First record of *Rhabdoceras suessi* (Ammonoidea, Late Triassic) from the Transylvanian Triassic Series of the Eastern Carpathians (Romania) and a review of its biochronology, paleobiogeography and paleoecology

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The occurrence of the heteromorphic ammonoid *Rhabdoceras suessi* Hauer, 1860, is recorded for the first time in the Upper Triassic limestone of the Timon-Ciungi olistolith in the Rârâu Syncline, Eastern Carpathians. A single specimen of *Rhabdoceras suessi* co-occurs with *Monotis (Monotis) salinaria* that constrains its occurrence here to the Upper Norian (Sevatian 1). It is the only known heteromorphic ammonoid in the Upper Triassic of the Romanian Carpathians. *Rhabdoceras suessi* is a cosmopolitan species widely recorded in low and mid-paleolatitude faunas. It ranges from the Late Norian to the Rhaetian and is suitable for high-resolution worldwide correlations only when it co-occurs with shorter-ranging choristoceratids, monotid bivalves, or the hydrozoan *Heterastridium*. Formerly considered as the index fossil for the Upper Norian (Sevatian) Suessi Zone, by the latest 1970s this species lost its key biochronologic status among Late Triassic ammonoids, and it generated a controversy in the 1980s concerning the status of the Rhaetian stage. New stratigraphic data from North America and Europe in the subsequent decades resulted in a revised ammonoid biostratigraphy for the uppermost Triassic, the Rhaetian being reinstalled as the topmost stage in the current standard timescale of the Triassic. The geographic distribution of *Rhabdoceras* is compiled from published worldwide records, and its paleobiogeography and paleoecology are discussed.

Key words: *Rhabdoceras suessi*, Ammonoidea, Upper Triassic, Rârâu Syncline, Transylvanian Triassic Series, Eastern Carpathians, biochronology, paleogeography, paleoecology.

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Introduction

The ammonoid faunas of the Transylvanian Triassic carbonate rocks that made up an array of olistoliths embedded in the Lower Cretaceous Wildflysch Formation from the Rârâu, Hâghimaș and Perșani Mts, and also build up a set of large klippen in the Perșani Mts, are referred to in numerous papers (e.g. Patrulius 1971; Patrulius 1996; Turculet 1971 to 2005). However, no occurrence of Late Triassic heteromorphic ammonoids were recorded until now in the Transylvanian Triassic Series of the Eastern Carpathians.

While examining the fossils collected by the senior author in an old quarry in limestone of the Timon-Ciungi olistolith, the junior author, whose aim was to study the nautiloids, identified a fragment of a specimen of Rhabdoceras suessi Hauer, 1860, in the material. Consequently the purpose of the present paper is to describe this specimen, and to discuss the biostratigraphic range, chronostratigraphic relevance, and the paleobiogeographic distribution and paleoecology of this Late Triassic heteromorphic ammonoid.

Geologic and stratigraphic settings

The Timon-Ciungi olistolith, along with many other olistoliths composed of Triassic sedimentary and/or ophiolitic rocks, is embedded in Lower Cretaceous wildflysch that infills the Rârâu Syncline of the Bucovinian Nappe in the northern part of the inner Eastern Carpathians (Sandulescu 1973). The Triassic rocks of the olistoliths and also of several large klippen scattered along the inner zone of the Eastern Carpathians, in the Rârâu, Hâghimaș and Perșani Mts, are assigned to several, facially distinctive Transylvanian Triassic Series (Patrulius 1996).

The Timon-Ciungi olistolith is located on the left side of the drainage of the Timon Creek, which is a tributary of the Moldova River at the Fundu Moldovei locality (Fig. 1). The olistolith, several tens of meters in length, was largely quarried in the 1960s. The limestone quarry was abandoned for a long time and the area is now entirely reforested, with only few small exposures remaining. The main mass of the olistolith seems to be represented by thick-bedded light-grey limestone that is cut by Neptunian dykes filled with ammonoid-bearing, reddish nodular limestone. Monotis-bearing, Hallstatt-type reddish limestone occurs on the south-eastern side of the olistolith, its stratigraphic relationships within the olistolith being concealed by soil.


The ammonoid fauna consists of more than fifty described taxa. Age-diagnostic taxa for the Middle Norian include Cyrtopleurites sp. ex. gr. C. socius Mojsisovics,
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Parathisbites sp. ex gr. P. meleagri Mojsisovics, Himavatites sp. aff. H. watsoni Diener, Halorites alexandri Mojsisovics, Halorites excentricus Turculet, Halorites sp. ex gr. H. mitis (Mojsisovics); and for the Upper Norian to Lower Rhaetian, Megaphyllites insectus Mojsisovics, Placites polydactylus (Mojsisovics), Tragorhacoceras occultum (Mojsisovics), Stenarcestes sp. aff. subumbilicatus Hauer, Rhacophyllites invalidus Mojsisovics. The described ammonoid assemblage includes numerous other stratigraphically less useful species of leiostracan ammonoids, such as Placites, Arcestes, Cladiscites, Rhacophyllites and Megaphyllites, all of them have long ranges in the Norian–Rhaetian interval in the Hallstatt facies of the Northern Calcareous Alps (e.g. Krystyn 2008b).
The lack of a precise ammonoid stratigraphic log hinders the establishment of an accurate biostratigraphy for the Timon-Ciungi olistolith. The published ammonoid fauna reflects a "rucksack-condensation", in the sense given to this term by Krystyn (2008b). However, taking into account the known ranges of the above mentioned age-diagnostic ammonoids, one can conclude that the Hallstatt-type limestone of the Timon-Ciungi olistolith spans a stratigraphic interval ranging from the Middle to Upper Norian (Sevatian 1), and higher into the Lower Rhaetian (Sevatian 2).

The specimen of Rhabdoceras suessi comes from Monotis-bearing reddish limestone. An orthocerid specimen of Trematoceras sp. is found on the same rock slab (Fig. 2). The monotid bivalves are assigned to Monotis (Monotis) salinaria (Schlotheim 1820) (Turculet 2005).

The top-Norian occurrence and the pre-Rhaetian disappearance of the pectinoid bivalve M. (Monotis) salinaria, as documented in the Austrian Northern Calcareous Alps (McRoberts et al. 2008; Krystyn 2008b), allows determining a Late Norian (Sevatian 1) age for the occurrence of Rhabdoceras suessi in the Timon-Ciungi olistolith.

The Rhabdoceras suessi specimen found in the Hallstatt-type limestone of the Timon-Ciungi olistolith is the only record to date of a Late Triassic heteromorphic ammonoid in the Eastern Carpathians, as well as in the other Carpathian regions of Romania.
Systematic paleontology

Class CEPHALOPODA CUvier, 1797
Subclass AMMONOIDEA ZITTEL, 1884
Order CERATITIDA HYATT, 1884
Suborder CERATITINA HYATT, 1884
Superfamily CHORISTOCERATACEAE (HYATT 1900) TOZER 1979
Family RHABDOCERATIDAE TOZER 1979
Genus Rhabdoceras HAuer, 1860
Type species: Rhabdoceras suessi HAuer, 1860

Rhabdoceras suessi HAuer: Hauer 1860, p. 125, Pl. 2, figs 9–16; Mojsisovics 1893, p. 571, Pl. 133, figs 10–17; Gemmellaro 1904, p. 76, Pl. 18, figs 45–46; Arthaber 1906, Pl. 47, fig. 19a–b; Janensch 1906, p. 710, text-figs 1–2; Wanner 1910, p. 739; Jaworski 1927, p. 165, Pl. 6, fig. 8a–c.

Rhabdoceras suessi HAuer: Kutassy 1932, pp. 646–647; Kutassy 1936, p. 1041, Pl. 13, fig. 36; Muller and Ferguson 1939, p. 1605; Spatham 1951, p. 86; Kummel 1957, p. 169, fig. 1997; Popov 1958, p. 43, Pl. 13, fig. 2; Tozer 1958, p. 15; Tozer 1963, Pl. 12, figs 18, 19a–c; Tozer 1965, p. 222; Kushlin 1965, p. 139, text-fig. 1a–d; Kushlin 1966, p. 844, text-fig. 1a–d; Zapfe 1965, p. 300, Pl. 1, fig. 8; Tozer 1967, pp. 38–40, 54, 55, 75, 77, 79–80, Pl. 10, figs 6, 7a–c; Sachariewa-Kowatschewa 1967, p. 76, Pl. 5, fig. 9; Tozer 1970, p. 634, Pl. 18, fig. 18a–b; Tozer 1971, p. 1020; Wiedmann 1972, p. 588, Pl. 3, fig. 3a–b; Urlichs 1972, pp. 668, 670; Krystyn 1973, pp. 131–132; Catalano et al. 1974, p. 1034; Wiedmann et al. 1979, p. 136, text-fig. 1a–b; Tozer 1979, p. 127, Pl. 16.1, figs 8–10; Kochanová and Kollárová-Andrusovová 1983, p. 577, Pl. 12, figs 3, 6, 7, 9; Krystyn 1987, pp. 23–25; Golebiowski 1988, p. 63; Tozer 1994a, p. 264, Pl. 144, figs 1–8, Pl. 147, figs 1–3, text-fig. 117c–g (p. 636), text-fig. 120i–j (p. 644).

Rhabdoceras (Rhabdoceras) suessi HAuer: Wiedmann 1973, p. 238, Pl. 1, figs 9a–c, text-fig. 1e; Shevyrev 1990, p. 137, Pl. 8, fig. 1; Shevyrev 2001, p. 144, text-fig. 23, Pl. 61, figs 6a–c; Shevyrev 2005, pp. 617–619, figs 3a–c, 4, 5.


Rhabdoceras (Cyrtorhabdoceras) curvatum MOJSISOVICS: Wiedmann 1973, p. 238, Pl. 1, figs 8a–b; Shevyrev 1990, p. 139, Pl. 8, figs 3–4; Shevyrev 2001, p. 145, Pl. 62, figs 1–2; Shevyrev 2005, p. 617, figs 3d–e.

Rhabdoceras russelli HYATT: Hyatt 1892, p. 398; Hyatt and Smith 1905, p. 203, Pl. 47, figs 13–15, Pl. 56, fig. 26; Smith 1927, p. 99, Pl. 47, figs 13–15, Pl. 56, fig. 26; Spatham 1951, p. 86.

Rhabdoceras boreale AFITSKY: Afitsky 1965, p. 137, text-fig. 1; Afitsky 1970, p. 107, Pl. 3, fig. 1a–b.
Rhabdoceras leave KUSHLIN: Kushlin 1965, p. 140, text-fig. 2a–d; Kochanová and Kollárová-Andrusovová 1983, p. 580, Pl. 12, figs 8, 10, Pl. 13, figs 1–16; Rhabdoceras (Rhabdoceras) leave KUSHLIN: Shevyrev 1990, p. 138, Pl. 8, fig. 3; Shevyrev 2001, p. 145, Pl. 61, fig. 7a–c.
Rhabdoceras cf. R. suessi HAUER: González-León et al. 2000, p. 493, figs 5, 8, 9, 10.
Rhabdoceras sp.: v. Hillebrandt 1994, p. 299, Pl. 1, fig. 17; Afitsky 1970, pp. 20, 26, 40;
Bychkov 2000, p. 105.
Rhabdoceras nov. sp.: Jaworski 1915, p. 135, Pl. 45, fig. 16a–b.

Material. One specimen (UBLG-GE 1065). The illustrated specimen is housed in the Laboratory of Geology, Faculty of Geology and Geophysics, University of Bucharest.

Dimension. Length of fragment – 22 mm; height adapical – 4.6 mm; width adapical – 4.2 mm; h/w – 0.91.

Description. The single available specimen is a fragment of the straight part of the conch, one half representing the last part of the phragmocone and other the beginning of the body chamber. The ribbing is well preserved on the conch of the body chamber, and is projected ventrally, becoming stronger than on the flank, while on the dorsum it is weaker. The preserved portion of the body chamber is ornamented by six ribs. On the phragmocone, which is preserved as a steinkern, there are six visible suture lines showing a narrow and deep lateral lobe, a broad rounded marginal saddle and a shallow external lobe incised by a median saddle, that characterize the goniatitic suture lines of choristoceratids.

Discussion. The heteromorphic ammonoid Rhabdoceras is known commonly as fragmentary specimens, the initial coiled part, as described and illustrated by Janensch (1906), not even being found in the case of the large collections of Canadian material (Tozer 1994a). The rhabdoceratids commonly show variable morphologies, with straight and variable curved shells, showing also variable sculpture, from ribbed to virtually smooth. Morphologically different variants occur even in the same population, as emphasized by Tozer (1994a, p. 265), and it is also evident in the Slovakian and Pamirs materials (Kochanová and Kollárová-Andrusovová 1983; Kushlin 1966/1965; Shevyrev 1990, 2001). Several species of Rhabdoceras were described by different authors, as shown in the present synonymy, although there is no compelling evidence that these represent biochronologically distinct species. Wiedmann (1973) defined two distinct subgenera, Rhabdoceras (Rhabdoceras), with Rh. suessi Hauer, 1860, as the type species, and Rhabdoceras (Cyrtorhabdoceras), with Rh. suessi Hauer var. curvata Mojsisovics, 1893, as the type species. This typological taxonomy was followed by Shevyrev (1990, 2001, 2005). Kochanová and Kollárová-Andrusovová (1983) have not recognized the two subgenera of the genus Rhabdoceras, but they maintained the species oversplitting of the genus. In treating the taxonomy of the genus

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Rhabdoceras, a heteromorphic ammonoid that displays considerable variation in morphology and sculpture, we follow here the taxonomy adopted by Tozer (1994a). As the rhabdoceratids usually occur in fragmentary condition, in many cases it is not even possible to assign smaller pieces to straight or curved variants. Some geographically isolated rhabdoceratids, such as Rhabdoceras boreale which occurs along with specimens of Rhabdoceras sp. in Northeast Russia (Afitsky 1965/1966, 1970), despite showing slight differences in the suture line, are also included in the synonymy.

A separate case exists for Rhabdoceras curvatum Jaworski (Jaworski 1923, p. 153, Pl. 6, figs 1–2), not Rhabdoceras suessi Hauer var. curvata Mojsisovics, 1893, which was assigned to the genus Peripleurites by Geyer (1973, p. 24), then renamed as Choristoceras (Peripleurites) peruvianum by Wiedmann (1973, p. 239, Pl. 1, figs 6–7), and later considered as a representative of Rhabdoceras, i.e. Rh. peruvianum, by Krystyn (1990, p. 20). It is placed by Tozer (1994a, p. 265) in the synonymy of Peripleurites roemeri Mojsisovics, 1893.

**Occurrence.** The heteromorphic ammonoid Rhabdoceras suessi had a very broad geographic distribution during the Late Triassic in low and middle latitudes both in the Northern and Southern Hemispheres. In western North America, Rh. suessi is well documented from the Cordilleranus, Amoenum and Crickmay Zones, occurring in some localities in sequence within all zones, such as in British Columbia in western Canada. Along the Alpine–Himalayan–Indonesian orogenic belt, Rh. suessi occurs from Alpine Europe to the Pamirs, and further on to southeast Indonesia, being known together with age-diagnostic choristoceratids from all Upper Norian and Rhaetian biozones.

**Biostratigraphic range and chronostratigraphic relevance**

For a long time, the use of the heteromorphic ammonoid Rhabdoceras suessi for the chronostratigraphy of the uppermost Triassic was closely related to the progressive knowledge increase of the biostratigraphic ranges of Late Triassic ammonoids in general, and of the aforementioned heteromorphic ammonoid in particular. This in turn deeply influenced the evolution of ammonoid zonal concepts and their impact on the definition of the Norian–Rhaetian boundary, as well as on establishing the chronostratigraphic status of the Rhaetian, respectively.

**Biostratigraphic range.** Rhabdoceras suessi is now known to be a long-ranging heteromorphic ammonoid spanning almost the whole interval of the Upper Norian (Sevatian 1) to Rhaetian (Fig. 3). However, it was not known as such until the latest 1970s.

**Before the latest 1970s.** The Northern Calcareous Alps in Austria represents the homeland of the Late Triassic heteromorphic ammonoid Rhabdoceras suessi. From here Hauer (1860) first described and presented data on the occurrence of
Rhabdoceras suessi in the Hallstatt limestone. Afterwards, Mojsisovics (1893) reported the occurrence of *Rhabdoceras suessi* in various facies of Hallstatt limestone assigned to the so-called "Juvavische Stufe" (= Norian Stage; see Tozer 1965, p. 223) and also from the "Cochloceras" beds in the Zlambach Formation. In the Hallstatt limestone *Rhabdoceras suessi* was recorded from the *Sagenites giebeli* and *Cladiscites ruber* Zones, as well as from the *Pinacoceras metternichi* Zone, which in Mojsisovics's (1902) zonal scheme were assigned to the "Lower Juvavic" (Lacian) and "Upper Juvavic" (Sevatian) Substages, respectively. As later proved by Krystyn et al. (1971), the ammonoid assemblages in the "Hangendrotkalk" facies of the Hallstatt Limestone, such as those of the Gastropod Beds of Millibrunnkogel (*Cladiscites ruber* Zone), and from Leislingwand (*Sagenites giebeli* Zone) and Ferdinandstollen (*Glyphidites docens* lens), had been wrongly emplaced by Mojsisovics (1902) into the "Lower Juvavic" (Lacian).

Kittl (1903) provided the first exact known data on the stratigraphic occurrences of *Rhabdoceras suessi* in the Hallstatt limestone occurrences of the Salzkammergut region (at Siriuskogel, in the "Pinacoceras metternichi" Zone) together with "Cochloceras" *amoenum* and *Monotis salinaria*; at Taubenstein, together with *Sagenites quinquepunctatus*; at Steinbergkogel near Hallstatt and "Franzberg", together with "Cochloceras", *Pinacoceras metternichi*, *galeate Arcestidae* and *Heterastridium*) and also in the Zlambach Formation (at Stambachgraben near Goisern, in the Cochloceras-beds). In Kittl’s (1903, p. 16, tab. 2) stratigraphic scheme of the Triassic from the Salzkammergut region, the ammonoid faunas of the

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**Table 1: Stratigraphic Zones of Rhabdoceras suessi and Monotis salinaria in Central Europe**

<table>
<thead>
<tr>
<th>Stage</th>
<th>Tethys Zone</th>
<th>North America Zone</th>
<th>Rhabdoceras suessi and Monotis salinaria stratigraphic range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lower Sevatian</td>
<td><em>Sagenites reticulatus</em> (Paracocloceras suessi)</td>
<td><em>Paracocloceras amoenum</em></td>
<td>??</td>
</tr>
<tr>
<td>Middle Norian</td>
<td><em>Sagenites quinquepunctatus</em> (Metasphaerites spinoceri)</td>
<td><em>Gnomohalites cordilleranus</em></td>
<td>??</td>
</tr>
<tr>
<td>Upper Norian</td>
<td><em>Halogites macer</em></td>
<td><em>Mesohimarvites columbiaus</em></td>
<td>??</td>
</tr>
<tr>
<td>Ladinian</td>
<td><em>Himarvites hogarti</em></td>
<td><em>Himarvites watsoni</em></td>
<td>??</td>
</tr>
<tr>
<td></td>
<td><em>Cyrtopleurites bicornutus</em></td>
<td><em>Drepanites rutherfordi</em></td>
<td>??</td>
</tr>
</tbody>
</table>

**Fig. 3**

"Pinacoceras metternichi" Zone" and of the "Cochloceras"-beds are assigned to the Upper Norian. Arthaber (1904, pp. 382, 385) reaffirmed the Upper Norian (Sevatian) age for the "Metternichi-Kalke der Hallstätter Facies" and for the "Cochloceras-Bänke der Zlambach-Facies".

Following the glorious period of the second half of the 19th century, when studies of the Triassic ammonoids were initiated and extensively developed by the famous "Geologic School of Vienna", a gap of more than five decades elapsed, when studies of the Tethyan Triassic ammonoids were only occasionally carried out in Europe. The studies of Alpine Triassic ammonoids resumed in the early 1960s and mostly extended into the 1970s in Austria and a few other European countries.

In Italy, Gemmellaro (1904, 1923) and Catalano et al. (1974) reported the occurrence of *Rhabdoceras suessi* together with *Heterastridium conglobatum* (Hauer) from the Upper Norian limestone in the Palermo region of Sicily.

In Hungary, Kutassy (1927, 1936) mentioned the occurrence of *Rhabdoceras suessi* in the Norian Dachstein-type limestone.

In Austria, Zapfe (1962, 1965, 1967a) found *Rhabdoceras suessi* in the Dachstein-Riffkalk of the Gosaukamm in the Dachstein Mts. Krystyn (1973, p. 132) reported the occurrence of *Rhabdoceras suessi* in the Upper Norian (Sevatian) from the Suessi Zone (sensu Tozer 1967), and in support of this the author referred to the ammonoid faunas described by Mojsisovics from the Hangendrotkalk and Hangengraukalk facies of the Hallstatt Limestone, and also from the Zlambach Beds in the Salzkammergut region. Wiedmann (1972) found *Rhabdoceras suessi* in the Zlambach Marls, and on this basis the author assigned the "Bereich III–IV" to the Suessi Zone (sensu Tozer 1967), regardless of his several available options for the position of the Norian–Rhaetian boundary.

In the Balkans, Sachariewa-Kowatschewa (1967) described *Rhabdoceras suessi* in an ammonoid assemblage including several species of *Metasibirites* (M. spinescens, M. uhligi, M. crassus, etc.), and *Cochloceras fischeri*, together with other long-ranging ammonoids that in the standard zonation of the time were assigned to the Upper Norian.

Outside of Alpine Europe, the occurrence of *Rhabdoceras suessi* was mentioned by Wanner (1910) and Jaworski (1915) in the Upper Norian *Nucula*-Mergel from the Misool Archipelago of Indonesia, occurring together with different species of *Cochloceras* and *Paracochloceras*. Tozer (1971, p. 1020) reported the occurrence of *Rhabdoceras suessi* at Aliambata in Timor-Leste (East Timor) in a Late Norian ammonoid assemblage including *Glyphidites docens* and other age-diagnostic ammonoid genera. From Central Asia, Kushlin (1965) described *Rhabdoceras suessi* from the Norian of the southeast Pamirs, without any other specification on its exact stratigraphic occurrence.

In the Western Hemisphere, the occurrences of *Rhabdoceras suessi* were recorded in the United States in the first half of 20th century by Hyatt and Smith in their classical studies on Triassic ammonoids. Later, more data on the
stratigraphic occurrence of this heteromorphic ammonoid were provided by collections made by S.W. Muller of Stanford University in 1930s–60s, and starting in the early 1950s, by the studies of E.T. Tozer in Canada and those by N.J. Silberling in the United States.

In the United States, *Rhabdoceras russelli* was described by Hyatt (1892) from the Taylorsville area in northern California, and reported in California and Nevada by Smith (1927) from the Norian *Pseudomonotis subcircularis* Zone [this monotid species is now referred to the genus *Monotis* (*Pacimonotis*), and was considered a junior synonym of *Rhabdoceras suessi* by Tozer (1967, p. 39; 1994a, p. 265). Later, the occurrence of *Rhabdoceras suessi* was reported by Muller and Ferguson (1939, p. 1605, tab. 4) in the Gabbs Formation in Nevada from the upper part of the Upper Norian Suessi Zone, as revised by Silberling and Tozer (1968, p. 32). Silberling and Tozer (1968) reported occurrences of *Rhabdoceras suessi* at a number of localities in western Nevada, and also in northern California, occurring together with *Metasibirites spinescens* (Hauer), *Monotis subcircularis*, *Monotis cf. M. salinaria* and the hydrozoan *Heterastridium*.

In Canada, Tozer (1958, 1965) found that *Rhabdoceras suessi* occurs both in and above the beds with *Monotis subcircularis* (Gabb) in the Yukon Territory, British Columbia and Vancouver Island. Tozer (1965, p. 224) mentioned that at Tyaughton Creek, southern British Columbia, strata with *Rhabdoceras* are overlain by beds with *Choristoceras cf. C. marshi* Hauer (now *Choristoceras crickmayi*, Tozer 1979), the latter assumed to be correlative with the Kössen Beds of the northern Alps. Taking into account that the Kössen Beds were at that time considered the standard for the uppermost Triassic Rhaetian Stage and these were regarded as younger than the Norian in the European Triassic chronostratigraphic scheme, Tozer (1965, p. 225) concluded that all above-mentioned occurrences suggest that in Canada *Rhabdoceras suessi* is restricted to the Upper Norian. On the basis of the data from the Canadian Norian ammonoid sequence, Tozer (1965, pp. 224–225; 1971, p. 1020) was also able to demonstrate that the two Salzkammergut zones of *Sagenites giebeli* and *Cladiscites ruber* regarded by Mojsisovics (1902) as Lower Norian and where the occurrence of *Rhabdoceras suessi* was reported, are essentially correlative with the Upper Norian *Pinacoceras metternichi* Zone. Moreover, the occurrences of *Monotis* in the Salzkammergut evidently support an approximate correlation with the North American *Monotis subcircularis* Zone. Thus, based on the available data, Tozer (1965) found no apparent conflict in the revised Mojsisovics's Alpine Norian ammonoid sequence and the occurrences of *Rhabdoceras suessi* in Canada. Subsequently, Schlager (1969, p. 293) and Krystyn et al. (1971, pp. 286–288) provided field evidence in support of Tozer's Canadian findings, demonstrating that Mojsisovics's Norian ammonoid zonal sequence does not represent a normal sequence, being based on more or less isolated occurrences of ammonoid faunas supposedly arranged in a zonal scheme.

On the basis of the ammonoid succession in North America, Tozer (1967, p. 40; 1971, p. 1020) and Silberling and Tozer (1968, p. 16) emphasized that the North
American Suessi Zone newly named by them, with *Rhabdoceras suessi* as the nominal index fossil and stratotype in Nevada, may be correlated with the *Piracoceras metternichi* Zone of Austria, as represented in the Hallstatt Limestone of the Steinbergkogel, and with the *Cochloceras*-bearing part of the Zlambach Beds, as exposed in the Stambachgraben. *Rhabdoceras suessi* is reported in North America from both ‘Lower Suessi Zone’, equivalent to the *Monotis subcircularis* Zone, and the ‘Upper Suessi Zone’, which includes the Norian beds that overlie *Monotis subcircularis* (referred to as the Supramonotis Beds). Since an adequate boundary between the lower and upper parts of the Suessi Zone cannot yet be defined, it is stressed by Silberling and Tozer (1968, p. 33) that *Rhabdoceras suessi* and some other long-range ammonoid species appear to range through most or all of the zone, but species of *Cochloceras* (or *Paracochloceras*) and *Cycloceltites* may be restricted to its upper part. Since this pattern in the faunal sequence inside the North American Suessi Zone was also known long before by Kittl (1903) in the Austrian Alps, it is relevant because it concerns the further evolution in chronostratigraphic nomenclature and concepts of the Norian–Rhaetian boundary (this question will be dealt with later). It bears the biostratigraphic premise for splitting the classical Sevatian Substage into two distinct parts and to equate the Sevatian 2, characterized by the occurrence of *Cochloceras* (or *Paracochloceras*), with the lower part of the Rhaetian as it is actually defined by Krystyn et al. (2007a–b).

To summarize the data of this period, in terms of the chronostratigraphic nomenclature applied to the North American zonal sequence, as promoted by Tozer (1967, 1970, 1971, 1974), which was also adopted in Europe by Krystyn (1973, 1974, 1980), Zapfe (1974), Tollmann (1976) and Wiedmann et al. (1979), the occurrence of *Rhabdoceras suessi* was customarily confined to the Upper Norian (Sevatian) Suessi Zone, that in most chronostratigraphic schemes underlies the Rhaetian Marshi Zone (Fig.4).

**The latest 1970s and onwards.** In the Northern Calcareous Alps, Urlichs (1972) and Möstler et al. (1978) stated that the beds with *Rhabdoceras suessi* underlie those with *Choristoceras marshi* in the Kössen Beds, and consequently they assigned the beds with *Rhabdoceras suessi* to the Upper Norian and those with *Choristoceras marshi* to the Rhaetian. In the first instance, the Kössen data were promptly taken by Tozer (1974, pp. 203–204) to justify the North American Suessi-Marshi zonal scheme. However, the finding of *Rhabdoceras suessi* in the lower part of the Kössen Beds, traditionally considered as the stratotype for the classical Rhaetian, represented for Tozer (1971, 1974) the turning point from which he began to doubt the validity of the Rhaetian as a valid chronostratigraphic unit for the uppermost Triassic, by advancing the idea that the Sevatian and Rhaetian overlap in their scope.

New data on the ammonoid succession in Canada provided by Tozer (1979, 1980b–c, 1984), later fully developed by Tozer (1994a) in his excellent monograph on the Canadian Triassic ammonoid faunas, shed a completely different, new
light on the biostratigraphic range of *Rhabdoceras suessi*. Tozer found that *Rhabdoceras suessi* is present in all of the new three zones he defined for the uppermost part of the North American Triassic, the *Gnomohalorites cordilleranus, Cochloceras amoenum* and *Choristoceras crickmayi* Zones, in ascending order. Compared with the previous North American scheme, the first two zones replace the two informal divisions of the Upper Norian Suessi Zone, while the Crickmayi Zone replaces the Rhaetian Marshi Zone. Tozer classified all three newly-named zones as Upper Norian (Sevatian) and argued against the Rhaetian as a valid chronostratigraphic unit, an opinion that has caused considerable controversy in the following years (this question will be dealt with later). Based on the new data, which proved a more extended biostratigraphic range for *Rhabdoceras suessi* in North America than was known before, Tozer concluded that the former Suessi Zone serves no purpose in the chronostratigraphic subdivision of the uppermost Triassic, and extended the Upper Norian (Sevatian) to the top of the Triassic (Fig. 5, columns 1 and 2).

The subsequent data obtained in the Northern Calcareous Alps also confirmed the more extended biostratigraphic range of *Rhabdoceras suessi* in the uppermost part of the Triassic. These data came not from the Hallstatt Limestone but from the time-equivalent Kössen and Zlambach beds. Wiedmann et al. (1979) reported that *Choristoceras marshi* – an index fossil of the restricted Rhaetian – was found in the lower part of the Kössen Beds of the Lahnewiesgraben, equivalent to the former *Rhabdoceras suessi* Zone. Upon this discovery Wiedmann et al. (1979, p. 142, tab. 2) made four proposals for defining the Alpine uppermost Triassic chronostratigraphy, none of them being later validated. Golebiowski (1986, figs 3–4) reported that in the Kössen Beds the occurrence of *Rhabdoceras suessi* reaches up into the lower part of the Marshi Zone, where it co-occurs with *Choristoceras ammonitiforme*, underlying the beds with *Ch. marshi*. A similar ammonoid sequence was also found by Krystyn (1988) in the Zlambach Marls. On the basis of a new, detailed ammonoid sequence defined in the Zlambach Marls, Krystyn (1988, p. 24, fig. 1) developed a new, shorter concept for the Rhaetian, as the ultimate stage of the Triassic (Fig. 5, column 4). By adopting Krystyn’s new ammonoid zonal scheme for the Zlambach Beds, Golebiowski (1990, fig. 1) restricted the occurrence of *Rhabdoceras suessi* to the Rhaetian section of the Kössen Formation, i.e. in the *Vandaites stuerzenbaumi* Zone and to the lower part of the *Choristoceras marshi* Zone, respectively. Although Krystyn (1990, p. 15) had earlier claimed that the *Cochloceras* fauna “for a long time served as the topmost Norian ammonoid standard and would remain in this position in the future too”, subsequent new detailed data on the ammonoid biostratigraphy from the Hallstatt Limestone at Steinbergkogel demonstrated that the *Paracochloceras/Cochloceras* fauna is chronostratigraphically equivalent to the Lower Rhaetian *Sagenites reticulatus* Zone (Krystyn and Kuerschner 2005, fig. 1, p. 18; Krystyn et al. 2007a–b). Hence, a new definition for a larger Rhaetian Stage was proposed, with the *Paracochloceras suessi* Zone, equivalent of the North American
Paracochloceras amoenum Zone, as its basal ammonoid zone (Fig. 5, column 5). In this case, the Sevatian 2 becomes the Lower Rhaetian, in opposition with the former usage of the Sevatian 1 and 2 as lower and upper substages for the Upper Norian, having as index fossils Sagenites quinquepunctatus and Sagenites reticulatus and/or Paracochloceras suessi, respectively (Gallet et al. 1996, 2003, 2007).

As a consequence of the new detailed ammonoid zonal sequence in the Hallstatt basin of the Northern Calcareous Alps, objective data demonstrate that the biostratigraphic range of Rhabdoceras suessi extends, as in North America, to include almost the entire interval of the newly-defined Upper Norian (=Sevatian 1) Substage and the Rhaetian Stage (Krystyn 2008b; Maslo 2008), and that this ammonoid represents a less-time diagnostic choristoceratid.

The other reported occurrences of Rhabdoceras suessi throughout the world are also proving that the stratigraphic range of this heteromorphic choristoceratid spans the whole interval of the Upper Norian to Rhaetian.

In the Slovakian Carpathians, Kollárová-Andrusovová (1983) and Kochanová and Kollárová-Andrusovová (1983) mentioned the occurrence of Rhabdoceras suessi in the Sevatian Hallstatt limestone.

In the southeast Pamirs Shevyrev (1990, p. 98; 2001, pp. 144–145) reported Rhabdoceras suessi together with other long-range ammonoids, along with Monotis salinaria and Heterastridium conglobatum, that are assigned to the Sagenites quinquepunctatus Subzone in the Suessi Zone. This subzone was initially regarded by Shevyrev (1990, tab. 12, p. 94) as equivalent to the Lower Rhaetian, where the Rhaetian Stage (sensu Wiedmann et al. 1979, p. 145) includes both the Suessi and Marshi Zones. Later, the ammonoid assemblage of the Sagenites quinquepunctatus Subzone in the Pamirs was regarded as Upper Norian (Dronov 2001, p. 12, tab. 2).

On the Alaska Peninsula, Pálfy et al. (1999) mentioned the occurrence of Rhabdoceras together with Metasibirites, Monotis and Heterastridium from the Upper Norian.

In South America, Geyer (1973, 1979) reported the occurrence in Columbia of Rhabdoceras sp. ex gr. suessi, together with Metasibirites spp. and Monotis subcircularis in the Upper Norian, while Hillebrandt (1994, p. 299, fig. 2) recorded the occurrence in Peru of Rhabdoceras sp. in the Lower Rhaetian Suessi Zone (sensu Wiedmann et al. 1979, p. 145).

In Mexico, González-León et al. (2000) found Rhabdoceras cf. R. suessi together with Choristoceras cf. C. nobile Mojsisovics, and interpreted them as indicative for the uppermost Triassic Crickmayi Zone.

To summarize the data of this period, and taking into account the most recent Alpine chronostratigraphic scheme for the uppermost Triassic, with a new definition of the Norian–Rhaetian boundary, it is now known that Rhabdoceras suessi Hauer is a long-ranging heteromorphic ammonoid covering the entire interval of the newly defined Upper Norian (=Sevatian 1) Substage and the Rhaetian Stage (Fig. 3).
However, despite the fact that *Rhabdoceras suessi* has lost its quality as a zonal index species, the main result of the newly acquired data is that this long-ranging choristoceratid can contribute to dating and high-resolution correlation of uppermost Triassic strata only in co-occurrence with short-range, biostratigraphically diagnostic choristoceratids or with monotid bivalves and the hydrozoan *Heterastridium*.

**Chronostratigraphic relevance.** As far as its relevance for the Upper Triassic chronostratigraphy is concerned the heteromorphic ammonoid *Rhabdoceras suessi* Hauer experienced a period of celebrity during the 1970s, when it had the status of a zonal index species, but fell into the shadows by the latest 1970s, when it lost this status. This change in its chronostratigraphic relevance was the direct consequence of newly-gained knowledge of the true biostratigraphic range of Late Triassic ammonoids in general, and of this heteromorphic ammonoid in particular.

In the 1970s, *Rhabdoceras suessi* Hauer was designated by Tozer (1967) and Silberling and Tozer (1968) as an index fossil for the Upper Norian (Sevatian) Suessi Zone (= *Rhabdoceras suessi* Zone), underlying the Rhaetian Marshi Zone (= *Choristoceras marshi* Zone) in the standard Triassic time scale for North America, and this stratigraphic scheme was also adopted for the uppermost Triassic in the Alpine Europe (Fig. 4).

As subsequently demonstrated in the 1980s, the designation of *Rhabdoceras suessi* as an index fossil for the Upper Norian Substage in fact reflected an as yet poor knowledge at that time of the ammonoid succession in the uppermost part of the Triassic, both in North America and in Alpine Europe.

Starting with the latest 1970s and mostly in the 1980s, Tozer (1979, 1980b–c, 1984) introduced a new ammonoid zonal scheme for the North American uppermost Triassic based on a detailed time-diagnostic ammonoid biostratigraphy in a stratigraphically well-ordered sequence. Tozer also changed the former chronostratigraphic nomenclature of the uppermost Triassic, as used for the European Alpine Triassic timescale, by extending the Norian Stage to the top of the Triassic, and questioned the status of the Rhaetian as a stage at the top of the Triassic (Fig. 5, columns 1, 2 and 1–2). From this Tozer (1980b, p. 413) concluded that the "Upper Norian", "Sevatian" and "Rhaetian" should be treated as synonymous substages. Even in the early 1970s, Tozer (1971, p. 1020) questioned the status of the Rhaetian, when he claimed that "in terms of ammonoid faunas it is difficult to justify recognizing a Rhaetian Stage". In support of his early opinion, Tozer recalled an inference made by Zapfe (1967a, p. 13), who found that a genuine similarity exists between the Upper Norian "Sevatic" and Rhaetic (?Lower Rhaetic) ammonoid faunas of northern Alps. However, it must be emphasized that Zapfe (1967, p. 13) had not questioned in any case the status of the Rhaetian Stage; on the contrary, he merely underlined "it is probable that we shall have to revise the biostratigraphic range of some Upper Triassic index fossils and even of whole index faunas".
First record of *Rhabdoceras suessi* (Ammonoidea) from the Transylvanian Triassic Series

Central European Geology 53, 2010

**Fig. 4**


<table>
<thead>
<tr>
<th>North America</th>
<th>Alpine Europe</th>
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<tr>
<td>Stage</td>
<td>Substage</td>
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<tr>
<td>Rhaetian</td>
<td>Choristoceras marshi</td>
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<tr>
<td>Unt.</td>
<td>Choristoceras haueri</td>
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<tr>
<td>Upper Triassic</td>
<td>&quot;Upper Suessi&quot;</td>
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<tr>
<td>Norian</td>
<td>Himavatites columbianus</td>
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<tr>
<td>Upper</td>
<td>Drespanites ruthfordi</td>
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<tr>
<td>Lower</td>
<td>Malayites dawsoni</td>
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<td>Lower</td>
<td>Mosquitoicites kerri</td>
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Central European Geology 53, 2010


What must be emphasized from the beginning is that it was only the finding of the real biostratigraphic range of the heteromorphic ammonoid *Rhabdoceras suessi* in the North American Upper Triassic, of a greater extent than was known before, that prompted Tozer (1979) not only to eliminate the Suessi Zone as the time-equivalent for the Upper Norian Stage but also to question the value of the Rhaetian as a valid time-stratigraphic subdivision in the uppermost Triassic. Also, we shall emphasize that Tozer's rejection of Gümbel's Rhaetian received justified support because of the lack of a proper definition and of a valid stratotype for it in the European Alpine Triassic on the one hand, and due to the absence of a detailed ammonoid biostratigraphy for the Alpine uppermost Triassic on the other. All these enabled an unstable and confusing stratigraphic nomenclature for the European Alpine uppermost Triassic until the early 1980s, in contrast with new achievements in the North American Triassic stratigraphy.

In reply to Tozer's opinion, at the conference of the Subcommission on Triassic Stratigraphy, held in Munich in July of 1978, a resolution was adopted concerning the stratigraphic status of the Rhaetian. The Subcommission made the following recommendations: 1) the name Rhaetian should be applied exclusively to strict chronostratigraphic meaning, and 2) the term Rhaetian sensu Gümbel should be preserved and should be used as the denotation of the uppermost Stage of the Triassic System, i.e. including or representing the Sevatian or Upper Norian, respectively.


Ager (1987, 1990) defended the Rhaetian as the final stage of the Triassic, contrary to Tozer (1980, 1988, 1990) and Silberling and Nichols (1988), although unfortunately Ager referred to the Kössen Beds as the stratotype for the Rhaetian and thus directed the first discussions on the status of the Rhaetian in the wrong direction.

In his reply to Ager's (1988) defense of the Rhaetian in terms of the Kössen Beds, Tozer (1988), with good reason in this instance, classified the Rhaetian as "a
First record of *Rhabdoceras suessi* (Ammonoidea) from the Transylvanian Triassic Series

Central European Geology 53, 2010

Fig. 5


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<td>Stage</td>
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<td>Sagenites reticulatus</td>
<td>Sagenites quinquapunctatus</td>
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<td>Metasibitreites spinescens (Sagenites quinquapunctatus)</td>
<td>Halorites macer</td>
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<td>Himavitites hogarti</td>
<td>Cyrtopleurites bicornatus</td>
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<td>Juvaivites magnus</td>
<td>Malasites paulkei</td>
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<td>Stikinoceras kerri</td>
<td>Guembelites jandianus</td>
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two-faced creature”, i.e. a Rhaetian sensu lato classically defined in terms of the Alpine Kössen stratotype, and a Rhaetian sensu stricto that is chrono-stratigraphically defined by the *Choristoceras marshi* Zone (sensu Tozer 1974, p. 203), which is the upper part of the Kössen. It is quite surprising to see that Tozer (1986, 1980b, 1988, 1990), in his dispute on the Rhaetian, obsessively referred to the Kössen Beds as the standard of the classical Rhaetian, as it was defined by Gümbel in 1859. Although even he insisted repeatedly that the time-stratigraphic units, of which the stage is the fundamental category, are based on ammonoid zones, and these should be defined by their basal boundary in a stratotype, Tozer a priori rejected the Rhaetian as a distinct stage, instead of calling for a valid stratotype for it in the European Alpine Triassic. Furthermore, when Urlichs (1972) found that *Rhabdoceras suessi*, then the nominal index fossil for the Upper Norian (Sevatian s.l.), occurs in the lower part of the Kössen Beds, Tozer claimed that the Sevatian and the classical Rhaetian overlap more or less in their scope in the Alpine Kössen stratotype, by sharing common ammonoid faunas. Finally, Tozer (1990, p. 11; 1994b, p. 162) concluded that the classic Rhaetian represents only a provincial substage of the Norian, and thus has no place in the hierarchy of standard Triassic stages.

In the light of the actual stratigraphic rules, it is strange to see how at that time the dispute on the status of the Rhaetian was carried out in connection with the Kössen Beds, a purely lithostratigraphic unit, instead of recognizing the Rhaetian as a chronostratigraphic unit.

Ultimately, by adopting the Norian-Rhaetian boundary as defined by Krystyn (1988, 1990) on the basis of the ammonoid sequence in the Zlambach Marls, Golebiowski (1990, p. 30) definitely demonstrated that the Kössen Formation includes both Norian and Rhaetian beds, with *Rhabdoceras suessi* occurring in the lower Rhaetian. As the base of the Kössen Formation is situated somewhere within the Upper Norian without any time-significant fossils below, Golebiowski (1990) and Krystyn (1990) concluded that its base is not suitable as a chronostratigraphic boundary between the Norian and Rhaetian. Thus, for the first time a clear discrimination was made for the Kössen Formation as a lithostratigraphic unit and for the Rhaetian as a chronostratigraphic one; the latter, however, not yet having a proper definition.

The long controversy around the status of the Rhaetian as a stage, substage or unit with no significance in global chronostratigraphy as illustrated in the Figs 4 and 5, ended during the STS Meeting in Lausanne in 1991, when a significant majority of STS members decided to retain the concept of a separate Rhaetian Stage, a decision that was ratified at the STS Meeting in Kyoto on 31 August 1992 (Visscher 1992). Several operational definitions utilizing ammonoids have been used in Europe in the following years to define the base of the Rhaetian, i.e. the base of the *Vandaites stuerzenbaumi* Zone (Krystyn 1988), the base of the *Sagenites quinquepunctatus* Zone (Shevyrev 1991), the base of *Sagenites reticulatus* Zone (Dagys and Dagys 1994), or the base of the ‘*Cochloceras* suessi’ Zone (Kozur...
In North America, Carter (1993) revived the Rhaetian, with its base being marked by a strong change in radiolarians that occurred in close temporal proximity to the appearance of the ammonoid Paracochloceras. Afterwards, Orchard and Tozer (1997) selected the base of the Paracochloceras amoenum Zone to define the Norian/Rhaetian boundary, thus ultimately reinstalling the Rhaetian as the uppermost stage in the North American Triassic time scale. The stage status of the Rhaetian is now currently installed in the North American Triassic timescale (e.g. Orchard et al. 2007; Carter and Orchard 2007; Katvala and Stanley 2008; Caruthers and Stanley 2008; McRoberts 2010).

Following the STS 2003 Executive Notes (Albertiana 28), the lowest occurrence of the ammonite Cochloceras/Paracochloceras has officially been nominated as a proxy for an internationally agreed Norian/Rhaetian boundary, with possible GSSP candidates in key sections in Austria, British Columbia (Canada), and Turkey (Ogg 2004a–b).

Further studies in the Northern Calcareous Alps have been focused on the pelagic facies in the Hallstatt Basin with the aim to identify and define a Rhaetian stratotype reliable enough to fulfill the necessary requirements to define chronostatigraphic units achieving general consensus for a basal boundary supported by multiple proxies (Walsh et al. 2004). Results published by Krystyn and Kuerschner (2005), Krystyn et al. (2007a, b), Krystyn (2008a, b) have demonstrated the faunistic and biochronologic significance of the Steinbergkogel section near Hallstatt, in the Austrian Salzkammergut region, as a GSSP for the base of the Rhaetian Stage. In terms of the newly gained, detailed ammonoid biochronology, the Norian–Rhaetian boundary may be defined by the disappearance (LO) of the ammonoid genera Metasibirites and Sagenites s.l. (with lateral nodes) or by the appearance (FO) of Paracochloceras suessi and Sagenites s. str., while in terms of pelagic bivalve biochronology the same boundary is marked by the worldwide disappearance of Monotis salinaria/subcircularis in low and mid-paleolatitudes and M. ochotica group in the Boreal Zone.

However, by allocating the Paracochloceras suessi Zone to the Rhaetian Stage, it results that the Sevatian Substage of the classic Norian Stage in the Alpine Triassic time scale is now split in two distinct parts, whereby the Sevatian 2, with the ammonoid Paracochloceras as a biostratigraphic guide, becomes the equivalent of the Lower Rhaetian. As the chronostratigraphic nomenclature is essentially a matter of consensus, to avoid further conceptual and nomenclatural misunderstandings that can plague stratigraphers, it is necessary, as in many other cases in the Geologic Time Scale, when the GSSP levels defining stages have necessitated a revision of the historical usage (Ogg 2004a), that the STS
should limit the Sevatian only to the Upper Norian in the sense of the actual Triassic time scale standard. This is already given, but not explicitly stated, by Krystyn et al. (2009), Lucas (2010) and Balini et al. (2010).

In summary, after more than 150 years of long-lasting controversy over the scope, content, acceptance or refusal of the Rhaetian, it is now unanimously accepted as a distinct stage for the uppermost Triassic having a GSSP candidate for its basal boundary in the Steinberkogel section that exposes a pelagic basin facies of the red and gray Middle Norian to Lower Rhaetian Hallstatt Limestone, and having a highly resolved ammonoid chronology.

**Paleobiogeography**

The geographical distribution of *Rhabdoceras suessi* has been formerly summarized and mapped by Wiedmann (1973), Tozer (1980b–c, 1982a) and Shevyrev (2005). We present here an up-to-date worldwide distribution map, on both present-day and Triassic geographic coordinates, including all occurrences recorded in the published papers (Fig. 6).

As shown by the distribution map, the heteromorphic ammonoid *Rhabdoceras suessi* occurs mainly along the Pacific margins of North and South America, in numerous locations along the Alpine–Himalayan orogenic belt, and also has isolated occurrences in Indonesia and Northeast Asia. The ammonoid *Rhabdoceras* had a pandemic distribution during Late Triassic (Late Norian and Rhaetian) time in low- and mid-paleolatitude faunal provinces along the eastern margin of the Panthalassa (paleo-Pacific Ocean) and also in the Tethys Seaway, this distribution being constrained by other groups of biogeographically significant macrofossils. This heteromorphic ammonoid did not inhabit the Boreal and Notal provinces.

The most spectacular, and also the most intriguing, occurrences of *Rhabdoceras* are those in the North American Cordillera, where they extend over a broad latitudinal range, which is not reflected in the original Triassic biogeography, and is the consequence of the complex accretionary and post-accretionary tectonics.
First record of Rhabdoceras suessi (Ammonoidea) from the Transylvanian Triassic Series
that affected the western North American margin. A large amount of varied data, paleontological, stratigraphic, paleogeographic, biogeographic, paleomagnetic and tectonic, have contributed to the deciphering of the terrane puzzle of the North American Cordillera (e.g. Howell et al. 1985; Haggart et al. 2006; Blodgett and Stanley 2008).

**Pacific margins of North and South America**

Along the Pacific margins of North and South America, from Alaska to Peru, the heteromorphic ammonoid *Rhabdoceras suessii* has known occurrences in both craton-bound Upper Triassic strata and in those of the American Cordillera terranes, many of them being reported from the accreted terranes.

Although the occurrences of *Rhabdoceras* do not provide positive evidence by itself for the paleolatitude assessment and displacement of the various American Cordilleran accreted terranes, the intrinsic character of the co-occurring Upper Triassic faunas, which include various groups of biogeographically significant biotas, ammonoids, monotids and reef biotas, is suggestive for its occurrence in low and middle paleolatitudes.

An obvious paleolatitudinal control existed on the distribution of different Upper Triassic ammonoid and monotid faunas from different segments of the North American cratonic margin and the Western Cordillera (Westermann 1973; Nichols and Silberling 1979; Tozer 1980c, 1982a, 1984; Silberling 1985; Silberling et al. 1997). Various fossil biotas give precious insight into the Upper Triassic marine biogeography of the continental shelf along the western margin of the North American craton, much of which was subsequently obscured by the complex accretionary tectonics of Triassic terranes (e.g. Tozer 1982a; Stanley 1982; Silberling 1985; Blodgett and Stanley 2008).

In the Western Cordillera and Arctic North America, Upper Triassic ammonoid and monotid faunas are apparently distributed according to original paleolatitude in rocks depositionally or sedimentologically related to the North American craton. The regional differences among North American Upper Triassic ammonoid and monotid faunas provide a good basis for paleobiogeographic and tectonostratigraphic terrane analysis. Distinct ammonoid and monotid faunas are recognized on the basis of their mutual occurrence or exclusion of certain of the taxonomic groups, and these have discrete geographic distribution. Paleomagnetic control on the paleolatitudes of the accreted terranes of the North Pacific margin generally corroborates the assumption that latitude was the primary biogeographic control. Tozer (1982a), Silberling (1985) and Silberling et al. (1997) segregated craton-bound ammonoid and monotid faunas of broadly different paleolatitudes in the Northern Hemisphere. Inboard of the Phanerozoic accreted terranes, exposures of craton-bound, or craton-related, fossiliferous marine Upper Triassic rocks from western Nevada, the Rocky Mountain Foothills of western Canada, Arctic Alaska and the Canadian Arctic Islands (Sverdrup
allow comparisons between, respectively, low, low-middle, middle-high and high, northern paleolatitude faunas.

Comparison between the North American craton-bound Monotis faunas and those of the Western Cordilleran terranes indicates that all of the Monotis-bearing terranes were paleoequatorial in latitude during Late Triassic time. Paleolatitudinal distribution of the Upper Triassic ammonoids and of the different species of Monotis varied, and thus they provide important paleogeographic constraints for interpreting the displacement histories of the various Western Cordilleran accreted terranes. Large-scale displacement of the accreted terranes is evidently required to explain the present distribution of the Upper Triassic ammonoid and monotid faunas, and it represents a major constraint in assessing the paleobiogeographic distribution of the heteromorphic ammonoid Rhabdoceras in the eastern part of the Panthalassa.

**North American craton.** The western margin of the North American craton preserves autochthonous and para-autochthonous marine Triassic, where three faunal provinces have been distinguished by Tozer (1982a) on the basis of their diagnostic fossils, and designated by their present-day latitude as the low, middle and high paleolatitude provinces. From south to north, these paleolatitudinal provinces are in their approximate hemispheric position along the North American Pacific craton margin. Low-paleolatitude faunas occur in the Triassic strata of the para-autochthonous terranes in the western Great Basin of western Nevada, while mid- to high-paleolatitude faunas are found in the Upper Triassic craton-bound strata of northeastern British Columbia and Arctic Canada, respectively.

The province now at low latitude has intrinsic Upper Triassic characteristics, such as reefs and reef-like buildups, suggestive of deposits in warm water. These are absent in the province now at higher latitudes, suggesting that their faunas inhabited cooler waters, so these provinces more or less match the primary Triassic paleolatitudes (Tozer 1982a). In cratonic North America the occurrence of Rhabdoceras suessi is recorded only in the middle and low paleolatitude provinces, in the craton-bound Upper Triassic strata in northeastern British Columbia in Canada, and in the para-autochthonous strata of western Nevada in the United States, and in northwestern Sonora in Mexico, respectively (Fig. 7).

In northeastern British Columbia, the occurrence of Rhabdoceras suessi is mentioned from the Cordilleranus and Amoenum Zones (Figs 6 and 7, Locs 1–2).


**Loc. 2 –** Mount Ludington, *Monotis* beds, Pardonet Formation (Tozer 1967, pp. 54–55; 1979, p. 127, pl. 16.1, figs 8a–c; 1982b, p. 387; 1994a, pp. 45, 265; pl. 144, figs 5–8, pp. 331–332, 345); Cordilleranus Zone.

Both localities are in the Eastern Belt of the Canadian Cordillera, which adjoins and is essentially autochthonous with respect to the North American craton (Tozer 1982a, 1994a). This region is the only one in western North America where
Fig. 7
Sketch map of Western North America showing the distribution of *Rhabdoceras suessi* as discussed in text. Craton-bound occurrences of middle paleolatitude: Locs 1–2 – northeastern British Columbia; Craton-related occurrences of low paleolatitude: Locs 3–7 – western Nevada; Loc. 8 – northwestern Sonora, Mexico; Occurrences in accreted terranes of North American Cordillera: Peninsular, Loc. 9 – Puale Bay, Alaska; Stikinia, Loc. 10 – southern Yukon, Loc. 11 – southern British Columbia; Southern Wrangellia, Locs 12–14 – Vancouver Island, Loc. 15 – Queen Charlotte Islands; Eastern Klamath, Loc. 16 – Brock Mt; Northern Sierra Nevada, Loc. 17 – Sierra Nevada. DF – Denali Fault, TF – Tintina Fault, MS – Mojave–Sonora megashear. Terrane map compiled from Silberling (1990), Senowbari-Daryan and Stanley (2009), and Blodgett and Frýda (2001b)
Rhabdoceras suessi occurs in sequence within the Cordilleranus and Amoenum Zones, and this served for Tozer (1967, pp. 39, 55) to divide the former Upper Norian Suessi Zone into two parts, i.e. the Lower Suessi Zone, and the Upper Suessi Zone that overlie Monotis (P) subcircularis-bearing strata. The Monotis fauna which is well documented in the Upper Triassic cratonic shelf of northeast British Columbia (Westermann and Verma 1967; Tozer 1967, 1979, 1982a–b, 1994a), indicates northern, mid- to high-paleolatitudes (Silberling 1985; Silberling et al. 1997). In the Peace River area, beds with Monotis (P) subcircularis and M. (Entomonotis) ochotica, which are correlatives of the Upper Norian Cordilleranus Zone, overlie M. (Eomonotis)-bearing strata of the late Middle Norian Columbianus Zone. The Peace River Foothills represent the southernmost occurrence of M. (Eomonotis) pinensis on the craton. The presence of M. (Entomonotis) ochotica and the absence of corals and megalodonts are characteristic features for the mid-paleolatitude province. The scleratinian coral and spongiomorph-bearing patch reefs in the Upper Carnian Baldonnel Formation at Pardonet Hill in northeastern British Columbia document the occurrence of Triassic corals on the North American craton margin at ~30° N paleolatitude, the extreme latitudinal edge of the subtropical zone (Zonneveld et al. 2007). Their absence in younger Triassic strata of the Rocky Mountain Foothills could be explained by the northward displacement of the North American plate to higher, mid-latitudes in the Northern Hemisphere during Late Triassic time, which is demonstrated by the paleobiogeographic signature of the monotid fauna.

In western Nevada, Rhabdoceras suessi is mentioned in several localities (Figs 6 and 7, Locs 3–7), most of the occurrences being in the Cordilleranus Zone, and a single occurrence being recorded in the Amoenum Zone.

**Loc. 3** – Northern Clan Alpine Range, Hoyt Canyon Formation (Silberling, in Silberling and Tozer 1968, p. 31); Cordilleranus Zone.

**Loc. 4** – West Humboldt Range, Muttleberry Canyon, Monotis beds (Hyatt and Smith 1905, pp. 17, 26, 33, 203, pl. 56, fig. 26; Smith 1927, pp. 2, 9, 20, 99, pl. 56, fig. 26); Cordilleranus Zone.

**Loc. 5** – Humboldt Range, Buffalo Mountain; Monotis beds, Upper unit of post-Dun Glen strata (Silberling and Wallace 1969, p. 47); Cordilleranus Zone.

**Loc. 6** – Pine Nut Mountains, Oreana Peak Formation (Silberling, in Stewart 1997, p. 32); Cordilleranus Zone.

**Loc. 7** – Gabbs Valley Range, Gabbs Formation, Nun Mine Member (Muller and Ferguson 1939, p. 1605; Silberling and Tozer 1968, p. 31; Laws 1982; Taylor et al. 1983); Amoenum Zone.

The Triassic in the first two localities are in the Jungo terrane, while those in the third locality belong either to the Jungo or the Golconda terrane. The Triassic of the last two localities are in the Pine Nut and Paradise subterranees, respectively, both being included in the Walker Lake terrane (Silberling 1990). All these terranes and subterranees are regarded as belonging to a tectonically disrupted continuation of the Mesozoic continental margin and unlike truly allochthonous terranes they are para-autochthonous, and thus are not exotic with respect to the North American craton at about their present latitude (Silberling 1985; Lupe and Silberling 1985).
In the Cordilleranus Zone of these localities, *Rhabdoceras suessi* occurs together with *Monotis (Monotis) alaskana* Smith, *M. (M.) haueri* Kittl, *M. (Pacimonotis) subcircularis* Gabb and the hydrozoan *Heterastridium*. In terms of the monotid biogeography, *M. (M.) alaskana* is considered a biogeographic hallmark of low paleolatitudes. Other significant biogeographic evidence for an originally low-paleolatitude deposition of the Upper Triassic strata in the Nevadan craton-bound terranes is provided by the Middle Triassic pteriomorphian bivalves and scleractinian corals from the Augusta Mountain Formation, and also the Late Triassic brachiopods, spongiomorphs and wallowaconchid bivalves (Sandy and Stanley 1993; Roniewicz and Stanley 1998; Yancey et al. 2005; Senowbari-Daryan and Stanley 2009).

In *Mexico*, *Rhabdoceras suessi* has its southernmost known occurrence in the Western Cordillera (Figs 6 and 7, Loc. 8).

**Loc. 8** – Sierra del Álamo, northwestern Sonora, Antimonio Formation (González-León et al. 2000, pp. 492–494, text-fig. 5.8–10); Crickmayi Zone.

An Upper Triassic shallow-water, reef-like invertebrate fauna, including calcified sponges, spongiomorphs, corals, along with the hydrozoan *Heterastridium*, ammonoids, wallowaconchid bivalves, suggestive of a tropical-paratropical climatic zone, occur within a biostromal limestone in the lower member of the Antimonio Formation (Stanley et al. 1994; Stanley and González-León 1995; Goodwin and Stanley 1997). For the Cordilleran region the Antimonio fauna shows its closest biogeographic ties with those of craton-bound Norian strata of para-autochthonous North American terranes in the Great Basin of west-central Nevada (Luning Allochthon). Middle Norian gastropod faunas of the Antimonio Formation were noted by Blodgett and Frýda (2001a) and Frýda and Blodgett (2003) to be nearly identical to those of western Nevada, and they suggested a single province, the "Nevada-Sonora", to encompass them. Paleobiogeographic links with Nevada appear stronger than with Cordilleran terranes of the United States or Canada. To explain stratigraphic and paleontological similarities between west-central Nevada and northwestern Sonora, Stanley and González-León (1995) postulated that the Antimonio terrane could have been tectonically displaced southward along the Mojave-Sonora megashear, by as much as 1000 km, into its present-day position in northwestern Sonora, by left-lateral transcurrent faulting along the truncated Mesozoic edge of the North American craton, from original depositional settings in the southwestern United States. The Antimonio para-autochthonous terrane appears to be a detached portion of the Cordilleran miogeocline that remained physically in contact with the North American craton (Yancey et al. 2005).

**North American Cordillera.** Most of the known occurrences of *Rhabdoceras suessi* in North America, as plotted in Figs 6 and 7, are reported from the Western Cordillera of North America, which represents a belt of fault-bounded, accreted or displaced (also referred to as allochthonous, suspect or exotic) tectono-stratigraphic (also referred to as lithotectonic) terranes and subterranes (e.g.
Coney et al. 1980; Jones et al. 1983, 1986, 1987; Saleeby 1983; Howell et al. 1985; Monger and Berg 1987; Silberling et al. 1984, 1992; Gabrielse et al. 1991; Nokleberg et al. 1994; Dickinson 2004) that extends from Alaska to Mexico. More than 20 accreted terranes with marine Triassic rocks became amalgamated during the Jurassic, prior to Cretaceous accretion to the North American continental margin (Tozer 1982a), in a tectonic collage of a great structural complexity, most of them with geologic histories independent of the craton and also of each other. Since their accretion to North America, extensive right-lateral transcurrent faulting further modified the primary configuration and relationships of these terranes and dispersed them from their original latitudes to higher northern latitudes along the western edge of the North American craton. These tectonic complexities complicate correlation and matching of the terranes, as well as the reconstruction of their pre-accretionary paleogeography.

Biogeography is a powerful tool for interpreting the paleogeographic position of the accreted terranes and for assessing their large-scale displacements within the North American Cordillera. Taxonomic studies and biogeographic interpretation of different fossil biotas help to elucidate relations among accreted terranes and to constrain their past geographic positions over time with respect to the craton, thus being of utmost utility in unraveling the tectonic history of the North American Cordillera (e.g. Silberling and Jones 1983; Carter et al. 1991; Haggart et al. 2006; Blodgett and Stanley 2008). To test paleogeographic and tectonic hypotheses, fossil evidence in conjunction with paleomagnetic data must be considered to result in a more precise estimate of the origin of the allochthonous terranes, as well as the timing of their accretion to North American craton.

Most of the Triassic faunas throughout the North American Cordilleran accreted terranes include fossils diagnostic for the low-paleolatitude province defined on the North American craton. All are now north of the craton-bound occurrences in the Clan Alpine and Gabbs Valley ranges, in western Nevada. Some are now aligned latitudinally with the mid-paleolatitude province on the craton in western Canada. In Alaska and Yukon they are about 3000 km north of their counterparts on the North American craton and about 1500 km north of the mid-paleolatitude province in British Columbia (Tozer 1982a).

The significance of various Upper Triassic faunas in assessing the former paleogeographic position of displaced terranes has been highlighted by numerous authors (e.g. Westermann 1973; Tozer 1970, 1971, 1982a, 1984, 1994a; Stanley 1982; Newton 1988; Silberling 1985). The ammonoids and monotid bivalves are the most investigated among the biogeographically significant biotas for the Late Triassic paleogeography of the Cordilleran accreted terranes (Tozer 1982a, 1994a; Silberling 1985; Silberling et al. 1997). Scleractinian coral, spongiomorph and sponge-dominated reef biota represent the most significant fossil group for assessing the paleogeographic signature of the accreted terranes. Upper Triassic Dachstein-type, massive tropical reefs, and coral-rich biostromal
and patch-reef buildups occur within island-arc settings of many of inboard displaced terranes of the North American Cordillera, such as in the Chulitna terrane in Alaska, the Alexander, Wrangellia, Stikinia and Quesnellia terranes in Canada, the Wallowa and Eastern Klamath terranes in the western United States, and the Antimonio terrane in Mexico (Stanley and Senowbari-Daryan 1986; Reid and Tempelman-Kluit 1987; Goodwin and Stanley 1997; Yarnell et al. 1999; Stanley and Senowbari-Daryan 1999; Stanley and Yarnell 2003; Caruthers and Stanley 2008; Senowbari-Daryan and Stanley 2009). The reef biota, together with wallowaconchid bivalves (Yancey et al. 2005), and gastropods (e.g. Blodgett et al. 2001; Blodgett and Frýda 2001b; Nuetzel et al. 2003), provide compelling biogeographic evidence for a low-paleolatitude origin of these terranes and indicate tropical-subtropical climate regimes in the eastern region of the Panthalassa Ocean. The spherical, planktonic hydrozoan *Heterastridium conglobatum* Reuss, 1865, a common associate of *Monotis* faunas in the Upper Norian Cordilleranus Zone, is also noteworthy because of its biogeographic significance. It is abundant in a large number of accreted terranes and subterranes, i.e. Chulitna, Peninsular, Alexander, Wrangellia, Susitna, Farewell (Nixon Fork subterrane), Quesnellia, and Antimonio, where it is often closely associated with strata bearing other warm-water elements such as scleractinian corals, spongiomorphs, etc. (Silberling and Tozer 1968; Tozer 1982a, 1994a; Silberling et al. 1997; Stanley and González-León 1995; González-León et al. 1995; Blodgett and Clautice 2000; Katvala and Stanley 2008). All these fossil biotas, occurring in Upper Triassic strata of the tectonostratigraphic terranes accreted along the North American continental margin, show that the Western Cordillera contains shallow-water carbonate buildups, many of which once rimmed volcanic oceanic islands situated in the equatorial region of eastern Panthalassa (paleo-Pacific Ocean) during Late Triassic time.

The wide latitudinal range in terms of present-day geographic distribution (not reflective of their original tropical origin) of all these Upper Triassic biotas in the accreted terranes of the Western Cordillera, express the post-Triassic, northward, large-scale tectonic displacements of these terranes with respect to the contemporary non-accretionary occurrences on the North American craton, as earlier pointed out by Tozer (1982a), Stanley (1982) and Silberling (1985).

In regards to the broad latitudinal occurrences of *Rhabdoceras suessi* in the accreted terranes of the Western Cordillera and their paleobiogeographic signature, this heteromorphic ammonoid shares a low-paleolatitude origin in common with the coevally-occurring biotas.

In the Western Cordillera of Alaska, the only known occurrence of the heteromorphic ammonoid *Rhabdoceras* is reported from southwestern Alaska (Figs 6 and 7, Loc. 9).

*Loc. 9* – Alaska Peninsula, Puale Bay, Kamishak Formation (Pálfy et al. 1999, p. 1538), Peninsular terrane, Chignik subterrane; Cordilleranus Zone.

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This is the northernmost occurrence of *Rhabdoceras suessi* in the accreted terranes of the North American Cordillera. It co-occurs in the Kamishak Formation with *Monotis (Pactimonotis) subcircularis* Gabb, *Monotis (Monotis) alaskana* Smith, *M. (Entomonotis) cf. M. (En.) ochotica densistriata* (Tellier) and the hydrozoan *Heterastridium* (Grant-Mackie and Silberling 1990; Silberling et al. 1997; Blodgett 2008). Paleomagnetic data, the lithology and the paleobiogeographic affinities of the various Late Triassic faunas found in the Kamishak corroborate its low paleolatitude in a definite northern hemisphere location, indicating that the Peninsular terrane was situated in a tropical to subtropical setting during the Late Triassic (Wilson et al. 1985; Detterman 1988, 1996; Blodgett 2008).

In the *Western Cordillera of Canada*, the accreted terranes are found in both the Intermontane and Insular belts, and all are interpreted as indicating that the Triassic rocks are allochthonous with respect to the North American craton. They show signs of having been deposited in relatively warm water at a lower paleolatitude than contemporary rocks now at the same present-day latitude in the cratonic Eastern Cordillera (Tozer 1970, p. 635; 1982a; 1994a, p. 20).

In the Intermontane Belt of the Cordillera, the occurrence of *Rhabdoceras suessi* is reported from both the Cordilleranus and Amoenum Zones (Figs 6 and 7, Locs 10–11).

**Loc. 10** – Southern Yukon, Lewes River, Laberge area, Formation D, Lewes River Group (Tozer 1958, p. 15; 1963, pl. 12, figs 18–19; 1967, pp. 79–80, pl. 10, figs 6–7; 1970, p. 634, pl. 18, fig. 18a–b; 1994a, p. 265, pl. 144, figs 3–4, p. 303); Cordilleranus Zone.

**Loc. 11** – Southern British Columbia, Castle Peak-Tyaughton Creek area and southern Coast Mountains, *Cassianella* Beds, Tyaughton Group (Tozer 1967, pp. 75–80; 1979, p. 127, pl. 16.1, fig. 10; 1994a, p. 265, pl. 147, figs 1–2, p. 322; Umhoefer and Tipper 1998, p. 21); Amoenum Zone.

Structurally the Triassic rocks of the Lewes River are included in the Stikine terrane while the Triassic rocks from Tyaughton Creek are uncertainly assigned either to the Stikine terrane by Tozer (1982a, p. 1082), to the Methow-Tyaughton terrane by Monger and Berg (1987) and Silberling et al. (1997, p.12), or to the Cadwallader terrane by Umhoefer and Tipper (1998) and McRoberts and Blodgett (2000, p. 58). The last two of these terranes could be fragments of the larger Stikine terrane. In the northern part of Stikinia, which relative to the North American craton lies in an inboard setting, only *M. (P.) subcircularis* and *M. (M.) haueri* are known to occur, while species of *M. (Entomonotis)*, such as those that characterize craton-bound Late Norian Monotis faunas farther inland at about the same present-day latitude in north-eastern British Columbia, are unknown (Silberling et al. 1997). In the same stratigraphic succession as that containing the *Monotis* faunas, one of the few developments of paleoequatorial Dachstein-type Upper Triassic coral reefs in North America (Stanley and Senowbari-Daryan 1986; Reid and Tempelman-Kluit 1987; Yarnell et al. 1999) is displayed at Lime Peak in southern Yukon, the other being in the Wallowa terrane of eastern Oregon. Wallowaconchid megalodontoid bivalves are associated with coral-rich biotas in both terranes, indicating tropical-subtropical climate regimes in the eastern region of the Panthalassa Ocean from where these terranes originated (Yancey et
al. 2005). The implications of the coral reefs for appreciable northward displacement of the Stikinia terrane relative to the craton was first recognized by Tozer (1970, 1982a).

In the Insular Belt of the Cordillera, *Rhabdoceras suessi* occurs in the Vancouver and Queen Charlotte Islands, in Cordilleranus, Amoenum and Crickmayi Zones (Figs 6 and 7, Locs 12–15).

**Loc. 12** – Southern Vancouver Island, Cowichan Lake, Cape Flattery area, Sutton Formation (Tozer 1967, pp. 78–79; 1979, p. 128, pl. 16.1, fig. 9a–b; 1980c, pp. 854–855; 1994a, p. 265, pl. 147, fig. 3; p. 302); Crickmayi Zone.


**Loc. 15** – Queen Charlotte Islands; *Monotis* beds, Peril Formation (Tozer 1980c, pp. 854–855); Cordilleranus Zone.

On Vancouver Island, *Rhabdoceras suessi* occurs in sequence within the Cordilleranus, Amoenum and Crickmayi Zones. This is the first North American locality where it was proved that *Rhabdoceras* ranges up into the latest Triassic Crickmayi Zone (Tozer 1979, p. 128), although its co-occurrence here with *Choristoceras* had been earlier noticed and considered unusual (Tozer 1967, p. 78). The Triassic rocks on Vancouver and Queen Charlotte islands are located in the southern Wrangellia terrane (e.g. Tozer 1982a, p. 1082). *Monotis* fauna, with *M. (Pacimonotis) subcircularis* and *M. (M.) alaskana*, is indicative of low paleolatitudes (Tozer 1982a; Silberling 1985; Silberling et al. 1887). This is also corroborated by the paleobiogeographic signature of the Rhaetian scleractinian coral fauna described by Caruthers and Stanley (2008) from the Cowichan Lake region.

In the **Western Cordillera of the United States**, *Rhabdoceras*-bearing allochthonous terranes are present in northern California, with known occurrences in the Cordilleranus Zone (Figs 6 and 7, Locs 16–17).

**Loc. 16** – Brock Mountain, Shasta County, Brock Shale (Hyatt and Smith 1905, pp. 16, 33, 203, Smith 1927, pp. 2, 4, 20, 99); Cordilleranus Zone.

**Loc. 17** – Sierra Nevada, Genesee Valley, Plumas County, *Monotis* beds (Hyatt and Smith 1905, pp. 26, 33, 203; pl. 47, figs 13–15; Smith 1927, pp. 2, 8, 20, 99; pl. 47, figs 13–15); Cordilleranus Zone.

The first occurrence is located in the Eastern Klamath terrane, akin to the inboard Quesnel superterrane (Wyld et al. 2006), while the second is located in the Northern Sierra Nevada terrane, or possibly in the part of the Eastern Klamath terrane structurally juxtaposed with the Northern Sierra terrane at its northern end (Silberling, pers. commun.). The *Monotis* fauna and reef biota of the Quesnella, which like the Stikinia lies in an inboard setting relative to the North American craton, show that these accreted island arc terranes were situated within tropical-subtropical paleolatitudes of the Panthalassa Ocean (Grant-Mackie and Silberling 1990; Stanley and Senowbari-Daryan 1999; Senowbari-Daryan and Stanley 2009).
South American Cordillera. The heteromorphic ammonoid *Rhabdoceras suessi* has known occurrences in the Andes Mountains of Colombia and Peru (Fig. 6, Locs 18–19).

**Loc. 18** – Payandé Formation, Ortes Payandé, Central Cordillera, Colombia (Geyer 1973, p. 24; Geyer 1979, p. 352); Cordilleranus and/or Amoenum Zones.

**Loc. 19** – Aramachay Formation, Pucará Group, Utcubamba Valley, Levanto, northern Oriental Cordillera, Peru (Steinmann 1909, p. 617; Prinz and Hillebrandt 1994, pp. 35, 38; Hillebrandt 1994, p. 299, pl. 1, fig. 17); Amoenum Zone.

Specimens of *Rhabdoceras* sp. *ex gr. suessi* Hauer have been recorded along with *Metasibirites annulosus* Mojsisovics, *M. tolymensis* Geyer and *Monotis* (Pacimonotis) *subcircularis* Gabb from Colombia, while in Peru *Rhabdoceras* sp. and *Metasibirites annulosus* were found above *Monotis* (Pacimonotis) *subcircularis* Gabb. This is the only known *Monotis* species of the South American Cordillera (Westermann 1973; Tozer 1980c), and Silberling (1985) questioned whether its occurrences here are within accreted terranes. Both Mesozoic epicontinental series, the "Oriente Andino" of Colombia and the Mesozoic Pucará Basin in Peru define a pre-Andean paleogeography (Geyer 1979; Rosas et al. 2007). Although collisional docking of allochthonous terranes could have triggered local tectonism, it is believed that terrane accretion has not played a critical role in the Andean orogenesis (Dalziel and Forsythe 1985). The paleobiogeographic signature of the Upper Triassic sponges, corals, spongiomorphs and other associated shallow-water biotas from the Pucará Group is typical for low, southern paleolatitudes in the eastern Panthalassa Ocean (Stanley 1994).

Pacific margins of Northeast Asia

A remote occurrence of the heteromorphic ammonoid *Rhabdoceras* in Arctic Siberia is known from Western Chukotka (Fig. 6, Loc. 20).


Representatives of *Rhabdoceras*, with *Rhabdoceras* sp. and *Rhabdoceras boreale*, have been reported in the northeastern part of Northeast Russia by Afitsky (1965/1966, 1970). The Late Norian *Monotis* fauna shows a mixed character, with the *Monotis* (Entomonotis) *ochotica* group, *M. (En.) pachypleura*, and *M. (En.) jakutica* commonly typifying high and mid-paleolatitudes, along with low-paleolatitude monotids such as *M. (M.) alaskana* and *M. (Pacimonotis) subcircularis* (Bychkov 2000). The ammonoid assemblage includes Tethyan-type haloritids and long-ranging, cosmopolitan leiostracan genera. Hence, the species etymology for *Rhabdoceras boreale* Afitsky, 1965, does not properly reflect its occurrence at a high, northern paleolatitude during the Late Triassic, but its present-day occurrence at a high, northern latitude. On the Circum-North Pacific tectonostratigraphic terrane map of Nokleberg et al. (1994, p. 56) and Parfenov et al. (2009, p. 23) the Triassic volcano-sedimentary sequence from the upper reaches of the Bol’shoy

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Anyuy River is allocated to the Yarakvaam island arc terrane of the Kolyma-Omolon Superterrane. This superterrane consists of a tectonic collage of cratonic, passive continental margin, island arc and ophiolite terranes accreted to the northeast Verkhoyansk (North Asian) craton margin in Late Jurassic to Early Cretaceous time. The *Monotis* fauna of the Yarakvaam terrane, where the Middle Norian *Monotis (Eomonotis) scutiformis* Zone is followed by Late Norian monotids of the *Monotis ochotica* group (Bychkov and Solov'ev 1992), is comparable in its taxonomic composition with the mid-paleolatitude *Monotis* fauna from the Nixon Fork subterrane of the Farewell terrane in west-central Alaska, as described by Silberling (1985), Grant-Mackie and Silberling (1990) and Silberling et al. (1997). Both terranes also have in common the northernmost occurrence of the hydrozoan *Heterastridium* in the accreted terranes of the North American Cordillera and Northeast Asia, respectively.

**Alpine–Himalayan–Indonesian orogenic belt**

In the Neotethyan Alpine–Himalayan–Indonesian orogenic belt, the heteromorphic ammonoid *Rhabdoceras suessi* is discontinuously recorded from Alpine Europe and Central Asia, from Sicily, the Alps, the Carpathians, the Hungarian Transdanubian Range and the Balkans, and farther east the Pamirs and, after a large geographic gap, from the Moluccan Archipelago and Timor Island in Southeast Asia, along more than 20,000 km of Tethyan margin. Most of the occurrences are from Hallstatt limestone, which for the most part is allochthonous. An original distribution within 30° of the Triassic equator for the Tethyan ammonoid and monotid bivalve faunas is generally accepted and is corroborated by the reef biotas, some internal paleomagnetic control and by the paleolatitudinal constraints provided by the continental blocks to the north (Eurasia) and south (Gondwana) of the Alpine–Himalayan orogenic belt (e.g. Tozer 1980b, 1982a; Silberling 1985; Krystyn and Piller 2000). In comparison with the broad latitudinal range of occurrences of *Rhabdoceras suessi* along the western North American margin, resulting from complex post-Triassic northward tectonic displacements, the geographic distribution of this ammonoid in the different regions of the Alpine-Himalayan-Indonesian orogenic belt remained closely confined within the belt, although the tectonostratigraphic units hosting it were also involved in large-scale post-Triassic movements.

**Alpine Europe.** The most numerous occurrences of *Rhabdoceras suessi* in Alpine Europe are known from the Northern Calcareous Alps in Austria (Fig. 6, Locs 21–29). This heteromorphic ammonoid is known from varied facies: pelagic facies of Hallstatt Limestone, basinal marly facies of Zlambach Beds, shallow-water facies of Dachstein carbonate platform, and mixed intraplatform facies of the Kössen Beds. Following the ammonoid biozonation for the uppermost Triassic of Alpine Europe, the biostratigraphic range of *Rhabdoceras suessi* extends from the Upper Norian (=Sevatian 1) into the Rhaetian.

*Loc. 21* – Zlambach Beds, Mühlgraben, Grünbachgraben, Bad Goisern (Kittl 1903, p. 16; Wiedmann
(1972; Bolz 1974; Krystyn 1988); Stuerzenbaumi and Marshi Zones (= Crickmayi Zone).

**Loc. 22** – Kösseen Beds, Weißenlocherbach near Kösseen, Achensee, Lahnwiesgraben near Garmish (Urlichs 1972; Wiedmann 1972; Möstler et al. 1978; Golebiowski 1986, 1990); Stuerzenbaumi and Marshi Zones (=Crickmayi Zone).

**Loc. 23** – Dachstein-Riffkalk, Gosaukamm, and "erratische Blöcke", Falmbergalm near Gosau (Zapfe 1962, p. 348; Zapfe 1965, p. 300, pl. 1, fig. 8; Zapfe 1967, p. 20; Krystyn et al. 2009); Reticulatus Zone (= Amoenum Zone).

**Loc. 24** – Gray Hallstatt Limestone, Steinbergkogel, Hallstatt (Mojsisovics 1893, p. 808; 1902, p. 343; Krystyn et al. 2007a–b; Krystyn 1991, 2008); Quinquepunctatus, Reticulatus and Stuerzenbaumi Zones (= Cordilleranus – lower Crickmayi Zones).

**Loc. 25** – Red Hallstatt Limestone, Scheiblkogel, Bad Aussee, Austria (Gallet et al. 1996, p. 116); Quinquepunctatus Zone (= Cordilleranus Zone).

Beside the above-listed occurrences, which were found in sections of normal stratigraphic succession, *Rhabdoceras suessi* is known from several ammonoid assemblages, described in classical monographs, which came from fissure fillings, some of them with polyzonal ammonoid faunas (Krystyn et al. 1971; Tozer 1967, 1980c).

**Loc. 26** – Fissure with 'Weisser Crinoidenkalk', Steinbergkogel (Mojsisovics 1893, p. 808; 1902, p. 343; Krystyn 2008, p. 95); Middle Rhaetian.

**Loc. 27** – Fissure with *Cladiscites ruber*, Millibrunkkogel (Hauer 1860, p. 125, pl. 2, figs 9–16; Mojsisovics 1893, p. 804; 1902, p. 341); Mixed faunas: Middle Norian to Lower Rhaetian.

**Loc. 28** – Fissure with *Sagenites giebeli*, Lieslingwand (Mojsisovics 1893, p. 803; 1902, p. 804; 1902, p. 341); Mixed faunas: Middle and Upper Norian (=Sevatian 1).

**Loc. 29** – Lens with *Glyphidites docens*, Röthelstein near Aussee (Mojsisovics, 1893, p. 804; 1902, p. 341); Mixed faunas: Middle and Upper Norian (=Sevatian 1).

Several isolated occurrences of *Rhabdoceras suessi* in Alpine Europe are known from Sicily in the southern Apennines, from Hungary in the NE Transdanubian Range, from Slovakia and Romania in the Carpathians, and from Bulgaria in the Balkans (Fig. 6, Locs 30–34).

**Loc. 30** – Formazione Sciacca, Panormide Carbonate Platform, Monti di Palermo, Sicily, Italy (Gemmellaro 1904, p. 76, pl. 18, figs 45-46; Gemmellaro 1923, p. 138; Catalano et al. 1974, p. 1034; Antonelli et al. 1992, p. 163); Cordilleranus Zone.


**Loc. 32** – Hallstatt Limestone, Silická Brezová, Slovakian Karst, Western Carpathians, Slovakia (Kochanová and Kollárová-Andrusovová 1983, p. 577, pl. 12, figs 3, 6, 7, 9); Cordilleranus Zone.

**Loc. 33** – *Monotis*-bearing Hallstatt-type limestone, Ciungi-Timon olistolith, Fundu Moldovei, Eastern Carpathians, Romania (Grădinaru and Sobolev, this paper); Cordilleranus Zone.

**Loc. 34** – Glogova Formation, Luda Kamchia Zone, Kotel, Balkans, Bulgaria (Sachariewa-Kovatschewa 1967, p. 76, pl. 5, fig. 9); Cordilleranus and/or Amoenum Zones.

Most of the above-listed occurrences of *Rhabdoceras suessi* are from the northern margin or central part of the western Tethys, such as those from the Northern Calcareous Alps, Carpathians and Balkans, and the Hungarian Transdanubian Range; only the occurrence from the Panormide Carbonate Platform in Sicily are from the southern part.
Central Asia. East of an extended gap in its occurrence in the Tethyan regions of Middle Asia, various morphotypes of *Rhabdoceras* are known from the Upper Norian of the Pamirs (Fig. 6, Loc. 35).

**Loc. 35** – *Monotis salinaria* beds, southeastern Pamirs, Tajikistan (Kushlin 1965, 1966; Shevyrev 1990, p. 137, pl. 8, fig. 1; Shevyrev 2001, p. 144, text-fig. 23, pl. 61, fig. 6a–c); *Quinquepunctatus* Zone (= Cordillerus Zone).

In the southeastern Pamirs *Rhabdoceras suessi* is reported from a limy-marly sequence in the upper part of the Aktash Series, including several isochronous formations (Nayzatash, Igrimyuz and Kamarutek Formations), where it co-occurs with *Monotis salinaria, Heterastridium conglobatum* and ammonoids indicative of the Upper Norian *Sagenites quinquepunctatus* Zone (Shevyrev 2001; Dronov 2001). The other two morphotypes of the genus *Rhabdoceras* are included in the same ammonoid assemblage, *Rhabdoceras curvatum* Mojsisovics and *Rhabdoceras laeve*, the last species being originally described in this region by Kushlin (1965/1966). The occurrence of *Rhabdoceras* representatives in the Pamirs is as yet the only one reported in shelf deposits on the northern rim of the Neo-Tethys, which was inhabited by low-paleolatitude faunas.

Southeast Asia. The easternmost occurrences of *Rhabdoceras* are in Misool and Timor islands, in southeastern part of the Indonesian Archipelago (Fig. 6, Locs 36–38).

**Loc. 36** – *Nucula* Marl/Lios Member, Bogal Formation, Misool Island, Moluccan Archipelago, eastern Indonesia (Wanner 1910, p. 739; Jaworski 1915, p. 133, pl. 45, figs 14–15; Campbell and Grant-Mackie 2000, p. 249; Hasibuan 2008, p. 324; Hasibuan 2010, pp. 36, 43, fig. 1); *Amoenum* Zone.

**Loc. 37** – Hallstatt Limestone, Noe Bihati (Baun), West Timor, eastern Indonesia (Tatzreiter 1981, p. 13); *Cordillerus* Zone.

**Loc. 38** – Gray Limestone of Aliambata, Timor-Leste (East Timor) (Tozer 1971, p. 1020; Tozer 1980c, p. 855); *Cordillerus* Zone.

Misool Island is located in the northern Banda Arc province, where the Triassic rocks are included in the para-autochthonous sequence of the Salawati Basin, while Timor Island is located in the forearc of the southern Banda Arc province, both of these tectonostratigraphic provinces being interpreted as belonging to Gondwanan eastern Indonesia (e.g. Charlton 2001). The occurrence of *Rhabdoceras suessi* in West Timor, within an extremely rich Tethyan-type ammonoid assemblage along with the planktonic hydrozoan *Heterastridium*, is in a Hallstatt-type condensed limestone, occurring as isolated blocks in the so-called Allochthonous Series of Sonnebait, which is included in the tectonic mélangé of the accretionary prism of the Banda Arc (Martini et al. 2000). The allochthonous pelagic Triassic of Timor, which facially is definitely distinct from that of the Australian margin, represents obducted remnants of Hallstatt-topped seamounts littered in the south-eastern Tethys Seaway, where it reached the Panthalassa Ocean. The occurrence of *M. (Pacimonotis) subcircularis* in Upper Norian strata in several microcontinents (Seram, Timor, Roti, etc.) in eastern Indonesia (Campbell and Grant-Mackie 2000) supports their emplacement at a southern, approximately 30° Triassic paleolatitude in the eastern part of Gondwanaland, a
conclusion that is also supported by the paleobiogeographic signature of the Upper Triassic corals from Timor-Leste (East Timor) (Roniewicz et al. 2005, fig. 9).

**Paleoecology**

In the eastern part of Panthalassa (paleo-Pacific Ocean), *Rhabdoceras* is found in pelagic assemblages, along with thin-shelled monotid bivalves and the planktonic hydrozoan *Heterastridium*, in Cordilleranus Zone deposits on the North American craton margin, and also in many oceanic island arcs. Craton-bound, or craton-related deposits of this age include those from the Great Basin in western Nevada, and especially those of the Pardonet Formation in the Rocky Mountain Foothills of western Canada, from where the most abundant occurrences of this heteromorphic ammonoid are known, in open-marine deposits (Tozer 1970, 1982a, 1994a). On the other hand, the occurrences of *Rhabdoceras* in the Amoenum Zone (Cassianella Beds in southern British Columbia, the Arenaceous Member of Parson Bay Formation in Vancouver Island, and the Nun Mine Member of the Gabb’s Formation in the New Canyon, western Nevada), in the Crickmayi Zone (Sutton Formation in Vancouver Island, and in the Antimonio Formation in Mexico) are all in benthos-related assemblages (Tozer 1970, 1994a; Laws 1982; González et al. 2000), with their most notable abundance being in the Gabb’s Formation in western Nevada. Comparable pelagic and benthos-related biofacies are those from the Cordilleranus and Amoenum Zones in the Pacific Cordillera of South America, such as of the Payandé Formation from the "Oriente Andino" in Colombia (Geyer 1979) and of the Aramachay Formation from the Pucará Basin in Peru (Stanley 1994), and also of the Privalny Formation in Western Chukotka (Bychkov and Solov’ev 1992). Faunal facies changing from pelagic in the Upper Norian to benthos-dominated in the Rhaetian reflects an upward marine shallowing during the end-Triassic in northern Circum-Panthalassa (e.g. Laws 1982; Taylor et al. 1983; González-León et al. 1995; Hallam and Wignall 2000; Lucas et al. 2007).

In the western Tethys, as known from Austrian Northern Calcareous Alps, *Rhabdoceras* inhabited various pelagic and benthonic biotopes: on the outer slope of Bahamian-type Dachstein carbonate platforms, in mixed intraplatform Kössen basins, in Hallstatt facies on pelagic carbonate plateaus, and in marly Zlambach basins, in autochthonous/para-autochthonous assemblages (Zapfe 1967b; Wiedmann 1972, 1973, 1974; Krystyn 1991; Krystyn et al. 2009). Similar biotopes are also found in Sicily, the Hungarian Transdanubian Range, the Carpathians, the Balkans, the Pamir Mts and in southeastern Indonesia. The reported occurrences in fissure-fillings in both Dachstein and Hallstatt Limestone in the Alps must be interpreted as incidental, and not as a normal habitat as inferred by some authors (e.g. Hornung 2005).

As regards the life habits and feeding modes of the Late Triassic heteromorphic ammonoids, they are interpreted as either planktonic or benthic animals (Tozer 1970, 1994a; Wiedmann 1973, 1974; Laws 1982; Wang and Westermann 1993;
There is compelling evidence that the end-Triassic regressive trend had led the heteromorphic ammonoids to change, after the Late Norian, from a planktonic to an epibenthic scavenger-micropredator habit, which is demonstrated by the Rhaetian trophic nucleus in the Gabbs Formation in western Nevada (Laws 1982).

Conclusions

The occurrence of the heteromorphic ammonoid *Rhabdoceras suessi* is for the first time reported here from the Romanian Carpathians, and this record fills a gap in our current knowledge on the distribution of this ammonoid in the Western Tethyan regions.

As shown in the present paper, in the second part of the 1970s *Rhabdoceras suessi* held a privileged position among the uppermost Triassic ammonoids, being nominated and used in North America and Europe as the index fossil of the former Upper Norian Suessi Zone (= *Rhabdoceras suessi* Zone). The remarkable achievements in North American Triassic biostratigraphy that resulted from the outstanding studies carried out by Tozer during second half of 20th century, deposed this ammonoid from its status as an index taxon by the end of the 1970s. A coincident controversial dispute about the status of the Rhaetian as a stage arose during the 1980s. The achievements resulting from studies in the Austrian Alps have reinstalled the Rhaetian as the topmost stage of the Triassic, its base now having a biostratigraphically well-documented standard stratotype. The history of the long debated bio- and chronostratigraphy of the uppermost Triassic is a lesson from which stratigraphers must learn that only a general consensus based on objective data in biostratigraphically well-calibrated stratotypes can contribute to the continuous and endless work to improve the Triassic timescale, bearing in mind at all times that the biostratigraphic record is imperfect and incomplete by its very nature.

Biogeographically, the heteromorphic ammonoid *Rhabdoceras suessi* is a pandemic, long-ranging Late Norian and Rhaetian ammonoid widely dispersed in the low- and mid-paleolatitude faunas of western North and South America, Alpine Europe, Pamirs and southeast Indonesia. The heteromorphic ammonoid *Rhabdoceras suessi* is suitable for worldwide correlations only when it occurs together with age-diagnostic, short-range choristoceratids, or with monotid bivalves and the hydrozoan *Heterastridium*.

The distribution of present-day occurrences of *Rhabdoceras suessi*, together with contemporaneous biotas, shows an intriguingly broad latitudinal range in the Western Cordillera of North America, not representative of their original Late Triassic paleobiogeography. The various allochthonous tectonostratigraphic terranes where this ammonoid occurs were dispersed in the tropical/subtropical belt of eastern Panthalassa, subsequently accreted to and tectonically displaced northward by large-scale post-Triassic faulting to higher latitudes along the
disrupted Mesozoic margin of the North American craton. This Late Triassic ammonoid, along with other coeval fossil assemblages, contributed to the deciphering of the terrane puzzle of the North American Cordillera, and also of other regions, such as Northeast Asia. Triassic biotas appear especially useful for the biogeographic interpretation and paleogeographic analyses of the accreted terranes of the North American Cordillera. The utility of the Triassic fossils for fueling and testing paleogeographic and tectonic hypotheses has greatly contributed to the emerging and growing concepts of the exotic or displaced terrane theory, which in turn helped to explain the anomalies of their actual occurrences.

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