BULLETIN 299

EURASIAN CRASPEDITID GENERA *TEMNOPTYCHITES* AND *TOLLIA* IN THE LOWER VALANGINIAN OF SVERDRUP BASIN, DISTRICT OF FRANKLIN

With comments on taxonomy and nomenclature of Craspeditidae

J.A. Jeletzky

EURASIAN CRASPEDITID GENERA *TEMNOPTYCHITES* AND *TOLLIA* IN THE LOWER VALANGINIAN OF SVERDRUP BASIN, DISTRICT OF FRANKLIN

With comments on taxonomy and nomenclature of Craspeditidae

EURASIAN CRASPEDITID GENERA *TEMNOPTYCHITES* AND *TOLLIA* IN THE LOWER VALANGINIAN OF SVERDRUP BASIN, DISTRICT OF FRANKLIN

With comments on taxonomy and nomenclature of Craspeditidae

J.A. Jeletzky

Preface

Fossils provide the principal means of dating Phanerozoic rocks as a basis for understanding the geological framework of a region. As such the present study is a significant contribution to increasing our knowledge of the stratigraphy of the Sverdrup Basin, a region where there seems to be a good chance of finding natural gas and oil. Detailed geological studies are essential in evaluating these and other resources and this report forms part of the Geological Survey of Canada's contribution to meeting this responsibility.

Ottawa, October 1977

D.J. McLaren
Director-General
Geological Survey of Canada

Contents

EURASIAN CRASPEDITID GENERA *TEMNOPTYCHITES* AND *TOLLIA* IN THE LOWER VALANGINIAN OF SVERDRUP BASIN, DISTRICT OF FRANKLIN
with comments on taxonomy and nomenclature of Craspeditidae

Abstract

Lower Valanginian beds of the Deer Bay Formation in Sverdrup Basin, Arctic Canada, are characterized by the numerous representatives of the boreal ammonite *Temnoptychites* Pavlow 1914 (including subgenera *Temnoptychites* s. str. and *Costamenjaites* Sazonova 1971). They are accompanied by rare representatives of the boreal genus *Tollia* (s. lato) Pavlow 1914. The following representatives of these craspeditid genera are described and figured from the Deer Bay Formation:

> *Temnoptychites (Temnoptychites) borealis* Bodylevsky 1967
> *T. (T.) kemperi* n. sp.
> *Temnoptychites (Costamenjaites) grandiosus* Voronets 1962
> *T. (C.) aff. T. (C.) grandiosus* Voronets 1962
> *T. (C.) troelseni* n. sp. subsp. *troelseni* n. subsp.
> *T. (C.) troelseni* n. sp. subsp. *crassus* n. subsp.
> *Tollia* (s. lato) aff. *T. tolli* Pavlow 1914
> *T.* (s. lato) n. sp. aff. *T. klimovskiensis* Krimgolts 1953
> *T.* (s. lato) n. sp. aff. *T. vai* Krimgolts 1953
> *T.* (s. lato) n. sp. aff. *T. subtilis* Voronets 1962

A revision of taxonomy and nomenclature of *Temnoptychites*, *Tollia* and the family Craspeditidae Spath 1924 in general is undertaken in connection with the description of the Deer Bay representatives of the above-mentioned genera. This revision stresses the outstanding taxonomic value of the external suture line for the recognition of representatives of Craspeditidae in general and that of its individual genera. The details of sculpture and the whorl shape are considered to have a subordinate taxonomic value for the same purposes.

The current proliferation of subgenera, genera and subfamilies of the Craspeditidae is directly attributable to the neglect of the taxonomic value of the external suture line by modern workers combined with an exaggeration of the value of the sculpture and the whorl shape. This taxonomic procedure is severely criticized and rejected as causing an unnecessarily complicated nomenclature and obstructing interregional zonal correlation of the uppermost Jurassic and early Early Cretaceous rocks.

None of the recently proposed subfamilies of the Craspeditidae are recognized as valid. Furthermore, some craspeditid subgenera and genera (e.g., *Volgidiscus* Casey 1973; *Runctonia* Casey 1973; *Lynnia* Casey 1973; *Bojarkia* Shulgina 1969; *Neotollia* Shulgina 1969; *Pronjaites* Sazonova 1971; *Bodylevskyiceras* Sazonova 1971; *Mosquites* Sazonova 1971; *Caseiceras* Sazonova 1971; and *Nikitinoceras* Sokolov 1913) are considered to be entirely superfluous and are synonymized with *Craspedites*, *Surites*, *Temnoptychites*, *Praetollia*, and *Tollia* on the generic and subgeneric level. Other genera are either considered to be of doubtful validity (e.g., *Shulginites* Casey 1973; *Borealites*

Résumé

Les couches d'âge valanginien inférieur de la formation de Deer Bay dans le bassin Sverdrup de l'archipel Arctique canadien sont caractérisées par de nombreux représentants de l'ammonite boréale *Temnoptychites* Pavlow 1914 (y compris les sous-genres *Temnoptychites* s. str. et *Costamenjaites* Sazonova 1971). Ces ammonites sont accompagnées par de rares représentants du genre boréal *Tollia* (s. lato) Pavlow 1914. Dans la formation de Deer Bay, on a découvert et décrit les représentants suivants de ces genres de Craspeditidés:

> *Temnoptychites (Temnoptychites) borealis* Bodylevsky 1967
> *T. (T.) kemperi* n. sp.
> *Temnoptychites (Costamenjaites) grandiosus* Voronets 1962
> *T. (C.) aff. T. (C.) grandiosus* Voronets 1962
> *T. (C.) troelseni* n. sp. subsp. *troelseni* n. subsp.
> *T. (C.) troelseni* n. sp. subsp. *crassus* n. subsp.
> *Tollia* (s. lato) aff. *T. tolli* Pavlow 1914
> *T.* (s. lato) n. sp. aff. *T. klimovskiensis* Krimgolts 1953
> *T.* (s. lato) n. sp. aff. *T. vai* Krimgolts 1953
> *T.* (s. lato) n. sp. aff. *T. subtilis* Voronets 1962

Dans le présent article, on a entrepris une révision générale de la taxonomie et de la nomenclature de *Temnoptychites*, *Tollia* et de la famille Craspeditidae Spath 1924 en fonction des descriptions des représentants des genres susmentionnés rencontrés dans la formation de Deer Bay. Cette révision s'appuie sur l'excellente valeur taxonomique de la ligne de suture externe pour l'identification des représentants des Craspeditidés en général, et des genres qui composent cette famille. On juge que les détails de la sculpture et le configuration de la coquille n'ont qu'une valeur taxonomique secondaire, a cet égard.

La prolifération actuelle des sous-genres, des genres et sous-familles des Craspeditidés est directement imputable au fait que les chercheurs actuels ont négligé la valeur taxonomique de la ligne de suture externe, et qu'ils ont en outre exagéré l'importance de la sculpture et du configuration de la coquille. Cette méthode taxonomique a fait l'objet d'une critique sévère, et a été rejetée, puisqu'elle complique inutilement la nomenclature et empêche d'établir d'une région à l'autre une corrélation entre les zones du Jurassique terminal et du Crétacé basal.

Aucune des sous-familles des Craspeditidés récemment proposées n'est acceptée. De plus, quelques sous-genres et genres de Craspeditidés (par example, *Volgidiscus* Casey 1973; *Runctonia* Casey 1973; *Lynnia* Casey 1973; *Bojarkia* Shulgina 1969; *Neotollia* Shulgina 1969; *Pronjaites* Sazonova 1971; *Bodylevskyiceras* Sazonova 1971; *Mosquites* Sazonova 1971; *Caseiceras* Sazonova 1971; et *Nikitinoceras* Sokolov 1913) sont considérés comme entièrement superflus, et comme des synonymes de *Craspedites*, *Surites*, *Temnoptychites*, *Praetollia*, et *Tollia* aux niveaux du genre et du sous-genre. On considère un certain nombre d'autres genres comme d'une validité douteuse (par exemple, *Shulginites* Casey 1973; *Borealites* Klimova 1969; *Bogoslovskia* Sazonova 1971; *Stchirowskiceras* Sazonova 1971), ou bien ils ont été replacés dans des sous-genres (par exemple, *Swinnertonia* Shulgina 1972, *Menjaites* Sazonova 1971; *Costamenjaites* Sazonova 1971).

Klimova 1969; *Bogoslovskia* Sazonova 1971; *Stchirowskiceras* Sazonova 1971) or downgraded to subgenera (e.g., *Swinnertonia* Shulgina 1972, *Menjaites* Sazonova 1971; *Costamenjaites* Sazonova 1971).

All representatives of *Temnoptychites* and *Tollia* known from the lower Valanginian of Sverdrup Basin are either closely related to or specifically identical with the species previously described from central Russia, European Arctic and northern Siberia. Therefore they are interpreted as migrants from these boreal regions via the early Valanginian seas of northern Siberia. This circumstance greatly facilitates the intercontinental correlation of the lower Valanginian beds of Sverdrup Basin and the dating of its regional Valanginian and Berriasian fossil zones in terms of the international standard stages and the classical fossil zones of western Europe.

At least two well defined *Temnoptychites* faunas are recognizable in the lower Valanginian beds of the Deer Bay Formation: *Temnoptychites (Temnoptychites) kemperi* fauna and *Temnoptychites (Costamenjaites) troelseni* fauna. These two faunas define ammonite zones within the lower part of the lower to middle Valanginian *Buchia keyserlingi* Zone.

The *Temnoptychites (Temnoptychites) kemperi* Zone immediately underlies the *Thorsteinssonoceras ellesmerense* Zone and the two faunas mingle in its topmost part. The *Temnoptychites (Temnoptychites) kemperi* Zone is therefore equated, completely or in part, with the *T. (T.) hoplitoides* Zone of central Russia and the *T. (T.) syzranicus* Zone of northern Siberia. It is assigned the latest early Valanginian age whereas the next younger *Thorsteinssonoceras ellesmerense* Zone is placed in the earliest mid-Valanginian as defined by the author.

Though *Temnoptychites (Temnoptychites) kemperi* and *Temnoptychites (Costamenjaites) troelseni* zones were not observed in superposition, the latter zone is inferred to be the older of the two and equivalent, in part, to the basal Valanginian *Pseudogarnieria undulatoplicatilis* Zone of central Russia. First, there is no room for another fossil zone between *Temnoptychites (Temnoptychites) kemperi* Zone and the next younger *Thorsteinssonoceras ellesmerense* Zone. Second, the two Canadian zones contain specifically and subgenerically distinct *Temnoptychites* forms and so could hardly be faunal facies of one and the same zone. Third, *T. (C.) grandiosus* and *T. (C.) troelseni* n. sp. belong to the same subgenus as, and are closely related specifically to, *Temnoptychites (Costamenjaites)* ex gr. *jucundus-suraense* of Central Russian Basin. There the latter species characterize the basal Valanginian *Pseudogarnieria undulatoplicatilis* Zone which immediately underlies the regional *Temnoptychites (Temnoptychites) hoplitoides* Zone.

The bulk of *Tollia* (s. lato) forms hitherto found in Sverdrup Basin are associated either with *Temnoptychites (Costamenjaites) troelseni* or with *Temnoptychites (Temnoptychites) kemperi* fauna. This puts in doubt the previously held idea about the presence of the basal Valanginian *Tollia tolli* Zone stratigraphically below the generalized *Temnoptychites* Zone in the Deer Bay Formation. It is not known whether or not the *Temnoptychites (Costamenjaites) troelseni* Zone corresponds to all of the central Russian *Pseudogarnieria undulatoplicatilis* Zone and to all of the presumably equivalent *Tollia klimovskiensis* and *Tollia mesezhnikowi* subzones (of *Tollia tolli* Zone) of northern Siberia. If it corresponds only to the upper part of the *Pseudogarnieria undulatoplicatilis* Zone and the *Tollia klimovskiensis* Subzone, the equivalents of the lower part of the *Tollia tolli* Zone may be present in those beds in the Deer Bay Formation containing *Buchia keyserlingi* but so far barren of ammonites, which immediately underlie the *Temnoptychites (Costamenjaites) troelseni* Zone. However, these lowermost Valanginian beds may be represented only by a regional late Berriasian and basal (?) Valanginian hiatus recently discovered in the Sverdrup Basin.

Tous les représentants de *Temnoptychites* et *Tollia* identifiés dans le Valanginien inférieur du bassin Sverdrup sont soit étroitement apparentés, soit identiques aux espèces déjà décrites en Russie centrale, dans l'Arctique européen et le nord de la Sibérie. Par conséquent, on estime que ces représentants ont migré des régions boréales en traversant les mers du Valanginien inférieur du nord de la Sibérie. Ceci nous permet d'établir beaucoup plus facilement une corrélation entre les couches du Valanginien inférieur du bassin de Sverdrup et ceux des autres continents et de dater les zones fossilifères régionales du Valanginien et Berriasien par rapport aux étages internationaux et aux zones classiques d'Europe occidentale.

On a identifié au moins deux faunes bien définies de *Temnoptychites* dans les couches de la formation de Deer Bay qui datent du Valanginien inférieur: la faune à *Temnoptychites (Temnoptychites) kemperi* et la faune à *Temnoptychites (Costamenjaites) troelseni*. Ces deux faunes permettent de définer des zones à ammonites dans la partie inférieure de la zone à *Buchia keyserlingi*, d'âge valanginien inférieur à valanginien moyen.

La zone à *Temnoptychites (Temnoptychites) kemperi* est située immédiatement au-dessous de la zone à *Thorsteinssonoceras ellesmerense*, et ces deux faunes s'imbriquent à la limite entre les deux zones. La zone à *Temnoptychites (Temnoptychites) kemperi* est par conséquent équivalente, en tout ou en partie, à la zone à *T. (T.) hoplitoides* de Russie centrale et à la zone à *T. (T.) syzranicus* du nord de la Sibérie. On lui attribue un âge correspondant à la fin du Valanginien inférieur, tandis que la zone ultérieure à *Thorsteinssonoceras ellesmerense* est placée au tout début du Valanginien moyen, comme l'a précise l'auteur.

Bien que les zones à *Temnoptychites (Temnoptychites) kemperi* et *Temnoptychites (Costamenjaites) troelseni* n'aient pas été observées l'une au-dessus de l'autre, on suppose que la seconde est la plus ancienne des deux, et qu'elle est équivalente en partie à la zone à *Pseudogarnieria undulatoplicatilis* de la base du Valanginien, en Russie centrale. D'une part, on ne peut placer aucune autre zone fossilifère entre la zone à *Temnoptychites (Temnoptychites) kemperi*, et la zone ultérieure à *Thorsteinssonoceras ellesmerense*.D'autre part, les deux zones canadiennes contiennent aux niveaux de l'espèce et du sous-genre des formes distinctes de *Temnoptychites*, et pourraient donc difficilement représenter les faciès fauniques de la même zone. Ensuite, *T. (C.) grandiosus* et *T. (C.) troelseni* n. sp. appartiennent au même sous-genre que *Temnoptychites (Costamenjaites)* ex gr. *jucundus-suraense* du bassin de Russie centrale, et lui sont étroitement apparentés au niveau de l'espèce. En Russie, la seconde espèce citée caractérise la zone à *Pseudogarnieria undulatoplicatilis* de la base du Valanginien, zone située immédiatement au-dessous de la zone régionale à *Temnoptychites (Temnoptychites) hoplitoides*.

Dans leur majorité, les formes de *Tollia* (s. lato) rencontrées jusqu'à présent dans le bassin Sverdrup sont associées à la faune à *Temnoptychites (Costamenjaites) troelseni* ou à celle à *Temnoptychites (Temnoptychites) kemperi*. Ceci nous oblige de mettre en doute la notion que la zone à *Tollia tolli* de la base du Valanginien se situe au-dessous de la zone globale à *Temnoptychites* dans la formation de Deer Bay. On ne sait pas si la zone à *Temnoptychites (Costamenjaites) troelseni* correspond à l'ensemble de la zone à *Pseudogarnieria undulatoplicatilis* de Russie centrale. On ne sait même pas si elle correspond à l'ensemble des sous-zones à *Tollia klimovskiensis* et *Tollia mesezhnikowi* (c. à d. à l'ensemble de la zone à *Tollia tolli*) du nord de la Sibérie, qui sont probablement équivalentes à la zone à *Pseudogarnieria undulatoplicatilis*. Si elle ne correspond qu'à la partie supérieure de la zone à *Pseudogarnieria undulatoplicatilis* et à la sous-zone à *Tollia klimovskiensis*, il est possible que les équivalents de la partie inférieure de la zone à *Tollia tolli* existent dans les couches de la formation de Deer Bay contenant *Buchia keyserlingi*, mais apparemment dépourvus totalement d'ammonites, et situés immédiatement au-dessous de la zone à *Temnoptychites (Costamenjaites) troelseni*. Cependant, il est possible que ces couches de la base du Valanginien ne soient représentés que par une lacune régionale de la fin du Berriasien et de la base (?) du Valanginien, lacune récemment découverte dans le bassin Sverdrup.

Introduction

Early Valanginian ammonites collected from the Deer Bay Formation of Sverdrup Basin, District of Franklin, Northwest Territories by officers of the Geological Survey of Canada and others include numerous, generally well preserved representatives of the stratigraphically and biochronologically important craspeditid genus *Temnoptychites* Pavlow 1914 and rare representatives of the craspeditid genus *Tollia*. Represented are at least two distinct *Temnoptychites* faunas that are related closely to *Temnoptychites* faunas of central Russia and Novaya Zemlya. These faunas contain some species in common with the latter faunas, and also rare representatives of *Tollia* that are closely allied to and possibly specifically identical with typical Eurasian species. Some of the Sverdrup Basin *Temnoptychites* and *Tollia* forms have been figured previously and briefly described or mentioned by the writer (e.g., Jeletzky, 1964, p. 38, Pl. V, figs. 1, 3, 4, 5; 1973, p. 66, Figs. 2, 3). Because of their outstanding biochronological, paleogeographical and purely paleozoological interest, these *Tollia-Temnoptychites* faunas of Sverdrup Basin have been made the subject of a special study, the results of which are presented in this paper.

The Canadian Arctic Archipelago in general and the Sverdrup Basin in particular remain remote regions accessible only with difficulty for geological work in spite of remarkable logistical achievements of the last two decades. For this reason and because most lower Lower Cretaceous ammonite localities so far discovered in this region are predominantly unique and easily exhaustible (most are completely exhausted already), additional, better material is unlikely to become available in the near future. Therefore this report includes descriptions and figures of a number of unique fragmentary specimens and even mere fragments which did not permit exact specific identification. This was done also because all of these poorly preserved specimens and fragments appear to be new to North America while being closely allied to biochronologically and paleobiogeographically important *Temnoptychites* and *Tollia* species previously known from northern Eurasia.

Acknowledgments

Sincere thanks are expressed to the following persons who have contributed to the preparation of this bulletin. R. Thorsteinsson, Geological Survey of Canada, Institute of Sedimentary and Petroleum Geology, Calgary, Alberta, Edwin Kemper, Bundesanstalt für Geowissenschaften und Rohstoffe, Hannover, Federal German Republic, J.C. Troelsen, Petrobras-Serdeste, Brazil (formerly Curator, Mineralogisk-geologisk Institut, University of Copenhagen, Denmark) and D. W. Organ, Chevron Standard Ltd., Calgary, Alberta, collected all of the Canadian *Temnoptychites* and *Tollia* specimens used in this paper and provided the writer with important stratigraphical information about their paleontological collections. Hans Frebold, Geological Survey of Canada (retired) kindly permitted the writer to study unpublished duplicate material of *Temnoptychites* and other Valanginian ammonites from Novaya Zemlya and Spitzbergen preserved in his private collection. Valdar Janasson, Curator, Palaeontology Department, Naturhistoriska Riksmuseum, Stockholm, Sweden and David Worsley, Curator,

Palaeontology Department, University of Oslo, Norway kindly permitted the study of valuable comparative material of *Temnoptychites, Tollia* and other Valanginian ammonites from Novaya Zemlya and Spitzbergen preserved in those institutions, and facilitated the writer's research in Stockholm and Oslo. The writer's assistant F. M. McLaughlin drew most of the suture lines, prepared all of the textfigures from drafts provided by the writer, assembled the list of references, ably supervised the photographing of all specimens published in this paper and helped in many other ways. J. White prepared all of the ammonite photographs reproduced in this paper.

Paleontological descriptions

Family Craspeditidae Spath, 1924
General taxonomic and nomenclatorial remarks

The writer adheres to an expressly conservative concept of all taxa used, as in his previous publications dealing with Late Mesozoic ammonites (e.g., Jeletzky, 1964, 1965a, b, 1966, 1971a, p. 16). At the generic and higher levels, the writer's approach is appreciably more conservative than the 'middle of the road' taxonomic procedures adopted in the *Ammonoidea* volume of the *Treatise on Invertebrate Paleontology* (Arkell *et al.*, 1957) and the *Ammonoidea-Endocochlia* volume of the Soviet *Osnovy Paleontologii* (Luppov and Drushchits, 1958). The more radical taxonomic approach practised by a great many contemporary Jurassic and Cretaceous ammonitologists (e.g., Casey, 1973; Shulgina, 1968, 1969; Sazonova, 1971; Saks *et al.*, 1972; Bodylevsky, 1967) is rejected outright. In the writer's opinion, the latter approach results in excessive splitting and grossly overcomplicated, entirely artificial paleontological systematics at the specific and higher levels. This approach appears to hinder rather than further the understanding of the evolutionary development and paleobiotic radiation of Jurassic and Cretaceous ammonites and hence their biochronological utilization. Casey's (1973) erection of subgenus *Volgidiscus* and genus *Runctonia* for ammonites that are typical representatives of the northern Siberian subgenus *Taimyroceras* Bodylevsky 1960 is a characteristic example of such a hindrance. As pointed out below (footnote on p. 6), this action confused the position of the Jurassic-Cretaceous boundary in eastern England and elsewhere in the Boreal Realm. Most of the reasons underlying the decided opposition of the writer to such an extensive splitting of ammonite taxa (and of many other fossil invertebrates) have been published already (e.g., Jeletzky, 1950, 1955, 1965a, p. 3–15) and do not need to be repeated in this section.

They will be commented on more specifically in connection with the description of the individual ammonitid taxa.

As in his previous publications dealing with the Craspeditidae (Jeletzky, 1965b, p. 1; 1966, p. 3), the writer refuses to recognize the validity of the proposed separation of the subfamily Tollinae Spath 1952 from the subfamily Craspeditinae Spath 1924. Furthermore the writer feels that the subfamily Garniericeratinae Spath 1952 is invalid also. In his opinion none of these three 'subfamilies' represents a major, morphologically and stratigraphically well defined and

hence conceivably monophyletic group of genera deserving such a high taxonomic rank. Like Tollinae, the Garniericeratinae is believed to comprise a number of short-lived, unrelated offshoots of the main stem of the Craspeditidae (e.g., *Garniericeras* and *Hectoroceras*) erroneously amalgamated with other keeled genera (e.g., *Proleopoldia*, *Pseudogarnieria* and *Platylenticeras* sensu lato) unrelated to the family Craspeditidae Spath 1924. The subfamilies and families (e.g., Suritidae, Suritinae, Menjaitinae) of craspeditid ammonites proposed recently by Sazonova (1971, p. 24, 25) are minor, mostly completely artificial taxa, which do not deserve a suprageneric status. Therefore no subfamilies are recognized for the time being within the family Craspeditidae Spath 1924.

Taxonomic value of suture line

Regardless of whether or not the harshly negative general appraisal of the taxonomic value of the suture line given in Part L of the *Treatise on Invertebrate Paleontology* (Arkell, in Arkell *et al.*, 1957, p. L97, L98, L111, L112) is valid for other ammonitid families and suborders, it most certainly does not apply to Craspeditidae, Dorsoplanitinae and Polyptychitinae.

Suture line of Polyptychitinae. The outstanding taxonomic value of the external suture line for the recognition of taxa of the subfamily Polyptychitinae Spath 1924 and their differentiation from the homeomorphically similar taxa of the family Craspeditidae Spath 1924 has been stressed already by Jeletzky (1965b, p. 2, 3). These comments are not repeated here, but will be dealt with comprehensively in a joint paper by Kemper and Jeletzky (*in prep.*) treating of the Sverdrup Basin Polyptychitinae. It must be pointed out, however, that the analysis of the external suture line alone does not solve the problem of the origin of the Polyptychitinae. The suture lines of Dorsoplanitinae (Textfig. 1A–1D) do not differ much from those of Spiticeratinae (Luppov and Drushchits, 1958, Fig. 78a). On morphology alone either of these types of external suture lines could have been ancestral to that of the Polyptychitinae. Therefore one has to use the biochronological data to infer the ancestry of the Polyptychitinae. The external suture lines of all presently known Polyptychitinae genera (Textfig. 1E–H) are so unlike those of all presently known representatives of the contemporary and older (Berriasian) Early Cretaceous representatives of Craspeditidae that these two major taxa could hardly be directly connected genetically. The prolonged time gap (all of the Berriasian and most of the early Valanginian, *sensu* Jeletzky, 1973) separating the last known representatives of Dorsoplanitinae (*Chetaites sibiricus*) from the earliest known representatives of Polyptychitinae makes equally improbable a direct genetic connection between these two taxa, in spite of a general similarity in their external suture lines (Textfig. 1). Consequently, the writer follows Wright (in Arkell *et al.*, 1957, p. L348) in deriving the subfamily Polyptychitinae directly from the Berriasian Spiticeratinae. Polyptychitinae appear to be a specialized offshoot of the Olcostephanidae Haug 1910, which became superficially similar to the Craspeditidae after it migrated to the southern part of the Boreal Realm either late in the Berriasian or at the onset of the Valanginian.

None of the elements of the external suture line, judged

to be taxonomically valuable at the subfamily level, seems to change materially within the subfamily Polyptychitinae (Textfig. 1). These features (see Jeletzky, 1965b, p. 2, 3 for further details) are considered accordingly to be the most reliable means now available for its recognition.

Suture line of Dorsoplanitinae. The external suture line of all presently known Dorsoplanitinae genera, including that of the latest known representatives of *Dorsoplanites* (*Chetaites*) ex gr. *D.* (*C.*) *chetae-sibiricus* (Shulgina, 1968, p. 102, Pl. XIII, fig. 4), is essentially uniform and characteristically perisphinctid. Its entire auxiliary part is strongly retractive (or suspensive) and forms an obtuse angle with the subradially directed to ascendant lateral part (the part consisting of the first and second lateral lobes and first and second lateral saddles). Furthermore, the auxiliary part of the dorsoplanitine suture consists of either one or two auxiliary lobes, which are ill defined and commonly difficult to segregate from intervening (one or more) lobules (Luppov and Drushchits, 1958, p. 89, Fig. 73b, v, g; Jeletzky, 1966, Figs. 1A, 2; Casey, 1973, Fig. 4g, n; Textfig. 1 of this paper). Except for the previously questioned (e.g., Spath, 1947, p. 15) but by now well documented (e.g., Casey, 1973, Fig. 4b, c, g, i, m, l, n) transmutation of the dorsoplanitine suture line into the craspeditid suture line, the former is not known to change substantially within the subfamily.

Suture line of Craspeditidae. The external suture line of Craspeditidae is quite different from that of Dorsoplanitinae. Beginning with the evolutionarily and morphologically transitional early craspeditids (e.g., *Swinnertonia* Shulgina 1972; see Casey, 1973, p. 238 for further details) mentioned above, the strongly retractive (suspensive) character of the entire auxiliary part of the ancestral dorsoplanitine suture and its abrupt directional break with the subradially directed or ascendant lateral part have disappeared never to be seen again in the descendant Craspeditidae (Textfig. 1I–V). The ill defined and crowded appearance of dorsoplanitine auxiliary lobes followed suit, even though its vestiges are still perceptible in the adumbilicalmost* parts of auxiliary sutures of some primitive, latest Jurassic craspeditids (e.g., Casey, 1973, Textfig. 4g, i; Jeletzky, 1966, Textfig. 1L). All dorsoplanitine features mentioned are replaced by a basically linear arrangement of more numerous (three to rarely four), well spaced and defined auxiliary lobes separated from each other by well spaced and defined, considerably smaller lobules. The orientation of this craspeditid suture line may vary from strongly ascendant to subradial or even to feebly forward convex or knicked within the auxiliary part with a resulting slightly retractive (or suspensive) character of its adumbilicalmost part (Luppov and Drushchits, 1958, p. 92, Textfigs. 76a, b, v, g, z; Casey, 1973, Textfigs. 4b, c, g, i, m, 5a, b, k, l, m, 6d, e, h, k, m, o, p, r; Jeletzky, 1965b, Textfig. 1a–e; 1966, Textfigs. 1B–L; this paper, Pl. 9, fig. 1F, Pl. 14, fig. 1D, Textfig. 1). However, these minor variations do not affect in the least the fundamental morphological unity of all known

---

*The new term 'adumbilicalmost' is being proposed herein for that part of the external suture line immediately adjoining the umbilical seam and confined between the umbilical seam and the umbilical shoulder.
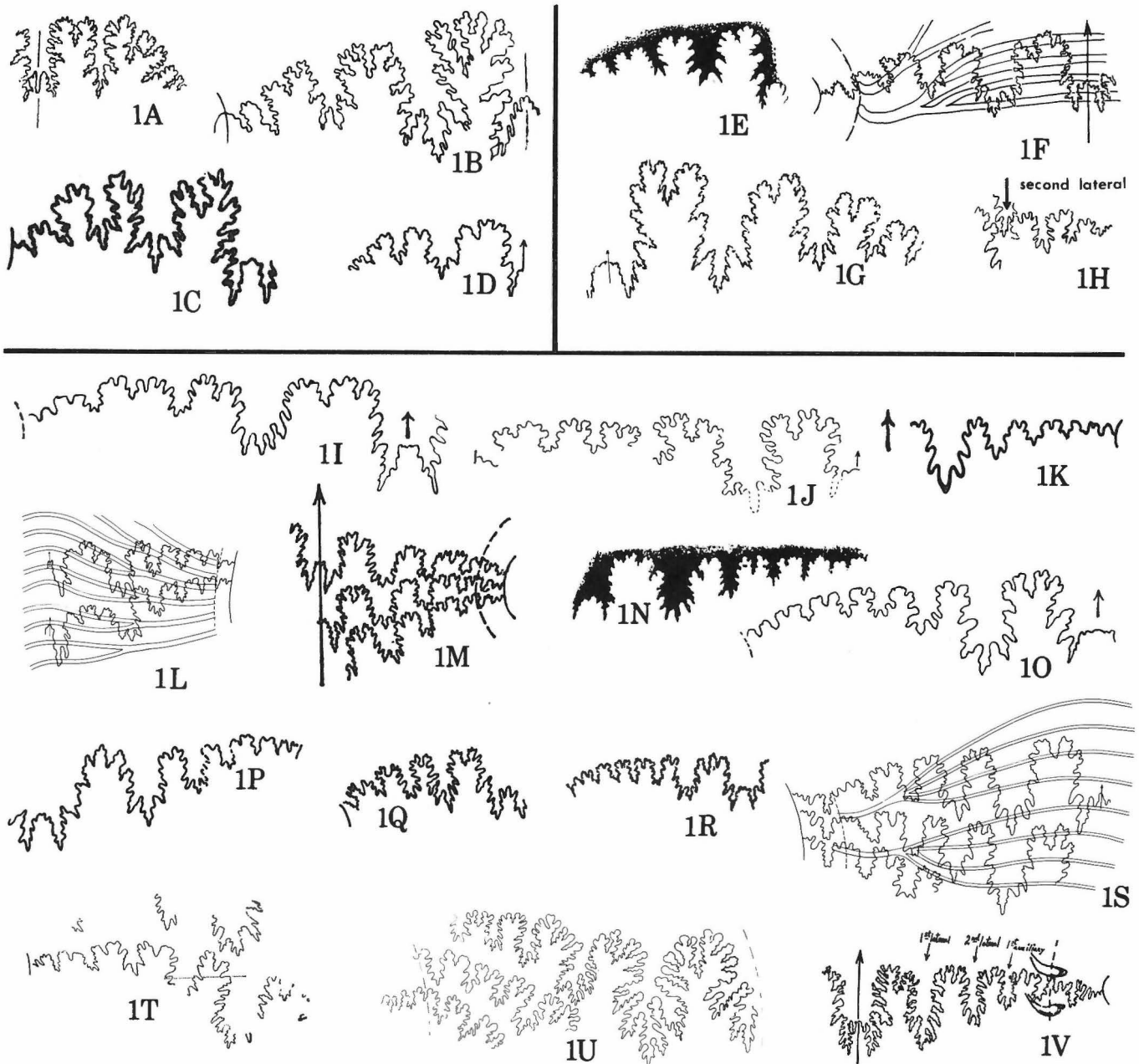
Texfigure 1. Selected external suture lines of Dorsoplanitinae (1A to 1D), Polyptychitinae (1E to 1H), and Craspeditidae (1I to 1V) arranged to illustrate the constancy of their principal morphological features within each of these taxa (see text). All suture lines are complete to almost complete in their auxiliary parts and are reproduced approximately natural size.

(1A) *Virgatosphinctes broilii* Uhlig (from Uhlig, 1903–1910); (1B) *Dorsoplanites* (*Dorsoplanites*) *dorsoplanus* (Vishniakov) (from Michalski, 1890); (1C) *Dorsoplanites* (*Chetaites*) *chetae* Shulgina (from Shulgina, 1968); (1D) *Paracraspedites stenomphaloides* Swinnerton (from Casey, 1973); (1E) *Polyptychites keyserlingi* (Neumayr and Uhlig) (from Neumayr and Uhlig, 1881–82); (1F) *Polyptychites* (*Siberiptychites*) *stubendorffi* Schmidt var. *middendorffi*, Pavlow (from Jeletzky, 1965b); (1G) *Dichotomites* (*Prodichotomites*) sp. (from Pavlow, 1892; figured as *Dichotomites bidichotomus*); (1H) *Astieriptychites astieriptychus* Bodylevsky (from Voronets, 1957); (1I) *Craspedites* (*Swinnertonia*) *primitivus* Swinnerton (from Spath, 1947); (1J) *Craspedites* (*Craspedites*) *plicomphalus* (Sowerby) (from Casey, 1973); (1K) *Praetollia aberrans* Spath (from Spath, 1952); (1L) *Praetollia antiqua* Jeletzky 1973. Holotype. Described in Jeletzky (1973, p. 74, 76) but figured originally herein; (1M) *Craspedites* (?*Taimyroceras*) *canadensis* Jeletzky (Jeletzky 1966); (1N) *Surites spasskensis* (Nikitin) (from Nikitin, 1888); (1O) *Hectoroceras kochi* Spath 1947 (from Casey, 1973); (1P) *Tollia mesezhnikowi* (Shulgina) (from Shulgina, in Saks et al., 1972); (1Q) *Tollia tolli* Pavlow (from Shulgina, in Saks et al., 1972); (1R) *Tollia klimovskiensis* Krimgolts (from Shulgina, in Saks et al., 1972); (1S) *Temnoptychites* (*Temnoptychites*) *kemperi* n. sp. Paratype, GSC 49324; (1T) *Tollia tolli* Pavlow (from Pavlow, 1914); (1U) *Homolsomites quatsinoensis* Crickmay (from Imlay, 1960; figured as *Homolsomites stantoni*); (1V) *Thorsteinssonoceras ellesmerense* Jeletzky (from Jeletzky, 1965b).

5

craspeditid suture lines and their pronounced distinctiveness from those of directly ancestral Dorsoplanitinae.

It must be stressed that, contrary to the opinion of Arkell (in Arkell *et al.*, 1957, p. L197), the principal features of the external craspeditid suture line do not appear to be appreciably influenced by even the most general morphological changes of the whorl shape or sculpture known within the family. The suture lines of such craspeditid oxycones as *Hectoroceras* (e.g., Casey, 1973, Textfig. 5a–c) or *Garniericeras* (e.g., *ibid.*, Textfig. 5m) retain the same basic features (e.g., the linear arrangement and a large number of auxiliary lobes) as of the most extreme cadicones – e.g., *Thorsteinssonoceras* (Jeletzky, 1965b, Textfig. 1a–e) or *Temnoptychites* (*Temnoptychites*) ex gr. *T.* (*T.*) *triptychiformis-kemperi-borealis* (this paper, Pl. 1, fig. 2B, Pl. 3, figs. 2A, 4, Textfig. 1). The same craspeditid suture line persists, finally, in all slender, discus-shaped representatives of the family – e.g., *Tollia* (Pavlow, 1914, Pl. XII, figs. 1a, 2c, 3, Pl. XIII, fig. 2) or nodeless forms of *Temnoptychites* (*Costamenjaites*) (Jeletzky, 1964, Pl. V, figs. 3D, E, 4A, B; Bodylevsky, 1967, Pl. III, fig. 1a, Pl. IV, fig. 1a).

While retaining all its fundamental characters, the craspeditid suture line becomes gradually less Dorsoplanitinae-like in the course of evolution of the family. These slow evolutionary changes appear to be irreversible, for the most part at least, and so represent the same, so-called 'irreversible orthogenetic' (better named 'orthoselectionary') trend as defined by Jeletzky (1955, p. 483, Textfig. 1; 1965a, p. 4) in Belemnitellidae and *Buchia*. This 'orthogenetic' mode of evolution of the suture line contrasts strongly with the pronounced iterative mode of evolution of all other presently known morphological elements in the craspeditid shell (see below).

The following general trend is discernible (Textfig. 1). The short and stubby, sparsely and shallowly indented external sutures with only three auxiliary lobes are restricted almost to the earliest (late Tithonian or late Volgian) stage of craspeditid evolution typified by genus *Craspedites* sensu lato (including subgenera *Swinnertonia*, *Subcraspedites*, *Taimyroceras*). By latest Tithonian (= latest Volgian), this suture line transmutates into the morphologically more advanced, markedly ascendant suture line of *Praetollia* (? = *Borealites*). Some of these advanced sutures have more (four to five) auxiliary lobes (e.g., *Praetollia*) and so are transitional to yet more advanced, more strongly indented, entirely to largely ascendant suture lines with four to five auxiliary lobes characteristic of such early Berriasian and early to mid-Valanginian Craspeditidae as *Surites*, *Tollia* (= *Neotollia* = *Bojarkia*), *Temnoptychites* sensu lato (including subgenera *Temnoptychites* sensu stricto, *Menjaites* and *Costamenjaites*), and *Thorsteinssonoceras* (= *Russanovia*). This basically irreversible, orthoselectionary evolution of the craspeditid suture line reaches its acme in some of the late Valanginian representatives of the genus *Homolsomites* with which the writer (Jeletzky, 1966, p. 4; 1973, p. 73, Textfig. 3, column 2) synonymizes the genus *Wellsia* Imlay 1960. In spite of their extremely long- and narrow-stemmed, abundantly and very deeply incised (with long, fingerlike lateral and terminal accessory lobes), commonly overlapping character, the external suture lines of *Homolsomites* ex gr. *H. quatsinoensis*

(e.g., Imlay, 1960, Pl. 27, figs. 5, 14; Jeletzky, 1964, Pl. XII, fig. 4, Pl. XIII, fig. 6b; this paper Textfig. 1U) do not differ from those of older early Early Cretaceous craspeditids in such things as the number of sutural elements and their general arrangement. The same is true of the considerably less complex external suture lines of the immediately descendant early Hauterivian *Homolsomites* (= *Wellsia*) forms (e.g., Imlay, 1960, Pl. 32, fig. 11, Pl. 33, fig. 26) closing the evolutionary history of Craspeditidae.

Admittedly there are some exceptions to the 'irreversible orthogenetic' trend of the development of the external suture line in Craspeditidae. For example, the general direction of the trend toward the progressively more complex, florid, long- and narrow-stemmed, commonly overlapping suture line appears to be reversed in the latest Valanginian. The last known, early Hauterivian representatives of *Homolsomites* (e.g., *H. oregonensis*, *H. packardi*), which appear to be the immediate descendants of *H.* ex gr. *H. quatsinoensis*, have a considerably more simple external suture line than the latter form. Furthermore, the evolutionary trend from primitive *Craspedites* toward *Garniericeras* and that from the more advanced *Craspedites* (*Taimyroceras*) (of which *Volgidiscus* and *Runctonia* appear to be junior synonyms) toward *Hectoroceras** are characterized by an increased number of auxiliary elements of the suture line combined with its marked forward convexity and shortened lobes (Spath, 1947, Textfigs. 1, 2, 3i, 5a, b; Casey, 1973, Textfigs. 4b, c, g, i, l, m,

---

*In the writer's opinion, the monotypic subgenus *Volgidiscus* Casey 1973 and the monotypic genus *Runctonia* Casey 1973 are entirely superfluous. Their type species "*Craspedites* (*Volgidiscus*)" *lamplughi* (Spath 1936) and "*Runctonia*" *runctoni* Casey 1973 are interpreted herein as representatives of the late late Volgian subgenus *Taimyroceras*. This is indicated by the presence of an interruption or weakening of secondary ribs on the venter of their intermediate whorls described as 'smooth venter' or 'ventral smoothness' and well figured by Casey (1973, p. 239, 242, Pl. 4, fig. 9a, b, Pl. 7, figs. 6a, 7b). This diagnostic feature of *Taimyroceras* is combined with a typical *Craspedites* suture line; compare the external suture lines figured by Casey, 1973, Fig. 5 h, i, k with those of *Craspedites* (?*Taimyroceras*) *canadensis* figured by Jeletzky, 1966, Figs. 1C, 1F, and particularly Fig. 1J. Furthermore the ribbing habit and the whorl shape of representatives of *Craspedites* (*Taimyroceras*) *lamplughi* figured by Casey (1973, Pl. 4, figs. 8, 9, Pl. 6, figs. 2a, 3) resemble closely those of the representatives of *C.* (?*T.*) *canadensis pseudosubditus* reproduced by Jeletzky (1966, Pl. II, figs. 2–5). The somewhat more aberrant ribbing habit of *Craspedites* (*Taimyroceras*) *runctoni* (Casey), which features dichotomous rib bundles with long and sharp primaries separated from each other by one to three intercalated secondaries (see Casey, 1973, Pl. 7, figs. 5a, 6b, 7a), is closely matched in some representatives of *C.* (?*T.*) *canadensis* figured by Jeletzky (1966, Pl. II, figs. 4A, 9A, Pl. III, figs. 5A, 6A).

The medioventral interruption of secondaries in the basal Cretaceous and uppermost Jurassic *Hectoroceras*, excellently figured but not described by Casey (1973, Pl. 7, fig. 3), can now be reinterpreted as indicative of its derivation from *Craspedites* (*Taimyroceras*) ex gr. *C.* (*T.*) *lamplughi-runctoni*. ?*Hectoroceras tolliense* (Nikitin), made the basis of the doubtful genus *Shulginites* by Casey (1973, p. 239, 240, Pl. 6, fig. 4), may well be but another connecting link between *Craspedites* and *Hectoroceras*.

The above taxonomic reappraisal of "*Craspedites* (*Volgidiscus*)" *lamplughi* and "*Runctonia*" *runctoni* as representatives of the latest Jurassic subgenus *Taimyroceras* is important in indicating that the Jurassic-Cretaceous boundary in eastern England is situated higher than Casey believed (1973, p. 219, 220, Fig. 2). This boundary should be placed not between the zones of *Craspedites* (*Taimyroceras*) *lamplughi* and *Craspedites* (*Taimyroceras*) *runctoni* but higher, either at the base of or within the *Hectoroceras kochi* Zone.

Thus defined, the Jurassic-Cretaceous boundary in eastern England corresponds closely to this boundary in Canada, northern Siberia, central Russia, and eastern Greenland as defined by Jeletzky (1973, p. 47–52, Fig. 3; this paper, Textfig. 8).

n, 5a, b, c, i, k, m, Pl. 6, fig. 4a). This trend may fall outside the orthogenetic trend discussed above. However, these exceptions do not detract materially from the outstanding taxonomic and biochronological value of the principal orthogenetic trend of the development of the suture line in Craspeditidae, which permits the identification and dating of many homeomorphic representatives of the family simply on the evolutionary grade of their external suture lines. This trend, for example, makes it possible to distinguish at a glance the late (but not the latest) late Tithonian *Swinnertonia*, *Craspedites* and *Subcraspedites* from the otherwise almost indistinguishable (see below) latest Tithonian and earliest (?) Berriasian *Praetollia* (? = *Borealites*) and "*Subcraspedites*". Also, the trend makes it possible to differentiate easily the early Valanginian *Tollia* and *Temnoptychites* (*Costamenjaites*) ex gr. *T.* (*C.*) *jucundus-elegans* species group from the externally similar late Valanginian *Homolsomites* ex gr. H. *quatsinoensis* (Textfig. 1).

Taxonomic value of sculpture

All sculptural elements of the Craspeditidae shell, such as ribbing habit, the tendency to lose the sculpture (completely or in part) on the adult ultimate whorl and rarely the penultimate whorl, the presence or absence of umbilical nodes, and the presence or absence of a smooth midventral band are considerably less constant within the family than is the external suture line. Furthermore, their evolution appears to be dominated completely by 'reversible morphological shifts' as defined by Jeletzky (1955, p. 483, Textfig. 1; 1965a, p. 4, 5) in Belemnitellidae and *Buchia*. This 'iterative' mode of evolution results in the repeated appearance of similar to identical sculptural types in stratigraphically distant, demonstrably homeomorphic members of the family.

For example, the late Tithonian *Craspedites* (*Taimyroceras*) and the early Valanginian slender-whorled *Temnoptychites* (*Costamenjaites*) are characterized by similar loss or strong weakening of secondary ribs on the midventer of intermediate whorls. Another example is the recurrence of characteristic sculpture of the late, but not the latest, Tithonian (=Volgian) *Craspedites* (*Subcraspedites*) ex gr. *C.* (*S.*) *sowerbyi-praeplicomphalus* in the earliest Berriasian "*Subcraspedites*" *anglicus* Shulgina 1972 and "*Subcraspedites plicomphalus*" Shulgina 1972 (Saks *et al.*, 1972, p. 139–144, Pls. I–III) and the Canadian "*Craspedites* (*Subcraspedites*)" aff. *C.* (*S.*) *suprasubditus* Jeletzky (1964, Pl. II, figs. 1, 4). The prolonged controversy about the age and taxonomic status of the forms concerned (see Jeletzky, 1965a, p. 20, 21; Casey, 1973, for further details) was caused by the lack of data about the suture lines of the English *Craspedites* (*Subcraspedites*) ex gr. *C.* (*S.*) *sowerbyi-praeplicomphalus* and closely related true *Craspedites* (*Craspedites*) *plicomphalus* (Sowerby). This controversy was settled as soon as the drawings of primitive *Craspedites*-like external suture lines of the English forms became available (Casey, 1973, p. 233, Textfig. 4b, c, m) for comparison with much more advanced *Praetollia*- and *Surites*-like sutures of their northern Siberian and Canadian homeomorphs (Shulgina, in Saks *et al.*, 1972, Textfigs. 10.3, 10.4, 11.5, 11.9, 11.10, 12.13; Jeletzky, 1964, Pl. II, fig. 4A, C, Pl. III, fig. 3A, B). It must be stressed in this connection that in the writer's opinion the distinction in the costation of the

forms concerned, as claimed by Casey (1973, p. 236), is nonexistent. The specimen of "*Subcraspedites* (*Subcraspedites*)" *anglicus* reproduced by Shulgina (in Saks *et al.*, 1972, Pl. I, fig. 2v) exhibits exactly the same feeble impression of the costation on the internal mould as does the English representative of *Craspedites* (*Subcraspedites*) aff. *C.* (*S.*) *sowerbyi* figured by Casey (1973, Pl. 8, fig. 8).

The taxonomic value of all known elements of craspeditid sculpture is even more decreased by the fact that all types of sculpture known in the family are present in the morphologically convergent olcostephanid subfamily Polyptychitinae. The recent study of genus *Thorsteinssonoceras* (Jeletzky, 1965b) provides an excellent example of such recurrence of a completely polyptychitinid ribbing habit in Craspeditidae.

The late Valanginian to early Hauterivian genus *Homolsomites* Crickmay 1930 has a bidichotomous ribbing habit and a strong forward swing of secondaries on the venter, which completely duplicate those of the polyptychitinid genus *Dichotomites* Koenen 1902. The persistent taxonomic reliance on these recurrent features resulted in a prolonged refusal of ammonitologists at large to recognize the validity of *Homolsomites* and in an equally prolonged misidentification of North American and Middle Russian *Tollia* and *Homolsomites* (Jeletzky, 1965a, p. 39, footnote; 1973, p. 73, Textfig. 3).

A number of characteristic craspeditid sculptural types (especially ribbing habits), furthermore, are duplicated in the ancestral perisphinctid subfamily Dorsoplanitinae. This is exemplified by the recurrence of dorsoplanitine ribbing habit in the Berriasian *Surites*. This instance of homeomorphy resulted in a prolonged (since Swinnerton, 1935) misidentification of the early late Tithonian (late early Volgian) dorsoplanitine genus *Paracraspedites* Swinnerton 1935 with the Berriasian craspeditids now assigned to the genus *Surites* Sazonov 1951. The traditional neglect of the suture line is again responsible for this misidentification and the resulting prolonged but now settled controversy (Casey, 1973, p. 229, 230), as the completely different suture lines of all forms concerned were adequately figured a long time ago (Jeletzky, 1965a, p. 21, 22; 1966, p. 1, 2).

Other examples (e.g., the general similarity of ribbing habit of early Valanginian craspeditid *Virgatoptychites* Voronets 1958 with that of *Virgatites*; see Shulgina, in Saks *et al.*, 1972, p. 133, 134 for further details) could be cited to demonstrate the taxonomic unreliability of the craspeditid sculpture, but the examples quoted suffice to illustrate the point. The only sculptural feature commonly occurring in Craspeditidae (e.g., in *Taimyroceras* [= *Volgidiscus*, = *Runctonia*] or in *Temnoptychites*) but apparently absent either in Polyptychitinae or in Dorsoplanitinae, is the interruption or strong weakening of secondary ribs in the middle of the venter.

Taxonomic value of whorl shape and proportions

All details of craspeditid whorl shape and proportions are just as variable within the family as is the shell sculpture. Furthermore, their evolution is just as exclusively dominated by 'reversible morphological shifts'. As with the sculpture, this 'iterative' mode of evolution results in the repeated appearance of shells characterized by extremely similar whorl

shapes and proportions at different stages of craspeditid evolution. The much discussed (e.g., Spath, 1947, p. 15–20; Casey, 1973, p. 239, 240, 244, 258, 260) heterochronous appearance of keeled forms (e.g., *Garniericeras* and *Hectoroceras*) in the family Craspeditidae is a good example. The writer agrees with Casey (1973, p. 232) that these repeatedly arising, taxonomically low ranking modifications of the basic type should never have been raised to the status of a separate subfamily or family Garniericeratinae as is commonly done (e.g., Spath, 1947; Sazonova, 1971; Shulgina, in Saks *et al.,* 1972).

Another example is provided by the repeated recurrence of slender, discuslike whorl shapes closely resembling those of *Tollia* Pavlow, 1914 in various craspeditid genera not directly related (e.g., *Craspedites (Taimyroceras)* ex gr. *C. (T.) lamplughi,* *Praetollia* Spath 1953, *Temnoptychites (Costamenjaites)* ex gr. *T. (C.) jucundus-elegans, Homolsomites*).

Yet another example is the general morphological similarity of whorl shapes of the late, but not the latest, late Tithonian (= late Volgian) *Craspedites* (belonging to subgenera *Subcraspedites* and *Craspedites* sensu stricto) from the Spilsby sandstone in England to those of the earliest Cretaceous forms from northern Siberia erroneously placed in *Subcraspedites* by the writer (Jeletzky, 1973, p. 68, Pl. 6) and Shulgina (in Saks *et al.,* 1972, p. 139–144, Pls. I–III). This resemblance, coupled with the similarity of ribbing habits of the forms concerned (see preceding section), resulted in a prolonged international controversy that apparently has been settled by the recently published results of Casey's (1973) research.

Like the sculpture of the shell, all whorl types known in the Craspeditidae are duplicated in the morphologically convergent olcostephanid subfamily Polyptychitinae. Furthermore, a number of these whorl types are duplicated in the ancestral perisphinctid subfamily Dorsoplanitinae.

Perhaps the best known example is provided by the recent study of the variation of whorl shape and proportions in the genus *Thorsteinssonoceras* (Jeletzky, 1965b), which mimic those of *Polyptychites* subgenera *Polyptychites* sensu stricto and *Euryptychites*. This homeomorphic development is combined with an equally pronounced homeomorphic development of the shell sculpture in *Thorsteinssonoceras* (see preceding section).

Another good example is the recurrence of evolute, broad-ventured whorl shape characteristic of Dorsoplanitinae (e.g., *Paracraspedites* Swinnerton 1935) in several, only indirectly related, earliest Cretaceous craspeditid species groups (e.g., *Surites* and *Ronkinites*; see Shulgina, in Saks *et al.,* 1972, p. 137–156; Casey, 1973, p. 229, 230 for further details). This homeomorphy of the whorl shape is paralleled also by an equally far reaching homeomorphy of the shell sculpture.

Yet another example is the virtual duplication of the slender, discuslike whorl shape of *Tollia, Temnoptychites (Costamenjaites),* and *Homolsomites* in such Polyptychitinae genera as *Dichotomites* and *Neocraspedites*. This homeomorphy, again coupled with a general homeomorphy of the shell sculpture of the forms concerned (see preceding section), resulted in a prolonged misidentification of North American, eastern Greenland and Middle Russian *Tollia,*

Temnoptychites and *Homolsomites* species (Jeletzky, 1965a, p. 39, footnote; 1973, p. 73, Textfig. 3; Donovan, 1953, Pl. 23, figs. 2, 4).

As with the homeomorphy of shell sculpture, many more examples could be cited–e.g., that of sturdy-whorled *Temnoptychites (Temnoptychites)* ex gr. *T. (T.) borealis-kemperi* duplicating sturdy, low-whorled Polyptychitinae shells (see this paper). However, the examples already given are believed to be ample to illustrate the point.

Conclusions

Because of the above considerations, it is concluded that the external suture line, which alone was studied by the writer, is the most stable and, consequently, the taxonomically most reliable morphological character of Craspeditidae now available. The suture line alone permits the safe differentiation of all its known representatives from homeomorphically similar representatives of the convergent olcostephanid subfamily Polyptychitinae Spath 1924 and the ancestral perisphinctid subfamily Dorsoplanitinae Arkell 1950. All other presently used morphological features, such as the sculpture of the whorl and the shape and proportions of the whorl, can be used safely only for establishing subordinate taxa (genera, subgenera and species) within the family Craspeditidae under a constant control of the external suture line.

The truly chaotic present state of taxonomy and nomenclature of Craspeditidae, justly decried by Shulgina (in Saks *et al.,* 1972, p. 117, 118), appears to be caused largely by a widespread neglect of the suture line combined with an even more widespread overestimation in the past of the taxonomic value of shell sculpture, whorl shape and whorl proportions. This attitude is, for example, believed to be responsible for the erroneous attempts to connect the entirely superfluous family Suritidae with Polyptychitidae (e.g., Sazonova, 1971, p. 89); for the claim that *"Polyptychites"* pumilio Vogel occupies an intermediate position between genera *Tollia* and *Polyptychites* (e.g., Shulgina, in Saks *et al.,* 1972, p. 132, 133); for the attempts to subordinate the subfamily Polyptychitinae to Craspeditidae (e.g., Casey, 1973, p. 257); and for the recent description of a typical representative of a *Neocraspedites*-like dichotomitid ammonite with an excellently preserved polyptychitid suture line (Aristov, 1974, p. 152, Pl. XIV, figs. 1, 2, Pl. XV, figs. 1–3) as *Homolsomites ivanovi* n. sp.

The above discussion of the evolutionary development of the craspeditid suture line (p. 4, 6, 7) indicates that it can be used also for the differentiation of craspeditid genera. However, it must be pointed out that such taxonomic use of the craspeditid suture line is an entirely empirical process presupposing a fair degree of understanding of the infraspecific and infrageneric ranges of variation of its elements used. One has to establish the individual, ontogenetic and intraspecific variability of external suture lines before attempting to use them taxonomically at the generic level. Broadly speaking, only the more general morphological characteristics of the craspeditid suture lines, such as the number of auxiliary lobes, presence or absence of major retractive bends of the auxiliary part of the line measured in tens of degrees, or major and constant distinctions in the relative width, shape and degree of denticulation of major

sutural elements, can be utilized taxonomically at the family, subfamily and generic level. It is particularly important either to compare only the equivalent growth stages of the external suture lines or to take into account the ontogenetic development of the suture lines in the taxa concerned.

The description of infraspecific variation of external suture lines in the intermediate and advanced shells of *Temnoptychites* (*Costamenjaites*) *troelseni* and *T.* (*C.*) *elegans* (see below) provides an example of constraints imposed by nature on the taxonomic use of the suture lines in the ammonite groups discussed in this paper. Another example is the infraspecific variation of external suture lines in juvenile and adult representatives of *Craspedites canadensis* (Jeletzky, 1966, p. 12–14, Textfig. 1A–F). These examples illustrate clearly that it is inadmissible to propose new families of craspeditid ammonites merely on minor differences in general configuration of suture line supplemented by minor differences in its adventral bends not exceeding 5 degrees (e.g., Garniericeratidae and Suritidae; see Sazonova, 1971; and in Saks *et al.,* 1972, p. 175, 176). As admitted by Sazonova (in Saks *et al.,* 1972, p. 177) on the basis of "*Borealites*" *suprasubditus* as an example, such differences in general configuration, including those of adventral bends, may occur within a craspeditid species. The number of auxiliary lobes, the degree of denticulation of the suture line and other characteristics mentioned above were found, in contrast, to be rather constant not only within the individual species but within the genera and higher taxonomic units as well.

Genus *Temnoptychites* Pavlow 1914

Type species: *Olcostephanus hoplitoides* Nikitin 1888, p. 96, Pl. II, figs. 1–3. Selected originally by Pavlow (1914, p. 44), who erected the genus *Temnoptychites* expressly for (writer's translation from Russian): "representatives of the family Olcostephanidae forming the group of *Olcostephanus hoplitoides*."

Diagnosis. The following original diagnosis of Pavlow (*ibid.,* writer's translation from Russian) is almost entirely appropriate, in the writer's opinion:

"The genus *Temnoptychites* includes forms which are closely related to both the polyptychitids and craspeditids; they are characterized by a narrow umbo and by forward-inclined rib bundles which are either interrupted or decidedly weakened on the siphonal side. The arrangement of branches in the rib bundles repeats the types characteristic of the polyptychitids; they include dichotomous, tri- and quadrichotomous-polyptychitid, quadrichotomous-bidichotomous, and multibranched types, with intercalated ribs inserted between the bundles. The suture line is weakly dissected and has many auxiliaries (up to five); it advances more or less forward as it approaches the umbo."

As far as the writer is concerned, Pavlow (*loc. cit.*) erred only in suggesting a close affinity of *Temnoptychites* with *Polyptychites*.

Concept of genus and its subgenera. Because of the extremely *Tollia*-like morphology of all previously known Canadian representatives of *Temnoptychites* (e.g., *T.*

"*novosemelica* Sokolov 1913" and *T.* "*simplex* Bogoslowsky 1902"; see Jeletzky, 1964, p. 38, Pl. V, figs, 1, 3, 4), the writer treated this genus as a subgenus of *Tollia* Pavlow 1914. However, as Pavlow pointed out (1914, p. 44; see above) and Wright reiterated more recently (in Arkell *et al.,* 1957, p. L344), the genus *Temnoptychites* is based not on these high-whorled and slender, discuslike, almost to entirely nodeless forms but on the sturdy, moderately depressed, bullate species *Olcostephanus hoplitoides* Nikitin 1888 (see Bodylevsky, 1967, Pl. IV, fig. 2 for a photographic reproduction of the holotype). Furthermore, the recent work of Sazonova (1971, p. 23, 83, Fig. 4) revealed that it is the *Tollia*-like forms of *Temnoptychites* rather than the typical, moderately to strongly depressed, bullate representatives of the genus that occur mainly in older early Valanginian beds. Sazonova (1971) accordingly had introduced the new generic names *(Costamenjaites* and *Bodylevskyiceras)* for the former. Although such extreme splitting is unacceptable to the writer, the name *Costamenjaites* Sazonova 1971 (= *Bodylevskyiceras* Sazonova 1971) appears to be useful at the subgeneric level. This subgenus based on *Costamenjaites jucundus* Sazonova 1971 is employed in this report for the earliest Valanginian (*Pseudogarnieria undulatoplicatilis* Zone and its equivalents), nodeless *Tollia*-like forms of *Temnoptychites*—e.g., *T.* (*C.*) *suraense* Sazonova 1971; *T.* (*C.*) *elegans* Bodylevsky 1949 (? = *Dichotomites gregersoni* var. *paucicostata* Donovan 1953); *T.* (*C.*) *grandiosus* Voronets 1962; and *T.* (*C.*) *troelseni* n. sp.

The subgenus *Temnoptychites* sensu stricto is restricted herewith to the typical representatives of the genus (e.g., *T.* (*T.*) ex gr. *T.* (*T.*) *hoplitoides-borealis-kemperi*), which characterize the succeeding Hoplitoides Zone of central Russia and its equivalents.

Unlike Sazonova (1971, p. 23–26, Fig. 4), who assigns the typical *Temnoptychites* forms to a different lineage from *Costamenjaites* and places the two genera into different families of craspeditid ammonites, the writer interprets the two as successive evolutionary stages of a continuous early Valanginian plexus of highly variable *Temnoptychites* species (Textfig. 2). The evolutionary centre of this plexus apparently was situated in the Central Russian Basin throughout most or all of its known history. The origin of the oldest known representatives (subgenus *Costamenjaites*) of *Temnoptychites* plexus is uncertain. However, they may have evolved directly out of the last known, latest Berriasian representatives of *Praetollia* (= *Pronjaites* Sazonova 1971), such as *P. bidevexa* Bogoslowsky and *P. nikitinoense* (Sazonova). These representatives of *Praetollia* (Bogoslowsky, 1897, p. 55–58, Pl. III, fig. 1a, b; Sazonova, 1971, p. 54–56, Pl. IX, figs. 3, 5, Pl. XXIV, fig. 17) occur in the same Central Russian Basin as and are similar to *Temnoptychites* (*Costamenjaites*) ex gr. *T.* (*C.*) *jucundus-suraense* in most features of their shell morphology.

The extremely close affinity of *Menjaites* to *T.* (*C.*) *jucundus* is made evident by Sazonova's (1971, p. 83) statement (writer's translation from Russian) that the ribs of all sculptured representatives of her 'subfamily' Menjaitinae (which includes *Menjaites,* *Costamenjaites* and *Bodylevskyiceras*): "either are weakened or smoothed on the ventral side, forming a small furrow" and that "this subfamily unites ammonites with a uniform structure of the suture line." Furthermore, the early whorls of the most strongly sculptured

9

Menjaites species (e.g., *M. magnus*; see Sazonova, 1971, Pl. II, fig. 3, Pl. III, figs. 2, 2a, b) have an entirely *Costamenjaites*-like pattern of ribbing and the representatives of the two genera have been listed as co-occurring in the same beds in most of the fossil localities of the Undulatoplicatilis Zone listed by Sazonova (1971, p. 13, 74–87). Under these circumstances the remaining morphological distinctions of *Menjaites* from *Costamenjaites,* such as the presence of numerous deep constrictions on the early whorls of some *Menjaites* species (i.e., *M. imperceptus*; see Sazonova, 1971, Pl. II, fig. 1b, d, g, Pl. III, fig. 4, a, b), the generally very fine, threadlike appearance of *Menjaites* ribs, the very early disappearance of the sculpture and, finally, a complete absence of sculpture in some extreme forms (e.g., *M. levis*; see Sazonova, 1971, Pl. XIII, fig. 2, Pl. XIV, fig. 2), do not seem to be particularly significant on the generic, or even on the subgeneric level. In the writer's opinion, *Menjaites* is likely to be but a short-lived, specialized offshoot of the early phase of *Temnoptychites* plexus, ranking only as its subgenus. The writer favours this hypothesis (Textfig. 2). The alternative interpretation of *Menjaites* as a direct descendant and possible synonym of *Craspedites* (e.g., Shulgina, in Saks *et al.*, 1972, p. 130) appears to be less likely. Furthermore, the known infraspecific variability of some craspeditid ammonites is very great – e.g., in *Craspedites* (?*Taimyroceras*) *canadensis* (Jeletzky, 1966); or in *Thorsteinssonoceras ellesmerense* (Jeletzky, 1965b); or, finally, in *Temnoptychites* (*Temnoptychites*) *kemperi* n. sp. (see below in this report). It is so great that all representatives of *Menjaites* described and figured by Sazonova (1971) could possibly be but extreme morphological variants of a polymorphic species comprising all morphological forms from *Temnoptychites* (*Costamenjaites*) *suraensis* to *Temnoptychites* (*Menjaites*) *levis,* inclusive. The final decision on the subject is impossible without a restudy of the rich original material of the two subgenera collected and studied by Sazonova (1971).

The proposed direct ancestor-descendant relationship between *Costamenjaites* and *Temnoptychites* sensu stricto and their downgrading to subgenera of *Temnoptychites* are supported by the common coexistence and obvious intergradation of the shell types characteristic of these subgenera in the *Temnoptychites* sensu stricto populations of the Hoplitoides Zone. This appears to happen, for example, in the so-called *Temnoptychites hoplitoides* species group in the Central Russian Basin. Sazonova (1971, p. 84) proposes to split this species group to bolster the assignment of *Temnoptychites* and *Costamenjaites* to different genera and families favoured by herself. She assigns *Temnoptychites lgowensis* (Nikitin 1888) to *Costamenjaites* and thus separates it on the genus and family level from *T. hoplitoides* (Nikitin 1888) because of differences in the whorl cross-section and alleged difference in the ribbing habit. However, Nikitin (1888, Pl. II, fig. 2) figured a specimen of *T. hoplitoides* that obviously is transitional to *T. lgowensis* in the shape of its whorl and was found at the same locality as its holotype. Furthermore, Sazonova's (*loc. cit.*) claim of the diagnostic value of bidichotomous ribbing habit of *T. hoplitoides* is erroneous. Bodylevsky's (1967, Pl. IV, fig. 2a) photograph of the holotype displays the same highly variable ribbing habit as Nikitin's (1888, Pl. II, fig. 1) drawing with rare, irregularly dichotomous rib bundles alternating with prevalent

trichotomous-virgatitid and quadrichotomous-virgatitid bundles. This ribbing habit differs from that of the holotype of *T. lgowensis* (Nikitin, 1888, Pl. II, fig. 6) only in its somewhat more swollen (bullate) appearance and somewhat smaller length of primaries. This feature, furthermore, is rather variable in the representatives of these two 'species' figured by Nikitin (1888). As will be shown below, whorl shape and ribbing habit are even more variable in *T. kemperi* n. sp., which is the Canadian analogue of *Temnoptychites hoplitoides–T. lgowensis* species group. Because of this and considering a still greater infraspecific variability of whorl shape and ribbing habit in the related craspeditid *Thorsteinssonoceras ellesmerense* (Jeletzky, 1965b), the writer cannot accept *T. hoplitoides* and *T. lgowensis* even as truly independent species and therefore treats them in this paper as mere extreme morphological variants of one and the same polymorphic *Temnoptychites* species (see below).

Sazonova's (1971, p. 23, 83, 84, Textfig. 4) proposal to split the slender-whorled, nonbullate representatives of *Temnoptychites* into the genera *Costamenjaites* and *Bodylevskyiceras* also is erroneous, in the writer's opinion. This proposal is based largely on Sazonova's (1971, p. 83, 84) claim that *Bodylevskyiceras elegans* (Bodylevsky, 1967, Pl. III, fig. 1a, Pl. IV, fig. 1a) differs from *Costamenjaites* ex gr. *C. jucundus-suraense* in the narrower proportions of its lobes and saddles and in the presence of an archlike bend in the external suture line. However, a perusal of Bodylevsky's (*loc. cit.*) original illustrations leaves no doubt that these two features vary more within the species *T. elegans* than they do between this species and *T.* ex gr. *T. jucundus-suraense* (cf. Sazonova, 1971, Pl. XXVI, figs. 8, 10, 10a; and this report, p. 42). The same is true of Sazonova's (*loc. cit.*) claim that *Bodylevskyiceras* is characterized by a well developed interruption of secondaries in the midventer while in *Costamenjaites* they only weaken in this area. Actually this feature is present in all known representatives of *Temnoptychites* (including all representatives of *Costamenjaites*; see Sazonova, 1971, p. 85, 86) and is diagnostic of the genus as a whole. However, its strength and extent (presence on the early whorls and absence on the late whorls, etc.) is long known (e.g., Pavlow's, 1914, p. 44 original diagnosis of *Temnoptychites* cited earlier in this section) to vary widely but quite haphazardly from one species to another and even within one and the same species. Like *Costamenjaites* ex gr. *C. jucundus-suraense,* many typical *Temnoptychites* species either do not exhibit a complete midventral interruption of secondaries (but only their more or less marked weakening) or exhibit it only on very limited segments of their whorls. Finally, there is no reason to assume, as Sazonova (1971, p. 83) does, that *Costamenjaites* ex gr. *C. jucundus-suraense*: "apparently were ancestors of the genus *Bodylevskyiceras*, which inhabited the sea of the '*hoplitoides*' time." All representatives of "*Bodylevskyiceras*" *elegans* described by Bodylevsky (1967, p. 102, 107) have been found in glacial boulders of an unknown derivation which have yielded ammonites of the *Surites spasskensis, Tollia stenomphala* (=*Pseudogarnieria undulatoplicatilis*) and *Temnoptychites hoplitoides* zones. Inasmuch as the closest allies of "*B.*" *elegans* (i.e., *C.* ex gr. *C. jucundus-suraense*) in the Central Russian Basin appear to be restricted to the

Undulatoplicatilis Zone and those in Sverdrup Basin (*C. troelseni*) are assignable to beds underlying the equivalents of the Hoplitoides Zone and hence are correlative with the Undulatoplicatilis Zone, the Novaya Zemlya species probably was derived also from the Undulatoplicatilis Zone and not from the Hoplitoides Zone as Bodylevsky believed (1967, p. 107). Sazonova's (1971) purely iconographic taxonomic approach to the erection of ammonite genera does not serve any useful purpose, in the writer's opinion (Jeletzky, 1955, p. 485–490). The writer considers *Bodylevskyiceras* to be synonymous with *Costamenjaites* on the generic and subgeneric level. The name *Bodylevskyiceras* is nomenclatorially invalid in any case (see below).

Some recent workers (e.g., Bodylevsky, 1967, p. 103; Shulgina, in Saks *et al.,* 1972, p. 130, 131) felt concerned about *Temnoptychites* Pavlow 1914 falling into the synonymy of an almost unknown, ill defined name *Nikitinoceras* Sokolov 1913. Wright (in Arkell *et al.,* 1957, p. L344) and Bodylevsky (1967, p. 103) sought to avoid this pitfall by claiming that *Temnoptychites* was proposed not in 1914 but in 1913, that is, in the same year as *Nikitinoceras* Sokolov (1913, p. 84). Bodylevsky (1967, p. 103) based this claim on the fact that separates of Pavlow's (1914) paper are dated 1913. Whatever the merits of the above claim, there appears to be a better way to do away with the name *Nikitinoceras* Sokolov 1913. Sokolov (1913, p. 84) proposed the generic name *Nikitinoceras* for a most comprehensive complex of craspeditid ammonites corresponding to several genera of the modern usage. As originally proposed, the genus included four species groups arranged in the following order: *Olcostephanus okensis* group; *Olcostephanus spasskensis* group; *Olcostephanus hoplitoides* group; and *Olcostephanus juvenescens* group. No type species was indicated in the original definition and the writer knows of no subsequent formal selection. Therefore it is proposed herein to restrict *Nikitinoceras* Sokolov 1913 to the *Olcostephanus okensis* group only and to select *Ammonites okensis* d'Orbigny 1845 as its type species (see Jeletzky, 1966, p. 4, 5 for further details). This legitimate action makes *Nikitinoceras* Sokolov 1913 an objective synonym of *Craspedites* Pavlow 1892 and removes any possible doubts about the availability of *Temnoptychites* Pavlow 1914 for the group of craspeditid ammonites typified by *Olcostephanus hoplitoides* Nikitin 1888.

Diagnostic features. The early Russian workers (e.g., Nikitin, 1888; Bogoslowsky, 1902, p. 20, 63, 64) relied explicitly on the presence of a marked weakening or a complete interruption of secondary ribs in the midventer for the recognition of *Olcostephanus hoplitoides* Nikitin 1888 and allied forms long before Pavlow (1914, p. 44) erected the generic name *Temnoptychites* for this form group. The same midventral weakening or interruption of ribs continues to be used as the principal diagnostic character of *Temnoptychites* at present (e.g., Bodylevsky, 1949, p. 199; 1967, p. 101; in Luppov and Drushchits, 1958, p. 93; Klimova, in Golbert *et al.,* 1972, p. 155, 156). The writer's study of the Sverdrup Basin *Temnoptychites* and a review of the data available in the literature have fully confirmed the taxonomic validity of the above generic character. However, it is sometimes difficult to utilize this character in practice, particularly where the

early growth stages or the strongly weathered specimens of *Temnoptychites* are concerned. Some of these cases are discussed below in connection with the description of individual Canadian species (e.g., *T. grandiosus* and *T. troelseni* n. sp.).
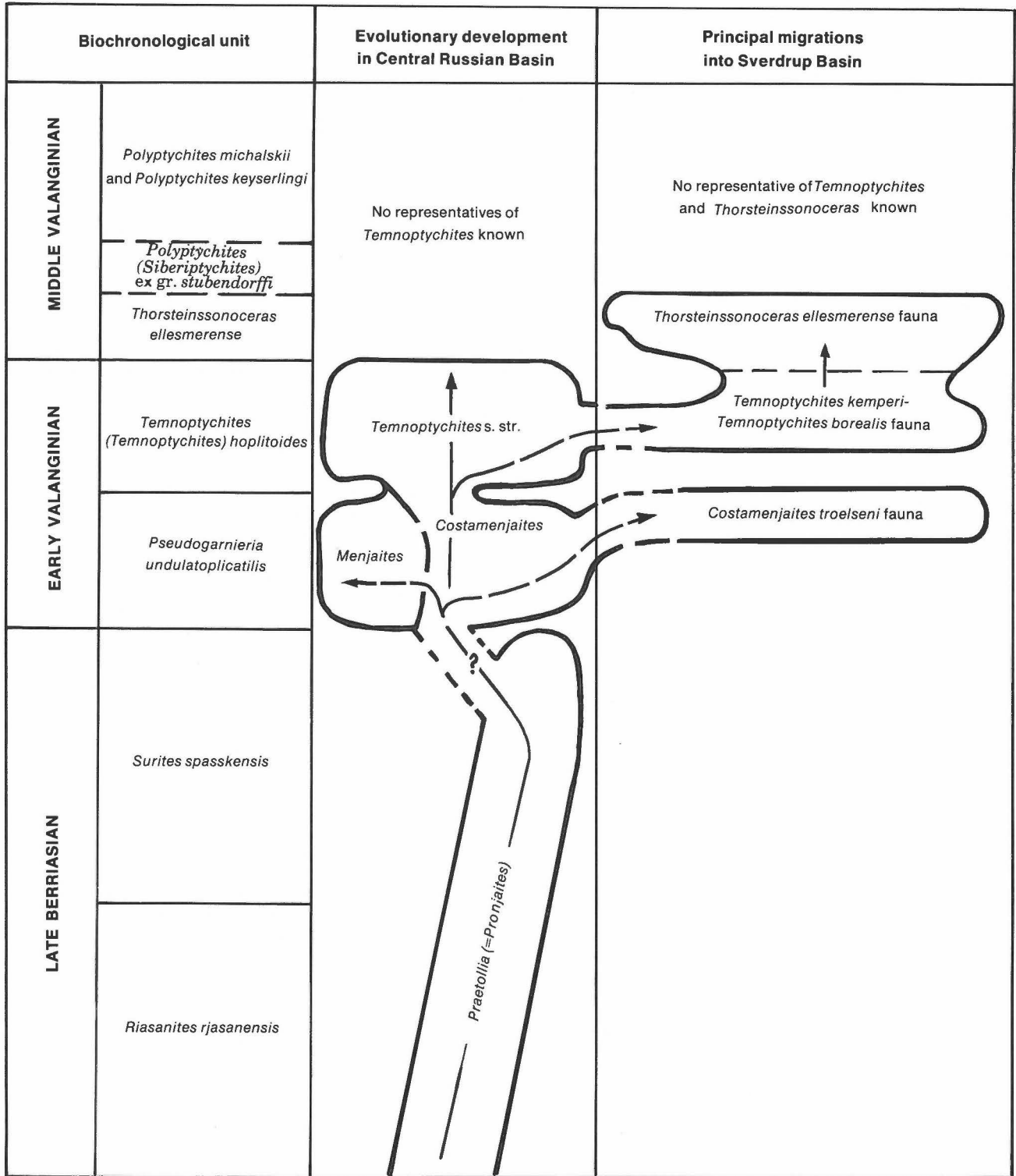
In the writer's opinion the medioventral weakening or interruption of secondary ribs remains the only immediately diagnostic morphological feature common to all representatives of the genus *Temnoptychites* as defined in this report, while apparently being totally absent in all otherwise similar early Early Cretaceous craspeditid genera. The more recent discovery of a similar medioventral weakening or interruption of secondary ribs in the not directly related latest Jurassic *Craspedites* (*Taimyroceras*) (Bodylevsky, 1960; Jeletzky, 1966) does not affect this conclusion. This craspeditid subgenus is easily distinguishable from *Temnoptychites* because of an entirely different, more primitive external suture line (see below) and a rather different ribbing habit at the intermediate and adult growth stages.

The external suture line is the only other feature providing morphological criteria diagnostic of nearly all known representatives of the genus *Temnoptychites*.

Only semiadult (those of sculptured intermediate whorls characterized by four auxiliary lobes) to adult (those of entirely to almost entirely smooth outer whorls) external suture lines of *Temnoptychites*, beginning with the whorl diameters of about 17 mm, have been available to the writer. As far as it was possible to judge, the earlier external suture lines of the genus were neither described nor figured by any of the previous workers either.

The semiadult to adult external suture lines of all better known *Temnoptychites* species (see Bogoslowsky, 1902, Pl. IV, fig. 3d, Pl. XIV, fig. 7c; Bodylevsky, in Luppov and Drushchits, 1958, p. 92, Fig. 76g; Bodylevsky, 1967, Pl. III, fig. la, Pl. IV, fig. 1b, Pl. V, fig. 1b; Jeletzky, 1964, Pl. V, figs. 3E, 4A; Klimova, in Golbert *et al.,* 1972, Pl. IV, fig. 1; this paper, Pl. 1, fig. 2B, Pl. 3, figs. 2A, 4, Pl. 6, fig. 2D, Pl. 8, fig. 3D, Pl. 9, figs. 1A, C, 2B, C, F, Pl. 10, fig. 1H, Pl. 12, fig. 1D, E, Textfigs. 3–6) are characterized by an early appearance of the fourth auxiliary lobe (usually already on the second to third whorl before the adult ultimate whorl) and the presence of four to five auxiliary lobes throughout the rest of the ontogeny. This feature is diagnostic of the early Early Cretaceous evolutionary phase of the Craspeditidae (p. 6, 7).

In the semiadult external suture lines of *Temnoptychites*, the presence of four to five auxiliary lobes is usually combined with the parallel-sided appearance of lateral and auxiliary lobes, regular spacing of these lobes, equally regular decrease of their size toward the umbilical seam, and their insignificant to moderate frilling. The adult suture line is much more variable within the genus. It usually acquires narrow- to very narrow stemmed, adorally contracted or parallel-sided lateral and auxiliary lobes. However, its saddles become either correspondingly narrowed (e.g., in *T. borealis* and *T. kemperi* n. sp.) or, in contrast, broad to very broad, square shaped to adorally expanding (in some representatives of *T. elegans* and *T. troelseni* n. sp.). Generally, the adult suture lines become considerably more frilled than semiadult suture lines. However, the last few suture lines of some representatives of

Biochronological unit		Evolutionary development in Central Russian Basin	Principal migrations into Sverdrup Basin
MIDDLE VALANGINIAN	*Polyptychites michalskii* and *Polyptychites keyserlingi*	No representatives of *Temnoptychites* known	No representative of *Temnoptychites* and *Thorsteinssonoceras* known
	Polyptychites (Siberiptychites) ex gr. stubendorffi		
	Thorsteinssonoceras ellesmerense		*Thorsteinssonoceras ellesmerense* fauna
EARLY VALANGINIAN	*Temnoptychites (Temnoptychites) hoplitoides*	*Temnoptychites* s. str.	*Temnoptychites kemperi-Temnoptychites borealis* fauna
	Pseudogarnieria undulatoplicatilis	*Costamenjaites* *Menjaites*	*Costamenjaites troelseni* fauna
LATE BERRIASIAN	*Surites spasskensis*	*Praetollia (=Pronjaites)*	
	Riasanites rjasanensis		

MFM

Textfigure 2. Suggested course of evolutionary development of *Temnoptychites* stock in Central Russian Basin, principal migrations of its representatives into Sverdrup Basin and the *Temnoptychites-Thorsteinssonoceras* transmutation there.

T. troelseni n. sp. become markedly simplified instead (Textfig. 6D, F).

Most semiadult and adult suture lines alike are strongly ascendant (form angles of 15 to 40 degrees with the shell's radius) throughout or almost throughout (with the exception of the adumbilicalmost segment of the suture lines usually confined to the umbilical wall) the distance between the ventral lobe and the umbilical seam. Therefore the semiadult suture lines of *Temnoptychites* usually are indistinguishable from those of *Praetollia* (? = *Borealites*; see Spath, 1952, p. 14, Textfig. 1a, b; Jeletzky, 1973, p. 74, 75; this paper, Textfig. 1K) and *Surites* sensu lato (inclusive of *Caseiceras*, *Lynnia*, ?*Bogoslovskia*, ?*Stchirowskiceras*). The exceptions to this rule will be described below in connection with the comparison of external suture lines of *Tollia* and *Temnoptychites*.

The semiadult suture lines of *Temnoptychites* are not much more advanced morphologically than those of *Craspedites* sensu lato (inclusive of such subgenera and complete synonyms as *Swinnertonia*, *Subcraspedites*, *Mosquites* and *Taimyroceras*) in the degree of stubbiness and frilling of their elements. However, like the sutures of *Praetollia* and *Surites* sensu lato, they can be distinguished easily from suture lines of *Craspedites* sensu lato because of their pronounced ascendant character and the presence of four or five (instead of three) auxiliary lobes.

The adult suture lines of *Temnoptychites* can be distinguished easily from those of *Praetollia*, *Surites* sensu lato and *Craspedites* sensu lato because of their considerably longer, more narrow, adorally constricted and abundantly frilled lobes combined with square-shaped to adorally expanding saddles. In the case of *Craspedites* sensu lato, the adult suture lines of *Temnoptychites* also differ markedly in their strongly ascendant character.

The differentiation of semiadult to adult external suture lines of *Temnoptychites* from the equivalent suture lines of *Tollia* sensu lato (see below for the interpretation of this genus) presents considerable difficulty since the two may be similar in the major morphological features (e.g., the number of auxiliary lobes, regularity of spacing and of gradual adumbilical decrease in size of the lobes). Consequently it is necessary to use differences in other less taxonomically significant features of these suture lines.

As already mentioned, the external suture lines of *Temnoptychites* are rather variable within every sufficiently well known species (e.g., *T. kemperi* n. sp., *T. troelseni* n. sp., and *T. elegans* Bodylevsky 1949). Furthermore the suture lines of different *Temnoptychites* species studied differ appreciably from one another in a number of morphological details. There is a considerable overlap of the range of variation of most morphological details of *Temnoptychites* suture lines with the corresponding morphological details of *Tollia* suture lines, which may make it difficult to differentiate these two genera on the evidence of external suture lines alone.

The rather persistent difference in orientation and general shape of external suture lines of *Tollia* and *Temnoptychites* provides perhaps the most diagnostic distinction. As mentioned previously, the semiadult and adult external suture lines of *Temnoptychites* are, as a rule, strongly ascendant and approximately straight throughout or almost throughout (with the exception of the adumbilicalmost part) the distance

between the ventral lobe and the umbilical seam. In this respect, they resemble closely the external suture lines of *Praetollia* (Jeletzky, 1973, p. 74, 75; this paper, Texfig. 1K) and *Surites* ex gr. *S. spasskensis* (Textfig. 1N). In contrast, the external suture lines of *Tollia*, as exemplified by those of *Tollia tolli* sensu lato and *Tollia maimetschensis* (Pavlow, 1914, Pl. XII, figs. 1a, 2c, 3, Pl. XIII, fig. 2; Shulgina, in Saks *et al.*, 1972, p. 140, 141, Textfigs. 10-6a, b, 10-8, 11-1, 11-4, 12-4, 12-11; this paper, Textfig. 1Q, R and T) and by *Tollia klimovskiensis* Krimgolts (Shulgina, in Saks and Shulgina, 1960, Pl. II, fig. 1g; in Saks *et al.*, 1972, p. 140, 141, Textfigs. 10-7, 10-10; this paper, Textfig. 1R) differ from those of *Temnoptychites* (Pl. 1, fig. 2B, Pl. 3, figs. 2A, 4, Pl. 6, fig. 2D, Pl. 7, fig. 1E, G, Pl. 8, fig. 3D, Pl. 9, figs. 1A, B, 2B, C, F, Textfigs. 1S, 3–6) in the restriction of distinctly to markedly ascendant orientation of the suture line to its adventral part consisting either of the first and second lateral lobes and first and second lateral saddles alone or to those elements plus the first auxiliary lobe and first auxiliary saddle, or (quite exceptionally) to the lateral elements plus first and second auxiliary lobes and saddles. The remaining adumbilical part of the external suture line is either only very feebly ascendant or subradially directed. It may be even feebly suspensive in some *Tollia* forms (e.g., *Tollia venusta*; see Klimova, in Saks *et al.*, 1972, Pl. XXXIX, fig. 1a). The more strongly ascendant adventral part of the *Tollia* suture line may grade into its very weakly to weakly descendant adumbilical part causing a more or less regularly adorally arched overall appearance of the suture line, resembling that of *Hectoroceras* (Casey, 1973, Textfig. 5a, b, c; this paper, Textfig. 1-O). In other *Tollia* forms each of these two parts of the external suture line is approximately straight. This results in the development of an adorally directed knick of the suture at their junction. Furthermore the ascendant adventral part of the *Tollia* suture line is considerably less ascendant normally than the corresponding part of the *Temnoptychites* suture line. It forms angles of 5 to 10 degrees with the direction of the shell's radius whereas the suture line of *Temnoptychites* normally forms angles of 15 to 40 degrees with the direction of the shell radius. There are exceptions, however, as the external suture lines of some apparently typical *Tollia* species such as *Tollia anabarensis* (Pavlow, 1914, Pl. 4, fig. 3a) and *Tollia* n. sp. aff. *T. klimovskiensis* (p. 51, Textfig. 7) appear to be just as strongly ascendant as those of the *Temnoptychites* and to lack either the adoral arch described above or the knick characteristic of most *Tollia* species. Similarly, there are some otherwise typical *Temnoptychites* species (e.g., *T. borealis* Bodylevsky; see p. 16, 17, Pl. 1, fig. 2B, Textfig. 3) the external suture lines of which are only very weakly ascendant and slightly convex adorally.

Another considerably less constant but nevertheless significant distinction of *Temnoptychites* and *Tollia* suture lines consists in the common development of thin- to very thin stemmed, partly adorally constricted lobes in adult suture lines of the former genus; see the descriptions of adult suture lines of *Temnoptychites* (*Costamenjaites*) *grandiosus*, and *T.* (*C.*) *troelseni* n. sp., below and in Textfigures 5 and 6. This development is accompanied by a strong simplification of lateral and auxiliary lobes in some representatives of *T.* (*C.*) *troelseni* n. sp. (Pl. 12, fig. 1D, E, Pl. 13, fig. 2C, Textfig. 6D,

F). Whenever this happens, the intervening adult saddles are correspondingly expanded, becoming two to three times wider than the adjacent adumbilical lobes (e.g., Pl. 7, fig. 1A, B, Pl. 12, fig. 1D, Textfigs. 5A–C, 6D–G and in the holotype of *T.* (*C.*) *grandiosus*; see Voronets, 1962, Pl. XXXVIII, fig. 2). Because of the adoral constrictions of the adult lobes, the adult saddles of such *Temnoptychites* forms tend to acquire an adorally widening, somewhat egg-shaped outline instead of the approximately square outline characteristic of most semiadult *Temnoptychites* saddles.

The taxonomic value of this morphological distinction is decreased by the circumstance that the lobes of advanced, presumably adult external suture lines of *Temnoptychites* (*Temnoptychites*) *kemperi* n. sp. (Pl. 3, fig 4, Textfig. 4A, D) become relatively thin stemmed and adorally constricted without the intervening saddles becoming relatively wider. Furthermore the lobes of advanced, presumably adult suture lines of *T.* (*T.*) *borealis* (Textfig. 3B) do not seem to become attenuated and constricted at all. Finally some adult representatives of *Temnoptychites elegans* Bodylevsky 1967 and *T.* (*C.*) *troelseni* n. sp. (Textfig. 6A, C) retain relatively broad stemmed, parallel-sided to adapically tapering lobes and relatively narrow, square-shaped to adorally tapering saddles, which are indistinguishable from those of some *Tollia* species (e.g., *T. klimovskiensis* or *T. anabarensis*; see Pavlow, 1914, Pl. IV, fig. 3A; Shulgina, in Saks and Shulgina, 1969, Pl. II, fig. 1g) throughout their ontogeny. However, these exceptions appear to be relatively rare in the Canadian and Eurasian *Temnoptychites* hitherto described.

In contrast to the adult lines of *Temnoptychites* discussed above, the latest known, presumably adult suture lines observed in large (120–180 mm in diameter), entirely smooth but still fully septate shells of *Tollia* (e.g., *Tollia tolli* sensu lato; see Pavlow, 1914, Pl. XIII, fig. 2; Shulgina, in Saks *et al.*, 1972, Pl. XX, fig. 1, Pl. XXI, fig. 1a; Klimova, in Saks *et al.*, 1972, Pl. XXXIX, fig. 1a, b; this paper, Textfig. 1Q, R, T) retain the broad-stemmed, florid lobes and relatively more narrow, square-shaped to adorally tapering saddles characteristic of semiadult external suture lines of *Tollia*.

Other marked morphological distinctions of the suture lines of *Tollia* and *Temnoptychites* are even less constant than those discussed above. For example, the broad and florid first and second lateral lobes and the first auxiliary lobes of some *Tollia* forms such as *T. tolli* sensu lato (Pavlow, 1914, Pl. XII, figs. 1a, 2c, 3, Pl. XIII, fig. 2; Shulgina, in Saks *et al.*, 1972, p. 140, 141, Textfigs. 10-8, 11-4, 12-11) or *T. venusta* (Klimova, in Saks *et al.*, 1972, Pl. XXXIX, fig. 1a, b) are separated by relatively narrow, adorally contracting saddles that are either narrower or only a little wider than the next adumbilical lobes. These lobes and saddles are markedly different from the relatively narrower corresponding lobes and relatively wider corresponding saddles of most *Temnoptychites* species known. However, there are a number of apparently typical *Tollia* forms, such as *Tollia klimovskiensis* (Shulgina, in Saks and Shulgina, 1969, Pl. II, fig. 1g; in Saks *et al.*, 1972, p. 140, Textfigs. 10-7, 10-10), *T. klimovskiana* (Shulgina, in Saks *et al.*, 1972, p. 141, Textfig. 11-3) or *T. anabarensis* (Pavlow, 1914, Pl. IV, fig. 3a), in which the above-discussed lobes and saddles closely match those of *Temnoptychites*. Moreover the relative width of the lobes and saddles is known to vary greatly within

the same *Tollia* species (cf. Shulgina, in Saks *et al.*, 1972, p. 140, Textfigs. 11-1, 11-4) or even within the same specimen of *Tollia* (cf. Shulgina, *ibid.*, p. 140, Textfig. 6a, b). The same is true of some otherwise typical *Temnoptychites* species (see below in the description of *T. borealis* and *T. troelseni* n. sp.) where the relative width of the lobes and saddles may vary so markedly from one species to another and within one and the same species (e.g., in *T. elegans* and *T. troelseni* n. sp.) that some of their extreme morphological modifications are impossible to differentiate from those of some *Tollia* lobes and saddles.

The difference commonly present in the degree of frilling of lateral and auxiliary lobes and saddles and in the length of lateral and terminal accessory lobes of *Tollia* and *Temnoptychites* (see below in the description of the suture line of *T. troelseni* n. sp.) is valid on the specific but not on the generic level as the range of variation of these features may overlap greatly.

The intermediate external suture line of *Temnoptychites* differs from that of *Thorsteinssonoceras*, as exemplified by *T. ellesmerense* (Jeletzky, 1965b, p. 10, 11, Textfig. 1A, E) primarily in the absence or slight expression of the widening of the second auxiliary saddle. In all better known *Temnoptychites* forms (Textfigs. 3–6; Bodylevsky, in Luppov and Drushchits, 1958, p. 92, Textfig. 76g), the second auxiliary saddle is either about as wide as the adjacent saddles or only insignificantly (up to 1½ times) widened in comparison with them. The second auxiliary saddle of *T. ellesmerense*, erroneously designated as the first auxiliary saddle by the writer (Jeletzky, 1965b, p. 10), in contrast, is markedly to strongly (two to four times) widened compared with the adjacent saddles. As indicated by a study of still unpublished material of early growth stages of Canadian and European *Thorsteinssonoceras* forms, this relative widening of the second auxiliary saddle decreases only to values comparable with those observed in the intermediate to advanced suture lines of *Temnoptychites* in their earliest known (less than 10 mm in diameter) whorls. Another distinction consists of the considerably less florid appearance and either the absence or weak development of long fingerlike lateral and terminal accessory lobes in the intermediate suture line of *Temnoptychites*.

The adult external suture lines of *Thorsteinssonoceras* are closely comparable to those of *Temnoptychites* in the degree of their frilling. However, their lobes do not become as narrow as the adult lobes of typical representatives of *Temnoptychites* and all saddles, except for the second auxiliary saddle, remain narrower than the saddles of these *Temnoptychites*. The adult second auxiliary saddle of *Thorsteinssonoceras* is just as unlike that of *Temnoptychites* as is its semiadult second auxiliary saddle.

The above-discussed, constant morphological distinctions of *Temnoptychites* suture line from that of *Thorsteinssonoceras* support the generic distinction of these taxa in spite of their now inferred direct ancestor-descendant relationships (p. 18, Textfig. 2).

The semiadult and adult suture lines of *Homolsomites* Crickmay 1930 cannot be confused easily with those of *Temnoptychites* because of the much greater degree of frilling of their extremely long stemmed, wavering lobes (Textfig. 1U).

14

The great length and ramification of accessory lobes of *Homolsomites* and the close approximation to overlap of its adjacent suture lines is not matched even in *Temnoptychites troelseni* n. sp.

Contrary to Arkell's sweeping assertion (in Arkell *et al.*, 1957, p. L97), major distinctive features of the *Temnoptychites* suture line generally hold true regardless of the thickness and shape of the whorl of the *Temnoptychites* species concerned. However, as illustrated in Textfig. 6A–I, the external suture line of the most slender Canadian species known – *T. troelseni* n. sp. – tends to be considerably more ascendant and more markedly frilled than the approximately equivalent external suture lines of the sturdiest known Canadian species (e.g., *T. borealis* and *T. kemperi* n. sp.; see Textfigs. 3, 4). The approximation and partial overlap of the semiadult and adult external suture lines also were observed only in the most slender, nodeless Canadian species (e.g., *Temnoptychites troelseni* n. sp.).

Other than the medioventral weakening or interruption of secondary ribs and the morphological details of suture lines, only the presence of umbilical bullae or bullate primary ribs in combination with the very low position of the branching points of primary ribs on the flank has some independent value for the recognition of representatives of *Temnoptychites*. This feature permits a safe differentiation of all the intermediate and adult growth stages of nodose *Temnoptychites* forms assigned herein to the subgenus *Temnoptychites* sensu stricto (e.g., *T.* ex gr. *T. triptychiformis-hoplitoides-lgowensis*, *T. mokschensis*, *T. borealis*, *T. vylkoi*, *T. rudis*, *T. prontschistchtevi*, and *T. kemperi*) from representatives of the genera *Tollia* and *Homolsomites* whenever the weakening or interruption of secondary ribs is primarily (on the early whorls) or secondarily (weathered or fragmentary state of preservation) absent and the suture line is not visible. However, these features do not permit the differentiation of nodose *Temnoptychites* forms from such craspeditid genera as *Thorsteinssonoceras*, fully ribbed *Craspedites* sensu lato or heavily ribbed and bullate basal Cretaceous "*Subcraspedites*" ex gr. "*S.*" *anglicus* Shulgina 1972. The suture line must be used to differentiate these craspeditids from the homeomorphic forms of bullate *Temnoptychites*.

None of the supplementary distinguishing features discussed above permits the differentiation of the nodose representatives of *Temnoptychites* sensu stricto from those of such craspeditid genera as *Praetollia* and *Surites* sensu lato. Only the presence of the medioventral weakening or interruption of secondary ribs is diagnostic in this case.

None of the presently known features of the ribbing habit, whorl shape, or whorl proportions provides a reliable means of differentiation of nodeless *Temnoptychites* forms assigned herein to the subgenus *Costamenjaites* Sazonova 1971 (e.g., *T. grandiosus*, *T. elegans* and *T. troelseni* n. sp.) from homeomorphically similar representatives of *Praetollia*, *Surites* and *Tollia* sensu lato (see below for definition). The ribbing habits and the whorl shapes of the latter craspeditid genera may be so similar as to make their safe differentiation from nodeless *Temnoptychites* (*Costamenjaites*) impossible if the diagnostic medioventral weakening or interruption of secondaries is primarily (on the inner whorls) or secondarily (in fragmentary or weathered specimens) absent and the

suture line is not visible in the latter. The long-standing misidentification of *Surites simplex* (Bogoslowsky 1902) is a case in point (p. 28). The practical impossibility of differentiating the isolated early whorls of *Tollia tolli* sensu lato from the equivalent, still fully ribbed whorls of *Temnoptychites* (*Costamenjaites*) ex gr. *T.* (*C.*) *elegans-troelseni* n. sp. on the sculpture and whorl shape alone is another example. Even with the aid of the suture line, the writer remains uncertain about the generic nature of some nuclei of *Tollia tolli*–like ammonites from the glacial boulders of Novaya Zemlya (e.g., Salfeld and Frebold, 1924, Pl. IV, figs. 2, 3; Bodylevsky, 1967, Pl. III, fig. 2a, b, Pl. IX, fig. 5a, b), which are too small to decide whether or not their strong secondary ribs, not weakened on the venter, are diagnostic of genus *Tollia* or represent the early growth stage of *Temnoptychites* (*Costamenjaites*) *elegans* devoid of any midventral weakening of the secondaries.

As with most other craspeditid genera (see above in section on taxonomic value of sculpture), the adult whorls of *Temnoptychites* can be differentiated from immature whorls because of a complete to almost complete (except for umbilical bullae, constrictions and striae) loss of sculpture. There does not seem to be any exception to this rule either in the Canadian or in the Eurasian (judging by the data available in the literature) representatives of the genus, though the sculpture may be lost at various growth stages (either on the fully septate part of penultimate whorl or on the ultimate whorl occupied by the adult living chamber) in different representatives of the genus. This morphological feature seems to provide a better means of recognition of adult representatives of *Temnoptychites* than the crowding and simplification of the last few suture lines before the living chamber (see discussion of the suture line). All ribbed living chambers are assigned tentatively to the prematurely deceased nonadult individuals preserved with their last living chambers.

Geographical range. Until recently, representatives of *Temnoptychites* were known only in the U.S.S.R., where they occur abundantly in the lower Valanginian of central Russia (e.g., Nikitin, 1888; Bogoslowsky, 1902; Bodylevsky, 1949; Sazonova, 1971), Novaya Zemlya (e.g., Sokolov, 1913; Salfeld and Frebold, 1924; Bodylevsky, 1949, 1967), western Siberia (Klimova, 1960, p. 172, 173, Pl. XX, figs. 10, 11, Pl. XXI, figs. 1–4; in Golbert *et al.*, 1972) and northern Siberia (Pavlow, 1914; Voronets, 1962; Bodylevsky, 1967; Saks *et al.*, 1972). The genus was not known from any other region of the Boreal Realm until Jeletzky (1964, p. 38, Pl. V, figs. 1, 3, 4) recorded its presence in the Sverdrup Basin, Canadian Arctic Archipelago and Bodylevsky (1967, p. 103) recognized the presence of misidentified representatives of the genus in eastern Greenland. As pointed out by Bodylevsky (*ibid.*; writer's translation from Russian): "The representatives of this genus are now known from East Greenland ("*Dichotomites*"(?) sp. nov. – Pl. 23, fig. 2 and, possibly "*Neocraspedites*" *groenlandicus* – Pl. 23, fig. 4 (Donovan, 1953) . . . .". To this must be added that Donovan (1953, p. 103, 105, Pl. 21, figs. 1, 3) also records generically misinterpreted *Polyptychites* (*Polyptychites*) aff. *P.*(*P.*) *triptychiformis* (Nikitin) and *Polyptychites* (*Polyptychites*)

mokschensis (Bogoslowsky). Though not identifiable definitively as to the species from photographs and brief descriptions, these specimens definitely belong to nodose *Temnoptychites* ex gr. *T. triptychiformis-kemperi* based on a distinct interruption of secondary ribs in the middle of the venter of their last preserved whorls (*ibid.*, Pl. 21, figs. 1b, 3b) combined with their sturdy whorl shape and the presence of bullate primary ribs in the early growth stages.

Though a definitive decision is impossible without a restudy of the actual specimen (especially of its unfigured suture line), *"Dichotomites" gregersoni* var. *paucicostatus* of Donovan (1953, p. 110–112, Pl. 23, fig. 1a, b) seems more likely to belong to either a *Temnoptychites lgowensis*–like variant of *T. kemperi* n. sp. or to a nodeless *Temnoptychites* ex gr. *T. elegans-troelseni* than to a *Tollia* ex gr. *T. anabarensis* (Pavlow 1914). This is suggested by the apparent weakening of secondary ribs in the midventer of this specimen (see Donovan, 1953, Pl. 23, fig. 1b) combined with the narrow umbilicus (22%) and the low point of branching of primary ribs on the flank.

The above data suggest that the eastern Greenland fauna of *Temnoptychites* is just as rich as and very closely allied to the *Temnoptychites* faunas of the U.S.S.R. and the Canadian Arctic Archipelago. Although the data available are scarce and unevenly distributed, *Temnoptychites* likely occurs throughout the Boreal Realm and represents an extremely valuable intercontinental index fossil of the early Valanginian time throughout that realm.

Subgenus *Temnoptychites* Pavlow 1914 sensu stricto

Type species: As for the genus.

Diagnosis. Temnoptychites forms characterized by moderately sturdy to sturdy *Polyptychites*-like whorls and/or moderately well developed to pronounced umbilical bullae in the intermediate to late growth stages.

Concept of subgenus. The reasons for treating the nodose *Temnoptychites* ex gr. *T. hoplitoides* as a typical subgenus of *Temnoptychites* have been explained fully in connection with the discussion of the genus (p. 9).

Temnoptychites (Temnoptychites) borealis Bodylevsky 1967

Plate 1, figure 2, Textfig. 3

1902 *Olcostephanus* cf. *triptychiformis* et *syzranicus* Bogoslowsky, p. 62, Pl. XVII, figs. 1–5
1967 *Temnoptychites borealis* Bodylevsky, p. 106, Pl. IX, figs. 1, 2
1975 *Russanovia diptycha* Jeletzky, in Kemper, 1975, p. 248

Holotype. Juvenile specimen reproduced by Bodylevsky (1967, Pl. IX, fig. 1) (by original designation).

Material and locality. A solitary, incomplete, somewhat deformed specimen GSC 49309 from GSC locality 91313. Collected by Edwin Kemper. See description of *Temnoptychites kemperi* n. sp. for further details.

Description. Bodylevsky (1967, p. 106) describes *Temnoptychites borealis* as follows (writer's translation from Russian): "Shell with thick whorls and a deep, moderately narrow umbilicus. Cross-section low and wide with a flattened outer [i.e., ventral (translator's remark)] side. The Novaya Zemlya

representatives are represented by chambered whorls only. The sculpture consists of strong dichotomous ribs which are weakened on the outer side. One rib of the holotype is single (after a feeble constriction). The suture line has four auxiliary lobes, three of which are situated on the umbilical shoulder.

"From the most closely allied species – *T. triptychiformis* – the new species differs in: flattening of the outer side; sharper and stronger ribs, especially on the umbilical shoulder; more definite weakening of ribs on the outer side. The number of [studied (translator's remark)] specimens – 3. Middle Valanginian, zone of *T. hoplitoides* on Izhma River, in boulders on Novaya Zemlya."

The above description is rather incomplete since the material available to Bodylevsky (1967) was restricted to the early whorls of *Temnoptychites (Temnoptychites) borealis*. The only representative of the species found in the Amund Ringnes Island fauna (Pl. 1, figs. 2A–E) is a much larger but still fully septate intermediate (possibly penultimate) whorl. This somewhat deformed (secondarily compressed) specimen has the following approximate dimensions (at whorl's end): shell diameter, 69.5 mm; whorl height, 39.5 mm; whorl width, 34 mm (almost certainly too low because of a secondary compression); width of the umbilicus, 22 mm; coefficient of involution, 55 per cent.

Suture line. The characteristically craspeditid, weakly ascendant semiadult external suture line of the early half of exposed whorl closely resembles that of *Surites* and *Praetollia* in the shape, proportions and degree of denticulation of its elements (Pl. 1, fig. 2B, Textfig. 3A). The lateral part of the suture is somewhat more ascendant than the auxiliary part but there is no definite *Tollia*-like bend or knick anywhere. The broad, only moderately denticulated ventral lobe is slightly longer than the first lateral lobe. The latter is broad and stubby (about twice as long as broad), approximately parallel-sided and asymmetrically trifid with most accessory lobes very short and pointed. The first and second lateral saddles are unlike those of other Canadian *Temnoptychites* species and closely resemble those of typical *Tollia* forms in being considerably narrower (about one half and one third, respectively) than the first lateral lobe and roughly square shaped. The second lateral lobe has the same general shape and degree of denticulation as the first lateral lobe but is appreciably more slender. It is only about half as long as the first lateral lobe. First and second auxiliary lobes are similar to the second lateral lobe in the shape, proportions and degree of denticulation. However, they are, respectively, two thirds and one third as long as the second lateral lobe. All three lobes are almost symmetrically trifid.

The lengths of these four lobes decrease gradually and almost evenly toward the umbilicus so that the line connecting their tips deviates only slightly from the straight course (i.e., is only slightly convex adorally). This, and the equally regular adventral decrease of general size of the four lobes, results in a rather neat and regular appearance of this part of the suture line. However, this regularity disappears farther toward the umbilicus because the third auxiliary lobe is almost as long as the second auxiliary, in spite of being a slender, only slightly indented, tacklike structure. The fourth and last auxiliary lobe is a tiny, simple-pointed notch which is only slightly longer

than the similarly shaped intervening lobule. One more similarly shaped lobule separates the fourth auxiliary lobe from the umbilical seam (Textfig. 3A). The almost completely undifferentiated character of this adumbilicalmost part of the external suture line appears to be a characteristic feature of semiadult sutures of the Canadian representatives of *Temnoptychites* sensu stricto (see description of *T. kemperi* n. sp.).

The second auxiliary saddle is only slightly wider than the first. Thus it is typical of *Temnoptychites* and contrasts with the second auxiliary saddle of *Thorsteinssonoceras* (cf. Jeletzky, 1965b, p. 10, Textfig. 1A–E). However, the third auxiliary saddle is unusually broad (about three times wider than the adjacent saddles) and subdivided into three parts by two lobules. The more adventral of these lobules is only slightly shorter and smaller than the following third auxiliary lobe. The exceptionally widened third auxiliary saddle is situated almost entirely on the flank with the regularly rounded umbilical shoulder situated on the outer (adventral) side of the third auxiliary lobe, which is still parallel sided, slightly denticulated and faintly trifid. The fourth auxiliary saddle is almost as wide as the third and divided in two by a short, broadly triangular lobule which is about half as long as the following fourth auxiliary lobe. The latter is only slightly smaller than the third auxiliary lobe but matches it closely in the shape and very feeble denticulation.

Only the ventral and lateral parts of the more advanced, probably adult external suture line are visible on the already smooth adoralmost part of the exposed whorl (Textfig. 3B). This suture differs from corresponding parts of the semiadult suture described above only in a considerably greater degree of frilling of lobes and saddles and in the ventral lobe being appreciably shorter than the first lateral lobe.

Shape and proportions of the whorl. The shape of the early whorls is adequately described in the previously cited original description. The rounded-rectangular, strongly depressed cross-section of the almost undeformed earliest exposed third of the whorl (Pl. 1, fig. 2C) closely matches that of the considerably smaller specimens figured by Bodylevsky (1967, Pl. IX, figs. 1a, 2a). The height of the whorl at the earliest exposed point is 17 mm and the corresponding width 22 mm (approx.). Within the adoral two thirds, the whorl seems to acquire an adventrally narrowing, rounded-trapezoidal cross-section with weakly convex flanks, fairly rapidly but gradually converging toward the truncated but nevertheless distinctly convex venter (Pl. 1, fig. 2C, E). The maximum width of the whorl is situated at the umbilical rim throughout this interval. This rounded-trapezoidal cross-section may be influenced considerably by postmortem deformation of the corresponding part of the shell. However, similar cross-sections recur in the similarly large intermediate whorl and in the much larger outer whorl of *Olcostephanus* cf. *O. triptychiformis* et *syzranicus* figured by Bogoslowsky (1902, Pl. XVII, fig. 1a, b). This specimen is assigned tentatively to *Temnoptychites (Temnoptychites) borealis* in this report contrary to the opinion of Bodylevsky (1967, p. 108), who compares it with *T. (T.) vylkoi*. The deep, moderately narrow umbilicus covers the inner whorls almost completely. The slightly convex umbilical wall is approximately perpendicular

to the plane of symmetry. The umbilical seam is furrowlike. The umbilical shoulder is regularly rounded and ill defined.

Sculpture. The earliest exposed part of the whorl is covered by fairly widely spaced, strong, sharp-topped dichotomous ribs described by Bodylevsky (see above). The primary ribs are either subradial or slightly inclined backward. These primaries are not appreciably thickened and only slightly elevated at the umbilical shoulder. They rapidly disappear on the outer part of the umbilical wall leaving its greater part entirely smooth or covered by fine transversal striae. Some of the primaries split into two secondary ribs within the lower third of the flank but most subdivide in two at the midflank. There is no weakening of ribs in the midflank. The initially subradial secondary ribs become increasingly but gradually inclined forward as they approach the ill defined, almost regularly rounded ventral shoulder and form broad, forward convex bends on the broad, flattened venter (Pl. 1, fig. 2C). On the earliest third of the whorl, the secondary ribs are only slightly weakened in the middle of the venter wherever it is shell covered. However, the same ribs are considerably weakened, albeit not completely interrupted, wherever the shell is removed. The same is the case in the small area of the venter of the preceding whorl (Pl. 1, fig. 2D) exposed immediately adorally of the segment discussed here.

The dichotomous ribbing habit described above is replaced by an indistinctly trichotomous habit within the poorly preserved (ventral part missing) middle part of the exposed whorl. There the primary ribs become moderately thickened and distinctly elevated (i.e., become distinctly bullate). These bullate ribs are now restricted to the lower third of the flank with most of the umbilical wall remaining only striated as before. Higher upflank, these somewhat commalike bullate primaries almost disappear at the level where they split into either three or rarely two strong, forwardly inclined (as before) secondary ribs (Pl. 1, fig. 2A, B). This results in an invariably indistinct connection between the primaries and the secondaries. Apparently the bullate primaries first split in two and then the posterior secondary rib splits once more at about the whorl's middle. At least one of the secondaries is intercalated between a trichotomous and a dichotomous rib bundle on the upper third of the flank. In the early part of this shell interval, the forward-bent secondary ribs are only weakened and/or attenuated in the middle of the broadly rounded venter which is shell covered throughout. However, in its adoral part (Pl. 1, fig. 2C) the ribs become completely interrupted within the broad median zone of the venter regardless of its shell-covered or steinkern mode of preservation. Only fine, mostly faint striae bent broadly forward occur in this midventral zone.

The ornament described above becomes gradually lost within the oralmost preserved third of the whorl. The ribs disappear first in the middle third of the flanks and in the above-described median zone of the venter where they become replaced by fine, ill defined striae. The still extant segments of secondary ribs on the upper thirds of the flanks are detached completely from the now strongly elevated, oval-shaped, round-topped bullae restricted to the adumbilical quarter of the flanks (Pl. 1, fig. 2A, B). Still farther adorally, the secondary ribs disappear completely and the oralmost fifth of

the whorl appears to be completely smooth except for the bullae. There are 18 primary ribs and bullae on the preserved whorl. The shape of the umbilical wall and shoulder does not change compared with the earliest third of the whorl. No constrictions have been noted.

Discussion. This description of the Canadian representative of *Temnoptychites borealis* Bodylevsky 1967 necessitates a somewhat drastic change of the original interpretation of this species. It indicates that the early, square-shaped and heavily ribbed but not bullate whorls of *T. borealis* are followed by at least one sturdily built, fully septate, rounded-trapezoidal-shaped whorl where the primary ribs are transformed into bullae. First the dichotomous rib bundles are replaced by indistinctly trichotomous rib bundles; then the ornament, with the sole exception of prominent, round-topped bullae and some striae, is lost on the outermost preserved part of the whorl (at whorl's height of about 29 mm).

The ontogenetic changes described above of *T. borealis* suggest strongly that the largest specimen of *Olcostephanus* cf. *O. triptychiformis* et *syzranicus* described and figured by Bogoslowsky (1902, p. 62, Pl. 17, fig. 1a, b) is but an adult of this species. The ribbing habit and the whorl shape of the inner whorl of this specimen match closely the similarly large trichotomous growth stage of the Canadian specimen. Under this interpretation, which does not depend only on the Middle Russian specimen described and figured by Bogoslowsky (1902), since the Canadian specimen exhibits much the same ontogeny, the adult of *T. borealis* is a large, strongly depressed form superficially indistinguishable from the *Polyptychites keyserlingi*–like variant of *Thorsteinssonoceras ellesmerense* (Jeletzky, 1965b, Pl. II, fig. 1A–C). However, *T. borealis* is not a *Thorsteinssonoceras* but an aberrant *Temnoptychites* as shown by its external suture line which resembles that of other *Temnoptychites* species. This suture line is much less denticulated than the comparable external suture line of *Thorsteinssonoceras ellesmerense* (*ibid.*, fig. 1A–D). Furthermore, it lacks the florid appearance, long fingerlike lateral and terminal accessory lobes, and the unusually widened second auxiliary (erroneously called first auxiliary by Jeletzky, 1965b, p. 10) saddle. The placement of *T. borealis* (including the larger specimen figured by Bogoslowsky, 1902, Pl. XVII, fig. 1a, b) in *Temnoptychites* is indicated also by the weakening and then complete interruption of secondary ribs in the middle part of the venter. *Thorsteinssonoceras ellesmerense* exhibits, at the most, a faint suggestion of weakening of ribs on the midventer of the early whorls. Although not a *Thorsteinssonoceras*, *Temnoptychites borealis* has a closer morphological resemblance to *Thorsteinssonoceras* than to any other *Temnoptychites* form known. Therefore, and because of its apparently greater age (see below in the biochronological section), *T. borealis* is considered tentatively to be a direct ancestor of *Thorsteinssonoceras* in general and of *T. ellesmerense* in particular (Textfig. 2).

Temnoptychites borealis forms part of the heavily built, mostly depressed, bullate species group of *Temnoptychites* typified by *T. hoplitoides* and including *T. rudis* Bodylevsky 1967, *T. simplicissimus* Bodylevsky 1967, *T. vylkoi* Bodylevsky 1967, *T. triptychiformis* (Nikitin 1888), *T. mokschensis* (Bogoslowsky 1902), *T. ribkinianus* (Bogoslowsky 1902), and

T. syzranicus (Pavlow 1892). Among these species, *T. borealis* resembles most closely *T. rudis* (Bodylevsky 1967, Pl. 1, figs. 1–3) and *T. vylkoi* (*ibid.*, Pl. IV, fig. 3, Pl. V, fig. 1). Of these species *T. rudis* differs markedly in the considerably coarser and more widely spaced ribbing habit at all comparable growth stages. Its holotype has only 14 primary ribs per whorl and the larger paratype reproduced in Bodylevsky's (1967) Plate 1, figure 3 has only 13 primaries. Other taxonomically significant distinctions consist of the much stronger development of the midventral smooth band in *T. rudis,* its considerably more slender inner whorls (compared with Bodylevsky's 1967, Pl. IX, figs. 1, 2 specimens of *T. borealis*) and, apparently, in its much smaller size.

Temnoptychites vylkoi (*ibid.*, p. 108, Pl. IV, fig. 3, Pl. V, fig. 1a, b) is based on a unique large, apparently adult specimen whose early and intermediate growth stages (with the exception of the smooth innermost whorl) are known only in cross-sections. The latter match closely the cross-sections of the early growth stages of *Temnoptychites rudis* (*ibid.*, Pl. I, figs. 1v, 2b), including its holotype, and it is possible that these two forms are different growth stages of one and the same species. The cross-section of the large paratype of *T. rudis* (Bodylevsky, 1967, Pl. I, fig. 3) is comparable with the cross-section of intermediate growth stages of *T. vylkoi* (*ibid.*, Pl. IV, fig. 3).

The holotype of *T. vylkoi* matches closely the Canadian representative of *T. borealis* in most of its features. However, it has an appreciably wider, ladder-shaped umbilicus which exposes about a fifth of the inner whorls and has an oblique (instead of subperpendicular) wall. Furthermore, the sculpture is appreciably coarser, the exposed whorl of the holotype being ornamented by about 14 bullaelike primary ribs. Because of the above distinctions, the writer cannot now synonymize *T. vylkoi* with *T. borealis*.

Temnoptychites simplicissimus (*ibid.*, Pl. II, figs. 2, 3) has an entirely different ribbing habit consisting of single ribs and a much stronger developed, smooth midventral band on the early growth stages.

Temnoptychites mokschensis (Bogoslowsky, 1902, p. 23, Pl. III, figs. 2, 3) differs in early replacement of the square-shaped early whorls first by more or less regularly rounded, *Temnoptychites triptychiformis*–like intermediate whorls and then by markedly rounded-triangular-shaped outer whorls combining almost straight, rapidly converging flanks with regularly arched venter.

Temnoptychites hoplitoides differs in the predominantly quadrifurcate ribbing habit of the intermediate growth stages comparable in size to the trifurcate growth stage of *T. borealis* (Bodylevsky, 1967, Pl. IV, fig. 2). In combination with the regularly rounded, *Temnoptychites triptychiformis*–like cross-section, considerably denser ribbing habit and strong development of smooth midventral band, this feature precludes the confusion of the two species concerned. The earlier, relatively slender, regularly rounded, densely ribbed whorls of *T. hoplitoides* (*ibid.*, Pl. I, fig. 4) are even more unlike the early whorls of *T. borealis*.

Temnoptychites ribkinianus (Bogoslowsky, 1902, p. 23, Pl. III, fig. 1) differs pronouncedly in the apparently complete absence of square-shaped whorl cross-sections in all known early to intermediate growth stages equivalent to those

represented by *T. borealis* specimens figured by Bodylevsky (1967, Pl. IX, figs. 1, 2). This form is probably a morphological variant of *T. triptychiformis* Nikitin 1888.

Temnoptychites triptychiformis (Nikitin, 1888, p. 97, Pl. II, figs. 4, 5; Bogoslowsky, 1902, p. 19, Pl. II, fig. 2, Pl. IV, figs 1–3; Bodylevsky, 1967, p. 105, Pl. IX, fig. 3) differs in the apparently complete absence of square-shaped whorl cross-sections in early and intermediate growth stages equivalent to those represented by the Novaya Zemlya and Canadian specimens of *T. borealis*. Furthermore this form, treated as a variant of *T. (T.) hoplitoides* below, is characterized by a much earlier appearance of trichotomous rib bundles (Bogoslowsky, 1902, Pl. II, fig. 2a), immediately followed by the quadrifurcate growth stage (*ibid.*, Pl. IV, fig. 1a), which does not occur in *T. borealis*. Finally *T. triptychiformis* lacks the forward swing of secondaries on the venter in all growth stages known.

Temnoptychites syzranicus (Pavlow, 1892, p. 521, footnote, Pl. VIII, fig. 12; Bogoslowsky, 1902, p. 21, Pl. II, fig. 6) is difficult to compare with other *Temnoptychites* forms because it is known only from two fragmentary early whorls. This species differs from the equivalent growth stages of *T. borealis* in having a considerably more slender cross-section of the whorl and in the low arched (instead of flattened) appearance of the venter.

Temnoptychites (Temnoptychites) kemperi n. sp.

Plate 1, figures 1, 3; Plate 2, figures 1–3; Plate 3, figures 1–5; Plate 4, figures 1–3; Plate 5, figures 1, 3; Plate 6, figure 2; Plate 8, figure 2; Textfigures 1S, 4

?1953 *Polyptychites (Polyptychites)* aff. *triptychiformis* Donovan, p. 103, 104, Pl. 21, fig. 1a, b
1973 *Tollia (Temnoptychites) novosemelica* (partim) Jeletzky, p. 66 (the specimen from Blackwelder Mountains section only)
1975 *Temnoptychites* ex gr. *lgowensis-syzranensis-simplex* (pro parte) Jeletzky, in Kemper, p. 248

Holotype. GSC 49312, Plate 2, figure 2A, B, Pl. 5, figure 3, Textfigure 4B.

Derivation of name. The species is named for Dr. Edwin Kemper, Bundesanstalt für Geowissenschaften und Rohstoffe, Hannover, Federal German Republic, who collected the bulk of the material studied, made excellent collections of many other early Early Cretaceous and latest Jurassic faunas of Sverdrup Basin, Canadian Arctic Archipelago, and provided the writer with important stratigraphic information.

Material and localities. The bulk of the material studied is from two adjacent fossil localities (GSC locs. 91313, 93757) on Amund Ringnes Island. GSC loc. 91313 (Kemper, 1975, p. 248, Fig. 2) has yielded 20 invariably incomplete (only two immature living chambers were seen), more or less damaged (parts of whorls missing) and slightly to fairly strongly deformed (mostly on one side only) specimens consisting of intermediate and early whorls. It also yielded eight identifiable fragments including some large (70–85 mm in whorl diameter) but still fully septate fragments. GSC loc. 93757 (Kemper, 1977, p. 3, Figs. 1, 3) has yielded 12 invariably incomplete, mostly fully septate, almost invariably strongly deformed to almost completely flattened specimens and 10 identifiable fully septate fragments. All but one of the

specimens figured in this report have been selected from the better preserved material from GSC loc. 91313. However, the range of infraspecific variation of *Temnoptychites kemperi* n. sp. is exactly the same at these two localities.

All the material was collected by Kemper in the course of field work in the Valanginian part of the Deer Bay Formation undertaken in 1974 and 1976 under the title of a joint project organized by the Geological Survey of Canada and the Bundesanstalt für Geowissenschaften und Rohstoffe, Federal German Republic. GSC loc. 91313 represents a single fossiliferous bed in a measured section of the Deer Bay Formation representing its still poorly known midbasin facies (Kemper, 1975, p. 248, Fig. 2). This fossiliferous bed is situated approximately 20 m stratigraphically above the base of the section and 230 m stratigraphically below the level at which *Polyptychites (Siberiptychites) stubendorffi* appears for the first time. The section was measured on the northern part of Amund Ringnes Island between latitudes 78°38'20"N and 78°38'35"N and longitudes 97°56'W and 97°52'W (*ibid.*, p. 248, Figs. 1, 2 for further details). GSC loc. 93757 (Kemper, 1977, p. 3, Figs. 1, 3) is from the lateral extension of the section. This locality is situated about 30 m above the base of the section and only about 20 m stratigraphically below the bed containing an abundant *Thorsteinssonoceras ellesmerense* fauna. The stratigraphic distance between GSC loc. 93757 and the oldest bed containing *Polyptychites (Siberiptychites) stubendorffi* fauna is about 130 m.

Though collected loose on the surface, all specimens and fragments of *Temnoptychites (Temnoptychites) kemperi* n. sp. found at GSC locs. 91313 and 93757 apparently were derived from the same isolated band of fossiliferous clay ironstone concretions (Kemper, *pers. com.*, 1976). They are considered therefore to be geologically contemporary and to form part of a single paleontological population. The solitary representative of *Temnoptychites (Temnoptychites) lgowensis*–like variant of *Temnoptychites (Temnoptychites) kemperi* n. sp. found in the Blackwelder Mountains section, Ellesmere Island by R. Thorsteinsson (GSC loc. 52489) represents the only other Canadian occurrence of the species known to date. The species probably is present in the Valanginian beds of Traill Island, eastern Greenland as the solitary juvenile specimen of *Polyptychites (Polyptychites)* aff. *P. (P.) triptychiformis* described and figured by Donovan (1953, p. 103, 104, Pl. 21, fig. 1) from these beds appears to represent the *Temnoptychites (Temnoptychites) triptychiformis*–like variant of *T. (T.) kemperi* n. sp.

Diagnosis. The whorl shape of early (at shell diameters less than 55–65 mm), *Temnoptychites hoplitoides*- or *T. lgowensis*–like sculptured growth stages is highly variable. It ranges from sturdy, regularly arched *Temnoptychites triptychiformis*–like shapes through intermediate *Temnoptychites hoplitoides*–like shapes to slender discuslike, *Temnoptychites lgowensis*–like shapes. The ornament, except for sparse (10–14 per whorl), prominent umbilical bullae, becomes rapidly obsolete and then completely lost at shell diameters ranging from 55 to 70 mm. Simultaneously with the loss of ribbing, the whorl cross-section becomes rounded-triangular and *Temnoptychites mokschensis*–like, with proportions ranging from somewhat wider than high to

considerably higher than wide. The resulting ribless but bullate appearance and rounded-triangular cross-section are retained to the largest known, mostly still fully septate shell diameters approaching 150 mm. At these growth stages, the previously characteristically *Temnoptychites*-like external suture line acquires very narrow lobes with long fingerlike accessory lobes and equally narrow saddles.

Measurements. The following measurements of best preserved specimens are all approximate since these are invariably slightly to appreciably deformed.

GSC no.	Figure	Diameter	Umbilicus	Height	Thickness
			mm		
Temnoptychites triptychiformis–like variant					
49308	Pl. 1, fig. 1	90	23 (0.25)	39	48
49324	Pl. 6, fig. 2	64	14 (0.21)	31	37
49321	Pl. 4, fig. 3	87	20 (0.22)	41	49
49319	Pl. 4, fig. 1	–	32	71	75
49317	Pl. 3, fig. 4	91	19 (0.20)	42	37
(middle of exposed whorl)					
Temnoptychites hoplitoides–like variant					
49312	Pl. 2, fig. 2	86	20 (0.23)	39	37
49311	Pl. 2, fig. 1	124	32 (0.25)	55	55
49315	Pl. 3, fig. 2	78	17 (0.21)	35	36
49318	Pl. 3, fig. 5	89	22 (0.24)	38	31
49310	Pl. 1, fig. 3	–	–	27	24
Temnoptychites lgowensis–like variant					
49316	Pl. 3, fig. 3	62	14 (0.22)	28	23
49313	Pl. 2, fig. 3	83	15 (0.18)	39	29
49314	Pl. 3, fig. 1	83	23 (0.27)	36	29

( ) Fraction of diameter.

Description

Suture line. The examples studied of the semiadult external suture line of the intermediate whorls (Textfigs. 1S, 4C), up to 35 mm high, closely resemble the corresponding suture lines of *Temnoptychites borealis* in the presence of four auxiliary lobes combined with almost undifferentiated character of their adumbilicalmost parts. The ventral, lateral and first auxiliary lobes and saddles of the two are all but identical in all essential features (cf. Textfigs. 3A and 4C) and the same is true of the second auxiliary saddles and second and third auxiliary lobes. The third auxiliary saddle of *T. kemperi* n. sp. (Textfig. 4C) is just as wide proportionately as that of *T. borealis*. However, the third auxiliary lobe of *T. kemperi* n. sp. is a tiny single pointed notch followed by three more even smaller notchlike lobes that cannot be differentiated into the fourth auxiliary lobe and lobules on the basis of their relative size and morphology. The middle of these three lobes, which must be the fourth auxiliary according to its position, is actually smaller than the other two. This completely undifferentiated adumbilicalmost part of the semiadult suture line matches closely that of the equivalent suture line of *T. borealis* (cf. Textfigs. 3A and 4C).

The fourth auxiliary lobe of *T. kemperi* n. sp. becomes clearly differentiated only later at the whorl diameters ranging from 40 to 45 mm. There it has the same distinctly incised, indistinctly trifid appearance as the third auxiliary lobe but it is about four fifths as long as the latter. The third auxiliary saddle is unusually wide (twice as wide as the second and 1½ times wider than the fourth), just as it is in *Temnoptychites (Temnoptychites) borealis*.

The advanced, presumably adult external suture lines of the ribless growth stage were observed only in several disconnected segments on fragments of completely smooth, still fully septate specimens with approximate whorl diameters of 75 to 80 mm (Pl. 3, fig. 4, Textfig. 4A, B, D). As reconstructed from their segments, these suture lines differ from the semiadult sutures first of all in a strong, *Temnoptychites (Costamenjaites) grandiosus*-like constriction of the stems of most or all lobes accompanied by a considerable elongation and ramification of their previously short and pointed (Textfig. 4C, E, F) lateral and terminal accessory lobes. The increased elongation and ramification of accessory lobes is equally strongly expressed in all elements of these presumably adult suture lines. However, the constriction of the lobes, generally speaking, is expressed most strongly in the auxiliary lobes and tends to decrease adventrally. The second lateral lobe is still strongly constricted while the first lateral lobe is either feebly constricted (Textfig. 4A) or not constricted at all (e.g., in the lower suture of Textfig. 4D). The ventral lobe is not known to be constricted in any of the suture lines studied.

The constriction of auxiliary and lateral lobes of the presumably adult suture line of *T. (T.) kemperi* n. sp. usually is accompanied by a slight to pronounced narrowing of some of the intervening saddles. This narrowing of the adult(?) saddles is most strongly expressed in the lateral part of these suture lines. There the first lateral saddle is considerably narrower than the first lateral lobe in all presumably adult suture lines studied (Textfig. 4A, D). This contrasts with the semiadult suture lines where the first lateral saddle is somewhat wider than or about as wide as the first lateral lobe (Textfig. 4C, E, F). This narrowing of the adult(?) saddles is much less strongly expressed in the second lateral saddle and is either feebly developed or absent in the auxiliary saddles.

The second auxiliary saddle of the ribless growth stage is not appreciably wider than the adjacent saddles (Textfig. 4D). This provides a reliable distinguishing feature from the otherwise closely matching external suture line of *Thorsteinssonoceras*. The number of auxiliary lobes (four) of the ribless growth stage does not increase in comparison with the later phase of the intermediate growth stage.

The previously regularly subtransversal (i.e., in relation to the radius of the shell) orientation of the individual lobes and the more or less regular decrease of their length and average size toward the umbilicus (Textfig. 4C, E, F) is either disturbed or largely lost in adult(?) suture lines of the ribless growth stage. The first lateral lobe may be about as long as the ventral lobe (Textfig. 4A) or considerably shorter (Textfig. 4D), whereas the second lateral lobe is about two thirds as long as the first lateral lobe. The first auxiliary lobe is appreciably to markedly inclined adventrally and its length is about three quarters that of the second lateral lobe (Textfig. 4A, D). The second auxiliary lobe is almost as long as the first. The third and fourth auxiliary lobes are almost as long as the second auxiliary, markedly denticulated and narrower than any of the preceding lobes (Textfig. 4B). Only the first lateral lobe retains the regularly trifid appearance whereas all other lobes become irregularly trifid.

No change in the overall orientation of the lateral and auxiliary parts of the external suture has been noted in the ribless and intermediate growth stages of *T. (T.) kemperi* n. sp.

3B **3A** **4B** **4A**

4E **4F** **4C** **4D**
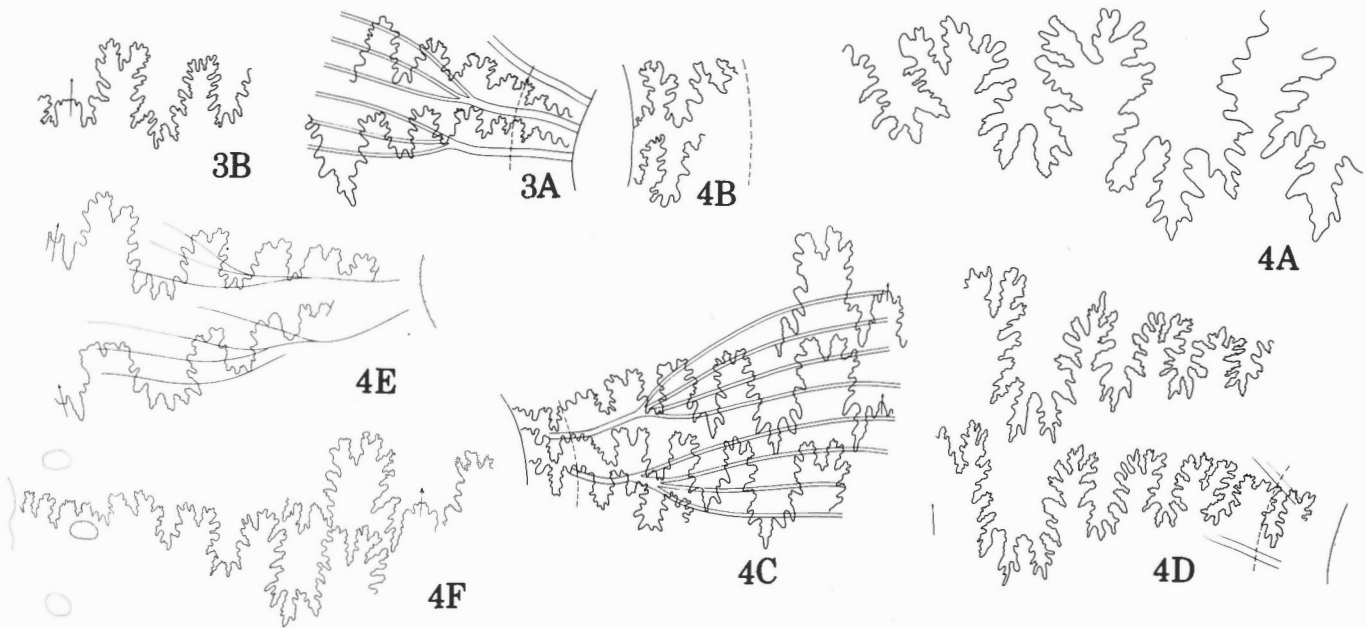
Textfigure 3. *Temnoptychites* (*Temnoptychites*) *borealis* Bodylevsky 1967. Partial external suture lines of specimen GSC 49309 reproduced in Pl. 1, fig. 2A–E. (3A) The lower of the two suture lines outlined in white in fig. 2B. (3B) Ventral and lateral parts of the fragmentary suture dimly visible on the adoralmost preserved, smooth part of the same specimen (Pl. 1, fig. 2B).

Texfigure 4. *Temnoptychites* (*Temnoptychites*) *kemperi* n. sp. (4A) Ventral and lateral parts of a suture line of unfigured large (whorl diameter about 80 mm) fragmentary specimen GSC 47508 representing the ribless but nodose growth stage of the sturdy variant of the species. The specimen is septate to the end. (4B) Adumbilicalmost parts (fifth auxiliary lobe and adjacent lobules) of two external suture lines of GSC 47508. The lower suture is the continuation of the suture line shown in fig. 4A. (4C) Three partial external suture lines of GSC 49324 reproduced in Pl. 6, fig. 2A–D. The lower of these sutures is visible in fig. 2D, reproducing the middle part of the otherwise unfigured flank of this specimen. (4D) Lateral and auxiliary parts of two adjacent, incomplete external suture lines of GSC 49317, reproduced in Pl. 3, fig. 4. These sutures are somewhat dimly visible in the middle part of that photograph closely

adapical of the pronounced construction. (4E) Two almost complete external suture lines of GSC 49315 reproduced in Pl. 3, fig. 2A–C. These suture lines, which are clearly visible in the middle parts of fig. 2A, C, are strongly weathered. This resulted in the loss of a great deal of fine detail visible in the better preserved, equivalent suture lines shown in 4C. As they are preserved, the external suture lines of GSC 49315 closely resemble those of the latest Jurassic *Craspedites* forms (cf. Textfig. 1I, J, M). (4F) Two adoralmost preserved external suture lines of the holotype GSC 49312 reproduced in Pl. 2, fig. 2 and Pl. 5, fig. 3. The preserved part of the oralmost suture complements the almost complete preceding suture line.

All suture lines of Textfigs. 3 and 4 are camera lucida drawings reproduced approximately natural size. The arrows within the ventral lobes are directed adorally. The dotted line indicates the approximate position of the umbilical shoulder while the solid line indicates the approximate position of the umbilical seam. Approximate positions of nodes and/or ribs are shown in some drawings. It was not possible to reproduce faithfully the orientation of the suture lines relative to the radius of the shell and the reader is referred to the corresponding photographs for this information.

Proportions and shape of the whorl. As indicated by the measurements and fossil plates 1 to 6, the whorl shape and proportions of *Temnoptychites kemperi* n. sp. are extremely variable. In the material studied, the shape of the early whorls ranging from about 15 to 35 mm in diameter varies from (i) sturdy, regularly rounded (flanks and venter are inseparable), invariably wider than high shapes, through (ii) feebly to moderately high oval shapes with slightly to feebly convex flanks and regularly arched venter; the whorl proportions range from slightly to appreciably higher than wide, to (iii) slender, much higher than wide, discuslike shapes.

The extreme forms i and iii are connected by more numerous (about two thirds of the material available) representatives of the intermediate form. Therefore, and because all the material presumably was collected from one and the same thin bed (see previous sections), all three forms are interpreted as morphological variants of a single polytypic paleontological species (as defined by Jeletzky, 1955, p. 485–490).

The morphologically extreme variant i is exemplified by specimens reproduced in Plate 1, figures 1, 3, Plate 3, figure 4,

Plate 4, figures 1, 3, Plate 5, figures 1, 3 and Plate 6, figure 2. It resembles closely the corresponding growth stages of *Temnoptychites triptychiformis* (see Nikitin, 1888, p. 97, Pl. 2, figs. 4, 5; Bogoslowsky, 1902, p. 19, Pl. 2, fig. 2, Pl. 4, figs. 1–3; Bodylevsky, 1967, Pl. 9, fig. 3) from Middle Russia and Novaya Zemlya. The other morphologically extreme variant iii is exemplified by specimens reproduced in Plate 2, figure 3A–B, Plate 3, figures 1A–C, 3A–C and Plate 8, figure 2. It resembles closely the somewhat smaller representatives (no larger representatives have ever been figured or described) of *Temnoptychites lgowensis* (Nikitin, 1888, p. 98, Pl. 2, figs. 6, 7) and *T.* aff. *lgowensis* (Bogoslowsky, 1902, p. 25, Pl. 1, fig. 5) from Middle Russia. The intermediate morphological variant ii, finally, is exemplified by specimens reproduced in Plate 2, figure 2A, B, Plate 3, figures 2, 5, Plate 4, figure 2 and Plate 5, figure 3. The whorl shape and proportions of most of its representatives (e.g., Pl. 3, fig. 5A, C, Pl. 4, fig. 2A, C) match closely those of the more slender, distinctly smaller representatives of *Temnoptychites hoplitoides* (Nikitin, 1888, p. 96, Pl. 2, fig. 2; Bodylevsky, 1967, Pl. 1, fig. 4) from Middle Russia and Novaya Zemlya. Others (e.g., Pl. 2, fig. 2A, B) are

transitional between this slender form of *T. hoplitoides* and its holotype (Nikitin, 1888, Pl. 2, fig. 1; Bodylevsky, 1967, p. 105, Pl. 4, fig. 2) in these two respects. However, the specimens closely matching the whorl shape and proportions of the holotype are rare in the material studied (e.g., Pl. 3, fig. 2).

It must be stressed in this connection that the range of morphological variation of the whorl shape and proportions is best documented for the growth stages with whorl diameters ranging from 20 to 30 mm. The data about earlier growth stages are limited largely to their cross-sections visible in the accidentally split larger specimens (e.g., Pl. 1, fig. 1D, Pl. 3, figs. 2B, 5B, C, Pl. 4, figs. 1B, C, D, 3B). To begin with, the preservation of all material available is extremely unfavorable for its development (extremely weathered and cracked state of specimens combined with the frequent replacement of innermost whorls by large calcite prisms). Furthermore, the earliest whorls are either strongly deformed or completely squashed even in the specimens with well preserved and slightly deformed intermediate whorls.

The whorl shapes of the *Temnoptychites triptychiformis–* and *T. hoplitoides*–like variants described above are transformed rapidly into a rounded-triangular cross-section at whorl diameters ranging from 20 to 40 mm. This rounded-triangular cross-section is characterized by only slightly convex flanks that converge rapidly but evenly adventrally from the umbilical shoulder to the broadly arched, medially flattened venter (e.g., Pl. 1, fig. 1C, D, Pl. 4, fig. 3B, C) and matches closely that of the advanced growth stages of Middle Russian *Temnoptychites mokschensis* (Bogoslowsky, 1902, p. 23. Pl. 3, Fig. 2B, C).

The time of the first appearance and the proportions of the *T. mokschensis*–like advanced cross-section vary within wide limits. However, the variation exhibits a definite trend which parallels the previously discussed variation of the whorl shape and proportions characteristic of the earlier growth stages of *T. kemperi* n. sp. In representatives of the *T. triptychiformis*–like variant, the *T. mokschensis*–like cross-section first appears at whorl diameters ranging from 20 to 25 mm and is characterized by sturdy whorl proportions which are always considerably wider than high (e.g., the whorl width of 46.5 mm vs. the height of only 37 mm in GSC 49308; see Pl. 1, fig. 1C, D). In the *Temnoptychites hoplitoides*–like variant, the *T. mokschensis*–like whorl shape first appears at whorl diameters ranging from 30 to 40 mm and is characterized by more slender proportions. Here the cross-section is invariably higher than wide (e.g., the whorl width of only 35.5 mm vs. its height of 39 mm in GSC 49315; see Pl. 3, fig. 2B). In some other specimens transitional to the *Temnoptychites lgowensis*–like variant, however, the whorl shape changes much earlier than in either of the other two variants, namely at whorl diameters ranging from 10 to 15 mm (e.g., in GSC 49318, Pl. 3, fig. 5C). In such specimens, the *T. mokschensis*–like cross-section has the same proportions as in more typical representatives of *T. hoplitoides*–like variant. In the typical representatives of the *Temnoptychites lgowensis*–like variant, finally, the whorl shape changes very little in any of the growth stages accessible to observation (cf. cross-sections of specimens GSC 49316 and 49313; see Pl. 3, fig. 3B, Pl. 2, fig. 3C). However, it is assumed that in this variant the characteristic extremely slender but nevertheless

rounded-triangular, and so *Temnoptychites mokschensis*–like, cross-section of the whorl is acquired in very early growth stages (probably at whorl diameters less than 10 mm), which are not exposed in any of the few specimens available.

The *Temnoptychites mokschensis*–like whorl section described above is retained to the largest known, still fully septate growth stages of the *T. triptychiformis*–, *T. hoplitoides*–, and *T. lgowensis*–like (e.g., Pl. 8, fig. 2) variants of *T. kemperi* n. sp., some of which have whorl diameters approaching 80 mm (e.g., Pl. 4, fig. 1B).

The shell is mostly moderately involute with the umbilicus comprising from 20 to 25 per cent of the whorl diameter. However, in some representatives of the slender *Temnoptychites lgowensis*–like variant, the umbilicus width decreases to 18 per cent of the whorl's diameter (e.g., GSC 49313). Furthermore, the width of the umbilicus in the representatives so far known of *T. lgowensis*–like variant varies more widely than that of the other variants (e.g., from 27% to 18% in GSC 49313 and 49314).

The deep (in *T. triptychiformis*–like variant) to moderately shallow (in *T. lgowensis*–like variant) umbilicus is funnellike in most known representatives of all three morphological variants of *T. kemperi* n. sp. (e.g., Pl. 1, fig. 1A, B, Pl. 3, figs. 2A, 3A, Pl. 4, figs. 1A, 2A, Pl. 6, fig. 2A). Whenever this is the case, the earlier whorls are concealed entirely or almost entirely. However, the umbilicus of some rare representatives of all three variants may become distinctly ladderlike. In such cases, one sixth (e.g., Pl. 3, fig. 5A) to one fifth (e.g., Pl. 4, fig. 3A) of the preceding whorls may be exposed in the umbilicus. The funnellike umbilicus is associated with a straight to only slightly convex umbilical wall directed either subperpendicularly to the direction of the flank or forming a 60 to 70° angle with it (e.g., Pl. 5, Fig. 1D). The umbilical shoulder tends to be well defined, albeit rounded rather than angular, in all such instances. However, there are exceptions to this rule where the deep and narrow, funnellike umbilicus is combined with distinctly convex umbilical walls and ill defined, almost regularly rounded umbilical shoulders (e.g., GSC 49313 and 49315; Pl. 2, fig. 3C, Pl. 3, fig. 2A, B).

The shallower, distinctly ladderlike umbilicus tends to be associated with a more oblique but nevertheless straight to only slightly convex umbilical wall forming a 45 to 60° angle with the direction of the flanks (e.g., Pl. 3, fig. 5A–C). The umbilical shoulder tends to be well defined but rounded rather than angular in this type of umbilicus also. However, there are exceptions to this rule as some specimens (e.g., GSC 49321, Pl. 4, fig. 3B) combine a distinctly ladderlike umbilicus with an umbilical shoulder that forms a subvertical angle with the direction of the flank. As far as is known, the umbilicus does not become more evolute in the course of ontogeny. The apparently slightly unrolled appearance of some specimens (e.g., GSC 49316, Pl. 3, fig. 3A) is believed to be caused by the slight deformation of these specimens.

Sculpture. Information about the sculpture of the earliest whorls, less than 20 mm in diameter, is extremely limited for reasons already mentioned. As indicated by a few poorly preserved examples available (e.g., Pl. 3, figs. 2B, 5B, C, Pl. 4, fig. 1C, D), the whorls with 5 to 10 mm diameters are covered by fine, closely spaced, sharp-topped, approximately radially

directed primary ribs, which mainly bifurcate on the lower third of the flank. These primaries do not seem to be thickened anywhere but may be elevated slightly just below the branching point. They either begin at the umbilical shoulder or extend onto the outer third of the umbilical wall before petering out completely. The fine, sharp-topped secondary ribs are either subradially directed throughout or become gradually but increasingly inclined forward as they approach the ventral shoulder. If the latter, they may acquire a feebly sicklelike appearance. The secondaries that are directed subradially cross the venter without or almost without forward bends (Pl. 4, fig. 1C) and the secondaries that are deflected forward form feeble to marked but broad, forward convex bends (Pl. 3, fig. 5B, C) on the venter. The subradially directed secondaries seem to be characteristic of the sturdy *Temnoptychites triptychiformis*-like whorls and the secondaries that are bent forward seem characteristic of more slender *T. hoplitoides*-like and especially *T. lgowensis*-like whorls (e.g., GSC 49316, Pl. 3, fig. 3B). However, the data available are too limited to be certain of the general validity of this observation. Regardless of the appearance of secondaries, they do not seem to become weakened, let alone interrupted, in the middle of the venter in the earliest accessible growth stage.

The earliest known instances of a distinct midventral weakening of the secondaries have been noted in the next following growth stage at whorl diameters ranging from 10 to 15 mm. This early weakening was observed in the *Temnoptychites hoplitoides*-like (e.g., specimen GSC 49314, Pl. 3, fig. 1B) and in the *T. lgowensis*-like (e.g., GSC 49316, Pl. 3, fig. 3C) representatives of the species. The density of ribbing and its general appearance at this growth stage match closely those of the early whorl of *Temnoptychites hoplitoides* partly visible inside the larger whorl reproduced in Bodylevsky (1967, Pl. I, fig. 4a, v). However, none of the fragmentary specimens available is sufficiently complete or well preserved to allow a count of primaries and secondaries per whorl.

In the still scanty material available the dichotomous ribbing habit discussed persists to whorl diameters ranging from 15 to 17 mm in all three morphological variants of the species. At any rate, this habit is invariably replaced by a trichotomous ribbing habit at whorl diameters ranging from 18 to 20 mm (Pl. 1, fig. 3B, Pl. 4, fig. 3A, Pl. 6, fig. 2A). The primary ribs become distinctly thickened and elevated (weakly bullaelike) earlier in the late dichotomous growth stage. As far as is known, the earliest distinctly bullate primary ribs appear at a whorl diameter of about 10 mm but they may appear somewhat earlier in the sturdy *Temnoptychites triptychiformis*-like forms than in the slender *T. lgowensis*-like forms. At any rate, the primaries are always markedly bullate in all known representatives of *T. kemperi* at whorl diameters ranging from 12 to 15 mm and still ornamented by bidichotomous ribs. The length of bullate primaries varies from one fifth to one third of the whorl's height in the late dichotomous growth stage. The shorter primaries appear to prevail in the sturdy *Temnoptychites triptychiformis*-like variant while the longer are more frequent in the slender *T. lgowensis*-like variant. The secondaries of the late dichotomous growth stage do not appear to differ materially from those of the previously discussed early dichotomous

growth stage, except for an invariably present but rather variably expressed (with regard to its strength) weakening in the midventer.

The trichotomous growth stage is characterized by stronger elevated and shorter, distinctly commalike, bullate primary ribs than the late dichotomous growth stage. The bullate primaries usually are restricted to the umbilical shoulder and only rarely extend for any appreciable distance upflank. However, they extend as round-topped ribs gradually attenuating adventrally across most or all of the width of the umbilical shoulder. The bullate primaries split into three fine, closely spaced secondary ribs either just above the umbilical shoulder or, more rarely, within the adumbilical fifth of the flank (Pl. 4, fig. 3A). Usually the primary splits in two with either the anterior or posterior secondary rib splitting in two again slightly higher upflank. This results in virgatitid rib bundles. However, it is not uncommon for the primary rib to branch into three secondaries right away producing fasciculate rib bundles. Some additional secondaries restricted to the upper two thirds to three quarters of the flank are intercalated between the rib bundles either singly or, very rarely, in pairs. Dichotomous rib bundles may be intercalated in some specimens between the trichotomous rib bundles. The secondary ribs do not change materially compared with the previously described earlier growth stages; as a rule they are weakened in the midventer, as in the late dichotomous growth stage. The connection between the bullate primaries and the secondaries remains distinct throughout the trichotomous growth stage in all specimens studied. As a rule, the secondaries are more definitely elevated and better delimited in the immediate proximity of the bullate primaries than farther upflank.

Judging by somewhat scanty material available (this stage was observed mainly in segments of older whorls exposed in somewhat fragmentary larger whorls; see Pl. 1, fig. 1A, Pl. 4, fig. 3A), the trichotomous growth stage is brief in all three morphological variants of *Temnoptychites kemperi* n. sp. It appears to last usually through only one third to one half of the whorl before being replaced by the quadrichotomous growth stage characterized by the prevalence of quadrichotomous rib bundles. In most specimens where the trichotomous growth stage could be observed, it ends before the whorl diameter of 25 mm. This appears to be so in all sturdy forms belonging to the *Temnoptychites triptychiformis*-like variant. However, the trichotomous growth stage may last, in some cases, through the greater part of one whorl and end at whorl diameter of about 26 to 27 mm. This was observed in one specimen transitional between the *T. hoplitoides*-like and *T. lgowensis*-like variants (GSC 49310, Pl. 1, fig. 3A) and in the most slender representative of *T. lgowensis*-like variant known (GSC 49313, Pl. 2, fig. 3B).

The quadrichotomous growth stage is abundantly represented in the material studied. This stage differs from the preceding trichotomous one mainly in the strong prevalence of quadrichotomous rib bundles. The trichotomous bundles were seen only in the initial part of this stage where they may alternate with quadrichotomous bundles.

The bullate primaries of the quadrichotomous growth stage are essentially similar to those of the trichotomous growth stage. They exhibit a regular pattern of variation

paralleling the previously described variation of the whorl shape that was observed in the quadrichotomous growth stage. In all representatives of the sturdy *Temnoptychites triptychiformis*–like variant (Pl. 1, fig. 1B, Pl. 4, fig. 3A), the primaries are developed as regular, short, strongly elevated bullae restricted to the umbilical rim. These bullae are markedly to distinctly commalike, sharp topped when shell covered but less prominent and round topped in the steinkern preservation. In the intermediate *T. hoplitoides*–like variant, the primaries tend to be more elongate and less prominent; they are developed mainly as commalike bullate ribs (Pl. 3, fig. 2A, Pl. 4, fig. 2A), even though regular bullae similar to those of the *T. triptychiformis*–like variant are present in some specimens (e.g., GSC 49312, Pl. 2, fig. 2A). In the available, somewhat scanty material of the slender, *T. lgowensis*–like variant, finally, the primaries are invariably developed as markedly thickened but only slightly to weakly elevated, straight to almost straight bullate ribs extending over the adumbilical one fifth to one quarter of the flank (e.g., GSC 49316, Pl. 3, fig. 3A). The number of primaries in the quadrichotomous growth stage (at whorl diameters from about 20 to about 40 mm) exhibits a variation pattern paralleling that of the shape of primaries. In the sturdy *T. triptychiformis*–like variant, there are 12 to 14 bullae whereas the bullate primary ribs in the slender *T. lgowensis*–like variant number 15 to 16. The representatives of the intermediate *T. hoplitoides*–like variant usually have 14 to 15 bullae per whorl but the number may increase to 16 in some representatives. The bullae (or bullate primaries) extend onto the umbilical wall as in the preceding growth stages.

The primaries give rise to four fine and closely spaced secondary ribs. As far as is known, the density and the overall appearance of secondary ribs of the quadrichotomous growth stage does not differ materially in any of the three morphological variants of *T. kemperi* n. sp. Virgatitid bundles appear to be prevalent throughout. Either the anterior or the posterior secondary may remain single in these bundles (Pl. 4, fig. 3A, Pl. 5, fig. 1A). Distinctly to indistinctly bidichotomous rib bundles (Pl. 2, fig. 2A) are common and some fasciculate rib bundles (Pl. 8, fig. 2A) were noted. One or more trichotomous rib bundles, finally, may be intercalated between the prevalent quadrichotomous rib bundles at the beginning of the quadrichotomous growth stage (Pl. 1, fig. 3B). The first three kinds of rib bundles appear to alternate irregularly throughout the duration of quadrichotomous growth stage. Some single secondaries restricted to the upper half to two thirds of the flank are intercalated between adjacent bundles.

The number of secondaries fluctuates between about 50 and at least 85 per whorl in the trichotomous and quadrichotomous growth stages alike. The variation pattern of the thickness, spacing and number of secondaries per whorl parallels, once more, the previously discussed variation pattern of the whorl shape and the appearance of primary ribs. All representatives of the sturdy *Temnoptychites triptychiformis*–like variant have the least number of secondaries per whorl (from about 50 to about 60; see Pl. 6, fig. 2A). These secondaries are somewhat heavier built and less closely spaced than those of other varieties. The representatives of the slender *T. lgowensis*–like variant have considerably more secondaries per whorl, ranging from about

65 to at least 85 (Pl. 8, fig. 2A, Pl. 3, fig. 1A), and its secondaries are noticeably finer and closer spaced than those of the sturdy variant. However, there are exceptions to this rule since the spacing and thickness of secondaries of specimen GSC 49313 (Pl. 2, fig. 3A, B) are comparable to those of most representatives of the sturdy variant. Most representatives of the intermediate *T. hoplitoides*–like variant approach the sturdy *T. triptychiformis*–like variant in the number and appearance of secondaries. However, the secondary ribs of some representatives of this variant are considerably more elevated and sharper than those of either of the other two variants and are separated from each other by considerably wider, flat-bottomed interspaces (Pl. 3, fig. 5A, Pl. 4, fig. 2A, B).

Throughout the quadrichotomous and trichotomous growth stages the secondaries gradually incline more forward as they approach the ill defined ventral shoulder. Then they cross the venter in feeble to pronounced but always broad forward bends. The forward inclination and bending of secondaries is the least developed in the sturdy *Temnoptychites triptychiformis*–like variant (Pl. 1, fig. 1C, Pl. 4, fig. 3C, Pl. 6, fig. 2B, C). In contrast, these features are the most strongly developed in the slender *T. lgowensis*–like variant, where they resemble those of *Tollia* (Pl. 3, figs. 1B, C, 3B, C, Pl. 8, fig. 2B). The intermediate *T. hoplitoides*–like variant is characterized mainly by the degree of forward inclination and bending of secondaries (e.g., GSC 49315 and 49320; Pl. 3, fig. 2C, Pl. 4, fig. 2C) comparable to that of the sturdy variant. However, there are specimens of the intermediate variant that approach closely the slender *T. lgowensis*–like variant in this respect (e.g., GSC 49312, Pl. 2, fig. 2B).

The quadrichotomous growth stage usually lasts for 1 to 1½ whorls and is followed immediately by the last known sculptural growth stage – the ribless growth stage – characterized by a complete loss of ribbing (except sometimes for fine striation) combined with the retention of strong umbilical bullae and constrictions.

The quadrichotomous growth stage grades into the ribless growth stage through a more or less protracted interval of gradual weakening of the sculpture. As in other representatives of Craspeditidae, the sculpture weakens first in the middle of the flanks. This results initially in the indistinct connection between umbilical bullae (or bullate primary ribs) and secondary ribs and then in a complete interruption of this connection within a broad median zone of the flank regardless of the shell-covered or steinkern mode of preservation (Pl. 1, fig. 1A, B, Pl. 2, figs. 2A, 3B, Pl. 4, fig. 2A). The still extant segments of secondary ribs on the upper thirds of both flanks are detached completely from the strongly developed umbilical bullae or bullate primaries in this growth stage. The bullae (or bullate primaries) become gradually stronger throughout this stage. Still farther adorally the secondary ribs disappear completely at the whorl diameters ranging from 35 to 45 mm while the umbilical bullae become even more prominent than before but considerably sparser (Pl. 2, figs. 1B, 3A, Pl. 3, fig. 4, Pl. 4, fig. 1A). This is the beginning of the final, ribless growth stage of *Temnoptychites kemperi* n. sp.

Because of the intergradation of the quadrichotomous and ribless growth stages, only the early phase of the former is characterized by the presence of well defined rib bundles

firmly attached to the oral ends of umbilical bullae. The duration of this early phase of quadrichotomous growth stage varies greatly. In some specimens belonging mainly to the sturdy *Temnoptychites triptychiformis*–like variant (e.g., GSC 49322, Pl. 5, fig. 1A) it lasts through almost the whole whorl. In other specimens belonging either to the intermediate *T. hoplitoides*–like (Pl. 2, fig. 2A) or to the slender *T. lgowensis*–like (Pl. 3, fig. 3A) variant the early quadrichotomous growth stage may last less than a quarter of a whorl. In yet other representatives of the last two variants, the weakening of the ornament in the midflank begins immediately after the end of the trichotomous growth stage (Pl. 2, fig. 3B). In the quadrichotomous growth stage the secondary ribs remain sharp-topped whenever the specimen is covered by a well preserved shell layer (e.g., Pl. 4, fig. 2A–C) but are round topped in the steinkern preservation (e.g., GSC 49310, Pl. 1, fig. 3A, B).

Constrictions were noted first in the trichotomous growth stage in some specimens (e.g., GSC 49324, Pl. 6, fig. 2A) belonging to the sturdy *Temnoptychites triptychiformis*–like variety. However, they are rare and commonly ill developed in the trichotomous and quadrichotomous growth stages, in contrast with the following ribless growth stage.

The characteristic *Temnoptychites*–like weakening of secondary ribs in the midventer is always found in better preserved specimens. However, the strength of this feature varies widely from one specimen to another and on different parts of the same specimen. A complete interruption of ribs is rare (e.g., GSC 49320, Pl. 4, fig. 2B, C); it appears to be restricted to the late phase of the quadrichotomous growth stage when the secondary ribs become confined to the upper parts of the flanks. Only a greater or lesser weakening of secondaries in the midventer was observed in the early phase of the quadrichotomous growth stage (Pl. 2, fig. 2B, Pl. 3, figs. 1B, C, 2C, 3C, Pl. 6, fig. 2B). This weakening is best developed on the shell-covered parts of the venter. However, it may be absent completely over larger parts of the whorl even in shell-covered specimens (e.g., GSC 49310, Pl. 1, fig. 3D). The representatives of the slender *T. lgowensis*–like variant devoid of this weakening may be extremely *Tollia*–like in the appearance of their upper flank and venter. However, they are easily distinguished from *Tollia* by their umbilical bullae (or bullate primaries) and the extension of characteristically quadrichotomous secondary ribs almost to the umbilical shoulder.

The previously mentioned ribless growth stage is characterized by a complete absence of secondary ribs and, on some specimens, the presence of fine, closely spaced striae (Pl. 2, fig. 1A) combined with prominent umbilical bullae. The latter essentially resemble those of the preceding quadrichotomous growth stage but are relatively more prominent and more widely spaced (e.g., GSC 49311, 49319 and 49322; Pl. 2, fig. 1B, Pl. 3, fig. 4, Pl. 4, fig. 1A, Pl. 5, fig. 1B). All known sufficiently complete specimens representing the ribless growth stage have only 10 to 12 umbilical bullae per whorl and the same seems to be true of all other less complete representatives of this growth stage. No bullate primary ribs have been observed in the ribless growth stage of the intermediate variant of *T. kemperi* n. sp. Another characteristic feature of the ribless growth stage is the almost

invariable presence (they are absent in only one specimen) and strong development of forward inclined constrictions (e.g., Pl. 3, fig. 4), which are absent or rare in the preceding growth stages of *Temnoptychites kemperi* n. sp. In the ribless growth stage, however, they number one to four per whorl.

The ribless growth stage extends to the oral ends of the largest known representatives of *T. (T.) kemperi* n. sp., the whorl diameter of which approaches 80 mm. All of these largest known ribless whorls are septate to the end and their adoralmost preserved suture lines are not distinctly crowded (e.g., Pl. 3, fig. 4, Pl. 4, fig. 1A). Therefore, the three considerably smaller representatives of the species preserved with parts of living chambers (e.g., Pl. 3, fig. 2, Pl. 4, fig. 2, Pl. 5, 1A, B) are all assumed to be prematurely deceased specimens. Consequently, the full size of *T. (T.) kemperi* n. sp. remains unknown.

Discussion. Like *Temnoptychites borealis*, *T. kemperi* n. sp. forms part of the heavily built, mostly depressed, bullate species group of the genus typified by *T. (T.) hoplitoides*. However, unlike all its previously described representatives it has a seemingly unique range of infraspecific variation, from heavily built, invariably wider than high *T. triptychiformis*–like forms to slender, discus-shaped *T. lgowensis*–like forms. These extreme morphological variants are connected by transitions and morphologically are united by an identical sequence of fine and closely spaced ribbing habits beginning with the dichotomous bundles, changing first into trichotomous and then into quadrichotomous bundles and ending with a complete loss of ribbing. Another characteristic feature of the species as a whole is the presence of umbilical bullae (including bullate primaries) in the intermediate and late (?) growth stages.

Among the previously known bullate *Temnoptychites* species, *T. kemperi* n. sp. is allied most closely with the following three Middle Russian 'species': *Temnoptychites triptychiformis* (Nikitin 1888), *T. hoplitoides* (Nikitin 1888) and *T. lgowensis* (Nikitin 1888). Judging by the range of infraspecific variation of *T. kemperi* n. sp. and the extremely close correspondence of its extreme and intermediate forms with these three Middle Russian 'species', the latter are but morphological varieties of one and the same polytypic species; they are being treated as such in this paper. So considered, the species *T. triptychiformis-hoplitoides-lgowensis* differs from *T. kemperi* n. sp. primarily in the considerably greater number of primary ribs and/or bullae at all comparable growth stages. As Bogoslowsky pointed out (1902, p. 20), *T. triptychiformis* has 17 bullate primaries and 45 secondaries at the whorl diameter of 34.5 mm. The *T. triptychiformis*–like variant of *T. kemperi* n. sp. has only 12 to 14 bullae at comparable growth stages. The holotype of *T. hoplitoides* has either 19 or 20 bullate primaries and about 60 secondaries at the whorl diameter of about 23 mm (Nikitin, 1888, Pl. II, fig. 1; Bodylevsky, 1967, p. 105, Pl. IV, fig. 2a) and the smaller paratype (Nikitin, 1888, Pl. II, fig. 2), about 19 primaries. Finally, the imperfectly preserved holotype of *T. lgowensis* (*ibid.,* fig. 6) is estimated to have about 17 primaries and about 80 secondaries at the whorl diameter of about 25 mm. The comparable growth stages of intermediate *T. hoplitoides*–like and the slender *T. lgowensis*–like variants of *T. kemperi* n. sp.

have mainly 14 to 15 primaries and are not known to have more than 16 primaries. Another distinction of *T. kemperi* n. sp. from the three Middle Russian *Temnoptychites* forms taken together consists of the considerably later appearance, much weaker development and only sporadic presence of the midventral interruption or weakening of secondary ribs. These morphological distinctions are ample for the specific differentiation of the two form groups concerned.

Another morphologically similar Middle Russian species – *Temnoptychites mokschensis* Bogoslowsky 1902 – may be indistinguishable from the *T. triptychiformis*–like variant of *T. kemperi* n. sp. in the final ribless growth stage (cf. Bogoslowsky, 1902, Pl. III, fig. 2a–c with Pl. 5, fig. 1A–E of this paper). However, the earliest growth stages of *T. mokschensis* are quite unlike those of *T. kemperi* n. sp. in the pronouncedly rounded-rectangular whorl cross-section and the much coarser and sparser appearance of primary and secondary ribs. The far-reaching similarity of the late growth stages of *T. mokschensis* to those of the *T. triptychiformis*–like variant of *T. kemperi* n. sp. is obviously caused by homeomorphy.

Temnoptychites rudis Bodylevsky 1967, *T. borealis* Bodylevsky 1967, and *T. simplicissimus* Bodylevsky 1967 (Bodylevsky, 1967, p. 103, 104, 106–108, Pl. I, figs. 1–3, Pl. II, figs. 2, 3, Pl. IX, figs. 1, 2; and in this paper) cannot be confused easily even with the sturdy *T. triptychiformis*–like variant of *T. kemperi* n. sp. because of their entirely different ornament. *Temnoptychites rudis* is ornamented by much coarser and more widely separated dichotomous ribs than the above variant of *T. kemperi* n. sp. These bundles are followed by only a few similarly coarse and widely spaced trichotomous ribs before all ribbing is lost. Furthermore, *T. rudis* has a much stronger developed, smooth band appearing earlier in the midventral zone. *Temnoptychites simplicissimus* is a similarly coarse-ribbed form which is ornamented by single ribs throughout. It also differs from this variant of *T. kemperi* n. sp. in the rounded-rectangular, flat-ventered shape of the whorl and in the stronger development of the weakening and/or interruption of ribs in the midventer. *Temnoptychites borealis* differs from the sturdy variant of *T. kemperi* n. sp. in the same way that *T. rudis* does. Furthermore it has entirely different, extremely low whorled, rounded-rectangular, flat-ventered early whorls resembling those of *Thorsteinssonoceras*.

Temnoptychites vylkoi (*ibid.*, p. 108, 109, Pl. IV, fig. 3, Pl. V, fig. 1) differs in the rounded-trapezoidal, flat-ventered cross-section of the intermediate whorls and in the absence of a quadrichotomous sculptural growth stage between the trichotomous and ribless growth stages. As is clearly visible in Bodylevsky's (1967, Pl. V, fig. 1a) photographs, the ribbing is completely lost immediately following the trichotomous growth stage.

The poorly understood *Temnoptychites syzranicus* Pavlow 1892 (p. 521, footnote, Pl. VIII, fig. 12; Bogoslowsky, 1902, p. 21, Pl. II, fig. 6) apparently cannot be distinguished from the corresponding growth stages of the sturdy *T. triptychiformis*–like variant of *T. kemperi* n. sp. where the ornament and the whorl shape are concerned (cf. Pl. 1, fig. 1D, Pl. 4, fig. 3B). However, its holotype exhibits a completely smooth midventral band which appears to be completely

absent in the corresponding growth stages of the Canadian form. It must be stressed, however, that the holotype of *T. syzranicus* is too small to be definitely identified specifically.

The holotype and only known specimen of *Temnoptychites ribkinianus* Bogoslowsky (1902, p. 23, Pl. III, fig. 1) is extremely similar to the corresponding early whorls of the sturdy *T. triptychiformis*–like variant of *T. kemperi* n. sp. (cf. Pl. 4, fig. 3B, C, Pl. 6, fig. 2A, C) in the degree of refinement and density of ribbing, presence of quadrichotomous (partly bidichotomous) bundles arising out of umbilical nodes on the last-preserved whorl, and the only local weakening of secondaries in the midventral zone of the whorl. However, all exposed whorls of *T. ribkinianus* are considerably lower and wider than the sturdiest known comparable whorl cross-sections of the Canadian form concerned. Furthermore, the secondaries of *T. ribkinianus* cross the venter transversally without any noticeable forward bends. Those of the corresponding growth stages of the Canadian form invariably form weak (Pl. 4, fig. 3C) to marked (Pl. 1, fig. 1C) forward bends on the venter. These morphological distinctions appear sufficient for a specific differentiation of the two forms concerned. However, it must be mentioned that the suture line of the *T. ribkinianus* is not known. Should the sporadic weakening of secondaries in the midventer of its only known representative be caused by weathering or other secondary factors, the customary generic assignment of *T. ribkinianus* would have to be revised.

The unique representative of *Temnoptychites prontschischtevi* Voronets (1962, p. 72, Pl. XXXVII, fig. 2) from the Anabar River area in northeastern Siberia closely resembles the intermediate growth stage of the *Temnoptychites triptychiformis*–like variant of *T. kemperi* in the shape and proportions of the whorl, the degree of coarseness of the ribbing and particularly in the shape and spacing of bullate primary ribs. The latter number about 14 per whorl and become transformed into regular commalike bullae on the adoralmost third of the preserved whorl just as in the corresponding growth stages of the *T. triptychiformis*–like variant of *T. kemperi* n. sp. (cf. Pl. 4, fig. 3A, Pl. 6, fig. 2A). However, *T. prontschischtevi* differs from this variant of *T. kemperi* n. sp. in the following:

1. The secondary ribs disappear in the broad zone occupying most of the venter (*ibid.*, Pl. XXXVII, fig. 2b) within the adoral half of the preserved whorl, which is preserved as an internal cast. None of the available specimens of the sturdy variant of *T. kemperi* n. sp. exhibits comparably strongly expressed and wide smooth medioventral band, least of all when preserved as internal casts.

2. The sculpture of the earliest preserved third of the whorl (*ibid.*, Pl. XXXVII, fig. 2a) consists predominantly of distinctly *Temnoptychites grandiosus*–like dichotomous rib bundles intercalated with single ribs extending all across the flank. Only one trichotomous rib bundle occurs in this interval and it is followed immediately by several indistinctly formed, apparently trichotomous to quadrichotomous rib bundles. The corresponding growth stages of the *Temnoptychites triptychiformis*–like variant of *T. kemperi* n. sp. are characterized by an entirely different ribbing habit consisting either of well developed trichotomous bundles alone or of the

alternation of well developed trichotomous and quadrichotomous rib bundles (see above and Pl. 6, fig. 2A).

The above morphological distinctions appear to be sufficient for the specific differentiation of *T. prontschischtevi* Voronets 1962 from *T. kemperi* n. sp. The differences of ribbing habit are believed to be particularly significant taxonomically.

Subgenus *Costamenjaites* Sazonova 1971
(= *Bodylevskyiceras* Sazonova 1971, nomen nudum)

Type species: *Costamenjaites jucundus* Sazonova 1971. Original designation by Sazonova (1971, p. 83).

Diagnosis. The original diagnosis of Sazonova (*ibid.*; writer's translation from Russian) is as follows: "An involute shell of intermediate size. The cross-section is an oval elongated in the direction of the diameter and attenuated in the upper part. The primary ribs are protruding, sharpened and feebly inclined forward to the diameter of 50 mm. In the lower part of the flanks they split into a bundle consisting of three to four and sometimes of up to six ribs. The marginal ribs of the bundles are indistinctly attached to the primaries. Some bundles have a bidichotomous structure. As the shell grows the ribs disappear throughout its surface including the ventral side. The suture line consists of four lateral lobes, two of which are situated on the lateral side while the third is situated on the umbilical shoulder and the fourth(?) on the umbilical wall. The saddles are very broad and rounded."

Discussion. The preceding diagnosis is incomplete and partly misleading. As pointed out in the discussion of the genus *Temnoptychites* (p. 10), the secondary ribs of both *Costamenjaites* species described by Sazonova actually become weakened or interrupted on the venter well before the rest of the ribbing fades out. Furthermore, the statement regarding the presence of only four lateral lobes conflicts with the following statement made by Sazonova (1971, p. 83, 84) under the discussion of the affinites of *Costamenjaites* (writer's translation from Russian): "These ammonites were apparently ancestral also to the genus *Bodylevskyiceras* which lived in the sea of the '*hoplitoides*' time. This is indicated by the comparison of the development of the suture lines of *Costamenjaites* (see Pl. XXVI, figs. 8, 10, 10a) and *Bodylevskyiceras* (see Pl. XXIV, fig. 16). The suture line of the latter has more narrow lobes and saddles and is bent archlike but the number of lateral lobes is the same." None of the *Costamenjaites* suture lines reproduced by Sazonova (1971, Pl. XXVI, figs. 6, 8, 10, 10a) is sufficiently complete to count the total lateral and auxiliary lobes. However, *Bodylevskyiceras elegans* referred to in the above quotation does have four auxiliary lobes (Bodylevsky, 1967, p. 104, Pl. III, fig. 1a, Pl. IV, fig. 1a). Hence the same is assumed to be true of *Costamenjaites* and the contrary statement made in the generic diagnosis must be some kind of *lapsus calami*. Most likely one should read 'four auxiliary' instead of 'four lateral' lobes. However, this definition is not correct either as the number of auxiliary lobes is known to vary from four to five in adult suture lines of some *Costamenjaites* species (e.g., in *T. troelseni* n. sp.; see below).

Because of these defects of the generic diagnosis of *Costamenjaites* and the rather poor quality of most of its

photographs published by Sazonova (1971), the writer would much prefer to suppress this name in favour of the generically and subgenerically synonymous (p. 9–11) name *Bodylevskyiceras* proposed in the same publication (Sazonova, 1971, p. 74, 83, 84, 87) for the excellently described and figured *Temnoptychites elegans* Bodylevsky 1949. However, this cannot be done since the genus *Bodylevskyiceras* is a *nomen nudum* under the Code of Zoological Nomenclature. Although she cites *T. elegans* as the example of this genus, Sazonova (*loc. cit.*) does not designate this species as its genotype as required under Article 13a of the Code.

Temnoptychites (Costamenjaites) grandiosus Voronets 1962

Plate 7, figure 1; Textfigure 5

1902 *Olcostephanus* n. sp. aff. *simplex* Bogoslowsky, p. 60, Pl. XIV, fig. 7a–c
1913 *Olcostephanus simplex* Sokolov, p. 78, Pl. 3, fig. 1
1924 *Tollia simplex* Salfeld and Frebold, p. 7, Pl. IV, fig. 1
1949 *Temnoptychites simplex* Bodylevsky, p. 201, 202, Pl. LIV, fig. 3a, b, Fig. 26
1954 *Tollia* cf. *tolli* (partim) C. W. Wright, in Troelsen, p. 16
1962 *Temnoptychites grandiosus* Voronets, p. 73, Pl. XXXVIII, figs. 1, 2, Pl. XLVII, fig. 1, Pl. L, fig. 1
1964 *Tollia (Temnoptychites) simplex* Jeletzky, p. 38, Pl. V, fig. 3A–E
1967 *Temnoptychites simplex* subsp. *inflatus* Bodylevsky, p. 106, Pl. VI, figs. 1, 2, Pl. VII, figs. 1, 2, Pl. VIII, fig. 1
1972 *Temnoptychites grandis* Klimova, in Golbert, *et al.*, p. 154–156, Pl. II, fig. 1, Pl. III, fig. 1, Pl. IV, fig. 1
1973 *Tollia (Temnoptychites) simplex* var. *grandiosus* Jeletzky, p. 63, 64

Holotype. Giant specimen from northern Siberia, Pronchistchev Range, figured by Voronets (1962, p. 73, Pl. XXXVIII, figs. 1, 2, Pl. XLVII, fig. 1, Pl. L, fig. 1) (by monotypy).

Material and locality. The only known Canadian representative of *Temnoptychites grandiosus* (Voronets 1962) was collected by J.C. Troelsen (then Curator of Mineralogisk-geologisk Institut, University of Copenhagen) in 1952 during a geological reconnaissance trip to Ellesmere Island sponsored by the Arctic Institute of North America, Montreal, Canada.

This ammonite formed part of an originally unidentified ammonite collection (Troelsen, 1952, p. 208). The ammonites of this collection later were identified summarily as *Tollia* cf. *T. tolli* Pavlow by C.W. Wright, London, England in an unpublished terminal report of J.C. Troelsen (1954, p. 16). The ammonite collection concerned eventually was turned over to the Geological Survey of Canada and assigned the locality number GSC 24075. The fossil locality was recorded as situated in the bed of Reptile Creek, 3.2 to 4 km northeast of Eureka Weather Station, Slidre Fiord, Ellesmere Island.

The ammonite subsequently was reidentified by Jeletzky (1964, p. 38, Pl. V, fig. 3A–E) as *Tollia (Temnoptychites) simplex* (Bogoslowsky 1902) while the bulk of the ammonite collection was reidentified as *Tollia (Temnoptychites) novosemelica* (Jeletzky, 1964, p. 38, Pl. V, figs. 1, 4). It is not known whether or not this unique Canadian representative of *T. simplex* was found in exactly the same bed with the bulk of the ammonite collection at GSC loc. 24075. However, this is most likely since the subsequent, more numerous fossil collection at GSC loc. 28713 made by R. Thorsteinsson from

what appears to be the same section and locality yielded a very similar ammonite fauna consisting of ammonites then identified by the writer as numerous representatives of *Tollia* (*Temnoptychites*) *novosemelica* (Sokolov 1913), two fragmentary specimens of *Tollia tolli* Pavlow 1914, and one specimen of *T.* aff. *T. grandiosus* Voronets 1962.

Thorsteinsson's fossil locality GSC 28713 is shown as loc. 144 on GSC Map 1298A, where the Reptile Creek is renamed as Weather Station Creek; it is recorded as follows: "Arctic Reptile Creek, Slidre Fiord, Ellesmere Island. About 1 mile directly north of airstrip."

According to the geological profile compiled by Tozer (see Thorsteinsson and Tozer, in Douglas *et al.*, 1970, p. 581, Fig. X-12), GSC locs. 24075 and 28713 occur at about the middle of the Deer Bay Formation as developed in the Weather Station Syncline. Neither the exact stratigraphic position of these fossil localities nor the stratigraphic relationships of their *Tollia*–nodeless *Temnoptychites* (*Costamenjaites*) fauna with other Valanginian and Berriasian ammonite faunas of Sverdrup Basin are known. However, this fauna is inferred to be from the equivalents of the lowermost Valanginian Undulatoplicatilis Zone for reasons explained below in the biochronological section (Textfig. 8).

Historical remarks. The unique original specimen of *Olcostephanus simplex* described and figured by Bogoslowsky (1902, p. 56, Pl. XIV, fig. 6a–d) from a boulder in Pechora Basin, was considered until recently a juvenile representative of *Temnoptychites* that had not yet developed the characteristic interruption of secondary ribs in the middle of the venter (e.g., Bodylevsky, 1967, p. 107). This idea led to the persistent identification of the similarly ornamented but much larger and more sturdily built *Temnoptychites* form from glacial boulders on Novaya Zemlya with the Middle Russian *Olcostephanus simplex* Bogoslowsky 1902 (e.g., Sokolov, 1913; Salfeld and Frebold, 1924). This *"Temnoptychites simplex"* was named formally *T. simplex* subsp. *inflatus* by Bodylevsky (1967, p. 106, 107, Pl. VI, figs. 1, 2, Pl. VII, figs. 1, 2, Pl. VIII, fig. 1) because of the above-mentioned morphological distinctions from Bogoslowsky's (1902) original of *O. simplex*.

Recent investigations of Sazonova (1971, p. 41–43, Pl. II, fig. 4, Pl. V, fig. 3, Pl. X, fig. 3, Pl. XIX, fig. 3, Pl. XX, fig. 3, Pl. XXVI, fig. 7) revealed the common occurrence of *Olcostephanus simplex* Bogoslowsky 1902 in the late Berriasian (Spasskensis Zone) and basal Valanginian (Undulatoplicatilis Zone) of the Ssura Basin. Sazonova's (*loc. cit.*, Pl. XX, fig. 3) material of the species included large specimens with shell diameter of 80 mm which were devoid of any weakening, let alone interruption, of secondary ribs in the midventer. *Olcostephanus simplex* was assigned, therefore, to the genus *Surites* Sazonov 1951 and *Temnoptychites simplex inflatus* Bodylevsky 1967 was treated as an appreciably younger (Hoplitoides Zone) homeomorphic representative of *Temnoptychites* Pavlow 1914 to which a full specific status was accorded. Except for the Hoplitoides zonal dating of *T. simplex inflatus*, these conclusions of Sazonova (1971, p. 42, 43) are accepted tentatively in this report as valid in spite of the fact that *O. simplex* and *O.* aff. *O. simplex* of Bogoslowsky (1902, p. 60) have been obtained from the same boulder at the mouth of Ussa River. However, *Temnoptychites inflatus*

Bodylevsky 1967 is a subjective junior synonym of *Temnoptychites grandiosus* Voronets 1962, in the writer's opinion, which necessitates the corresponding renaming of the Canadian specimen described here and previously assigned to *T. simplex* (see above in the synonymy).

Concept of species and synonymy. In the writer's opinion, the species *Temnoptychites* (*Costamenjaites*) *grandiosus* Voronets 1962 is characterized by the combination of a somewhat sturdy to moderately slender, generally discuslike and moderately narrowly to narrowly umbilicated (15–30%) whorl with fairly long (two fifths to one half of the whorl's height), prominent but fine, widely to moderately spaced, *Tollia*-like primary ribs in all ornamented growth stages. The primaries subdivide exclusively, or at least predominantly, dichotomously until shell diameters reach 45 to 55 mm. This uniquely prolonged simple dichotomous growth stage is followed by a brief (one half to one whorl) indistinctly trichotomous growth stage, which is followed by a growth stage in which the ornamentation completely disappears. Umbilical bullae or bullate ribs are absent at all growth stages and the rapidly adventrally converging whorl flanks are either slightly or feebly convex. The final, entirely smooth growth stage extends over two or more whorls, which may result in very large shells. For example, the holotype of *T. grandiosus* Voronets 1962 with the smooth, fully septate shell reaches a diameter of at least 260 mm and so does the holotype of *T. grandis* Klimova 1972.

As defined above *Temnoptychites grandiosus* is a morphologically unique representative of the subgenus *Costamenjaites*. It is entirely isolated morphologically from all other known representatives of this subgenus and cannot be confused with any of them. The sculptured inner whorls of the northern Siberian holotype of *T. grandiosus* differ only from the equivalent inner whorls of the Novaya Zemlya representatives of the species (*T. inflatus* Bodylevsky 1967) in (Voronets, 1962, p. 73): "the trapezoidally-shaped cross-section, a more narrow umbilicus, and a more coarse sculpture," and is only an extreme morphological variant of the latter species. *Temnoptychites grandis*, recently described from the Polar Transuralian region by Klimova (in Golbert, *et al.*, 1972, p. 154–156, Pl. II, fig. 1, Pl. III, fig. 1, Pl. IV, fig. 1) is another junior synonym of *T.* (*C.*) *grandiosus*, in the writer's opinion. As noted by Klimova (*loc. cit.*, p. 156), this form resembles *T.* (*C.*) *grandiosus* very closely in its large dimensions, early disappearance of sculpture and character of the suture line. The only distinctions noted by Klimova (*loc. cit.*) consist of: "a wider umbilicus, a broader cross-section, a greater number of secondary ribs per one umbilical rib and less coarse ribs." All these distinctions are extremely trivial and in the writer's opinion fall within the individual variability of the species. The holotype of *T. grandis* particularly indicates this because it is clearly intermediate in all of the morphological features between the holotype of *T.* (*C.*) *grandiosus* and some of its Novaya Zemlya representatives described by Sokolov (1913) and Bodylevsky (1967). As pointed out in the following description of the Canadian specimen, the holotype of *T. grandis* resembles most closely the Canadian representative of *T.* (*C.*) *grandiosus* in these same morphological features. The discovery of *T.* (*C.*)

grandiosus in the Polar Transuralian region points once more to an extremely wide geographical range, and hence an outstanding biochronological value, of this presumably early early Valanginian (*Pseudogarnieria undulatoplicatilis* Zone; see Textfig. 8) index species.

Description of Canadian representative of T. grandiosus. The unique specimen GSC 17173 from Ellesmere Island has the following dimensions at the place where the dichotomous growth stage ends: shell diameter, 49 mm (approx.); whorl height, 25 mm (est.); whorl width, 20 mm (est.); width of the umbilicus, 13.5 mm (approx.); involution index (the umbilicus in per cent of shell diameter), 27 per cent (approx.). The same measurements at the oralmost end of the shell are: shell diameter, 114 mm (approx.); whorl height, 54 mm (approx.); whorl width, 39 mm (est.); width of the umbilicus, 27 mm (est.); involution index, 24 per cent (est.). All measurements are only approximate to estimated since the specimen consists of a complete but partly deformed intermediate whorl representing the late part of the ribbed growth stage of the species and parts of the next following, also partly deformed, still fully septate intermediate whorl representing the transition between the ribbed and the entirely smooth growth stages and the very beginning of the latter stage. The dichotomous growth stage lasts from the earliest visible part of the inner whorl with a diameter of about 17 mm (est.) to its middle part with a diameter of about 25 mm (est.). This part of the shell (Pl. 7, fig. 1A, D) is ornamented with prominent but fine and distinctly pinched, *Tollia*-like primary ribs, which are sharp topped in the shell-covered and steinkern preservation alike. These primaries begin as faint ribs on the innermost part of the umbilical wall; they gradually thicken and become more elevated toward the umbilical shoulder and reach full strength thereabouts. On the umbilical shoulder the primaries are inclined distinctly backward, only to become subradial or weakly inclined forward just above the umbilical shoulder. This course of primaries is maintained over the lower two fifths of the flank to their bifurcation points. The secondary ribs are exactly like the primaries in strength and appearance and are attached firmly to them. The secondaries become progressively more inclined forward as they approach the narrowly rounded venter until they begin to form acute angles with the plane of symmetry of the whorl on both sides of the venter. This results in the pronounced forward bends of the secondaries on the venter and their chevronlike appearance (Pl. 7, fig. 1C, F). The secondaries weaken abruptly and then all but disappear in the middle part of the venter, forming a narrow, semismooth to almost smooth band there. There are 9 to 10 primaries and about 19 secondaries on the half whorl discussed here, which suggests 19 to 20 primaries and 38 to 39 secondaries per complete whorl of the dichotomous growth stage of our specimen.

All sculptural features match very closely those visible in the corresponding growth stages of specimens of *T. grandiosus* reproduced by Bodylevsky (1967, Pl. VII, fig. 2a, b).

At the whorl diameter of about 25 mm (est.), corresponding to the shell diameter of about 50 mm (est.), the dichotomous rib bundles are replaced by trichotomous bundles. The primaries and secondaries of the earliest four or five trichotomous bundles are similar to those previously described in strength and appearance, except that all ribs are considerably closer spaced (Pl. 7, fig. 1B, D). The secondaries remain firmly attached to the primaries in these bundles. The strong forward bends of secondaries on the venter are chevronlike and they notably weaken or almost completely disappear in the midventer, as in the dichotomous growth stage (Pl. 7, fig. 1F).

The late phase of trichotomous growth stage, visible about a half whorl later (after a completely covered interval) at the whorl diameter of about 30 mm (est.), is characterized by subdued sculpture on the midflank contrasting with the continuing prominence of the lower parts of the still fine and sharp-topped primaries and the similar prominence of the forward-inclined upper parts of secondaries. The chevronlike forward bends of the secondaries at the ventral shoulders and their pronounced weakening to almost complete interruption on the midventer persist unchanged. The sculpture must continue to weaken rapidly and disappear almost completely within the next following, now missing, fifth of the whorl because the next-preserved segment of the whorl, beginning with whorl diameter of about 40 mm (est.) (Pl. 7, fig. 1A), is smooth except for faint vestiges of fine and *Tollia*-like primary ribs just above the umbilical shoulder and barely discernible traces of secondary ribs at the ventrolateral shoulder. These vestiges of sculpture disappear completely about one quarter of the whorl later. The preserved parts of the remaining oralmost segment of the outer whorl are completely smooth (Pl. 7, fig. 1A).

A pronounced forward-inclined constriction occurs on the earliest exposed part of the inner whorl (Pl. 7, fig. 1D) and another similarly inclined, well defined constriction occurs at the end of the earliest third of the outer whorl (Pl. 7, fig. 1A).

Most of the visible details of the trichotomous and entirely smooth growth stages of the Canadian specimen agree closely with those visible in the corresponding growth stages of larger specimens of *Temnoptychites grandiosus* figured by Bodylevsky (1967, Pl. VI, fig. 1b, Pl. VII, fig. 1a, Pl. VIII, fig. 1). The ribbing of the trichotomous growth stage is appreciably denser than that of the corresponding growth stages of Bodylevsky's (*ibid.*) specimens. However, it matches fairly closely the density of trichotomous ribbing of the specimen from Novaya Zemlya figured by Sokolov (1913, Pl. 3, fig. 1a, b).

The considerably higher than wide (see measurements), rounded-angular, essentially flat-flanked cross-section of the inner whorl visible in Plate 7, figure 1F seems to be considerably more slender than the cross-sections of all known comparably large whorls of *Temnoptychites grandiosus* figured by Sokolov (*ibid.*, fig. 1b), Salfeld and Frebold (1924, Pl. IV, fig. 1a), Bodylevsky (1967, Pl. VI, fig. 1a, Pl. VII, figs. 1a, 2b) and Voronets (1962, Pl. L, fig. 1b). However, this cross-section is strongly deformed laterally so as to appear considerably more slender, more narrow-ventered, and essentially flat-flanked (instead of weakly convex) than it actually is. Some other relatively little to almost undeformed cross-sections of the same whorl (Pl. 7, fig. 1G) indicate that its original cross-section matched closely the cross-section of the equally large inner whorl of *T. grandiosus* illustrated by Voronets (*loc. cit.*) in all taxonomically important respects.

The virtually undeformed cross-section of the outer whorl

of the Canadian specimen (Pl. 7, fig. 1C) is comparable to the cross-section of the equally large next outer whorl of *T. grandiosus* illustrated by Voronets (*loc. cit.*) in all taxonomically important aspects such as the whorl proportions, an only slightly convex appearance of rapidly adorally converging flanks of the whorl, and the narrowly rounded appearance of the venter.

The shell is involute with the somewhat deformed umbilicus comprising from 24 to 27 per cent of the whorl diameter (see measurements). On the best preserved side of the shell, the moderately deep, narrow umbilicus is funnellike, covers the preceding whorls almost entirely, and does not become more evolute in the course of the preserved part of the ontogeny (Pl. 7, fig 1A). The slightly more evolute, weakly steplike appearance of the umbilicus on the other side of the shell (Pl. 7, fig. 1B), is believed to be the result of a slight deformation. The slightly convex umbilical walls are inclined outward at about 30 to 35 degrees and form an almost 90 degree angle with the flanks wherever they are least deformed. However, the umbilical shoulder is rounded narrowly rather than truly angular. All these features match closely the corresponding features of previously described representatives of *T. grandiosus* from Novaya Zemlya.

The semiadult external suture line of the inner whorl is essentially *Surites*- and *Praetollia*-like (Textfig. 5C). However, it differs from the suture lines of comparably large intermediate whorls of previously discussed representatives of *Temnoptychites* (*Temnoptychites*) *kemperi* n. sp. (Textfig. 4C, E, F) and *T.* (*T.*) *borealis* (Textfig. 3A) in several respects. The first lateral lobe is slightly shorter than the ventral lobe. Unlike the equivalent first lateral lobes of nodose *Temnoptychites* species, this lobe is appreciably narrower in the adoral part compared with the adapical part and its terminal (adapicalmost) accessory lobes are long, slender and directed backward (Pl. 7, fig. 1E, F, Textfig. 5C). The lobe is almost regularly trifid. The first lateral saddle also is peculiar in being from 1½ to 2 times broader than the first lateral lobe and markedly widened adorally instead of approximately square.

The second lateral lobe is only slightly more than half as long as the first lateral lobe. This unusually narrow lobe is approximately parallel sided but the irregularly shaped (irregularly bifid rather than irregularly trifid) terminal accessory lobes are distinctly larger than the lateral accessory lobes. This deprives the second lateral lobe of the square shape characteristic of nodose *Temnoptychites* species. The second lateral saddle is only slightly wider than the second lateral lobe and distinctly widened adorally instead of square.

The first auxiliary lobe is shaped and proportioned approximately like the second lateral lobe but is about three quarters as long. The first auxiliary saddle is only slightly wider than the second lateral saddle and is similarly shaped.

The second auxiliary lobe is about three fifths as long as the preceding auxiliary. This even more slenderly proportioned lobe is shaped much like the preceding two lobes, except for being almost regularly trifid (Textfig. 5C). Unlike the preceding two saddles the second auxiliary saddle is twice as wide as any of the adjoining lobes and is subdivided into three parts by two lobules. The distinctly aberrant, somewhat *Thorsteinssonoceras*-like appearance of this saddle appears to

be a 'prophetic' feature in the sense of Pavlow (1901, p. 62, 63) since it is largely lost in the later growth stages (see below).

The very slender, still frilled third auxiliary lobe differs from the second auxiliary lobe only in its length, which is about three quarters that of the latter. This auxiliary lobe is situated almost exactly on the umbilical shoulder in the growth stage beginning with the whorl diameter of about 17 mm. However, it occurs in the middle part of the umbilical wall in the earlier growth stages visible in the umbilicus of the inner whorl. The almost regularly square-shaped third auxiliary saddle is even wider, relatively speaking, than the second auxiliary saddle. It is 2½ to 3 times wider than the adjoining auxiliary lobes (Textfig. 5C).

The fourth and last auxiliary lobe is a tiny, hardly indented and single-pointed, tacklike structure about half as long as the third auxiliary lobe. In the growth stage discussed herein it is situated in the middle of the umbilical wall and is followed by a still smaller lobule visible at the umbilical seam (Textfig. 5C). The fourth auxiliary saddle is again approximately square but somewhat narrower than the third auxiliary saddle.

The semiadult external suture line described above closely resembles the much more advanced, presumably adult suture lines of *Temnoptychites* (*Temnoptychites*) *kemperi* n. sp. (Textfig. 4A, B, D) in the adoral constriction and the mode of denticulation of its lobes. However, this semiadult suture has relatively much wider saddles than the latter sutures. Furthermore this suture is more strongly ascendant throughout than semiadult and presumably adult suture lines of *T.* (*T.*) *kemperi* n. sp. Except for the part nearest the umbilicus confined to the third and fourth auxiliary lobes and situated entirely on the umbilical wall, the all but straight suture line forms an angle of about 30 degrees with the radius of the shell. The imaginary line connecting the tops of both lateral lobes and those of the first and second auxiliary lobes is consequently almost straight (Textfig. 5C). Though somewhat deflected backward in comparison with the rest of the external suture line, the part nearest the umbilicus remains slightly ascendant to the umbilical seam, forming an angle of 10 to 15 degrees with the radius of the shell. The change in direction of these two parts of the suture line is gradual rather than abrupt.

The suture line described above does not change materially to the adoralmost preserved part of the outer whorl, as indicated by two complimentary segments of the external suture line exposed on the flanks and venter of the latter (cf. Pl. 7, fig. 1E with Pl. 7, fig. 1A, B, Textfig. 5A, B). Except that all elements of this advanced suture line are proportionately larger and indented deeper, it differs from the semiadult suture line only in the relatively narrower proportions of the second auxiliary saddle (which has largely lost its previously somewhat *Thorsteinssonoceras*-like appearance) and in the appearance of one additional, fifth auxiliary lobe and a lobule between the fifth auxiliary lobe and the umbilical seam (Textfig. 5A). This almost complete absence of significant ontogenic changes in the external suture line of the Canadian representative of *Temnoptychites grandiosus* appears to be because the species grew regularly to a huge size comparable with that of the holotype. This is indicated by a rather different appearance of adult external suture lines of the Polar

Transuralian representative of *T. (C.) grandiosus* (see Klimova, in Golbert *et al.*, 1972, Pl. II, figs. 1, 1a, Pl. IV, fig. 1). This adult suture line resembles very closely the advanced, presumably adult suture lines of *T. (T.) kemperi* n. sp. (Textfig. 4A, E) in the constricted and wavy appearance of the lobes, their abundant and deep indentation, and in the narrow, adorally widening appearance of both lateral saddles and the first auxiliary saddle.

The only evident peculiarity of the Canadian representative of *Temnoptychites grandiosus* consists in its combining the relatively fine and closely spaced ribbing habit comparable to that of the morphologically extreme representative of *T. grandiosus* figured by Sokolov (1913, Pl. 3, fig. 1a, b) with the relatively slender whorl shape and proportions lacking in the sturdy variant, but present in equivalent intermediate whorls of the much coarser and more distantly ribbed holotype of *T. grandiosus*. It shares all of these morphological features with the Polar Transuralian representative of the species described as *T. grandis* by Klimova (in Golbert *et al.*, 1972, p. 154–156, Pl. II, fig. 1, Pl. III, fig. 1, Pl. IV, fig. 1). The writer does not doubt that this new combination of morphological characters is of an infraspecific rank only. As yet there does not seem to be any reason to introduce even a new subspecific name for the Canadian representative of *T. grandiosus* and its Polar Transuralian counterpart.

Discussion. Because of the previously mentioned unique morphology of *Temnoptychites grandiosus,* there is no need to compare this species with any of the foreign nodeless *Temnoptychites* species belonging to the subgenus *Costamenjaites* and recognized to be valid in this paper. The distinctions of *T. grandiosus* from the only other Canadian nodeless species, *Temnoptychites troelseni* n. sp. will be discussed in the description of the latter.

Temnoptychites (Costamenjaites)
aff. *T. (C.) grandiosus* Voronets 1962

Plate 7, figure 2

Material and locality. One fragmentary, somewhat deformed specimen GSC 49325, from GSC locality 28713. It consists of about one third of the ultimate whorl (almost entirely the early part of the adult living chamber) which conceals almost entirely the corresponding parts of partly squashed early whorls. The discussion of the material and locality of *T. grandiosus* gives further information about GSC loc. 28713.

Measurement. The best preserved intermediate (second earliest discernible; see Pl. 7, fig. 2A, C) whorl has the following measurements (approx.): shell diameter, 42.5 mm; whorl's height (at the oral end), 20 mm; whorl's width (the same place), 16 mm; width of the umbilicus, 11 mm; coefficient of involution, 22 per cent. The oral end of the living chamber has the following measurements: shell diameter cannot be measured but is assumed to be in order of 105 mm; whorl height, 51 mm; whorl width, 35 mm; width of the umbilicus (est.), 17 mm.

Description. The earliest clearly discernible whorl is visible only in cross-section (Pl. 7, fig. 2C), which is too distorted to

be described. An uncertain number of still earlier whorls are completely squashed.

The earliest reasonably well preserved whorl (see measurements) is somewhat deformed laterally. Allowing for postmortem deformation, the shape and proportions of this moderately sturdy, higher than wide whorl would be comparable to those of the equivalent whorls of *Temnoptychites grandiosus* figured by Bodylevsky (1967, Pl. VI, fig. 2v, g) and the writer (Pl. 7, fig. 1D, F). The short exposed segment of the earliest visible whorl (Pl. 7, fig. 2A) is ornamented to the oral end by dichotomous ribs closely resembling those of *T. grandiosus* in strength and orientation. The long (*Tollia*-like), prominent but pinched and entirely nonbullate primaries are sharp topped in the shell-covered and steinkern preservation. They begin at the umbilical seam and cross the umbilical wall on a somewhat backward directed course, gradually thickening toward the umbilical shoulder. At the umbilical shoulder, the primary ribs swing into a subradial to slightly adoral direction and continue on this course across the lower three fifths of the flank before splitting into two similarly prominent and pinched secondary ribs. There is no weakening of ribs in the midflank and the secondaries are firmly attached to the primaries. The sharp-topped, secondary ribs become progressively more and more inclined adorally as they approach the venter until they form an angle of about 35 to 40 degrees with the plane of symmetry of the shell at the ill defined ventral shoulder. The secondaries cross the venter on this course forming sharp chevronlike, forward-directed bends there (Pl. 7, fig. 2D); as far as one can tell, they are weakened only slightly on the exposed part of the midventer at the exposed adoralmost part of the whorl discussed herein. The primaries and secondaries closely match those of the equivalent whorl of *T. grandiosus* mentioned above (see Bodylevsky, 1967, Pl. VI, fig. 2a) in strength and appearance. However, they are considerably more closely spaced and the primary ribs are considerably longer. None of the primaries on the whorl of *T. grandiosus* is longer than one half of the flank and some of them are considerably shorter.

The next adoral whorl of our specimen is too deformed for its shape and proportions to be described. However, it apparently had originally somewhat more slender, appreciably higher than wide proportions similar to those of the more advanced whorls of *T. grandiosus*. The sculpture of this, still completely septate, penultimate whorl is exposed somewhat imperfectly in its short oralmost segment (Pl. 7, fig. 2A). As far as one can tell, it consists of indistinctly trifurcating rib bundles. The still nonbullate primaries are just as long as those of the preceding whorl and resemble the latter closely in every other respect. The same is true of the secondary ribs, except that the third secondary rib is attached only indistinctly to the primary rib in the only completely visible bundle. The midventer is too poorly exposed to say whether or not the ribs are weakened there. There is no appreciable weakening of the ribs in the midflank.

The strength and spacing of the ribs on the oralmost part of the penultimate whorl match closely those of indistinctly trichotomous rib bundles on the oralmost end of the specimen of *T. (C.) grandiosus* figured by Sokolov (1913, Pl. 3, fig. 1).

The preserved part of the ultimate whorl is smooth, except for very weakly expressed basal parts of two or three

only slightly thickened primary ribs on its apicalmost part and a well developed constriction inclined forward on its oralmost part (Pl. 7, fig. 2A). Except for the apicalmost 2.5 cm or so, the preserved part of this whorl is occupied by the living chamber. The shape and proportions of this somewhat deformed whorl do not seem to differ materially from those of the Canadian specimen of *T. grandiosus* if one restores mentally the lower parts of its flanks to their approximate original position.

The moderately deep, narrow umbilicus of the best preserved whorl fragments has vertical to subvertical but slightly to markedly (on the outermost whorl) convex walls. Except for the squashed innermost whorls, the inner whorls are covered completely by the subsequent whorls in this strongly involute umbilicus.

The parts of external suture lines visible on the exposed part of the intermediate, indistinctly trichotomously ribbed whorl (Pl. 7, fig. 2A) duplicate the corresponding parts of equivalent suture lines of the Canadian representative of *T. grandiosus*. The mainly poorly preserved auxiliary parts of the adoralmost three or four external suture lines visible on apicalmost segments of both flanks of the smooth outer whorl (Pl. 7, fig. 2A) have relatively much shorter, narrow, adorally pinched lobes and extremely wide saddles. The lobes and saddles are strongly frilled in spite of their relative shortness. The shortness of the elements and strong crowding of these adoralmost suture lines indicates that the adjoining living chamber belonged to the adult individual and that the shells of adult representatives of the form concerned did not exceed 110 to 115 mm in diameter.

Except that their elements are short, the oralmost suture lines described above closely resemble the corresponding parts of the most advanced suture lines (those of the ribless growth stage) observed in *Temnoptychites (Temnoptychites) kemperi* n. sp.

Discussion. As mentioned in the description, specimen GSC 49325 closely resembles *Temnoptychites grandiosus* Voronets 1962 in most morphological features visible. However, it differs from it in the considerably closer spacing of ribs, considerably greater length of primary ribs in the dichotomous growth stage and apparently in a considerably smaller adult shell. The specific value of these features cannot be evaluated until better preserved specimens are found.

Temnoptychites (Costamenjaites) troelseni n. sp.

Plate 5, figure 2; Plate 8, figure 3; Plate 9, figures 1, 2;
Plate 10, figure 1; Plate 11, figure 1; Plate 12, figures 1, 2;
Plate 13, figures 1–3; Plate 14, figures 1, 2;
Textfigure 6

1954 *Tollia* cf. *tolli* (partim) C. W. Wright, in Troelsen, p. 16
1964 *Tollia (Temnoptychites) novosemelica* Jeletzky, p. 38, Pl. V, figs. 1, 4
1964 *Tollia (Tollia) tolli* var. *latelobata* Jeletzky, p. 38, Pl. V, fig. 5
1972 *Temnoptychites elegans* Shulgina, in Saks *et al.*, p. 113 (Canadian specimens only)
1973 *Tollia (Temnoptychites) novosemelica* Jeletzky, p. 66, Figs. 2, 3

Holotype. GSC 17174 (Pl. 9, fig. 1A–F).

Derivation of name. The species is named for Dr. J.C. Troelsen, Petrobras-Serdeste, Brazil, who discovered the first

(GSC loc. 24075) and apparently the only known (see below) locality which yielded abundant and well preserved material of this *Temnoptychites* species.

Material and localities. Three almost complete (including parts or all of an apparently adult living chamber), undeformed to appreciably deformed specimens and one somewhat questionable large fragment from GSC loc. 24075. Nine almost complete (including parts or all of an apparently adult living chamber) specimens and four readily determinable fragments from GSC loc. 28713 (see description of *Temnoptychites grandiosus* for further information concerning stratigraphy and geographical position of these localities). An almost completely flattened specimen GSC 49334 collected by the Chevron Standard Co. Ltd. in 1974 from Section 007152 (No. 67F) situated at lat. 80°39′N, long. 84°55′W in Blackwelder Mountains, Ellesmere Island (Pl. 14, fig. 2) is the only other representative of the species known to the writer. This specimen is recorded as found at approximately 248.5 m (815 ft) level stratigraphically above the base of the Deer Bay Formation. However, the total thickness of the formation measured by the Chevron Standard geologists considerably exceeds that measured by the Geological Survey geologists in the same area. This makes it impossible to relate the GSC loc. 94731 to those containing the *Thorsteinssonoceras ellesmerense* fauna (Jeletzky, 1965b, p. 14).

Diagnosis of species. A fairly sturdy to moderately slender (width of adult whorl is from 0.93 to 0.65% of the diameter), nodeless species shaped and proportioned like *Temnoptychites grandiosus* to *T. elegans*, characterized by a uniquely large number of primary ribs (19–23) per whorl, by marked weakening of sculpture on the midflank almost immediately after the appearance of the first trichotomous rib bundles, and by the initially crowded and then partly touching to overlapping character of semiadult to adult external suture lines. The fine and closely spaced, superficially *T. elegans*-like sculpture is characterized by the presence of one to two intercalated secondaries between irregularly alternating, well to poorly formed dichotomous and trichotomous rib bundles throughout the intermediate growth stage. This results in a bundling coefficient ranging from about 3.7 to about 4.6. This intermediate growth stage is followed immediately by the final completely smooth (except for constrictions) growth stage. The midventral interruption of secondary ribs is mostly complete on the adoral half of the penultimate whorl representing the late intermediate growth stage but is weakly developed (a weakening of ribs only) or absent on earlier growth stages; the interruption of ribs is only weakly impressed on the surface of the internal cast.

General remarks. Though it is considerably less variable morphologically than *Temnoptychites (Temnoptychites) kemperi* n. sp., *T. (C.) troelseni* n. sp. is rather difficult to describe because the population sample available is relatively small. The scarcity of the material apparently is responsible for the paucity of morphologically transitional forms connecting what is believed to be the extreme morphological variants of the species. This scarcity of morphologically transitional forms, combined with rather remote but nevertheless possible doubts about the geological contemporaneity of fossil localities GSC 24075 and 28713 (see

description of *T.* (*C.*) *grandiosus* for further details), which provided the bulk of the material studied, makes it possible that more than one taxon of the specific rank was included in *T. troelseni* n. sp. as erected in this paper. However, no attempt was made to subdivide the material available into 'morphological species' as the writer firmly believes that it is preferable to 'lump' rather than to 'split' whenever in doubt about the validity of new taxa to be proposed (Jeletzky, 1950; 1955, p. 479, 485–490). It was decided instead to designate the extremely slender morphological form with *Tollia*-like suture line as the typical subspecies, *T.* (*C.*) *troelseni* subsp. *troelseni* n. subsp., and to segregate the considerably sturdier *T.* (*C.*) *grandiosus*–like form with a *Temnoptychites*-like external suture line as another subspecies, *T.* (*C.*) *troelseni* subsp. *crassus* n. subsp. (see below).

The sample of fossil population of *T.* (*C.*) *troelseni* studied herein is peculiar in that it apparently consists exclusively of adult representatives of the species. All but one (e.g., GSC 17167, Pl. 8, fig. 3) of the specimens studied are similarly large and retain at least the early part of the almost completely smooth, apparently adult living chamber. No traces of juvenile to half-grown shells prematurely deceased (with the intermediate living chamber of parts thereof) or even possible fragments of these have been found either by Troelsen or by Thorsteinsson. This can hardly be an accident of collecting as GSC loc. 28713 was visited repeatedly by Thorsteinsson after the original collection of *T.* (*C.*) *troelseni* and other ammonites was gathered there. Thorsteinsson (*pers. com.*, Dec. 1975) was unable to find any additional ammonite material at this locality or anywhere in the vicinity in spite of an intensive search. The writer interprets the evidence available in the sense that a small group of adult representatives of *T.* (*C.*) *troelseni* n. sp., possibly representing part of a migrating school consisting of individuals of the same age, fell victim to some kind of accident and was speedily buried before the cadavers were mutilated seriously by scavengers.

Description

Sculpture. The sculpture of the early whorls of *T.* (*C.*) *troelseni* n. sp. with diameters less than 17 mm is known only poorly. None of the large specimens available was found to be suitable for the extraction of these almost invariably strongly distorted or completely squashed early whorls and only very few examples of naturally weathered out or otherwise exposed inner whorls are available in the collections studied.

The earliest growth stage observed is a segment, about a third of a whorl long, of a still globose whorl about 3 mm high and 2.5 mm wide (est.) exposed in the cross-section of the holotype (Pl. 5, fig. 2, Pl. 9, fig. 1D). This early whorl, which is preserved mainly as an internal cast, is comparable in size and shape to the completely smooth innermost whorl of *Temnoptychites* (*Costamenjaites*) *grandiosus* figured by Bodylevsky (1967, Pl. VI, fig. 2v, g) under the name of *Temnoptychites simplex* var. *inflatus*. However, it is distinctly sculptured with sparce (some 5 or 6 ribs on the exposed third of the whorl) but prominent, sharp-topped primary(?) ribs inclined markedly forward. At least one of these ribs splits into two indistinctly attached secondary ribs on the upper third of the flank. These ribs are somewhat indistinctly visible

in Plate 5, figure 2A and Plate 9, figure 1D. The lower thirds of these primary(?) ribs were not observed, since only the venter and upper two thirds of one flank of the whorl concerned are exposed. None of the ribs discussed above appears to extend beyond the barely suggested ventral shoulder and the regularly rounded, broad venter of the whorl appears to be smooth, except for a few faint striae that are bent forward and one shallow constriction also bent forward on the exposed flank. The venter may appear smooth, however, because it is preserved only as a steinkern (Pl. 5, fig. 2B).

A similarly long segment of a slightly larger (estimated to be 3.5–4 mm in diameter) but still nearly globose early whorl exposed inside the umbilicus of adult specimen GSC 49329 shows that the primary ribs begin as heavy, closely spaced bullae at the umbilical rim (Pl. 9, fig. 2 G, H). These bullae are sharp topped whenever shell covered but round topped whenever preserved as a steinkern. They are restricted to the adumbilical one fifth to one quarter of the flank. On the early two thirds of the exposed segment each bulla gives rise to a single, prominent rib of the same type as those observed in the early whorl of the holotype. These primary ribs are relatively fine and sharp topped whenever shell covered but round topped and much broader when the shell is stripped off; they are separated by gently depressed intervals which are about four times wider than the ribs. Whenever the shell substance is preserved, these intervals are covered by fine, closely spaced striae which parallel the course of the ribs. Otherwise the intervals between appear to be smooth. The primary ribs were not observed to subdivide on this part of the whorl, nor to extend onto its apparently smooth, regularly rounded, broad venter, which is preserved as a steinkern throughout.

On the adoral third of the exposed segment, the bullae are mainly poorly preserved but do not seem to differ from those covering the earlier part of the whorl. However, they split into three and four (?) closely spaced secondaries that are sharp topped (in shell-covered and steinkern preservation alike) and inclined distinctly forward within the lower fifth of the flank (Pl. 9, fig. 2G, H). Only three bundles are visible but they consist of two trichotomous bundles which seem to flank a quadrichotomous bundle. The adoralmost rib of each bundle is considerably more prominent than the rest and so is recognizable as the equivalent of solitary primaries of the preceding two thirds of the segment. Each bundle is separated from the adjacent bundles by an interspace that is somewhat wider than the adjacent ribs. Otherwise the width of interspaces about equals the width of the ribs. The somewhat curving, secondary ribs become progressively more forwardly inclined upflank. They extend at least to the ventrolateral shoulder but could not be traced any farther since the corresponding part of the venter is not exposed.

The ribbing habit discussed is strongly reminiscent of that present on much larger, intermediate whorls of such bullate *Temnoptychites* (*Temnoptychites*) species as *T.* (*T.*) *kemperi* n. sp. and *T.* (*T.*) ex gr. *T.* (*T.*) *triptychiformis-hoplitoides-lgowensis*. It seems likely that it is another instance of the 'prophetic phase' of Pavlow (1901, p. 62, 63) foretelling the adult characters of these racial descendants of nodeless *Temnoptychites* (*Costamenjaites*) ex gr. *T.* (*C.*) *suraense-jucundus-novosemelicus-elegans* (Textfig. 2). It is impossible to

test this hypothesis on the Novaya Zemlya material because the stratigraphic relationships of nodeless and nodose *Temnoptychites* species found there remain obscure (see stratigraphic and biochronological sections below). However, this hypothesis finds support in stratigraphic relationships of nodeless and nodose *Temnoptychites* species observed in Middle Russia and in Sverdrup Basin. In the former region the nodeless *Temnoptychites* (*Costamenjaites*) *jucundus* (Sazonova 1971) and *T.* (*C.*) *suraense* (Sazonova 1971) are reported to be restricted to the topmost Berriasian (uppermost part of *Surites spasskensis* Zone), basal Valanginian (zone of *Pseudogarnieria undulatoplicatilis*), and the basal part of the overlying zone of *Temnoptychites hoplitoides* (Sazonova, 1971, p. 12, 13, 83–87). These beds are followed immediately by the main part of *Temnoptychites hoplitoides* Zone characterized by the nodose *Temnoptychites* (*Temnoptychites*) – e.g., *T.* (*T.*) ex gr. *T.* (*T.*) *triptychiformis-hoplitoides-lgowensis*. The same stratigraphic relationships of *Costamenjaites* and *Temnoptychites* sensu stricto faunas are inferred to exist in the Sverdrup Basin (see below and in Texfig. 8).

A segment, about one fifth of a whorl long, of a more advanced, parallel-flanked, higher than wide (*Craspedites canadensis*–like; see section on whorl shape) juvenile specimen, estimated to have a diameter of about 5 mm, is exposed inside the very large adult specimen GSC 49331 (Pl. 11, fig. 1A, C, F, G). This segment is covered by extremely fine, very closely spaced, sharp-topped secondary ribs, which appear to be grouped into trichotomous and quadrichotomous bundles on the poorly preserved lower third of the flanks. The nature of the closely spaced, relatively more prominent primary ribs remains somewhat uncertain but they appear to be much less bullate but longer than those of the preceding growth stage. There are 18 to 19 secondary ribs on the exposed segment of the whorl discussed here, which suggests 95 to 100 secondaries per whorl of the *Craspedites canadensis*–shaped growth stage of *T.* (*C.*) *troelseni* n. sp. The curving secondaries incline progressively more forward adventrally and form pronounced, fairly narrow forward bends on the venter. No midventral weakening, let alone interruption, of secondaries occurs anywhere on the exposed segment of the whorl.

A couple of small fragments of still more advanced early whorls with estimated diameters of 6 to 8(?) mm were obtained when the large specimen GSC 49330 was broken up. The subparallel upper flanks and the narrowly rounded venter of these fragments are covered by very fine, very closely spaced, secondary ribs like those of the immediately preceding growth stage observed inside specimen GSC 49331. The mode of branching was not observed since the fragments do not include the lower third of the flank. The secondary ribs are sharp topped in the shell-covered and steinkern preservation alike; they incline forward near the ventral shoulder and cross the already narrowly rounded venter in marked but broad forward loops without exhibiting any weakening in the midventer.

No specimens exhibiting the sculpture of whorls with diameters ranging from 8 to 17 mm were available. The sculpture of the next larger whorls available, with diameters of 17 to 18 mm is best exposed in specimen GSC 49332 (Pl. 12,

fig. 2B, C). A small area of this growth stage is visible also in the holotype of the species (Pl. 9, fig. 1B). The growth stages of these two specimens are covered by moderately widely spaced, fine but elevated ribs forming simple dichotomous bundles. Specimen GSC 49332 has about 13 primaries and 32 secondaries per half of the whorl in this sculptural growth stage which amounts to about 25 to 26 primaries and 64 to 65 secondaries per whorl. This dichotomous mode of bundling closely resembles that of the comparable growth stages of some advanced *Tollia* species recently referred to the genus *Neotollia* by Shulgina (in Saks et al., 1972, Pl. XXII, fig. 2a, b). It is named herewith the dichotomous growth stage of *T. troelseni* n. sp.

In these two specimens of *T. troelseni* n. sp. the primary ribs of the dichotomous growth stage are deflected markedly backward and begin faintly in the middle part of the umbilical wall; they cross the outer part of the wall on that course, gradually becoming more prominent and sharper, until they reach their full strength at the umbilical shoulder. At the latter point the now pinched and sharp-topped primaries swing narrowly around until they incline distinctly forward (Pl. 12, fig. 2B) on the lowermost part of the flank. Thereafter the primary ribs continue on this course upflank until they split in two at somewhat variable levels ranging from the lower two fifths to about one half of the flank's height. The resulting secondary ribs are firmly attached to the primaries and are just as strongly pinched and sharp as the latter whenever they are shell covered. In the steinkern preservation the secondaries and the primaries both remain elevated and narrow but their sharp-topped appearance is either lost or greatly reduced (Pl. 12, fig. 2B). The secondary ribs become progressively more forwardly inclined as they approach the ill defined ventral shoulder until they bend forward at angles of 30 to 40 degrees at the shoulder. Thereafter the secondaries cross the venter forming narrow, pronounced (sometimes chevronlike), forward-directed bends. In the holotype the shell-covered secondary ribs are distinctly weakened and partly interrupted in this growth stage. However, in specimen GSC 49332, the venter of which is mainly preserved as a steinkern, the secondaries are only occasionally somewhat weakened in the midventer (Pl. 12, fig. 2C).

On the exposed part of the whorl of specimen GSC 49332 the dichotomous growth stage persists over only about a third of the whorl before becoming replaced by the intermediate growth stage (Pl. 12, fig. 2A) described below at the whorl diameter of about 21 mm. However, the dichotomous stage is assumed to have started at least one half whorl earlier, at a whorl diameter of about 15 mm, judging by the coarse appearance of basal parts of primaries in the umbilical walls inside the umbilicus and by that of the secondaries on the locally visible, poorly preserved ventral part of this specimen. The considerably shorter segment of the dichotomous growth stage observed in the holotype does not add any information about its extent.

Because both the exceptionally finely and densely ribbed specimen GSC 49333 (Pl. 13, fig. 1C) and the less finely ribbed but similarly sized specimen GSC 17167 (Pl. 8, fig. 3A, C) are covered by well formed rib bundles of the next following intermediate growth stage at the approximate whorl diameter of 18 mm, the dichotomous growth stage is believed

to end considerably earlier (see below) in the very finely and densely ribbed variant of *T. troelseni* n. sp. than it does in its coarser and sparser ribbed variant exemplified by specimens GSC 49332, 49334, 17175 and the holotype.

As far as is known, the dichotomous growth stage of *T. troelseni* n. sp. is always followed immediately by the so-called intermediate growth stage dominated by an irregular to fairly regular alternation of dichotomous and trichotomous rib bundles. These rib bundles are, as a rule, separated from each other by one or two intercalated secondaries restricted to the upper one third to two thirds of the flank. The earliest exposed whorl segments of most of the studied representatives of *T. troelseni* n. sp. exhibit this intermediate sculptural growth stage. Judging by the limited data available (see above), the intermediate sculptural stage makes its first appearance at rather different whorl diameters.

In the material studied the intermediate sculptural growth stage extends over a lesser or greater part (possibly over the whole length in specimen GSC 49333) of the second whorl from the last (from adult ultimate) and then extends farther adorally over most or all of the penultimate whorl. It grades imperceptibly into the final, so-called sculptureless growth stage of *T. troelseni* n. sp. either on the oralmost part of penultimate whorl or on the apicalmost part of the ultimate whorl (Pl. 12, fig. 1A, Pl. 13, fig. 2A, B, Pl. 14, fig. 2A).

For convenience the intermediate sculptural stage may be subdivided into the following two sculptural phases: (i) the early intermediate, characterized invariably by a markedly elevated appearance of primary and secondary ribs, by the lack of any weakening of ribbing on the midflank, and by well defined bundling of the primary ribs; and (ii) the late intermediate, characterized by a rapidly progressive weakening of sculpture on the midflank, which is later followed by a complete loss of sculpture in the same area. This gradual weakening of sculpture is coupled with a concurrent strengthening and commonly noticeable coarsening of the upper parts of the secondaries and of the lower parts of the primaries. Furthermore, the secondary ribs become completely interrupted on the midventer during most or all of this phase. The duration of the early intermediate phase appears to be highly variable. It may be limited to one quarter of the whorl or thereabouts, judging by the only specimen (i.e., GSC 49332, Pl. 12, fig. 2A, B) where the whole length of that phase is visible. The visible duration of this phase at least is even shorter in specimens GSC 49329 (Pl. 9, fig. 2A) and 49333 (Pl. 13, fig. 1C), where its beginning is not visible. However, this phase extends over the whole whorl of the specimen GSC 17167 (Pl. 8, fig. 3a), although its beginning is not exposed there.

The transition from the early to the late intermediate phase is invariably rapid in the relatively abundant material available. As exemplified by specimens GSC 49332 (Pl. 12, fig. 2A), 17174 (Pl. 9, fig. 1A, B) and 49333 (Pl. 13, fig. 1A), the semismooth appearance of midflanks of the whorl accompanied by a distinct strengthening and thickening of ribs on the upper and lower parts of the flanks is acquired within one fifth to one quarter of the whorl from the last sharply defined rib bundle. The transition is fastest in the coarsest ribbed specimens (e.g., GSC 49332), while the slowest transition was observed in the exceptionally finely and densely

ribbed specimen GSC 49333. The transition from the late intermediate to the final ribless sculptural stage lasts much longer than that from the early to the late intermediate phase. It takes from three quarters of a whorl (e.g., GSC 49329, Pl. 9, fig. 2B, C) to somewhat more than one whorl (e.g., GSC 49333 and 49330; Pl. 13, fig. 1A, B, Pl. 10, fig. 1A, B) in the material available.

The early intermediate phase is characterized by the same extent, direction and length of the primary ribs as the previously discussed dichotomous growth stage. However, the primary ribs gradually become distinctly thicker in comparison with those of the dichotomous growth stage. This thickening (sometimes amounting to a faintly bullate appearance) is more marked in the steinkern preservation, where the exposed, relatively wider internal casts of primaries are round-topped (e.g., GSC 49332, Pl. 12, fig. 2A, B), than in the shell-covered preservation, where the narrower to pinched and sharp-topped primaries proper are preserved (e.g., GSC 49329, Pl. 9, fig. 2A).

The style and alternation of rib bundles in the early intermediate phase is highly variable. In the very finely and closely ribbed specimen GSC 49333 (Pl. 13, fig. 1B, C), only well formed trichotomous rib bundles, which are not separated from each other by intercalated ribs, have been observed in this phase. These bundles are all fasciculate. In the specimen having very coarse and widely spaced ribs (GSC 49332, Pl. 12, fig. 2B), the phase is represented by an irregular alternation of more common dichotomous with less common trichotomous bundles. The latter are mostly virgatotome with the two successive secondaries jutting forward from the continuing primary. A solitary nondividing primary rib was noted immediately adorally of a deep, wide constriction that is inclined forward. Intercalated secondary ribs are very rare in the specimen discussed here. Specimen GSC 49329 (Pl. 9, fig. 2A) and the holotype (Pl. 9, fig. 1A, B) exemplify the prevalent variant of bundling in the early intermediate phase, consisting of a more or less regular alternation of dichotomous bundles with fasciculate or virgatotome trichotomous bundles and including one or two intercalated secondaries separating the individual rib bundles. These secondaries are restricted to the upper third to two thirds of the flank.

The secondary ribs of the early intermediate phase have exactly the same appearance and direction as the secondaries of the previously described dichotomous growth stage, except at the ventral shoulder and on the venter proper. Because of the stronger variation of the degree of forward bends of the secondaries at the ventral shoulder, which ranges from about 45 degrees (e.g., GSC 49332, Pl. 12, fig. 2B, C) to less than 30 degrees (e.g., GSC 49333, Pl. 13, fig. 1A, C; GSC 49329, Pl. 9, fig. 2A, B), the ribs may cross the venter forming either sharp, chevronlike forward bends (e.g., GSC 49332, Pl. 12, fig. 2C) or marked but broad forward loops (e.g., GSC 49333, Pl. 13, fig. 1E; GSC 49329, Pl. 9, fig. 2D). These extremes are connected by transitions (e.g., GSC 49330, Pl. 10, fig. 1F) and it seems that the sharpest forward bends (and the strongest forward inclinations) of the secondary ribs on the venter occur in the coarsest and most sparsely ribbed specimens. The finest and most densely ribbed specimens seem to have the broadest forward bends (and the weakest forward inclinations) of the secondary ribs on the venter.

The weakening of secondary ribs on the midventer is invariably present in the early intermediate phase, provided that the specimens concerned are sufficiently well preserved (not weathered to any great extent); this is more marked in the shell-covered specimens than in the internal casts (cf. GSC 49329, Pl. 9, fig. 2D, with GSC 17174, Pl. 9, fig. 1C). However, no complete interruption of the secondaries was observed in the growth phase discussed here.

Some of the most characteristic sculptural features of the late intermediate phase have been discussed previously in its definition. However, the following details should be added. No traces of primary ribs have been seen on the umbilical walls of any specimen studied throughout the duration of the late intermediate phase. The general appearance, spacing and direction of the lower parts of the primary ribs still preserved on the lower parts of the flanks are not changed compared with the early intermediate phase. However, the internal casts of these reduced primaries are considerably thicker in comparison with their already thickened internal casts in the early intermediate phase in most of the specimens studied (e.g., GSC 17164, Pl. 13, fig. 2A; GSC 49330, Pl. 10, fig. 1B; GSC 49332, Pl. 12, fig. 2A). It is not an exaggeration to call the most marked examples of these thickened internal casts bullate primaries (e.g., Pl. 12, fig. 2A, Pl. 13, fig. 2A). There are, however, some specimens where the residual primary ribs become weakened instead of strengthened during the late intermediate phase and disappear completely long before its end as defined by the disappearance of strengthened upper parts of the secondary ribs (e.g., GSC 17174, Pl. 9, fig. 1A, B). Unlike the internal casts, the shell-covered residual primary ribs of the late intermediate phase retain the distinctly pinched, sharp-topped appearance characteristic of the previously described early intermediate phase (e.g., GSC 49329, Pl. 9, fig. 2A, B; GSC 17176, Pl. 12, fig. 1F) regardless of whether they become somewhat strengthened or somewhat weakened.

The above-discussed residual primary ribs on the lower parts of the flanks usually increase gradually in prominence at the umbilical shoulder through part or all of the late intermediate phase as they become more and more shortened because of the gradual widening of the smooth to almost smooth zone of the midflank. Finally, these residual primaries disappear abruptly, either within the penultimate whorl or on the early part of the living chamber. If the former, they mainly disappear just before the oral end of the phragmocone (e.g., GSC 17176, Pl. 12, fig. 1A; GSC 49330, Pl. 10, fig. 1A, B). However, there are instances where the residual primaries disappear earlier on the penultimate whorl, in some cases even within its apicalmost quarter (Pl. 14, fig. 2A). If the residual primaries persist onto the living chamber, they are restricted invariably to its apical part (e.g., GSC 17164, Pl. 13, fig. 2A). As a rule, the residual primaries disappear approximately at the same time as the strengthened upper parts of secondary ribs (e.g., GSC 17164, Pl. 13, fig. 2A) but, as already mentioned, there are some exceptions to this rule (e.g., GSC 49329, Pl. 9, fig. 2A, B; GSC 17174, Pl. 9, fig. 1A, B).

The extent of the residual upper parts of secondary ribs on the penultimate and ultimate whorls varies within the same limits as do the residual primaries (see above); they gradually become thickened and more widely spaced as they become shorter in the course of the late intermediate growth phase because of a gradual widening of the smooth to almost smooth midflank zone. As with the residual primaries, the thickening is pronounced in the round-topped internal casts of the residual secondaries (e.g., GSC 17176, Pl. 12, fig. 1A, C; GSC 17174, Pl. 9, fig. 1A, E) and becomes less and less evident in partly shell covered specimens as more and more external shell layers are preserved (e.g., GSC 17164, Pl. 13, fig. 2A). The specimens locally retaining the outermost shell layers (e.g., GSC 49329, Pl. 9, fig. 2A, E; GSC 17174, Pl. 9, fig. 1A, E; and especially GSC 49334, Pl. 14, fig. 2A, B) reveal that the topmost parts of residual secondaries remain just as strongly pinched and sharp topped throughout the late intermediate phase as they were in the preceding early intermediate phase and dichotomous stage. However, the perfectly preserved, residual secondaries of the late intermediate phase are separated from each other by slightly concave interspaces which are considerably (1½ to 2 times) wider than the interspaces of the preceding sculptural stages (GSC 17174, Pl. 9, fig. 1A, E; GSC 49329, Pl. 9, fig. 2B, E; GSC 49334, Pl. 14, fig. 2A, B). These relationships indicate that the thickening of internal casts of reduced secondaries in the late intermediate (and also in the early intermediate; see above) stage is caused by the appearance of broad, transversal corrugations of inner shell surface which diminish in intermediate shell layers and do not extend into the outermost shell layers. Superimposed on the general regularities of development of reduced secondaries is a trend for the perfectly preserved secondaries to become gradually thicker and more prominent adorally and for the perfectly preserved interspaces to widen gradually in the same direction (e.g., GSC 17164, Pl. 13, fig. 2A; GSC 49330, Pl. 10, fig. 1D, G; GSC 49334, Pl. 14, fig. 2A, B).

The forward inclination of residual secondary ribs in the late intermediate phase varies within about the same limits as that in the previously described early intermediate phase, and the same is true of the variation in the shape of forward bends or loops formed by these secondaries on the venter.

Unlike the secondaries of the early intermediate stage, those of the late intermediate stage are interrupted completely in the midventer. In all better preserved, shell-covered specimens (e.g., GSC 17174, Pl. 9, fig. 1E; GSC 49329, Pl. 9, fig. 2E; GSC 49334, Pl. 14, fig. 2B) this interruption lasts through part or all of the intermediate phase and disappears together with the oralmost reduced secondary ribs (Pl. 10, fig. 1G, Pl. 14, fig. 2B). Only faint striae may cross the midventral smooth band in these specimens and all shell-covered, nearly perfectly preserved secondaries stop abruptly at its borders. The midventral smooth band is much less distinctly expressed in less satisfactorily preserved specimens (or their parts) retaining only the inner shell layers (e.g., GSC 17164, Pl. 13, fig. 2B; GSC 49330, Pl. 10, fig. 1D, G). However, it is definitely present also in these specimens.

Apart from these structural details and ontogenetic trends confined either to the early or to the late intermediate phase, there are some details and trends shared by both phases. For example, the coarseness and spacing of primary and secondary ribs vary in rather wide limits from one specimen to another throughout the intermediate sculptural stage. One extreme is represented by specimen GSC 49333 (Pl. 13, fig. 1A, C), which is covered by much finer and much

closer spaced ribs than the rest throughout the intermediate stage. It is conservatively estimated that this specimen has 18 primaries and 45 to 50 secondaries on the early half of the penultimate whorl beginning with the diameter of about 18 mm and ending with the diameter of about 30 mm. About the same density of primaries and secondaries is maintained on the less satisfactorily preserved late half of the penultimate whorl, which does not permit counting of ribs.

The secondaries become slightly less numerous on the preserved earliest part of the living chamber. It appears safe to estimate that specimen GSC 49333 has about 35 to 36 primaries and from 90 to 100 secondaries on the penultimate whorl with resulting branching coefficient between 2.7 and 3.

The ribbing habit of specimen GSC 49333 is unique in the studied population sample of *T. troelseni* n. sp. Therefore one might feel tempted to exclude it from this species, considering the absence of morphologically intermediate forms connecting it with the rest of the specimens studied and the lack of data about the morphology of its earlier growth stages. However, this idea is rejected as improbable. In contradiction, specimen GSC 49333 was found together with the rest of the material of *T. troelseni* n. sp. and agrees closely with its sculpturally more typical representatives in all other taxonomically significant features (e.g., the similar whorl shape, the similar size and shape of the umbilicus, and the entirely similar morphology of the external suture line).

The other extreme is represented by specimens GSC 49332 and 17164 (Pl. 12, fig. 2A, B, Pl. 13, fig. 2A, B) with very coarse and widely spaced ribs. Of these specimens, GSC 49332 has about 23 primaries (counted) and only 60 to 65 secondaries (est.) per whorl on the late half of the second whorl from the last (beginning with whorl diameter of about 17 mm) and early half of the penultimate whorl ending with whorl diameter of about 35 mm. Specimen GSC 17164, also with coarse and widely spaced ribs, has 18 primaries (counted) and about 82 secondaries (est.) per whorl on the late half of penultimate and the early half of the ultimate whorl between the diameters of 29 and 42 mm. This results in a bundling coefficient of about 4.5.

The majority of specimens studied are somewhat less coarse and closer ribbed than the extreme specimens GSC 49332 and 17164 while resembling them more closely than specimen GSC 49333 in these respects. They are exemplified by specimens GSC 49329 (Pl. 9, fig. 2A, B), 17174 (Pl. 9, fig. 1A, B) and 49330 (Pl. 10, fig. 1B, C). The last specimen, which most closely approaches specimen GSC 17164 in its ribbing habit, has 20 primaries (counted) and only 79 to 80 secondaries (est.) on the penultimate whorl beginning with the diameter of 24.5 mm and ending with that of about 43 mm. This results in a bundling coefficient of only 4. Specimen GSC 49329 has about 19 primaries and between 88 and 90 secondaries (est.) on the entirely septate penultimate whorl beginning with the diameter of about 23 mm (estimated because of whorl's distortion) and ending with that of about 40 mm. This results in a bundling coefficient of between 4.6 and 4.7. Finally, specimen GSC 17174 (the holotype) has between 8 and 9 primaries and between 30 and 35 secondaries on the earliest quarter whorl exposed. This specimen is too incomplete to permit either a counting or a really close estimation of the number of ribs on the whole whorl.

Considering the uncertainties involved in estimation of the number of secondaries and primaries per whorl from this meager data, the bundling coefficient of specimen GSC 17174 may be anywhere between 3.5 and 4.

The last sculptural stage of *Temnoptychites troelseni* n. sp. is named herewith the structureless growth stage because as a rule sculpture is completely absent, except for the almost invariably present, well developed constrictions (see following text).

The extent of the structureless growth stage is variable. In some specimens it extends over most or the whole of the adult living chamber. For example, it comprises between three quarters and seven eighths of the ultimate whorl in the three complete specimens GSC 49330 (Pl. 10, fig. 1A), 17176 (Pl. 12, fig. 1A) and 49335 (Pl. 14, fig. 1A). In these specimens the beginning of the sculptureless growth stage almost coincides with the last suture line. However, there are specimens (e.g., GSC 49334, Pl. 14, fig. 2A) where the structureless growth stage begins in the middle of the penultimate whorl and so must have extended for about 1½ whorls. The other extreme is represented by two other specimens (e.g., GSC 17164 and 17175; Pl. 13, figs. 2A, 3A), where the structureless growth stage is restricted to the adoral half to adoral two thirds of the adult living chamber. These two specimens are considerably smaller than those in which the structureless growth stage extends over most or all of the living chamber. The last few suture lines (Pl. 13, fig. 3A, B) of specimen GSC 17175 are relatively simple but distant and one could argue that immaturity was the reason for this anomaly. However, this hypothesis does not at all fit specimen GSC 17164, characterized by considerably narrowed, touching to interlocking lobes of its last few suture lines (Pl. 13, fig. 2C, Textfig. 6F).

Most of the complete specimens and some of the fragments of *Temnoptychites troelseni* n. sp. carry numerous well developed *Tollia tolli*–like (Pavlow, 1914, Pl. XII, figs. 1a, 3, Pl. XIII, figs. 1c, d, 2) constrictions on the last three whorls. Only one such constriction was seen on the early whorls (e.g., specimen GSC 49329; see above) with diameters less than 17 mm. However, this appears to be because these whorls are scarce in the material studied.

The two specimens exposing the greater part of the second from last whorl (i.e., GSC 49332, Pl. 12, fig. 2A, B; GSC 49333, Pl. 13, fig. 1A–C) carry, respectively, two and four relatively shallow and narrow constrictions per whorl. The constrictions are even more common and pronounced on the penultimate and ultimate whorls of most of the studied specimens, where they usually count two to four per whorl (e.g., GSC 49329, Pl. 9, fig. 2B; GSC 49330, Pl. 10, fig. 1A, B; GSC 17176, Pl. 12, fig. 1A; GSC 49331, Pl. 11, fig. 1A, D). However, there are exceptions to this rule since specimen GSC 17164 carries only one constriction on the penultimate and none on the ultimate whorl (Pl. 13, fig. 2A) and the holotype of *T. troelseni* n. sp. (Pl. 9, fig. 1A, B) lacks constrictions on preserved parts of the penultimate whorl.

The constrictions generally are deeper, wider and better defined on the penultimate and ultimate whorls than they are on the second from last whorl. The constrictions are round-bottomed and either symmetrical (on the second from last whorl and sometimes on subsequent whorls) or

asymmetrical (on penultimate and ultimate whorls only). If the latter, the adoral flank is elevated above the adjacent whorl surface and forms a kind of round-topped broad bulge (e.g., GSC 17176, Pl. 12, fig. 1A).

The constrictions incline moderately to strongly backward on the umbilical wall but turn around in a broad loop at the umbilical shoulder and become moderately to strongly inclined forward on the flank; they may be weakly or markedly curved on the flank (Pl. 11, fig. 1A, Pl. 12, fig. 1A). Generally, the constrictions follow closely the course of adjacent primary and secondary ribs and form forward loops or bends on the venter that resemble closely those of adjacent secondary ribs. The constrictions normally (there are exceptions) extend all around the outer whorl, beginning at umbilical seams; in no case were they seen to weaken or to become interrupted in the midventer. The constrictions are much more pronounced on internal casts than on the completely shell-covered specimens or sections of the same specimens and may be completely invisible on the latter.

The living chamber comprises between seven eighths and eight ninths of the adult ultimate whorl in all completely to nearly completely preserved specimens (e.g., GSC 49330, Pl. 10, fig. 1A; GSC 17175, Pl. 13, fig. 3A; GSC 17176, Pl. 12, fig. 1A; GSC 49335, Pl. 14, fig. 1A). There is every reason to think that it was similarly long in all other less complete specimens (e.g., GSC 17164, Pl. 13, fig. 2A). Whenever the mouth border is preserved, it coincides with one of the constrictions discussed above (e.g., GSC 49330, Pl. 10, fig. 1A; GSC 49335, Pl. 14, fig. 1A).

Whorl shape and proportions. The whorl shape and proportions of the early whorls less than about 17 mm in diameter are very poorly known. These poorly preserved to completely squashed early whorls could not be extracted from any of the adult specimens available and the collections studied contain only very few naturally weathered out or otherwise exposed examples.

Judging by the cross-section of the early whorls visible in the accidentally broken, undeformed holotype (Pl. 5, fig. 2A, B, Pl. 9, fig. 1D) the earliest visible whorls up to the diameter of about 3 mm have a globose appearance. These sturdy-proportioned, somewhat broader than high whorls have regularly rounded flanks which merge imperceptibly into the equally regularly rounded, broad venter. The umbilical walls are markedly convex and merge almost inperceptibly into the rounded flanks. Other less satisfactorily preserved specimens (e.g., GSC 49329, Pl. 9, fig. 2B, F, G, H) appear to have whorls that are similarly shaped.

Beginning with whorl diameters ranging between 5 and 6 mm, the juvenile whorls become somewhat higher than wide (in the holotype the whorl width is 8 mm at the whorl height of 9 mm, or 88%; see Pl. 9, fig. 1D) and the flanks become gradually less convex. However, the venter remains regularly and broadly rounded (Roman arch–like; e.g., GSC 49331, Pl. 11, fig. 1G) throughout this growth stage, which lasts to the whorl diameters from 13 to 15 mm in the few specimens studied. The above changes result in a generally *Craspedites canadensis* subsp. *canadensis*–like cross-section (cf. Jeletzky, 1966, Pl. I, figs. 5B, 6C, 8C) of the early whorls.

Beginning with whorl diameters of 12 to 15 mm (the

changeover is gradational anyway), the umbilical wall becomes essentially straight and directed obliquely (at 40 to 45 degrees) outward while the almost imperceptible, rounded umbilical shoulder is replaced gradually by a much better defined, rounded-angular shoulder. At the same time, the whorl gradually becomes considerably more slender with only weakly convex flanks. These flanks contract rapidly and almost evenly all the way from the level of maximum diameter situated at the umbilical shoulder to the rounded but distinctly defined ventral shoulder. The venter becomes narrowly rounded in this growth stage but with its middle part distinctly flattened. In the holotype GSC 17174 (Pl. 9, fig. 1D), the whorl is only 10 mm wide at the diameter of 13 mm or about 75 per cent. The fairly slender, considerably higher than wide, rounded-triangular cross-section of the intermediate whorls of *Temnoptychites troelseni* n. sp. does not differ materially from that of the equivalent growth stages of the *T. lgowensis*–like variant of *T. kemperi* n. sp. (cf. Pl. 3, fig. 3B) and closely resembles that of the equivalent growth stages of *T. lgowensis* itself (Nikitin, 1888, Pl. II, figs, 6, 7; Bogoslowsky, 1902, Pl. I, fig. 5b). This cross-section does not change much throughout the remainder of the ontogeny of *T. troelseni* n. sp., including the sculptureless, presumably adult growth stage. The range of variation of the whorl's cross-section recognized at whorl diameters greater than 17 mm (see below) may be present in the above-discussed earlier growth stages but remains unrecognized there because the material available is extremely scarce.

In the half-grown to adult representatives of *T. troelseni* n. sp., with whorl diameters ranging from 17 to about 62 mm, the shape and proportions of the whorl are variable in spite of the few specimens available. One extreme, exemplified by specimen GSC 17176 (Pl. 12, fig. 1B, C, G), is characterized by a moderately sturdy, rounded-triangular shape with flattened flanks and narrowly rounded venter. The flanks of this form, designated *T. t.* subsp. *crassus* n. subsp. (see below), converge rapidly and almost to entirely evenly all the way adventrally from the maximum whorl diameter situated at the umbilical shoulder. This whorl shape matches closely that of *T. (C.) grandiosus* (Pl. 7, fig. 1C) and also closely resembles the slender, rounded-triangular cross-section of more sturdy representatives of the *Temnoptychites hoplitoides*–like variant of *T. (T.) kemperi* n. sp. and forms transitional to its *T. triptychiformis*–like variant (e.g., Pl. 5, fig. 1C, D, Pl. 3, fig. 2B, C). Furthermore, it is not unlike the considerably sturdier whorl shape of the final growth stages of *T. mokschensis* (Bogoslowsky, 1902, Pl. III, fig. 2b, c). In this best preserved representative of this sturdy form of *T. troelseni* n. sp. (e.g., GSC 17176, Pl. 12, fig. 1B, C) the only feebly deformed part of the living chamber has the whorl width of 39.5 mm at the whorl height of only 44 mm, which corresponds to 89 per cent of the diameter. Other known representatives of the variant (e.g., GSC 17164, Pl. 13, fig. 2A, B) have nearly identical whorl proportions.

In the other extreme represented by the holotype (GSC 17174, Pl. 9, fig. 1D) and some other known representatives of *T. troelseni* n. sp., the rounded-triangular whorl cross-sections gradually become appreciably more slender in the semiadult to adult growth stage. Simultaneously, the flanks of the whorl become almost flat in this variant and the venter of most of

the representatives known (e.g., Pl. 9, figs. 1C, 2D) loses the midventral flattening characteristic of the previously discussed earlier growth stages. At the same time, this venter becomes even more narrowly rounded than before. The above-described gradual change of whorl proportions of the slender variant is illustrated by the width of the whorl becoming only 17.5 mm at the whorl diameter of 27 mm in the holotype (Pl. 9, fig. 1D), which corresponds to only 65 per cent of the diameter. The shape and proportions of cross-sections of semiadult to adult whorls of the slender form of *T. troelseni* n. sp., designated as *T. t.* subsp. *troelseni* n. subsp. (see below), are indistinguishable from those of the holotype of *T. elegans* (Bodylevsky, 1967, Pl. IV, figs. 1v, g).

All better preserved specimens of *Temnoptychites troelseni* n. sp. have a strongly involute (see tables of dimensions), funnellike, moderately deep umbilicus. The succeeding whorls either conceal the preceding whorls completely or expose only their very umbilical shoulders (e.g., Pl. 9, fig. 1A, D). A slight uncoiling of the last whorl appears to be restricted to the adoral half of the adult living chamber (Pl. 12, fig. 1A). The angle of the umbilicus ranges from 20 to 50 degrees in the material studied. As already mentioned, all umbilical walls, except for those of the earliest two or three whorls studied, are straight to only slightly convex and directed subvertically to the direction of the flanks of the whorl. The umbilical seams are depressed only slightly, except in the earliest growth stages, and the umbilical shoulders are well defined, albeit narrowly rounded rather than truly angular (Pl. 9, fig. 1D, Pl. 11, fig. 1C).

Suture line. The external suture line of *Temnoptychites (Costamenjaites) troelseni* n. sp. was studied only in intermediate and late growth stages beginning with whorl diameters ranging from 17 to 20 mm and ending with those ranging from 35 to 44 mm. These suture lines include fairly numerous examples of the few oralmost suture lines adjoining the adult body chamber.

The studied semiadult to adult, external suture lines of *T. (C.) troelseni* n. sp. remain *Temnoptychites*-like (see generic description above) in such major morphological characters as the strongly ascendant orientation of most or nearly all its elements, the square to adorally contracted shape of lobes, and the presence of five or, more rarely, four well differentiated auxiliary lobes on the penultimate whorl. However, these suture lines appear to be unique within the genus *Temnoptychites* in the degree of crowding and overlapping of the adjacent suture lines. The earliest studied semiadult suture lines observed at the whorl diameter of about 18 mm are already considerably more crowded than the approximately equivalent suture lines of any other *Temnoptychites* species the writer is familiar with.

The equivalent elements of adjacent semiadult suture lines of all better known *Temnoptychites* species, such as *T. (T.) borealis* (Pl. 1, fig. 2B, Textfig. 3A), *T. (T.) kemperi* n. sp. (Textfig. 4C, E, F), *T. (C.) grandiosus* (Pl. 7, fig. 1E, G), and *T. (C.) elegans* (Bodylevsky, 1967, Pl. III, fig. 1a, Pl. IV, fig. 1a), are separated from each other by considerable distances. In contrast, the tips of semiadult suture lines of *T. (C.) troelseni* n. sp. almost touch the topmost parts of the saddles of preceding sutures already at whorl diameters ranging between

18 and 22 mm (e.g., Pl. 8, fig. 3D, Textfig. 6I). The tips of adventral terminal lobules of the first lateral lobe begin to touch the top part of the second lateral saddle of the preceding suture already at the whorl diameter of about 25 mm (Textfig. 6C). Then the tips of terminal lobules of the second lateral and the first auxiliary lobes begin to touch, and sometimes overlap, the tops of the corresponding saddles of the preceding sutures at whorl diameters ranging from 30 to 35 mm when the terminal lobules of the first lateral lobes already overlap markedly the tops of preceding second lateral saddles (Textfig. 6E, H). Thereafter most or all of the elements of the suture lines continue either to touch or overlap (interlock) all the way to the beginning of the adult living chamber regardless of whether they become more and more complex or simplified as they approach the oral end of the phragmocone (e.g., Textfig. 6A, B, F, G and H). The degree of this contact or overlapping gradually increases oralward in most of the specimens studied.

The only exception from this mode of ontogenetic development of the suture line known to the writer (Pl. 13, fig. 3A, B) appears to be caused by the weathering of the shell surface of specimen GSC 17164 to the depth of 1.5 to 2 mm. This weathering had destroyed all of the tips of the lobes, and the topmost parts of the adjacent saddles, which either touch or overlap in all other representatives of the species.

Because of pronounced crowding and partial overlapping, semiadult and adult external suture lines of *T. (C.) troelseni* n. sp. resemble the equivalent suture lines of *Homolsomites* ex gr. *quatsinoensis* (Whiteaves) (cf. Textfig. 1U with Textfig. 6A, B, C, E, F and H). However, the stems of the lobes of *T. (C.) troelseni* n. sp. are relatively much wider than those of *H.* ex gr. *quatsinoensis* and lack its characteristic waving. Furthermore, they are much less ramified and denticulated than those of *H.* ex gr. *quatsinoensis*.

It is not certain whether the similarity of the suture lines of *T. (C.) troelseni* n. sp. to those of *H.* ex gr. *quatsinoensis* is a matter of homeomorphy alone or reflects their genetic affinity, including a possible ancestor-descendant relationship. The writer intends to study this problem in connection with the planned description of the Canadian representatives of *Homolsomites*.

In contrast to the relationships in *T. (C.) troelseni* n. sp. discussed above, the adjacent external suture lines of *Temnoptychites (Costamenjaites) grandiosus* remain completely separated at least to the whorl diameters of 44 mm (e.g., Pl. 7, fig. 1A, E, G). The same appears to be true of the sutures of *Temnoptychites (Temnoptychites) kemperi* n. sp., which begin to touch each other only at the whorl diameters of 75 to 80 mm (Pl. 3, fig. 4, Pl. 4, fig. 1A). Finally, all elements figured so far of the external suture lines of *T. (C.) elegans* (Bodylevsky, 1967, Pl. III, fig. 1a, Pl. IV, fig. 1a) and *T. (C.) novosemelicus* (Sokolov, 1913, Pl. 3, fig. 2a) remain well spaced throughout the presumably adult penultimate whorl with terminal whorl diameters of 45 to 55 mm.

The early crowding followed by partial contacts and then overlapping of semiadult suture lines of *T. (C.) troelseni* n. sp. appears to be diagnostic of the species. However, it is the only such feature known, since all other structural details of semiadult and adult suture lines exhibit a wide range of infraspecific variation which may be summarized as follows.
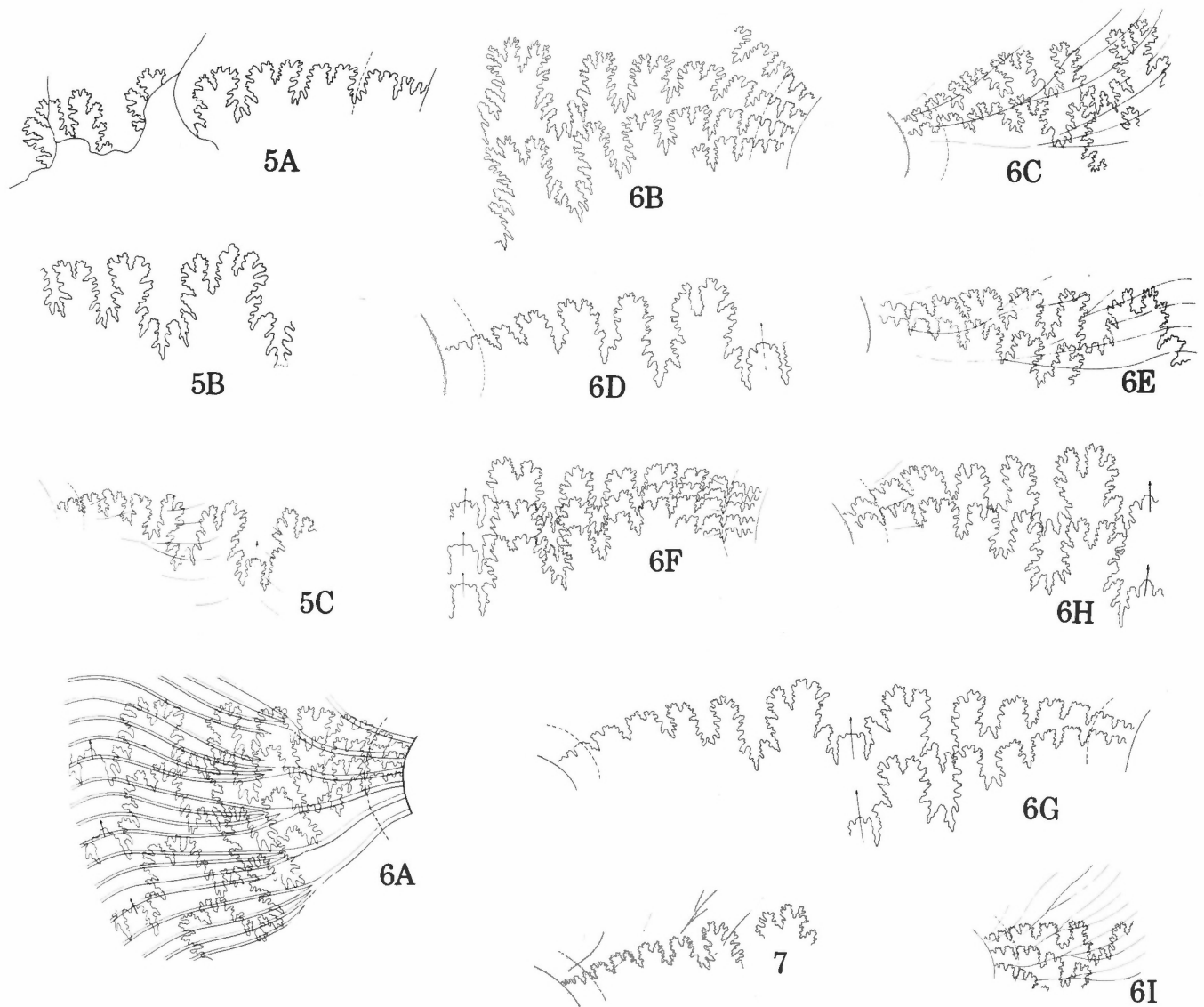
Textfigure 5. *Temnoptychites (Costamenjaites) grandiosus* Voronets 1962. External suture lines of specimen GSC 17173 reproduced in Pl. 7, fig. 1A–G. (5A) Almost complete suture visible on the completely smooth, adoralmost preserved part of the right flank of the specimen (Pl. 7, fig. 1B). (5B) Ventral and lateral parts of the adoralmost suture line dimly visible on the adoralmost preserved part of the left flank of the specimen (Pl. 7, fig. 1A). This suture is introduced to supplement the fragmentary part of the equivalent suture line in 5A. (5C) Complete suture line outlined in black on the middle part of the earliest exposed, completely ribbed whorl of the same specimen (Pl. 7, fig. 1E, G).

Textfigure 6. *Temnoptychites (Costamenjaites) troelseni* n. sp. (6A) A group of four excellently preserved, complete external suture lines visible on the early part of the whorl of the holotype GSC 17174 (Pl. 9, fig. 1B). (6B) Two excellently preserved, complete external suture lines outlined in white on the middle part of the left flank and venter of specimen GSC 49329 reproduced in Pl. 9, fig. 2C, E, F. (6C) Two almost complete, well preserved, external suture lines of GSC 49332 (Pl. 12, fig. 2A–C). These suture lines are dimly visible beneath ammonium chloride layer on the oralmost preserved part of penultimate(?) whorl (Pl. 12, fig. 2B). (6D) Almost complete, well preserved, terminal external suture line of GSC 17176 (Pl. 12, fig. 1A–F). The lateral and auxiliary parts of this suture are reproduced in Pl. 12, fig. 1D, E. Its lateral part also is outlined in white in Pl. 12, fig. 1A. (6E) Two almost complete external suture lines of GSC

49331 (Pl. 11, fig. 1A–H). These suture lines are dimly visible beneath the layer of ammonium chloride on the earliest exposed part of the inner whorl in Pl. 11, fig. 1A. They are reproduced also unwhitened in Pl. 11, fig. 1H. (6F) Three terminal external suture lines of GSC 17164 (Pl. 13, fig. 2A–C). The lateral and auxiliary parts of these suture lines are reproduced in Pl. 13, fig. 2E. (6G) A complete external suture line of GSC 49333 (Pl. 13, fig. 1A–E). The lateral and auxiliary parts of the right half of this suture line are reproduced in Pl. 13, fig. 1B (whitened) and 1C (unwhitened). (6H) Two complete external suture lines of GSC 49330 (Pl. 10, fig. 1A–H). These suture lines are dimly visible beneath the layer of ammonium chloride in the middle part of the penultimate whorl in Pl. 10, fig. 1B; they also are reproduced ×2 and in an unwhitened state in Pl. 10, fig. 1H. (6I) Lateral and auxiliary parts of three external suture lines of GSC 17167 (Pl. 8, fig. 3A–D). The external suture lines of this half-grown specimen still have only three auxiliary lobes, the third of which appears at the very umbilical rim. These suture lines are reproduced ×2 in Pl. 8, fig. 3D.

Textfigure 7. *Tollia* n. sp. aff. *T. klimovskiensis* Krimgolts 1953. The almost complete, terminal external suture line of specimen GSC 17172 in Pl. 8, fig. 5A–D. This suture line is reproduced at the lower end of Pl. 8, fig. 5A.

All suture lines are camera lucida drawings at approximately natural size. See Textfigs. 3 and 4 for legend.

One morphological extreme is exemplified by specimens GSC 17167 (Pl. 8, fig. 3D, Textfig. 6I), GSC 17174 (Pl. 9, fig. 1A, B, C, Textfig. 6A), GSC 49329 (Pl. 9, fig. 2B, C, F, Textfig. 6B), GSC 49332 (Pl. 12, fig. 2A, B, Textfig. 6C) and GSC 49335 (Pl. 14, fig. 1A, D, E), in which the suture lines resemble those of half-grown and adult representatives of *Tollia tolli* Pavlow sensu lato (including *T. tolmatschowi* and *T. latelobata*), other typical *Tollia* species as defined below (see generic description of *Tollia*), and adult representatives of *Temnoptychites* (*Temnoptychites*) *kemperi* n. sp. and *Temnoptychites* (*Costamenjaites*) *grandiosus* in the following respects:

1. The first and second lateral lobes, and in some cases the first auxiliary lobe, are either relatively broader than the preceding saddles (Pl. 8, fig. 3D, Textfig. 6I) or, at least, not much narrower (e.g., Pl. 9, fig. 1A, B, C, Pl. 12, fig 2A, B, Textfig. 6A, C).

2. The first and second lateral saddles and at least the first auxiliary saddle of the above-mentioned specimens are narrow and square. The shape and proportions of these saddles resemble closely those of the equivalent saddles of the adult suture line of *T.* (*C.*) *grandiosus* (Klimova, in Golbert *et al.*, 1972, Pl. IV, fig. 1) and those of the advanced, presumably adult suture lines of *T.* (*T.*) *kemperi* n. sp. (Textfig. 4A, D), which are even narrower in part. Furthermore, these saddles closely resemble the equivalent saddles of the adult suture lines of *Thorsteinssonoceras ellesmerense* (Textfig. 1V).

The remaining auxiliary saddles are much wider than the equivalent saddles of the adult sutures of *Temnoptychites* (*T.*) *kemperi* n. sp. and *Thorsteinssonoceras ellesmerense* and their width gradually increases adumbilically. The respective widths of these saddles are comparable with those of the equivalent saddles of adult (Klimova, *loc. cit.*) and advanced (Textfig. 5A) suture lines of *T.* (*C.*) *grandiosus* and with those of the equivalent saddles of *Tollia tolli* (e.g., Textfig. 1T). The gradual adumbilical widening of saddles represents a rather characteristic distinction of the herein discussed extreme form of *T.* (*C.*) *troelseni* n. sp.

3. The first and second lateral lobes and either the first auxiliary lobe or the first and second auxiliary lobes are intricately and deeply frilled, like those of *Tollia tolli* sensu lato (Textfig. 1Q, R, T). The first, and sometimes the second, lateral lobe ends in long, fingerlike, very acutely pointed terminal accessory lobes closely resembling those of the first (and sometimes the second) lateral lobe of *T. tolli* sensu lato (Pl. 8, fig. 3D, Pl. 9, figs. 1A, 2B, C, Textfig. 6A, B, C, I). These florid, *Tollia*-like lobes contrast with much more shallowly and simply indented lobes of most other *Temnoptychites* forms known.

4. The strongly ascendant *Temnoptychites*-like orientation of the suture line is restricted to the first and second lateral lobes and the first auxiliary lobe. The second to fourth (and the fifth, wherever present) auxiliary lobes become progressively less ascendant. Consequently the imaginary line connecting the tops of the lateral and auxiliary lobes forms a gentle, *Tollia*-like, forward convex curve (Pl. 9, figs. 1A, B, 2B, C, F, Textfig. 6A, B, C).

5. The fourth auxiliary lobe appears late. It is barely visible at the umbilical seam of specimen GSC 17167 at the whorl diameter of about 23 mm (Pl. 8, fig. 3D, Textfig. 6I), where the second auxiliary lobe still straddles the umbilical shoulder.

These characteristic features of the extreme form are maintained essentially unchanged from the earliest semiadult suture lines observed (e.g., Pl. 8, fig. 1D, Pl. 12, fig. 2B, Textfig. 6C, I) to the oralmost suture lines immediately adjoining the adult body chamber (e.g., Pl. 9, figs. 1A, B, C, 2B, C, F, Textfig. 6A, B). In particular, none of the studied representatives of this extreme form exhibits the slightest tendency toward the simplification of the oralmost suture lines so characteristic of the other extreme form of *T.* (*C.*) *troelseni* n. sp. (see below). Instead the suture lines gradually become more complex all the way to the beginning of the adult living chamber (Pl. 9, fig. 2B, C).

The *Tollia*-like features of semiadult to adult external suture lines of this extreme form of *T.* (*C.*) *troelseni* n. sp. were one of the reasons which prompted the proposed downgrading (Jeletzky, 1964, p. 38, Pl. V, figs. 1, 3, 4; 1973, p. 66) of the genus *Temnoptychites* to a subgenus of *Tollia* Pavlow 1914. Furthermore, they have resulted in the misidentification of one half-grown representative of the form (GSC 17167; *ibid.*, Pl. V, fig. 5D) for *Tollia tolli* Pavlow var. *latelobata* Pavlow.

The other morphologically extreme form of *T.* (*C.*) *troelseni* n. sp. is exemplified by specimens GSC 17176, 17164 and 49330 (Pl. 12, fig. 1A, D, E, Pl. 13, fig. 2A, C, Pl. 10, fig. 1A, Textfig. 6D, F, H). Specimens GSC 49333 (Pl. 13, fig. 1C, Textfig. 6G) and GSC 49331 (Pl. 11, fig. 1H, Textfig. 6E) probably belong to this extreme form also. However, the character of their terminal suture lines is unknown.

The semiadult suture lines of this extreme form lack all of the previously discussed *Tollia*-like features. These much more stubby and less denticulated suture lines resemble instead the semiadult suture lines of *T.* (*C.*) *grandiosus* (cf. Textfig. 5C) in most of their morphological features. The relative proportions (degree of diminution of lobes toward the umbilicus) of adjacent elements of the external suture line and the orientation of lateral and auxiliary parts of semiadult suture lines of the form of *T. troelseni* n. sp. discussed here do not appear to differ materially from those of equivalent suture lines of *T. grandiosus*. Furthermore, the number of auxiliary lobes is the same (four to five) in these two forms.

The semiadult suture lines of this extreme morphological form of *T.* (*C.*) *troelseni* n. sp. differ from those of *T.* (*C.*) *grandiosus* in an earlier appearance (at the whorl diameter of 17–18 mm) of the fourth auxiliary lobe. Furthermore, the constriction of oral parts of the lobes so characteristic of *T.* (*C.*) *grandiosus* tends to be either absent or very poorly developed in most representatives of our form (e.g., Pl. 11, fig. 1H, Pl. 13, fig. 1C, Textfig. 6E, G). However, this character is rather variable in the material studied and some well preserved specimens of our form (e.g., Pl. 10, fig. 1H, Textfig. 6H) exhibit lobes which are just as strongly constricted adorally as those of equivalent suture lines of *T.* (*C.*) *grandiosus*. It should be noted in this connection that the adoral constriction of semiadult lobes may yet be found to be just as variable in *T.* (*C.*) *grandiosus* as it is in *T.* (*C.*) *troelseni*. This character was observed only in the solitary Canadian specimen and in the northern Siberian holotype (Voronets, 1962, Pl. XXXVIII, fig. 2) but not in the Novaya Zemlya

representatives (e.g., Sokolov, 1913, Pl. 3, fig. 1a) of the species.

Generally, the representatives of the form of *T. (C.) troelseni* n. sp. discussed herein, characterized by the least denticulated sutures, exhibit the most markedly constricted lobes. In contrast, the specimens with the most strongly denticulated sutures tend to have lobes characterized by parallel to subparallel sides (cf. Pl. 10, fig. 1H, Pl. 12, fig. 1A, Pl. 13, fig. 1C, Textfig. 6E, G, H).

The lobes of the form of *T. troelseni* n. sp. discussed herein gradually become relatively narrower and correspondingly more elongated within the last half whorl or so before the beginning of the adult body chamber in all its appropriately preserved specimens. The intervening saddles gradually become correspondingly wider in the same interval. Finally, in most specimens the stems of all lobes become regularly pinched and their accessory lobes reduced to mere notches in the last three to four sutures approximately corresponding to the oralmost sixth of the last septate whorl (Pl. 10, fig. 1A, B, Pl. 12, fig. 1A, C, D, E, Textfig. 6D, F, G). Generally this gradual narrowing and simplification of the external lobes become apparent first in the adumbilicalmost lobes and then spread gradually to the more adventral lobes. The second and first lateral lobes are the last to be affected by this narrowing and simplification. The ventral lobe does not become appreciably narrowed even in the oralmost suture in any of the specimens studied, although it becomes appreciably simplified (Pl. 12, fig. 1C, E, Textfig. 6D, F).

Subspecies. It does not seem feasible to utilize the far-reaching morphological variation of semiadult to adult suture lines and other features of *T. (C.) troelseni* n. sp. for its subdivision into two or more independent species, let alone subgenera, for the following reasons:

1. All extreme morphological types of *T. (C.) troelseni* n. sp. described above are connected by at least some transitional forms. Where the extreme morphological types of external suture lines are concerned, specimens GSC 49329 and 49335 are obviously transitional. Specimen GSC 49329 (Pl. 9, fig. 2B, C, D, Textfig. 6B), which exhibits the beginning of the adult living chamber, is the best example of such a transitional form. The lateral and auxiliary lobes of this specimen are relatively deeply and abundantly denticulated in a *Tollia*-like fashion. Furthermore, the first lateral lobe is almost as wide as the first lateral saddle whereas the second lateral lobe is somewhat wider than the second lateral saddle. Finally, the lobes do not become appreciably narrowed, let alone pinched, even in the last few suture lines adjoining the living chamber. Hence it was left in the *Tollia*-like form of the species. However, the first and second lateral lobes are considerably longer and narrower than those of specimen GSC 17174 and other representatives of the *Tollia*-like variant of *T. troelseni* n. sp. and the first lateral lobe exhibits a distinct adoral constriction. Furthermore, the suture lines are distinctly crowded and the first lateral lobes begin to touch at the whorl diameter of about 33 mm well within the early half of the penultimate whorl. And yet this crowding does not develop into regular overlap even in the last few suture lines adjoining the living chamber.

As already mentioned in the description of *T. (C.)*

troelseni n. sp., all morphological extremes in the whorl shape (e.g., specimens GSC 17174 and 17176; Pl. 9, fig. 1, Pl. 12, fig. 1) also are connected by transitional forms (e.g., specimens GSC 49330, 17164 and 17175; Pl. 10, fig. 1, Pl. 13, figs. 2, 3). Furthermore, the same is true of all sculpturally extreme forms of the species as illustrated by the series of its representatives reproduced in Plates 8 to 14 of this paper.

2. The bulk of the morphologically extreme forms of *T. (C.) troelseni* n. sp. (except for specimen GSC 49334, Pl. 14, fig. 2) and all of the forms transitional between them have been found together and appear to be a sample of a single paleontological population.

3. All of the presently known morphological features of *T. (C.) troelseni* n. sp. appear to vary either independently, or semi-independently, from one another. Even the above-discussed far-reaching variation of the external suture line exhibits only a limited amount of correlation with the shape of the whorl and none whatsoever with the coarseness and mode of ribbing. It is true that all extremely slender and relatively small representatives of *T. (C.) troelseni* n. sp. studied do have *Tollia*-like external suture lines (e.g., GSC 17174, 49329, 49332; Pl. 9, figs. 1, 2, Pl. 12, fig. 2, Textfig. 6A–C). However, there are some sturdy and relatively small (e.g., GSC 17175, Pl. 13, fig. 3) or very large, presumably sturdy (GSC 49335, Pl. 14, fig. 1) forms possessing this type of suture line. The strong weathering of the suture line of GSC 17175 (p. 39) does not invalidate this conclusion. Its unweathered terminal suture lines must have been even more *Tollia*-like than their deeply weathered remnants.

4. An even greater range of infraspecific variation in all morphological characters, including the external suture line, is known to exist in other representatives of *Temnoptychites*. A good example is provided by *T. (T.) kemperi* n. sp. described earlier in this paper. Furthermore, just as great infraspecific variation is known to exist in at least some representatives of other craspeditid genera (e.g., Jeletzky, 1965b, 1966).

A pronounced infraspecific variation in the morphology of external suture lines characterizes, for example, *T. (C.) elegans* Bodylevsky, which seems to be closely allied to *T. (C.) troelseni* n. sp. Excellent photographs of one of the paratypes of *T. (C.) elegans* (Bodylevsky, 1967, Pl. III, fig. 1a) reveal that its semiadult to adult external suture lines resemble those of that extreme variant of *T. (C.) troelseni* n. sp. characterized by *Tollia*-like sutures in this respect at least. This paratype exhibits external suture lines that are even more *Tollia*-like than the equivalent sutures of the Canadian specimens GSC 17175 (Pl. 13, fig. 3E, D) or GSC 49332 (Pl. 12, fig. 2B, Textfig. 6C) in the adapically tapering shape of the lobes, in the relatively greater width of the lobes combined with the relatively lesser width of the preceding saddles, and in the deep indentation of the accessories of the first and second lateral lobes. However, these suture lines of *T. (C.) elegans* differ from the equivalent sutures of *T. (C.) troelseni* n. sp. in a much wider spacing of adjacent suture lines. Only the considerably earlier external suture lines of the Canadian specimen GSC 17167 (Pl. 8, fig. 3D, Textfig. 6I) are at all comparable to the advanced (possibly adult) external suture lines of this paratype of *T. elegans* in this respect.

In contrast, the holotype of *T. elegans* (see Bodylevsky, 1967, Pl. IV, fig. 1a) exhibits much more *Temnoptychites*-like

external suture lines than the paratype. Except for their much wider spacing, the suture lines of the holotype are comparable with the equivalent suture lines of the Canadian specimen GSC 49329 (Pl. 9, fig. 2, Textfig. 6B) in the relatively greater length, parallel-sided appearance and lesser indentation of its lateral lobes and in the relatively greater width of the first and second lateral saddles. As was already pointed out, this Canadian specimen is transitional between the two morphologically extreme forms of *T. troelseni* n. sp. where the appearance of its external suture line is concerned.

Craspedites (?*Taimyroceras*) *canadensis* Jeletzky exhibits a still greater subspecific range of variation of semiadult to adult suture lines, which parallels exactly that observed in *T.* (*C.*) *troelseni* n. sp. (Jeletzky, 1966, Fig. 1B–L).

Following the widely accepted explanation of similar distinctions in other ammonitid taxa (see Arkell *et al.,* 1957, p. L97, L98, Fig. 143), one might feel tempted to interpret the previously mentioned (p. 42) prevalent restriction of the *Tollia*-like external suture line to relatively small, extremely slender representatives of *T.* (*C.*) *troelseni* n. sp., in the sense that they are immature representatives of a much larger *Temnoptychites* form which died before reaching maturity, and were preserved with part or all of their immature living chamber intact. The representatives of the other extreme form characterized by simplified, closely approximated to partly overlapping penultimate and ultimate suture lines would then have to be interpreted as adult representatives of this same *Temnoptychites* form. Alternatively, one could assume that these two forms were respectively the male (the smaller form) and the female (the larger form) of *Temnoptychites troelseni* n. sp. Unfortunately these two hypotheses are contradicted by the observed breakdown of the correlation between the size of the shell and the character of the suture line. Some smaller specimens of about equal size may possess the last few suture lines, which have the character either of those of the *Tollia tolli*–like extreme form (e.g., GSC 17175, Pl. 13, fig. 3A, B) or of those of the other extreme morphological form (e.g., GSC 17164, Pl. 13, fig. 2C, D, Textfig. 6F). The same is true of the largest known specimens of *T. troelseni* n. sp. (e.g., GSC 49330, 49335, 49331) reaching a shell diameter of between 140 and 155 mm and retaining the almost complete living chamber. Of these GSC 49335 (Pl. 14, fig. 1A, E, F) and GSC 49331 have the last three suture lines, which are distinctly *Tollia tolli*–like in the width and denticulation of the first and second lateral and the first auxiliary lobes and saddles. Furthermore, these adjacent suture lines are somewhat crowded only insofar as their ventral and first lateral lobes barely begin to touch. Finally, these suture lines have only four auxiliary lobes. In specimen GSC 49330, in contrast, the last five or six suture lines are quite typical of the other extreme form (Pl. 10, fig. 1A, B, H), in spite of the fact that its living chamber begins at a considerably smaller whorl diameter than those of the other two specimens. Under these circumstances, it appears best to separate the morphologically extreme forms of *Temnoptychites* (*Costamenjaites*) *troelseni* n. sp. as its subspecies while leaving the rare and poorly preserved intermediate forms formally unnamed. Two such subspecies are recognized at present and named formally according to the Code of Zoological Nomenclature. The grouping of the studied representatives of *T.* (*C.*) *troelseni* n.

sp. according to the variation in the morphology of external suture line was preferred to other possible groupings since it commonly, if not always, correlates with the variation of the shape and proportions of the whorl. The proposed subspecies are as follows:

1. *Temnoptychites* (*Costamenjaites*) *troelseni* n. sp. subsp. *troelseni* n. subsp. Specimen GSC 17174, previously designated as the holotype of the species and reproduced in Plate 9, figure 1A–F and Textfigure 6A also is designated the holotype of this subspecies. The measurements of the holotype and two other best preserved representatives of the subspecies are as follows:

GSC no.	Figure	Diameter	Umbilicus	Height	Thickness
			mm		
17174	Pl. 9, fig. 1	74	11 (0.14)	36	24
17167	Pl. 8, fig. 3	57	10 (0.17)	28	23
49332	Pl. 12, fig. 2	68	11 (0.16)	34	20

( ) Fraction of diameter.

Temnoptychites (*C.*) *troelseni* subsp. *troelseni* n. subsp. is characterized by the *Tollia*-like appearance of all semiadult to adult external suture lines. This suture line remains extremely florid and deeply denticulated all the way to the beginning of the adult living chamber. The oralmost few suture lines do not exhibit any signs of either constriction of the lobes or widening of the intervening saddles. This *Tollia*-like appearance of the external suture lines is usually, but not invariably, coupled with an extremely slender and high, discuslike cross-section of the adoralmost three whorls (including the adult living chamber), in which the width comprises 0.60 to 0.70 per cent of its diameter. The subspecies is generally, but not always, characterized by moderately small adults, the whorl diameter of which usually does not exceed 100 to 110 mm.

2. *Temnoptychites* (*Costamenjaites*) *troelseni* n. sp. subsp. *crassus* n. subsp. Specimen GSC 17176 reproduced in Plate 12, figure 1A–G and Textfigure 6D is designated herewith as the holotype of this subspecies. The approximate measurements of the weakly deformed holotype and the only other almost undeformed representative known are as follows:

GSC no.	Figure	Diameter	Umbilicus	Height	Thickness
			mm		
17176	Pl. 12, fig. 1A–H	93	21 (0.22)	43	40
17164	Pl. 13, fig. 2A–C	89.3	15 (0.16)	40	31

( ) Fraction of diameter.

Temnoptychites (*C.*) *troelseni* subsp. *crassus* n. subsp. is characterized by a semiadult external suture line which differs from that of *T.* (*C.*) *troelseni* subsp. *troelseni* n. subsp. in having a considerably stubbier and less denticulated appearance of all its elements. This semiadult suture line, which closely resembles that of *T.* (*C.*) *grandiosus,* except in the characteristic crowding and partial overlap of adjacent sutures, gradually becomes progressively more simplified in the adult growth stage. Finally, in the oralmost few suture lines immediately preceding the adult living chamber, all lateral and auxiliary lobes become very narrow to regularly pinched, with their accessory lobes reduced to mere notches in most specimens studied. The intervening saddles of these suture lines become two to three times wider than the adjacent

lobes. This diagnostic suture line is usually, but not invariably, coupled with a fairly sturdy, rounded-triangular cross-section of the intermediate and adult whorls in which the width comprises 0.80 to 0.95 per cent of the diameter; these whorls generally are *T. (C.) grandiosus*–like.

Discussion: Temnoptychites troelseni n. sp. was identified previously with *Olcostephanus novosemelicus* Sokolov 1913, which is a representative of the same nodeless species group of the genus *Temnoptychites* (Jeletzky, 1964, p. 38, Pl. V, figs. 1, 4; 1973, p. 66, Figs. 2, 3). This Novaya Zemlya species is indistinguishable from the subspecies *troelseni* n. subsp. of the Canadian form in the shape and proportions of the whorl (including those of the umbilicus). The ribbing habits of these two forms also are similar at all comparable growth stages (Sokolov, 1913, Pl. 3, fig. 2a, b). However, the Novaya Zemlya form exhibits the following morphological distinctions, which are judged to be sufficiently important taxonomically for its specific separation from the Canadian analogue.

1. As pointed out by Sokolov (1913, p. 74, 75), the secondary ribs of the unique representative of *T. novosemelicus* known are completely interrupted in the midventer at whorl diameters of 48 to 56 mm. However, they begin to cross the midventer again soon thereafter on the early part of the living chamber. This does not happen in any of the studied representatives of *T. troelseni* n. sp. in which the midventral interruption of secondaries persists until the complete loss of the sculpture on the living chamber.

2. As is clearly visible in Sokolov's (1913, Pl. 3, fig. 2a) photograph of the ultimate whorl of *T. novosemelicus,* the trichotomous rib bundles remain well defined and the sculpture does not become effaced on the midflank even on the preserved part of the presumably adult living chamber. This feature, too, is absent in all studied specimens of *T. troelseni* n. sp. In these specimens, the connection between the strengthened upper parts of secondary ribs and the likewise strengthened lower parts of primary ribs is invariably and permanently lost much earlier on the early, still fully septate part of the penultimate whorl.

3. The primary ribs of *T. (C.) novosemelicus* are relatively much more widely spaced on the preserved fragment of the living chamber (*ibid.,* p. 74, Pl. 3, fig. 2a) than the primaries of the corresponding growth stages of *T. (C.) troelseni* n. sp. Furthermore, unlike the primaries of *T. (C.) troelseni* n. sp., the primaries of *T. (C.) novosemelicus* become much more widely spaced on the living chamber than they are on the earlier whorl. As far as it is possible to judge from the fragmentary holotype, which is the only known representative of *T. (C.) novosemelicus,* the primaries of the Novaya Zemlya species differ from those of *T. (C.) troelseni* n. sp. in exactly the same way as do those of *T. (C.) elegans* (see below for further details).

4. The semiadult external suture line of *Temnoptychites novosemelicus* (*ibid.,* p. 72, Pl. 3, fig. 2a) differs pronouncedly from that of *T. (C.) troelseni* n. sp. in a complete absence of crowding, let alone partial overlap, of adjacent sutures so characteristic of the Canadian species (see above). The suture line of *T. (C.) novosemelicus* also differs in the considerably stubbier, adapically tapering shapes of the first and second lateral and the first and second auxiliary lobes. Furthermore,

its auxiliary part bends abruptly adapically and becomes radially oriented. This does not happen even in the most *Tollia tolli*–like examples of *T. troelseni* n. sp. suture lines. Finally, and most important (*ibid.,* p. 72), the suture line of *T. novosemelicus* is said to be the same as that of *Olcostephanus juvenescens* Keyserling and *Olcostephanus diptychus* Keyserling. Should this be true (cf. Sokolov, 1913, p. 83, Fig. IVb, c, Pl. 2, fig. 4b), and the issue cannot be decided without inspecting the holotype, *Olcostephanus novosemelicus* would have a rather primitive craspeditid suture line with no more than three auxiliary lobes at the growth stage, where *Temnoptychites troelseni* n. sp. has a much more advanced suture line with at least four auxiliary lobes. Because of these important morphological distinctions, *T. (C.) troelseni* n. sp. is not believed to be either conspecific with or closely related to *T. (C.) novosemelicus* (Sokolov). However, there seems to be no good reason to segregate the two species on the subgeneric level (see below under the comparison of *T. (C.) troelseni* and *T. (C.) elegans*).

A number of morphological features of *Temnoptychites (Costamenjaites) troelseni* n. sp. subsp. *troelseni* n. subsp., as typified by the holotype, match closely those of *T. elegans* Bodylevsky 1949. Its previously figured representatives (Jeletzky, 1964) have been synonymized with this Novaya Zemlya species by Shulgina (in Saks *et al.,* 1972, p. 113). The Canadian form is indeed indistinguishable from *T. elegans* Bodylevsky in the shape and proportions of adult ultimate and penultimate whorls (including those of the umbilicus). However, the two differ markedly in the ornamentation of the penultimate whorl (the earlier whorls of *T. elegans* were not described by Bodylevsky, 1949, 1967).

As Bodylevsky pointed out (1967, p. 104), *T. elegans* is characterized by the secondary ribs forming well defined bundles consisting mainly of five to seven ribs. This arrangement of ribs is clearly visible in at least two of three specimens of *T. elegans* figured by Bodylevsky (1967, Pl. III, fig. 1b, Pl. IV, fig. 1b), including its holotype. The alternation of these complex virgatitid, bidichotomous or polyptychitid rib bundles appears rather early in the ontogeny of *T. elegans*. For example, in the holotype (see Bodylevsky, 1949, Pl. LIV, fig. 2; 1967, Pl. IV, fig. 1b), quadrichotomous to quintichotomous rib bundles, which are attached somewhat indistinctly to the short primaries, are already present on the earliest exposed part of the whorl with the diameter of about 22 mm.

The corresponding growth stages of *T. troelseni* n. sp. subsp. *troelseni* n. subsp. exhibit an entirely different ornament consisting of irregularly alternating dichotomous and trichotomous rib bundles separated by one or two intercalated secondaries restricted to the upper third to two thirds of the flank (Pl. 8, fig. 3A, Pl. 9, figs. 1A, B, 2A, Pl. 10, fig. 1B, Pl. 12, fig. 2A, B). In most of the representatives studied of *T. troelseni* n. sp. subsp. *troelseni* n. subsp., including the holotype, the ribbing habit persists onto the early part of the penultimate whorl where it grades into the sculptureless growth stage, which begins with the weakening and then complete loss of sculpture on the middle parts of flanks. As far as it is possible to tell, even the quadrichotomous rib bundles, such as are common on the earliest part of penultimate whorl of the holotype of *T. elegans*

(Bodylevsky, 1967, Pl. IV, fig. 1b), never appear on the distinctly sculptured part of the penultimate whorl of this form of *T. troelseni* n. sp. immediately preceding its sculptureless, final growth stage. There is no trace of even more complex rib bundles consisting of five to seven secondaries, such as are common in the largest paratype (*ibid.,* Pl. III, fig. 1b) of *T. elegans,* on any part of the penultimate whorl of *T. troelseni* n. sp. subsp. *troelseni* n. subsp.

The third representative of *T. elegans* figured by Bodylevsky (1967, Pl. II, fig. 1a, b) resembles more closely *T. troelseni* n. sp. subsp. *troelseni* n. subsp. where the ribbing habit (mostly trichotomous rib bundles) is concerned. However, this specimen differs from all known representatives of the Canadian species because its primary ribs become relatively much more widely spaced on the adoral third of the preserved penultimate whorl. This results in a much smaller number of primaries per penultimate whorl of this specimen as compared with the analogous form of *T. troelseni* n. sp. As pointed out by Bodylevsky (1967, p. 104, table of measurements) and clearly visible in his photographs, the specimen concerned has only 13 primary ribs on the exposed whorl. These relatively fewer primary ribs on the penultimate whorl are a constant feature of *T. elegans* since it occurs in its other figured and measured specimens (*ibid.,* p. 104, table of measurements, Pl. IV, fig. 1b), including the holotype. The latter has 17 primary ribs on the preserved penultimate whorl. In contrast, all representatives of the studied population sample of *T. troelseni* n. sp., including its subsp. *troelseni* n. subsp., have 19 to 23 primaries on the penultimate whorls. Furthermore, the primary ribs of the Canadian species do not become much more widely spaced than before on the adoralmost part of penultimate whorl and retain their close spacing until they disappear completely either on the adoralmost part of the phragmocone (Pl. 10, fig. 1B) or on the early part of the adult living chamber (Pl. 13, fig. 2A).

Another important distinction of the ornament of *T. elegans* from that of *T. troelseni* n. sp. subsp. *troelseni* n. subsp. is that the former has a much greater coefficient of branching. For example, the paratype of *T. elegans* reproduced in Bodylevsky's (1967) Plate II, figure 1 has 92 or 93 secondary ribs per whorl, which is ornamented with only 13 primary ribs. This results in the branching coefficient of 7.1. Even the coarser ribbed holotype (*ibid.,* p. 104, table of measurements, Pl. IV, fig. 1) has a branching coefficient of 4.9. In contrast, the branching coefficient in the studied material of *T. troelseni* n. sp. does not exceed 4.6.

Yet another distinction of *T. troelseni* n. sp. from *T. elegans* consists in its sculpture, which begins to weaken on the flank at a considerably earlier growth stage. This happens on the earliest part of the penultimate whorl (at whorl diameters ranging from 17 to 32 mm) soon or immediately after the trichotomous rib bundles and intercalated secondaries make their first appearance in most of the specimens available. In *T. elegans,* in contrast, well defined rib bundles persist over most or all of the penultimate whorl (*ibid.,* Pl. II, fig. 1b, Pl. III, fig. 1b, Pl. IV, fig. 1b).

Finally, *T. elegans* is characterized by an interruption or a marked weakening of secondary ribs on the midventer in all growth stages studied (*ibid.,* p. 104). This is not the case in any of the studied representatives of *T. troelseni* n. sp. where the secondary ribs are only somewhat to moderately weakened on the midventer until the last third of penultimate whorl. Moreover, the secondaries are completely interrupted only in the shell-covered parts of the venter of *T. troelseni* n. sp. on this part of the penultimate whorl (e.g., Pl. 9, figs. 1E, 2E) as the interruption is imprinted only weakly on the inner surface of the shell.

The semiadult and adult external suture lines of *T. (C.) elegans* differ pronouncedly from those of all studied representatives of *T. (C.) troelseni* n. sp., including its subsp. *troelseni* n. subsp., because they lack the above-discussed crowding and partial overlapping of the adjacent sutures so characteristic of the latter species. Nor do any of the external suture lines figured by Bodylevsky (1967, Pl. III, fig. 1a, Pl. IV, fig. 1a) exhibit the simplified and constricted lateral and auxiliary lobes in the proximity of the adult living chamber, which are characteristic of *T. (C.) troelseni* subsp. *crassus* n. subsp.

The distinctions of ornament and external suture lines discussed above are deemed to be ample for the specific differentiation of even the most slender representatives of *T. (C.) troelseni* n. sp. subsp. *troelseni* n. subsp. from *T. (C.) elegans.* The sturdier forms of *T. (C.) troelseni* n. sp. are even more unlike this Eurasian species. Therefore, the two species are believed to be homeomorphic, shortlived offshoots of the main stem of the subgenus *Costamenjaites* rather than closely related, vicarious species of this subgenus. These offshoots apparently evolved independently in different basins of the early Valanginian Boreal Ocean following the initial migration of *Costamenjaites* into the Canadian Arctic region (Textfig. 2).

Temnoptychites (Costamenjaites) troelseni n. sp. cannot be confused easily with *T. (C.) grandiosus* Voronets 1962 (inclusive of *T. inflatus* Bodylevsky 1967) because the latter species is characterized by the persistence of a sparse and more prominent, exclusively dichotomous ribbing habit to the whorl diameters of 50 to 60 mm, and grows incomparably larger. Furthermore, the external adult suture lines of these two species differ greatly.

Temnoptychites (Costamenjaites) jucundus (Sazonova 1971) and *T. (C.) suraense* (Sazonova 1971), belonging to the same subgenus as *T. (C.) troelseni* n. sp., lose their sculpture much earlier. In *T. jucundus,* the shell surface becomes completely smooth at the whorl diameter of about 25 mm. Furthermore, the sculpture of this species is sharp only at whorl diameters less than 15 mm and the rib bundles become trichotomous at a whorl diameter of about 18 mm (Sazonova, 1971, Pl. XX, fig. 4, Pl. XXI, fig. 1). The shell surface of *T. suraense* becomes completely smooth at the whorl diameter of about 25 mm and the rib bundles become either trichotomous or bidichotomous on the earliest exposed part of the holotype at approximate whorl diameter of 12 mm (*ibid.,* Pl. XXI, fig. 2b).

As presently known, the morphological distinctions of *T. (C.) troelseni* n. sp. do not seem to warrant the erection of a new, endemic subgenus of *Temnoptychites* for it alone. However, this tentative conclusion may have to be revised in the future when the mode of the morphological variation of *T. (C.) troelseni* and its subspecies will be better understood and the stratigraphic position of the species in the lower Valanginian succession of the Sverdrup Basin will be

definitely established. Furthermore, the previously mentioned similarity of the external suture line of *T. (C.) troelseni* to that of *Homolsomites* ex gr. *quatsinoensis* must be studied closely before any final conclusion about the subgeneric status of *T. (C.) troelseni* n. sp. can be reached.

<div align="center">

Genus *Tollia* Pavlow 1914
(= *Neotollia* Shulgina 1969 subj.
= *Bojarkia* Shulgina 1969 subj.)

</div>

Type species: *Tollia tolli* Pavlow 1914. Selected originally by Krimgolts (in Krimgolts, *et al.*, 1953, p. 74). This selection was repeated subsequently by Arkell (in Arkell *et al.*, 1957, p. L344), apparently in ignorance of the preceding selection made in a local Soviet publication difficult to find.

Historical remarks. The genus *Tollia* was erected by Pavlow (1914, p. 38) for (writer's translation from Russian): "an interesting group of Olcostephanidae, close to *Simbirskites* and differing [from that genus (translator's remark)] in absence of clearly expressed small nodes at points of division of umbonal ribs, [presence of (translator's remark)] distinctly expressed constrictions, and the suture line with a greater number (two more) of auxiliary saddles than in *Simbirskites*. This suture line advances forward as it progresses from the siphonal margin to the first auxiliary saddle.

"The forms belonging herein exhibit a considerable similarity to *Simbirskites* of the *Discofalcati* group and appear to be genetically connected with it. *Simbirskites payeri* with very feebly expressed small nodes and with constrictions on inner whorls is a form situated near the borderline of the two genera."

Three similar species from Klimovsky Bluff on Anabar River, eastern Siberia have been assigned to the genus *Tollia* by Pavlow (1914, p. 39–42, Pl. XII, figs. 1–3, Pl. XIII, figs. 1, 2). These species – *Tollia tolli, T. tolmatschowi* and *T. latelobata* – are, in the writer's opinion, morphological variants and morphologically different growth stages of the same polytypic species *T. tolli* Pavlow 1914.

Many *Tollia*-like early Early Cretaceous ammonites from central Russia (e.g., Bodylevsky, 1956), Novaya Zemlya (e.g., Salfeld and Frebold, 1924; Bodylevsky, 1967), western Siberia (Klimova, 1960), eastern Siberia (Krimgolts, in Krimgolts *et al.*, 1953; Voronets, 1962), eastern Greenland (Spath, 1936; Donovan, 1964), Canada (Jeletzky, 1964, 1965a, 1968, 1973), western U.S.A. (Imlay and Jones, 1970) and northwestern Europe (e.g., Kemper, 1964, 1968; Neale, 1962) have been assigned to *Tollia* since the beginning of this century. A few more species from northern and western Siberia have been published recently in the paleontological part of a comprehensive Soviet work on the Jurassic-Cretaceous boundary beds and the Berriasian stage in the Boreal Realm (e.g., Shulgina and Klimova, in Saks *et al.*, 1972). An attempt was made recently (Shulgina, in Saks and Shulgina, 1969, p. 42, 48, 49, Pl. I, fig. 3, Pl. II, figs. 1, 2) to return to the original concept of *Tollia* promulgated by Pavlow (1914) by segregating the somewhat sturdier and more widely umbilicate latest Berriasian and earliest Valanginian forms similar to *Tollia payeri* (Toula 1874) into a new genus *Bojarkia* Shulgina 1969 and by placing other somewhat aberrant, allegedly early

Valanginian forms previously assigned to *Tollia* (e.g., by Krimgolts *et al.*, 1953) to a new genus *Neotollia* Shulgina 1969.

Concept of genus. The numerous records of *Tollia* in many regions of the Boreal Realm contributed considerably to our understanding of its morphology, genetic relationships with other craspeditid genera, time range, and geographic distribution. However, they have made it somewhat difficult to interpret and to delimit *Tollia* from its craspeditid, polyptychitine and dorsoplanitine homeomorphs. As pointed out in the general taxonomic and nomenclatorial comments, these difficulties are caused primarily by the tendency of many recent workers on Craspeditidae to neglect, or even to ignore completely, the evidence of external suture line and to rely almost exclusively or even exclusively on details of shell sculpture and whorl shape when either assigning their geographically isolated *Tollia*-like ammonites to the genus *Tollia* or excluding them from it. Some of these workers, particularly Soviet (Voronets, 1962; Bodylevsky, 1967; Sazonova, 1971), northwestern European (e.g., Kemper, 1964, 1968) and British (e.g., Neale, 1962; Casey, 1973) workers, either did not figure any external suture lines of ammonites concerned, or figured only nondiagnostic fragments of such suture lines. This makes it impossible to decide whether such recently introduced *Tollia*-like genera as *Peregrinoceras* Sazonova 1971, *Paratollia* Casey 1973 and *Subpolyptychites* Sazonova 1971 are but junior synonyms based on somewhat aberrant representatives of *Tollia,* valid craspeditid genera, or polyptychitid homeomorphs of *Tollia.* Furthermore, this makes questionable the current generic assignment of some sculpturally aberrant forms, such as *Tollia kordikovi* (Bodylevsky MS, published by Voronets, 1962), *Tollia subtilis* Voronets 1962, *Tollia emelianzevi* Voronets 1962, or *T. pakhsaensis* Voronets 1962.

In the writer's opinion, "*Subcraspedites*" *groenlandicus* (Spath, 1936, p. 84, footnote, Pl. 34, fig. 5, Pl. 36, figs. 3–5) is not *Tollia,* as assumed by Shulgina (in Saks *et al.*, 1972, p. 132) and some other workers, but *Praetollia,* either closely allied to or possibly conspecific with *P. antiqua* Jeletzky (1973, p. 74–76, Pl. 4, fig. 1a–d, Pl. 5, fig. 1a–d, Pl. 7, fig. 1a–d). The widely spaced, apparently considerably heavier primaries of the holotype are internal casts which compare favourably with the similarly preserved primaries of the largest known representative of *P. antiqua* (Jeletzky, 1973, Pl. 7, fig. 1a) while the much finer, sharp-topped, and closely spaced primaries of the smaller paratypes (Spath, 1936, p. 4, 5, Pl. 36) match closely those of the shell-covered inner whorls of *P. antiqua* (Jeletzky, 1973, Pl. 5, fig. 1b, d). The suture lines of the two forms also resemble each other very closely. Finally, the stratigraphic position of "*Subcraspedites*" *groenlandicus,* which is only about 8 m stratigraphically above the *Titanites* horizon containing true *Craspedites* (Spath, 1936, p. 84), strongly suggests its uppermost Jurassic (late late Tithonian or late late Volgian) age corresponding to that of *Praetollia antiqua* in the Sverdrup Basin (Jeletzky, 1973, p. 47, Figs. 2, 3).

The scarcity of data regarding the external suture lines of many *Tollia*-like forms and the scarcity or absence of comparative material of these forms and of typical representatives of *Tollia* from Novaya Zemlya and northern Siberia in the western European and Canadian (the private

collection of Dr. Hans Frebold) collections studied by the writer prevent him from attempting a comprehensive review of the genus at this time. This is not critical for the purpose of this paper because no *Tollia*-like forms comparable to *Peregrinoceras, Propolyptychites* or *Paratollia* are present in the Sverdrup Basin collections studied. However, it is necessary at this time to deal with a part of the problem, namely the taxonomic validity of the genus *Neotollia* Shulgina 1969. Three out of four *Tollia*-like forms described below (*Tollia* n. sp. aff. *T. klimovskiensis, T.* n. sp. aff. *T. subtilis* Voronets, and *T.* n. sp. aff. *T. vai*) are closely comparable with *Neotollia*, whereas the remaining form (i.e., *Tollia* aff. *T. tolli*) is more closely comparable with *Tollia* as restricted by Shulgina (in Saks and Shulgina, 1969; and in Saks *et al.*, 1972).

The assignment by recent authors of a great bulk of morphologically diverse *Tollia*-like forms from various, usually geographically remote, regions of the Boreal Realm into the genus *Tollia* certainly makes it advisable to try to subdivide this genus. However, the attempted subdivision into *Tollia* sensu stricto and *Neotollia* is unacceptable to the writer for the following reasons. Shulgina (in Saks *et al.*, 1972, p. 166, 167; writer's translation from Russian) uses the following morphological features for separation of *Neotollia* from *Tollia* sensu stricto:

"1) The shape of *Tollia* shells differs, as a rule, from that of *Neotollia* in a greater flattening of the flanks. At equal diameters the average thickness of the shell of *Tollia tolli* Pavlow comprises 30 to 35 per cent of the diameter. That of *Neotollia* comprises 40 per cent, though there are some representatives of *Neotollia* which possess flattened flanks.

"2) The shape of whorl cross-section of *Tollia* has the appearance of an oval the height of which is strongly elongated. In *Neotollia* the cross-section is wider and lower; it becomes trapezoidally shaped in the adult whorls.

"3) The shell of *Tollia* is more evolute than that of *Neotollia*. In similarly large shells, the width of the umbilicus comprises 25 to 30 per cent of the diameter in *Tollia* while in *Neotollia* it comprises 15 to 25 per cent.

"4) The sculpture of early and middle growth stages of *Tollia* up to the diameters of 50 to 60 mm is represented predominantly by trichotomous rib bundles while that of *Neotollia* is represented predominantly by dichotomous rib bundles.

"In the growth stages with diameters of 60 to 70 mm, representatives of the two genera resemble each other very closely. However, the above-cited distinctions suffice to differentiate these two ammonite genera."

Shulgina (in Saks and Shulgina, 1969, p. 49; writer's translation from Russian) also notes: "The suture line [of *Neotollia* (writer's remark)] closely resembles that of representatives of the genus *Tollia* in its structure and orientation. However, the suture line differs in having narrower and longer lobes. It is considerably denticulated and consists of nine lobes, five or six of which are auxiliaries. The suture line is fanlike directed; that is, it goes up [i.e., adorally (writer's remark)] at first and then begins to descend as it approaches the umbilical shoulder."

Finally, Shulgina attempts (*loc. cit.*) to support the proposed subdivision of the genus *Tollia* by the differences in stratigraphic ranges of *Tollia* sensu stricto and *Neotollia*.

According to Shulgina (*ibid.*, p. 44, 48, 49, Table 1), representatives of *Tollia*, as restricted by herself, are all but confined, to the upper Berriasian Zone of *"Bojarkia" mesezhnikowi* while those of *Neotollia* are confined to the immediately overlying lowest Valanginian *"Neotollia" klimovskiensis* zone.

The tenuous nature of distinctions discussed in paragraphs 1 to 3 is readily apparent from Shulgina's (*loc. cit.*) own differential diagnosis. The ranges of all dimensions stated to be diagnostic of *Tollia* and *Neotollia* either overlap or differ by a maximum of 5 per cent. In the writer's experience, such trivial distinctions usually fall well within the range of infraspecific variation of craspeditid ammonites (see above descriptions of *Temnoptychites kemperi* n. sp. and *T. troelseni* n. sp.; also descriptions of *Craspedites canadensis* and *Thorsteinssonoceras ellesmerense*, in Jeletzky, 1965b, 1966; and description of *Tollia mutabilis* provided by Imlay, 1960, and Imlay and Jones, 1970), which were collected from the same locality and bed and freely intergrade morphologically. The intergradation of the morphological features in Siberian *Tollia* and *Neotollia* is admitted by Shulgina (in Saks *et al.*, 1972, p. 166, 167) in the differential diagnosis translated above and in the following remarks on the individual representatives of *Neotollia*. It is obviously wrong to try to use the trivial distinctions listed under paragraphs 1 to 3 of the differential diagnosis for definition of any supraspecific taxons.

The morphological distinctions between the external suture lines of *Tollia* and *Neotollia* also are unsuitable for differentiation of either genera or subgenera because of their extremely strong infraspecific and infrageneric variability fully discussed earlier in this paper (see generic description of *Temnoptychites*). A good example of the extreme infraspecific and infrageneric variability of these suture lines is provided by Shulgina (*ibid.*, p. 140, 141, Figs. 10-6a, 10-6b, 10-8, 11-1, 11-3, 11-4, 11-11, 12-4, 12-11, 12-12). Her drawings of the suture lines of *Tollia* and *Neotollia* clearly indicate that the sutures of specimens assigned to *Tollia tolli* vary all the way from characteristically *Tollia* sensu stricto–like (*ibid.*, Fig. 10-8) to equally characteristically *Neotollia klimovskiensis*–like (*ibid.*, Fig. 11-1). The same is true of the sutures of specimens assigned to *Neotollia*, since the sutures of *"Neotollia" maimetschensis* are completely *Tollia tolli*–like (*ibid.*, Figs. 10-6a, 10-6b) and contrast with the *Neotollia*-like sutures of *"Neotollia" klimovskiensis* (*ibid.*, Figs. 10-7, 10-10) or *"Neotollia" klimovskiana* (*ibid.*, Fig. 11-3).

The sculptural differences of early and intermediate growth stages of *Tollia* and *Neotollia* mentioned in paragraph 4 above do not seem to be taxonomically significant on the generic, or even subgeneric, level either, because conclusions of Saks and Shulgina (1969, p. 42–44, Table 1; and in Saks *et al.* 1972) about time ranges and infraspecific variability of all *Tollia* species distributed by them between *Tollia* sensu stricto and *Neotollia* are apparently invalid. The writer questions the validity of Saks and Shulgina's (*loc. cit.*) claim that representatives of the genus *Tollia* sensu stricto are confined largely to the upper Berriasian beds (*"Bojarkia" mesezhnikowi* Zone of northern Siberia) immediately underlying the lower Valanginian beds (*"Neotollia" klimovskiensis* Zone of northern Siberia) characterized by predominant representatives of *Neotollia*. As Shulgina admits (in Saks *et al.*, 1972, p. 162), the

exact age of beds in Klimovsky Bluff, Anabar River, which have yielded the type material of *Tollia tolli* sensu lato (including *T. tolmatschowi* and *T. latelobata*), remains uncertain. In the writer's opinion, this is an understatement of the evidence opposed to the late Berriasian age of beds containing *Tollia tolli* sensu lato in the Klimovsky Bluff section. The early Valanginian age of Pavlow's (1914) original species material is indicated by Saks and Shulgina's (in Saks *et al.*, 1972, p. 106) citation of *Tollia tolli* sensu lato, *T.* cf. *T. vai*, *Tollia* sp., *Neotollia klimovskiensis* and *N. klimovskiana* from the same 7 to 8 m thick unit of glauconitic aleurolites of this section. Furthermore, the numerous craspeditid and polyptychitid ammonites from Klimovsky Bluff described or listed by Pavlow (1914) and subsequent workers (e.g., Krimgolts, in Krimgolts *et al.*, 1953, p. 15; Shulgina, in Saks and Shulgina, 1969, p. 49–52, Pl. II, figs. 1, 2; Shulgina, in Saks *et al.*, 1972, p. 162, 167) do not include any late Berriasian forms comparable with those found in *"Bojarkia" mesezhnikowi* Zone of Khatanga Basin where *Tollia tolli* sensu lato was also found (Bassov *et al.*, in Saks *et al.*, 1972, p. 28). Finally, *Tollia tolli* sensu lato was reported to range into the lower lower Valanginian beds on Novaya Zemlya (e.g., Bodylevsky, 1967, p. 101, 102, Pl. IX, fig. 5; Salfeld and Frebold, 1924, p. 8, Pl. IV, figs. 2, 3) and almost to the base of beds containing the first representatives of *Polyptychites conferticosta* and *Euryptychites pateraeformis* in the stratigraphic section measured by T.M. Emeliantsev (in Voronets, 1962, Fig. 3) along the left shore of Anabar Bay and the eastern shore of Paks Peninsula. The sum of these data points to the conclusion that, contrary to Shulgina's (*loc. cit.*) ideas, *Tollia tolli* sensu lato ranges through and is equally common in the beds containing *"Bojarkia" mesezhnikowi* and those containing *Tollia klimovskiensis*, regardless of whether or not these beds are regionally superimposed faunal zones or are essentially contemporary faunal facies of the same lowest Valanginian *Tollia tolli* Zone. Furthermore, there is little doubt that in northern Siberia typical *Tollia* ex gr. *T. tolli* range still higher up into the beds containing *Temnoptychites* spp. and assigned to *Temnoptychites syzranicus* Subzone of *Polyptychites stubendorffi* Zone by Saks and Shulgina (in Saks *et al.*, 1972, p. 106).

Finally, the writer's conclusions are supported by Shulgina's statement (*ibid.*, p. 167; writer's translation from Russian) that: "among *Neotollia*, apart from typical forms similar to *Neotollia klimovskiensis* (Krimgolts), there are specimens with strongly convex flanks and a suture line in which the lobes and saddles are considerably shorter than those of the holotype. On the other hand, specimens occur which have considerably flatter flanks than those of *T. klimovskiensis*. These specimens are very close to *Tollia tolli* Pavlow in the shape of their shells. However, there is no need to separate them into independent genera or subgenera. First, they are all united by the uniform type of sculpture, and second there are intermediate forms among them."

On the whole, the writer is convinced that Shulgina's (*loc. cit.*) genera *Tollia* sensu stricto and *Neotollia* are not natural supraspecific paleontological taxons succeeding each other in time but merely extreme morphological types intergrading with each other through most or all of the time range of *Tollia*. It may be that *Tollia tolli*–like morphological types appear

earlier than the *Tollia klimovskiensis*–like morphological types and become rare near the top of the known span of existence of *Tollia* in northern Siberia and elsewhere. However, the apparent persistence of *Tollia* aff. *T. tolli* into the equivalents of *Pseudogarnieria undulatoplicatilis* Zone in Sverdrup Basin (Textfig. 8) is against such a hypothesis. Even if this hypothesis were true, such restriction of *T. tolli* and *T. klimovskiensis* time ranges would indicate their interpretation as successive paleontological species of *Tollia* plexus and not as independent genera or subgenera of Craspeditidae.

Shulgina's proposal (in Saks and Shulgina, 1969, p. 43, Table 1) to exclude *Tollia payeri* (Toula 1874) and morphologically similar, newly erected northern Siberian *Tollia* forms (e.g., *Bojarkia mesezhnikowi* Shulgina 1969 and *B. bodylevskii* Shulgina 1972) from the genus *Tollia* and to place them into the new genus *Bojarkia* Shulgina 1969 also is unacceptable to the writer. As Shulgina pointed out (in Saks *et al.*, 1972, p. 159; writer's translation from Russian): "The new forms are allied to representatives of *Tollia* in the character of sculpture of their inner whorls. Namely, they are characterized by the presence of fine and closely spaced, bifurcating and trifurcating ribs (Tollias also have bifurcating and trifurcating ribs). The sculpture of large outer whorls also is similar to that of *Tollia*. However, the sculpture of the intermediate whorls is distinctive. That of *Bojarkia* consists predominantly of bifurcating ribs which are very elevated throughout while *Tollia* has no less than 3 to 4 secondary ribs which are subdued in the middle of the flanks. Tollias are characterized also by a relatively higher cross-section and by a more involute shell."

In the writer's opinion, all of these distinctions are extremely trivial. The values of relative height of the cross-section and of the degree of involution of the shell of *Bojarkia bodylevskii* given by Shulgina (*ibid.*, p. 160) do not differ materially from those given for a number of sturdier and widely umbilicate *Tollia* and *Neotollia* forms (Shulgina, *ibid.*, p. 161, 166, 167). The same is true of *B. mesezhnikowi* (Shulgina, in Saks and Shulgina, 1969, p. 48). The predominantly bifurcating sculpture of intermediate whorls alleged to be characteristic of *Bojarkia* also occurs in *Tollia*, particularly in those relatively lower whorled forms unnecessarily assigned to *Neotollia* by Shulgina (in Saks *et al.*, 1972, p. 166). The prominent ribs on intermediate whorls and the lack of their weakening in their midflanks is by no means diagnostic of forms assigned to *Bojarkia*. In fact, *Tollia* aff. *T. tolli* Pavlow and *Tollia pakhsaensis* Voronets, which were left in *Tollia* sensu stricto by Shulgina (*ibid.*, p. 163–166, Pl. XVIII, fig. 1b, Pl. XIX, fig. 2a) have even more prominently ribbed intermediate whorls, at least some of which do not exhibit any weakening of ribs in the midflank. As Shulgina pointed out (*ibid.*, p. 163), the weakening of ribs in the middle of the flank of specimens referred to the species *T. tolli* Pavlow is the most unstable character, which may begin at diameters from 50 to 70 mm.

Of other potentially diagnostic features, the external suture line of *Bojarkia* ex gr. *B. mesezhnikowi-bodylevskii* does not differ materially from that of the more typical *Tollia* species (cf. Textfig. 1P, Q, R, T). It has the same number of morphologically similar principal elements and has an adorally arched appearance similar to that of *Tollia tolli* or *T.*

klimovskiensis. Like the latter suture lines, it differs markedly from the external suture lines of *Surites* and *Praetollia*, which are much more strongly ascendant and rise evenly through most or all of their extent (cf. Textfig. 1K, N).

Finally, *Bojarkia* ex gr. *B. mesezhnikowi-bodylevskii* apparently is not restricted to the late Berriasian beds underlying those containing the first typical *Tollia* ex gr. *T. tolli*. As already pointed out earlier in this section, typical *T. tolli* coexists with *B.* ex gr. *B. mesezhnikowi-bodylevskii* in these beds designated as *Bojarkia mesezhnikowi* Zone by Saks and Shulgina (1969). Furthermore, there are reasons to believe that these *Bojarkia* forms are present also in the definitely lower Valanginian *Pseudogarnieria undulatoplicatilis* Zone of central Russia (e.g., Shulgina, in Saks *et al.*, 1972, p. 89, 160). For these reasons the writer has assigned the *Bojarkia mesezhnikowi* Zone to the basal Valanginian (Textfig. 8).

Because of the foregoing considerations, the genus *Bojarkia* Shulgina 1969 is interpreted herein as a junior subjective synonym of the genus *Tollia* Pavlow 1914. Because the external suture line and other morphological features of typical northern Siberian representatives of *Bojarkia* resemble more closely those of *Tollia* ex gr. *tolli-klimovskiensis* than those of typical *Surites*, Casey's (1973, p. 250) proposal to treat this genus as a subgenus of *Surites* is not followed by the writer. There is no doubt that the northern Siberian *Bojarkia* forms, *Tollia payeri* Toula 1874 and at least some of the eastern English forms assigned by Casey (1973) to *Bojarkia* are morphologically transitional between the more typical *Surites* ex gr. *spasskensis-analogus* and the typical *Tollia tolli* Pavlow. However, this is not a valid reason either for separating them generically (or even subgenerically) from *Tollia* or for subordinating them subgenerically to *Surites*. As far as it is possible to judge, the Berriasian to earliest Valanginian genus *Surites* sensu lato is a plexus of highly variable, morphologically intergrading forms that grade imperceptibly into the genus *Praetollia* on the one hand and into the typical late Berriasian to early Valanginian *Tollia* ex gr. *tolli* on the other. The current tendency to arbitrarily 'slice' this plexus further and further is completely unjustified, in the writer's opinion. Consequently the genus *Tollia* Pavlow 1914 is interpreted herein as comprising all craspeditid forms recently assigned to the genera *Bojarkia, Tollia* and *Neotollia* by Shulgina (in Saks *et al.*, 1972, p. 130–133, 158–171). None of these 'genera' deserves recognition on either generic or subgeneric level, in the writer's opinion. As will be pointed out in the description of *Tollia* n. sp. aff. *T. subtilis* Voronets 1962, one might sooner doubt whether or not such very coarsely and distantly ribbed forms as *Tollia pakhsaensis* Voronets (1962, p. 66, Pl. XLVI, figs. 1, 3) or such widely umbilicate or peculiarly ornamented forms as *Tollia kordikovi* Voronets (1962, p. 65, 66, Pl. XXXIII, fig. 2, Pl. XXXV, fig. 1) should be retained in *Tollia* in the sense adopted here. However, these *Surites*- or *Virgatoptychites*-like forms are too poorly known to be made a basis of a new subgenus, let alone a genus.

Comparison. The morphological distinctions of *Tollia*, as interpreted in this paper, from the homeomorphically similar, nodeless forms of *Temnoptychites* (*Costamenjaites*) have been discussed in detail in the description of the latter genus. In summary, they are basically limited to

(1) a complete absence of weakening, let alone interruption, of secondary ribs on the venter at any of the sculptured growth stages; and

(2) a differently oriented and shaped external suture line, which is considerably less ascendant (about 5 to 10 degrees) than that of *Temnoptychites* (about 20 to 40 degrees) even in its most strongly ascendant adventral part (usually including only lateral and first auxiliary lobes and saddles) and becomes less ascendant, subradial or even slightly descendant in its remaining adumbilical part.

Morphological distinctions of *Tollia* from the apparently indirectly related older genus *Praetollia* Spath 1952 (? = *Borealites*) have been comprehensively discussed by Jeletzky (1973, p. 74, 75). It should be added only that the numerous drawings and photographs of external suture lines of *Tollia* species published by Shulgina (in Saks *et al.*, 1972, p. 140, 141, figs. 10–12) fully confirm the persistent nature of distinctions in the orientation of external suture lines of these two genera, as suggested by the writer on the basis of more limited data.

The genus *Surites* sensu lato (including *Caseiceras, Lynnia*, ?*Bogoslovskia* and ?*Stchirowskiceras*) differs from *Tollia* in having an appreciably to much sturdier and considerably lower cross-section of the whorl, an appreciably to considerably wider (30–40%) umbilicus, and an appreciably to much more elevated and sparser ornamentation, which commonly includes markedly thickened to clearly bullate primary ribs. The external suture line of *Surites* sensu lato commonly does not differ much from that of *Praetollia* (e.g., Sazonova, 1971, Pl. VII, fig. 1a, Pl. XXIV, figs. 7, 11, 14; Casey, 1973, Fig. 6m, r; Shulgina, in Saks *et al.*, 1972, Figs. 10–9, 11–7, 12–8) and so should represent another valuable distinguishing feature from *Tollia*. However, it is either unknown or poorly known in many forms placed by the writer in *Surites* sensu lato. Therefore it is uncertain whether or not Sazonova's claim (1971, p. 26) – that the adumbilical part of the external suture in her subfamily Suritinae, beginning with the second lateral saddle, is characteristically deflected backward as compared with the adventral part of the same suture at angles up to 15 degrees – has any validity outside of *Surites*-like forms placed in the genus *Bojarkia* by Shulgina (in Saks and Shulgina, 1969, p. 47, Pl. I, fig. 3). As mentioned previously, this *Tollia*-like orientation of the external suture line of "*Bojarkia*" *mesezhnikowi* Shulgina and *Tollia payeri* (Toula, 1874, Pl. I, fig. 1a) indicates that they are transitional between the genera *Surites* and *Tollia* as interpreted in this paper. However, this is not a valid reason for separating "*B.*" *mesezhnikowi* either generically or even subgenerically from other more typical *Tollia* forms with which it is so closely connected morphologically and stratigraphically. The intergradation of *Surites* and *Tollia* makes it extremely difficult to draw a distinct morphological boundary between these two genera and dooms all attempts to segregate morphologically distinct forms, or groups of forms, forming part of the *Surites* plexus into genera or subgenera (e.g., *Caseiceras, Lynnia*, ?*Bogoslovskia* and ?*Stchirowskiceras*) of their own.

The morphological differences of *Homolsomites* Crickmay 1930 and *Tollia* have been discussed already by Jeletzky

(1965a, p. 39) based on the examples of *Homolsomites quatsinoensis* (Whiteaves) and *Tollia mutabilis* (Stanton). However, *Homolsomites* was considered then to be a junior synonym of *Dichotomites*, except in a subsequently added footnote.

Homolsomites, inclusive of the genus *Wellsia* Imlay 1960 (Jeletzky, 1966, p. 4; 1973, p. 73) is believed now to differ from *Tollia* in the following respects:

1. In the intermediate and late growth stages, its venter is much more narrowly rounded and the whorl is markedly subtriangular in cross-section with rapidly adorally converging flat flanks.

2. Coarse, chevronlike secondary ribs incline markedly forward on the venter. This ribbing and, in places, weak but swollen basal parts of the primary ribs are retained on the penultimate and ultimate whorls after the flanks become almost or completely smooth.

3. The intermediate and adult external suture lines are strongly ascendant, much like those of *Praetollia, Surites* and *Temnoptychites* and are strongly crowded to overlapping as in *Temnoptychites* (*Costamenjaites*) *troelseni* n. sp.; the lobes have very long, slender, waving stems and the lateral and terminal accessory lobes are much longer and much more ramified than those of *Tollia*.

4. Ribbing is predominantly bidichotomous in the middle growth stages with *Tollia*-like dichotomous and trichotomous rib bundles restricted to early growth stages.

5. The umbilicus is strongly involute to almost occluded (10–15%) at all growth stages and completely conceals the preceding whorls; it is nearly always narrower than that of *Tollia* (15–30%).

6. The ribs are more crowded and finer in the early and middle growth stages. The primary ribs are considerably shorter than those of *Tollia* and their branching points generally are situated close above to almost at the umbilical shoulder at all stages of growth.

All known species of *Homolsomites* in North America and northern U.S.S.R. are restricted to upper Valanginian or lower Hauterivian beds (Jeletzky, 1973, p. 73, 74, Fig. 3) overlying those containing the youngest known *Tollia*. *Homolsomites* is believed to be a direct descendant of morphologically advanced *Tollia* forms (*Tollia mutabilis* Stanton or *T. klimovskiensis* Krimgolts), combining a narrow umbilicus with dense and fine ribbing and with narrow-lobed, crowded and strongly denticulated external suture lines (Jeletzky, 1965a, p. 40, 41, Pl. XIV, figs. 7–9).

Tollia aff. *T. tolli* Pavlow 1914

Plate 8, figure 1

1973 *Tollia* (*Tollia*) *tolli* var. *latelobata* Jeletzky, p. 64 (partim; unfigured specimen from Reptile Creek section only)

Material and locality. One partly deformed fragment of the living chamber GSC 49326 comprising somewhat less than one quarter of the whorl from GSC locality 28713 (see description of *Temnoptychites grandiosus* for further details).

Description. The imprint of a fragment of an undeformed penultimate whorl preserved inside the fragmentary living chamber gives a good idea of the shape, proportions and sculpture of the inner whorls of our form (Pl. 8, fig. 1C, D). In all these respects, the fragment GSC 49326 does not differ materially from the smaller specimen of *Tollia tolli* figured by Pavlow (1914, Pl. XII, fig. 2a, b). The absence of basal parts of primaries in our fragment permits the conclusion that the penultimate whorl concerned left some of the adumbilical part of the preceding whorl exposed just as it happens in the specimen figured by Pavlow (*ibid.*, fig. 2a). If anything, the secondary ribs are slightly sharper topped and more prominent on the midventer than elsewhere.

The fragment of the living chamber is an internal cast with a few small patches of poorly preserved shell present locally. The surface is entirely smooth, except for one shallow, possibly weathered constriction and a few striae on the umbilical wall where the shell is best preserved. The constriction is bent commalike on the adumbilicalmost part of the flank and inclines progressively more forward upflank (Pl. 8, fig. 1A). Its ventral part is not preserved. On the only umbilical wall preserved, the constriction disappears beneath the shell and the same happens on the other, more fragmentary and partly deformed flank. As far as it is possible to judge, the slightly convex flanks converge gradually and almost evenly all the way toward the narrowly rounded but not appreciably flattened venter from the level of maximum width of the whorl, which is situated at the umbilical shoulder (Pl. 8, fig. 1B). The obliquely oriented umbilical wall is slightly convex and the umbilical shoulder is broadly rounded. The shape and proportions of the living chamber (Pl. 8, fig. 1A, B) do not appear to differ materially from those of the larger, still fully septate specimen of *Tollia tolli* figured by Pavlow (*ibid.*, fig. 1b).

Fragments of the last suture line, preserved on the unfigured flank, include adoral parts of very broad, markedly adapically tapering first lateral lobe and somewhat narrower but broad and adapically tapering second lateral lobe separated by a fairly narrow second lateral saddle. The saddle could hardly be much wider than the second lateral lobe. Apparently these elements of the suture line do not differ materially from the corresponding parts of the external suture line of *Tollia tolli* (*ibid.*, figs. 1a, 2c; this paper, Textfig. 1T) and other typical representatives of *Tollia*. Small fragments of the auxiliary part (second? and third auxiliary lobes) of the last suture line preserved on the other figured flank (Pl. 8, fig. 1A) are very strongly ascendant (between 30 and 40 degrees) and so resemble the corresponding parts of *Temnoptychites, Surites* or *Praetollia* suture lines (cf. Textfig. 1K, N, S) more than they do those of typical *Tollia* species (cf. Textfig. 1R, Q, T). However, the last suture lines are apt to be somewhat irregular in their orientation, shape of elements and degree of denticulation.

Discussion. The fragment discussed herein was unreservedly referred previously to *Tollia tolli* var. *latelobata* Pavlow (e.g., Jeletzky, 1973, p. 64). However, all known representatives of *Tollia tolli* sensu lato (including *T. tolmatschowi* and *T. latelobata*) remain septate to much larger whorl diameters (more than 120 mm; see Shulgina, in Saks *et al.*, 1972, p. 163) than the Canadian fragment. In the latter, the living chamber begins at the approximate whorl diameter of 47 mm. This distinction possibly could be because the Canadian fragment

represents a half-grown individual of *Tollia tolli* that died prematurely and was preserved with the interim living chamber intact. However, our specimen also has an aberrant (too strongly ascendant) auxiliary part of the last suture line that differs markedly from that of all typical *Tollia* forms with which the writer is familiar. Therefore, it seems best to describe the fragment concerned by the open nomenclature pending the discovery of additional, better preserved material.

Tollia n. sp. aff. *T. klimovskiensis* Krimgolts 1953

Plate 8, figure 5; Textfigure 7

Material and locality. One fragment of the living chamber GSC 17172 from GSC locality 28713 (see description of *Temnoptychites grandiosus* for further details).

Description. The unique, almost undeformed fragment comprises somewhat less than one third of the whorl. It includes the adoralmost part of the phragmocone and the early part of the presumably adult living chamber (see below). The whorl is about 38 mm high and 22.5 mm wide (est.) in its best preserved middle part, which results in the width of the whorl comprising about 59 per cent of its diameter.

The bundling habit and the density of ribbing of specimen GSC 17172 does not differ materially either from that of the similarly large inner whorl of the previously described specimen GSC 49326 assigned to *Tollia* aff. *T. tolli* or from Pavlow's (1914) originals of that species. However, the secondary ribs of our specimen are much less curved and do not incline forward nearly as strongly as those of *Tollia* aff. *T. tolli* (Pl. 8, fig. 1C, D) or *T. tolli* itself (Pavlow, 1914, Pl. XII, figs. 1a, 2a). Furthermore, the secondaries form considerably broader and shorter forward bends on the venter (Pl. 8, fig. 5C), which match closely those of *Tollia klimovskiensis* (Shulgina, in Saks and Shulgina, 1969, Pl. II, figs. 1b, v, 2b, v) or those of *Tollia mutabilis* (Imlay, 1960, Pl. 28, figs. 10, 15, 19). The secondaries do not become weakened at all in the middle of the venter (Pl. 8, fig. 5C).

The whorl of GSC 17172 is considerably sturdier than that of either the previously described specimen of *T.* aff. *T. tolli* or of Pavlow's (1914) originals of *T. tolli*. This is well illustrated by the width to height ratio of our specimen, which is about 59 per cent compared with only 30 to 34 per cent for *Tollia tolli* (Shulgina, in Saks *et al.*, 1972, p. 163). The cross-section of the whorl is an elongated, almost egg-shaped oval with a moderately broadly rounded venter and virtually flat flanks. The flanks converge slowly and evenly all the way from the level of maximum width (at the almost regularly rounded umbilical shoulder) to the ill defined ventral shoulder (Pl. 8, fig. 5D). This cross-section again closely resembles that of *Tollia klimovskiensis* or *T. mutabilis*. The ultimate whorl does not completely cover the poorly preserved and partly deformed inner whorls and the umbilicus apparently had a steplike shape and was comparable to that of *Tollia tolli* in width. The obliquely directed umbilical wall of the ultimate whorl is only slightly convex (Pl. 8, fig. 5D). It was not possible to extract the slender, discuslike inner whorls and the details of their morphology remain unknown.

Although it is largely a living chamber, the surface of specimen GSC 17172 is strongly ribbed throughout and its secondary ribs become only slightly weakened on the midflank in its adoral half (Pl. 8, fig. 5B). Because of a strong approximation and partial overlap of preserved parts of the last two external suture lines adjoining the living chamber (Pl. 8, fig. 5A), it does not seem feasible to interpret our specimen as a fragment of a half-grown individual that died before reaching maturity and was preserved with the early part of its interim living chamber intact. On the other hand, all *Tollia* species with which the writer is familiar lose their ribbing long before the beginning of the adult body chamber.

Of the last two external suture lines visible on one flank of our specimen (Pl. 8, fig. 5A), only the adoralmost suture is sufficiently preserved to be drawn and evaluated. This suture line (Pl. 8, fig. 5A, Textfig. 7) is markedly ascendant throughout and forms an angle of 20 to 25 degrees with the direction of shell radius. However, the adumbilical part of the suture line beginning with the third auxiliary saddle is somewhat less ascendant than the rest. All four well differentiated auxiliary lobes are situated on the flank, the fourth straddling the umbilical shoulder. Only four tiny spicular lobules which gradually diminish in size toward the umbilical seam occur on the umbilical wall. No distinctive, well differentiated auxiliary lobes are recognizable among these closely spaced lobules. All lateral and auxiliary lobes closely resemble those of *Temnoptychites* and advanced *Tollia* species, which Shulgina (in Saks and Shulgina, 1969; and in Saks *et al.*, 1972, p. 132, 133, 166, 167) placed in the genus *Neotollia*, in their narrow stems, parallel sides and shallow denticulations. The length of the incompletely preserved first lateral lobe appears to be about equal to that of the ventral lobe whereas the length of the asymmetrically trifid second lateral lobe comprises slightly more than one half of that of the first lateral lobe. The first and second auxiliary lobes have about the same shape and proportions as the second lateral lobe but their lengths comprise, respectively, two thirds and one third of the latter. The symmetrically trifid third auxiliary lobe is almost as long as the second auxiliary lobe and the fourth, only slightly notched, spicular auxiliary lobe is only slightly shorter than the third auxiliary. All saddles are approximately square-shaped and considerably wider (2 to 2½ times) than the subsequent lobes. The unusual width of the slightly adapically widening first lateral saddle and its subdivision into two symmetrical halves by a large, distinctly denticulated lobule is particularly striking (Pl. 8, fig. 5A, Textfig. 7). The two adjacent suture lines are approximated closely throughout with apical ends of most of the lobes of the succeeding line either touching or slightly overlapping the tops of the saddles of the preceding line.

The terminal suture line described above is rather unlike the equivalent suture line of *Tollia tolli* or other typical *Tollia* species (see generic description of *Tollia*). However, it is similar to that of some advanced *Tollia* species, such as *Tollia anabarensis*, *Tollia klimovskiensis* and *Tollia mutabilis* (Pavlow, 1914, Pl. IV, fig. 3a; Shulgina, in Saks and Shulgina, 1969, Pl. II, fig. 1g; Imlay, 1960, Pl. 28, fig. 11; Jeletzky, 1965a, Pl. XIV, fig. 9).

Discussion. The unique specimen GSC 17172 is a *Tollia* form which exhibits a peculiar combination of morphological features characteristic of *Tollia tolli* (the appearance of ribbing

on the flank) and *T. klimovskiensis* (sturdy, broad-ventered whorl, weak forward bends of secondaries on ventral shoulder and the venter, and morphology of external suture line). This specimen appears most closely related to *T. klimovskiensis* but differs from that species radically in the persistence of the normal *Tollia*-like ribbing habit onto the apparently adult living chamber. The Canadian specimen is peculiar also because it is much smaller than the adults of any previously described *Tollia* species (with the possible exception of *Tollia mutabilis*; see Jeletzky, 1965a, Pl. XIV, fig. 9). The persistence of ribbing onto the adult living chamber is a particularly important morphological feature which does not occur in any *Tollia* species the writer is familiar with. In combination with the other morphological peculiarities of our specimen, this feature leaves little doubt that it belongs to a new *Tollia* species. However, this unique specimen is inadequate to serve as the holotype of a new species and so is described herewith by the open nomenclature.

Tollia n. sp. aff. *T. vai* Krimgolts 1953

Plate 8, figure 4

1973 *Tollia (Tollia) tolli* var. *tolmatschowi* Jeletzky, p. 63 (the specimen from GSC loc. 52491 only)

Material and locality. One partly pyritized internal cast GSC 49328 comprising about two fifths of somewhat deformed, intermediate (fully septate) whorl enclosing parts of at least four poorly preserved early whorls from GSC locality 52491 on Axel Heiberg Island, at the point about 7 km southwest of Buchanan Lake. It was collected from float about 46.5 m stratigraphically above the highest occurrence of *Buchia okensis*–"*Craspedites (Subcraspedites)* aff. *C. (S.) suprasubditus*" fauna (Jeletzky, 1973, p. 63 for further details).

Description. The best preserved outermost preserved whorl has the following dimensions: estimated shell diameter at the oral end, 88 mm; approximate whorl diameter at the least deformed apical end, 29 mm; approximate whorl width (max.; same place as for whorl diameter), 23.5 mm; estimated width of the umbilicus (same place as for shell diameter), 28 mm; umbilicus as percentage of shell diameter, 32 per cent; approximate ratio, whorl width/whorl diameter, 80 per cent.

The earliest discernible (fourth from last preserved), appreciably distorted whorl has an almost equidimensional (slightly wider than high), apparently regularly rounded cross-section and the same appears to be true of the third from last preserved similarly distorted whorl representing the shell diameter of about 28 mm (Pl. 8, fig. 4A). The indistinctly visible second from last whorl appears to have an entirely different, distinctly higher than wide, rapidly adventrally converging, almost flat-sided cross-section with a narrowly rounded venter. This rounded-trapezoidal cross-section is similar to that of the inner whorl of the holotype of *Tollia vai* (Krimgolts, in Krimgolts *et al.*, 1953, p. 78, fig. 12). The least deformed cross-section of the last preserved whorl (Pl. 8, fig. 4B) is basically similar to that of the above-described second from last whorl. It appears to differ from the cross-section of the last preserved whorl of the holotype of *Tollia vai* (Krimgolts, *loc. cit.*) in having more slender proportions (in whorl width to whorl diameter ratio of 0.80 compared with

0.90 for *T. vai*). However, this distinction may be largely or even entirely caused by lateral deformation of the Canadian specimen.

The moderately wide and shallow, pronouncedly steplike umbilicus of *T. n. sp.* aff. *T. vai* resembles closely that of *Tollia tolli* Pavlow sensu lato and *T. vai* Krimgolts in its depth, shape and direction of umbilical walls, and appearance of the umbilical shoulder. However, it is appreciably wider (32% of shell diameter) than the umbilicus of any *Tollia* (including *Neotollia*) species known (Shulgina, in Saks *et al.*, 1972, p. 167), including that of *T. vai* (Krimgolts, in Krimgolts *et al.*, 1953, p. 78, table of measurements).

The ornament of the shell is characteristically *Tollia*-like. The primary ribs, bent markedly backward, begin near the umbilical seam and maintain this course to the umbilical shoulder while gradually becoming more and more prominent in this direction. On the umbilical shoulder, these high, sharp-topped, distinctly thickened primary ribs rapidly turn around until they incline weakly forward. Then the primaries maintain this course across the lower part of the flank, which results in their essentially straight appearance (Pl. 8, fig. 4A). There are about nine primaries on the preserved two fifths of the outermost whorl, which suggests 22 to 23 primaries per whorl.

The primary ribs bifurcate and trifurcate at variable levels above the umbilical shoulder, fluctuating between one quarter and three fifths of the flank's height (Pl. 8, fig. 4A). The mainly well defined trichotomous and dichotomous rib bundles alternate irregularly and are separated mainly by one or two intercalated ribs restricted to the upper third to two thirds of the flank. All secondary ribs are more or less straight and maintain about the same course, inclined somewhat forward, across the middle and upper parts of the flank. Then the forward inclination increases rapidly at the ill defined ventral shoulder, which results in the secondary ribs forming broad and fairly short forward bends on the venter (Pl. 8, fig. 4B) before joining the secondaries of the opposite flank. Wherever they are satisfactorily to well preserved, the secondaries do not weaken at all in the midventer of the last preserved whorl. If anything, they become somewhat more elevated and heavier there. Nor do the secondary ribs exhibit any signs of interruption on the venter of a short, exposed segment of the third from last whorl. The density and prominence of distinctly pinched and sharp-topped secondary ribs of the last preserved whorl match closely that of the equivalent growth stages of *T. tolli* var. *tolmatschowi* (Pavlow, 1914, Pl. XIII, fig. 1b, c, d).

The external suture line is not visible anywhere.

Discussion. Though similar to the equivalent growth stages of the *Temnoptychites lgowensis*–like variant of *T. kemperi* n. sp. in the shape and proportions of the shell and in the ribbing habit (cf. Pl. 8, fig. 2A, B), specimen GSC 49328 differs from this form in having a much wider umbilicus, considerably longer primary ribs, a fine and pinched appearance of the primary ribs, and a complete absence of any weakening, let alone interruption, of the secondary ribs in the midventer. These features indicate the assignment of specimen GSC 49328 to the genus *Tollia* Pavlow 1914 as defined above. The specimen was identified previously as *Tollia tolli* var.

tolmatschowi and assigned to the lowest Valanginian *Tollia tolli* Zone by the writer (Jeletzky, 1973, p. 63) but this assignment cannot be maintained. The ribbing habit of specimen GSC 49328 resembles very closely that of the equivalent growth stages of this northern Siberian form. However, the outermost preserved whorl is appreciably sturdier and lower, as illustrated by its maximum width, which comprises about 80 per cent of the diameter in contrast to 30 to 34 per cent for *Tollia tolli* sensu lato, including *T. tolli* var. *tolmatschowi* (Shulgina, in Saks *et al.*, 1972, p. 163). Furthermore, unlike *T. tolli* sensu lato, the flanks of the outer two whorls of the Canadian specimen are virtually flat and converge rapidly and evenly all the way up to the narrow but distinctly flattened venter, whereas the inner two whorls are almost globose in cross-section. Finally, the umbilicus is distinctly wider than that of the variants of *Tollia tolli* sensu lato (*T. tolmatschowi* and *T. latelobata*), where it is not known to exceed 30 per cent of the shell diameter (*ibid.*, p. 131, 163, table of measurements).

As already mentioned, the whorl shape and proportions of specimen GSC 49328 resemble closely those of *Tollia klimovskiensis* Krimgolts (in Krimgolts *et al.*, 1953, p. 76, 77, Pl. XI, fig. 1, Textfig. 9) and *T. vai* Krimgolts (*ibid.*, p. 78, 79, Pl. XI, fig. 2, Textfig. 12). However, it cannot be referred to any of these northern Siberian species because of an entirely *T. tolli* sensu lato–like ribbing habit (characterized by relatively much more widely spaced primary ribs) and a much wider umbilicus. As Shulgina pointed out (in Saks and Shulgina, 1969, p. 51, Table 3, Pl. II, figs. 1a, 2a), *T. klimovskiensis* has an umbilicus that is appreciably narrower than that of *T. tolli* sensu lato, not to mention that of the *T. n. sp.* aff. *T. vai* described herein. The same is true of the umbilicus of *T. vai* (Krimgolts, in Krimgolts *et al.*, 1953, p. 76, table of measurements, Pl. XI, fig. 1).

Of all other *Tollia* species known to the writer, specimen GSC 49328 resembles closely only that of *Tollia n. sp.* aff. *T. klimovskiensis* from GSC loc. 28713, described earlier in this report (p. 51, 52). However, the apparently adult living chamber of *T. n. sp.* aff. *T. klimovskiensis* begins at the whorl diameter of about 32 mm in its only known representative. The specimen GSC 49328 is, in contrast, fully septate to the oralmost preserved end where the whorl diameter is about 33.5 mm. Furthermore, the whorl of *T. n. sp.* aff. *T. klimovskiensis* is considerably more slender than that of *T. n. sp.* aff. *T. vai*, and its maximum width comprises only about 67 per cent of the diameter at a comparably large growth stage. Finally, the shape and slenderness of the innermost preserved whorls of *T. n. sp.* aff. *T. klimovskiensis* are comparable to those of its outermost preserved whorl. The similarly large (and even larger) inner whorls of *T. n. sp.* aff. *T. vai* are, in contrast, almost regularly rounded and only slightly higher than wide.

Tollia n. sp. aff. *T. vai* evidently is a representative of a new, rather aberrant *Tollia* species. However, its only known representative is too incomplete and too poorly preserved to serve as a type specimen. Therefore it was decided to describe and figure this specimen by the open nomenclature and to stress its apparently close affinity with *Tollia vai* Krimgolts pending the discovery of additional, better preserved material.

Tollia n. sp. aff. *T. subtilis* Voronets 1962

Plate 6, figure 1

1975 *Tollia* ex gr. *T. mira* Voronets–?*mutabilis* Jeletzky, in Kemper, 1975, p. 248
1977 *Tollia* n. sp. aff. *T. subtilis* Jeletzky, in Kemper, 1977, p. 3

Material and locality. One large and almost complete but moderately deformed specimen GSC 49323 from GSC locality 91313: see description of *Temnoptychites (Temnoptychites) kemperi* n. sp. for further details.

Measurements. The best preserved, almost undeformed part of the shell at the beginning of the living chamber (see Pl. 6, fig. 1A, where it is marked by an arrow) has the following measurements (approximate only): shell diameter, 99 mm; whorl height, 43 mm; whorl width, 39.5 mm; width of the umbilicus (measured at umbilical shoulder), 30 mm; coefficient of involution (width of the umbilicus in per cent of shell diameter), 30 per cent.

Description. The only specimen available consists of about three quarters of the septate penultimate whorl (Pl. 6, fig. 1B) followed by the fragmentary but apparently almost complete adult body chamber. Except for the earliest two fifths of the chamber, where it is almost completely preserved, only one of its umbilical walls and one lower flank are preserved. The mouth border is not preserved but the body chamber appears to be all but complete because it extends over about five sixths of the whorl. The shell diameter at the preserved end of this apparently adult body chamber is estimated to be about 140 mm (Pl. 6, fig. 1A). The earlier whorls are very poorly preserved and apparently greatly deformed. It was impossible either to extract them or to discern any features of their morphology in the umbilicus.

The external suture line is too poorly preserved to be either drawn or photographed. However, it is of a general craspeditid type with the large, wide and florid first lateral lobe (Pl. 6, fig. 1A) that resembles closely that of *Tollia tolli*. This lobe is either equal to or only slightly shorter than the ventral lobe. The first lateral lobe is followed by a considerably smaller second lateral lobe and either four or five gradually diminishing auxiliary lobes separated from each other by lobules. The first three or four auxiliaries are trifid whereas the fourth or fifth auxiliary is tacklike and situated almost at the umbilical seam. The suture line appears to be moderately ascendant throughout and to lack the characteristic *Tollia*-like arched or angular bend within the auxiliary part (see description of the genus).

The early half of the only exposed flank of the penultimate whorl (Pl. 6, fig. 1B) is ornamented by about nine ill defined but distinctly thickened (subbullate), markedly adorally inclined but apparently straight primary ribs. The adoral half of this whorl is extremely weathered and does not exhibit any primaries, but it is assumed that there are some 17 to 18 primaries per whorl. The preserved primaries apparently begin at the umbilical seam and cross the umbilical wall obliquely, gradually thickening away from the seam and farther upflank. At or near the boundary between the lower and middle third of the flank, the primaries end by subdividing into secondary ribs. The primaries are separated from each other by ill defined, shallowly depressed interspaces

that are two to three times wider than the primaries. As far as one can see, these interspaces gradually widen adorally within the early half of the penultimate whorl (Pl. 6, fig. 1B).

On the earliest exposed quarter of the penultimate whorl, most of the primary ribs split into three or four very fine and closely spaced secondary ribs. However, at least one bundle (the sixth adorally; see Pl. 6, fig. 1B) consists of five secondaries arranged in the regular virgatitid fashion. The ribbing is somewhat to distinctly weakened in the midflank throughout the part of the penultimate whorl discussed herein, which results in a somewhat indistinct attachment of most secondaries to the primaries. This makes it difficult to infer the exact mode of bundling of most of the other bundles. However, some of the bundles may be virgatitid rather than fasciculate. As far as one can see, one to three secondaries are intercalated between every one of the rib bundles discussed here.

About 60 secondary ribs have been counted on the early half of the penultimate whorl and this results in a ratio of between six and seven secondaries to each primary. The secondary ribs are approximately straight to slightly curved on the flank. They incline forward slightly at first and this inclination increases somewhat upflank. The ribs cross the venter, forming shallow and broad forward bends (Pl. 6, fig. 1C, D) and are neither interrupted nor weakened there.

Adorally, the ribs weaken more and more in the midflank until this part of the flank becomes smooth on the anterior part of the penultimate whorl and throughout the preserved part of the ultimate whorl. However, the secondary ribs persist and gradually become coarser on the upper flanks and the venter throughout the adoral half of the penultimate whorl and at least on the preserved adapical half of the body chamber (Pl. 6, fig. 1A, D). The lower parts of subbullate primaries apparently persist throughout the adoral half of the penultimate whorl and on the apicalmost part of the body chamber (Pl. 6, fig. 1A). However, they appear to be absent on the adoral two thirds of the body chamber. The sparce bullaelike elevations on the lower flanks of the body chamber invariably flank the broad but shallow and ill defined adorally inclined constrictions commonly occurring there (Pl. 6, fig. 1A). At least seven such constrictions have been counted on the preserved flank of the adoral half of the body chamber.

The whorl is relatively low and broad for the genus (see measurements); the height only slightly exceeds the width. The whorl diameter increases only slowly during the investigated growth stages (from about 35 mm to about 47 mm over 1¼ whorls). It has a distinctly rounded-trapezoidal shape with a broadly rounded venter. The slightly convex sides converge gradually and more or less evenly all the way upflank from the level of maximum diameter situated at the umbilical shoulder (Pl. 6, fig. 1C). The ventrolateral shoulder is broadly rounded. The moderately wide umbilicus (about 30% of the shell diameter; see measurements) appears to be shallow, but this may be an illusion caused by the lateral deformation of the shell. The umbilical wall is regularly rounded and merges imperceptibly into the flank.

Comparison and affinities. The Canadian specimen described is closely comparable to such previously described, aberrant but poorly known *Tollia* species as *T. emelianzevi* Voronets 1962

and *T. subtilis* Voronets. Voronets (1962, p. 66) introduced the latter form as a variety of *Tollia kordikovi* Bodylevsky 1957 (MS) but the writer considers it as an independent species. However, the Canadian specimen cannot be assigned to either of these two northern Siberian species since it combines the moderately wide umbilicus (about 30%), the presence of numerous constrictions on the living chamber, the low, fairly broad whorl shape, and the slight adoral bends of the secondaries characteristic of *T. subtilis* with the early loss of the ribbing on the midflank, exceptional persistence of secondaries on the ventral shoulder and the venter, unusually high ratio of secondaries to primaries, and the unusually large ratio of intercalated secondary ribs characteristic of *T. emelianzevi*. The somewhat to distinctly thickened appearance of primaries on the penultimate and ultimate whorls of the Canadian specimen is equally characteristic of *T. subtilis* (see Voronets, 1962, Pl. XXXIX, fig. 1a) and *T. emelianzevi* (*ibid.*, p. 68, Pl. XXXII, fig. 2a; Shulgina, in Saks *et al.*, 1972, Pl. XIX, fig. 1), while absent in all other previously described *Tollia* species. This feature allies all three forms concerned with such aberrant representatives of *Virgatoptychites* as *V. trifurcatus* Shulgina (*ibid.*, p. 171, Pl. XXIV, fig. 1a).

Because of this unique combination of morphological features combined with at least one five-ribbed virgatitid bundle on the early part of the penultimate whorl, the Canadian specimen GSC 49323 is believed to be a representative of a new *Tollia* species closely allied to *T. subtilis* and *T. emelianzevi*. However, the only specimen known is inadequate to serve as the type of a new species. The form concerned accordingly is described by means of open nomenclature and compared with *T. subtilis* to which it is judged to be particularly closely allied.

The above-mentioned *Virgatoptychites*-like features of *Tollia* n. sp. aff. *T. subtilis* Voronets 1962 do not seem to be taxonomically significant in the present state of our knowledge. Virgatitid rib bundles are known to be present rarely also on the outermost ribbed whorls of typical *Tollia* species, including *T. tolli* Pavlow. The taxonomic value of the thickened to bullaelike, relatively short primaries occurring on the outer whorls of *T. subtilis*, *T. emelianzevi* and *T.* n. sp. aff. *T. subtilis* is impossible to assess at present. Therefore *T.* n. sp. aff. *T. subtilis* and its northern Siberian allies are left in the genus *Tollia* Pavlow at this time.

The previously made comparison of the specimen with *Tollia* ex gr. *T. mira* Voronets–?*mutabilis* (Stanton) (see Jeletzky, in Kemper, 1975, p. 248) is now believed to be less apt than the comparison proposed herein. Although comparatively fine ribbed, the solitary specimen described as *Tollia* (*Polyptychites*?) *mira* by Voronets (1962, p. 69, 70, Pl. XLI, fig. 3) lacks the very fine and closely spaced ribbing habit and numerous intercalated secondaries of our specimen. Furthermore, it develops prominent commalike, sharp-topped, bullate primaries at the adoralmost part of the preserved whorl and lacks *Tollia*-like primary ribs on the earlier part of the same whorl. This specimen would have been assignable to *Astieriptychites* ex gr. *A. astieriptychus* Bodylevsky, except that its suture line seems to have a craspeditid character (*ibid.*, p. 70, Fig. 26). The comparably fine-ribbed *Tollia mutabilis* Stanton 1895 is a much smaller form that has a much smaller ratio of primaries to secondaries (between 3 and 4) on the

penultimate whorl and becomes completely smooth at whorl diameters ranging from 40 to 50 mm (Jeletzky, 1965a, Pl. XIV, fig. 9, Pl. XV, fig. 1A).

The solitary specimen of *Tollia* n. sp. aff. *T. subtilis* discussed above is important in demonstrating the presence of fairly typical representatives of *Tollia* in *Temnoptychites kemperi* beds of Sverdrup Basin closely below the lowermost middle Valanginian beds containing *Thorsteinssonoceras ellesmerense* (Textfig. 8).

Stratigraphy

Most of the *Tollia-Temnoptychites* faunas (in the sense of Kemper, 1975, p. 248, 249, Fig. 2; 1977, p. 3, Figs. 2, 3) of Sverdrup Basin described in this report have been found either in stratigraphically isolated fossil localities or in sections of the Deer Bay Formation lacking other diagnostic ammonite faunas. In this respect, they conform to the characteristically random distribution of latest Jurassic and early Early Cretaceous ammonite faunas in the Deer Bay Formation; this fact has considerably complicated their biochronological use (Jeletzky, 1973, p. 47).

The bulk of the ammonites described in the preceding sections of this report forms part of two distinctive *Tollia-Temnoptychites* faunas that were not found either in association or in superposition in the same section. One of these faunas is the *Temnoptychites (Temnoptychites) kemperi* n. sp. fauna, the stratigraphic relationships of which with the overlying Valanginian ammonite faunas are well established by Kemper's field work (1975, 1977). Thus, in the very thick midbasin facies of the lower and middle Valanginian (in the sense of Jeletzky, 1973, p. 62, Fig. 3) part of the Deer Bay shale on Amund Ringnes Island, the *Temnoptychites kemperi* fauna occurs about 130 m stratigraphically below the oldest known occurrence of *Polyptychites (Siberiptychites) stubendorffi* fauna and about 20 m stratigraphically below the *Thorsteinssonoceras ellesmerense* fauna (Kemper, 1975, p. 248, 249, Fig. 2; 1977, p. 3, figs. 2, 3). In the marginal facies of the Deer Bay shale in Blackwelder Mountains, a solitary representative of *Temnoptychites kemperi* (p. 19) was found about 7.6 m stratigraphically below beds containing the *Thorsteinssonoceras ellesmerense* fauna (Jeletzky, 1965b, p. 14; see below). The stratigraphic relationships of *Temnoptychites kemperi* fauna with the older Valanginian and the late Berriasian ammonite faunas are obscure since the latter are unknown in Sverdrup Basin (Jeletzky, 1973, p. 46, Fig. 2; and below).

According to the preliminary identifications of the writer (Kemper, 1975, p. 248), the *Temnoptychites kemperi* fauna included "*Temnoptychites* ex gr. *T. lgowensis-syzranensis-simplex, Tollia* ex gr. *T. mira* Voronets–?*mutabilis* (Stanton), and *Russanovia diptycha* (Keyserling)." Further study of this fauna necessitated a change of some of the above identifications while revealing an extremely close affinity to complete specific identity of all its better preserved ammonites with those of *Temnoptychites* beds of Middle Russia and Novaya Zemlya described and figured by Nikitin (1888), Bogoslowsky (1902) and Bodylevsky (1967). As now known, this fauna consists mainly of *Temnoptychites (Temnoptychites) kemperi* n. sp. supplemented by very rare *T. (T.) borealis*

Bodylevsky 1967, and *Tollia* n. sp. aff. *T. subtilis* Voronets 1962. The first, rare representatives of *Thorsteinssonoceras* ex gr. *T. ellesmerense* also have been found in this fauna (Kemper, 1977).

The second fauna is the *Temnoptychites (Costamenjaites) troelseni* n. sp. fauna of the Camp (= Reptile) Creek area on Ellesmere Island (near Eureka Weather Station). No older or younger diagnostic Valanginian ammonite faunas of the Deer Bay Formation have been found in the Camp Creek section that yielded the *T. (C.) troelseni* fauna (Jeletzky, 1973, p. 66, 67, Fig. 3; Kemper, 1975, p. 248, 249, Fig. 2). Therefore, its stratigraphic position within the lower Valanginian part of the Deer Bay shale remains obscure. The stratigraphic relationships of the solitary representative of *T. (C.) troelseni* found more recently in Blackwelder Mountains (GSC loc. 94731; see p. 32) are similarly obscure.

The absence of any common ammonite species in *Temnoptychites (Temnoptychites) kemperi* and *Temnoptychites (Costamenjaites) troelseni* faunas and, even more important, the fact that all the species of *Temnoptychites* belong to distinct, well defined subgenera suggest strongly that these faunas represent successive evolutionary stages of a *Temnoptychites* plexus rather than its geologically contemporary faunal facies. Furthermore, this idea is supported by the following, even more compelling, lines of evidence:

1. *Temnoptychites (Temnoptychites) borealis* found at GSC loc. 91313 of *Temnoptychites (Temnoptychites) kemperi* n. sp. fauna is a form very closely related and apparently ancestral to *Thorsteinssonoceras* (p. 18). Such forms are more likely to be found in a stratigraphic position adjacent to their apparent descendants.

2. The Reptile Creek *Temnoptychites (Costamenjaites) troelseni* n. sp. fauna consists almost exclusively of nodeless *T. (C.) troelseni*, which is similar morphologically to the basal Valanginian (*Pseudogarnieria undulatoplicatilis* Zone; see Jeletzky, 1973, Fig. 3) *Temnoptychites (Costamenjaites) jucundus-suraense* species group of central Russia (Sazonova, 1971, p. 86, 87, table opp. p. 4).

3. *Temnoptychites (Temnoptychites) kemperi* n. sp. is a nodose, partly low-whorled form, which morphologically resembles *Thorsteinssonoceras* more closely than it does the basal Valanginian representatives of *Temnoptychites (Costamenjaites)* listed under paragraph 2. Furthermore, this species is very closely allied to the Middle Russian *T. (T.) hoplitoides* which appears to be restricted to beds (*Temnoptychites hoplitoides* Zone) directly overlying the *Pseudogarnieria undulatoplicatilis* Zone (Jeletzky, 1973, Fig. 3).

4. The solitary representative of the *Temnoptychites lgowensis*–like variant of *T. (T.) kemperi* n. sp. found in the Blackwelder Mountains section (Jeletzky, 1965b, p. 14; Kemper, 1975, p. 248, 249, Fig. 2) occurs only 7.6 m stratigraphically below the *Thorsteinssonoceras ellesmerense* fauna while GSC loc. 93757 of *T. (T.) kemperi* n. sp. on Amund Ringnes Island occurs only about 20 m stratigraphically below the *Thorsteinssonoceras* fauna. These stratigraphic relationships make it difficult to assume the presence of another, entirely different *Temnoptychites* fauna in the intervening unfossiliferous interval. The circumstance that this 7.6 to 20 m thick shale interval represents but a minuscule

part of the obviously rapidly deposited lower Valanginian part of the Deer Bay Formation supports this idea.

5. The presence of an additional, morphologically distinctive *Temnoptychites* fauna in the narrow stratigraphical interval separating *Temnoptychites* (*Temnoptychites*) *kemperi* n. sp. and *Thorsteinssonoceras ellesmerense* faunas (see paragraph 4) is all but ruled out by the recent discovery (Kemper, 1977, p. 9) of the first, rare representatives of *Thorsteinssonoceras ex gr. ellesmerense* in the former fauna at GSC loc. 93757.

As with the *Temnoptychites* (*Temnoptychites*) *kemperi* fauna (see above), the stratigraphic relationships of the *Temnoptychites* (*Costamenjaites*) *troelseni* fauna with the oldest Valanginian and late Berriasian ammonite faunas are obscure because of the complete absence so far of the latter faunas in the Sverdrup Basin (Jeletzky, 1973, p. 46, Fig. 2; and below).

The *Temnoptychites* (*Costamenjaites*) *troelseni* fauna originally was believed to consist of prevalent *Tollia* (*Temnoptychites*) *novosemelica* Sokolov 1913, very rare *Tollia* (*Temnoptychites*) *simplex* (Bogoslowsky 1902), and rare *Tollia* (*Tollia*) *tolli* Pavlow 1914 sensu lato (Jeletzky, 1964; 1973, p. 63, 64, figs. 2, 3). However, most of these indentifications had to be adjusted later either nomenclatorially or taxonomically and the fauna is considered now to consist of prevalent *Temnoptychites* (*Costamenjaites*) *troelseni* n. sp. and the following very rare forms: *Temnoptychites* (*Costamenjaites*) *grandiosus* Voronets 1962, *T.* (*C.*) aff. *T. grandiosus* Voronets 1962, *Tollia* aff. *T. tolli* Pavlow 1914, and *T.* n. sp. aff. *T. klimovskiensis* Krimgolts 1953.

Biochronology

The regional stratigraphic evidence summarized in the preceding section indicates that the *Temnoptychites* (*Temnoptychites*) *kemperi* n. sp. fauna is considerably older than the early mid-Valanginian (in the sense of Jeletzky, 1973, p. 66, Fig. 3) *Polyptychites* (*Siberiptychites*) *stubendorffi* fauna, and slightly older than the earliest middle Valanginian *Thorsteinssonoceras ellesmerense* fauna. This *T.* (*T.*) *kemperi* n. sp. fauna is still of an early Valanginian age based on its occurrence in the lower part of the generalized *Buchia keyserlingi* Zone (see Jeletzky, *ibid.*; Kemper, 1975, p. 248, 249, Fig. 2; 1977, p. 3, Fig. 2). The *Temnoptychites* (*Costamenjaites*) *troelseni* fauna can be assigned only a next older zonal position within the early Valanginian. It occurs somewhere near the base of the generalized *Buchia keyserlingi* Zone because it is inferred to be of an older age than the *Temnoptychites* (*Temnoptychites*) *kemperi* n. sp. fauna and because of its association with numerous and typical representatives of *B. keyserlingi*.

The two above-mentioned Canadian *Temnoptychites* faunas can be placed much more precisely within the zonal sequence of the boreal lower Valanginian using the stratigraphical and biochronological data available in the European and Asiatic parts of the U.S.S.R. As discussed by Jeletzky (1973, p. 66, 67), the Eurasian boreal zone characterized by the prevalence of typical *Temnoptychites* species allied to *T. hoplitoides* (Nikitin) is confined essentially (see below for apparent exceptions) between the basal Valanginian *Tollia tolli* Zone below and the mid-Valanginian

Polyptychites keyserlingi–P. michalskii–P. (*Siberiptychites*) *stubendorffi* Zone above over all of the Arctic Belt of the U.S.S.R. However, in the Middle Russian sections, this *Temnoptychites* (*Temnoptychites*) or Hoplitoides Zone is confined between the basal Valanginian *Pseudogarnieria undulatoplicatilis* Zone below and the mid-Valanginian *Polyptychites keyserlingi–P. michalskii* Zone above (Textfig. 8). In these Middle Russian sections, all previously described representatives of *Temnoptychites* (*Costamenjaites*) ex gr. *T.* (*C.*) *jucundus-suraense* are all but confined to the basal Valanginian *Pseudogarnieria undulatoplicatilis* Zone (Sazonova, 1971, p. 83, 84, 86). Sazonova (1971, table opp. p. 4) concluded accordingly that the *Pseudogarnieria undulatoplicatilis* Zone of the Middle Russian region is equivalent to the *Tollia tolli* Zone of northern Siberia and other Arctic regions of the U.S.S.R. (Textfig. 8). This correlation was proposed independently by Jeletzky (1971b, p. 2, 4, Fig. 2; 1973, Fig. 3) and continues to be treated as valid in this report.

This distribution of *Temnoptychites* subgenera and species in the lower Valanginian zonal sequence of the U.S.S.R. indicates the approximate correlation of the Canadian *Temnoptychites* (*Temnoptychites*) *kemperi* n. sp. fauna with the *Temnoptychites hoplitoides* Zone of the Middle Russian region and with the *Temnoptychites syzranicus* Zone of northern Siberia. The presumably next older *Temnoptychites* (*Costamenjaites*) *troelseni* fauna is correlative with part (upper?) or all of the *Pseudogarnieria undulatoplicatilis* Zone of Middle Russia and part (upper?) or all of the *Tollia tolli* Zone of northern Siberia (Textfig. 8). These two Canadian faunas are treated herein as regional ammonite subzones of the *Buchia keyserlingi* Zone. At the same time they represent refined subzones (or zones) of the interregional generalized *Temnoptychites* Zone of the Boreal Realm.

The correlation of the *Temnoptychites* (*Temnoptychites*) *kemperi* n. sp. Subzone with most or all of the Hoplitoides and Syzranicus zones of the U.S.S.R. proposed herein (Textfig. 8) necessitates an updating of the next younger *Thorsteinssonoceras ellesmerense* Subzone. This subzone previously was correlated tentatively with the middle parts of *Temnoptychites syzranicus* and *Temnoptychites hoplitoides* zones (Jeletzky, 1973, p. 66, 67, Fig. 3). However, the subsequent discovery of faunal equivalents of these zones in beds immediately underlying those containing *Thorsteinssonoceras ellesmerense* (Kemper, 1977, p. 3, Fig. 2; and in the preceding sections of this paper) indicates the correlation of the latter beds with the basal part of the overlying *Polyptychites michalskii* and *Polyptychites keyserlingi* Zone of the U.S.S.R. (Textfig. 8). The apparent total absence of any polyptychitid ammonites in the *Thorsteinssonoceras ellesmerense* Subzone of the Sverdrup Basin and their presence in its northern Siberian equivalents appears to be the result of a gradual arcticward and then eastward migration of these European forms (*ibid.*, p. 5, Fig. 2). The *Thorsteinssonoceras ellesmerense* Subzone accordingly is correlative with the basal part of the *Polyptychites* beds of northwestern Germany and with some beds low in the upper, subzonally unnamed, part of *Kilianella roubaudi* Zone of the zonal standard of southwestern Europe (Jeletzky, 1973, Fig. 3; this paper, Textfig. 8). The writer continues to place all these zones and subzones in the

Stages, zones and subzones of Southwestern Europe (after Le Hegarat, 1973 and Thieuloy 1973)	Sverdrup Basin (Kemper, 1977 and this paper)	Northern Siberia (rearranged from Jeletzky, 1973)	Russian Platform (rearranged from Jeletzky, 1973 and Kemper, 1977)
MID-VALANGINIAN			
Kilianella roubaudi	Polyptychites (s.str.) sphaeroidalis	Polyptychites (Siberiptychites) ex gr. stubendorffi	Polyptychites (s.str.) polyptychus
	Polyptychites (s.str.) keyserlingi	Polyptychites (s.str.) michalskii and Polyptychites (s.str.) ex gr. keyserlingi (undivided)	Polyptychites (s.str.) michalskii and Polyptychites (s.str.) ex gr. keyserlingi (undivided)
	Polyptychites (Siberiptychites) ex gr. stubendorffi		
	Thorsteinssonoceras ellesmerense		
EARLY VALANGINIAN			
Thurmanniceras pertransiens (subzone)	Temnoptychites (Temnoptychites) kemperi n.sp.	Temnoptychites (Temnoptychites) syzranicus	Temnoptychites (Temnoptychites) hoplitoides
	Temnoptychites (Costamenjaites) troelseni n.sp.	Tollia klimovskiensis	Pseudogarnieria undulatoplicatilis
		Tollia mesezhnikowi	
		Tollia tolli and allied forms	
BERRIASIAN			
Berriasella (Fauriella) boissieri s.str.	Unknown and possibly absent throughout the basin	Surites analogus	Surites spasskensis
Berriasella (Tirnovella) occitanica	Buchia okensis and "Craspedites (Subcraspedites)" aff. suprasubditus	Hectoroceras kochi (may include some topmost Tithonian beds at the base)	Berriasella (Riasanites) rjasanensis / Ryasanian beds
Berriasella (Pseudosubplanites) grandis			Absent by nondeposition

Buchia keyserlingi s. lato

MFM

Textfigure 8. Biochronology and external correlation of some Valanginian and Berriasian ammonite and Buchia faunas of Sverdrup Basin.

middle Valanginian as he prefers the tripartite subdivision of this stage used by himself (Jeletzky, 1973, p. 66, 67, Fig. 3) to the more commonly used bipartite subdivision. Kemper's (1977, p. 5, Fig. 2) proposal to subdivide the Canadian boreal Valanginian into the lower and upper Valanginian substages is not followed in this paper since the modified tripartite subdivision is more refined and results in three subequal groups of paleontological zones and subzones roughly corresponding to the *Platylenticeras*, *Polyptychites*, and *Dichotomites* (plus "*Astieria*") beds of northwestern Germany (see Jeletzky, 1973, Fig. 3; this paper, Textfig. 8).

The previously held idea (Jeletzky, 1973, p. 63, 64, Figs. 2, 3) about the presence in the Sverdrup Basin of the basal Valanginian *Tollia tolli* Zone stratigraphically below the generalized *Temnoptychites* Zone is regarded now as unproven and rather doubtful. All presently known finds of *Tollia* forms in the Sverdrup Basin are either assignable to the subzones of the *Temnoptychites* Zone defined above (e.g., that of *Tollia* n. sp. aff. *T. klimovskiensis* and *Tollia* aff. *T. tolli* at GSC loc. 28713 or that of *Tollia* n. sp. aff. *T. subtilis* at GSC loc. 91313) or are of an uncertain stratigraphic position (e.g., that of *Tollia* n. sp. aff. *T. vai* at GSC loc. 52491 near Buchanan Lake). The previous interpretation of the latter find as representing an "unmixed" *Tollia* fauna (Jeletzky, 1973, p. 63) is withdrawn herewith following Kemper's detailed study of the Buchanan Lake section (1975, p. 248, 249, Fig. 2).

If the *Temnoptychites* (*Costamenjaites*) *troelseni* Subzone of the Sverdrup Basin corresponds to all of the Middle Russian *Pseudogarnieria undulatoplicatilis* Zone, the rare and scattered occurrences of various *Tollia* species in this zone (and also those made in the Sverdrup Basin in general) likely represent only sporadic incursions of the contemporary northern Siberian *Tollia tolli* fauna into the Sverdrup Basin. If so, this endemic basal Valanginian fauna of northern Siberia is even more restricted paleogeographically than previously believed. Should this hypothesis be confirmed by further research, one would expect the *Temnoptychites* (*Costamenjaites*) *troelseni* Subzone to be underlain directly by the equivalents of the upper Berriasian *Buchia* n. sp. aff. *B. volgensis* and *Tollia* cf. *T. payeri* Zone of the Richardson Mountain–Porcupine Plain Trough (Jeletzky, 1971b, p. 5, Fig. 2; 1973, p. 56, Figs. 2, 3). However, it is also possible that the *Temnoptychites* (*Costamenjaites*) *troelseni* Subzone corresponds only to the upper part of the Middle Russian *Pseudogarnieria undulatoplicatilis* Zone and the presumably equivalent *Tollia klimovskiensis* Subzone of the northern Siberian *Tollia tolli* Zone (Jeletzky, 1973, Fig. 3, column 5). In that case, a teilzone of *Tollia tolli* fauna may be found yet in the beds, so far barren of ammonites, of the Deer Bay Formation immediately underlying the *Temnoptychites* (*Costamenjaites*) *troelseni* Subzone. Finally, there is yet another possibility: the presence of a widespread hiatus that cuts out at least the upper Berriasian beds in the nearshore facies of the Deer Bay Formation recently was discovered by Kemper (1975, p. 248, 249, Fig. 2). This hiatus may also embrace the basal Valanginian beds corresponding to the lower part of the

Pseudogarnieria undulatoplicatilis Zone of Middle Russia and the *Tollia mesezhnikowi* Subzone of the northern Siberian *Tollia tolli* Zone (Jeletzky, 1973, Fig. 3, columns 5, 6). Further field work in the critical sections of the Deer Bay Formation is needed to solve this problem and the writer's doubts are indicated by an empty space and a query at the boundary of the Berriasian and Valanginian compartments in Textfig. 8.

As far as is known, all *Temnoptychites* and *Tollia* found in the Sverdrup Basin occur in beds appreciably older than those containing the earliest *Polyptychites* (*Siberiptychites*) ex gr. *P. (S.) stubendorffi* (Kemper, 1977, p. 3). This conflicts with the reported association of *Temnoptychites* with *Polyptychites* sensu stricto, *Euryptychites*, *Astieriptychites*, and "*Neotollia*" in the subzone of *Temnoptychites syzranicus* of the *Polyptychites* (*Siberiptychites*) *stubendorffi* Zone in northeastern Siberia (Saks and Shulgina, in Saks et al., 1972, p. 104; Chirva et al., 1975). The Canadian sequence of faunas also conflicts with the apparent association of *Temnoptychites* with various representatives of *Polyptychites* sensu stricto and *Siberiptychites* in the late early Valanginian fauna of Traill Island, eastern Greenland (Bodylevsky, 1967, p. 103; and in the previous sections of this report). As pointed out by Jeletzky (1965a, p. 43; 1973, p. 67), the Traill Island fauna may represent a depositional accumulation (condensation) of several early Valanginian ammonite faunas in a thin, very slowly deposited layer of limy ooze. The same may be true of a similar faunal mixture recently described by Chirva et al. (1975) from a thin sequence of shallow-water sandstone in the Khatanga Basin. One is tempted to think that the recently made claims of the association of *Tollia* and *Neotollia* with *Temnoptychites*, *Euryptychites* and *Neocraspedites* (e.g., Saks et al., 1963; Saks and Shulgina, 1974, p. 145) are based solely on such marginal thin sections and are the results of either redeposition or condensation of several zonal ammonite faunas in a single thin layer or bed. However, *Tollia tolmatschowi* was reported also to be associated with *Polyptychites* ex gr. *P. keyserlingi* and *P. conferticosta* in the 9 to 10 m thick unit of the thick (about 200 m) entirely argillaceous offshore facies of the Valanginian on Paks Peninsula (Bassov et al., in Saks et al., 1972, p. 42). However, this claim conflicts with the results of Saks et al. (1963, p. 176, 181) and those of a careful bed-by-bed collecting of the same section by T.M. Emeliantsev (Voronets, 1962, p. 17, 18, Fig. 3). According to Voronets (*loc. cit.*), the highest *Tollia* (i.e., *Tollia tolli*) found in this section occurs some 20 m stratigraphically below the lowest *Polyptychites* (i.e., *Siberiptychites*) *conferticosta*. The Paks Peninsula section did not yield any *Temnoptychites* whatsoever. Further detailed study of critical sections in Arctic Canada and northeastern Siberia obviously is needed to clarify these conflicting biochronological data. However, like the previously mentioned absence of polyptychitid ammonites in the Canadian *Thorsteinssonoceras ellesmerense* Subzone, the variable time ranges of diagnostic middle Valanginian ammonites may be a result of their gradual interregional migrations within the Boreal Realm (Kemper, 1977, p. 5, Fig. 2).

References

Aristov, V. N.
1974: About ammonites of the genus *Homolsomites* from the Lower Cretaceous of Russian Platform; Akad. Nauk SSSR, Sib. Otd., Inst. Geol. Geofiz., Tr., No. 136, p. 149–154, Pls. XIV, XV (in Russian).

Arkell, W. J. *et al.*
1957: Treatise on Invertebrate Palaeontology, R. C. Moore, ed.; Part L: Mollusca 4, Cephalopoda, Ammonoidea; Geol. Soc. Am. and Univ. Kansas Press, p. L1–L490.

Bodylevsky, V. J.
1949: Atlas of index forms of fossil faunas of U.S.S.R., *in* Berg, L. S. *et al.*, Vol. X, Lower part of the Cretaceous System; VSEGEI (All Soviet Sci.-Res. Geol. Inst. Ministry Geol. U.S.S.R.), Gosud. Izdatelstvo Geol. Literatury, Moskva (in Russian).
1956: The significance of some ammonites for the stratigraphy of Jurassic and Lower Cretaceous deposits of the Russian Platform; Vses. Nauchno-Issled. Geol. Inst. n.s., Tr., v. 12, p. 137–142 (in Russian).
1960: New late Valanginian ammonites of northern Siberia; *in* New species of plants and invertebrates of the U.S.S.R.; Vses. Nauchno-Issled. Geol. Inst., pt. II, p. 172–175, Pl. 39 (in Russian).
1967: Jurassic and Cretaceous faunas of Novaya Zemlya; Zap. Leningrad. Gorn. Inst., v. 53 (2), p. 99–112, Pls. I–X (in Russian).

Bogoslowsky, N. A.
1897: Der Rjasan-Horizont, seine Fauna, seine stratigraphischen Beziehungen und sein wahrscheinliches Alter; Mater. Geol. Ross. t. 18, p. 1–158, Pls. 1–6.
1902: Materialien zur Kenntnis der Untercretacischen Ammonitenfauna von Central- und Nord-Russland; Geol. Kom. n.s., Tr., v. 2, p. 1–161, Pls. I–XVIII.

Casey, R.
1973: The ammonite succession at the Jurassic-Cretaceous boundary in eastern England: The Boreal Lower Cretaceous; Geol. J., Spec. Issue no. 5, p. 193–266.

Chirva, S. A., Shulgina, N. I. and Burdykina, M. D.
1975: *Menjaites* in the lower Valanginian deposits of northern Siberia; Akad. Nauk SSSR, Dokl., v. 225(5), p. 1162–1164 (in Russian).

Donovan, D. T.
1953: The Jurassic and Cretaceous stratigraphy and palaeontology of Traill Ø , East Greenland; Medd. om Grønland, v. 111 (4), p. 1–150, Pls. 1–125.
1964: Stratigraphy and ammonite fauna of the Volgian and Berriasian rocks of East Greenland; Medd. om Grønland, v. 154 (4), p. 1–34, Pls. 1–9.

Douglas, R. J., Gabrielse, H., Wheeler, J. A., Stott, D. F. and Belyea, H. R.
1970: Geology of Western Canada; *in* Geology and economic minerals of Canada; Geol. Surv. Can., Econ. Geol. Rept. No. 1, p. 366–488, Pls. VIII-1–VIII-20.

Golbert, A. V., Klimova, I. G. and Saks, V. N.
1972: The standard section of the Neocomian for West Siberia in Polar Transuralian region; Sib. Sci. Res. Inst. Geol. Geophy. Econ. Minerals (SNIIGGIMS), Nauka Press, Novossibirsk (in Russian).

Imlay, R. W.
1960: Ammonites of Early Cretaceous age (Valanginian and Hauterivian) from the Pacific Coast States; U.S. Geol. Surv. Prof. Pap. 334-F, p. 167–228, Pls. 24–43.

Imlay, R. W. and Jones, D. L.
1970: Ammonites from the *Buchia* zones in northwestern California and southwestern Oregon; U.S. Geol. Surv., Prof. Pap. 647-B, p. 1–57, Pls. 1–15.

Jeletzky, J. A.
1950: Some nomenclatorial and taxonomic problems in paleozoology; J. Paleontol., 24(1), p. 19–38.
1955: Evolution of Santonian and Campanian *Belemnitella* and palaeontological systematics; exemplified by *Belemnitella praecursor* Stolley; J. Paleontol., 29 (3), p. 478–509, Pls. 56–58.
1964: Illustrations of Canadian fossils. Lower Cretaceous marine index fossils of the sedimentary basins of Western and Arctic Canada; Geol. Surv. Can., Paper 64-11.
1965a: Late Upper Jurassic and early Lower Cretaceous fossil zones of the Canadian Western Cordillera, British Columbia; Geol. Surv. Can., Bull. 103.
1965b: *Thorsteinssonoceras:* A new craspeditid ammonite from the Valanginian of Ellesmere Island, Arctic Archipelago; Geol. Surv. Can., Bull. 120.
1966: Upper Volgian (latest Jurassic) ammonites and buchias of Arctic Canada; Geol. Surv. Can., Bull. 128.
1968: Macrofossil zones of the marine Cretaceous of the western interior of Canada and their correlation with the zones and stages of Europe and the western interior of the United States; Geol. Surv. Can., Paper 67-72.
1971a: Marine Cretaceous biotic provinces and paleogeography of Western and Arctic Canada: illustrated by a detailed study of ammonites; Geol. Surv. Can., Paper 70-22.
1971b: Biochronology of Jurassic-Cretaceous transition beds in Canada; Geol. Surv. Can., Paper 71-16.
1973: Biochronology of the marine boreal latest Jurassic, Berriasian and Valanginian in Canada: The Boreal Lower Cretaceous; Geol. J., Spec. Issue no. 5, p. 41–80.

Kemper, E.
1964: Über eine deutsche *Tollia*-Fauna und den Ursprung der Polyptychiten (Ammonoidea, Mittelvalendis); Fortschr. Geol. Rheinl. Westf., 7, p. 15–26, Pls. 1, 2.
1968: Geologischer Führer durch die Grafschaft Bentheim und die angrenzenden Gebiete (3rd ed.); Nordhorn, Bentheim, 1–172, Pls. 1–25.
1975: Upper Deer Bay Formation (Berriasian-Valanginian) of Sverdrup Basin and biostratigraphy of the Arctic Valanginian; Geol. Surv. Can., Paper 75-1B, p. 245–254.
1977: Biostratigraphy of the Valanginian in Sverdrup Basin, District of Franklin; Geol. Surv. Can., Paper 76-32.

Klimova, I. G.
1960: Valanginian ammonites of the West Siberian Lowland; SNIIGGIMS, Tr., Mater. po paleont. i Stratigr. Zap. Sibiri, No. 8, 163–175, Pls. XIX–XXI (in Russian).

Koenen, A. von
1902: Die Ammonitiden des Norddeutschen Neocom; Abh. Preuss. Geol. Landesanst., N.F. v. 24, p. 1–451 and Atlas with 55 pls.

Krimgolts, G. Ya., Petrova, G. T. and Pchelintsev, V. F.
1953: Stratigraphy and fauna of marine Mesozoic rocks of northern Siberia; Nauchno-Issled. Inst. Geol. Arktiki, Tr., t. XLV (in Russian).

Le Hegarat, G.
1973: Le Berriasien du sud-est de la France; Docum. Lab. Géol. Fac. Sci. Lyon, no. 43 (fasc. 1).

Luppov, N. P. and Drushchits, V. V.
1958: Ammonoidea (Ceratites and Ammonites), Dibranchiata; *in* Principles of Paleontology, Mollusca-Cephalopoda II, Yu. Orlov, ed.; Moscow (in Russian).

Michalski, A.
1890: Die Ammoniten der unteren Wolga-Stufe; Mém. Comité géol. Russie, livr. 8, no. 2.

Neale, J. W.
1962: Ammonoidea from the Lower D Beds (Berriasian) of the Speeton Clay; Palaeontology, v. 5, p. 272–296, Pls. 40–45.

Neumayr, M. and Uhlig, V.
1881-82: Ueber Ammonitiden aus den Hilsbildungen Norddeutschlands; Palaeontogr., vol. 27 (3).

Nikitin, S.
1881: Die Jura-Ablagerungen zwischen Rybinsk, Mologa und Myschkin an der oberen Volga; Mém. Acad. Imp. Sci., St. Pétersb. v. 7.
1888: Les Véstiges de la période Crétacé dans la Russie Centrale; Mém. Com. géol., St. Pétersb., t. V.

Pavlow, A. P.
1892: Parts I–III *in* A. P. Pavlow and G. W. Lamplugh: Argilles de Speeton et leurs équivalents; Bull. Soc. Impér. Nat., Moscou, n.s., t. V.
1901: Le Crétacé inférieur de la Russie et sa faune; Nouv. Mém., Soc. Imp. Nat., Moscou, t. XVII.
1914: Jurassic and Lower Cretaceous Cephalopoda of northern Siberia; Zap. Imp. Akad. Nauk, Cl. Phys.-Maths., v. 21 (4), p. 1–68, Pls. I–XVIII (in Russian).

Saks, V. N. *et al.*
1972: Jurassic-Cretaceous boundary and Berriasian stage in Boreal Realm; Izd. Akad. Nauk SSSR (in Russian) (also available in English translation by the Israel Program for Scientific Translation, Jerusalem, 1975, from the U.S. Dept. of Commerce).

Saks, V. N., Ronkina, Z. Z., Shulgina, N. I., Bassov, V. A. and Bondarenko, N. M.
1963: Stratigrafiia yurskoi i melovoi system severa SSSR; Press of Acad. Sci. U.S.S.R., Moscow (in Russian).

Saks, V. N. and Shulgina, N. I.
1969: New zones of the Neocomian and the boundary between the Berriasian and Valanginian stages in northern Siberia; Geol. Geofiz., no. 12, p. 42–52 (in Russian).
1974: Valanginian stage of the Boreal Realm; Akad. Nauk SSSR, Sib. Otd., Inst. Geol. Geofiz., Tr., no. 136, p. 142–149 (in Russian).

Salfeld, H. and Frebold, Hans
1924: Jura und Kreidefossilien von Nowaja Zemlja; Rep. Sci. Results, Norw. Exped. Nowaja Zemlya 1921, v. 11, Nr. 23.

Sazonova, I. G.
1971: The Berriasian of the Russian Platform (stratigraphy, fauna of ammonites and aucellas); Vses. Neft. Nauchno-Issled. Geol.-Razv. Inst., Tr., v. 110, p. 1–110, Pls. I–XXVI (in Russian).

Shulgina, N. I.
1968: Ammonites of the genus *Chetaites* from the Jurassic-Cretaceous boundary beds of Siberia; Inst. Geol. Geofiz., Sib. Otd., Tr., v. 48, p. 101–107, Pls. XI–XIX (in Russian).
1969: Volgian ammonites, *in* Key section of the Upper Jurassic deposits of the Kheta River basin, Nauka, Leningrad, V. N. Saks, ed.; p. 125–162, Pls. 22–38 (in Russian).

Sokolov, D. N.
1913: Sur les fossiles des blocks erratiques de Novaja Zemlia; Trav. Mus. géol. Pierre-le-Grand, t. 7, p. 59–92, Pls. 1–3.

Spath, L. F.
1924: On the ammonites of the Speeton Clay and the subdivisions of the Neocomian; Geol. Mag., v. 61, p. 73–89.
1936: The Upper Jurassic invertebrate faunas of Cape Leslie, Milne Land; II: Upper Kimmeridgian and Portlandian; Medd. om Grønland, v. 99 (3), p. 1–180.
1947: Additional observations on the invertebrates (chiefly ammonites) of the Jurassic and Cretaceous of East Greenland; I: The *Hectoroceras* fauna of S.W. Jameson Land; Medd. om Grønland, v. 132 (3), p. 1–69, Pls. 1–5.
1952: Additional observations on the invertebrates (chiefly ammonites) of the Jurassic and Cretaceous of East Greenland; II: Some Infra-Valanginian ammonites from Lindermans Fjord, Wollaston Foreland, with a note on the base of the Cretaceous; Medd. om Grønland, v. 133 (4), p. 1–40, Pls. 1–4.

Swinnerton, H. H.
1935: The rocks below the Red Chalk of Lincolnshire and their cephalopod faunas; Quart. J. Geol. Soc. London, v. 91, p. 1–46, Pls. 1–4.

Thieuloy, J. P.
1973: The occurrence and distribution of boreal ammonites from the Neocomian of southeast France (Tethyan Province): The Boreal Lower Cretaceous; Geol. J., Spec. Issue no. 5, p. 289–302.

Toula, F.
1874: Beschreibung mesozoischer Versteinerungen von den Kuhn-Insel; Zweite Deutsche Nordpolarfahrt, Bd. 2, p. 497–501.

Troelsen, J. C.
1952: Geological investigations in Ellesmere Island; Arctic, v. V, p. 198–210.
1954: A geological study of Canyon Fiord, Ellesmere Island, with particular reference to the geological history of the Franklinian Geosyncline; Arctic Inst. North America, Project No. ONR-73 (unpubl. MS on file with Geol. Surv. Can., Ottawa).

Uhlig, Victor
1903–10: The fauna of the Spiti shales; Palaeont. Indica (XV), v. 4, fasc. 1–3.

Voronets, N. S.
1957: New ammonites of the Paks Peninsula on the southern shore of Laptevs' Sea; Collection of Papers in Paleontol. and Biostratigr. No. 2, Press of the Inst. Arctic Geol., Leningrad (in Russian).
1962: The stratigraphy and cephalopod molluscs of the Jurassic and Lower Cretaceous deposits of the Lena-Anabar area; Inst. Geol. Arkt., Tr., v. 110, p. 1–237, Pls. I–LXI (in Russian).

Plates 1 to 14

All specimens are reproduced natural size unless otherwise indicated in the explanations of the figures concerned.

Plate 1

All fossils from late early Valanginian Deer Bay Formation, Amund Ringnes Island, GSC loc. 91313 (see text for further details)

Figure 1. *Temnoptychites (Temnoptychites) kemperi* n. sp. Paratype. GSC 49308. Intermediate whorl of the sturdy *T. (T.) triptychiformis*–like variant of the species. (A) Lateral view of fragmentary, strongly weathered side showing a segment of a distinctly trichotomously sculptured inner whorl corresponding to that reproduced in Pl. 6, fig. 2A–D. (B) Lateral view of the other, better preserved side exhibiting the transition from the indistinctly quadrichotomously ribbed growth stage to the ribless but bullate growth stage. (C) Ventral view of the earliest exposed part of the whorl exhibiting marked weakening of secondaries in the median part of the venter and the rounded-triangular, *T. (T.) mokschensis*–like cross-section of its oral end. (D) Cross-section illustrating gradual transformation of the regularly rounded early whorls into the rounded-triangular, outermost preserved (intermediate) whorl.

Figure 2. *Temnoptychites (Temnoptychites) borealis* Bodylevsky 1967. GSC 49309. An intermediate, fully septate whorl exhibiting transition from the dichotomous, nonbullate growth stage first to the indistinctly trichotomous, bullate growth stage, then to the ribless, bullate growth stage. (A) View of the mostly poorly preserved, almost completely shell-covered side exhibiting indistinctly trichotomous rib bundles and well developed umbilical bullae. (B) View of the other, better preserved but almost entirely shell-less side exhibiting all three above-mentioned types of ornament in succession. Lateral and umbilical parts of external suture lines are inked in on the middle part of the whorl. The steinkerns of umbilical bullae are low and round-topped in contrast to the elevated and pointed shell-covered bullae visible in fig. A. (C) Ventral view of the early part of the whorl and cross-section of its oral end. Note the distinct weakening of shell-covered secondary ribs in the midventer and the complete interruption of adjacent secondary ribs preserved as steinkerns. In combination with broad but pronounced forward bends of the secondaries, these features distinguish intermediate whorls of *T. (T.) borealis* from similarly shaped intermediate whorls of the sturdy variant of *Thorsteinssonoceras ellesmerense*. (D) Ventral view of the fragmentary middle part of the whorl which exposes the midventral part of the preceding whorl with strong and sparse, broadly forward bent and medioventrally weakened ribs. (E) Ventral view of the adoralmost part of the whorl which exhibits a complete midventral interruption of the still preserved, heavy and elevated ventrolateral parts of the secondary ribs.

Figure 3. *Temnoptychites (Temnoptychites) kemperi* n. sp. Paratype. GSC 49310. Fragment of two considerably laterally deformed early whorls of the sturdy *T. (T.) triptychiformis*–like variant. (A) Lateral view of the side which exposes outer, distinctly quadrichotomously sculptured whorl only. (B) Lateral view of the other side which exposes a segment of the inner, pronouncedly trichotomously sculptured whorl in addition to that of the outer distinctly quadrichotomously sculptured whorl. (C) Cross-section of the two whorl fragments. (D) Ventral view of the outer fragment exhibiting the broadly forward bent secondaries with weakening generally absent in the midventer.
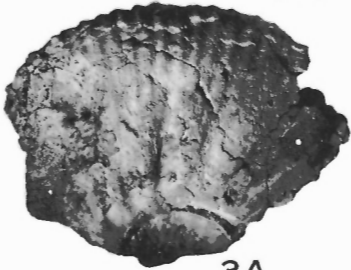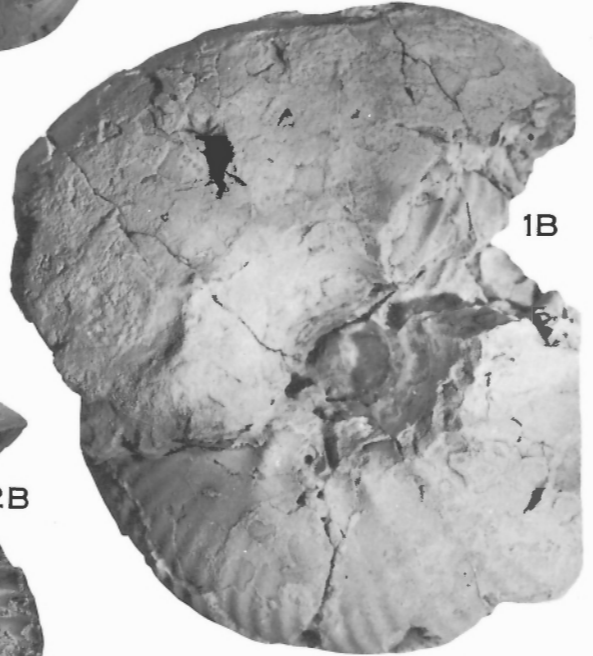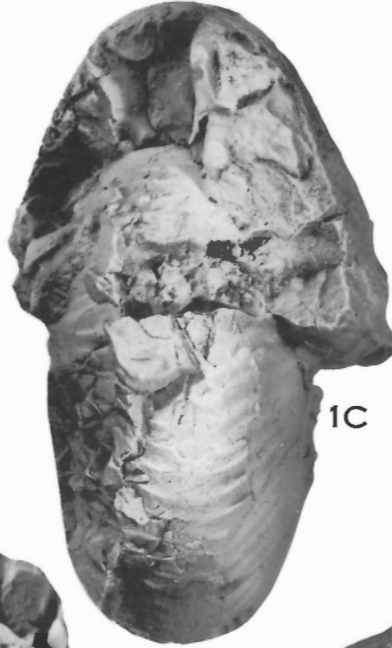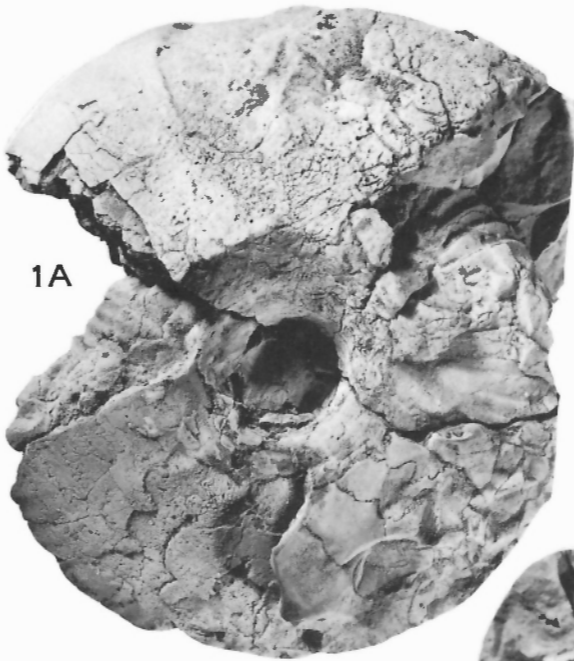
Plate 1

1A

1C

1D

2C

1B

2A

2B

3A

3B

3C

3D

2D

2E
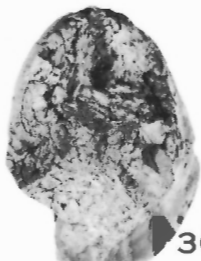
Plate 2

All fossils from late early Valanginian Deer Bay Formation, Amund Ringnes Island, GSC loc. 91313 (see text for further details)

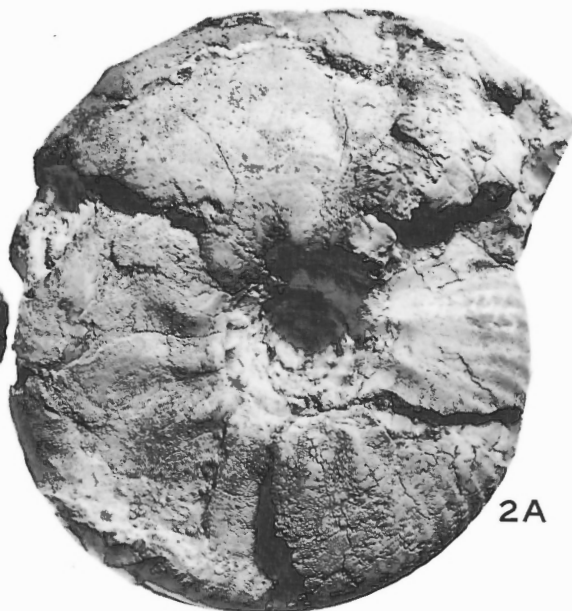Figure 1. *Temnoptychites (Temnoptychites) kemperi* n. sp. Paratype. GSC 49311. Late (penultimate?) but fully septate whorl representing the ribless but bullate growth stage. The specimen appears to be transitional between the sturdy *T. (T.) triptychiformis*–like and the intermediate, *T. (T.) hoplitoides*–like variants of the species. However, it may represent a laterally deformed (the inner whorls are almost completely crushed) representative of the former variety. (A) Ventral view of the mainly shell covered earliest third of the whorl and the cross-section of its oral end. The sculpture consists only of sparse but prominent umbilical bullae, three constrictions and locally numerous fine striae. (B) Lateral view of the almost entirely shell covered side. Sculpture as on the venter.

Figure 2. *Temnoptychites (Temnoptychites) kemperi* n. sp. Holotype. GSC 49312. Intermediate, fully septate whorl of the intermediate, *T. (T.) hoplitoides*–like variant of the species. The early and the end parts of the whorl are all but undeformed. (A) Lateral view of the almost entirely shell-less (a steinkern) side exhibiting the transition from the distinctly quadrichotomously ribbed growth stage (earliest fifth of the whorl), through the indistinctly quadrichotomously ribbed growth stage, to the ribless but bullate growth stage (oral half of the whorl). The whorl is ornamented by only 12 umbilical bullae. (B) Ventral view of the earliest exposed part of the whorl and the almost undeformed cross-section of its oral end. The secondary ribs are strongly weakened but not completely interrupted in the middle of the venter.

Figure 3. *Temnoptychites (Temnoptychites) kemperi* n. sp. Paratype. GSC 49313. Intermediate, fully septate whorl of the slender *T. (T.) lgowensis*–like variant of the species. The earliest and the adoralmost parts of the specimen are all but undeformed while the rest of the left side (fig. C) is all but flattened. (A) Lateral view of the undeformed (right) side partly covered by poorly preserved shell. The early two thirds of the whorl represent the indistinctly (due to weathering?) quadrichotomously ribbed growth stage while the oral third represents the beginning of the ribless but bullate growth stage. (B) Lateral view of the same side but with the oral third of the whorl taken off to expose the end phase of the distinctly trichotomously ribbed growth stage on the adoralmost quarter of the preceding whorl. The short primaries are distinctly bullate already in the trichotomous growth stage. (C) The undeformed earliest part of the whorl and its undeformed oral end. The entirely smooth appearance of the venter may be influenced partly by the strong weathering of the shell's surface.
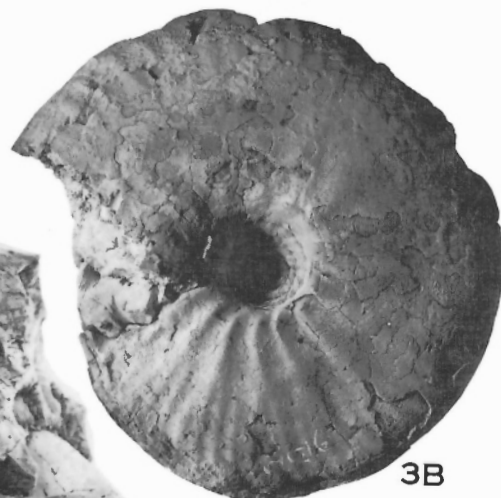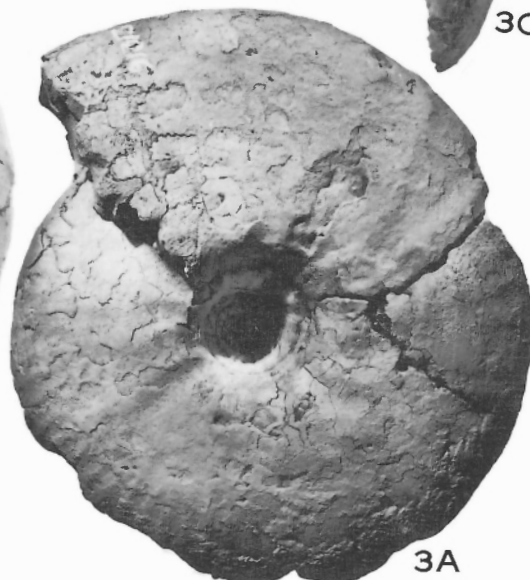
Plate 2

1A

2A

2B

3B

3C

1B

3A

Plate 3

All specimens are from GSC loc. 91313 (see previous plates and text for further details)

Figure 1. *Temnoptychites (Temnoptychites) kemperi* n. sp. Paratype. GSC 49314. Intermediate, completely septate whorl of the slender *T. (T.) lgowensis*–like variant of the species. This considerably deformed (laterally compressed) specimen is actually transitional to the intermediate *T. (T.) hoplitoides*–like variant (holotype, Pl. 2, fig. 2). The specimen is peculiar in that the secondaries cross the midventer without any appreciable weakening (fig. C), except near the adoralmost preserved part of the whorl (fig. B). (A) Lateral view of the better preserved, mostly shell-covered side. The earliest exposed fifth of the whorl exhibits the end phase of the distinctly quadrichotomously ribbed growth stage. The rest of the whorl exhibits the unusually prolonged, indistinctly quadrichotomously ribbed growth stage with the midflank becoming almost smooth near the oral end. (B) Ventral view of the adoral half of the whorl. The broadly forward-bent secondaries begin to weaken only in the midventer near the laterally deformed oral end of the whorl. (C) Ventral view of the earlier part of the whorl showing a complete lack of midventral weakening of the secondaries.

Figure 2. *Temnoptychites (Temnoptychites) kemperi* n. sp. Paratype. GSC 49315. Intermediate, completely septate whorl of a sturdy representative of the intermediate *T. (T.) hoplitoides*–like variant of the species morphologically transitional between its holotype (Pl. 2, fig. 2) and the more slender representatives of the sturdy *T. (T.) triptychiformis*–like variant (e.g., Pl. 1, fig. 1). This specimen is similar to the holotype of *T. (T.) hoplitoides* in its whorl shape and proportions. A small fragment of presumably immature living chamber adheres to the earliest preserved part of the whorl (fig. B). The specimen is almost undeformed (fig. B). (A) Lateral view. The ornament of the unweathered, largely shell-covered earliest part of the whorl is already indistinct in the midflank. (B) Cross-section of the whorl, cross-sections of two preceding whorls and the venter of the third preceding, early whorl. The coarse secondaries of the third whorl do not seem to be weakened, let alone interrupted, in the midventer. (C) Ventral view. The secondary ribs of the earliest preserved, shell-covered and almost unweathered part of the whorl are distinctly weakened to almost completely interrupted in the midventer. The greater adoral part of the venter is extremely weathered and unsuitable for any conclusions concerning the style of ribbing. The fragment of the living chamber attached to the left lower part of the whorl is marked by an arrow and 'L.ch.'

Figure 3. *Temnoptychites (Temnoptychites) kemperi* n. sp. Paratype. GSC 49316. Intermediate, completely septate whorl of the slender *T. (T.) lgowensis*–like variant of the species. The right side of the specimen shown in fig. A is almost undeformed whereas the left side is mostly squashed. (A) Lateral view of the right side mostly preserved as a steinkern. The whorl exhibits the indistinctly quadrichotomous ribbing habit throughout. The far-reaching obliteration of secondaries on the earliest preserved, still shell-covered part of the whorl appears to be an effect of the individual variability within the variant (cf. fig. 1A and Pl. 2, fig. 3B). An almost complete loss of ribbing on the adoralmost preserved part of the whorl probably is caused by its strong weathering. Note the swollen, bullate appearance of the primary ribs. (B) Ventral view of the strongly damaged early part of the whorl, its cross-section and the incomplete cross-section of the oral end. A segment of indifferently preserved ventral part of the preceding whorl is exposed also. The well developed, forward-bent secondaries of this whorl apparently are neither interrupted nor weakened on the midventer. (C) Ventral view of the best preserved, essentially undeformed early part of the whorl. The adapicalmost few ribs visible do not appear to be either interrupted or weakened on the midventer. However, the adoralmost secondaries visible appear to be distinctly weakened on the midventer.

Figure 4. *Temnoptychites (Temnoptychites) kemperi* n. sp. Paratype. GSC 49317. A late, possibly penultimate, entirely septate whorl of the sturdy *T. (T.) triptychiformis*–like variant of the species. This laterally deformed and, in part, flattened specimen exhibits the latest phase of indistinctly quadrichotomously ribbed growth stage and the early phase of the ribless but bullate growth stage. The reproduced side is a steinkern which exhibits some excellently preserved suture lines and several exceptionally well developed constrictions. Well developed umbilical bullae gradually become more distantly spaced and the lobes of the suture lines gradually become narrower adorally.

Figure 5. *Temnoptychites (Temnoptychites) kemperi* n. sp. Paratype. GSC 49318. Fragments of four early to intermediate, completely septate whorls of an extreme form of the intermediate *T. (T.) hoplitoides*–like variant of the species. This form combines an unusually early loss of the bulk of the ribbing with the unusually wide and shallow umbilicus and the early appearance and a great width of the medioventral interruption of secondary ribs. The flanks become semismooth and the secondary ribs are interrupted already on the earliest exposed part of the outermost of three inner whorls of the specimen (lower part of fig. A). (A) Lateral view of the two outer whorls. (B) Cross-sections of all four whorls. Oblique view of the oral and apical breaks of the fragmentary specimen shown in fig. A. Note the parallel-flanked and obtusely ventered but slender shape of cross-sections of the two almost undistorted inner whorls exposed in the apical break. The cross-section of the third (outer) whorl is already rounded-triangular shaped. (C) Cross-sections of all four whorls at the break in the middle of the specimen shown in fig. A. All cross-sections are distorted and that of the second earliest whorl is almost squashed. Note that the fine, noticeably forward bent secondary ribs covering the short exposed segment of the venter of the innermost whorl are neither weakened nor interrupted on the midventer.
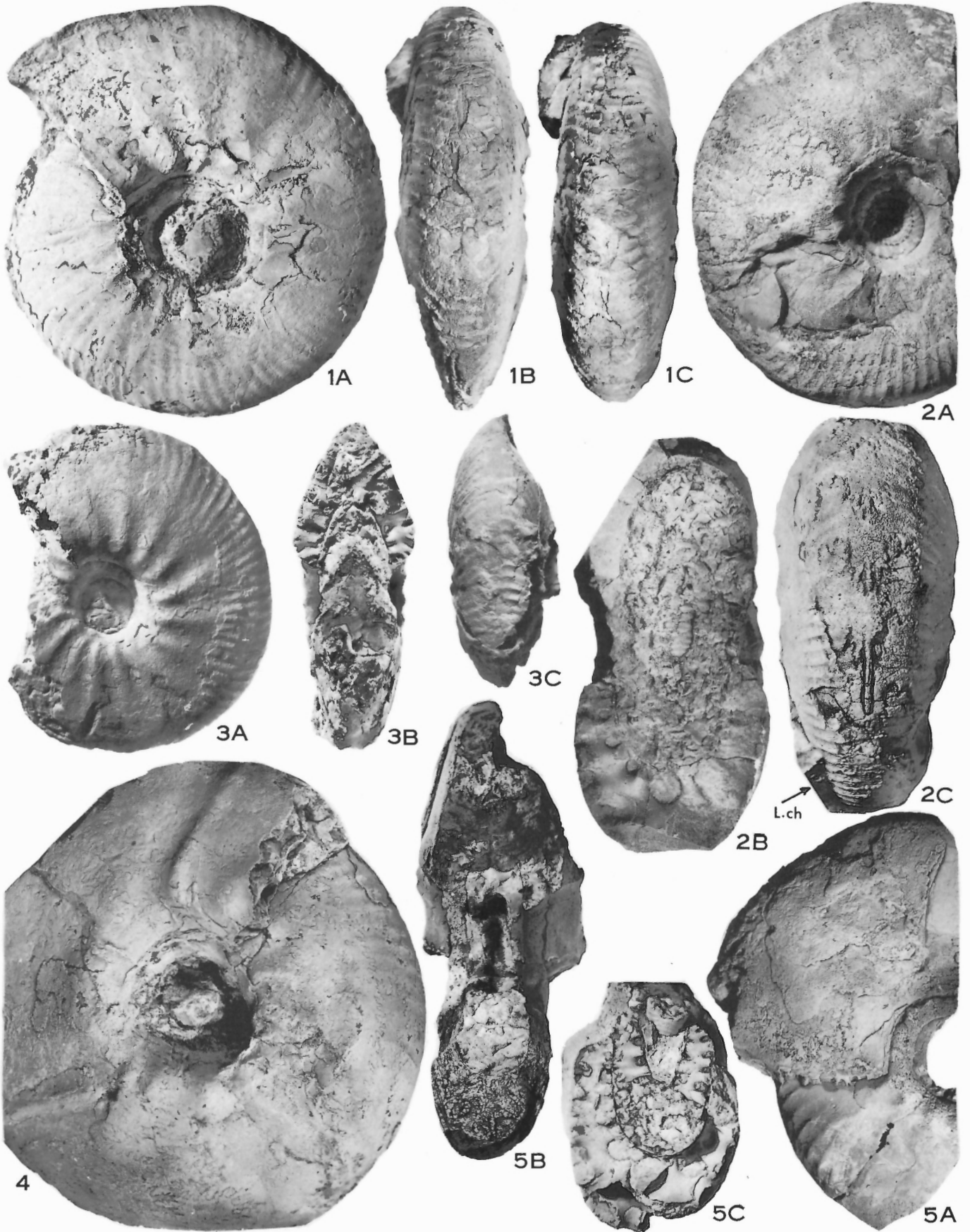
Plate 3

Plate 4

All specimens are from GSC loc. 91313 (see previous plates and text for further details)

Figure 1. *Temnoptychites* (*Temnoptychites*) *kemperi* n. sp. Paratype. GSC 49319. Fragments of four or five(?), mainly strongly deformed to squashed early to intermediate whorls. The almost undeformed fragment of completely septate, outermost preserved whorl reproduced in fig. A may be the early part of penultimate whorl. The specimen belongs to the same more slender form of the sturdy *T.* (*T.*) *triptychiformis*–like variant of the species as the earlier intermediate whorl reproduced in Pl. 1, fig. 1. (A) Lateral view of the outermost preserved whorl representing some (middle?) phase of the ribless but bullate growth stage. Note that the short segment of the preceding whorl exposed on the left side of the photograph already represents the same ribless but bullate growth stage which thus extends over 1½ septate whorls at least. (B) Rounded-triangular *T.* (*T.*) *mokschensis*–like shaped cross-section of the last preserved (penultimate?) whorl and the entirely smooth venter of a segment of the preceding whorl. (C) Ventral view of the distinctly and closely ribbed, regularly rounded innermost (fourth or fifth? inner) whorl visible inside GSC 49319. Note that the ribs are essentially straight all across the venter and are neither interrupted nor weakened in its middle part. (D) Lateral view of the same innermost visible whorl as that shown in fig. C. As far as it is possible to see, the elevated and sharp-topped secondaries of this whorl form dichotomous rib bundles.

Figure 2. *Temnoptychites* (*Temnoptychites*) *kemperi* n. sp. Paratype. GSC 49320. An intermediate, completely septate whorl of the same form of the species as that reproduced in Pl. 3, fig. 5. The specimen GSC 49320 differs from that reproduced in Pl. 3, fig. 5 only in the heavier build, narrower and deeper umbilicus and distinctly rounded-triangular (instead of subparallel-flanked) cross-section of equivalent growth stages. In these respects GSC 49320 is transitional between GSC 49318 and typical representatives of the intermediate *T.* (*T.*) *hoplitoides*–like variety of the species. As in GSC 49318, a fragment, about half a whorl long, of the living chamber attached to the right flank of the whorl and reproduced in fig. C is there marked 'L.ch.' (A) Lateral view of better preserved side exhibiting the same relatively sparse and sharp but early disappearing ribbing as the corresponding growth stages of GSC 49318 (Pl. 3, fig. 5A). The adapical half of the whorl exhibits the late phase of the indistinctly quadrichotomously ribbed growth stage whilst the adoral half is completely ribless. (B) Ventral view of the middle third of the whorl where the sparse and sharp, ventrolateral parts of secondaries fade out rapidly. Note the unusually great width of the medioventral smooth band characteristic of this extreme form of the variant. (C) Ventral view of the earliest third of the whorl. Unlike the middle third of the whorl shown in fig. B, the sparse and elevated secondaries are weakened only, but not completely interrupted, in the middle part of the venter.

Figure 3. *Temnoptychites* (*Temnoptychites*) *kemperi* n. sp. Paratype. GSC 49321. Fragmentary intermediate (completely septate) whorl of the sturdy *T.* (*T.*) *triptychiformis*–like variant of the species. GSC 49321 differs from the approximately equivalent growth stage of the same variant reproduced in Pl. 1, fig. 1 in the considerably lower and wider relative proportions of the whorl and in the considerably wider, distinctly steplike umbilicus. GSC 49321 is the sturdiest and the lowest whorled representative of *T.* (*T.*) *kemperi* n. sp. studied. (A) Lateral view. The adapical half of the whorl exhibits the latest phase of indistinctly quadrichotomously ribbed growth stage followed by the earliest phase of the ribless but bullate growth stage. The middle third of the whorl removed to expose a segment of the preceding whorl representing the distinctly trichotomous growth stage. (B) Cross-section of the above-discussed whorl and cross-sections of the preceding three intermediate and early whorls. Ontogenetic changes of the whorl's cross-section duplicate those of the specimen reproduced in Pl. 1, fig. 1D, except in the relatively wider and lower proportions of the equivalent whorls. (C) Two cross-sections of the whorl shown in fig. A and the ventral view of the segment of the preceding whorl. The midventral part of the preceding whorl is extremely weathered, except for the numbered uppermost visible part where the midventral interruption of some ribs and the decided midventral weakening of some others is clearly visible.
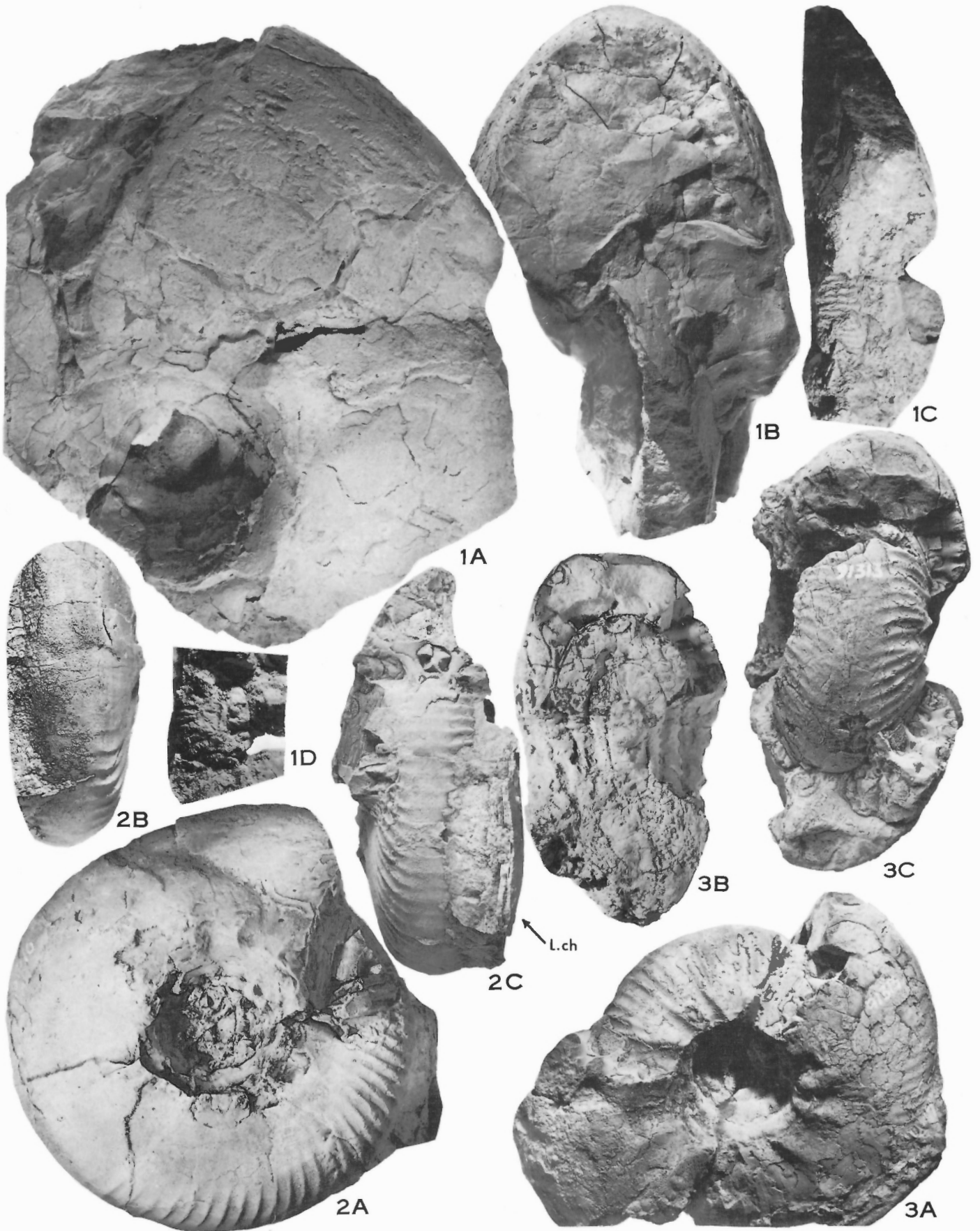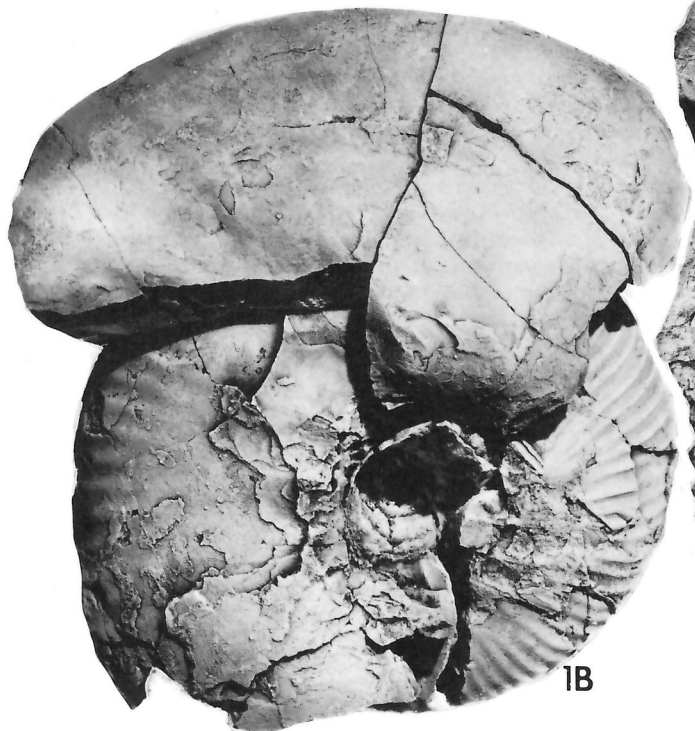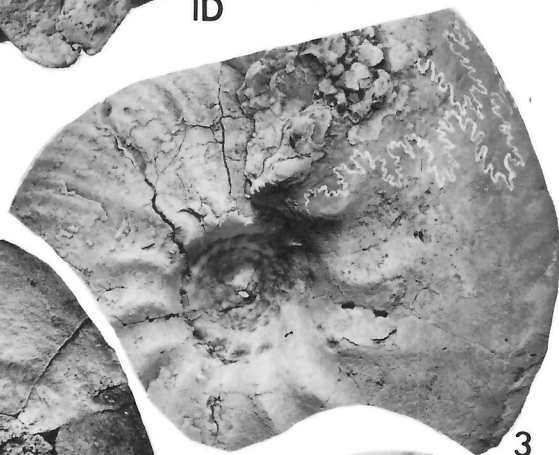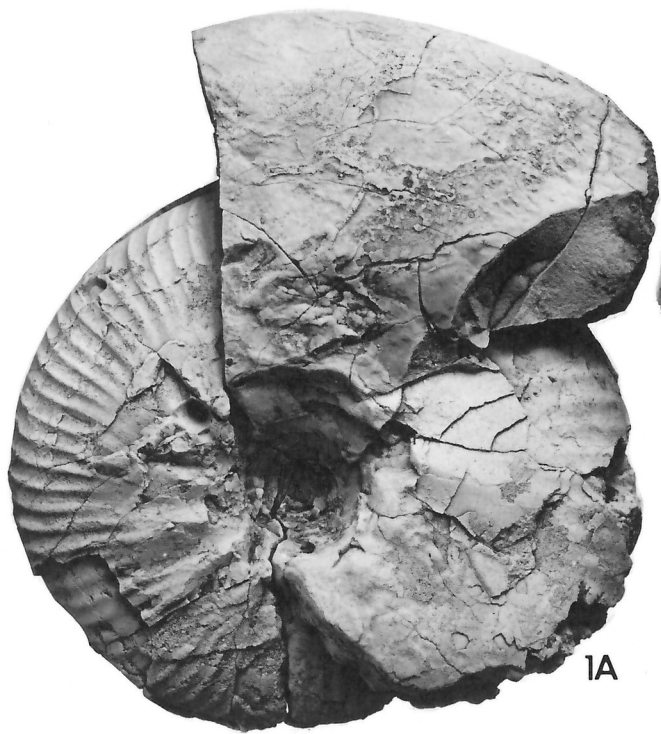
Plate 4

L.ch

Plate 5

Figure 1. *Temnoptychites (Temnoptychites) kemperi* n. sp. Paratype. Late early Valanginian, Deer Bay Formation, Amund Ringnes Island, GSC loc. 93757 (see text for further details). GSC 49322. An almost undeformed fragment of the apicalmost part of probably immature living chamber enclosing a slightly deformed to undeformed penultimate whorl and six moderately to slightly deformed earlier whorls apparently including the first whorl (fig. D). Specimen GSC 49322 is a slender representative of sturdy *T. (T.) triptychiformis*–like variant of the species transitional between its slender representative GSC 49308 (Pl. 1, fig. 1) and the sturdiest known representatives of the intermediate *T. (T.) hoplitoides*–like variant (e.g., GSC 49315; see Pl. 3, fig. 2) in the shape and proportions of the whorl. (A) Left-lateral view of penultimate whorl with a part of the fragmentary living chamber taken off. The early third of the penultimate whorl exhibits the distinctly quadrichotomously ribbed growth stage followed by the indistinctly quadrichotomously ribbed growth stage just before the superimposed fragment of the living chamber. The adoralmost preserved quarter of the penultimate whorl exhibits the late phase of indistinctly quadrichotomously ribbed growth stage where the ribs are all but lost in the midflank but strengthened and coarsened on the umbilical shoulder. (B) Right-lateral view with all of the fragment of the living chamber on. Two well developed constrictions and two prominent bullae are visible on the preserved fragment of the living chamber, which also shows two or three indistinctly defined but heavy ribs on the apicalmost part. This indicates that the fragment represents the apicalmost part of the living chamber. The sculpture of the penultimate whorl is similar to that of the other flank (fig. A). (C) Cross-section of the almost undeformed smaller half of the specimen consisting of seven whorls, including fragmentary living chamber. The innermost whorl is preserved only as an imprint. (D) Cross-section of the considerably more deformed larger half of the specimen. The exposed part of bodily preserved, globose innermost (seventh) whorl is smooth as is typical of the first whorls of Craspeditidae (e.g., Bodylevsky, 1967, p. 108, Pl. IV, fig. 3; Pl. VI, fig. 2v, g). It is assumed accordingly to be the first whorl. (E) Ventral view of the earliest quarter of the penultimate whorl visible from the side in fig. A. The markedly and fairly narrowly forward bent secondary ribs are greatly weakened but not interrupted, in the middle of the venter, in spite of its being well preserved and shell-covered.

Figure 2. *Temnoptychites (Costamenjaites) troelseni* n. sp. subsp. *troelseni* n. subsp. Holotype of the species and the subspecies. GSC 17174. Electron microscope photographs of the innermost visible (first?), almost smooth whorl visible in the cross-section reproduced in Pl. 9, fig. 1D, ×25. See description of that figure and the text (p. 33) for further details. (A) Lateral view; (B) ventral view.

Figure 3. *Temnoptychites (Temnoptychites) kemperi* n. sp. Holotype. GSC 49312. Lateral view of part of the otherwise unfigured flank of the specimen reproduced in Pl. 2, fig. 2. This flank is preserved almost exclusively as a steinkern and exhibits several excellently preserved external suture lines. The two oralmost of these suture lines are traced in white; they are also reproduced graphically in Textfig. 4F.

Plate 5

Plate 6

Both fossils are from late early Valanginian Deer Bay Formation, Amund Ringnes Island, GSC loc. 91313 (see text for further details)

Figure 1. *Tollia* n. sp. aff. *T. subtilis* Voronets 1962. GSC 49323. Partly fragmentary (adoral part) adult living chamber and complete but considerably deformed penultimate whorl. (A) Lateral view of the side consisting largely of the fragmentary living chamber. The beginning of the living chamber is marked by an arrow. Only the oralmost part of the phragmocone with a *Tollia*-like, large and florid first lateral lobe is exposed on the lower left side of the photograph. (B) Lateral view of the other side showing the completely preserved early part of the living chamber and about three quarters of the characteristically sculptured penultimate whorl. The beginning of the living chamber is marked by an arrow. (C) Ventral view of the early part of penultimate whorl visible from the side in fig. B and the deformed cross-section of the completely preserved but considerably deformed early part of the adult living chamber visible from the side in the right lower part of fig. A. The secondary ribs are neither weakened nor interrupted in the middle part of the venter, which indicates the placement of GSC 49323 in *Tollia*. (D) Ventral view of the completely preserved early third of the adult living chamber visible from the side in fig. A. Wherever the secondary ribs are well preserved, they are neither weakened nor interrupted in the middle part of the venter.

Figure 2. *Temnoptychites* (*Temnoptychites*) *kemperi* n. sp. Paratype. GSC 49324. Intermediate whorl of the sturdy *T.* (*T.*) *triptychiformis*–like variant corresponding to the preceding sculptured whorl partly exposed in GSC 49321 (Pl. 4, fig. 3A, C) but much better preserved and more slender. The specimen is mostly preserved as a steinkern. Proportions of GSC 49324 are the same as those of the earliest exposed part of the whorl of GSC 49308 (Pl. 1, fig. 1A, C, D) and it is morphologically transitional between the typical representatives of the sturdy, *T.* (*T.*) *triptychiformis*–like variant (e.g., that reproduced in Pl. 4, fig. 3) and the sturdiest representatives of the intermediate *T.* (*T.*) *hoplitoides*–like variant (e.g., that reproduced in Pl. 3, fig. 2) in the whorl proportions. (A) Lateral view of the better preserved side. All of the whorl exhibits the distinctly trichotomously ribbed growth stage. (B) Ventral view of the adoral part of the whorl. Secondary ribs are already interrupted in the middle part of the whorl even though most of the ventral side is preserved as a steinkern. (C) Ventral view of the earliest visible part of the whorl and the undeformed cross-section of its adoral part. The secondary ribs are almost always markedly weakened and sometimes interrupted on the middle part of the venter. (D) Lateral view of a segment of the unfigured side showing well preserved auxiliary part of external suture line. The second lateral lobe is in the middle whereas the first lateral lobe is out of focus on the right side of the photograph.
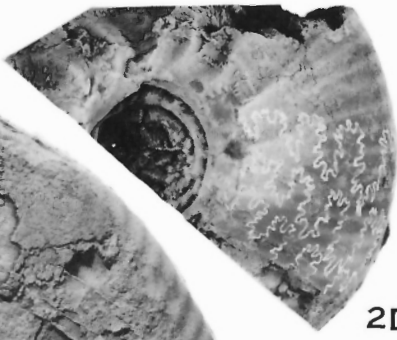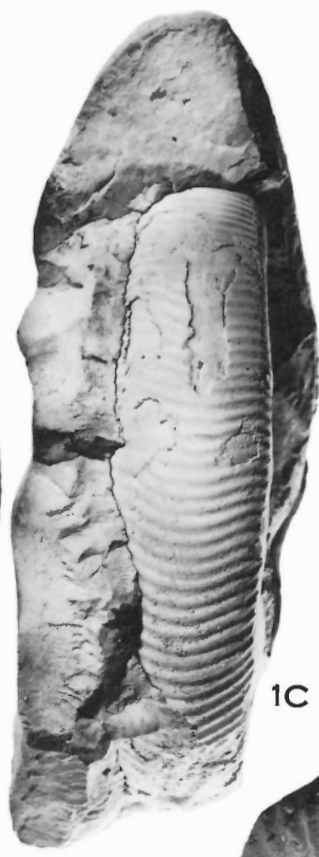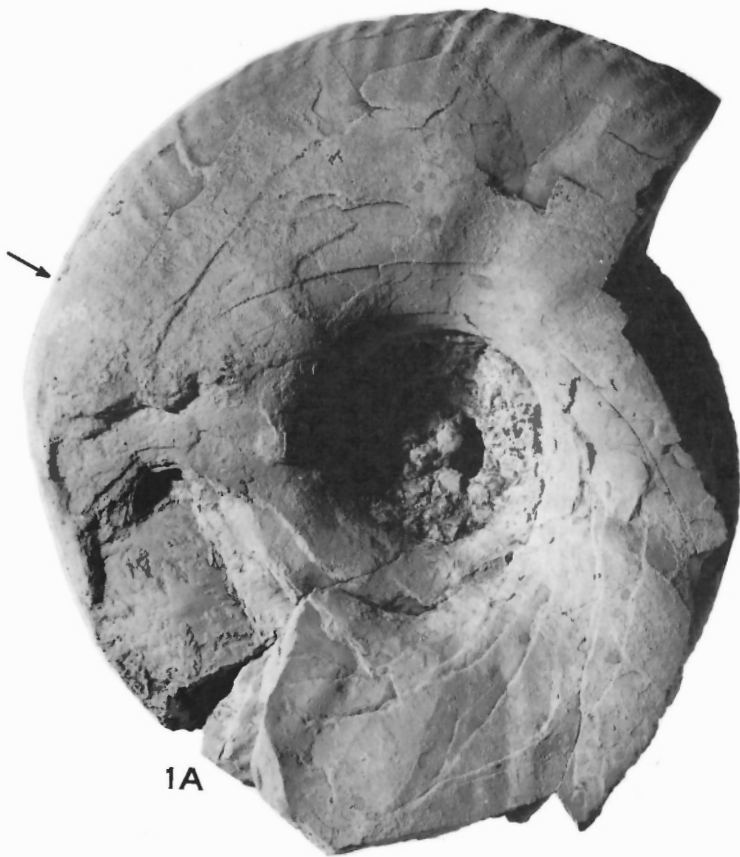
Plate 6

Plate 7

Figure 1. *Temnoptychites* (*Costamenjaites*) *grandiosus* Voronets 1962. Hypotype. Early early Valanginian, Deer Bay Formation, Ellesmere Island, GSC loc. 24075 (see text for further details). GSC 17173. A fragmentary specimen including a late intermediate, possibly penultimate (completely septate) whorl representing the early phase of final sculptureless growth stage. The enclosed, complete but considerably deformed preceding whorl represents most of indistinctly trichotomously ribbed growth stage and the latest phase of dichotomously ribbed growth stage. (A, B) Two views of the outermost preserved, sculptureless whorl with parts of the preceding ribbed whorl visible inside. (C) Adoral and adapical cross-sections of the outermost preserved whorl and the ventral view of the middle part of the preceding whorl. Note the abrupt and complete interruption of the prominent secondaries in the midventer and the uniquely great width of the resulting medioventral smooth band. (D) Lateral view of the ribbed whorl with most of the last preserved, sculptureless whorl removed. (E) The same view as in fig. 1D but without whitening, to exhibit the external suture lines. (F) Ventral view of the middle part of the ribbed whorl exposed in figs. D and E and the strongly distorted adapical cross-section of the superimposed segment of the enclosing sculptureless whorl. (G) The same view as in fig. F but without whitening, to exhibit the ventral parts of external suture lines.

Figure 2. *Temnoptychites* (*Costamenjaites*) aff. *T.* (*C.*) *grandiosus* Voronets 1962. Early early Valanginian, Deer Bay Formation, Ellesmere Island, GSC loc. 28713 [see description of *T.* (*C.*) *grandiosus* for further details]. GSC 49325. Fragment of somewhat distorted (laterally compressed) adult living chamber which conceals almost entirely the fragments of more strongly deformed to almost squashed inner whorls. (A) Lateral view of the best preserved side. A short segment of penultimate whorl with an indistinctly trichotomous rib bundle and an even shorter segment of the preceding whorl, which bears a distinctly dichotomous rib bundle on the unfigured side, protrudes from the living chamber. (B) Ventral view of the living chamber. (C) Almost undeformed adapical cross-section of the living chamber and more strongly deformed to almost completely squashed cross-sections of the inner whorls. (D) Oblique view of oral cross-section of the living chamber and oblique ventral views of two preceding whorls. Note the sharp, chevronlike appearance of forward-bent secondaries on the venter of the earliest visible whorl. These secondaries are weakened but not completely interrupted on the midventer.
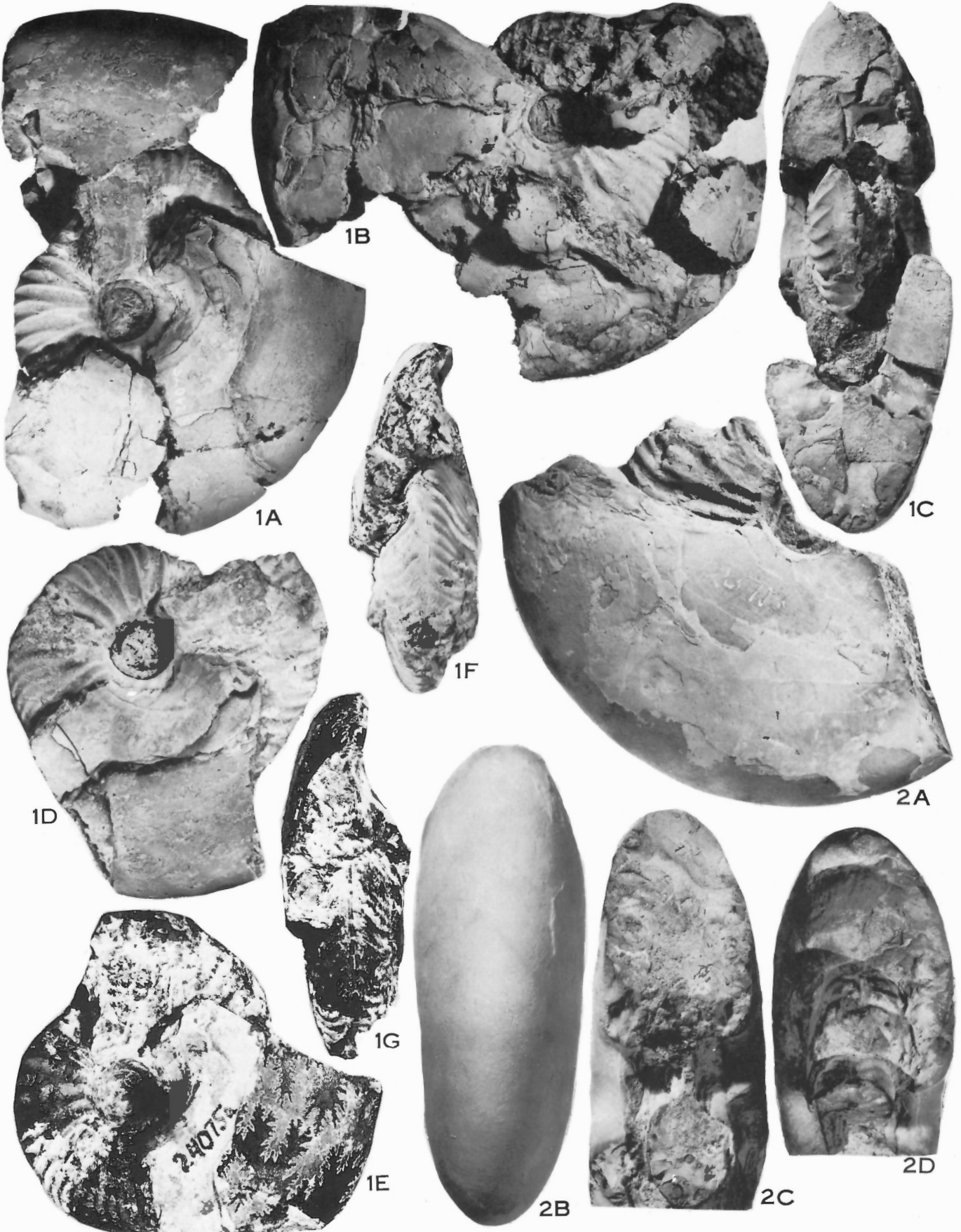
Plate 7

Plate 8

Figure 1. *Tollia* aff. *T. tolli* Pavlow 1914. Early early Valanginian, Deer Bay Formation, Ellesmere Island, GSC loc. 28713 [see description of *Temnoptychites* (*Costamenjaites*) *grandiosus* Voronets for further details]. GSC 49326. A fragment of adult living chamber with an imprint of a part of the penultimate whorl preserved inside. (A) Lateral view of the better preserved side of living chamber. (B) Ventral view of the living chamber. (C) Lateral view of the rubber mold of the imprint of a part of penultimate whorl preserved inside the living chamber in figs. A and B. Only the upper parts of long and elevated but not bullate primary ribs are preserved. (D) Ventral view of the same rubber mold. The markedly but regularly forward bent secondary ribs are neither interrupted nor weakened in the midventer of this penultimate whorl, indicating the reference of the specimen to the genus *Tollia.*.

Figure 2. *Temnoptychites* (*Temnoptychites*) *kemperi* n. sp. Hypotype. Late early Valanginian, Deer Bay Formation, Ellesmere Island, Blackwelder Mountains, GSC loc. 52489 on southeastern limb of syncline 3.7 km east of the mouth of a major unnamed river entering a prominent bay, which joins Greely Fiord 6.4 km east of Hare Fiord. Collected from the measured section 127.4 to 127.7 m above the base of the formation and about 7.6 m stratigraphically below GSC loc. 47879 of *Thorsteinssonoceras ellesmerense* fauna (Jeletzky 1965b, p. 14). GSC 49327. An incomplete, fairly strongly distorted intermediate whorl (completely septate) of the slender *T.* (*T.*) *lgowensis*–like variant of the species. (A) lateral view of the better preserved side exhibiting the indistinctly quadrichotomously ribbed growth stage on the early third of the whorl. The oral third of the whorl exhibits the early phase of the ribless but nodose growth stage. Note the very short, bullate appearance of primaries and the correspondingly low branching points of secondaries on the early third of the whorl. These features contrast with the long and elevated but not bullate primaries and much higher branching points of secondaries characteristic of the equivalent growth stages of *Tollia* (figs. 1C, 4A, 5A, B). (B) Ventral view of the early third of the whorl and the cross-section of its considerably distorted oral end. Some of the secondary ribs are considerably weakened whereas others are interrupted completely in the midventer of the almost undistorted early third of the whorl.

Figure 3. *Temnoptychites* (*Costamenjaites*) *troelseni* n. sp. subsp. *troelseni* n. subsp. Paratype. Same age, formation and locality as in fig. 1. GSC 17167. A well preserved, almost undistorted intermediate whorl which resembles closely the corresponding growth stages of *Tollia tolli* Pavlow 1914 and was mistaken for such in earlier publications (e.g., Jeletzky, 1964, p. 38, Pl. V, figs. 1, 4; 1973, p. 64, Fig. 3). The specimen is interpreted now as representing the dichotomously to trichotomously ribbed growth

stage of *T.* (*C.*) *troelseni* n. sp., visible within the penultimate whorl of its holotype (Pl. 9, fig. 1B), because of the distinct medioventral weakening of the secondaries on the adoralmost preserved part of the whorl (fig. B). (A) Lateral view. (B) Ventral view of the oralmost preserved part of the whorl. Note the weakening of the secondaries in the middle of the venter, which appears to increase adorally, ×2. (C) Ventral view of the earliest exposed part of the whorl and the somewhat deformed cross-section of the adoral end. The very strongly and narrowly forward bent (almost chevronlike) secondaries are neither interrupted nor weakened on the midventer. (D) Three partial external suture lines which are only dimly visible on the early third of the whorl in fig. A beneath the ammonium chloride cover. Although *Tollia*-like in proportions and shapes of its lateral lobes and saddles, this suture line is considerably more ascendant than is normal for *Tollia*. The fourth auxiliary lobe is almost concealed on the steep umbilical wall. It is barely visible at the umbilical seam in the middle of the three suture lines shown (cf. Textfig. 6I), ×2.

Figure 4. *Tollia* n. sp. aff. *T. vai* Krimgolts 1953. Early early Valanginian, Deer Bay Formation, Axel Heiberg Island, GSC loc. 52491 (see text for further details). GSC 49328. A fragment of intermediate, completely septate whorl. (A) Lateral view of the better preserved side exhibiting characteristically long and pinched but not bullate primaries and the high point of their bundling characteristic of *Tollia* (cf. fig. 2). (B) Ventral view. The apparent midventral weakening of secondaries in the middle part of the fragment appears to be caused by their pronounced weathering since better preserved secondaries on the oral part of the fragment (near the top of the photograph) are neither interrupted nor weakened. These ribs resemble those of advanced *Tollia* forms in their relatively broad and even forward bends (cf. figs. 1D, 5C) contrasting with the generally (but not always!) much narrower, almost chevronlike forward bends of secondary ribs characteristic of equivalent growth stages of *Temnoptychites* (*Costamenjaites*)*troelseni* n. sp. (cf. fig. 3C; Pl. 12, fig. 2C).

Figure 5. *Tollia* n. sp. aff. *T. klimovskiensis* Krimgolts 1953. The same age, formation and locality as in fig. 1. GSC 17172. A fragment of an almost undistorted, intermediate(?) living chamber with parts of the last two external suture lines preserved on its adapicalmost part (lower end of fig. A). (A) Lateral view of the right flank exhibiting the same characteristic *Tollia*-like ribbing habit as in *T.* n. sp. aff. *T. vai* in fig. 4A. (B) Lateral view of the left flank exhibiting the same ribbing habit as in fig. A but lacking the phragmocone. (C) Ventral view. None of the broadly and moderately forward bent secondary ribs shows any tendency to weaken in the middle of the venter. If anything, these ribs are more elevated and sharper there than on the flanks. (D) View of the somewhat distorted (laterally compressed) cross-section of the oral end of the fragment.
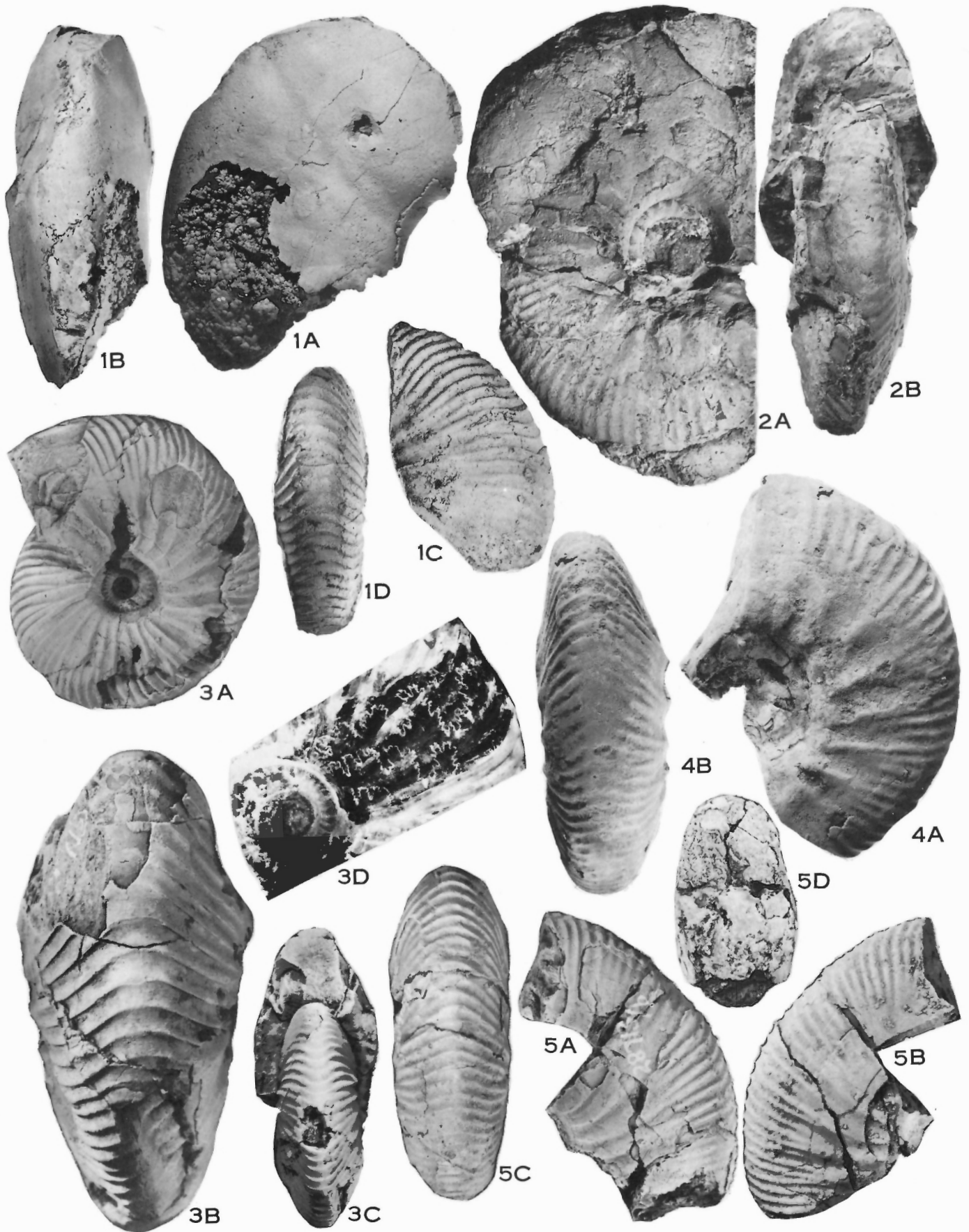
Plate 8

Plate 9

Early early Valanginian fossils from Deer Bay Formation, Ellesmere Island, GSC loc. 24075 (see description of *T. (C.) grandiosus* for further details)

Figure 1. *Temnoptychites (Costamenjaites) troelseni* n. sp. subsp. *troelseni* n. subsp. Holotype of species and subspecies. GSC 17174. An incomplete but undeformed, completely septate representative of the slender variant considered to be typical of the species and subspecies by the writer. Judging by the complete loss of sculpture on the flank and the preservation of secondary ribs on the umbilical shoulder on the adoral third of the whorl (fig. A) the adoralmost preserved whorl of the holotype extends almost to the beginning of the adult living chamber (cf. the similar paratype in fig. 2A–C). (A) Lateral view of the unweathered and partly shell-covered side. The already faint primaries and the even fainter lower parts of secondaries are marked in black on the painted early part of the whorl to illustrate the alternating dichotomous and trichotomous mode of bundling contrasting with that of the corresponding growth stages of *T. (C.) elegans* Bodylevsky (see text). The external suture lines visible on this flank are outlined in black and white to illustrate the gradual increase of their complexity in the course of the ontogeny. (B) Lateral view of the other, partly weathered side preserved exclusively as a steinkern. Whitened throughout to outline details of the ribbing habit. A short segment of upper flank and venter of the pronouncedly dichotomously ribbed next inner whorl is visible within the damaged part of the whorl on the right. The sculpture of this whorl apparently duplicates that of the intermediate whorl reproduced in Pl. 8, fig. 3A. (C) Ventral view of the early third of the whorl and the cross-section of its oral end. The fine and closely spaced secondary ribs are only broadly and moderately forward bent on the venter; they are only slightly to appreciably weakened but not interrupted in the midventer. (D) Cross-section of the early part of the last preserved whorl and those of four earlier whorls. The venter of the fifth inner whorl is visible also; it is completely smooth. All whorls are undeformed. (E) Ventral view of the adoralmost part of the last preserved whorl. The sharp and elevated secondary ribs terminate abruptly on the left side of the smooth medioventral band near the apical end of the venter where the shell is preserved. However, the ribs and the smooth band are only indistinctly developed on the steinkern's surface farther

adorally. This almost complete restriction of the sculpture to the shell's surface is characteristic of *T. (C.) troelseni* n. sp. (fig. 2C). (F) The apical quarter of the side shown in fig. B. Unwhitened and with the oralmost suture lines outlined in black and white to illustrate their complexity, pronounced crowding and partial overlapping.

Figure 2. *Temnoptychites (Costamenjaites) troelseni* n. sp. subsp. *troelseni* n. subsp. Paratype. GSC 49329. A representative of the same subsp. *troelseni* n. subsp. as the holotype, including all of the penultimate whorl and the beginning of adult living chamber. Specimen GSC 49329 is moderately to pronouncedly deformed (laterally compressed) throughout but excellently preserved otherwise. (A) Lateral view of the partly shell covered right side. The oralmost quarter of the whorl, including all of the living chamber (cf. fig. B), is removed to expose the strongly sculptured and distinctly tri- and dichotomously bundled adoral part of the penultimate whorl. The ribbing habit of this whorl duplicates that of the equivalent part of the holotype (fig. 1A, B), except that the ribs are considerably more elevated and more distinctly bundled. (B) Lateral view of the left side with the oralmost preserved quarter whorl on. This side is mostly preserved as a steinkern and exhibits some excellently preserved external suture lines. One of the earliest whorls squeezed out of its normal position is visible in the umbilicus (see text and explanations of fig. 2F–H). (C) Lateral view of the apical half of the same side as in fig. B but without whitening, to show better the details of external suture lines. (D) Ventral view of the early third of the whorl and the partly deformed cross-section of its oral end. The broadly and moderately forward bent secondary ribs are only weakened but not interrupted in the midventer, except in the oralmost visible part of the whorl. (E) Ventral view of the adoral, mostly strongly deformed third of the whorl. As in the holotype (fig. 1E), the sharp and elevated secondary ribs end abruptly at the medioventral, completely smooth band whenever the shell is preserved. This sculpture is only indistinctly expressed elsewhere on the surface of the steinkern. (F) Oblique, enlarged lateral view of the adumbilical part of the adoral third of the side shown in figs. B and C showing structural details of auxiliary parts of adult suture lines. Four auxiliary lobes are clearly visible, ×3. (G,H) Two enlarged views (×3 and ×2, respectively) of the squeezed out early whorl visible in the umbilicus of the flank shown in fig. B. These photographs elucidate sculptural details of this whorl discussed in the text (p. 33, 34).

Plate 9

1A

1D

1C

1F

2A
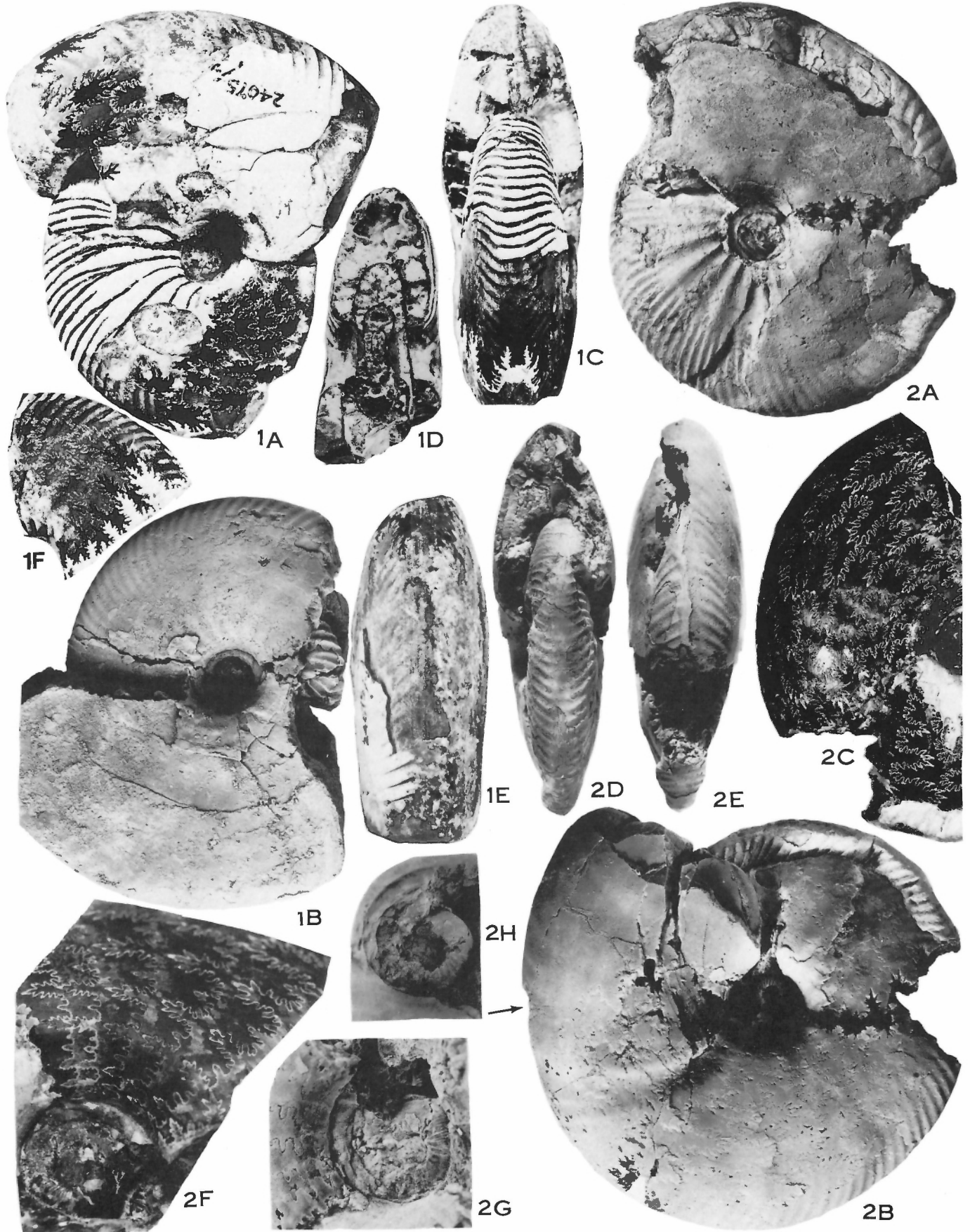
1E

2D

2E

2C

1B

2H

2F

2G

2B

Plate 10

Figure 1. *Temnoptychites (Costamenjaites) troelseni* n. sp. subsp. *crassus* n. subsp. Paratype. Early early Valanginian, Deer Bay Formation, Ellesmere Island, GSC loc. 28713 [see description of *T. (C.) grandiosus* for further details] GSC 49330. A deformed (moderately compressed laterally) but almost completely preserved representative of the subspecies *crassus* n. subsp. transitional to subsp. *troelseni* n. subsp., as represented by the holotype (Pl. 9, fig. 1) and the paratype GSC 49329 (Pl. 9, fig. 2), in the whorl shape and proportions. The almost completely preserved (the fragmentary constriction at the oral end of fig. A is believed to be the mouth border) adult living chamber of GSC 49330 and the thickened, elevated ventrolateral parts of secondary ribs preserved on its early third give an idea of what the missing living chamber of the holotype and that of the paratype GSC 49329 must have looked like. However, the external suture lines of GSC 49330 are typical of the subsp. *crassus* n. subsp. in being *T. (C.) grandiosus*–like on the early part of the last septate whorl (fig. H) and in becoming gradually more simplified later. At the same time the oralmost suture lines become more and more crowded (actually overlapping) and acquire more and more narrow to pinched lobes separated from each other by relatively wider and wider saddles (see the oralmost few suture lines in fig. B). (A) Lateral view of the best preserved side of the complete shell. The beginning of the living chamber marked by an arrow. (B) Lateral view of the same side with most of the living chamber removed to show the characteristic sculpture of and the above-mentioned ontogenetic changes of external suture lines on the penultimate whorl. The apparent differences of the sculpture of the penultimate whorl of GSC 49330 (especially the distinctly thickened, round-topped, almost bullate, appearance of its primaries) as compared with that of GSC 49329 (Pl. 9, fig. 2A) is caused by the former being preserved entirely as a steinkern while the latter is shell-covered (see p. 36). (C) Lateral view of the other, less satisfactorily preserved, partly shell-covered side of penultimate whorl to illustrate the effect of weathering on the sculpture. (D) Ventral view of the early third of the whorl of the complete shell visible in fig. A. The narrowly and strongly (almost chevronlike) forward bent secondary ribs are either only slightly weakened or unchanged in the midventer of this part of the whorl, except in the shell-covered patch near the lower margin of the photograph. As in other representatives of *T. (C.) troelseni* n. sp. (p. 36), this variable development of the medioventral ornament reflects the predominant restriction of the sculpture to the shell's surface. (E) Ventral view of the adoral, sculptureless third of the ultimate whorl visible in fig. A from the side. (F) Ventral view of the earliest third of the penultimate whorl visible in figs. B and C from the side. Although the photographed part of the venter is shell-covered and fairly well preserved, the narrowly and markedly forward-bent (almost chevronlike) secondary ribs do not seem to be even perceptibly weakened on the midventer of this part of the whorl. Their apparent weakening is an optical illusion. (G) Ventral view of the adoralmost sculptured part of the shell visible from the flank in fig. A and also shown in fig. D. Introduced to illustrate the variable appearance of the medioventral zone of this part of the whorl described in the discussion of fig. D but only dimly visible there. (H) Lateral and auxiliary parts of external suture lines less satisfactorily visible in the middle part of the penultimate whorl reproduced in fig. B, ×2. Introduced to illustrate the *T. (C.) grandiosus*–like appearance of these suture lines mentioned in general comments on GSC 49330. The fourth auxiliary lobe is concealed on the umbilical wall, except in the uppermost of the three suture lines shown.
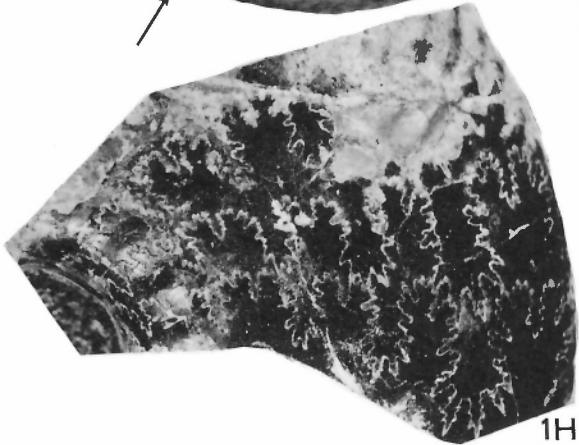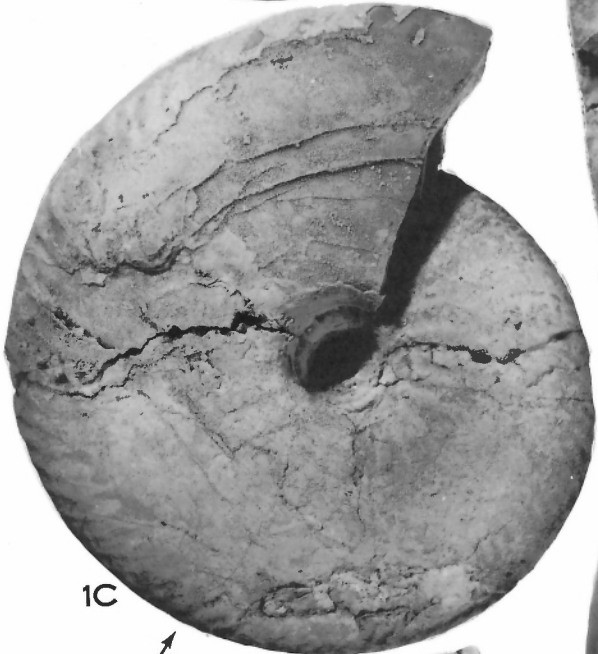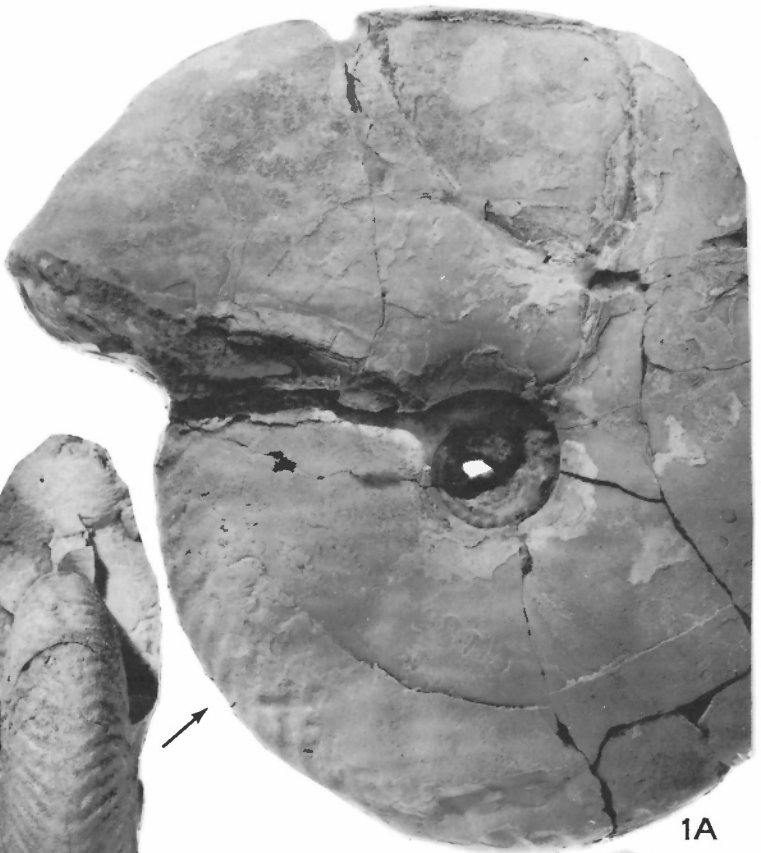
Plate 10

Plate 11

Figure 1. *Temnoptychites (Costamenjaites) troelseni* n. sp. subsp. *crassus* n. subsp. Paratype. Early early Valanginian, Deer Bay Formation, Ellesmere Island, GSC loc. 28713 [see description of *T. (C.) grandiosus* for further details]. GSC 49331. A fragment of adult, very large and sturdy representative of the subspecies. The specimen includes the oralmost third of the almost undeformed living chamber with a complete mouth border and mostly deformed fragments of preceding whorls. (A) Lateral view of the all but undeformed side of the living chamber with short segments of sculptured phragmocone (mostly penultimate whorl) protruding from the inside. The living chamber is completely sculptureless, except for four closely spaced constrictions, the oralmost of which appears to be the adult mouth border. The earliest visible segment of the penultimate whorl represents the still fairly distinct trichotomous growth stage with single secondaries intercalated between the trichotomous rib bundles. The less satisfactorily preserved oralmost segment of the penultimate whorl already exposes the indistinctly trichotomous growth stage. One of the earliest, finely and closely sculptured whorls, squeezed out of proper position, is visible inside the umbilicus. (B) Lateral view of the other, less satisfactorily preserved and partly distorted side with the earliest part of the living chamber removed to expose a greater segment of the early penultimate whorl. This segment exhibits the transition from the distinctly trichotomous to the indistinctly trichotomous growth stage. The oralmost ribs visible are all but effaced in the midflank. (C) Cross-section of the specimen showing the almost undistorted mouth border of the living chamber and the almost undistorted to strongly distorted cross-sections of the penultimate whorl and earlier whorls. The venter of one of the earliest whorls mentioned in explanation of fig. A is visible in the central part of the umbilicus. (D) Ventral view of the fragment of adult living chamber shown from the side in fig. A. The constrictions are clearly visible. (E) Ventral view of the apical half of the preserved fragment of the adult living chamber with some of it taken off to expose the venter of the segment of penultimate whorl shown from the side in fig. B. The four earliest visible (lowermost) secondaries are almost transversally directed; they are either only slightly weakened or remain unchanged in the midventer. However, the following nine secondaries are markedly forward bent and either markedly weakened or completely interrupted in the midventer. Finally, the adoralmost three secondaries visible are not only completely interrupted in the midventer but their tips on both sides of the resulting smooth band are displaced in relation to each other. (F) Enlarged lateral view of one of the earliest whorls visible in the umbilicus of the specimen (fig. A). Note very fine and dense, strongly forward bent appearance of primary and secondary ribs characteristic of this early growth stage of *T. (C.) troelseni* n. sp., ×2. (G) Enlarged ventral view of the whorl shown in fig. F, ×3. (H) Enlarged and unwhitened lateral view of lateral and auxiliary parts of two external suture lines dimly visible beneath the ammonium chloride layer on the earliest exposed segment of penultimate whorl in fig. A.
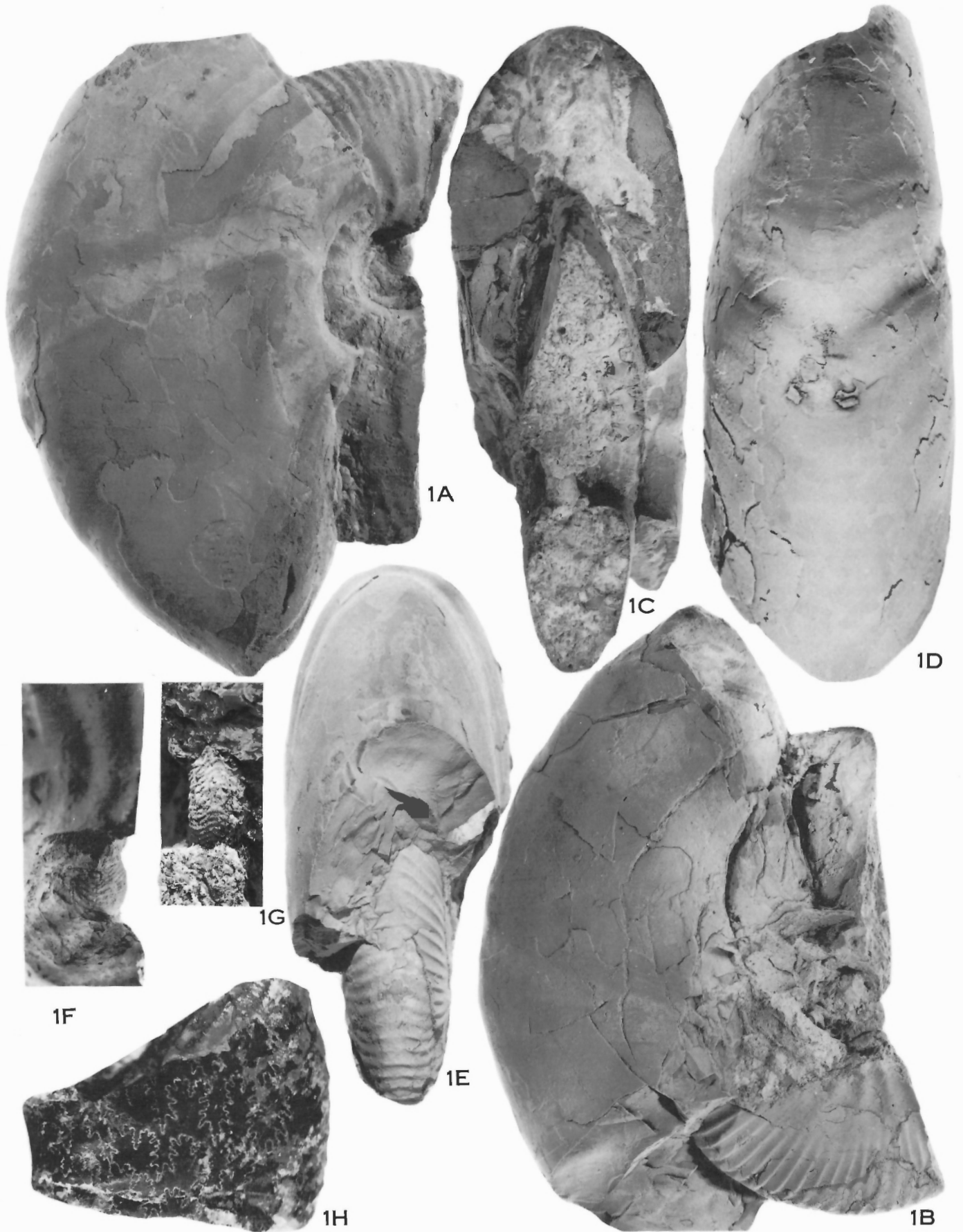
Plate 11

Plate 12

Both fossils are from early early Valanginian Deer Bay Formation, Ellesmere Island, GSC loc. 28713 (see description of *T. (C.) grandiosus* for further details)

Figure 1. *Temnoptychites (Costamenjaites) troelseni* n. sp. subsp. *crassus* n. subsp. Holotype of the subspecies. GSC 17176. Large, almost complete (except for the adoralmost quarter or so of adult living chamber), only feebly deformed representative of the subspecies. Specimen GSC 17176 is the sturdiest representative of the subspecies *crassus* n. subsp. and of the species *T. (C.) troelseni* n. sp. known to the writer. Other more slender representatives of the same subspecies reproduced in Pl. 11 and Pl. 13, figs. 2 and 3 connect it with the slendermost representative of the subspecies reproduced in Pl. 10. The shape and proportions of the adult whorl of specimen GSC 17176 resemble closely those of similarly sized intermediate whorls of *T. (C.) grandiosus* (Pl. 7, fig. 1). However, compared with this species, the adult is smaller, the ribbing habit is much more closely spaced, finer and mostly trifurcating at the equivalent growth stages, and the adult external suture line is entirely different (see below and in the text). (A) Lateral view of the better preserved side. The beginning of the living chamber is marked by an arrow. The lateral and auxiliary parts of the last suture line (outlined in white) feature strongly simplified and at the same time strongly attenuated lobes (cf. fig. D), compared with those of an earlier suture line visible at the shell's mouth border. (B) Ventral view of the middle part of the living chamber. (C) Ventral view of the early third of penultimate whorl and the slightly deformed (on the left side only) cross-section of the oral end. The relatively coarsened and more widely spaced ventrolateral parts of secondary ribs are restricted to the phragmocone; they are completely interrupted in the midventer. The ventral lobe of the last suture line is visible at the bottom of the photograph. (D) Lateral part of the oralmost external suture line featuring the greatly simplified and narrow lobes. The intervening saddles are widened accordingly. The fourth auxiliary

lobe is all but invisible on the umbilical shoulder. (E) Ventral part of the last external suture line, ×2. Note the contrast between the wide and florid ventral lobe, which does not differ materially from its earlier adult counterpart (fig. C) and the strongly attenuated and at the same time simplified first lateral lobe. (F) Lateral view of the same side of the shell as in fig. A with most of the living chamber removed to show the closely spaced, indistinctly trichotomously ribbed ornament of the adoral half of the penultimate whorl. This ornament still represents the late phase of the intermediate growth stage of penultimate whorl. (G) Ventral view of the middle part of the penultimate whorl seen from the side in fig. F. The slightly forward bent secondary ribs are completely interrupted in the midventer in spite of the prevalent steinkern preservation of this part of the whorl.

Figure 2. *Temnoptychites (Costamenjaites) troelseni* n. sp. subsp. *troelseni* n. subsp. Paratype. GSC 49332. An extreme representative of the subspecies combining unusually coarse and elevated ribs with a uniquely prolonged simple dichotomously ribbed growth stage (p. 34, 37). (A) Lateral view of the adoralmost part of the better preserved side exhibiting the late phase of intermediate growth stage. The ribs are characteristically weakened at first and then almost completely disappear on the midflank. (B) Lateral view of the other side. The adoralmost preserved third of the whorl removed to expose the unusually prolonged late phase of the simple dichotomous and the abbreviated early phase of the intermediate growth stages (p. 34, 35). The oralmost preserved quarter of the whorl exhibits the indistinctly trichotomously ribbed habit of the late intermediate growth stage (cf. fig. A). (C) Ventral view of the middle part of the whorl shown from the side in fig. B. The beginning of the damaged part of the whorl lacking the ventral part (fig. B) is at the upper margin of the photograph. The pronounced constriction visible in the lower part of fig. B is situated at about the middle of the photograph. The partly shell covered secondary ribs are not weakened, let alone interrupted, on the midventer, except at the oralmost preserved end of the whorl.
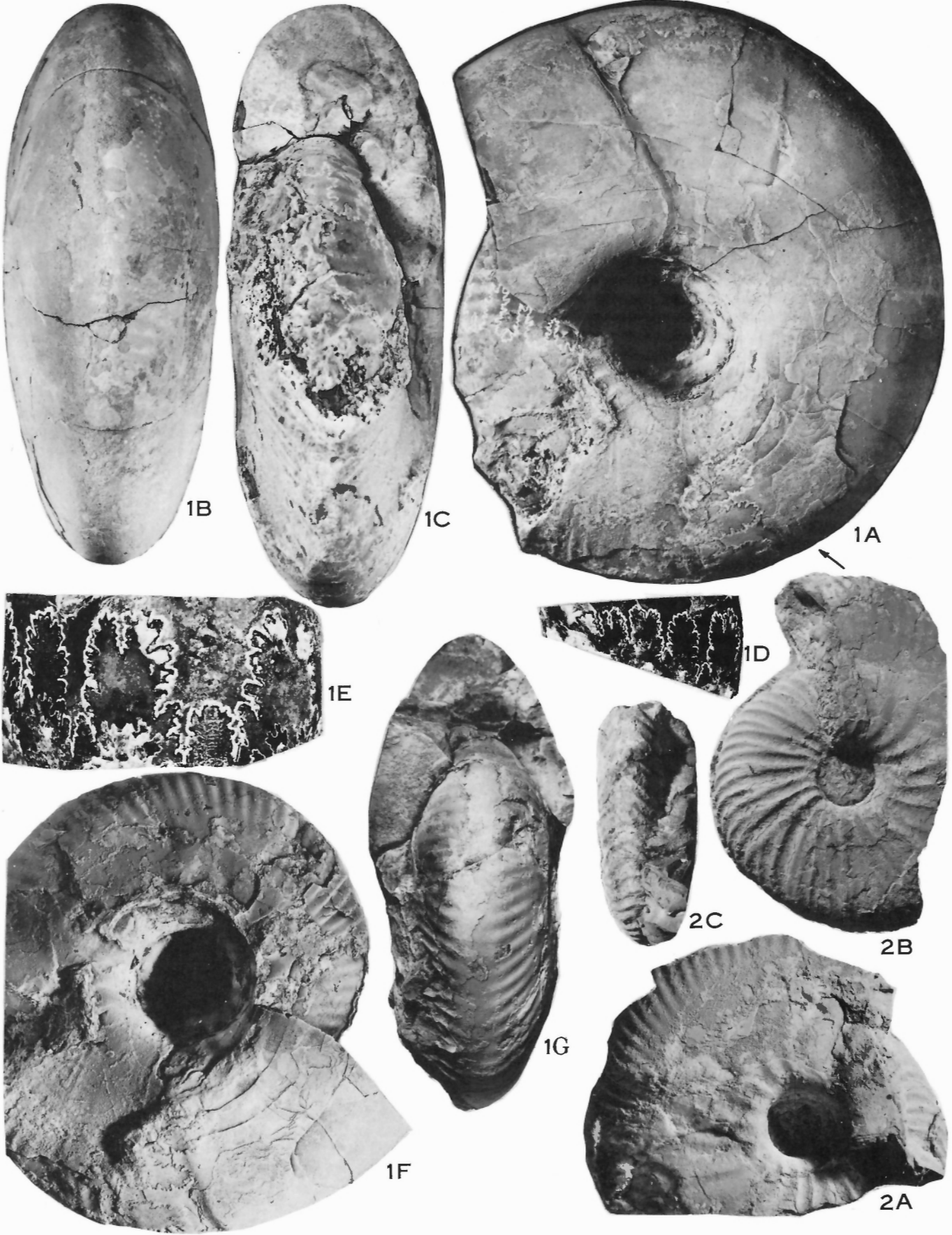
Plate 12

Plate 13

All specimens are from early early Valanginian Deer Bay Formation, Ellesmere Island, GSC loc. 28713 (see description of *T. (C.) grandiosus* for further details)

Figure 1. *Temnoptychites (Costamenjaites) troelseni* n. sp. subsp. *crassus* n. subsp. Paratype. GSC 49333. A moderately to strongly deformed, incomplete (lacks the oral half of the adult living chamber) representative of the extremely finely and closely ribbed and, at the same time, slender representative of the subspecies and species (p. 36, 37). The beginning of the adult living chamber is marked by an arrow. (A) Lateral view of the more nearly completely preserved side exhibiting a gradual weakening of the indistinctly trichotomous ribbing habit on the earliest visible part of the phragmocone followed by the relative coarsening of the residual secondary ribs on its oralmost part and the earliest part of the living chamber. Note well developed constrictions on the oralmost part of the phragmocone and on the oralmost preserved, fragmentary part of the living chamber. The markedly constricted lateral and auxiliary lobes and the correspondingly widened saddles of the terminal suture lines are dimly visible beneath the layer of ammonium chloride. (B) Lateral view of the other, less completely preserved, entirely septate side preserved almost to the end of the penultimate whorl. The earliest visible, mainly shell covered part of the whorl exhibits the early, distinctly trichotomously ribbed phase of the intermediate growth stage while its greater middle part preserved as a steinkern exhibits the late, indistinctly trichotomously ribbed growth stage. This stage grades into the final sculptureless growth stage on the oralmost preserved parts of the phragmocone. (C) Lateral view of the same side as in fig. B but without whitening to show the lateral and auxiliary parts of semi-adult suture lines (cf. Textfig. 6G). (D) Ventral view of the oralmost undeformed, earliest part of the living chamber visible from the side in fig. A. The residual secondaries are markedly weakened but not completely interrupted on the midventer which is preserved as a steinkern. (E) Ventral view of the earliest part of the whorl exposed in figs. B and C and the cross-section of the adoralmost completely preserved part of the whorl visible in fig. A. The septate part of the penultimate whorl is markedly deformed for the most part while the adoralmost cross-section (living chamber) is only feebly deformed. The closely spaced, slightly forward bent secondaries are only slightly weakened on the earliest visible part of the venter. However, their midventral weakening gradually increases adorally until they become markedly weakened on the oralmost part of the venter visible (near the bottom of the photograph).

Figure 2. *Temnoptychites (Costamenjaites) troelseni* n. sp. subsp. *crassus* n. subsp. Paratype. GSC 17164. Small, almost complete (except for the oralmost quarter or so of the adult living chamber), almost undeformed representative of the subspecies. This specimen and the large specimen in Pl. 12, fig. 1 illustrate the range of variation in size known to exist in this subspecies of *T. (C.) troelseni* n. sp. (A) Lateral view of better preserved side. The earliest visible part of the whorl exhibits the distinctly ribbed, intermediate growth stage featuring trifurcate rib bundles. This growth stage is followed by an unusually prolonged indistinctly ribbed growth stage, which persists through the early two fifths of the adult living chamber before being replaced by the sculptureless growth stage. The residual primary ribs of the indistinctly ribbed growth stage are distinctly bullate. The beginning of the living chamber is marked by an arrow. (B) Ventral view of the slightly deformed (laterally compressed) early

third of the whorl visible from the side in fig. A and of the only slightly deformed oral cross-section. The secondary ribs are weakened but not interrupted in the middle part of the venter in spite of its being mainly shell covered. (C) Unwhitened segment of the oralmost part of penultimate whorl of the unfigured flank. This segment corresponds approximately to the earliest part of the phragmocone visible in fig. A. This growth stage exhibits lateral parts of simple external suture lines which neither touch nor overlap. Such suture lines are characteristic of the penultimate adult whorl of subspecies *crassus* n. subsp., ×1. (D) Ventral lobe of the adapicalmost suture line reproduced on fig. C, ×3. (E) Unwhitened oralmost part of the phragmocone of the unfigured flank corresponding to part of the phragmocone immediately preceding that marked by the arrow in fig. A. The reproduced segment exhibits lateral and auxiliary parts of four adult suture lines immediately preceding the adoralmost suture line. The apical ends of the lobes of the latter are visible at the upper margin of the photograph. All suture lines (which are also drawn in Textfig. 6F) are strongly simplified, their lobes are pronouncedly constricted, and the saddles are correspondingly widened. This development is diagnostic of the few adoralmost external suture lines of adult representatives of *T. (C.) troelseni* subsp. *crassus* n. subsp., ×2.

Figure 3. *Temnoptychites (Costamenjaites) troelseni* n. sp. subsp. *troelseni* n. subsp. Paratype. GSC 17175. A mainly undeformed, completely preserved but pronouncedly weathered adult representative of the sturdy form of the subspecies superficially duplicating the specimen of subsp. *crassus* n. subsp. reproduced in fig. 2. This specimen is introduced to illustrate the subspecific differences in the morphology of adult suture line existing within the otherwise all but identical sturdy representatives of the species (see text). (A) Lateral view of the undeformed side. The indistinctly ribbed phase of the intermediate growth stage persists over the early half of the adult living chamber as in GSC 17164 (fig. 2A). The beginning of the living chamber is marked by an arrow. The adoralmost sixth of the living chamber, including a pronounced constriction which marks its partly preserved mouth border is removed to expose the unweathered, adoralmost part of the penultimate whorl. Another well developed constriction occurs in the middle part of the living chamber. The lateral and auxiliary parts of two oralmost external suture lines are painted white. Unlike the corresponding parts of the three oralmost external suture lines of GSC 17164 (fig. 2E, Textfig. 6F), these suture lines do not exhibit any widening of the saddles and attenuation of the lobes whatsoever. This indicates the reference of GSC 17175 to the subspecies *troelseni* n. subsp. The strongly simplified appearance of the suture lines and their fairly wide spacing is caused by their deep weathering discussed in the text (p. 39, 40). (B) Ventral view of the early third of the whorl (including the earliest part of the living chamber) visible from the side in fig. A and the cross-section of the adult living chamber. The whole cross-section of the specimen is all but undistorted. The strongly and narrowly forward bent secondary ribs appear to be weakened in the midventer on the earliest visible part of the whorl and seem to be completely interrupted there on its oralmost visible part. However, the shell is preserved as a steinkern throughout and its surface is weathered. The ventral lobe of one of the sutures painted white in fig. A is painted white. Unlike the lateral and auxiliary parts of these suture lines, this ventral lobe does not differ materially from the ventral lobe of equivalent suture lines of GSC 17164 (fig. 2D, Textfig. 6F).
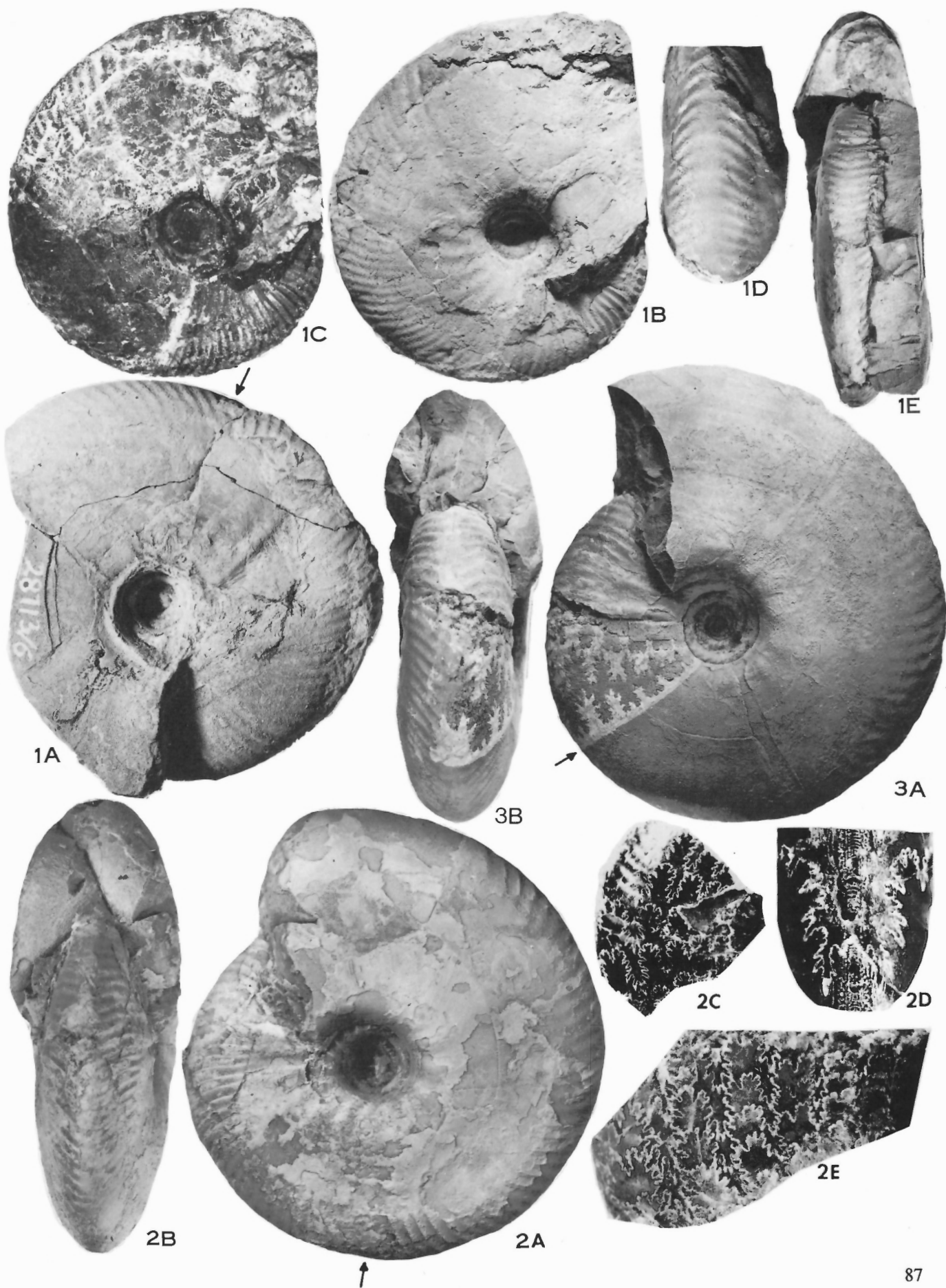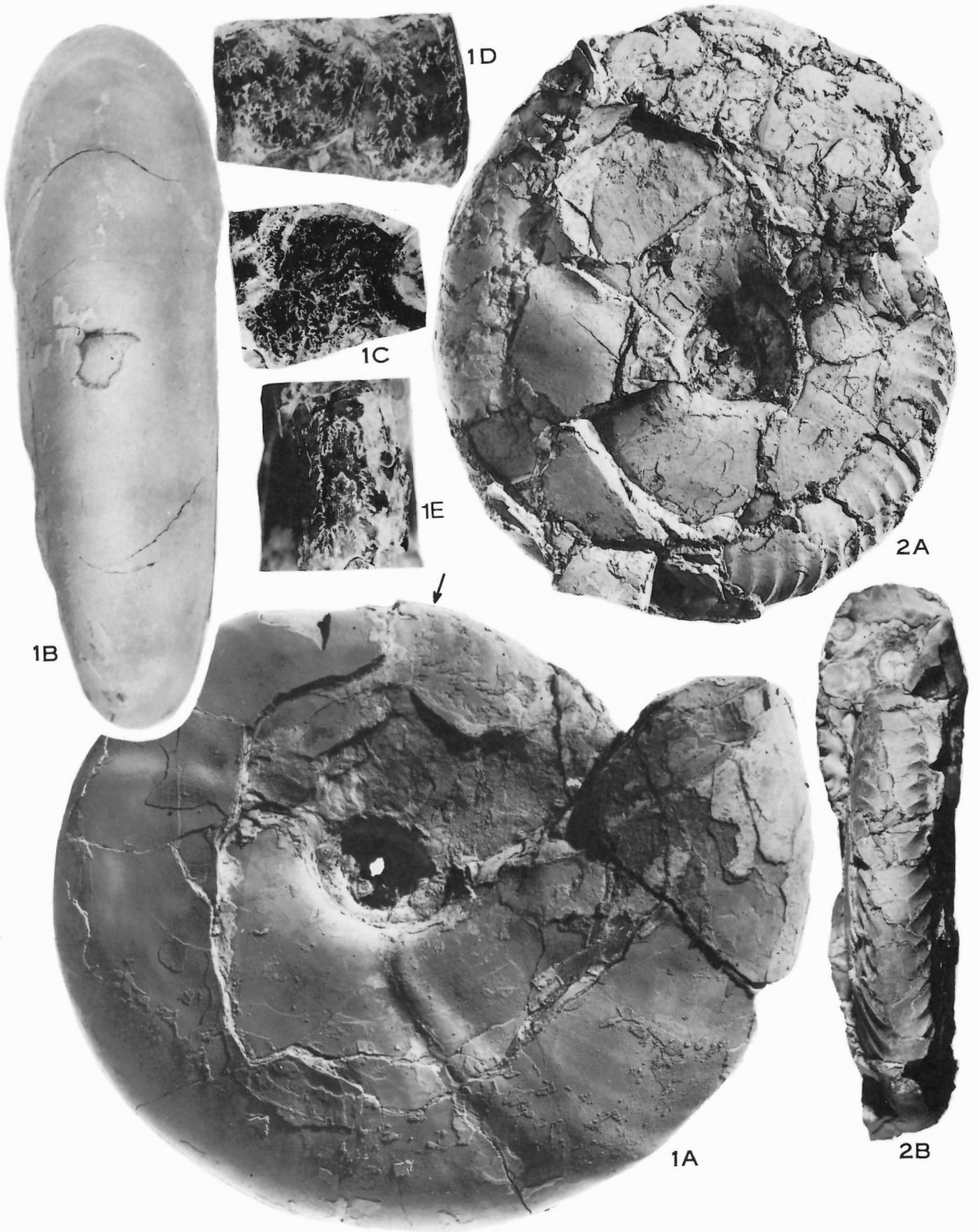
Plate 13

Plate 14

Figure 1. *Temnoptychites (Costamenjaites) troelseni* n. sp. subsp. *troelseni* n. subsp. Paratype. Early early Valanginian. Deer Bay Formation, Ellesmere Island, GSC loc. 28713 (see description of *T. (C.) grandiosus* for further details). GSC 49335. A strongly deformed (laterally compressed) but complete, adult ultimate whorl of the largest representative of the subspecies known. If it were undeformed, this shell would be of about the same size and would have about the same whorl shape and proportions as the largest known representative of *T. (C.) troelseni* subsp. *crassus,* reproduced in Pl. 12, fig. 1. Introduced to demonstrate that *T. (C.) troelseni* subsp. *troelseni* can reach dimensions as great as those of *T. (C.) troelseni* subsp. *crassus.* (A) Lateral view of the better preserved side. Note the broad and florid, completely *Tollia*–like appearance of the first lateral lobe of two oralmost suture lines clearly visible at the oral end of the phragmocone. The beginning of the adult living chamber marked by an arrow. The beginning of the sculptureless growth phase approximately coincides with the beginning of the living chamber and the riblike ridges on the latter are caused by warping of shell surface during its postmortal deformation. Note the presence of four well developed constrictions on the living chamber. The oralmost of them coincides with the oral end of the chamber and appears to represent its mouth border. (B) Dorsal view of the best preserved middle part of the living chamber. (C) The unwhitened oralmost part of the phragmocone shown in the whitened state in fig. A. Note the almost complete but locally fractured auxiliary parts of two oralmost external suture lines of a distinctly *Tollia*-like type. (D) The unwhitened oralmost part of the phragmocone of the otherwise unfigured other side exhibiting almost complete but locally fractured lateral and auxiliary parts of two oralmost external suture lines of the same *Tollia*-like type as in fig. C.

(E) The ventral view of the same oralmost part of the phragmocone shown in figs. A, C and D. Note the same *Tollia*-like appearance of ventral lobes as in the other parts of the suture lines visible in the above-mentioned figures.

Figure 2. *Temnoptychites (Costamenjaites) troelseni* n. sp. subsp. *crassus* n. subsp. Paratype. Early early Valanginian, Deer Bay Formation, Ellesmere Island, Blackwelder Mountains, GSC loc. 94731 from section 007152 (No. 67F) lat. 80°39′N; long. 84°55′W. Collected by the Chevron Standard Co. Ltd. in 1974. The locality was reported to be approximately 248.5 m (815 ft) above the base of the Deer Bay Formation. GSC 49334. A strongly deformed (almost flattened laterally), fully septate penultimate whorl of an unusually coarsely ribbed representative of the subspecies. Unlike all other representatives of the species, the adoral two thirds of this penultimate whorl are structureless except for two constrictions and some striae. (A) Lateral view. The flank is almost entirely shell covered. In spite of their exceptionally coarsened and distant character, the residual adventral parts of secondary ribs are strongly elevated and sharp because of a complete and excellent preservation of the shell layer. The markedly constricted appearance of first lateral lobes of three adjacent suture lines visible near the oral end of the phragmocone indicates the reference of the specimen to *T. (C.) troelseni* subsp. *crassus* n. subsp. These suture lines could hardly be the oralmost ones judging by the degree of their simplification and that of the constriction of the lobes. (B) Ventral view of the earliest third of the whorl showing a complete interruption of coarsened and distant, residual secondary ribs in the middle of the venter. The secondaries are completely interrupted regardless of whether the venter is shell covered or preserved as a steinkern only.

Plate 14

1A
1B
1C
1D
1E
2A
2B