Intraspecific variation of *Svalbardiceras spitzbergensis* (Frebold) from the Early Triassic (Spathian) of Spitsbergen

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Abstract

The ammonoid species *Svalbardiceras spitzbergensis* from the latest Early Triassic (Spathian, subrobustus Zone) shows a remarkable intraspecific variation. The more than 400 specimens studied come from one fossiliferous carbonate nodule layer within a sequence of mudstones and clayey siltstones of the Vikinghøgda Formation (Vendomdalen Member), mainly collected in the Sassendalen and Agardhbugta areas in central and eastern Svalbard, respectively. The preservation of the ammonoids is very good, usually with preserved shells and complete body chambers. Morphologically they range from compressed, more or less smooth platycones, with narrow umbilicus, to wide umbilicate, depressed forms with straight, prominent ribs. The morphological variation is continuous: all specimens belong to a single assemblage, and are variants of one biospecies. This phenomenon, which is quite common in Boreal Triassic ammonoid faunas, has in the past led to serious taxonomic oversplitting. Furthermore, this new example presents a serious challenge to current ideas about the close correlation between mode of life and shell morphology of ammonoids.

Intraspecific variation appears as a widespread and commonly overlooked character of ammonoid taxa. Recently, Dagys & Weitschat (1993), Dagys et al. (1999) and Dagys (2001) documented significant examples of intraspecific variation from the Spathian (*Parasibirites kolymensis*), the Early Anisian (*Czekanowskites rieberi*) and Middle Anisian (several genera of the Arctohungaritidae) from Arctic Siberia. They illustrated that the morphological variation is usually Gaussian in nature, which suggests that all specimens belong to a single genetically linked population. Recognition of this variation has led to the widespread simplification of nomenclature and to a reduction in the number of taxa.

In the course of joint biostratigraphic investigations in Svalbard and Siberia it became apparent that Boreal Triassic ammonoid assemblages are promising sources for this kind of investigation (Weitschat & Dagys 1989). Ammonoids usually occur in abundance in carbonate or phosphate nodular beds. Some of them are monospecific assemblages that seem to be embedded in situ, and probably represent the nearest approach to a "palaeopopulation" that is likely to be formed.

Remarkable intraspecific variability is seen among nearly all the studied Boreal Triassic ammonoid assemblages. The extent of morphological variation is not constant but may change within one family or even within one genus. In some groups the end members of the variation of one species are so different that on a basis of small samples even their assignment to the same genus would be an open question.

Intraspecific variability, but not always to a high degree, has already been reported from different groups of Triassic ammonoids. It was described from the Lower Triassic (Smithian) of Timor (Welter 1922) in the genus *Anasibirites*, and from Svalbard (Kummel 1961) within the genus *Arctoceras*. From the Anisian, similar variability was recorded by Silberling & Nichols (1982) among the genera *Gymnotoceras* and *Frechites*, by Dagis & Jermakova (1981) within the genus *Stenopopanoceras*, and by Rieber (1973) among tethyan ceratids from Monte San Giorgio. From Svalbard, strong intraspecific variation was reported by Weitschat & Lehmann (1983) within some Ladinian ptychitids and nathorstids, as well as by Lindhorst (2000) within the Carnian genus *Stolleyites*. In a number of other ammonoid groups, examples of intraspecific variation have been noted from the Jurassic and the Cretaceous. The most impressive examples are known from the Cardioceratidae (Jurassic), as described by Callomon (1985), and the Hoplitidae (Cretaceous), as described by Reeside & Cobban (1960).

The shape and the ornamentation of the ammonoid shell usually covary in a typical pattern. Involute, compressed and weakly sculptured variants grade into evolute, depressed and heavily sculptured ones. Based on a careful restudy of a single bed sample of *Sonninia adrica* from the Middle Jurassic of Dorset, Westermann (1966) clearly documented the biometric pattern of this covariation between the geometry of the shell tube and the intensity of the ornamentation. This covariation was first noted by Buckman (1892) on the very same sample, but he did not draw attention to the taxonomic and biological implications as did Westermann, who coined "Buckman's law of covariation" for the interdependance between the geometry of the shell and its ornamentation.

The great range of intraspecific variability that an ammonoid biospecies could accommodate points to some serious problems concerning stratigraphy, taxonomy and ecology. Frequently, successive faunas can be separated only on the basis of the mode of the population, whereas single morphotypes remain indeterminate (Dagys 2001; Hammer & Bucher 2005).

Location, material and stratigraphy

The horizon containing the *Svalbardiceras spitzbergensis* assemblage dealt with here was mainly sampled in the Sassendalen area (Stensiöfjellet, Wallenbergfjellet, Storfjellet, Milne Edwardsfjellet, Sticky Keep, Vendomdalen and Trehøgdene) and the Aghardhbukta area (Roslagenfjellet and Eistraryggen) of Spitsbergen. It belongs to the upper part of the Vikinghøgda Formation (Vendomdalen Member). At the type section, the Vendomdalen Member is 94 m thick and consists of silty, dark grey, laminated mudstone, thin-to-medium bedded, with silty yellow weathering dolomite beds and nodules (Mørk et al. 1999). The ammonoid assemblage occurs in its upper part in a single nodule layer about 10–12 m below the Early/Middle Triassic boundary. The carbonate nodules are rounded to oval, reaching the size of man's head, and have a typical pyrite crust.

The ammonoid sample consists of approximatively 600 specimens. *S. spitzbergensis* is by far the dominant species (90% of the whole fauna), and is represented by all of the ontogenetic stages. Other ammonoids present are: *Keyserlingites subrobustus* (Mojsisovics), *Popovites occidentalis* Tozer, *Monacanthites monceros* Tozer, *Procarnites* cf. *modestus* Tozer, *Olenekoceras nikitini* (Mojsisovics), *Arctomeekoceras* sp. nov. and *Pseudosageceras* sp. nov. The bivalve *Posidonia aranaea* (Tozer) and some orthoceratids are usually also present. This kind of assemblage—with one dominant ammonoid species and rare specimens of species of other genera—seems to be the most common in the Boreal Triassic. It is interpreted as a community that has been fossilized at the main living centre of a single species. Biostratigraphically the ammonoid assemblage belongs to the latest Lower Triassic ammonoid zone of *Keyserlingites subrobustus*.

Biostratonomy and taphonomy

The preservation of the ammonoids is very good. Nearly all of the specimens are complete individuals with preserved body chambers. They are randomly orientated in the middle of single concretions. On the whole, the biostratonomic data do not show any signs of condensation, lateral transportation, selection or preferred orientation. As some of them also have jaw apparatuses preserved in the body chamber, fossilization that occurred more or less in situ is postulated.

The original aragonitic shell material has been replaced by calcite. Sections have shown that the internal parts of the phragmocones are also well preserved and allow detailed ontogenetic study (Fig. 1). Half of each body chamber is filled by clayey sediments, and the other half is filled by calcareous sparite; phragmocones only consist of clear sparry calcite. All ontogenetic stages are found, with young specimens being the most numerous. Only very few specimens show the characteristic features of maturity, such as the approximation of the last septa, reduced ornamentation of the body chamber and uncoiling of the body chamber.

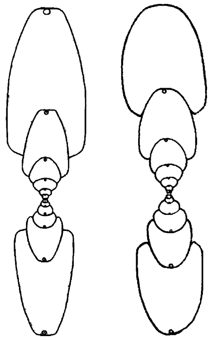

Fig. 1 Whorl sections showing the ontogeny of two different morphotypes of *Svalbardiceras spitzbergensis* (Frebold), from the Early Triassic, Spathian, Keyserlingites subrobustus Zone, Vikinghøgda Formation (Vendomdalen Member), and from Stensiöfjellet, central Spitsbergen.

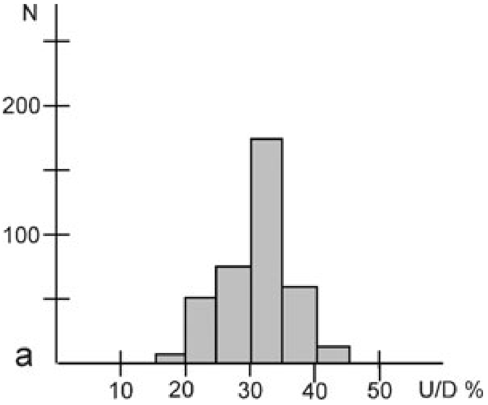

Fig. 2 Histogram illustrating the continuous variation of shell parameters in *Svabardiceras spitzbergensis* (Frebold), ($n = 400$). Abbreviations: *N*, number of specimens; *U*, umbilical width; *D*, diameter.

Description

Shell morphology and variation

The ammonoid assemblage shows quite varied coiling and ornamentation, ranging from involute, smooth compressed conchs to evolute depressed forms with straight prominent ribs. At first sight, a typological approach would split the fauna into at least several species. However, the biometric investigations suggest a different interpretation.

Geometry of the shell tube

The variation of the shell geometry is critical but not extreme (Fig. 2). On one side of the coiling spectrum are cadicones with a narrow umbilicus (U/D [umbilical width/diameter] = 19–23%), and relatively high and slender, tabulate whorls (H/D [whorl height/diameter] = 42–48%), with prominent ventral shoulders. At the other end there are more depressed forms with a relatively wide umbilicus ($U/D = 40–43\%$) and low and thicker whorls ($H/D = 30–35\%$), with more rounded ventral shoulders. Between these two morphological types there are various transitional forms, and it is possible to select a series of individuals that suggest complete gradation from one extreme to the other (Fig. 3). Intermediate conchs are numerically predominant.

Statistical analysis of the main shell measurements and their proportions shows continuous normal distributions, with rare extremes and dominating intermediate conchs. There are no breaks that might allow for a division of this population into different groups.

Ontogeny

The shape of the shells of the investigated sample undergoes remarkable ontogenetic changes. Up to the fourth whorl the whole assemblage is quite uniform. The shells are relatively evolute with subcircular whorl sections and rounded venters (Fig. 1). Within the fifth whorl, the shell proportions start to modify into different types. These changes occur relatively abruptly and may happen within less than half of a whorl. From this stage on, it usually becomes evident which tendency a single individual will follow.

Ornamentation

There are remarkable differences in the ornamentation among the ammonoid assemblage investigated. The compressed involute, platycone shells are quite smooth or bear low, closely spaced, fold-like ribs, some of which fade ventrally, whereas others cross the tabulate venter. Individuals with more depressed conchs are strongly sculptured. They have distinct straight, widely spaced ribs, which are most prominent at the umbilical shoulder, where they have a more node-like shape. This intercorrelation between whorl section and ornamentation is a well-known phenomenon, especially among Boreal Triassic ammonoid assemblages.

Results

Biostatistical analysis of the different morphological features shows that it is impossible to separate the fauna into discrete groups. Between the morphological variants of the main features there is a complete gradation (Fig. 3). All main shell measurements show a normal distribution, with a clear domination of intermediate forms and with comparably rare extremes.

Some of the variable morphological features described are clearly correlated:

A. Shape of whorl section and degree of involution of the conch.

B. Shape of conch and intensity of ornamentation.

From the statistical analysis of the different morphological features, as well as from biostratigraphic and taphonomic data, only one interpretation is possible: all specimens are members of a single genetically linked assemblage, and are variants of one species—a biospecies.

No discrete polymorphism, such as the possible sexual dimorphism expressed in the conch dimension of Boreal Jurassic and Cretaceous ammonites, exists in this similar Triassic case.

Wide intraspecific variability is quite common in Boreal Triassic ammonoid assemblages, but its range is not constant. Intraspecific variability differs within one family, or even within a genus (Dagys 2001). Similar examples of intraspecific variation have also been described from low-palaeolatitude Triassic ammonoid samples (Hammer

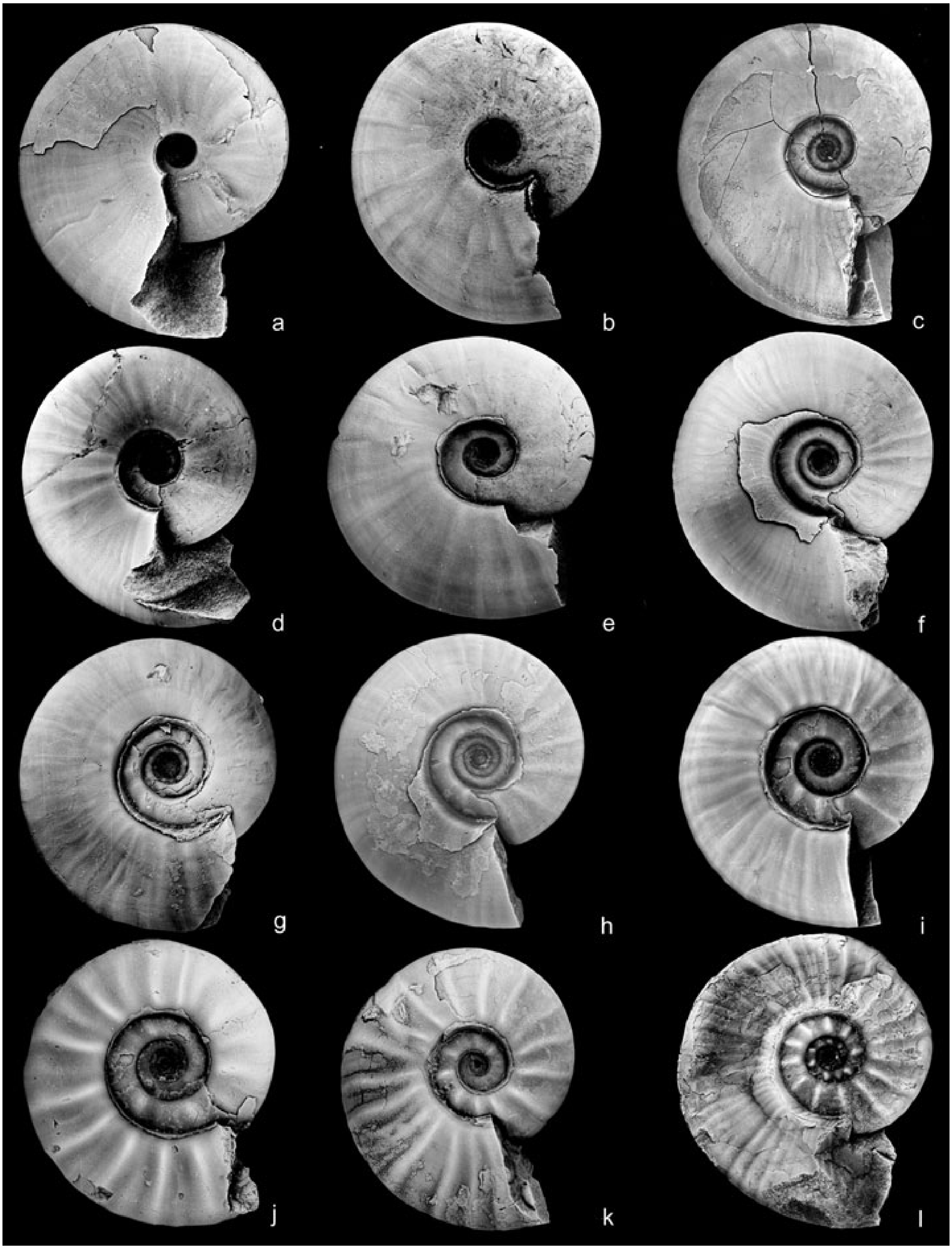

Fig. 3 *Svalbardiceras spitzbergensis* (Frebold). Side views of 12 specimens from a single nodule layer [Early Triassic Spathian, Keyserlingites subrobustus Zone, Vikinghøgda Formation (Vendomdalen Member)], illustrating the continuous morphological variation. (a, c–g, l) Specimens from Stensiöfjellet, central Spitsbergen; (b, h, i) specimens from Wallenbergfjellet, central Spitsbergen; (j) specimen from Roslagenfjellet, eastern Spitsbergen; (k) specimen from Trehøgdene, central Spitsbergen. Magnification: (a) 1.3 times natural size; (c) and (l) 0.8 times natural size; (j) 1.4 times natural size. All the other specimens are shown at their natural sizes. Note the variation represented at the two extremes by (a) and (l).

& Bucher 2005). In all of the different degrees of intraspecific variability there exists a distinct correlation between conch morphology and sculpture. The involute thin variants of a population are usually less costate than the evolute thicker ones.

The enormous range of variability that an ammonoid biospecies could accommodate has led to some serious problems concerning taxonomy, stratigraphy and ecology. Frequently, successive faunas can only be separated on the basis of the mode of the population, and single specimens remain indeterminable.

The consequences for ammonoid ecology also seem to be quite serious. The numerous described examples, especially from Boreal Triassic ammonoid assemblages, have shown that forms with extremely different conch morphologies, such as "streamlined" oxycones and "subbenthic" cadicones, lived together in the same biotope. This seriously undermines the prevailing opinion that there is a close correlation between ammonoid conch morphology and their mode of life. The streamlining of a shell cannot play any important role among such slow-swimming animals as ammonoids (Lehmann 1990; Weitschat & Bandel 1991).

Systematic descriptions

Family Dinaritidae

Genus *Svalbardiceras* (Frebold, 1930)

Type species: *Lecanites*? *spitzbergensis* Frebold 1929

Svalbardiceras spitzbergensis (Frebold, 1930)

1965 ?*Svalbardiceras freboldi* Tozer, pl. IV, figs. 12, 13, pl. V, fig. 2
1965 ?*Svalbardiceras chowdaei*, Tozer, pl. IV, figs. 9–11
1982 *Svalbardiceras spitzbergense* Frebold, Korčinskaja, pl. XII, figs. 1, 2
1982 *Svalbardiceras chowadei* Tozer, Korčinskaja, pl. IX, fig. 3, pl. XI, figs. 3, 4
1982 *Olenekites* ex. gr. *canadensis* Tozer, Korčinskaja, pl. IX, figs. 4, 5, pl. XII, fig. 4
1982 *Olenekites* cf. *canadensis* Tozer, Korčinskaja, pl. XII, fig. 4
1982 *Nordophiceras*? *costatus* Korčinskaja, pl. XI, figs. 1, 2, 5–7
1999 *Svalbardiceras spitzbergense* Frebold, Mørk et al., fig. 8G

Holotype: *Lecanites*? *spitzbergensis* Frebold, 1929, pl. I, fig. 1

Diagnosis: Shell size up to 85 mm in diameter, highly variable, from flat compressed platycones, to wide umbilicate, depressed subcadicones. Umbilical width: gradually increasing from platyconic to subcadiconic type of conch. Ventral side tabulate in platycones and subtabulate-to-rounded in subcadicones. Ornamentation highly variable, correlated to conch type. Platycones almost smooth, or with low fold-like, closely spaced ribs; subcadicones strongly sculptured, with straight distinct, widely spaced ribs, most prominent at the umbilical shoulder; some crossing subtabulate to rounded venter. Body chamber: about three quarters of a whorl, peristome simple. Suture line: with a deep external lobe with incised branches, two lateral lobes with only delicate shallow incisions, and a shallow unincised suspensive lobe.

Age and distribution: Early Triassic, latest Spathian, Keyserlingites subrobustus Zone; Sassendalen Group, Vikinghøgda Formation (Vendomdalen Member). Central Spitsbergen (Stensiöfjellet, Wallenbergfjellet, Storfjellet, Milne Edwardsfjellet, Sticky Keep, Vendomdalen and Trehøgdene); eastern Spitsbergen (Roslagenfjellet and Eistraryggen).

Material: Stensiöfjellet (250), Wallenbergfjellet (35), Trehøgdene (25), Sticky Keep (12), Storfjellet (15) and Vendomdalen (30) in central Spitsbergen; Roslagenfjellet (24) and Eistraryggen (25) in eastern Spitsbergen.

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