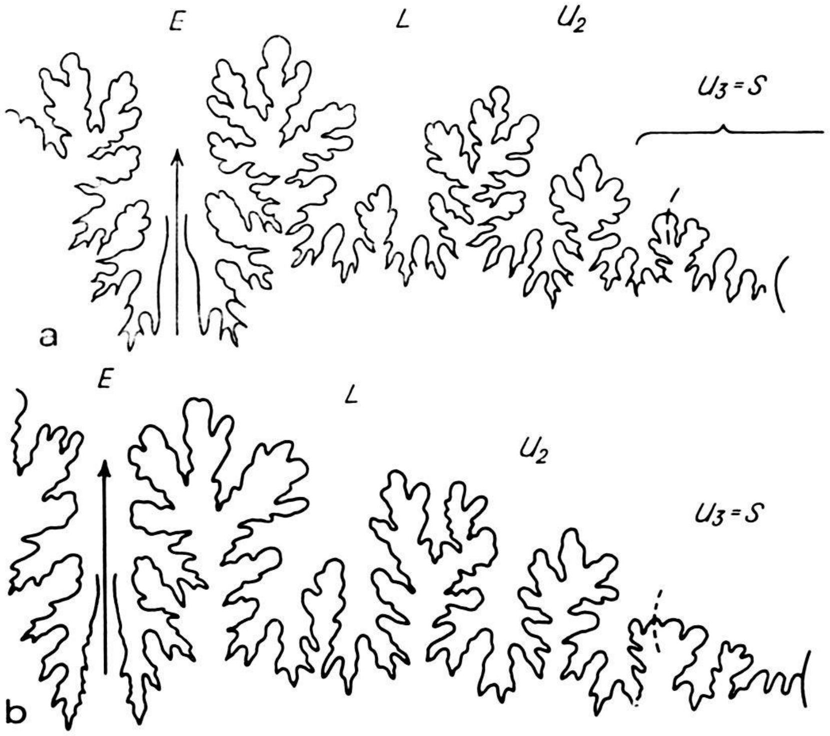

Fig. 5. External suture lines of *T. kitchini* (KRENKEL). *a* Holotype SMNS 22303. Upper Lower Albian, Lindi (Tanzania). At WH 6.5 mm. Ca. 5/1. *b* Hypotype GPIT Ce 1311/1. Middle Albian (?), Manohonda (Madagascar). At WH 12 mm. Ca. 5/1.

Description: Moderately evolute species with subquadrate whorl section. 5–7 projected constrictions per whorl seem to persist, but are of weak outline and recurved on the venter. Suture lines of the holotype and the Madagascan specimen are given in Textfigure 5. They confirm the complete identity of both forms, with the exception of the configuration of the saddle LU_2, but this is subject to variation (M. A. MURPHY 1967a, p. 56, Textfig. 30).

T. "hulenensis" described by MURPHY (1967a) from the upper Lower Albian of California and Alaska is indistinguishable to me from the present species, especially if the "different" whorl sections (and sutures) are compared (MURPHY 1967a, Textfig. 16a–e, 29; 16f, 30).

This identity is not as obvious in the specimens WHITEAVES (1876, Pl. 3, Fig. 2) and MCLEARN (1972, Pl. 4, Fig. 4, 5) described from the Hulenense Zone of Queen

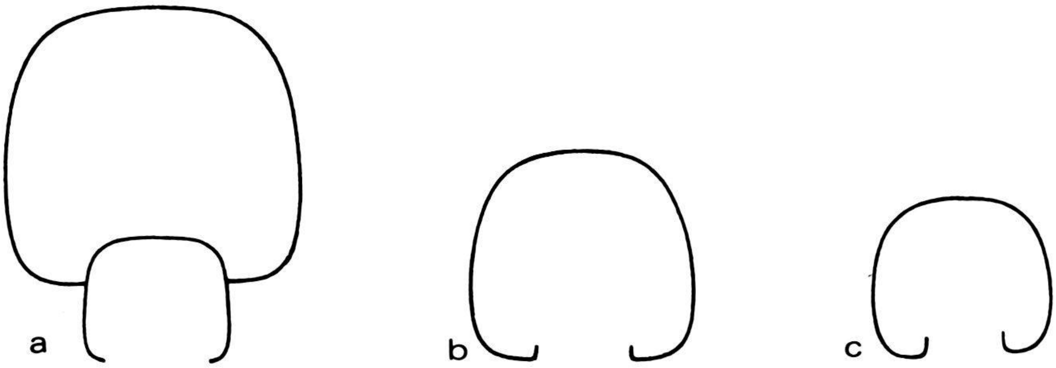

Fig. 6. Whorl sections of *T.* aff. *kitchini* (KRENKEL). *a* GSC 4970. Albian, Cumshewa Inlet, Q.Ch.I. (B.C., Canada). 1/1. *b* GSC 24527. Albian, Alliford Bay, Q.Ch.I. (B.C., Canada). 1/1. *c* GSC 24529. Middle Albian (QH A 9), Bearskin Bay, Q.Ch.I. (B.C., Canada). Ca. 1/1.

Charlotte Islands. As MCLEARN (1972, p. 27f.) pointed out, these forms – which agree completely in their general aspect – differ in some details of their dimensions, i.e. especially their degree of involution. Moreover in some of these specimens their subquadrate whorl section may be due to shell deformation. This means that they are, perhaps, crushed specimens of *T. subtimotheanus*. Therefore their whorl sections and some of the specimens MCLEARN mentioned only in the text are here reproduced (Pl. 6, Fig. 2–4, Textfig. 6). All these forms have a slightly higher degree of shell evolution, pointing to *T. subtimotheanus*.

Measurements:

Holotype, SMNS 22303	18 mm,	7 mm (0.39),	8.8 mm (0.49),	5.6 mm (0.33),	[1.26]
GPIT Ce 1311/1[3])	38 mm,	15.8 mm (0.42),	19 mm (0.50),	12 mm (0.32),	[1.20]
T. "hulenensis", holotype					
USGS 155481a	39.6 mm,	17.7 mm (0.45),	22 mm (0.56),	11.5 mm (0.29),	[1.25]
T. aff. *kitchini:*					
GSC 4970	67 mm,	28.5 mm (0.42),	30.5 mm (0.45),	18 mm (0.27),	[1.07]
Phragmocone-D 49 mm					
GSC 24527	43 mm,	18 mm (0.42),	19 mm (0.44),	11 mm (0.26),	[1.06]
Phragmocone-D 30 mm					
GSC 4978	34 mm,	15 mm (0.46),	17.5 mm (0.52),	10 mm (0.29),	[1.13]
GSC 24529	30 mm,	13 mm (0.43),	14.5 mm (0.48),	8.2 mm (0.27),	[1.12]

[3]) This specimen was erroneously attributed to the MHNG collection by MURPHY.

Distribution: *T. kitchini* is of upper Lower Albian age at Lindi (Tanzania), in Northern California (Lecontei Zone) and Southern Alaska (Hulenense Zone). The Madagascan occurrences are of Middle and, perhaps, of Upper Albian age, if MURPHY's identifications (1967a, p. 36) are correct. The doubtful hypotypes of British Columbia belong – as far as dated – to the Middle Albian Perezianum Zone.

Tetragonites blaisoni COLLIGNON

Pl. 1, Fig. 4; Pl. 6, Fig. 6, 7, 5?; Textfig. 7

? 1928 *Lytoceras (T.) Kiliani* mut. *Jacobi* COLLIGNON (*non* KILIAN), p. 18, Pl. 1, Fig. 19.
? 1940 *T. Collignoni* BREISTROFFER, p. 111.
1965 *T. Blaisoni* COLLIGNON, p. 31, Pl. 324, Fig. 1448.
? *T. rectangularis* WIEDM. – COLLIGNON, p. 5, Pl. 318, Fig. 1356, 1357 (only).
pars 1967 *T. collignoni* BREISTR. – M. A. MURPHY (1967a), p. 66, Textfig. 36a, Pl. 5, Fig. 2, 3.
pars *T. subtimotheanus* WIEDM. – M. A. MURPHY (1967a), p. 62, Textfig. 35a–d?, Pl. 6, Fig. 5–8.

Holotype: The specimen figured by M. COLLIGNON (1965) and here reproduced Plate 6, Figure 6, from the Lower Cenomanian of Beraketa (Madagascar); the specimen is preserved in the M. Collignon collection as No. 474.
Description: Small-sized and involute species with subtrapezoidal to semilunate whorl section. 5 distinct projected constrictions per whorl persist to the body chamber and are somewhat bent backward on the venter.

As visible from Textfigure 7 the suture line passes nearly straight over the umbilical seam.

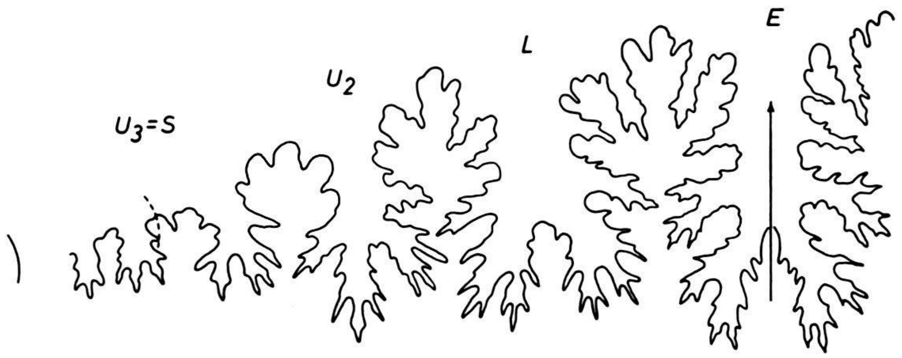

Fig. 7. External suture line of *T. blaisoni* COLLIGNON. Holotype, M. Collignon coll. No. 474. Lower Cenomanian, Beraketa-Sakondry (Madagascar). At WH 10 mm. Ca. 5/1.

One of the Utatur specimens available to me (Pl. 1, Fig. 4; Pl. 6, Fig. 7) is a perfect juvenile form of the present species. It is somewhat more evolute, but in all other characters corresponding perfectly with the type specimen. Moreover, it gives (Pl. 6, Fig. 7b) a clearer idea of the whorl section. The phragmocone-D does not exceed 20 mm.

Another specimen from Southern India (Pl. 6, Fig. 5) may be included in *T. blaisoni* with some hesitation. The restored whorl section of the crushed specimen may be identical with that of the type, but the number of constrictions is greater, the phragmocone attains a diameter of 32 mm, and also the degree of involution is lower than expected (and similar to that of the juvenile form). But also specimens from the Lower Cenomanian of Madagascar, recorded as *T. "rectangularis"* by COLLIGNON (1965) correspond completely with the species under discussion.

T. "collignoni" BREISTROFFER, based on *"L. (T.) kiliani* mut. *jacobi"* of COLLIGNON (1928, Pl. 1, Fig. 18) from the Lower Cenomanian of Madagascar cannot be identified with the present species with certainty. It is based on an immature specimen (D 14 mm) and should be regarded as invalid. Moreover the identification of *T. rectangularis ampakabensis* with the present species or *T. "collignoni"* respectively, as proposed by MURPHY (1967a, p. 66), cannot be accepted. *T. rectangularis ampakabensis* is of much larger size, has a more triangular whorl section and less pronounced constrictions of a greater number. But in any case both forms are close to each other or even joined by specimens such as the two Haida specimens here figured (Pl. 4, Fig. 3 4; Textfig. 4) and referred to *T. rectangularis ampakabensis*.

Measurements:

Holotype, Collignon coll. No. 474								
	39 mm,	18 mm	(0.46),	22 mm	(0.56),	9 mm	(0.23),	[1.22]
Phragmocone-D 25 mm								
MHNG Wi "T"/2	26 mm,	11 mm	(0.42),	15.5 mm	(0.60),	8 mm	(0.31),	[1.41]
Phragmocone-D 20 mm								
Doubtful hypotype								
MHNG Wi "T"/3	38 mm,	16 mm	(0.42),	20 mm	(0.53),	11 mm	(0.29),	[1.25]
Phragmocone-D 32 mm								

Distribution: T. blaisoni, thus defined, is a Lower Cenomanian species, which is restricted to Madagascar and the (?) Middle Utatur Beds of Odium (S. India).

Tetragonites makarovensis GLAZUNOVA

1960 *T. makarovensis* GLAZUNOVA, p. 161, Textfig. 25, Pl. 36, Fig. 3–5.

This species with its oval whorl section and a high degree of involution is similar in many aspects to *T. jurinianus*, but it seems to be constricted up to a great diameter and thus it may belong to the present group of forms. It is, however, impossible to interpret this species sufficiently due to the poor figures. Moreover, the given dimensions do not agree with these figures, and the new species has been compared by their author with *"Tetragonites" bhima* – which is a puzosiid – and with *"Tetragonites" leptonema* – which is a *Mesogaudryceras*. But nevertheless attribution to *Tetragonites* may be correct.

T. makarovensis has been described from the Cenomanian of Southern Sakhalin.

II. Group of *T. timotheanus*

Tetragonites balmensis BREISTROFFER

Tetragonites balmensis balmensis BREISTROFFER

Pl. 7, Fig. 3, 4; Textfig. 8

1908 *Lytoceras (T.) Timotheanum* PICT. – C. JACOB, p. 19, Pl. 1, Fig. 11.
Lytoceras (T.) Jurinianum PICT. – C. JACOB, p. 19, Pl. 1, Fig. 12.
pars *Desmoceras (Latidorsella) latidorsatum* MICH. – C. JACOB, Pl. 5, Fig. 1 (only).
1936 *T. balmensis* BREISTROFFER, p. 64.
pars 1967 *Eotetragonites balmensis* BREISTR. – M. A. MURPHY (1967a), p. 69, Textfig. 37, 38a–h, j, k, Pl. 3, Fig. 1–5, 8–11, Pl. 4, Fig. 9–11.

Holotype: Lytoceras (T.) jurinianum in C. JACOB 1908, Plate 1, Figure 12, from the Middle Albian of the Balme de Rencurel (Isère, France), preserved in the LGG collections.

Description: T. balmensis was proposed by its author (M. BREISTROFFER 1936, p. 64) without any description. The designated holotype in C. JACOB is so unsufficiently figured (constrictions seem to be absent, but exist; the whorl section was not taken vertically and thus seems to be broadly rounded instead of oval), that I included them (1962a, p. 176) with some reserve in the prior *T. jurinianus*. In the meantime I have become aware that *T. balmensis* is quite different from the latter, but very near to the recently proposed *T. epigonoides* WIEDM. In view of these facts, a short description of BREISTROFFER's species becomes necessary. *T. balmensis* s. str. is a large-sized and involute form, which preserves its phragmocone up to a diameter of 100 mm. The largest known specimen, described by C. JACOB (1908, Pl. 5, Fig. 1) as "*Desmoceras (Latidorsella) latidorsatum*" and now referred to the present subspecies, is always septate at its maximum D of 97 mm.

The most characteristic feature of the present form is the high number and irregular spacing of distinct constrictions (about 8 per whorl) which are restricted to the inner whorls. At a maximum D of 35 mm the whorls become smooth (Pl. 7, Fig. 3). Moreover the constrictions pass prorsiradiate over the lateral sides and nearly straight over the venter (Pl. 7, Fig. 4).

In addition the whorl section changes considerably during the ontogeny: it is broad-rectangular at an early D of 25 mm, thereafter the periphery becomes more and more rounded (Pl. 7, Fig. 4a), while it attains a more oval section at a D of 60 mm (Pl. 7, Fig. 3b; C. JACOB 1908, Pl. 1, Fig. 12b, Pl. 5, Fig. 1b). This tendency becomes evident also from the dimensions:

"*Desmoceras latidorsatum*" in JACOB 1908, Pl. 5, Fig. 1					
	97 mm,	48 mm (0.50),	53.5 mm (0.55),	22.3 mm (0.23),	[1.12]
Holotype	70 mm,	33 mm (0.47),	37.3 mm (0.53),	17 mm (0.24),	[1.13]
LGG Ce W 5	60 mm,	29.5 mm (0.49),	34.5 mm (0.57),	15.8 mm (0.26),	[1.17]
LGG Ce W 6	36 mm,	16.5 mm (0.46),	20 mm (0.55),	11 mm (0.30),	[1.21]
LGG Ce W 7	28 mm,	12 mm (0.43),	15.3 mm (0.54),	9 mm (0.32),	[1.27]

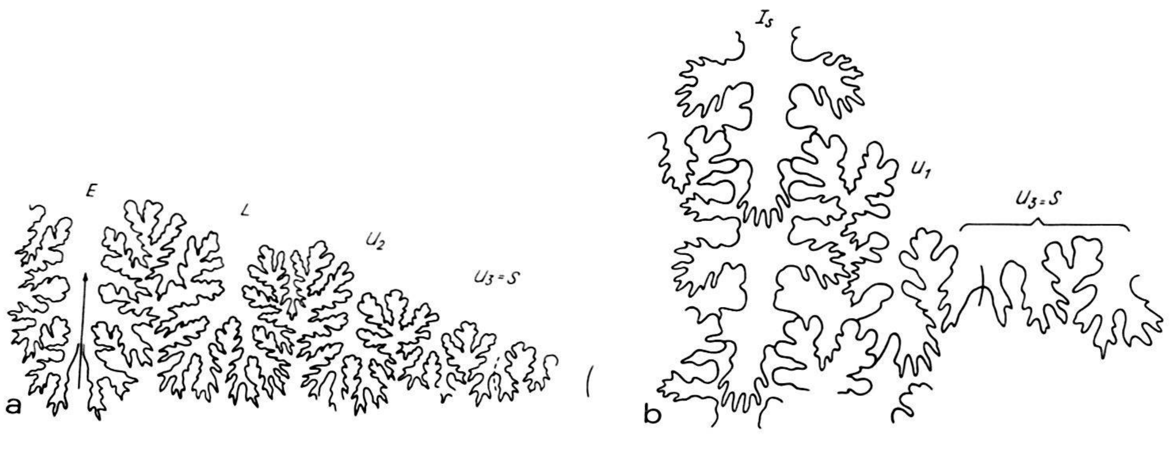

Fig. 8. Suture line of *T. balmensis balmensis* BREISTROFFER. *a* External suture line, hypotype LGG Ce W 5. Middle Albian, Balme de Rencurel (Isère, France). At WH 19 mm. Ca. 3/1. *b* Internal suture line, hypotype LGG Ce W 6. Same age and locality. At WH 15 mm. Ca. 5/1.

The suture line (Textfig. 8a, b) has a tendency to be retracted at the umbilical seam. There is a distinct U_1 in the internal part of the suture. Attribution of *T. balmensis* to *Eotetragonites* as proposed by MURPHY (1967a) thus cannot be accepted. Even MURPHY was not too sure about this attribution, since he correctly wrote "*T. balmensis*" in his diagrammatic Figure 37. Plate 7, Figure 3b gives an impression of the lytoceratid septal lobe (I_s), present in all tetragonitids.
Distribution: T. balmensis balmensis is a common representative in the Middle Albian of Southern France, especially of the Balme de Rencurel (Isère).

Tetragonites balmensis epigonoides WIEDMANN

Pl. 1, Fig. 3

1962 *T. epigonoides* WIEDMANN (1962b), p. 80, Textfig. 29, Pl. 6, Fig. 3, 4.

Holotype: The MSHNB specimen A94 from the Lower Albian of Son Suredeta near Palma de Mallorca, figured in WIEDMANN (1962b, Pl. 6, Fig. 4).
Description: Despite the striking similarity between *T. epigonoides* and *T. balmensis*, the first species of Lower Albian age differs in a number of constant peculiarities which may justify subspecific treatment. Additional specimens I studied in the meantime from the Mallorcan type region offer, as do the previously figured specimens, a larger umbilicus and a likewise higher WT/WH-ratio (see the Table I). A juvenile specimen is reproduced Plate 1, Figure 3, to allow a comparison with the typical subspecies. Its dimensions are, compared with the holotype:

Holotype MSHNB A94	43 mm,	18 mm (0.42),	23 mm (0.53),	14 mm (0.32),	[1.35]
LGG Ce W 8	20 mm,	8.8 mm (0.44),	11.8 mm (0.59),	6.8 mm (0.34),	[1.33]

The suture line formerly described (1962b, Textfig. 29) is retracted at the umbilical seam.
Distribution: The present subspecies occurs in the Lower Albian of Mallorca, especially in the outcrops near Palma de Mallorca.

Tetragonites balmensis diegoensis COLLIGNON

Pl. 2, Fig. 3; Textfig. 9

1963 *T. Jallaberti* var. *diegoensis* COLLIGNON, p. 24, Pl. 250, Fig. 1073.
T. aff. *Timotheanus* PICT. – M. COLLIGNON, p. 21, Pl. 249, Fig. 1067, 1068.
1967 *T. rectangularis diegoensis* (COLL.). – M. A. MURPHY (1967a), p. 44, Textfig. 21, Pl. 4, Fig. 8.

Holotype: COLLIGNON's Figure 1073, here reproduced Plate 2, Figure 3, from the Upper Albian of Mt. Raynaud (Madagascar).
Description: Large-sized, involute form with oval whorl section with rounded periphery. 9–10 constrictions per whorl are strongly projected on the flanks, in later stages recurved at the marginal border and with pronounced ventral sinuosity.

I am pleased to have the opportunity to reproduce, after *T. balmensis* s. str., the type specimen of this subspecies (Pl. 2, Fig. 3), which is in its measurements, whorl section and suture line (Textfig. 9) nearly indistinguishable from that form. The only trifling difference is the persistence of the constrictions to a D of about 55 mm, their more projected course and the stronger sinuosity on the venter at a larger size, and,

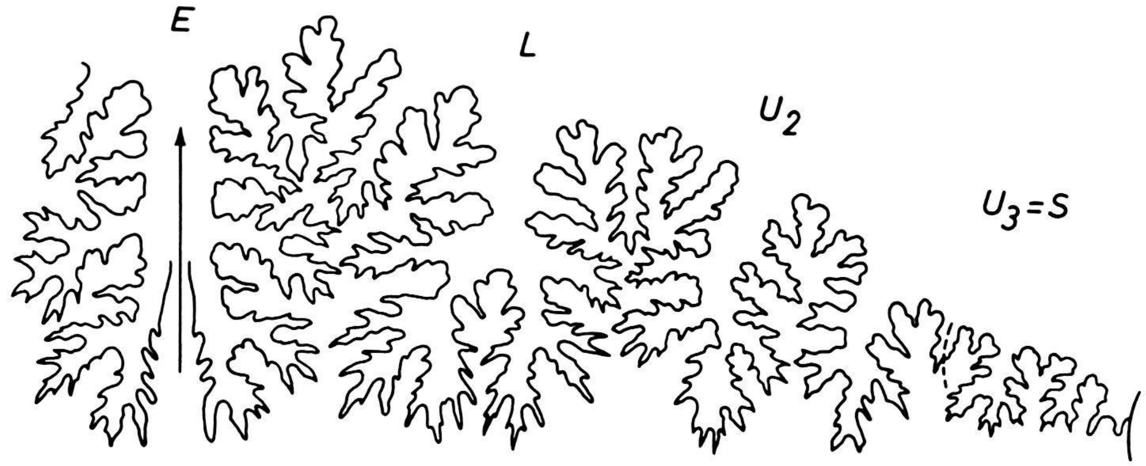

Fig. 9. External suture line of *T. balmensis diegoensis* COLLIGNON. Holotype, M. Collignon coll. No. 92–5. Upper Albian, Mt. Raynaud (Madagascar). At WH 18 mm. Ca. 5/1.

perhaps, the somewhat younger age. Also *T. balmensis diegoensis* is a large-sized form, which is still septate at a D of 65 mm. In the suture line the lobe U_2 has a different shape from that in the typical subspecies. From all these similarities it becomes obvious that the present form should be included in *T. balmensis* s. l., there is no real relationship to *Eotetragonites jallabertianus.*

T. aff. *timotheanus* in COLLIGNON (1963, Pl. 249, Fig. 1067, 1068) may represent the juveniles of the present subspecies.

Measurements:

Holotype	64 mm,	31 mm	(0.48),	35 mm	(0.55),	15 mm	(0.23),	[1.13]
COLLIGNON's fig. 1068	29 mm,	12 mm	(0.42),	17 mm	(0.59),	10 mm	(0.34),	[1.41]
COLLIGNON's fig. 1067	21 mm,	9 mm	(0.43),	12 mm	(0.57),	8 mm	(0.38),	[1.33]

Distribution: T. balmensis diegoensis is up to now restricted to the Upper Albian of Mt. Raynaud and the condensed (Upper?) Albian of Vohimaranitra (Madagascar).

Tetragonites timotheanus (PICTET)

Tetragonites timotheanus timotheanus (PICTET)

Pl. 7, Fig. 5–7

List of synonyms in J. WIEDMANN (1962a, p. 172), and
1967 *T. timotheanus* (PICTET). – M. A. MURPHY (1967a), p. 19, Textfig. 8, 9a–d, f–k, Pl. 1, Fig. 10–19.

Lectotype: Amm. timotheanus PICTET 1848, Plate 3, Figure 1 (reproduced in J. WIEDMANN 1962a, Pl. 14, Fig. 4, and here Pl. 7, Fig. 6) from the Upper Albian of Saxonet (Savoie, France), preserved in the MHNG coll. under Pi "GV"/3, 1.
Description: A complete redescription of this small-sized form was given on a previous occasion (1962a, p. 172). At that time, *T. timotheanus* was restricted to a small group of evolute forms with a distinctly trapezoidal whorl section and constrictions only on the inner whorl (up to a maximum D of 15 mm). The phragmocone terminates at a D of 20 mm.

The suture line (in WIEDMANN 1962a, Textfig. 31) is distinctly retracted at the umbilical seam.

It is not necessary to return to the extensive previous description. Two additional specimens with nearly complete body chamber are reproduced (Pl. 7, Fig. 5, 7), to accentuate the unusual characteristics of this exclusively European subspecies.

Measurements:

MHNG Wi "VK"/5	30 mm,	10 mm (0.33),	16 mm (0.53),	12.7 mm (0.42),	[1.60]
Phragmocone-D 22 mm					
MHNG Wi "T"/4	29 mm,	9.5 mm (0.33),	14 mm (0.48),	12 mm (0.42),	[1.48]
and	14 mm,	5 mm (0.36),	7 mm (0.50),	6 mm (0.43),	[1.40]
Phragmocone-D 22 mm					

Distribution: T. timotheanus s. str. should be restricted to the Upper Albian of Southern France. The Spanish specimens, doubtfully included in 1962 (1962a, Pl. 8, Fig. 10, Pl. 14, Fig. 5), may now be transferred to the following subspecies.

Tetragonites timotheanus australis Wiedmann and Dieni

Pl. 1, Fig. 6

1962 *T.* sp. juv. aff. *timotheanus* (Pict.). – J. Wiedmann (1962a), p. 172, Textfig. 32, 33, Pl. 8, Fig. 10, Pl. 14, Fig. 5.
1968 *T. timotheanus australis* Wiedmann and Dieni, p. 45, Textfig. 15, 16, Pl. 2, Fig. 12, 13, Pl. 4, Fig. 5, 6, 9.

Holotype: T. timotheanus australis Wiedmann and Dieni 1968, Plate 2, Figure 12, from the Upper Albian of Orosei (Sardinia), preserved in the IGP coll. as S 33.
Description: Normal-sized and moderately involute form. Moreover, having higher whorls and more convex lateral sides than the typical subspecies. One Sardinian specimen is reproduced (Pl. 1, Fig. 6) to give an impression of the similarity to *T. timotheanus* s. str., from which the present subspecies nevertheless can be distinguished by constant differences in the measurements (J. Wiedmann 1962a, p. 174; J. Wiedmann and I. Dieni 1968, p. 46):

GPIT Ce 1315/27	15 mm,	5.9 mm (0.39),	7.9 mm (0.52),	5.8 mm (0.38),	[1.34]
Holotype IGPS 33	18.5 mm,	7 mm (0.37),	10 mm (0.54),	6.8 mm (0.36),	[1.43]

The suture line (Wiedmann and Dieni 1968, Textfig. 15) is similar to that of the typical subspecies.
Distribution: While the typical subspecies is restricted to the Upper Albian of Southern France, *T. timotheanus australis* is found in the same beds of Northern Spain and Sardinia.

Tetragonites nautiloides (Pictet)

Tetragonites nautiloides nautiloides (Pictet)

Pl. 8, Fig. 2, 5–8; Textfig. 10

List of synonyms in J. Wiedmann 1962a, p. 174, and
1962 *T. nautiloides* (Pict.). – J. Wiedmann (1962b), p. 77, Textfig. 27, Pl. 5, Fig. 4.
1967 *T. nautiloides* (Pict.). – M. A. Murphy (1967a), p. 27, Textfig. 12, 13, Pl. 2, Fig. 5–10.
1968 *T. nautiloides* (Pict.). – J. Wiedmann and Dieni, p. 47, Pl. 4, Fig. 7, 10.

Neotype: The MHNG specimen Wi"VK"/4 from the Upper Albian of Saxonet (Savoie, France), figured in Wiedmann (1962a, Pl. 5, Fig. 4).

Description: Normal-sized (?) and involute form with trapezoidal whorl section (Pl. 8, Fig. 2, 5–8). *T. nautiloides* does not belong to the unconstricted tetragonitids as generally believed. As previously recorded (1962a, Pl. 8, Fig. 11) and here (Pl. 8, Fig. 2, 7) once more demonstrated, the innermost whorls of *T. nautiloides* s. str. preserve some extremely feeble constrictions, which do not exceed beyond a D of 10 mm. Thereafter the shell becomes completely smooth (Pl. 8, Fig. 5–8). Thus, *T. nautiloides* continuously links constricted and unconstricted tetragonitids. Therefore, subgeneric separation for the group of *T. jurinianus* seem unnecessary. The suture line of the typical subspecies (Textfig. 10) is only moderately retracted at the umbilical seam.

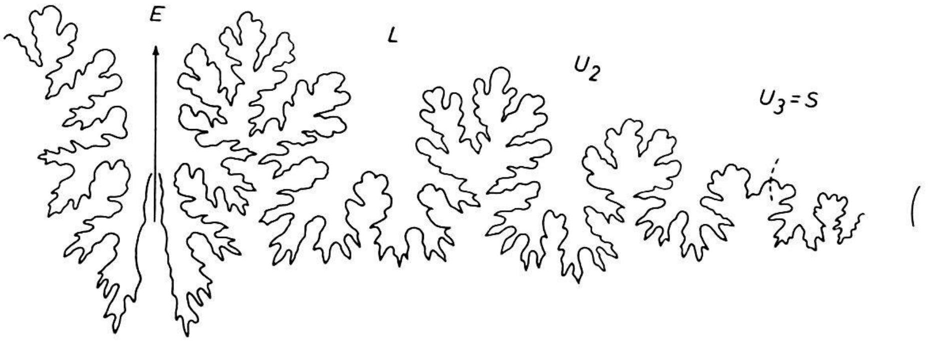

Fig. 10. External suture line of *T. nautiloides nautiloides* (PICTET). Hypotype MHNG Wi "VK"/7. Upper Albian, Saxonet (Savoie, France). At WH 15 mm. Ca. 5/1.

In the typical Upper Albian specimens the umbilical edge is distinctly sharpened (Pl. 8, Fig. 8), but there are some Lower and Middle Albian specimens (in WIEDMANN 1962b, Pl. 5, Fig. 4, and here Pl. 8, Fig. 5), in which the umbilical edge is rounded and the constrictions are somewhat more persistent. The complete identity of trapezoidal whorl section, suture line (Textfig. 10), and dimensions induce me to join them with *T. nautiloides* s. str. These forms may prove that *T. nautiloides* was not derived from *T. timotheanus* by progressive reduction of constrictions, but, probably, from the early *T. rectangularis*.

Measurements of Upper Albian specimens:

MHNG Wi "VK"/6	30 mm,	13.5 mm (0.45),	20 mm (0.66),	7.5 mm (0.25),	[1.49]
MHNG Wi "T"/5	29 mm,	13 mm (0.45),	19.2 mm (0.66),	7.2 mm (0.25),	[1.47]
GPIT Ce 1315/30	?29 mm,	13.6 mm (0.47),	17.2 mm (0.62),	6.5 mm (0.24),	[1.26]
and	14 mm,	6 mm (0.43),	7.8 mm (0.56),	3.5 mm (0.25),	[1.30]
GPIT Ce 1311/2	24 mm,	11 mm (0.46),	15 mm (0.63),	7 mm (0.29),	[1.36]

compared with those of the Middle Albian form (Pl. 8, Fig. 5)

MHNG Wi "VK"/7	27 mm,	11.2 mm (0.42),	17 mm (0.63),	8 mm (0.29),	[1.53]

Distribution: *T. nautiloides* s. str. is widespread in the Upper Albian of Western Europe, sporadic in the Lower and Middle Albian of Southern France and Mallorca.

Tetragonites nautiloides n. ssp.?

Pl. 8, Fig. 1

1963 *T.* aff. *nautiloides* PICT. – M. COLLIGNON, p. 24, Pl. 250, Fig. 1072.

In 1963 M. COLLIGNON presented a badly preserved specimen from the Upper Albian of Aontzy (Madagascar), which was only provisionally assigned to *T. nautiloides*. It is badly preserved and does not warrant a detailed description.

The dimensions taken from the specimen are

51 mm, 25 mm (0.49), >32 mm (0.63), 10 mm (0.20), [1.28]

While it (Pl. 8, Fig. 1) conforms well with *T. nautiloides* in trapezoidal whorl section and lack of constrictions, the outline of whorl section and, especially, the closed umbilicus differ from the latter in a way that might permit subspecific separation. With regard to the bad state of preservation of the single specimen, I prefer open nomenclature for the moment.

III. Group of *T. jurinianus*

Tetragonites jurinianus (PICTET)

Tetragonites jurinianus jurinianus (PICTET)

Pl. 8, Fig. 3, 4

List of synonyms in J. WIEDMANN 1962a, p. 176 (with exception of *T. balmensis* described above), and
1967 *T. jurinianus* (PICT.). – M. A. MURPHY (1967a), p. 23, Textfig. 10, 11, Pl. 2, Fig. 1–4.
1968 *T. jurinianus* (PICT.). – J. WIEDMANN and I. DIENI, p. 48, Pl. 4, Fig. 4, Pl. 5, Fig. 4.

Holotype: The MHNG specimen Pi "GV"/3,3 from the Upper Albian of Saxonet (Savoie, France), figured in F.-J. PICTET (1848, Pl. 3, Fig. 3), and reproduced by the author (1962a, Pl. 14, Fig. 2).

Description: Involute, unconstricted and large-sized form with broad-oval whorl section. In addition to the extensive description given in 1962a, page 176, two inner whorls are added here (Pl. 8, Fig. 3, 4) to demonstrate that oval whorl section and lack of any trace of constrictions are also characteristics of the inner whorls. Such smooth inner whorls are the American *T.* "*zacatecanus*" and "*brazoensis*" BÖSE, formerly (1962a) included in the synonomy.

T. jurinianus var. *angolana* HAAS, likewise included in the comprehensive species in 1962, may be preserved as subspecies in the present classification attempt. Distinguishing features are the high-oval whorl section and the nearly closed umbilicus.

The suture line was previously given (1962a, Textfig. 38) and is characterized by its slight retraction on the umbilical seam and an asymmetrical lateral lobe.

Measurements of the figured specimens:

MHNG Wi "VK"/8	25 mm,	12 mm (0.48),	14.5 mm (0.58),	6.5 mm (0.26),	[1.20]
MHNG Wi "T"/6	37 mm,	16.8 mm (0.45),	21 mm (0.57),	10 mm (0.27),	[1.25]

Both the present and the following subspecies are large-sized forms; the largest known specimens of 75 mm and 105 mm D respectively, are septate throughout.

Distribution: *T. jurinianus* s. str. is widespread in the Upper Albian of Western Europe, Africa, and Central America; it is also sporadically known from the Lower Cenomanian. One specimen (MHNG Wi "VK"/9), from La Goudinière (France), makes it highly possible that the typical subspecies evolved during the Middle Albian (presumably from *T. nautiloides*).

Tetragonites jurinianus angolanus HAAS

1942 *T. jurinianus* var. *angolana* HAAS, p. 170, Textfig. 25, Pl. 44, Fig. 3, Pl. 45, Fig. 1.

Holotype: The specimen cited above from the uppermost Albian of Hanha (Angola), deposited in the AMNH coll. as No. 25398.
Description: Large-sized and extremely involute form with high-oval whorl section, in which, with age, the whorl height exceeds the whorl thickness. The suture line (in O. HAAS 1942, Pl. 44, Fig. 3) is similar to that of the typical subspecies, the lateral lobe is, however, more symmetrical. These differences and the regional separation may justify the proposed subspecific treatment.
As mentioned above, the only known specimen is septate throughout up to a D of

	105 mm,	56 mm	(0.53),	51 mm	(0.48),	17 mm	(0.16),	[0.91]
and	63 mm,	32 mm	(0.51),	34 mm	(0.54),	?		[1.06]

From the small nuclei (between 11 and 19 mm), on which the synonymous *T.* "*zacatecanus*" and "*brazoensis*" were based, it is impossible to decide whether they belong to the present or to the typical subspecies. The degree of involution is similar to the former one, while the whorl sections resemble *T. jurinianus* s. str.
Distribution: T. jurinianus angolanus occurs in the uppermost Albian of Angola.

Genus *Carinites* n. gen.

Type species: Tetragonites spathi FABRE 1940.
Diagnosis: Normal-sized forms with subrectangular whorl section, numerous and irregularly spaced, but persistent constrictions and feeble ventral keel.
Description: The whorl section of *Carinites* n. gen. is high- to broad-rectangular with rounded marginal shoulders and convex venter. A characteristic feature of the genus is the feeble ventral keel which is unknown in any other tetragonitid species. The shells are moderately evolute and the whorls are irregularly constricted. The inner whorls may be smooth (?). The course of the constrictions also differs from that of true *Tetragonites:* they are projected on the lateral sides, but converge angularly on the venter. On the test the constrictions are accompanied by fine bulges.
Thus, the general aspect of *Carinites* n. gen. is somewhat desmoceratid. The suture line, however, is that of a *Tetragonites* (M. A. MURPHY 1967a, Textfig. 33c).
Distribution: Carinites n. gen. is known from one species occurring in the Lower Cenomanian of Southern France.

Carinites spathi (FABRE)
Pl. 8, Fig. 9, 10; Textfig. 11

1923 *T.* n. sp. – L. F. SPATH, p. 26.
1940 *T. Spathi* BREISTR. *in litt.* – S. FABRE, p. 214, Textfig. 26, Pl. 6, Fig. 1.
1967 *T. spathi* BREISTR. (in FABRE). – M. A. MURPHY (1967a), p. 61, Textfig. 33, Pl. 5, Fig. 6–10.

Holotype: The LGM specimen figured by S. FABRE (1940, Pl. 6, Fig. 1) from the Lower Cenomanian of Cassis (Bouches-du-Rhône, France), and here reproduced Plate 8, Figure 10.
Description: I am glad to have had the opportunity to study the holotype, because its whorl section (in S. FABRE 1940, Textfig. 26) needs some correction (Textfig. 11a).

It is subrectangular with slightly converging sides, rounded umbilical and marginal shoulders and slightly rounded venter. Constrictions seem to be restricted to the outer half whorl, where 6 constrictions of projected course and with irregular interspaces are present. The inner whorls seem to be smooth.

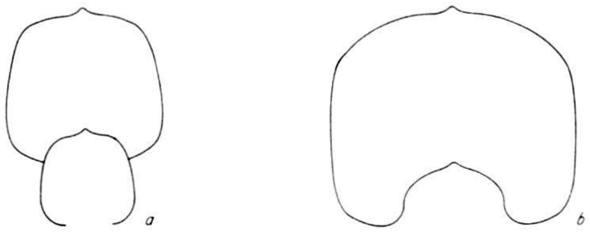

Fig. 11. Whorl sections of *Carinites spathi* (FABRE). *a* Holotype LGM coll. Lower Cenomanian, Cassis (B.-d.-Rh., France). 1/1. *b* Hypotype BMNH C 5896, Same age and locality. 2/1.

The specimen mentioned by L. F. SPATH (1923, p. 26) and here reproduced (Pl. 8, Fig. 9) differs in some aspects from the holotype. The whorl section (Text-fig. 11 b) is broad-rectangular with more distinctly rounded venter, the constrictions are accompanied by feeble bulges on the test (Pl. 8, Fig. 9 b) and already visible at a D of 20 mm. In all other characters the correspondence is complete. Identical origin and equal measurements are further arguments for the proposed identification:

Holotype	42 mm,	16.5 mm (0.39),	18 mm (0.43),	13 mm (0.31),	[1.09]
BMNH C 5896	27 mm,	11 mm (0.41),	13 mm (0.48),	8 mm (0.30),	[1.17]

Distribution: The species is only of limited abundance and restricted occurrences in the Lower and Middle Cenomanian of the departments Bouches-du-Rhône, Alpes-Maritimes and Basses-Alpes (France).

Some doubtful Albian-Cenomanian tetragonitids

As demonstrated at various occasions the inner whorls of several tetragonitid species are too similar for easy distinction or recognition of species. Therefore the following species based on small nuclei have not been accepted:
T. collignoni BREISTROFFER 1940
T. madagascariensis MURPHY 1967.
Others are included in synonomy:
T. kiliani JACOB 1908
T. brazoensis BÖSE 1927
T. zacatecanus BÖSE 1923
T. makarovensis GLAZUNOVA 1960 was doubtfully included in the present context. It needs, however, better documentation.
"*T.* sp." in W. J. KENNEDY (1971, p. 5, Pl. 1, Fig. 9) from the Lower Cenomanian of Southern England is an unconstricted form with rounded involute whorls which points to *T. jurinianus*. Since, however, rounded whorl section, involution and septal surface are so different from all known *Tetragonites* – and have much more affinity with some phylloceratids or desmoceratids – some more information and especially the suture line of the English form are needed[3]).

[3]) Addition de proof: The specimen now is identified as *Desmoceras latidorsatum* 'var. *medium*'.

Paleobiogeography, Paleoecology

As it becomes evident from Textfigure 12, Aptian to Cenomanian tetragonitids favoured the Western part of the European Tethys, the Indo-Madagascan-African realm and the North American Pacific trough. Random occurrences exist moreover in England, Tunisia, Angola, the Central American Tethys, Japan and Sakhalin.

Fig. 12. Distributional map of Aptian-Cenomanian tetragonitids (for explanation of numbers see Textfig. 13).

From the 19 species or subspecies here recognized, only two *(T. rectangularis rectangularis, T. jurinianus jurinianus)* can be regarded as cosmopolitan within the distributional limits of tetragonitids. Only one more species *(T. subbeticus)* joins Western Europe with Northern America and another one *(T. balmensis diegoensis)* Western Europe with Madagascar. The Indian, West African and Japanese (?) forms belong to the Madagascan faunal "province", the English one to Southwestern Europe and the Central American nuclei probably to the cosmopolitan *T. jurinianus* s. str. or *angolanus.* Single specimens known from Sakhalin and Angola are endemic forms, as well as the majority of the European species and subspecies (8 from the total of 11!), one (of 7) North American forms (*T. subtimotheanus maclearni* n. ssp.) and one (of the 8) Madagascan species or subspecies (*T. nautiloides* n. ssp.?). With the exception of Europe, no excessive endemism can thus be recognized. European endemism presumably is due to the fact that we are here in the centre of dispersal of this group of forms. Two other centres are Madagascar and the North American Pacific Coast where tetragonitids likewise are a remarkable element of the faunal association in diversity as well as in abundance.

This leads to reflections about the optimum biota of this most specialized (with respect to their primary sutures) group of ammonites and their possible mode of life. Not too much is known about the original environment, but from their distribution pattern given above we can assume that they had their optimum biota in the three areas just mentioned. If we discuss these areas separately with the traditional concept of ammonite provinces, we would attain quite contradictory conclusions. From their European occurrences we would believe in a climatic origin of this distribution, since the group respects the boreal-mediterranean boundary exactly. In Northern America we might come to the contrary conclusion. Here tetragonitids have a preferred boreal distribution and avoided the tethyan realm. Madagascar, however, had from the climatic point of view, an intermediate position in the moderate zone of the austral province. Consequently, climate cannot be the main controlling factor in tetragonitid distribution.

Most of North American, European and some Madagascan (i.e. Mt. Raynaud) occurrences point to a deep-water environment. Tetragonitids are, however, likewise abundant in littoral glauconites and extreme condensed deposits in Southern France (La Goudinière, Balme de Rencurel) as well as in Sardinia (Orosei) or Madagascar (Vohimaranitra). Even in British Columbia most tetragonitids are found in the Haida Sandstone Member associated with plant débris.

The shell morphology would likewise underline a preferential deep-sea mode of life of tetragonitids. This would be confirmed by their long stratigraphical ranges, if our previous reflections (1973, Textfig. 11) were correct. It is interesting that tetragonitids join the lytoceratid and phylloceratid morphological characters, which were separated for an extreme long time (Upper Triassic–Middle Albian). The advanced tetragonitid genus *Pseudophyllites* becomes absolutely convergent to some phylloceratids, some of the Albian-Cenomanian forms treated here *(T. jurinianus, Carinites spathi)* are indistinguishable from contemporaneous desmoceratids.

Therefore, the problem of tetragonitid mode of life – as a special adaptation in lytoceratids – can be solved only by restudying some of the favoured biota with their complete faunal association. Here, likewise, we come to divergent conclusions. In Southern Spain and Mallorca Aptian and Albian tetragonitids are found associated with smooth oxygones or smooth serpenticones (phylloceratids, desmoceratids, puzosiids) and with planktonic foraminifera within infraneritic sediments. The same is true for the tetragonitids of the Haida Formation of British Columbia, where they are joined, moreover, with the pseudohoplitid genus *Douvilleiceras*. The question why these heteromorphs regained the normal ammonitid coiling may have some adaptational response (hydrodynamically one would suppose: return to greater depth). But we are still far from approving any of these suppositions. As stressed by Murphy (1967a, p. 16) the association with other molluscs such as *Nucula*, *Acila*, *Anchura* and *Nerinea* is – once more – significant for a deep-water environment.

In Madagascar or Sardinia, however, tetragonitids are associated with a heavy sculptured fauna of hoplitids and mortoniceratids as is widespread within the boreal epicontinental seas. This discussion demonstrates the problems we still have in recognizing the facts of ammonite ecology.

Stratigraphy, Phylogeny

From the stratigraphical point of view, tetragonitids are a relatively unimportant group of forms. All necessary details can be seen in Textfigure 13, which tries to elucidate phylogeny of Aptian-Cenomanian tetragonitids. It becomes obvious that

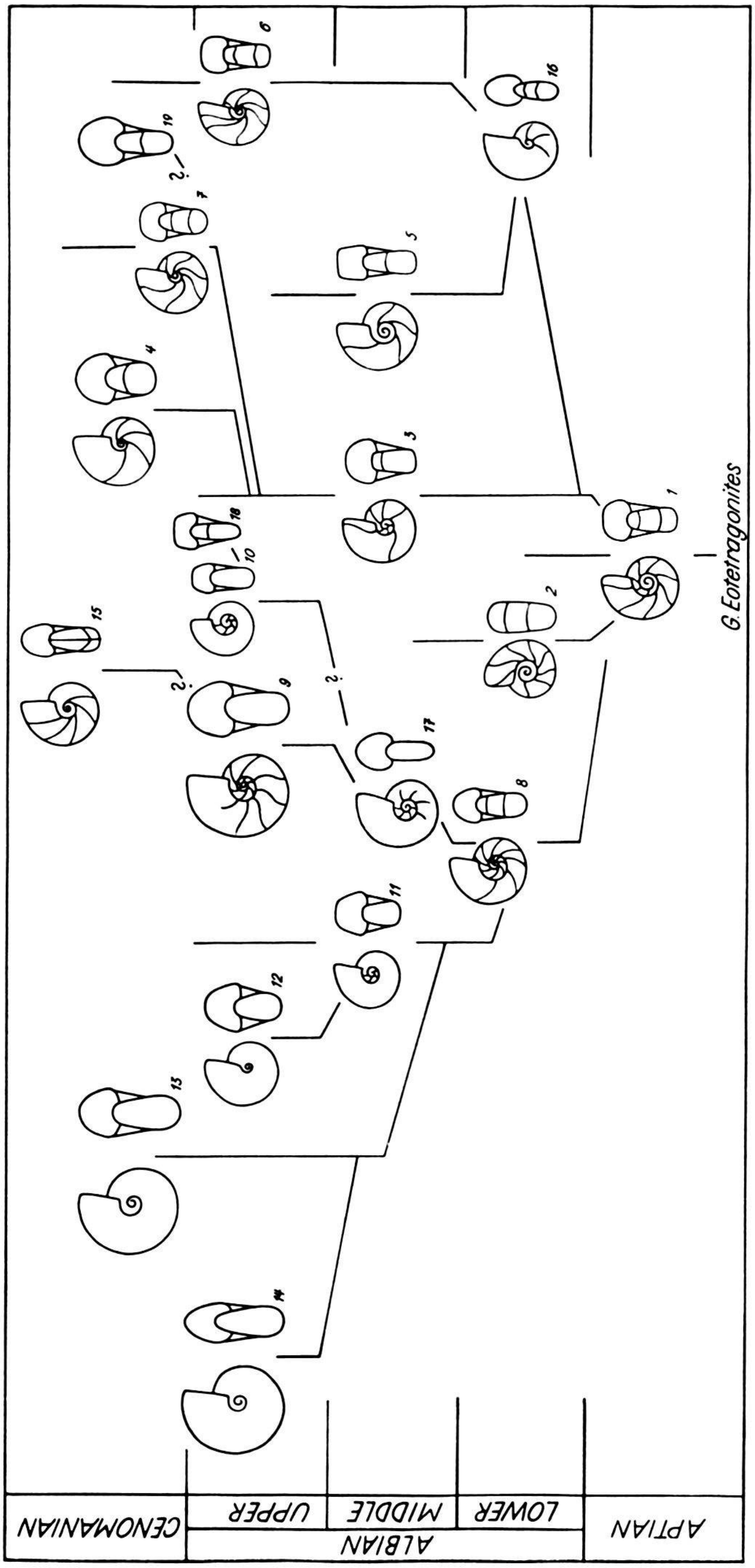

Fig. 13. Presumed phylogeny of Aptian-Cenomanian tetragonitids. *1 T. subbeticus* WIEDM., *2 T. marrei* THOM., *3 T. rectangularis rectangularis* WIEDM., *4 T. rectangularis ampakabensis* COLL., *5 T. kitchini* (KRENK.), *6 T. subtimotheanus subtimotheanus* WIEDM., *7 T. blaisoni* COLL., *8 T. balmensis epigonoides* WIEDM., *9 T. balmensis diegoensis* COLL., *10 T. timotheanus timotheanus* (PICT.), *11 T. nautiloides nautiloides* (PICT.), *12 T. nautiloides* n. ssp. ?, *13 T. jurinianus jurinianus* (PICT.), *14 T. jurinianus angolanus* HAAS, *15 Carinites spathi* (FABRE), *16 T. subtimotheanus maclearni* n. ssp., *17 T. balmensis balmensis* BREISTR., *18 T. timotheanus australis* WIEDM. and DIENI, *19 T. makarovensis* GLAZ.

there are some extremely long-ranging species (as *T. rectangularis*, *balmensis*, *subtimotheanus*, *nautiloides*) covering, with their subspecies, nearly the complete Albian and some even parts of the Cenomanian. There are some short-ranging species (like the true *T. timotheanus*) on the other hand, but in general tetragonitids are similar to their lytoceratid ancestors, to phylloceratids, haploceratids and desmoceratids, in their extreme stratigraphic ranges. As indicated above and has been shown elsewhere (1973, Textfig. 11) this might be related to life conditions in a stable environment, as there are in the infraneritic or even bathyal regions. Short ranging and generally strong ornamented ammonites, probably favoured the labile shelf seas and were, thus, much more obliged to environmental adaptation, resulting in an accelerated speciation or "differentiation index" (B. KURTÉN 1958). Similar phenomena were recently observed in other fossil groups (W. OHMERT 1971) which confirm the here presented assumption of relationship between shell morphology, stratigraphic range and the presumed mode of life.

SUMMARY

In a previous revision of European tetragonitids (1962a, 1962b), the Circum-Indic forms were regarded as distinct, but were only briefly treated. Here, Albian and Cenomanian species, especially those of the Indo-Madagascan faunal province, have been described in more detail and related to the remaining Aptian-Cenomanian forms. For the keeled *T. spathi* FABRE a new genus, *Carinites*, has been proposed.

The classification and phylogeny of these progressive lytoceratids has been represented more clearly, based on the natural hierarchy of all systematic features. The key given on page 589f. permits the easy recognition of this hierarchy, on which necessarily each classificational attempt should be based. In the present case, persistence, reduction, or absence of constrictions may be used for the distinction of species groups, which do not need generic separation in any case, because they are joined by a complete number of transitional forms. For specific separation the whorl section is to be recommended, whereas the degree of shell involution in some cases may justify subspecific treatment (of previous species). Two new subspecies have been proposed, one of them in open nomenclature. Some older species have been described in more detail (*T. balmensis*, *T. blaisoni*, *T. subtimotheanus*); and others interpreted anew (*T. ampakabensis*, *T. epigonoides*, *T. kitchini*); but in any case new and additional data have been added, which may – in addition to a short key for further determinations – facilitate future studies.

Finally, the problem of ecologic adaption and paleogeographic significance of these highly advanced ammonites has been discussed.

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Plate I

Fig. 1 *T. rectangularis rectangularis* WIEDMANN.
Hypotype MHNG Wi "VK"/11 (leg. Pictet).
Upper Albian, Saxonet (Savoie, France).
a: Lateral, b: frontal view of inner whorl with strong constrictions and rectangular whorl section. 2/1.

Fig. 2 *T. subbeticus* WIEDMANN.
Holotype GPIT Ce 1220/21 (leg. Wiedmann).
Upper Aptian, Alcoraya, Sierra Mediana (Alicante, Spain).
a: Ventral, b: lateral, c: frontal view. 2/1.

Fig. 3 *T. balmensis epigonoides* WIEDMANN.
Hypotype LGG Ce W 8 (leg. Fallot).
Lower Albian, Son Vida near Palma (Mallorca, Spain).
a: Lateral, b: frontal view. 2/1.

Fig. 4 *T. blaisoni* COLLIGNON.
Inner whorl of juvenile specimen MHNG Wi "T"/2 (see Pl. 6, Fig. 7) with subtrapezoidal whorl section (leg. Stoliczka). Middle (?) Utatur Group (Cenomanian), Odium (India).
a: Frontal, b: lateral view. 1/1.

Fig. 5 *T. subtimotheanus subtimotheanus* WIEDMANN?
? Hypotype GSC 34670 (leg. McLearn).
Albian, GSC locality 7613, Alliford Bay, Skidegate Inlet, Queen Charlotte Islands (B.C., Canada).
a: Ventral, b: frontal, c: lateral view of juvenile specimen. 2/1.

Fig. 6 *T. timotheanus australis* WIEDMANN and DIENI.
Paratype GPIT Ce 1315/27 (leg. Dieni).
Upper Albian, Orosei (Sardinia).
a: Frontal, b: lateral view. 3/1.

Fig. 7 *T. kitchini* (KRENKEL).
Holotype SMNS 22303.
Upper Lower Albian, Lindi (Tanzania).
a: Ventral, b: lateral, c: frontal view. 3/1.


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Plate II

All figures natural size

Fig. 1 *T. rectangularis ampakabensis* COLLIGNON.
Holotype, M. Collignon collection No. 417.
Lower Cenomanian, W of Ampakabo-Betioky (Madagascar).
a: Ventral, b: lateral, c: frontal view of adult (?) specimen.

Fig. 2 *T. subtimotheanus subtimotheanus* WIEDMANN.
Hypotype MHNG Wi "T"/1 (leg. Stoliczka).
Lower (?) Utatur Group (Upper Albian), Penangur (India).
a: Ventral, b: lateral view, c: cross section of adult (?) specimen.

Fig. 3 *T. balmensis diegoensis* COLLIGNON.
Holotype, M. Collignon collection No. 92–5.
Upper Albian, Mt. Raynaud (Madagascar).
a: Ventral, b: lateral, c: frontal view.

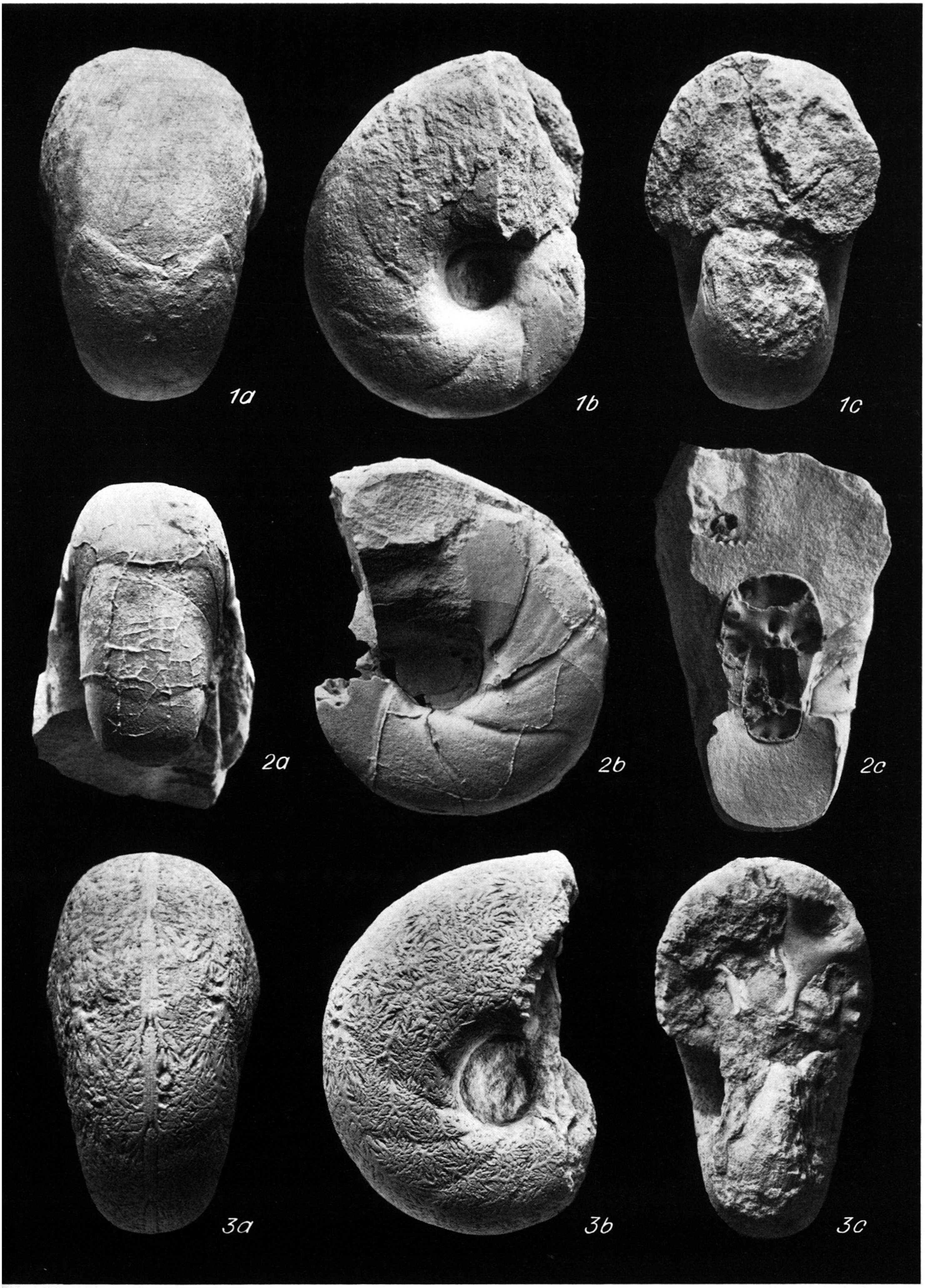
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Plate III

All figures natural size

T. subtimotheanus subtimotheanus WIEDMANN

Fig. 1 Hypotype GSC 34678 (leg. McLearn).
Upper Albian (Dawsoni Zone), GSC loc. 7578a (QH A 12a), North shore of Bearskin Bay, Skidegate Inlet, Q.Ch.I. (B.C., Canada).
a: Lateral, b: ventral view of juvenile (?) specimen with living chamber preserved. 1/1.

Fig. 2 Adult Hypotype GSC 34664 (leg. McLearn) with complete body chamber and mouth border.
Middle Albian (Perezianum Zone), GSC loc. 7575a (QH A 9), same locality as Figure 1.
a: Frontal, b: lateral view. 2/3.

Fig. 3 Hypotype GSC 34665 (leg. McLearn) with *Cleoniceras (Grycia?) perezianum* (WHIT.).
Middle Albian (Perezianum Zone), GSC loc. 7608 (QH F 6), North shore of Lina Island, Skidegate Inlet, Q.Ch.I. (B.C., Canada).
a: Lateral, b: ventral view. 1/1.

Fig. 4 Hypotype GSC 34668.
Albian, GSC loc. 8085, Skidegate Inlet, Q.Ch.I. (B.C., Canada).
a: Lateral, b: frontal, c: ventral view. 1/1.

Fig. 5 Hypotype GSC 34669.
Same age and locality.
a: Lateral, b: frontal, c: ventral view. 1/1.

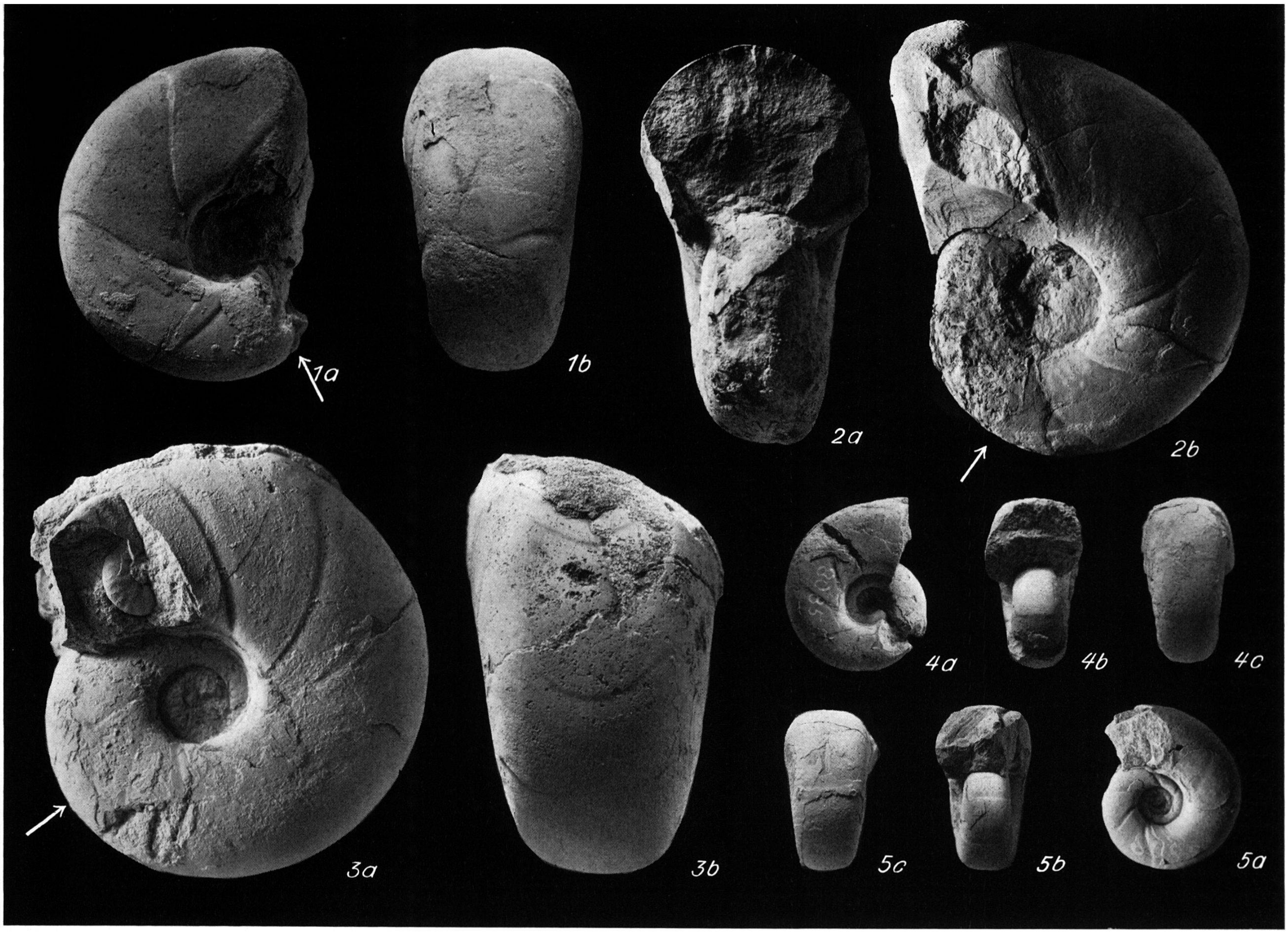
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Plate IV

All figures natural size

Fig. 1 *T. subtimotheanus maclearni* n. ssp.
Paratype GSC 24526 (leg. McLearn).
Upper Lower Albian (Hulenense Zone), GSC loc. 7572 (QH A 5), North shore of Bearskin Bay, Skidegate Inlet, Q.Ch.I. (B.C., Canada).
a: Lateral, b: ventral view of body-chamber fragment.

Fig. 2 *T. rectangularis rectangularis* WIEDMANN.
Holotype MHNG Wi "VK"/10.
Upper Albian, Saxonet (Savoie, France).
a: Lateral, b: frontal view.

Fig. 3 *T. rectangularis ampakabensis* COLLIGNON?
Hypotype GSC 34663 (leg. McLearn), possibly with body chamber preserved.
? Middle Albian, GSC loc. 7609a (QH F 8), North shore of Lina Island, Skidegate Inlet, Q.Ch.I. (B.C., Canada).
a: Ventral, b: lateral, c: frontal view.

Fig. 4 *T. rectangularis ampakabensis* COLLIGNON?
Hypotype GSC 34662, with body chamber preserved.
Albian, GSC loc. 8085, Skidegate Inlet, Q.Ch.I. (B.C., Canada).
Lateral view.

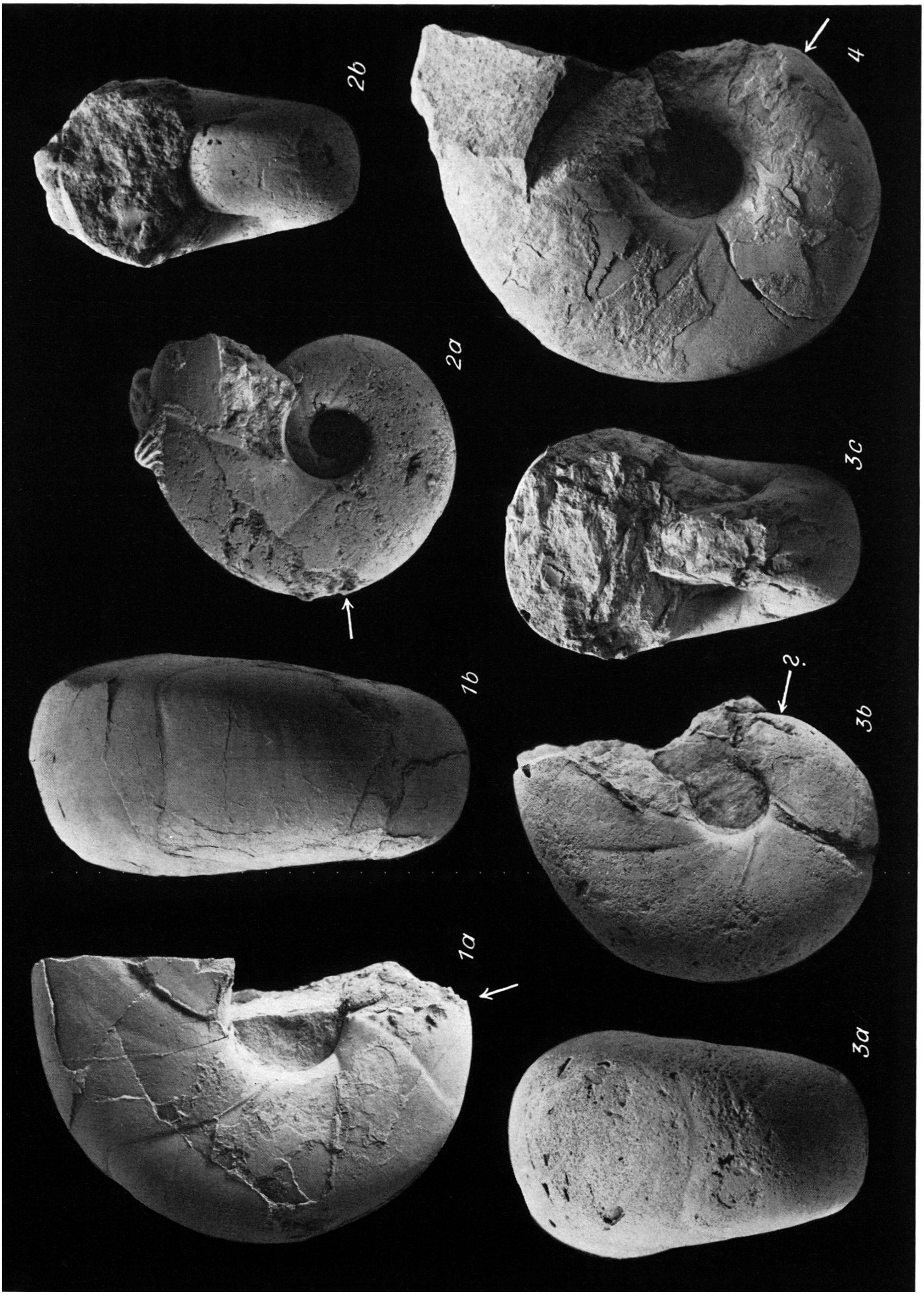
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Plate V

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T. subtimotheanus maclearni n. ssp.

Fig. 1 — Holotype GSC 34671 (leg. McLearn), with body chamber.
Middle Albian (Perezianum Zone), GSC loc. 7574a (QH A 8), North shore of Bearskin Bay, Skidegate Inlet, Q.Ch.I. (B.C., Canada).
a: Ventral view, b: cross section, c: lateral view.

Fig. 2 — Paratype GSC 34675 (leg. McLearn).
Middle Albian (Perezianum Zone), GSC loc. 7576a (QH A 10a), same locality.
a: Lateral, b: frontal view of inner whorl (?).

Fig. 3 — Paratype GSC 34672 (leg. McLearn).
Upper Lower Albian (Hulenense Zone), GSC loc. 7613 (QH P 2), Alliford Bay, Skidegate Inlet, Q.Ch.I. (B.C., Canada).
Lateral view of adult specimen.

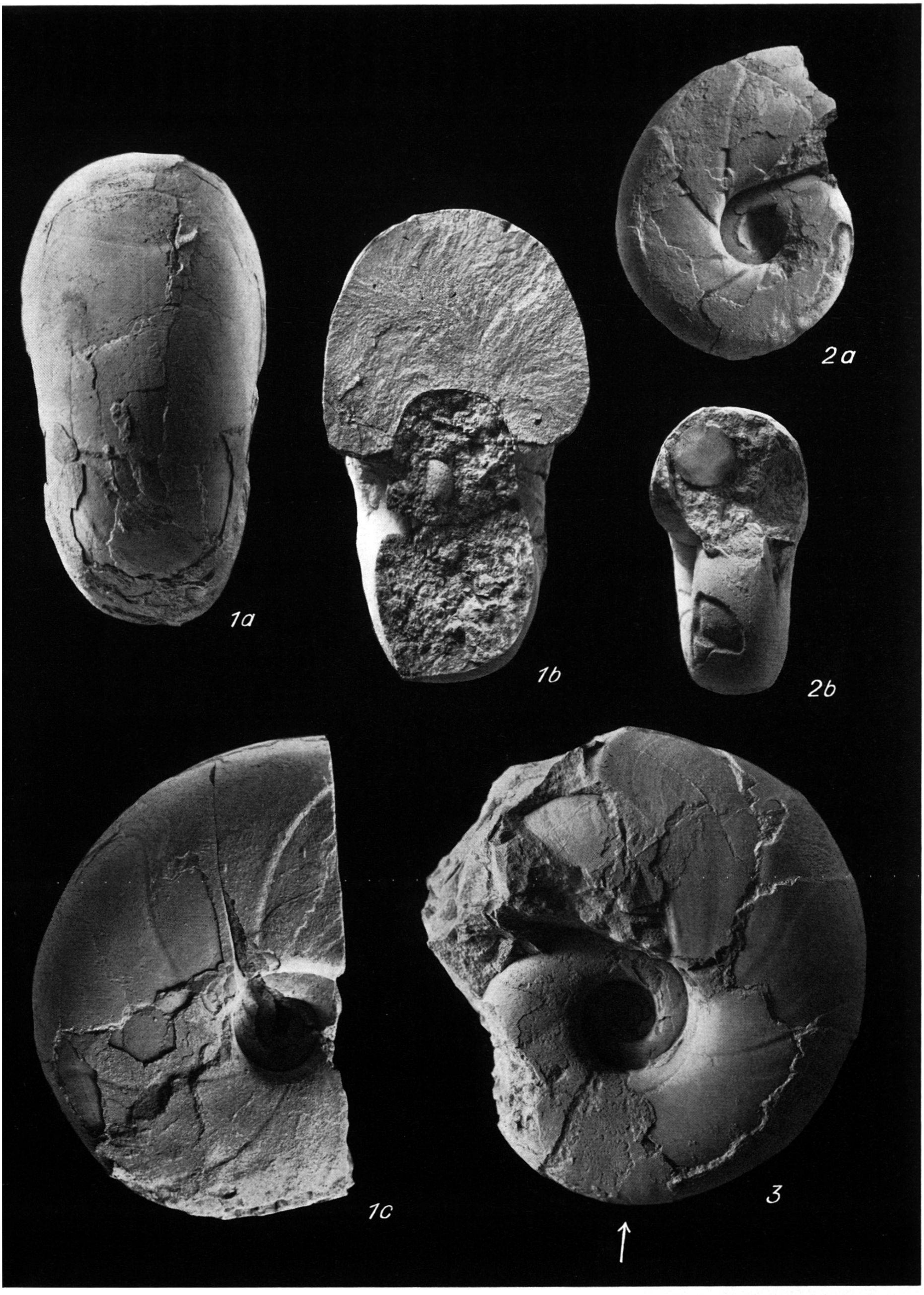
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Plate VI

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Fig. 1 *T. kitchini* (KRENKEL).
Hypotype GPIT Ce 1311/1.
? Middle Albian, Manohonda (Madagascar).
a: Ventral, b: lateral, c: frontal view.

Fig. 2 *T.* aff. *kitchini* (KRENKEL).
(= *Amm.* "*timotheanus*" in WHITEAVES 1876, Pl. 3, Fig. 2).
GSC 4978 (leg. Richardson), Albian. Alliford Bay, Skidegate Inlet, Q.Ch.I. (B.C., Canada).
a: Frontal, b: lateral, c: ventral view.

Fig. 3 *T.* aff. *kitchini* (KRENKEL).
Specimen GSC 24527, with body chamber.
Same age and locality.
a: Lateral, b: ventral view.

Fig. 4 *T.* aff. *kitchini* (KRENKEL).
Specimen GSC 24529 (leg. McLearn).
Middle Albian, GSC loc. 7579 (QH A 9), North shore of Bearskin Bay, Skidegate Inlet, Q.Ch.I. (B.C., Canada).
a: Lateral, b: ventral view.

Fig. 5 *T. blaisoni* COLLIGNON?
Doubtful hypotype MHNG Wi "T"/3, with part of body chamber (leg. Stoliczka).
Middle (?) Utatur Group (Cenomanian), Odium (India).
a: Ventral, b: lateral view.

Fig. 6 *T. blaisoni* COLLIGNON.
Holotype, M. Collignon collection No. 474.
Lower Cenomanian, Beraketa-Sakondry (Madagascar).
a: Frontal, b: lateral, c: ventral view.

Fig. 7 *T. blaisoni* COLLIGNON.
Juvenile hypotype MHNG Wi "T"/2, with part of body chamber (for inner whorls see Pl. 1, Fig. 4).
Same age and locality.
a: Lateral, b: frontal view.

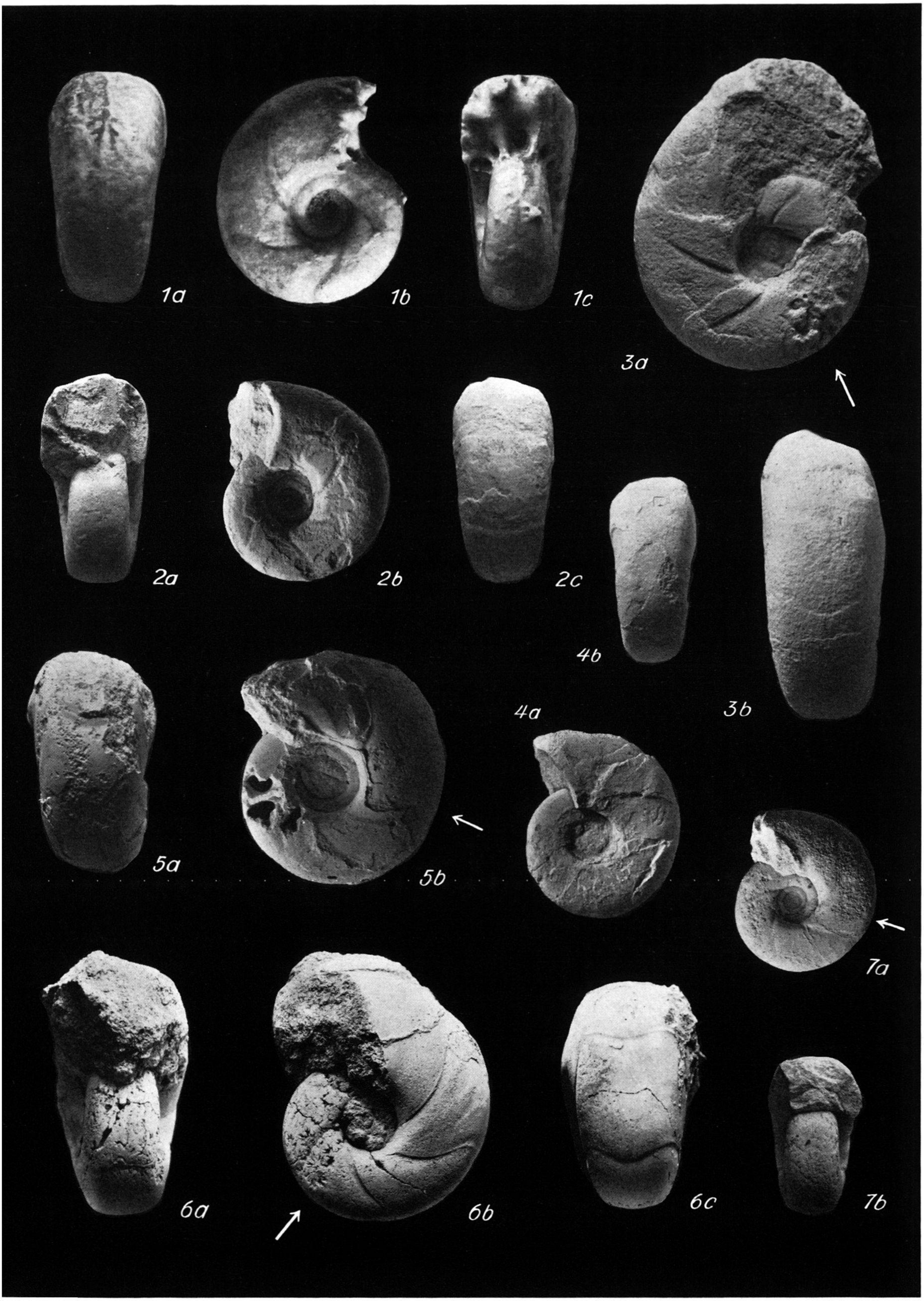
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Plate VII

All figures natural size

Fig. 1 *T. rectangularis rectangularis* Wiedmann.
Hypotype LGG Ce W 1 (leg. Fallot), medium-sized specimen.
Lower Albian, Son Vida near Palma (Mallorca, Spain).
a: Frontal, b: lateral, c: ventral view.

Fig. 2 *T. rectangularis rectangularis* Wiedmann.
Hypotype LGG Ce W 3 (leg. Fallot).
Same age and locality.
a: Lateral, b: frontal view of inner whorls.

Fig. 3 *T. balmensis balmensis* Breistroffer.
Hypotype, LGG Ce W 5 (leg. Jacob).
Middle Albian, Balme de Rencurel (Isère, France).
a: Lateral, b: frontal view with septal lobe.

Fig. 4 *T. balmensis balmensis* Breistroffer.
Inner whorls, LGG Ce W 6 (leg. Jacob).
Same age and locality.
a: Frontal, b: ventral, c: lateral view.

Fig. 5 *T. timotheanus timotheanus* (Pictet).
Hypotype MHNG Wi "T"/4 (leg. Pictet).
Upper Albian, Saxonet (Savoie, France).
Lateral view of adult specimen.

Fig. 6 *T. timotheanus timotheanus* (Pictet).
Lectotype MHNG Pi "GV"/3,1 (leg. Mayor), with complete body chamber.
Same age and locality.
Lateral view.

Fig. 7 *T. timotheanus timotheanus* (Pictet).
Adult hypotype MHNG Wi "T"/5 (leg. Pictet).
Same age and locality.
a: Lateral, b: frontal view.

Fig. 8 *T. subtimotheanus subtimotheanus* Wiedmann?
Doubtful hypotype GSC 34679 (leg. McLearn).
? Middle Albian, GSC loc. 7609a (QH F 8), North shore of Lina Island, Skidegate Inlet, Q.Ch.I. (B.C., Canada).
a: Lateral, b: frontal view.

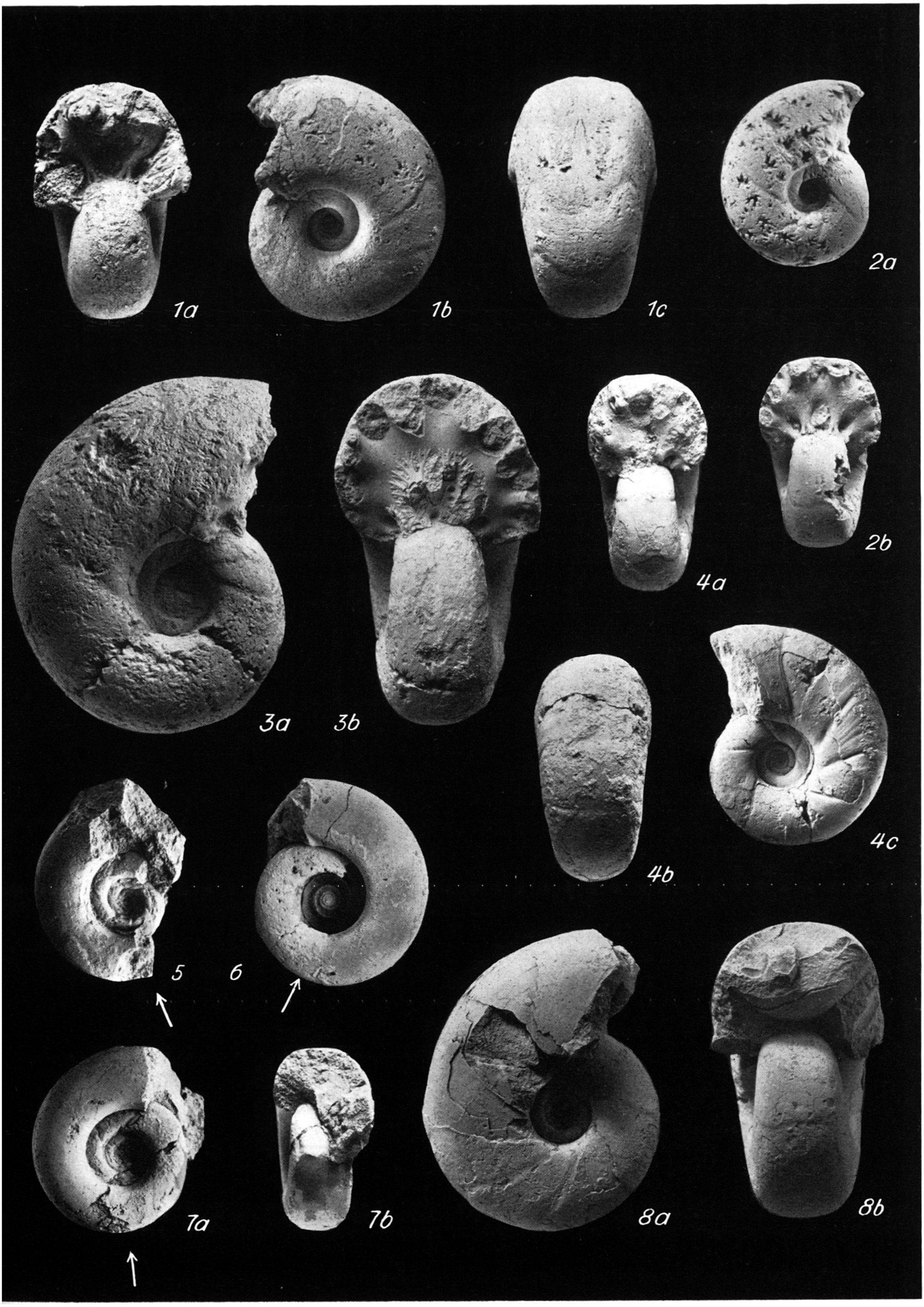
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Plate VIII

All figures natural size

Fig. 1 — *T. nautiloides* n. ssp.?
(= *T.* aff. *nautiloides* in M. Collignon 1963, Pl. 250, Fig. 1072).
Upper Albian, Aontzy (Madagascar).
a: Lateral, b: frontal view.

Fig. 2 — *T. nautiloides nautiloides* (Pictet).
Hypotype GPIT Ce 1311/2 (leg. Wiedmann).
Upper Albian, Cehegín (Murcia, Spain).
a: Ventral, b: lateral, c: frontal view.

Fig. 3 — *T. jurinianus jurinianus* (Pictet).
Hypotype MHNG Wi "T"/6 (leg. Pictet).
Upper Albian, Saxonet (Savoie, France).
Lateral view.

Fig. 4 — *T. jurinianus jurinianus* (Pictet).
Hypotype MHNG Wi "VK"/8 (leg. Pictet).
Same age and locality.
Lateral view of inner whorl.

Fig. 5 — *T. nautiloides nautiloides* (Pictet).
Hypotype MHNG Wi "VK"/7 (leg. Pictet).
Early form with rounded umbilical edge and somewhat longer persisting constrictions.
? Middle Albian, La Goudinière (Savoie, France).
a: Lateral, b: frontal view.

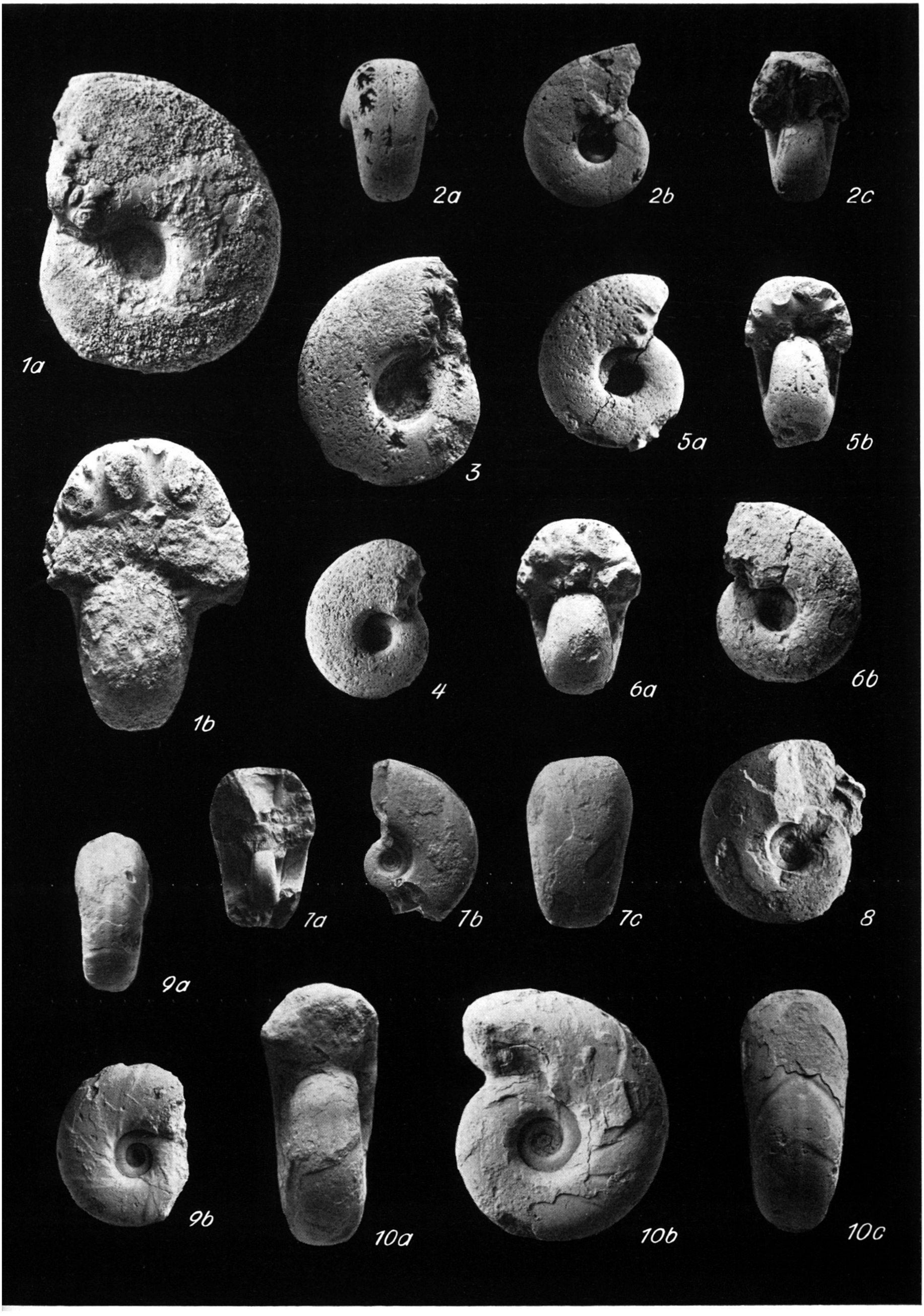
Fig. 6 — *T. nautiloides nautiloides* (Pictet).
Typical specimen MHNG Wi "VK"/6 (leg. Pictet).
Upper Albian, Saxonet (Savoie, France).
a: Frontal, b: lateral view.

Fig. 7 — *T. nautiloides nautiloides* (Pictet).
Hypotype GPIT Ce 1315/30 (leg. Dieni).
Upper Albian, Orosei (Sardinia).
a: Frontal, b: lateral, c: ventral view of inner whorls.

Fig. 8 — *T. nautiloides nautiloides* (Pictet).
Hypotype MHNG Wi "T"/5 (leg. Pictet).
Upper Albian, Saxonet (Savoie, France).
Lateral view of typical specimen with sharpened umbilical edge.

Fig. 9 — *Carinites spathi* (Fabre).
Hypotype BMNH C 5896 (leg. Michalet).
Lower Cenomanian, Cassis (Bouches-du-Rhône, France).
a: Ventral, b: lateral view.

Fig. 10 — *Carinites spathi* (Fabre).
Holotype LGM collection (see S. Fabre 1940, Pl. 6, Fig. 1).
Same age and locality.
a: Frontal, b: lateral, c: ventral view.


1a
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