RECENT DEVELOPMENTS ON TRIASSIC STRATIGRAPHY


J. Guex and A. Baud (eds)
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FOREWORD


The technical organization of the meeting was greatly eased by the Geological Museum of Lausanne (Mr E. Thibault), the University and the Institute of Geology (Mrs A. M. Magnenat and L. Dufresne). Several collaborators which are warmly acknowledged contributed to the preparation of the present Memoir: Mr M. Jaboyedoff (Institute of Mineralogy, Lausanne) for redrawing most of the text-figures.

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A. Baud and J. Guex
NEW AMMONOIDS FROM THE TAYLORI ZONE (MIDDLE ANISIAN, MIDDLE TRIASSIC) FROM NORTHWESTERN NEVADA (USA)

H. Bucher, Institut de Géologie, BFSH-2, 1015 Lausanne, Switzerland

Abstract
The biostratigraphic distribution of the Taylori Zone ammonoids is updated and four new species are described. A new subzone is introduced in the uppermost part of the Taylori Zone.

Introduction
Recognition of a distinct ammonoid fauna intercalated between the early middle Anisian Hyatti Zone and the late middle Anisian Shoshonensis Zone (see Silberling and Nichols 1982, Bucher 1992a & b) led to the introduction of the Taylori Zone by Bucher (1988). The present note is an update of the Taylori Zone as originally defined, with illustrations of all subzonal indexes.

Biostratigraphic distribution of the Taylori Zone ammonoids
Index species: Nevadisculites taylori Bucher (1988, Pl. 6, Figs.3-7).
Type locality: Favret Canyon, Augusta Mountains.
The biostratigraphic distribution of the ammonoids of the Taylori Zone is shown on Text-Figure 1. At present time, five subzones have been recognized. All of them are in close stratigraphic succession in Favret Canyon (Bucher 1988, Pl. 7).

Ismidites cf. I. marmarensis Arthaber, Intornites nevadanus (Hyatt and Smith), Nevadisculites smithi Bucher, Ussurites cf. U. arthaberi (Welter) and Sageceras cf. S. walteri Mojsisovics are long ranging forms which are common to the Hyatti, Taylori, and Shoshonensis Zones.

Megaphyllites wildhorsensis Bucher ranges from the Hadley Subzone (Hyatti Zone) up to the Taylori Zone. Acrochordiceras erucosum Arthaber, Eogymnotoceras tuberculatum Bucher, Gymnotoceras praeursor Bucher, and Constrictymnites robertsi Bucher range from the Taylori Zone up to the Shoshonensis Zone.

Platyceococeras favretense Bucher exactly ranges throughout the entire Taylori Zone, without any perceptible morphological change (see Pl. 1, Fig. 14-18).

Nicholsi Subzone
Index species: Pseudodanubites nicholsi Bucher; see Pl. 1, Figs. 21-26.
Type locality: Loc. HB 246, Favret Canyon, Augusta Mountains.
Occurrence: Loc. HB 28, 29, 30, 47, 68, northern Humboldt Range (Fossil Hill Member, Prida Formation). Loc. HB 99, 100, 102, 179, 215, 219, Favret Canyon, Augusta Mountains (Fossil Hill Member, Favret Formation).

Ptychites, Eogymnotoceras and Acrochordiceras of the carolinae-group have their oldest occurrence in the Nicholsi Subzone. Eogymnotoceras janvieri n. sp., Nicholsites parisi n. sp. and the index species are known only from this subzone.
Spivaki Subzone

Index species: *Anagymnotoceras spivaki* (McLear); see Pl. 2, Figs. 19-21.

Type locality: Loc. HB 226, Favret Canyon, Augusta Mountains.

Occurrence: USGS Mesozoic loc. M2822, loc. HB 1, northern Humboldt Range (Fossil Hill Member, Prida Formation). Loc. HB 101, Favret Canyon; loc. HB 197, Muller Canyon, Augusta Mountains (Fossil Hill Member, Favret Formation).

*Anagymnotoceras spivaki* is the only distinctive form that permits distinction of this subzone. *Nevadisculites taylori* has its earliest occurrence in the Spivaki Subzone.

Escheri Subzone

Index species: *Augustaceras escheri* Bucher; see Pl. 1, Figs. 19-20.

Type locality: Loc. HB 175, Favret Canyon, Augusta Mountains.

Occurrence: Loc. HB 224, Bloody Canyon; loc. HB 36, Congress Canyon, northern Humboldt Range (Fossil Hill Member, Prida Formation). Loc. HB 156, McCoy Mine; loc. HB 218, South Canyon, New Pass Range. Loc. HB 105, 163, 164, 165, 173, 176, 185, 189, 200, 216, 227, Favret Canyon; loc. HB 197, Muller Canyon, Augusta Mountains. Loc HB 217, southern Tobin Range (Fossil Hill Member, Favret Formation).

Within the Taylori Zone, the Escheri Subzone is the most frequently encountered fauna. It permits recognition of the Taylori Zone in the southern Tobin Range, the northern Humboldt Range and the New Pass Range, where the it is found in sequence with the Hyatti and Shoshonensis Zones. Ammonoids known only from the Escheri Subzone are *Eogymnotoceras thompsoni* Bucher, *Epigymnites* cf. *E. jollyanus* Diener, *Augustaceras staffordi* Bucher and the index species.

The uppermost part of the Escheri Subzone (locality HB 163) reveals minor changes in faunal composition as indicated in Figure 1. Depressed end-member variants of *Acrochordiceras* have a bituberculate immature stage similar to *A. ericosum* (Arthaber 1896, p. 88, Pl. 7, Fig. 9). They typically have their oldest occurrence in the Escheri Subzone and range further up into the entire Shoshonensis Zone.

Praebalatonensis Subzone

Index species: *Platyceucoceras praebalatonensis* Bucher; see Pl. 2, Figs. 17-18.

Type locality: HB 170, Favret Canyon, Augusta Mountains.

Occurrence: Loc 162, 228, Favret Canyon; loc. HB 221, 232, Muller Canyon, Augusta Mountains. Loc HB 148, southern Tobin Range (Fossil Hill Member, Favret Formation).

*Eogymnotoceras transiens* Bucher and the index species occur exclusively in the Praebalatonensis Subzone. *Gymnotoceras* has his earliest occurrence in this subzone.

Tozeri Subzone

Index species: *Platyceucoceras tozeri* n. sp.; see Pl. 1, Figs. 1-13.

Type locality: HB 229, Favret Canyon, Augusta Mountains.

Occurrence: Loc. HB 98, Favret Canyon; loc. HB 234, Muller Canyon, Augusta Mountains (Fossil Hill Member, Favret Formation). The type locality is placed stratigraphically 3 meters above loc. HB 228 which belongs to the Praebalatonensis Subzone, and about 14 m below the earliest occurrence of ammonoids indicative of the Shoshonensis Zone.
### MIDDLE ANISIAN

#### TAYLORI ZONE

<table>
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#### SUBSTAGE

#### ZONE

- *Subzone*
  - *Pseudodermites nicholai*
  - *Eogymnoceras janvieri*
  - Nicholaiites parsoni
  - Megaplychites widhoeelensis
  - *Phychoites* sp. A
  - *Platyceuchoceras ferracense*
  - *Acrochordiceras oestrina*
  - *Acrochordiceras auriculatum*
  - Intoritis nevadensis
  - *Vesiculites* cf. U. uthahaberi
  - *Eugymnoceras* o. *S. welleri*
  - *Nevadaptychites armilis*
  - *Lamellites* o. *I. marmorealis*
  - *Constrictiophyllum debelialis*
  - *Anagymnoceras spivaki*
  - *Nevadaptychites tozeri*
  - *Phychoites* sp. B
  - *Augusteoceras weberi*
  - *Augusteoceras staffordi*
  - *Eogymnoceras thompsoni*
  - *Eogymnoceras* o. *E. jolyanus*
  - Nicholaiites tozeri
  - *Platyceuchoceras praebalistovani*
  - *Eogymnoceras transiens*
  - *Gymnotoceras praepurpureor*
  - *Kolpoceras krafftii*
  - *Eogymnoceras tuberculatum*
  - *Platyceuchoceras tozeri*  

**Text-Fig.1:** Biostratigraphic distribution of the Taylori Zone ammonoids.

![Graph showing biostratigraphic distribution](image)

**Text-Fig.2:** Suture line of *Platyceuchoceras tozeri* n. sp. at H=15 mm. Paratype USNM 452807 (specimen not figured). Locality HB 229, Tozeri Subzone, Taylori Zone; Favret Canyon, Augusta Mountains.

![Suture line graph](image)

**Text-Fig.3:** Suture line of *Eogymnotoceras janvieri* n. sp. at D=42 mm. Paratype USNM 452817.
The index species and *Koipatoceras krafftii* n. sp. are known only from this subzone. *Eogymnotoceras tuberculatum* has its oldest occurrence in this subzone (see Pl. 2, Figs. 1-4).

**Systematic Descriptions**


**Order Ceratiida Hyatt 1884**

Superfamily *Dinartiaceae* Mojsisovics 1882

Family *Dinariidae* Mojsisovics 1882

Subfamily *Khvalinitinae* Shevyrev 1968

Genus *Koipatoceras* Silberling and Nichols 1982

Type species: *Koipatoceras discoideus* Silberling and Nichols 1982, p. 18, Pl. 4, Figs. 3-10 (Hyatti Zone).

*Koipatoceras krafftii* n. sp

Plate 1, Figures 27-29

Description: Shell moderately evolute, with compressed, high, rectangular whorl section. Venter narrowly rounded on innermost whorls, slowly decreasing in height until it becomes truncate on mature body chamber. Somewhat clavate, alternating marginal tubercles and lateral rounded nodes appear simultaneously at a diameter of about 7-8 mm. With further increase in shell size, weak falcoid folds develop on flanks. The progressively fading lateral node are placed at the inflexion point, just below mid-line of flanks. Marginal tuberculation enhanced at mature stage, whereas lateral tuberculation does not persist. Adult size estimated to about 4-5 cm in diameter.

Suture line not known.

Discussion: Distinguished from *Koipatoceras discoideus* Silberling and Nichols by having a lateral row of nodes and a truncated venter at later stage only.

Etymology: Species named in honor of A. von Krafft.

Figured specimens: Holotype USNM 452824

Occurrence: Loc. HB 234 (3), Muller Canyon, Augusta Mountains. Tozeri Subzone, Taylori Zone.

**Family Balatoniidae Spath 1951**

Genus *Platyacuococeras* Bucher 1988

Type species: *Platyacuococeras favretense* Bucher 1988, p. 729, Pl. 1, Figs. 16-20.

*Platyacuococeras tozeri* n. sp.

Plate 1, Figures 1-13; Text-Fig. 2

Description: Large sized, densely tuberculated *Platyacuococeras*. Umbilical, lateral, and marginal tuberculations extend to the entire phragmocone, with the exception of the innermost whorls. On venter, chevron-shaped ribs persist during all ontogenetic stages of the phragmocone. Although intraspecific variability is appreciable, lateral tuberculation generally becomes spinose on end of phragmocone and beginning of body chamber. Transition to mature body chamber enhanced by
concomitant approximation and decreasing strength of ornamentation. Umbilical tuberculation then fades out but thick, slightly prorsiradiate ribs persist on the subtabulate venter.

Suture line conforms to that of the genus.

Discussion: In many aspects, *P. tozeri* appears as a transition form between the stratigraphically underlying *P. praebalatonensis* Bucher 1988 (Praebalatonensis Subzone, Taylori Zone) and the overlying *Balatonites shoshonensis* Hyatt and Smith (Rieberi Subzone, Shoshonensis Zone). Absence of ventral tuberculation justifies generic assignment to *Platyecoceras*.


Figured specimens: Holotype USNM 452804, paratypes USNM 452801 to 452803, 452805 and 452806.

Occurrence: Loc. HB 229 (56), Favret Canyon, Augusta Mountains. Tozeri Subzone, Taylori Zone, middle Anisian.

Family *Ceratitidae* Mojsisovics 1879
Subfamily *Beyrichitidae* Spath 1934
Genus *Nicholsites* Bucher 1992

Type species: *Nicholsites newpassensis* Bucher, 1992b, Pl. 4, Figs. 12-23 (Hyatti Zone).

*Nicholsites parisi* n. sp.

Plate 2, Figures 22-23

Description: The complete, full grown holotype shows a compressed whorl section, with a narrowly rounded venter, at least on phragmocon. Although flattened by compaction, the venter apparently changes into a broader and lower outline on the body chamber. Thick, blunt, and sinuous distant ribs on phragmocon fade on mature chamber. Umbilical bullae weak or absent. Mature body chamber slightly egressive, of about a half of a whorl in length. Mature aperture preserved on holotype.

Suture line to poorly preserved to be drawn, but agreeing in plan with that of the genus (see Bucher 1992b).

Discussion: Differs from the older *N. newpassensis* Bucher 1992 (Hadleyi Subzone, Hyatti Zone) by its blunt and distant ribbing, also in having a more compressed whorl section. Distinguished from the younger *N. tozeri* (Bucher) 1988 (Escheri up to Tozeri Subzones, Taylori Zone) in being more widely umbilicated, and in having a simple, distant ribbing.


Figured specimen: Holotype USNM 452818.


Genus *Eogymnotoceras* Bucher 1988

Type species: *Eogymnotoceras thompsoni* Bucher

*Eogymnotoceras janvieri* n. sp.

Plate 26, Figs. 17-18; Plate 30, Figs. 5-18; Text-Fig. 3

1988 *Anagymnotoceras* sp. A.- Bucher 1988, p. 735, Pl. 4, Fig. 17-18.

Description: Phragmocon relatively compressed, evolute, with a subrectangular whorl section. Umbilical tuberculation consists of low, radially elongated to higher, oblique bullae from which stem two sinuous ribs. Conspicuous crescentic marginal tuberculation present on the adoral rib of
branched pairs. On ventral shoulder, both branched and single intercalated ribs are projected. Venter arched, and crossed by projected fading ribs and growth lines. Carination either weak or absent. With further increase in diameter, whorl height considerably increases, bullae become extremely radially elongated with their maximal elevation at mid-flanks. Marginal crescentic tubercles also disappear at this stage. At D = 47 mm (holotype), H = 48%, W = 31%, U = 23%.

Suture line subammonitic, with a deeply indented first lateral lobe.

Discussion: This is a somewhat intermediate form between *Anagymnotoceras variabilis* Bucher (1992b) and *Eogymnotoceras thompsoni* Bucher (1988). The style of ribbing is identical with that of *E. thompsoni*, but *E. janvieri* differs from the latter in having a weaker carination and by earlier acquisition of the high whorled, compressed shape. *E. janvieri* differs from *Anagymnotoceras variabilis* Bucher by its more projected and sinuous ribbing, frequent crescentic marginal tubercles and oblique umbilical bullae.

Earlier mention of *E. janvieri* from locality HB 179 (= *Anagymnotoceras* sp. A, Bucher 1988, p. 735, pl. 7) was erroneously assigned to the Spivaki Subzone. It now appears that locality HB 179 comes from the same horizon than that of the Nicholsi Subzone type locality.

Etymology: Species named for Ph. Janvier, Institut de Paléontologie, Museum national d'Histoire naturelle, Paris.

Figured specimens: Holotype USNM 452813, paratypes USNM 452812, USNM 452814 to 452817, plesiotype USNM 427261.

Occurrence: Loc. HB 179 (1), 246 (12), Favret Canyon. Nicholsi Subzone, Taylori Zone.

Acknowledgment

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References


PLATE 1
(All figures natural size unless otherwise indicated)

Fig. 1-13 *Platycoccoceras tozeri* n. sp. Tozeri Subzone, Taylori Zone. Loc. HB 229, Favret Canyon, Augusta Mountains.
1-2: paratype, USNM 452801.
3-4: paratype, USNM 452802.
5-7: paratype, USNM 453803.
8-9: holotype, USNM 452804.
10-11: paratype, USNM 452805.
12-13: paratype, USNM 452806.

Fig. 14-18 *Platycoccoceras favretense* Bucher. Tozeri Subzone, Taylori Zone. Loc. HB 229, Favret Canyon, Augusta Mountains.
14-16: plesiotype, USNM 452808.
17-18: plesiotype, USNM 452809.

Fig. 19-20 *Augustaceras staffordi* Bucher. Escheri Subzone, Taylori Zone. Plesiotype, USNM 452822. Single float specimen from spur between Coyote and Bloody canyons, northern Humboldt Range (loc. 72S-294, collected by N.J. Silberling).

Fig. 21-26 *Pseudodanubites nicholsi* Bucher. Nicholsi Subzone, Taylori Zone.
21-22: plesiotype, USNM 452819, loc. HB 246, Favret Canyon, Augusta Mountains
23-24: plesiotype, USNM 452820, loc. HB 219, Favret Canyon, Augusta Mountains
25-26: plesiotype, USNM 452821, loc. HB 246, Favret Canyon, Augusta Mountains

Fig. 27-29 *Koipatoceras krafti* n. sp. Tozeri Subzone, Taylori Zone. Holotype (x2), USNM 452824 Loc. HB 234, Muller Canyon, Augusta Mountains.

PLATE 2
(All figures natural size)

Fig. 1-4 *Eogymnotoceras tuberculatum* Bucher. Tozeri Subzone, Taylori Zone. Loc. HB 234, Muller Canyon, Augusta Mountains.
1-2. plesiotype, USNM 452810.
3-4. plesiotype, USNM 452811.

Fig. 5-16 *Eogymnotoceras janvieri* n. sp. Nicholsi Subzone, Taylori Zone. Loc. HB 246, Favret Canyon, Augusta Mountains.
5-6: paratype, USNM 452812.
7-9: holotype, USNM 452813.
10-11: paratype, USNM 452814.
12-13: paratype, USNM 452815.
14-16: paratype, USNM 452816.

Fig. 17-18 *Platycuccoceras praebalatonensis* Bucher. Praebalatonensis Subzone, Taylori Zone. Holotype USNM 427243. Loc. HB 170, Favret Canyon, Augusta Mountains.

Fig. 19-21 *Anagymnotoceras spivaki* (McLearn). Plesiotype USNM 452823. Spivaki Subzone, Taylori Zone. Loc. HB 226, Favret Canyon, Augusta Mountains.

Fig. 22-23 *Nicholsites parisii* n. sp. Nicholsi Subzone, Taylori Zone. Holotype, USNM 452818. Loc. HB 219, Favret Canyon, Augusta Mountains.
PROGRESS IN CONCEPTS ABOUT CONODONT AND FORAMINIFERA ZONAL STANDARDS OF THE TRIASSIC IN BULGARIA

K. Budurov and E. Trifonova, Geological Institute, Bulgarian Academy of Sciences, Acad. G. Bonchev str. Bl. 24, 1113 Sofia, Bulgaria

Introduction
The published Triassic conodont and foraminifera zonal standard of Bulgaria (Budurov and Trifonova, 1984) has been successfully applied to many stratigraphic problems. It elucidates the age, stratigraphy and correlation of some Triassic lithostratigraphic units, and has aided the study of new sections from both neighbouring and distant regions of Bulgaria. The general character of the zonation made correlations possible between the two Triassic types developed in this country regardless of their lithologic and paleontologic differences. The first type is in the territory of east and southeast Bulgaria, and according to its conodonts belongs to the Tethys. The other crops out in all the other parts of the country (west Bulgaria, west and central Balkan Mountains, west and central Sredna Gora Mountains, and northern Bulgaria; fig. 1) and is related to the Balkanid development of the Triassic. The conodont content also gives reason to refer to it as Tethys. The two parallel conodont zonal standards for the Tethys and for the Balkanid Tethys development during the Ladinian (Fig. 2) are integrated by the more universal foraminifera zonal standard. The Triassic foraminifers of Bulgaria are of a Tethys type. Irrespective of the more universal character of the foraminifera zonal standard for the Triassic in Bulgaria, some differences in the content and number of species within zonal associations of the same age are related to differences in the facies environments.

Fig. 1: Sketchmap of Bulgaria
In a previous paper (Budurov and Trifonova, 1984; Fig. 1) we indicated ties between the conodont and foraminifera standards with the ammonoid faunas, and tabulated the scarce macrofauna found. Particularly well-preserved macrofaunas of ammonoids are rare. This is the reason for the lack of a published ammonite zonal standard for the Triassic in Bulgaria. The determination of the chronostratigraphic score of the Triassic lithostratigraphic units from ammonites is relatively imprecise. The Triassic lithostratigraphic units yield more conodonts and foraminifers than ammonoids. The microfossils permit correlations not only between the sections within this country but also with typical foreign localities. Microfauna sampling within close (0.5-3m) intervals provides the opportunity to strictly define the boundaries between zones, substages and stages. In the case of foraminifers, species characteristic of the Tethyan development of the Triassic in Bulgaria and other countries have been found and introduced in the names of some of the zones and subzones. Comparisons with previous foraminifera zonal schemes (Trifonova, 1978a, b; Trifonova in Budurov and Trifonova, 1984) have not led to changes in the stratigraphic ranges of zones, but only made them more precise, as can be inferred when comparing Fig. 2 with Fig. 1 of Budurov and Trifonova (1984). The interval zones are named after the name of the species which appeared and had the main occurrence in the zone. In this manner, the current foraminifera zonation for the Triassic of Bulgaria (Trifanova in Salaj et al., 1988) has been introduced.

**Conodont zones**

Fifteen conodont zones characterizing Griesbachian and the interval Spathian - uppermost Norian are known (Fig. 2). They are as follows:

*Isarcicella isarcica Range-Zone.* The zone characterizes the middle to upper part of the Griesbachian (Lower Triassic). The single find of conodonts in the Strandza Mountains (SE Bulgaria) was not confirmed (Budurov and Trifonova, 1992). We therefore accept it with some doubt, because of the possibility of contamination with conodonts coming from foreign samples treated at the same time in the Micropaleontological Laboratory of the Geological Institute.

*Neospathodus triangularis Interval-Zone.* It characterizes the Spathian stage of Lower Triassic in the eastern Balkan and Strandza Mountains.

*Kashmiricella timorensis Range-Zone.* This zone characterizes the upper part of the Spathian stage of the Lower Triassic and part of the Aegean substage of the Anisian in the eastern Balkan and Strandza Mountains in southeast Bulgaria.

*Neogondolella regale Range-Zone.* It characterizes the upper part of the Aegean and lower part of the Pelsonian substages of the Anisian in the eastern Balkans and western Bulgaria.

*Paragondolella bulgarica Range-Zone.* The zone characterizes the middle and upper parts of the Pelsonian substage of the Anisian boreholes of western and north-central Bulgaria, as well as in the eastern Balkans and western Bulgaria.

*Neogondolella cornuta Range-Zone.* It characterizes the Illyrian substage of the Anisian in western and north-central Bulgaria, and the central and eastern Balkan Mountains.

*Neogondolella consticta Assemblage-Zone.* Without the presence of the typical Balkanid conodonts of the group of Neogondolella bakalovi Budurov & Stefanov, it characterizes the Fassanian substage of the Ladinian in the eastern Balkan and Strandza Mountains. The zone is an indicator for the development of typical Tethyan Triassic.

*Sephardicella mungoensis Assemblage-Zone.* This zone characterizes the lower and middle parts of the Longobardian substage of the Ladinian without presence of the Balkanid conodonts of the group of Neogondolella bakalovi Budurov & Stefanov. It is established in the eastern Balkan and Strandza Mountains.
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<th>Standard Foraminifera Zones and subzones (Trifonova in Salaj et al., 1988)</th>
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<td>(L. and M. Triasich from Kovacev &amp; Knezevic, 1980, emended, L. Triassic after Silverling and Tozer, 1964)</td>
<td>Typical</td>
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Fig. 2: Conodont and foraminiferal standard zones of the Triassic in Bulgaria
Neogondolella excentrica Assemblage-Zone. The zone characterizes the lower part of the Fassanian substage of the Ladinian in the Balkanid conodont province in boreholes of north central Bulgaria, the west and central Balkans and west and southwest Bulgaria.

Neogondolella bakalovi Range-Zone. It characterizes the upper part of the Fassanian substage and lower part of the Longobardian substage of the Ladinian in the Balkanid development in the central Balkans and southwest Bulgaria.

Paragondolella foliata Range-Zone. This zone characterizes the upper part of the Longobardian substage of the Ladinian in Tethyan development in the eastern Balkan and Strandza Mountains.

Paragondolella polygonathiformis Interval-Zone. It characterizes middle and upper parts of the Cordevolian, Julian and lower part of Tuvalian substages of the Karnian in Tethyan development in eastern Balkan and Strandza Mountains.

Paragondolella nodosa Range-Zone. This zone characterizes the middle and upper part of the Tuvalian substage of the Karnian in Tethyan development in the Strandza Mountains.

Metapolygnathus abneptis Interval-Zone. It characterizes the Lacian substage of the Norian in the Tethyan development in the eastern Balkan and Strandza Mountains.

Epigondolella posterza Range-Zone. The zone characterizes parts of the Aluunian substage of the Norian in Tethyan development in the eastern Balkan Mountains.

Foraminiferal zones and subzones

Seven foraminiferal zones and four subzones characterizing the chronostratigraphic interval Dienerian-Smithian to Norian, inclusive, are known (Fig. 2). They are as follows:

Meandrospira cheni Interval-Zone. It characterizes approximately the Dienerian-Smithian stages of the Lower Triassic in Southeast Bulgaria (Sveti Ilija Hills) only.

Meandrospira pusilla Interval-Zone. This zone characterizes the Spathian stage of the Lower Triassic in boreholes of northwest and northeast Bulgaria, as well as in outcrops of southwest Bulgaria and the central and eastern Balkan Mountains and Strandza Mountains.

Meandrospira deformata Interval-Zone. The zone characterizes the Aegean and lower part of the Pelsonian substages of the Anisian in boreholes of northern Bulgaria and in the western and central Balkans.

Pila minima densa Range-Zone. It characterizes the Pelsonian (without its lowermost part) and Illyrian (except its uppermost part) substages of the Anisian in boreholes in northern Bulgaria, in outcrops in the central and eastern Balkans and the Sveti Ilija Hills.

Meandrospira dinarica Interval-Subzone. The subzone characterizes the Pelsonian substage (without its lowermost part) of the Anisian in boreholes of all northern Bulgaria and in outcrops in southwest Bulgaria, the central Balkan Mountains, and the Sveti Ilija Hills.

Aulotortus pragensides Interval-Subzone. It characterizes the Illyrian substage (without its uppermost part) of the Anisian in boreholes of north-central and northeast Bulgaria.

Turricolmina mesotriassica Interval-Zone. The zone characterizes the uppermost part of the Illyrian substage and Ladinian in boreholes of north-central and northeast Bulgaria, as well as in outcrops in the central Balkan Range, southwest Bulgaria and the Strandza Mountains.

Aulotortus praegascheli Interval-Subzone. This subzone characterizes the Longobardian substage of the Ladinian in boreholes of northwest and northeast Bulgaria, as well as in outcrops of the central Balkan Range.

Paraophthalmidium carpathicum Range-Zone. The zone characterizes the Carnian in boreholes of northern Bulgaria and in outcrops of the central Balkan Range, southwest and southeast Bulgaria.
eastern Balkan and Strandza Mountains).

Aulotortus friedli Interval-Subzone. It characterizes the Cordevolian substage and part of the Julian substage of the Carnian in boreholes of northern Bulgaria, as well as in outcrops of the central Balkan Range, southwest and southeast Bulgaria (eastern Balkan and Strandza Mountains).

Miliolipora cuvillieri Range-Zone. This zone characterizes the Norian in outcrops of the central Balkan Range, and southwest Bulgaria (Strandza Mountains).

References


LOWER TRIASSIC STAGE, SUBSTAGE AND ZONAL SCHEME OF NORTH-EASTERN ASIA

A.S. Dagys, Institute of Ecology of the Lithuanian Academy of Sciences

Introduction
The biochronological scheme of the Lower Triassic of Siberia is now the most elaborate, not only in the Boreal regions, but in the world. It includes 21 biochronological divisions, zones and subzones traditionally united in two stages: Induan and Olenekian (Figs. 1, 2). Such a scheme at first seems to be paradoxical because ammonoid diversity in low paleolatitudes was 2-3 times higher than in high paleolatitudes, except Lower Induan (Griesbachian), yet differences between faunal diversity in low and high paleolatitudes were not evident. At low paleolatitudes a more intensive rate of evolution of ammonoids might be expected in comparison with the Boreal regions.

This paradox may be explained from the better paleontological investigation of Boreal ammonoid fauna and by the more favourable conditions of discovery of the sequences of geologic and paleobiologic events. The Lower Triassic in Siberia is represented mainly by siltstones with layers or lenses of carbonate concretions, usually containing natural assemblages of ammonoids (Tozer, 1971) in which species are often represented by abundant material ("paleopopulations"). In all Siberian sequences studied, the Lower Triassic is from several tens to several hundreds of meters thick and in the Boreal regions the condensed assemblages so characteristic for the Tethyan region are unknown (Tozer, 1971).

Discussion
The Siberian zonal scheme of the Olenekian stage is based on phylogenetic lineages of endemic Boreal ammonoid taxa: Anaxenaspis --> Lepiskites --> Chypeceras (Lower Olenekian); Xenocelites --> Bajanania --> Nordophiceras (Lower-Upper Olenekian); Boreoceras --> Praesibirites --> Parasibirites --> Sibirites (Upper Olenekian). In many cases the zones and subzones are based on sequence of endemic species, often connected by transitional forms.

Zonation of the Upper Olenekian of northeastern Asia is based on evolution of the endemic family Sibiritidae, showing natural development of this group from the simplest smooth conchs to intensively ornamented spinous forms (Dagys and Ermakova, 1988). The oldest in this line is genus Boreoceras, lacking ornamentation and showing a gradual change of whorl section from rounded (Boreoceras planorbis) to oval (Boreoceras demokidovi) and subrectangular (Boreoceras lenaense). The descendant of this genus at a higher stratigraphic level, genus Praesibirites, retained the shape of the youngest Boreoceras but is characterized by the appearance of bullae on its lateral sides (Praesibirites tuberculatus) which later were accompanied by ribs (Praesibirites egeri).

In the next step of this phylogenetic line, genus Parasibirites, there appeared additional ventro-lateral bullae and ribs on the ventral side. Species of genus Parasibirites from different subzones of the Grambergi Zone are distinguished by the time of origin of ventral ribs during ontogeny. In the oldest forms which were close to Praesibirites, ventral ribs and ventro-lateral bullae appear only on the living chamber of adult shells. Young specimens of Parasibirites kolymensis may be indistinguishable from Praesibirites. Species of Parasibirites from the Mixtus Subzone (Parasibirites mixtus, P. grambergi, P. subpretiosus) had ribbed ventral side starting at about the sixth whorl and the youngest Parasibirites efimovae was ribbed from about the third whorl. Terminal genus of this phylogenetic line, Sibirites, is characterized by the disappearance of lateral bullae (or spines).
In the phylogenetic lineage under consideration between successive species there existed intermediate forms and the lineage reflects all steps of the evolution of Sibiritidae. The stratigraphic scheme for the Siberian Olenekian stage based on this line is evidently without gaps and nears the limit for detailed elaboration of biostratigraphic schemes because the rate of evolution of other synchronous taxa of Boreal Olenekian ammonoids is much slower. There are some data showing that further subdivision is possible only for the Kolymensis Zone, in some sections genus *Lepiskites* being distributed only in the lower part of the zone and *Cypleoceratoidees* in the higher horizons. In the Spiniplicatus Zone a division is possible due to the appearance of genus *Frosphingites* and several other ammonoids in the upper part of the zone.

In the Induan stage of Siberia only short phylogenetic lines may be traced, e.g. *Otoceras concavum* --> *O. boreale*; *Tompophiceras pascoei* --> *T. morphaeos*. Chronostratigraphy of this interval is less elaborate. Probably there is a gap at the base of the Upper Induan in Siberia. Some problems of zonation remain for the Siberian Vavilovites beds. The Compressus Zone was described by Vavilov from an isolated section. The succession of assemblages with different species of *Vavilovites* is still questionable.

Correlation of the Siberian zonal scheme of the Lower Triassic with the Canadian scheme (Tozer, 1967, 1981; Dagys and Tozer, 1989) and other Boreal regions (Weitschat and Dagys, 1989) is clear enough (Fig. 3). More complicated are comparisons of the Siberian Lower Triassic with zonal schemes elaborated in low paleolatitudes. One stratigraphic level can be clearly recognized in all regions - the Tardus Zone. This correlation is confirmed by conodont zonation. Neogondolella milleri Zone, the exact equivalent of Tardus Zone (Dagys and Dagys, 1989), also had a worldwide distribution. Correlation of Kolymensis Zone is also clear, except in Perigondwanian Tethys. Analogues of the Siberian Hedenstroemi Zone are less certainly established (Dagys and Ermakova, 1990).

The next correlable level of the Boreal Lower Triassic are the beds with *Otoceras*, but they only correlate with Perigondwanian Tethys. Some problems are connected with precise correlations because the exact equivalents of the Concavum Zone in the Tethyan region are debatable (Dagys and Dagys, 1986).

Very problematic is a detailed correlation of the Upper Olenekian of Siberia. Kummel (1966, 1968, 1969), Kiparisova (1961) and Zakharov (1968) have described Boreal genera in low paleolatitudes but most of such determinations are not correct (Dagys and Ermakova, 1988). In Primorye true *Bajarania* was described from *Tirolites* beds (Zakharov, 1987) and *Olenekoceras* (Keyserlingites miroshnikovi) from the *Columbites* beds. In the western USA Smith (1932), Kummel (1969), Dagys and Ermakova (1988) recorded *Olenekoceras* (Keyserlingites stephensoni), *Bajarania* (Prionolobus jacksoni) and *Boreoceras* (Dieroeceras apostolicum). Dr. W. Weitschat has also determined from this level true *Nordophiceras* (personal communication).

According to these data the *Tirolites* beds may be correlated with the lower part of the Euomphala Zone of Siberia, and the *Columbites* beds correlate with the upper part of Euomphala Zone (Demokidov subzone), and the Contrarium and Grambergi Zones. In Siberia *Olenekoceras* appears in Efimovac Subzone of Grambergi Zone. Such correlations show that the Parisianus Zone of the western USA and Insignis Zone of Primorye are characterized by numerous ammonoid genera which are perhaps based on unnatural assemblages. They probably include several successive faunas. Tethyan two- or three-fold division of Upper Olenekian does not reflect the real evolution of ammonoids.
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Fig. 1: Correlation of the Siberian and Canadian schemes.
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Fig. 2: Stratigraphic distribution of the Siberian Lower Triassic ammonoids.
Correlation of the Boreal uppermost Spathian with the Haugi Zone of western USA is questionable. In the Haugi Zone there appear characteristic Anisian families, Acrochordiceratidae ("Acrochordiceras" inyoense) and Longobarditidae ("Hungarites" yatesi), but after Bucher’s (1989) opinion that "Tiroites" pacificus is conspecific with index-species of Canadian Subrobustus Zone, which was originally described in Spiniplacicus Zone of Siberia. Keyserlingites s.l. (including Durgaites) is known in China in the Lower Anisian (Japonites meridionalis Subzone) and Wang (1984) has considered that this genus was distributed in the Spathian of the Boreal province and in the Lower Anisian in the Tethyan province. This interpretation is doubtful. More probably Durgaites and Keyserlingites are heterochronous homoeomorphs (Dagys, 1988).

Traditionally only two stages are accepted in the Siberian Lower Triassic: Induan and Olenekian. Each stage now may be subdivided into two substages which are nearly exact correlatives of four Canadian stages proposed by Tozer (1965), with one principal difference: Upper Olenekian is much more comprehensive than the Spathian and includes several units which are unknown in the stratotypic region of the Spathian stage, as well as in the whole Canadian-Svalbardian region.

Subdivisions of the Boreal Lower Triassic reflect the main phase of evolution of ammonoids and regularities of their geographic differentiation. All Boreal Early Triassic ammonoid assemblages contain distinctive taxa, but degree of endemism shows great changes with time. The history of marine biota of this time distinguishes two cycles with relatively monotonous cosmopolitan fauna at the beginning, and endemic assemblages at the end (Fig.4). Enay (1980) has traced such changes in the Jurassic calling them “faunal rhythms” and has connected them with eustatic sea level changes.

During the Early Induan (Griesbachian) transgression, cosmopolitan genera dominated the Boreal regions. During Late Induan (Dienerian) distinctive Proptychitidae were dominant in high paleolatitudes and this endemism of ammonoids was probably related to the first considerable decrease of sea level in the Triassic. In Early Olenekian (Smithian) cosmopolitan genera became predominant again and their distribution perhaps was associated with rising of sea level. At the beginning of Late Olenekian or Spathian significant changes of ammonoid taxa are noted which were followed by intensive geographic differentiation of the fauna. (The rich ammonoid assemblages of Siberia contain only one widely distributed genus - Pseudosageceras).

Two- or four-fold division of the Lower Triassic, accepted in the Boreal regions, agrees with geological history as a first order with transgression-regression sedimentary cycles in the Arctic (Emby, 1985). The four fundamental subdivisions of the Lower Triassic have been united in different ways. According to one interpretation two stages are recognized in the Olenekian: Verkhoyanian or Ajaxian (= Ussurian), and Russian (Zakharov, 1973). Another proposal (Tozer, 1978; Guex, 1978) unites Upper Induan and Lower Olenekian in one stage - Nammalian. These differences in standard schemes for the Lower Triassic are based on different interpretations of the ammonoid evolution. Zakharov (1973, 1978) considered that at the base of the Lower Olenekian there occurred one of the biggest renovations of the Early Triassic fauna, whereas Tozer (1981, 1978) and Guex (1978) have united equivalents of Upper Induan and Lower Olenekian in one stage on the basis of similarity of their ammonoids. Advantages of both variants of three-fold division of Lower Triassic are doubtful. In northeast Asia acceptance of such propositions (especially of the Nammalian stage) would lead to nomenclature problems and great difficulties in geologic mapping.
Fig. 3. Correlation of the Lower Triassic zonal schemes.
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Fig. 4: Stratigraphy and geographic distribution of the Early Trissic ammonoids of Siberia
Acknowledgements
I wish to thank Dr E.T. Tozer who kindly revised the English of the present paper.

References
Bucher H. (1989): Lower Anisian ammonoids from the northern Humboldt range (northwestern Nevada, USA) and their bearing upon the Lower-Middle Triassic boundary. Eclogae Geol. Helv. 82: 945-1002.


GLOBAL CORRELATION OF THE TERMINAL TRIASSIC

A.S. Dagys and A.A. Dagys, Institute of Ecology of the Lithuanian Academy of Sciences

Introduction
The nineteen-eighties saw the last of the Rhaetian as a standard topmost Triassic stage. This stage was abolished from the 1983 time scale adopted for the new regional series of the geology of North America (Tozer, 1988), as well as from the standard accepted by the Stratigraphic Committee of the USSR in 1987. Such ideas were dominant among geologists and shared also by the authors (Dagys and Dagys, 1989).

During recent years, investigations of the stratotype of the Rhaetian stage (Koessen beds) and their ammonoid bearing equivalents in the Alps provided new stratigraphic and paleontological data which revived this question and the search for a compromise on the problem of the Rhaetian stage. According to Krystyn’s investigations (1987), the definition of Rhaetian in the sense one Marshi Zone (s.s.) is not acceptable. There are three other possible interpretations of the lower boundary of the Rhaetian:
1. At the base of Sturzenbaumi Zone (Kozur, 1973; Krystyn, 1987).
2. At the base of Reticulatus (or Amoenum) Zone (Tuchkov, 1962; Dagys, 1988).
3. At the base of Quinquepunctatus (or Cordilleranus) Zone (Popov, 1961; Zapfe, 1967; Wiedmann, 1973; Tollmann, 1967; see also Tozer 1988 who interpreted Rhaetian as substage of Norian).

A short analysis and comparison of different interpretations of the Rhaetian with respect to three aspects - priority, faunal changes at the lower boundary, and correlational capacity of the schemes, is given below.

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Fig. 1: Stratigraphic distribution of conodonts in the Terminal Triassic (Krystyn 1987).
Priority

Tozer (1988) has distinguished two Rhaetians: Rhaetian sensu stricto, including Marshi Zone alone and Rhaetian sensu lato, corresponding to the full section of the stratotype (alpine Koessen beds). Tozer (1988, 1990) considered that Rhaetian (s.l.) is essentially overlapping Sevatan and its lower boundary could not be correlated with the standard zonal scheme. "At the level of stage there is no room for both Norian and Rhaetian s.l.: one must go." (Tozer, 1988, p.10).

Thanks to investigations of Koessen and Zlambach beds by Wiedmann (1972), Wiedmann et al., (1979), Mostler et al. (1978) and especially by Krystyn (1987; 1990) and Golebiowsky (1990), we can now consider that correlation of the lower boundary of Koessen beds is not so hopeless as supposed by Tozer. Ammonoid and conodont zonation and correlation of Zlambach and Koessen beds show that Koessen beds are not older than the Reticulatus Zone and the Hochalm Member of the Koessen Formation and the Reticulatus Zone are more or less synchronous.

Consequently Krystyn's (1987) Rhaetian is more restricted in comparison with the original interpretation of this stage and is mainly correlative with the upper part of Koessen beds (Golebiowsky, 1990, Fig. 1). However, this variant permits retention of the traditional stage and substage scheme of the terminal Triassic.

The second proposition is in full agreement with the original interpretation of Rhaetian and also retains the principal stage and substage scheme (with some restriction of Sevatan).

The third interpretation of Rhaetian is a bit more general than Guemble's original proposition that equivalents of the Quinquepunctatus Zone in Koessen beds, according to conodont zonation, are certainly absent. If this third solution were accepted, the nomenclature of the terminal Triassic would require important changes.

Faunal changes

The end of the Triassic was a time of extinction of the ceratitids, and the main events at the stratigraphic boundaries were connected with vanishing of different taxa usually accompanied by their geographic localization. Stratigraphically important Rhaetian taxa were distributed only in low paleolatitudes (Choristocerataec from British Columbia were collected from allochthonous blocks originally situated in low paleolatitudes) and only long living genera of Ammonoidea Leiostraca of low stratigraphic value (Krystyn, 1987) were distributed in high paleolatitudes.

The most important extinctions took place before the Quinquepunctatus Zone (disappearance of Distichitidae, Clydonitidae, Thetiidae, etc.), before the Reticulatus zone (Metasibiritidae, Tibetidae, Arpadititae, etc.), and only rare genera of ammonoids (e.g. Cochloderas) vanished at the base of Sturzenbaumi Zone. Reconstruction of ammonoid assemblages on the three boundaries under consideration appears more or less equal: genera Rhabdoceras, Peripleurites appeared in the Quinquepunctatus Zone, Cochloderas, Cyclocelites in the Reticulatus Zone and Choristoceras, Vandaites in the Sturzenbaumi Zone.

Very important for the chronostratigraphy of the Upper Triassic were pelagic bivalves - monotids and halobiids. Genus Monotis (s.l.) appeared in Middle Norian but in the Quinquepunctatus Zone, and its analogues were distributed as the characteristic species Monotis salinaria and related forms (M. subcircularis, M. ochotica, etc.). At the lower boundary of the Reticulatus Zone genus Monotis, which dominated Late Norian bivalve assemblages especially in high paleolatitudes, fully disappeared. This boundary was also critical for another cosmopolitan genus, Halobia, and extinction of those two genera was the most important event in the evolution of bivalves in the terminal Triassic.
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<td></td>
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<tr>
<td>Megaphyllites insectus</td>
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<tr>
<td>Rhacophyllites debilis</td>
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<tr>
<td>Stenarcestes leiostracus</td>
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<tr>
<td>Arcestes ex gr. intuslabiatus</td>
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</tbody>
</table>

Fig. 2: Norian-Rhaetian "sandwich" in N-W Caucasus (Ytyrygarta).
<table>
<thead>
<tr>
<th>Norian</th>
<th>Rhaetian</th>
<th>Stage</th>
<th>Substratum</th>
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<tbody>
<tr>
<td>Sevalian</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Sagenites quengygeniculatus</td>
<td>Sagenites reticulatus</td>
<td>Vandaites sturzenbaumii</td>
<td>&quot;Choristoceras&quot; baneri</td>
</tr>
<tr>
<td>Red limestones with Mononis salinaria</td>
<td>Lower M. with Mononis salinaria</td>
<td>Vandaites sturzenbaumii</td>
<td>&quot;Choristoceras&quot; baneri</td>
</tr>
<tr>
<td>Krasjugai Formation</td>
<td></td>
<td>Vandaites sturzenbaumii</td>
<td>Vandaites ammonitiforme</td>
</tr>
<tr>
<td>Mononis salinaria</td>
<td></td>
<td></td>
<td>&quot;Choristoceras&quot; baneri</td>
</tr>
<tr>
<td>Krasjugai Formation</td>
<td></td>
<td></td>
<td>Vandaites ammonitiforme</td>
</tr>
<tr>
<td>Hahoria pedata</td>
<td></td>
<td></td>
<td>&quot;Choristoceras&quot; baneri</td>
</tr>
<tr>
<td>Borneo Formation</td>
<td></td>
<td></td>
<td>Vandaites ammonitiforme</td>
</tr>
<tr>
<td>Haabba Formation</td>
<td></td>
<td></td>
<td>&quot;Choristoceras&quot; baneri</td>
</tr>
<tr>
<td>Borneo Formation</td>
<td></td>
<td></td>
<td>Vandaites ammonitiforme</td>
</tr>
<tr>
<td>Haabba Formation</td>
<td></td>
<td></td>
<td>&quot;Choristoceras&quot; baneri</td>
</tr>
<tr>
<td>&gt; Vietnam &lt;</td>
<td></td>
<td></td>
<td>Vandaites ammonitiforme</td>
</tr>
<tr>
<td>&gt; South China (Xizang) &lt;</td>
<td></td>
<td></td>
<td>Vandaites ammonitiforme</td>
</tr>
</tbody>
</table>

**Alps (standard)**
- Black limestones with Koenen
- Khods Formation with "Choristoceras" baneri
- Koelen Formation with "Choristoceras" baneri

**East Carpathian**
- Upper M. with Khods

**North Caucasus**
- Upper M. with Koelen

**North Afghanistan**
- Upper M. with Koelen

**Panjir**
- Upper M. with Koelen

**Vietnam**
- Upper M. with Koelen

**South China (Xizang)**
- Upper M. with Koelen

**Fig. 3: Correlation of the Latest Triassic in the Northern Tethys.**
A specific complex of bivalves is known from the alpine Koessen beds and in the Rhaetian of the Germanic facies. Some renovation of bivalves (mainly at the species level) is noted in supramonotis beds (Efimovae Zone) of the Boreal regions (Polubotko and Repin, 1990) and Otatirian stage of the Notal region.

The Rhaetian cannot be recognized on bivalve data when its lower boundary is drawn at the base of Sturzenbaumi Zone. Rhaetian (s.s.) and Rhaetian (s.l.) in Koessen beds of the Alps contain the same assemblages of bivalves, migrating together with facies (Golebiowsky, 1990).

Conodont zonation is also very important for biostratigraphy and correlation of the terminal Triassic (Mostler et al., 1978; Gazdzicky et al., 1979; Krystyn, 1987, 1990; Golebiowsky, 1990; etc.). There were several events in the final evolution of conodonts in the Alpine region (Fig. 1): 1) appearance of the genus Misikella in the Reticulatus Zone; 2) extinction of genus Epigondolella (E. bidenta, incl. E. andrusovi) in the same zone; and 3) extinction of the genus Gondolella (G. steinbergensis) in the lower subzone of Sturzenbaumi Zone (Krystyn, 1987). The genus Misikella was distributed from the Alps to the Pacific region and appearance of this genus is an important event which may be used for determination of the lower boundary of the Rhaetian.

Some biostratigraphic standards for the Rhaetian have brachiopods widely distributed in the Tethyan, Boreal and Notal regions. Due to overestimating the stratigraphic value of Ammonidoidea Leiostraca it was considered that the Koessen assemblages of brachiopods in some regions (Slovakia, Caucasus, Pamir; Dagys, 1963) were distributed also in the Sevatian, but in fact brachiopods from the Quinquepunctatus Zone and the Reticulatus and younger zones are quite different. For the Quinquepunctatus Zone (or Monotis salinaria beds) the most characteristic were genera Halorella, Hallorelloidea, Austrellula, etc., while in supramonotic beds (Reticulatus, Sturzenbaumi and Marshi Zones) of the Alps and other Tethyan regions the dominant taxa were originally described from Koessen beds. Such sequences of brachiopod assemblages may be illustrated by the famous Norian - Rhaetian - Norian "sandwich" of Tozer (1988). In spite of Tozer's opinion, there is no alternation of Norian and Rhaetian fauna and in the terminal Triassic of this region two successive assemblages of brachiopods may be distinguished (Fig. 2): lower assemblage (beds 3-6) including mainly Norian taxa (Pexidella, Crurirhynchia, Camerothyris, etc.) accompanied by Monotis salinaria (Monotis kaukasica), and upper assemblage (beds 7-10) with characteristic genera and species (including Austrirhynchia cornigeru) of Koessen beds which are associated with 'Norian' ammonoids (bed 9) - Placites Polydactylus, Megaphyllites insectus, etc. (Dagys, 1974).

Essential changes in brachiopods are known also on the boundary of the Ochotica-Efimovae Zones (Dagys, 1965) in the Boreal region (Siberia), and certain differences are noted between brachiopod fauna of Warepan and Otatirian of the Notal region. Change of brachiopods on the boundary between the Reticulatus-Sturzenbaumi Zones is obscure and most probably insignificant.

The main tendencies of the stratigraphic distribution of corals in the topmost Triassic are similar to the development of brachiopods, and in the northern Tethys (at least from the Alps to the Pamir) the Koessen species predominated in supramonotis beds.

Global correlation

The value of biochronologic schemes depends on their correlational capacity. Paraphrasing Diener's famous saying (see Tozer, 1971, p. 1003) one can ask: "What good is a standard scheme which is acceptable only in one region?"

Very limited is the application of the Rhaetian with its lower boundary at the base of the Sturzenbaumi Zone. This scheme is based mainly on ammonoid distribution but ammonoids, as noted above, were very rare in the terminal Triassic (except Ammonidoidea Leiostraca) and are known only in limited sections of the Alpine region and the eastern Pacific. In most sections of the world the
Rhaetian is characterized only by bentonic fauna and adoption of this variant would be fraught with uncertainty of the lower boundary of Rhaetian and appearance of Norian-Rhaetian mixed beds.

The Rhaetian with its lower boundary at the base of Reticulatus Zone may be recognized in all regions of the world, which have known topmost Triassic marine sediments (e.g., northern Tethys, Perigondwanian Tethys, Pacific as well as the Boreal and Notal regions).

In the northern Tethys (Fig. 3) equivalents of Rhaetian may be distinguished in allochthonous blocks of the eastern Balkans where the topmost Triassic contains Koessen brachiopods (Ganev, 1961) and in famous localities Drnava and Hýbëe of the western Carpathian. A similar assemblage of Koessen brachiopods is described from the terminal Triassic of the Soviet Eastern Carpathian (Dagys and Chernov, 1974), allochthonous blocks of Crimea and topmost Triassic (Upper Member of Khods Formation) of the northern Caucasus (Dagys, 1963, 1974) where beds with Koessen brachiopods overlay beds with Monotis salinaria. Analogues of the Rhaetian with Koessen brachiopods and bivalves are known in eastern Iran (Douglas, 1929) and central Afghanistan (Karapetov and Kushlin, 1971). In the southeastern Pamir, the Rhaetian Bortepa Formation with Koessen brachiopods, corals and bivalves (Rhaetivalicula cf. contorta) overlies limestones of the Aktash Formation containing Monotis salinaria, Halorella pedata, Hallorelloidea rectifrons etc.

Some topmost formations in Vietnam overlying coal-bearing deposits may very probably be assigned to the Rhaetian. From the Pa-ma Formation (Vu Khuc et al., 1965) brachiopods (Laballa cf. suessi, rhaetina) and bivalves (Gervillia praexursor, Caridita cloacina) of Koessen appearance were collected. Koessen species of brachiopods are determined also from terminal Triassic of China, Xizang (Sun Dongli, 1981).

<table>
<thead>
<tr>
<th>Stages</th>
<th>Alps (standard)</th>
<th>Indonesia (Misol, Ceram)</th>
<th>Himalaya</th>
<th>Oman</th>
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<tbody>
<tr>
<td>Rhaetian</td>
<td>Choristoceras</td>
<td>Beds with Misola</td>
<td>Kyoto Formation, Lower M. with Misola</td>
<td>Asfal and Sumra Formation with Misola</td>
</tr>
<tr>
<td></td>
<td>marshi</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Choristoceras</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>ammonitiforme</td>
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<tr>
<td></td>
<td>Vandaletes</td>
<td></td>
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<tr>
<td></td>
<td>sturzenbaumi</td>
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<tr>
<td></td>
<td>&quot;Choritoceras&quot;</td>
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<tr>
<td></td>
<td>haueri</td>
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<td></td>
<td>Sagenites</td>
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<td></td>
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<tr>
<td></td>
<td>reticulatus</td>
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<tr>
<td></td>
<td>with Cochloceras</td>
<td></td>
<td>Beds with Monotis salinaria</td>
<td></td>
</tr>
<tr>
<td>Norian</td>
<td>Sagenites</td>
<td>Beds with Monotis salinaria</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sevastian</td>
<td>quinquepunctatus</td>
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</tbody>
</table>

Fig. 4: Correlation of the Latest Triassic in Perigondwanian Tethys.
<table>
<thead>
<tr>
<th>Norian</th>
<th>Rhaetian</th>
<th>Stage</th>
<th>Subst.</th>
</tr>
</thead>
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<tr>
<td>Sevatan</td>
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</tr>
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<td>Sagesites</td>
<td>Sagesites reticulatus</td>
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<td>quinquemucatus</td>
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<td>Nevada</td>
</tr>
<tr>
<td>Mopsis</td>
<td>Cochloceras</td>
<td></td>
<td>Pacific</td>
</tr>
<tr>
<td>salinae</td>
<td>Lower M.</td>
<td></td>
<td>British Columbia</td>
</tr>
<tr>
<td>Gnomohalites</td>
<td>Cochloceras amoenum</td>
<td></td>
<td>Chile</td>
</tr>
<tr>
<td>cordillerans</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>?</td>
<td>Beds with Ch. crickmani</td>
<td></td>
<td>Oceanic facies</td>
</tr>
<tr>
<td>Epigomolida</td>
<td>Misikella herteni</td>
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<td>Japan, Far East, Usal</td>
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<tr>
<td>bidentata</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Tospecten</td>
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<td></td>
<td>Siberia</td>
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<td>efimovae</td>
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<td>Boreal</td>
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<td>Monos</td>
<td>Camptonectes natus</td>
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<td></td>
</tr>
<tr>
<td>ochotica</td>
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<tr>
<td>Waregen</td>
<td>Oaptirian</td>
<td></td>
<td>Notal</td>
</tr>
</tbody>
</table>

Fig. 5: Correlation of the Latest Triassic in Pacific, Boreal and Notal regions.
On Misol Island, allochthonous blocks transported from the Perigondwanian Tethys contain equivalents of Reticulatus Zone - Nucula marls with Cochloceras (Jaworski, 1913) overlain by marls with specific brachiopod Misolia. On Seran Island beds with Misolia are situated above beds with Monotis salinaria and probably genus Misolia is characteristic for Rhaetian of the Perigondwanian Tethys (Fig. 4).

In the Himalaya above shales with Monotis salinaria there occur Quartzitic Series with Misolia manicensis and Kioto Formation containing Misolia and Triadimegalodon in its lower part, which may be interpreted as the Rhaetian. The Asfal and Sumra Formations in Oman are also most probably Rhaetian with Misolia and bivalves similar to the assemblage from the Nucula marls of Misol Island.

Correlation of the eastern Pacific Rhaetian was done recently by Krystyn (1990). If the lower boundary of the Rhaetian is accepted as the base of the Reticulatus zone, then the Rhaetian includes the Lower Member of the Gabbs Formation in Nevada and Ammoneum Zone (Cassianella beds) of British Columbia (Fig. 5). Revision of the benthonic fauna of this region should clarify biochronologic problems connected with the Rhaetian stage.

In the western Pacific analogues of the Rhaetian are known only in oceanic facies - deep water cherts. In the uppermost Triassic of Japan (Igo and Koike, 1983) and eastern Sikhote - Alin (Dagys et al., 1987, 1989) the genus Misikella is very common and local conodont zones Hernsteini and Posthernsteini are clear correlatives of the Rhaetian.

Equivalents of the Rhaetian stage are widely distributed in Siberia (from Siberian platform to the Okhotsk Sea) and represented by one bivalve zone, the Tosapetcen cfimovae, which overlies beds with Monotis ochotica and underlies the Lower Hettangian with Psiloceras. All marine invertebrates of the Efimovae Zone are endemic and correlation of Siberian Rhaetian with the standard is based on its stratigraphic position. At the base of the Efimovae Zone the genus Monotis and characteristic Norian brachiopods (Omofoenella, Ochotathyris, Orientospira, etc.) have disappeared. In bivalve and brachiopod assemblages, species of long living genera (Oxytoma, Tosapetcen, Piarorhynchia, Costispiriferina) and specific genera were very rare (Pseudohalotella). In the Efimovae Zone there appeared some characteristic Jurassic genera: Pseudomytiloides, Aequipecten, and Kolymonectes (Polubotko and Repin, 1990; Dagys, 1990). Ammonoids in the Siberian terminal Triassic are rare and belong exclusively to the Ammonoidea Leiostraca. Only from allochthonous blocks of Chukotka, originally probably situated in moderate paleolatitudes, in Ochotica Zone genera Halorites and Rhabdoceras are known (Afitsky, 1970).

The Otapiarian stage of New Zealand is an exact equivalent of the Siberian Efimovae Zone. Otapiarian overlies the Warepan stage with Monotis richmondiana and contains pure fauna: several new species of endemic brachiopod genera (Clavigera, Rastelligeria) and the characteristic bivalves Otapia. Correlation of the Otapiarian stage is also based on its stratigraphic position (supramonotis beds). The Rhaetian in the widest sense, with its lower boundary at the base of Qinquepunctatus (or Cordilleranus) Zone, may also be recognized around the world by the global distribution of Monotis salinaria and related species.

Conclusions
The Rhaetian, with its lower boundary at the base of Sturzenbaumi Zone, may be correlated with the upper part of the Koessen Formation (Eiberg Member and topmost part of Hochalm Member; Golebiowski, 1990) and is therefore in contradiction with the original interpretation of the Rhaetian stage. Biostratigraphy of this variant is based only on pelagic fauna (Krystyn, 1987) and the separation of Rhaetian from Sevatian in a majority of sequences where ammonoids and conodonts are absent is vague. Therefore this interpretation of the Rhaetian is unacceptable in high paleolatitudes - the Boreal and Notal regions.
The greater Rhaetian, including all the Sevatian with its lower boundary at the Quinquepunctatus Zone, is characterized by essential faunal changes and its equivalents on the whole may be recognized in almost all regions where topmost Triassic beds occur. The main drawback of this suggestion is its large deviation from the original interpretation of the Rhaetian stage.

The Rhaetian with its lower boundary at the base of the Reticulatus Zone is in full agreement with the principle of priority, has enough sharp distinctions of main groups of the marine invertebrates at the lower boundary and equivalents of such Rhaetian may be recognized throughout the world. Moreover, this last interpretation of the Rhaetian allows the preservation of the traditional standard scheme of stages and substages in the terminal Triassic.

Acknowledgement
We wish to thank Dr E.T. Tozer who revised the English of the present paper.

References


TRIASSIC MULTIELEMENT CONODONTS VERSUS EUSTATIC CYCLES

F. Hirsch, Geological Survey of Israel, Jerusalem

Abstract
Most Triassic multielement conodont types crossed the Permian/Triassic boundary. Anchignathodontidae range throughout the Griesbachian and Ellisoniidae until the end of the Early Triassic. Neogondolellidae offshoots include Dienerian-Spathian *Neospathodus*, Late Spathian-Early Carnian Gladigondolellinae, Anisian-Rhaetian *Paragondolella*, Ladinian *Pseudofurnishius* and *Sephardiella*, Late Carnian-Rhaetian *Epigondolella* and Rhaetian "Misikella".

Palaeobiogeography of conodonts is monitored by latitude, water depth and geographic isolation. The Early Triassic Panthalassic (mostly Boreal) Province of cosmopolite Neogondolellidae and Anchignathidontidae was bordered by the shallow to facially restricted (Smithian) Amerasian (Cratonic Cordilleran Sibero-Himalayan) Province of *Furnishius*, *Parachirognathus* and (Spathian) Western Tethys (Werfen) Province of *Hadrodontina-Pachycladina*. In the Late Spathian a low latitude pelagic Tethys Province of Gladigondolellinae appeared. Anisian through Early Carnian taxa subdivide into the low latitude pelagic Tethyan Province of *Gladi- and Paragondolella*, the mostly Boreal Panthalassic Province of the cosmopolite *Neogondolella* and *Sephardiella*, the Sephardic Province of *Pseudofurnishius* and the restricted Germanic Province. The Late Carnian-Rhaetian *Epigondolella* and the Rhaetian *Misikella* are Panthalassic Tethyan to Boreal. Norian *Paragondolella* species alone, define a Notal (Maori) Province (Jenkins and Jenkins, 1971; Marden et al., 1987). At the specific level of taxa further neritic/pelagic differentiation occurs as e.g. the Siberian Smithian *N.siberiensis* and Spathian *N.shveyrevi*, the North American cratonic Late Anisian *N.shoshonensis*, Late Carnian *P.sanueli* lineage, and Middle Norian *E. multidentata* and in the Germanic Realm the Ladinian lineage of *N.haslachensis-wattnaueri*.

Relationship between Triassic "third order" eustatic sea level cycles, conodont palaeobiogeography and conodont phylogeny is analyzed. It is tentatively suggested that eustatic sea level changes (most rises) may coincide with phylogenetic events: Griesbachian (Anisarcicus), Dienerian (Neospathodus), Smithian (Neogondolella), Spathian (Platyillosus), Late Spathian (Gladigondolella), Anisian (Paragondolella), Ladinian (Pseudofurnishius, Sephardiella), Tuvalian (Epigondolella) and Rhaetian (Misikella). As the result of a significant sea level drop and related "Saharan" salinity crisis in the western Tethys, faunal extinctions, including most conodont genera occurred during the Julian (Early Carnian) and Late Carnian-Rhaetian conodont taxa derived from *Paragondolella*.

Diversified marine environments became widely restored during the Rhaetian cycle, ending with global regression and extinction of multielement conodonts. Eustatic and phylogenetic conodont events support a Triassic stage subdivision that includes the Rhaetian as a stage.

Introduction
The starting point of this study was an attempt to reassess the phylogeny of Triassic conodonts, based on the study of the multielement apparatus. This led to the recognition of three basically different groups, all surviving the dreaded Permo-Triassic boundary.

Consequently it became obvious that the possible phylogeny of taxa, having the same apparatus, was relatively simple, once one became aware to which apparatus each single platform belongs. It also became obvious that, next to their evolution in time, a space differentiation of conodonts, controlled by latitude, depth and isolation, occurred, defining realms.
The next step consisted thus in tentatively plotting Conodont taxa into three Triassic Conodont Palaeogeographic Maps (Figs. 1-3).

The succession of Lower, Middle and Upper Triassic paleogeographies, being controlled by both local and global events, arose the question whether these changes were tectonic in origin or rather controlled by eustatic sea level changes. In other words the old question of catastrophism versus neptunism surfaced again. But this time detailed biostratigraphy based on ammonoids, conodonts and pelagic bivalves as well as absolute chronology allowed to differentiate between epeirogenic, orogenic and eustatic events.

The present study thus proposes a comparison of conodont bioevents (FOD and LOD of conodont taxa) with the global 'third order' eustatic sea level curve proposed by Haq et al. (1988).

**Triassic Multielement Conodonts**

Element taxonomy in Triassic conodonts has not yet replaced form taxonomy entirely. This is due to the fact that "reliable" multielements have still not been unilaterally accepted by conodont workers. Since Huckriede (1958), Hirsch (1969, 1981), Balogh et al. (1983), Ramovs (1977), Kozur & Mostler (1971) on one hand and Sweet (1970) on the other hand, two basically different views on Triassic multielements have been presented. This discrepancy partly rests on unsufficient relation by authors to ratio between 'platform' and 'ramiform' elements of conodont populations. The papers of Mosher (1968) and Krystyn (1983), e.g., clearly enhance the numerical relationships between P-elements and accompanying elements of their respective multielement apparatusus. This is sometimes obscured by the poor record of the non-platform elements in some samples, the reason for which may be related to primary environmental conditions, as facies, or to secondary factors as diageneisis. Preparation techniques used may also be invoked.

Three Lower Triassic multielement conodonts types are recognized: Anchignathodontid, Ellisoniid, and Neogondolellid. Formally these groups have Family rank. The statistical interrelation between the Anchignathodontid P-element and elements, formerly classified under the taxon Ellisonia (SWEET, 1970), that suggests their belonging to one single multielement (= *Hindeodus* in Sweet's Treatise).

The Ellisoniid type includes the genera *Ellisonia, Furnishus, Parachirognathus, Hadrodontina* and *Pachycladina*.

The statistical interrelation and concurrent range of morphospecies, belonging to the form genera *Neogondolella* (P-element), *Xanionathus* (Pa-element), and enantiognathid (Pb), lonchodinid (M), roundydid (Sa), prioniodinid (Sb) and hindeodellid (Sc) morphotypes similarly support their plotting into a natural apparatus. Sharing same apparatus are the genera *Neospathodus, Paragondolella, Pseudofurnishus, Sephardiella, Epigondolella* and "Misikella". The remarkable parallelism of the neogondollid apparatus with the apparatus of the genus *Gladiogondolella* suggests the Late Spathian phylogenic derivation of the latter from the neogondolellid stock. It may formally have the rank of a subfamily. *Neo- and Paragondolella* are homeomorph. Generic differentiations consist in the shape of the basal cavity or groove and the morphology of an amygdaloid (*Neospathodus, Gladiogondolella, Pseudofurnishus, Sephardiella, and Epigondolella*) versus a looipike pit (*Neo-, Paragondolella*) as well as in the continity of the phylogenic succession of monolobal to bilobal morphologies of the basal cavity, platform shape, lenght of free blade and cusp morphology. Specific differentiations consist in relative length of a free blade, length/ width/height ratios, platform ornamentation and number of denticles on the carina.

"Paedomorphic" or "neotenic retrogradation" in Post Carnian times, consisting in the reappearance of ancestral morphs, by the development of juvenile ontogenic stages as adults, may be due to the exhaustion of the genetic evolutionary potential of the conodont bearing organisms.
The Neogondolellid apparatus remains fairly the same throughout the entire Triassic. The succession however of species of Neogondolella remains problematic. Between Induan N.carinata and the array of Olenean species (e.g. N.nevadensis) there exists a Late Dienerian gap and the phylogeny of the genus across the Spathian-Anisian boundary is not well documented as well. The question remains whether the establishment of a new taxa is justified for Olenean and Middle Triassic "Neogondolella" species.

The only taxon that survived the Early Carnian extinction is Paragondolella. The platform element of this taxon reduces its platform from the Late Ladinian onward. P.polygnathiformis can develop in addition to its free blade a bifid basal cavity, that represents the transition to P.communis. Since the latter is a Paragondolella (MOSHER), the taxon Metapolygnathus (HAYASHI) becomes a junior synonym. As the result of paedomorphism (or neoteny), Norian morphs (P.navicula, P.steinbergensis) recall Middle Triassic Neogondolella. The development of nodes (e.g. P.nodoso and P.samueli group) on the platform occurs, setting in the transition to the parallel taxon Epigondolella (MOSHER). The lineage of Epigondolella consists in the Late Carnian of units with a large free blade, a bifid basal cavity and low nodes on the platform (E.echinata, E.primitia). Later on, in the Lower Norian, the bilobality of the basal cavity increases and the nodes of the platform grow into sharp denticles (E.abnetis). Orchard (1991) regards the latter as the first true representative of the taxon, a view that would require the establishment of an additional taxon. The Middle Norian group of Epigondolella poster (including the probably endemic E.multidentata forms) represents a paedomorphic development of morphs, resembling Ladinian Sephardiella, a trend culminating in the Late Norian E.bidentata.

Middle and Late Triassic recurrences of neospathid morphologies occur in the Bythinian-Pelsonian "Nicoraelia", Julian "Mosherella" and Rhaetian "Misikella". These phylogenetic "anomalies" seem to occur in periods of genetic "stress".

Sea Level Changes

The degree of resolution of the Triassic chart of sea level changes by Haq et al. (1988) has reached a level that allows to match sequences in far away regions, lithologically as well as biostratigraphically.

Sections in the Sverdrup Basin, Arctic Canada, (Embry, 1988) and the Namnl Gorge, Salt Range, Pakistan (Haq et al., 1988) serve as references for the Early Triassic. The Aegean, Hellenic, Southern Alpine, Northern Alpine and circummediterranean regions provide abundant references for the Middle and Upper Triassic (Hirsch, in press), as well as the sections of Kennecot Pt, Queen Charlotte Islands (Carter, Orchard and Tozer, 1990) and the New York Canyon, Nevada (Krystyn, 1990) for the terminal Triassic.

One can confidently differentiate global eustatic changes from local tectono-environmental "noise".

The nomenclature adopted by Haq et al. (1988) refers for the Triassic to most of the Upper Absaroka megacycle A (UAA) and to the base of UAB. Each megacycle is subdivided into numbered "second order" and "third order" cycles. A number of particular facies types can be discriminated as typical sedimentary responses to the different sea level - stands within each cycle.

Predominant sands with parallel and cross bedding and ripples are interpreted as Shelf Margin Wedges or Lowstand (L) deposits, as e.g. Gevainim Fm. (Late Anisian UAA2. 2), St. Cassian beds (Early Carnian UAA3. 1) and Raibl (Late Carnian UAA3. 2). Dolomitc limestones as e.g. Gutenstein (Anisian UAA2. 1) and coquoinid limestones as e.g. Saharonim and Riefling (Ladinian UAA2. 2) and Koessen (Rhaetic UAB1) point to transgressive deposits (T). Reef limestones as e.g. Wetterstein (Ladinian UAA2. 2) and Dachstein (Norian UAA4) may indicate highstands (H). Shales and limestones with sandstone, conglomeratic and volcanic interlayers as e.g. Partnach, Buchenstein and Wengen (Ladinian UAA2. 2) are the result of tectonic and volcanic activity, that "disturb" the
normal eustatic curve. The relative location of such deposits in relation to their basin edge give further clues as to the evolution, amplitude or intensity of eustatic cycles. Deposits such as Bunter or Bjorn Fm (Arctic Canada) represent continental edges (regressive when prograding toward the basin) and deposits such as Hallstatt facies represent seaway, channel or pelagic regime (transgressive when prograding toward the basin edge).

Ammonoid and conodont biostratigraphy provides the necessary age, palaeogeographic and environmental clues to the construction of a global Triassic scheme in space and time.

Paleogeography and Provincialism of Triassic Conodonts

Faunal Provinces share the three basic prerogatives of the classical theater: Unity of Action, Time and Space.

Faunal Provinces are characterized by different taxa of a given organism (at specific or generic level) competing for the available ecological niches (unity of Action), during the same geological timespan (unity of Time) in similar environmental-climatic, bathymetrical, chemical, physical and trophic conditions (unity of Space).

In other words when taxa, that dwelled in the same palaeolatitude, under similar conditions of temperature, depth, energy and salinity, are different, they may define faunal provinces. The cause of that difference is generally the presence of a separating landmass, distance or alien oceanic conditions (depth, temperature etc...).

The Triassic Pangea extended in both hemispheres, progressively separated into Gondwana and Eurasia by the low latitude Tethys that prograded from East to West. The Triassic Panthalassa was thus a super-Pacific ocean with westward flowing low latitude warm currents, most possibly temperate gulfstreams moving parallel to the Eurasian and Indo-Australian sides of Gondwana and cold currents moving from the boreal and austral oceans towards the equatorial zone along the American side of Pangea.

Conodonts were first recognized as excellent time markers. Their environmental dependence and provincialism has been emphasized only lately. They are strictly marine and often share the habitat of such molluscs as ammonoids and the bivalve taxa *Claraia* (Eotrias), *Daonella* (Mesotrias), *Halobia* (Carnian) and *Monotis* (Norian).

Early Triassic Conodont Palaeogeography (Fig. 1)

The worldwide distribution of *Neogondoella*, *Archignathodus* and "Isarcicella" (Early Induan) and of *Neogondoella* and *Neospathodus* (Late Induan-Olenekian) is similar to that of *Claraia*. On the west coast of North America ellisoniid genera *Fumishius* and *Parachirognathus* dwelled in Smithian times, whereas similar genera *Hadradorontina* and *Pachycladina* were found in the Spathian part of the Werfen facies of the western Palaeotethys. At the end of the Early Triassic the Neotethys seaway became characterized by the taxon *Gliadigondoella*. 
Fig. 1. Conodont palaeobiogeography of the Early Triassic: (1) Smithian Amerasian (Cordilleran - Sibero- Himalayan) Province of Furnishius-Parachirognathus. (2) Spathian Western Tethys Werfen Province of Hadrodontina- Pachycladina. (3) Late Spathian development of low latitude pelagic Tethys Province of Gladigondolella. (4) Induan-Olenekian Panthalassa.
Fig. 2. Conodont palaeobiogeography of the Middle Triassic: (1) Mostly Boreal Pan-Thalassic Province of cosmopolite Neogondoella and Sephardiella. (2) Sephardic Province of *Pseudofurnishius* (SEPH). (3) TETHYS: Low latitude pelagic Province of *Gladigondoella* and *Paragondoella*. (4) Germanic Province (GER). (5) Ameri-Boreal Province (e.g. *N.shoshonensis*).
Fig. 3. Conodont palaeobiogeography of the Late Triassic: (1) Ameri-Boreal Province (e.g. Late Carnian *P. samueli*, Middle Norian *E. multidentata*). (2) Late Carnian-Rhaetian Panthalassa (Tethys and Boreal Realms) of *Paragondolella*, *Epigondolella* and "Misikella". (3) Low Latitude pelagic Tethys realm of *Gladigondolella* (Early Carnian), *Paragondolella*, *Epigondolilla* and "Misikella" (Rhaetian). (4) Evidence of Norian *Paragondolella* (? Notal). (5) Rhaetian "Misikella" transgression. Arrows suggest Mesozoic displacements (terrane and thrusts).
Middle Triassic Conodont Palaeogeography (Fig. 2)

The Middle Triassic is a time of expanding Tethys. Its westernmost shelf regions remained however shallow and slightly hypersaline. An inland sea, communicating with the northern Tethys shelf extended over parts of Poland, Germany and eastern France, known as the Germanic Muschelkalk Province, characterized by endemic Ceratites genera and an the endemic lineage of Neogondolella (haslachensis). The entire southern Tethys shelf, extending from Arabia through North Africa to Iberia, developed Muschelkalk facies and a widely endemic fauna of ammonites (Gevanites, Israeletes, Iberites), bivalves (Costatoria) and conodonts (Pseudofurnishius), accompanied by the Tethyan bivalve Daonella and the cosmopolite conodont Sephardiella, represents the Sephardic Province (Hirsch and Marquez-Allaga, 1988). The Tethys sensu stricto is characterized by the pelagic Gladigondolella and the hemipelagic Paragondolella whereas the cosmopolitan genus Neogondolella has a worldwide distribution, including the north American Boreal Province, where endemic species of Daonella and Paragondolella developed.

Late Triassic Conodont Palaeogeography (Fig. 3)

The Early Carnian palaciobiogeography of pelagic and low latitude Gladigondolella cannot be dissociated from its Middle Triassic equivalent. The Early and Middle Carnian worldwide sea level drops generated an acute salinity crisis in the western part of the Tethys, accompanied by faunal extinctions. It represents the true turning point to the Late Triassic. The conodont taxa Paragondolella, Epigondolella and Rhaetian "Misikella" enjoyed wide cosmopolite distribution, similar to that of the bivalve taxa Halobia (Carnian) and Monotis (Norian). The distribution of the low latitude Early Norian Paragondolella hallstattensis recalls that of Late Spatian-Early Carnian Gladigondolella, and that of the Late Norian Monotis salinaria. Epigondolella extends from the Tethys to boreal regions. The distribution of the Late Norian Paragondolella steinbergensis coincides well with that of the rather low to midlatitude Monotis subcircularis, also occurring in New Zealand (Notal) terranes. In these terranes, the distinct lithologies (e.g. volcanidetric versus carbonatic) contrast with the similarity of their mutual faunas. Closely related taxa must have originated palaeogeographic domains that were not separated by alien realms. This concept of "vicinity" would infer that the areas of origin of the Late Triassic rocks of the Murihiku and Torlesse terranes, that share similar conodont and Monotis taxa, belonged within alitudinal range probably not exceeding 30 degrees.

The north American epicratonic province seems to be characterized in the Late Carnian by the group of Paragondolella samueli (Orchard) and in the Middle Norian by Epigondolella multidentata (Mosher).

During the Rhaetian rifting and transgression the last conodonts found their way as far as the British Isles (Swift, 1989).

Triassic Conodonts and Eustatic Cycles

Permian-Triassic boundary

Struggling against the faunal crowd in their receding marine environment, during the times of the fatidic shrinking of oceans, dropping sea levels, between icy seas and evaporating hypersaline gulfs, around the Kazanian-Tatarian boundary (Upper Permian) between 251 and 256 M Y ago, to be accurate (resp. sensu Harland et al, 1989 or Haq et al, 1988), all animal groups were grasping to their endangered lives but many did not make it into the Mesozoic.

Among the marine inhabitants of the post-hercynian leftovers of the world ocean, conodonts did not fare too badly as we find the latest Permian multielements of Neogondolella carinata, Ellisonia triassica and Anchignathodus typicalis well installed in their worldwide earliest Induan (Griesbachian)
The polemic around the Permian-Triassic boundary is merely the discussion of minor details concerning a natural division in biological history, retained for over 160 years (Harland et al., 1989). Irrelevant whether the boundary is located at a convenient break for brachiopod-, ammonoid-, foraminifer- or conodont biostratigraphy, the P-Tr boundary, between the Djulfian (Dorashamian) and Induan (Griesbachian) stages, is agreed upon at 245 MY (Harland et al., 1989) or 250 MY (Haq et al., 1988), following Tozer's (1967) ammonoid proposal. This Otoceras event coincides with the start of the transgressive deposits of the UAA-1. 2 cycle of Haq et al. (1988).

Lower Triassic (Fig. 4)

A convenient Griesbachian conodont marker, the short living Anchignathodus isarcicus, is first found in the O. commune ammonoid zone, in the middle part of the transgression of cycle UAA1. 2, shortly before the Late Griesbachian extinction of the ancient Anchignathodontid multielement. The start of the Nammalian (Dienerian) a stage occurs during the same transgression (UAA1. 2), marked by the first appearance of the neogondolellid genus Neospathodus (N.dieneri and N.kummeli). Later on, shortly before the Dienerian sea level highstand Neogondolella carinata disappeared. The Induan (Dienerian) highstand is marked by N.cristagalli, whereas the end of the Induan (Dienerian) coincides with the UAA1. 3 sea level lowstand (N.pakistanensis).

The start of the Olenekian (Smithian) corresponds to the transgression of cycle UAA1. 3 (Haq et al., 1988). It is marked by a new wealth of neogondolellids: Neogondolella sibirensis, N.nepalensis, N.nevadensis and Neospathodus waageni, followed later on by Neospathodus conservativus and Neogondolella milleri. In the shallow north american cratonic basins a wealth of Ellisoniids developed (Furnishius, Parachiropgnathus). The Middle Olenekian highstand of cycle (UAA1. 3) corresponds to the earliest Spathian, well defined by the appearance of the strange group of Playvillosum. The Spathian is further defined by the panthalassic Neospathodus triangularis and Neogondolella jubata. The Ellisoniid Hadrodontina and Pachycladina occurred in the shallow Werfen facies.

The transgression of Haq's et al. (op. cit) cycle UAA1. 4 is defined by Neospathodus homeri and the Late Olenekian (Late Spathian) sea level highstand is defined by Neospathodus timorensis, Neogondolella sheyrevyi and by the first appearance of the genus Gladigondolella.

The final Olenekian (Spathian) lowstand of cycle UAA1. 5 has no conodont signature.

The Early-Middle Triassic transition is characterized by further biological and tectono-environmental events: Late Spathian extinction of Ellisoniidae and of neogondolellid genus Neospathodus, appearance of Gladigondolellinae and of the genus Paragondolella, a neogondolellid homeomorph issued from Neospathodus (Mosher, 1968). These new taxa define since the latest Spathian and earliest Anisian the low latitude and more pelagic Tethyan seaway, whereas the higher latitude and shallower seas were populated by Neogondolella faunas.

Middle Triassic (Fig. 5)

Middle Triassic conodonts belong exclusively to the family Neogondolellidae, including the subfamily Gladigondolellinae.

The beginning of Early Anisian Aegean substage concurs with the transgression of cycle UAA1. 5, marked by Paragondolella aegaea in the Tethys and by Neogondolella regale in the Cordillerae realm. Its highstand coincides to the neo-Tethyan opening and progression to the Aegean region (Marcoux, 1978).
Fig. 4 Lower Triassic Eustatic Cycles, Range and tentative Phylogeny of Conodonts: The eustatic curve is after Haq et al. (1988), Upper Abasroka A supercycle (UAA), third order cycles 1.1-1.5. L Lowstand, T Transgression, H Highstand. ANCH Anchignathodontidae, ISAR "Isarcicella", ELLISON Ellisoniidae, FURN Furnishius, PAR Parachirognathus, HADR Hadrodontina, PACHY Pachycladina, NEOGONDOLLELLA Neogondolelliidae, PLATIV Plativillosus, NG Neogondolella, carin carinata, nepal nepalensis, sib sibiriensis, nev nevadensis, mill milleri, jub jubata, shev shevyrevi, NEOSPATH Neospathodus, dien dieneri, kumm kummeli, cristag cristagalli, pak pakistanensis, waag waageni, conserv conservativus, tri triangularis, hom homeri, tim timorensis, GLADI Gladigondolellinae.
Fig. 5 Middle Triassic Eustatic Cycles, Range and tentative Phylogeny of Conodonts: The eustatic curve is after Haq et al. (1988), Upper Absaroka A supercycle (UAA), third order cycles 1. 5-3. 1. L Lowstand, T Transgression, H Highstand. NEOG Neogondolella, const constricta, reg regale, sho shoshonensis, pt praetrameri, tram trammeri, momb mombergensis, hasl haslachensis, watz watznaueri, PF Pseudofumishius, hud huddei, murc murcianus, SEPH Sephardiella, tr truempi, mung mungoensis, dieb diebeli, NS Neospathodus, tim timorensis, NIC "Nicoraella", ko kockeli, PARA Paragondolella, aeg aega, bulg bulgarica, exc excelsa, incl inclinata, GLADI Gladigondolella, carin carinata, teth tethydis, mal malayensis.
Fig. 6 Upper Triassic Eustatic Cycles, Range and tentative Phylogeny of Conodonts: The eustatic curve is after Haq et al. (1988), supercycles Upper Absaroka A (UAA), third order cycles 3.1-3.1, and B (UAB), UAB1-2. L Lowstand, T Transgression, H Highstand. GLADI Gladigondolella, PARA Paragondolella, incl inclinata, pol polignathiforme, nsp newspassensis, car carnica, tadp tadpole, com communisti, sam samuelii, nod nodosa, ha hallstattensis, nav navicula, st steinbergensis, EPI Epigondolella, ech echinata, prim primitia, abn abneptis, tri triangularis, po postera group, bib bidentata group, M "Misikella".
The Early Anisian Bythinian substages correspond to the lowstand of cycle UAA2. 1., echoed by a hiatus in epicontinental waters. It is defined by the appearance of the neospathid morph "Nicoraelia".

The transgression of cycle UAA2. 1 is coeval to the base of the Late Anisian Pelsonian substages, defined by the first appearance of N.constricta, "N."kockeli, Neogondolella shoshonensis and Paragondolella bulgarica. The base of the late Anisian Illyrian substages starts during the hightstand of cycle UAA2. 1 and has no particular conodont signature, but the persistence of Pelsonian taxa N.constricta and P.bulgarica. The upper part of the Illyrian substages is defined by the appearance of N.mombergensis and by P.excelsa. The end of the Anisian stage corresponds to the lowstand of cycle UAA2. 2.

The base of the Ladinian stage is coeval to the transgression of Haq's et al. (op. cit.) cycle UAA2. 2 and most of the Ladinian Fassanian and Longobardian substages correspond to its hightstand. This time interval is defined by abundant Gladigondolella tethysis and P.excelsa in the expanding low latitude Tethys as well as by panthalassic Neogondolella and Sephardiella. Pseudofurnishius dwelled in the sephardic epigondwanic shelfscas and endemic neogondolellids in the germanic internal sea. The Longobardian is specifically defined by G.malayensis, P.inclinata and S.mungoensis, the last occurence of Neogondolella trameri occurs at the end of the hightstand of UAA2. 2, whereas the Ladinian ends in the lowstand of Haq's et al. (op. cit.) cycle UAA3. 1 with S.diebeli (ammonoid zone of Frankites or lower part of the "Cordevolian" substage). This lowstand (resp. 232 or 235 MY according to Haq et al. or Harland et al., op. cit.) is globally characterized by extinctions and catastrophes, as e.g. the development of huge salt and gypsum deposits around the western Tethys and the stratigraphic break between Kahiikuan and Oretian in New Zealand (Campbell, 1990), synchronous to massive faunal extinctions of molluscs (e.g. bivalves) and crinoids (Johnson and Simms (1989)).

Late Triassic (Fig. 6)

The Early Carnian transgression of the Julian substages is marked by the appearance of the neospathid neotenic morph "Mosherralla" newspassensis during the transgression of cycle UAA3. 1, whereas Paragondolella camica defines its hightstand at the end of which the pelagic Gladigondolellinae became extinct. Only Paragondolella survived the lowstand of the Tuvalian cycle UAA3. 2, and its stock secured the survival of conodonts in the later Carnian (Tuvalian) transgression of cycle UAA3. 2, defined by Paragondolella polygnathiformis, P.nodosa and a lineage of Cordilleran endemic species (e.g. P.samueli, ORCHARD). The hightstand of the Tuvalian cycle UAA3. 2 is marked by P.communis and by the first appearance of Epigondolella echinata. The end of the Carnian is coeval with the rather short lowstand and transgression of cycle UAA4 (Epigondolella primitia).

The base of the Norian stage corresponds to lower part of the hightstand of cycle UAA4. The lower Norian substages is defined by Paragondolella hallstattensis and the continued lineage of Epigondolella abnepesis and E.triangulatis as well as the appearance of Paragondolella navicula. The middle Norian substages corresponds to the upper part of the hightstand of cycle UAA4, being defined by the neotenic morphs of the Epigondolellaposteria group and of E.bidentata. The latter may extend to the Rhaetian stage, as does P.steinbergensis. The Late Norian substages corresponds to the lowstand of cycle UAB1, with no further conodont signatures.

The transgression and hightstand of cycle UAB1, marked by the neospathid morphs "Misikella" (e.g. hemsteini and posthemsteini) represent the lower and middle parts of the Rhaetian stage, whereas its upper part corresponds to the lowest stand of cycle UAB2, its transgressive stand belonging already to the Lower Jurassic Hettangian stage, devoid of conodonts.

Tectono-environmentaly the Rhaetian (Early Cimeric) events include a worldwide extension of the
marine realm, as witnessed by the inundation of Britain ("Misikella"). Biological events during that time interval include speciations and radiation of radiolarians (Carter, 1991) and calcareous nannoplankton (Moshkovitz, 1982), followed by the extinction of conodonts and almost all ammonoids.

It is remarkable that Haq et al. (op. cit) have put the limit between supercycles UAA and UABat the traditional Norian-Rhaetian boundary. Since, following Haq et al. 's (op. cit ) usage, stage limits are usually at the limit between a cycle's lowstand and the start of its transgression, the insertion of the ammonoid zone of cordilleranus (= quinquenectatus) and its cortege of Monotis, coeval to the lower global sea level stand of UAB1, in the Late Norian is no anomaly. Consequently the Rhaetian corresponds to a natural transgression, highstand and lowstand, coeval to the North American amoenum and crickmayi ammonoid zones or Tethyan reticulatus, stuerzenbaumi and marschi ammonoid zones.

The palaeogeographic distribution of Norian taxa is worldwide. However, Paragondolella is the only taxon found in the material from terranes, mostly originating Tethyan low to middle latitudes, presently in middle to high notal latitudes (New Zealand). Epigondolella occurs abundantly from the Tethys to the terranes and cratons presently in the northern hemisphere. Some taxa of the the genus Epigondolella are endemic to boreal cratonic realms only.

Conclusion

Palaeogeographic distribution of conodonts is monitored by latitude, depth and tectono-environmental isolation.

Conodont speciation and radiation occurs during transgressions and eustatic highstands. Conodonts, being tiny internal parts of a larger nektonic ?protocordate animal, evolved with less differentiation and less frequent changes than e.g. ammonoids. They may have nevertheless been particularly sensitive to the dramatic changes caused by changing sea levels and the "cortege" of accompanying side effects in the trophic chain, geography and size of their ecological niches, temperature, depth and salinity. Furthermore "cosmic" effects may have affected the genetic baggage of conodonts during the last 10 million years of the Triassic, until their final extinction.

Paraphrasing Magaritz (1991) it can be said that "since the formulators of the geological timescale used profound changes in fossil assemblages and prominent lithological breaks to divide the geological time, most time boundaries coincide with major extinction and/or radiation events. " A match between conodont bioevents and a global sea level curve is therefore most natural.

Stage boundaries correspond generally to the end of eustatic level lowstands. The base of a stage coincides generally with transgression, and accompanying new speciations and radiations. The Triassic third order cycles of Haq et al. (1988) correspond to the stages and substages given in table 1.

The question whether Anisian-Ladinian boundary coincides with the transgression (Nevadites/Neogondolella trammeri) or highstand (Eoprotrachyaceras curionii/Sephardiella) of cycle UAA2. 2 remains open. The Rhaetian stage includes the ammonoid zones amoenum and crickmayi (reticulatus, stuerzenbaumi and marschi) that concur with the volume of 'Misikella'. This time interval corresponds to the maximal development of the Koessen Formation in the Northern Calcareous Alps (Tirolikum), Austria (in Golebiowski, 1990). It is coeval with the proposal of Dagys (1988).
<table>
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**TABLE 1:** Triassic third order cycles and major bioevents
References


MICROFAUNA FROM THE UPPER TRIASSIC OF KARAVANKE MTS (SLOVENIA)

T. Kolar-Jurkovsek, Geoloski zavod Ljubljana, Dimiceva 14, 61000 Ljubljana

Abstract
The stratigraphical sequence at Sija in Karavanke Mts is composed of Upper Triassic platy limestone. A rich fossil fauna has been recovered. Zonal subdivision is based on conodonts. Two conodont zones, lower (Epigondolella bidentata-R.Z.) and upper (Misikella hernsteini-A.Z.) have been distinguished. The lower part of the bidentata-R.Z. is characterized by the cooccurrence of the E. bidentata and E. cf. humboldtensis, while the upper part of this zone is marked by the sole occurrence of index conodont taxa. Hernsteini-A.Z. is recognized by the presence of M. hernsteini in association with E. andrusovi in its lower portion. The collections of the higher part of the sequence also include ostracod species of Dicerobairdia bicornuta.

Introduction
This report deals with biostratigraphical study of Upper Triassic sequence at Sija in Karavanke Mts. Beside marker conodont taxa isolated microfauna also include an abundance of foraminifers, ostracods, and fish remains. Biostratigraphical dating of the sequence is based on microassemblages, as no identifiable associated macrofaunas were found. Present detailed biostratigraphic study of a short Upper Triassic sequence in Karavanke Mts emphasizes the extraordinary significance of conodonts as indicative microfossils in making biostratigraphic subdivision. Conodont assemblages from Karavanke Mts compare well with the faunas of other regions of the Tethyan-Pacific Realm. Correlation with assemblages from Eastern Alps and Western Carpathians is given.

Lithostratigraphy
In the roadcut approximately 200m east of the mountain hut at Sija in Karavanke Mts (Fig.1) a thin unit of carbonate rocks is exposed. On the geological map and explanation of the sheet Celovec these beds have been assigned to the Julian and Tuvalian substages (Buser 1980 a,b). During a program to establish the "Slovenian Geological Route" a sample for conodont analysis was collected by S.Buser. It yielded abundant microfauna. Therefore it was decided to study this section more in detail.

The carbonate sequence is approximately 10 m thick. It is mainly composed of micritic and sparitic limestone and in some places is marly. Some limestone beds (with thickness varying between 5 and 50 cms) contain nodules of pebbles. A 40 cm thick calcarenite bed occurs and contains frequent ammonoid and bivalve fragments. The beds are dipping 40 northeast.

Material and methods
Samples with minimum weight of 2 kg were collected. They were treated in mono-chlor acetic acid following standard conodont preparation techniques. Frequency of conodonts is approximately 10 elements per kg of rock, while foraminifers and ostracods are more abundant. Occurrences and vertical ranges of conodont taxa found in studied sequence are given in Figure 2.
Figure 1. Location map of the studied section in Slovenia.

Figure 2. Distribution of microfauna in the Sija section.
Biostratigraphic Correlation and Conodont Zonation

Due to the problem of "Rhaetian stage", age assignment of the youngest Triassic conodonts is rather difficult. Attempts at resolving this problem have been made by a number of authors studying the biostratigraphy of the Koessen and Zlambach beds. As a result, several re-definitions and subdivisions of the youngest Triassic stacta have been proposed lately. They generally differ in a) definition of Rhaetian as independent stage or substage within Norian stage and b) in correspondence with Rhaetian ammonoid zones/subzones (Mostler et al. 1978, Richter-Bernburg 1979, Wiedmann et al. 1979, Gazdzicki et al. 1979, Krystyn 1980, 1987, Golebiowski 1986).

Biostratigraphic subdivision of the Sija sequence is accomplished by microfossils. They are correlated with conodont associations from localities in the Eastern Alps and Western Carpathians. The stratigraphical interval at Sija is marked by the presence of four conodont taxa: *Epigondolella andrusovi*, *E.bidentata*, *E. cf. humboldtensis* and *Misikella hernsteini*. Vertical ranges of conodont species are interpreted in accordance with their ranges illustrated by Gazdzicki and co-authors (1979-table 1) and were considered in a later conodont zonation of Kozur (1980). The following two conodont zones have been recognized:

**Epigondolella bidentata-R.Z.**

This conodont zone is marked by the occurrence of index conodont species (samples 1-5), associated by the elements of *E. cf. humboldtensis* in lower part of this zone (samples 1-4). According to Orchard (1983) the stratigraphic range of bidentata-R.Z. is equivalent to the Gnomohololites cordilleranus ammonoid Zone and at least part of the Cochloceras amoenum Zone. First appearance of *E. bidentata* within Mesohimavatites colombianus ammonoid Zone is not precisely defined yet (Kovacs & Kozur 1980, Krystyn 1980, Orchard 1983).

**Misikella hernsteini-A.Z.**

Conodont marker taxa *M. hernsteini* is characterizing the upper part of the Sija section (samples 6,7) being accompanied by the elements of *E. andrusovi* in lowest portion of this zone (sample 6). Kovacs and Kozur (1980) interpret this species to occur in Cochloceras suessi Zone. Owing to the abundance of the elements *E. andrusovi* and *M. hernsteini* two conodont zones were proposed (*E.andrusovi-A.Z. and M.hernsteini-A.Z.*) (Gazdzicki et al.1979, Kozur 1980); whereas Krystyn (1980) and Budurov & Sudar (1990) claim, that bidentata Zone extends to the top of the suessi ammonoid Zone as they also include all forms lacking platforms to *E. bidentata*.

Microfauna from the uppermost part of the examined section has not yielded any individual with platform. Nonplatform epigondolellid elements have been therefore separated as an independent species i.e. *E. andrusovi*.

**Other Microfauna**

Other microfauna includes foraminifers, ostracods and fish remains. Foraminifers are a common component of all micro-associations. Among representatives of prevailing families Ophthahalmiidae, Nodosariidae, Ammodiscidae, Involutiniidae and Duostominidae are also important. The foraminifer fauna is largely recrystallized and reliable taxonomic determination of only a minor part of the fauna is possible. The following taxa have been recognized, none of which has stratigraphic significance:

*Ammodiscus sp.*
*Glomospirella densa* (Reitlinger)
*Glomospirella sp.*
*Tetraaxis humilis* Kristan
Gaudryina triassica Trifonova
Ophthalmidium lucidum (Trifonova)
Ophthalmidium triadicum (Kristan)
Ophthalmidium sp.
Nodosaria sp.
Rectoglandulina cf. holocostata Kristan-Tollmann
Rectoglandulina sp.
Dentalina sp.
Lenticulina (Lenticulina) subquadrate (Terquem)
Lenticulina sp.

Ostracods are diverse and abundant but only two families are represented. Polycopidae are very significant component of all faunas. Also, there are several undescribed species of Polycopae. The upper part of the section (samples 5, 6, 7) is marked by the occurrence of Bairdiidae. These collections are dominated by sculptured forms and include abundant species of Dicerobairdia bicornuta.

Fish remains are present in a few samples only, with sparse occurrences of genera Acodina (sample 2) and Nurrella (sample 4).

Significance of Micropaleontological Data for Slovenian Biostratigraphy

Four conodont taxa have been recognized in the studied sequence at Sija. Two of them (E. bidentata and M. hemsteini) have been found in Slovenian territory so far. Assemblage of lower E. bidentata-R.Z. (including E. abneptis, E. bidentata, E. postera and Gondolella steinbergenis) was established at Smarjetna gora (Kolar-Jurkovsek 1991).

Elements of Misikella hemsteini were recovered in western Slovenia only. On the Pokljuka plateau this species was found in Sevatin strata of Hallstatt facies together with elements of G. steinbergenis (Kolar-Jurkovsek et al. 1983).

The studied succession at Sija encompasses a confined stratigraphic interval, but its presence adds substantially new information on Sevatin micro-assemblages. Two conodont zones can be identified. Later yield the ostracod Dicerobairdia bicornuta; it appears in the highest part of bidentata-R.Z. and in hemsteini -A.Z.

Systematic Paleontology

Phylum: Conodonta
Class: Conodonta Eichenberg, 1930
Order: Conodontophorida Eichenberg, 1930
Genus: Epigondolella Mosher, 1968

Epigondolella andrusovi (Kozur & Mock, 1972)
Pl.1, Fig. 5
1972 Parvigondolella andrusovi n.gen.n.sp.-Kozur & Mock, 4-5,Taf.1, Fig.11, 12.
1972 Parvigondolella andrusovi Kozur & Mock - Kozur, Taf.7, Fig. 10.
1972 Parvigondolella andrusovi Kozur & Mock - Kozur & Mostler, Taf.4, Fig 4.
non 1976 Epigondolella andrusovi (Kozur & Mock) - Budurov, Pl.5, fig.6.
non 1977 *Epigondolella andrusovi* (Kozur & Mock) - Budurov, 45-46, Pl.5, figs. 8,9.
1980 *Parvigondolella andrusovi* Kozur & Mock - Kovacs & Kozur, Taf.15, Fig.3.

Material: eight specimens (sample 6).

Description: Unit is small and looks like ramiform conodont. Upper surface has extended row of laterally compressed denticles with pointed free tips and fused basal parts. Number of denticles varies between 7 and 9. The highest denticles are located at anterior half or third of the unit. Posterior two or three denticles are short and stronger, sometimes they stand isolated. Entire lower side is marked by narrow basal groove. Small basal pit is situated around posterior third of unit.

Remarks: *E. andrusovi* is differentiated from *E. bidentata* in the absence of a pair of lateral denticles.

*Epigondolella bidentata* Mosher, 1968
Pl.1, Figs. 1-4

1958 *Polygnathus abneptis* n.sp.- Huckriede, 156-157, Taf.14, Fig.32, 58.
1968a *Epigondolella bidentata* n.sp. - Mosher, 936, Pl.118, Figs.31-36.
1971 *Tardogondolella mosheri* n.sp. - Kozur & Mostler, 15.
1971 *Epigondolella bidentata* Mosher - Sweet et al., Pl.1, Fig.30.
1972 *Epigondolella bidentata* Mosher - Kozur & Mock, Taf.1, Fig.13-16.
1973 *Epigondolella bidentata* Mosher - Krystyn, Taf.5, Fig.7.
1976 *Epigondolella andrusovi* (Kozur & Mock) - Budurov, Pl.5, fig.6.
1977 *Epigondolella andrusovi* (Kozur & Mock) - Budurov, 45-46, Pl.1, figs.5,6, pl.2, figs.3,5,6.
1977 *Epigondolella bidentata* Mosher - Budurov, 45, Pl.1, fig.7, Pl.2, fig.4.
1977 *Epigondolella bidentata* Mosher - Sweet in Ziegler, 157-158, Pl.1, fig.6.
1977 *Epigondolella mosheri* (Kozur & Mostler) - Sweet in Ziegler, 173-174, Pl.1, fig.8.
1979 *Metapolygnathus bidentatus* (Mosher) - Gazdzicki et al., Pl.5, figs.10-12.
1980 *Metapolygnathus bidentatus* (Mosher) - Kovacs & Kozur, Taf.15, Fig.1.
1980 *Metapolygnathus mosheri* (Kozur & Mostler) - Kovacs & Kozur, Taf.14, Fig.6.
1980 *Epigondolella bidentata* Mosher - Kozur, Pl.14, figs. 1-3, non figs.4-6
1980 *Epigondolella bidentata* Mosher - Wardlaw & Jones, 900, Pl.64, fig.10.

Material: fifteen specimens (samples 1, 2, 4, 5).

Description: Small and slender unit is subsymmetrical in upper view. Platform is usually small or totally reduced. When present, platform is sometimes developed as widened base of lateral denticles. A single strong spike-like denticle is developed on either side of middlendlengh or posterior part of the unit. Carina bears 7 to 11 laterally compressed denticles with long free tips. Denticles of free blade are the highest and posterior denticles are low. Last denticle is inclined posteriorly. Slit-like basal groove entirely occupies lower conodont surface. Elliptical basal pit is located in posterior third of the
unit.
Remarks: *E. bidentata* can be clearly distinguished from *E. postera* and *E. andrusovi* by the number of lateral denticles; *E. postera* is characterized by numerous marginal denticles, while they are completely absent in *E. andrusovi*.

*Epigondolella cf. humboldtensis* Meek, 1987

Pl.1, Figs. 7,8
1984 *Epigondolella humboldtensis* n.sp.- Meek, Pl.1, figs.5-11,19.
1987 *Epigondolella humboldtensis* n.sp.- Meek, 196-197, Fig.1.1-1.4.

Material: sixteen specimens (samples 1 and 4).
Description: Elongate platform is developed along half of the unit length. Posteriorly it tapers to a point. Lateral platform margins are ornamented with several denticles; one prominent denticle on either side of the anterior platform is typical, additional denticles are smaller. Carina is composed of 4 to 7 discrete nodes and is anteriorly continuing as high free blade. In most specimens at hand, free blade is broken off. Lower side possesses distinctive groove which may occupy even half of unit width. Keel terminates into a point. Small basal pit is situated in the center.
Remarks: Exemplars of *E. cf. humboldtensis* from the studied section are much larger than *E. bidentata* what is in accordance to the statements of Meek (1987). In Norian of Nevada *E. humboldtensis* is reported from the sequence which corresponds to the interval with *E.bidentata* association (Meek 1987).

Genus: *Misikella* Kozur & Mock, 1974
*Misikella hermsteini* (Mostler, 1967)

Pl.1, Fig. 6
1967 *Spathognathodus hermsteini* n.sp.- Mostler, 182, Abb.1, Fig.1a-c.
1968a *Neospathodus lanceolatus* n.sp.- Mosher, 930, Pl.115, figs.10.11, non fig.7.
1971 *Neospathodus hermsteini* (Mostler) - Sweet et al., Pl.1, Figs.2,3.
1973 *Neospathodus hermsteini* (Mostler) - Sweet in Ziegler, 175, Pl.1, Fig.5.
1978 *Misikella hermsteini* (Mostler) - Mostler et al., Taf.1, Fig.11-19, Taf.2, Fig.5-7.
1979 *Misikella hermsteini* (Mostler) - Gazdzicki et al., Pl.15, Fig.3-6.
1980 *Misikella hermsteini* (Mostler) - Kovacs & Kozur, Taf.15, Fig.4-7.
1980 *Misikella hermsteini* (Mostler) - Krystyn, Pl.14, Figs.10-12.
1982 *Misikella hermsteini* (Mostler) - Nagao & Matsuda, Pl.1, figs.9-11.
1983 *Misikella hermsteini* (Mostler) - Kolar-Jurkovsek et al., 150, Tab.8, sl.2.

Material: nine specimens (samples 6,7).
Description: Unit is symmetrical in oral view. Basal cavity is posteriorly slightly expanded. There are laterally compressed denticles (3 to 5 in number) arranged in carina and they have fused bases. Denticles are inclined posteriorly, their height increase gradually to the last one which is strongest. Aboral edge is almost straight in lateral view. Shallow elliptical basal cavity which has rounded posterior edge occupies the whole lower surface.
Remarks: Main criteria in distinguishing *M. hemsteini* and *M. posthemsteini* Kozur & Mock is heart-shaped cavity outline of the latter.

**Phylum: Arthropoda**

*Subclass: Ostracoda Latreille, 1806*

*Order: Podocopida Mueller, 1894*

*Suborder: Podocopina Sars, 1866*

*Family: Bairdiidae Sars, 1888*

*Genus: Dicerobairdia Kollmann, 1963*

*Dicerobairdia bicomuta* Kollmann, 1963

Pl. 1, Figs. 9, 10

1963 *Dicerobairdia bicomuta* n.sp.- Kollmann, 182-183, Taf.1, Fig.3-8, Taf.9, Fig.1,2.

1970 *Dicerobairdia bicomuta* kollmanni n.sp.- Kristan - Tollmann, 292-293, Taf.37, Fig.1,2.

1971 *Triebelina* (Triebelina) *bicomuta* (Kollmann) - Bolz 192-195, Taf.9, Fig.132-136; Abb.26.

1980 *Dicerobairdia bicomuta kollmanni* - Kristan-Tollmann et al., 186, Taf.8, Fig.5-9.

**Material:** ten specimens (samples 5, 6).

**Description:** Carapace is subhexagonal in lateral outline. Dorsal margin is tripartite, its central part being straight; in left valve only slightly curved. Ventral margin is long and straight. Subdorsally two horn-like prolongations are located. Below horn bases, median swelling extends horizontally. Thick ridge tends subparallel to the ventral margin. Carapace surface is granulose or covered by pustulated-like bulges.

**Remarks:** This species has been described from Sevatan strata of Iran and Rhaetian of Alps in Austria. Sohn (1968) reports *Dicerobairdia* n.sp. 1 resembling *D. bicomuta* from Carnian strata of Israel.

**Repository:** Microfauna, illustrated as well as unfigured material, is deposited with Ljubljana Geological Survey (Geologski zavod Ljubljana) under numbers GZL 2290, 2450-2456. The SEM photographs were taken by J.Rode (Institut za biologijo, Ljubljana) and Z.Cadez-Pecar (Iskra-Keramika, Ljubljana).

**Phylogenetic Considerations**

During the Norian rapid evolution of genera Epigondolella occurred. Evolutionary changes were reflected in overall size reduction and gradual reduction of the platform with simultaneous reduction of marginal denticles. General agreement as to composition of the phylomorphogenetic lineage *E. abneptis-E. posteras-E. bidentata* has been used by Mosher (1968b), Kozur & Mostler (1971), Trammer (1974), Vrielynck (1978), Kolar (1979), Krystyn (1980) and Orchard (1983). Norian epigondolellids from the Pardonet Formation, British Columbia were studied by Orchard (1983). He examined eight successive *Epigondolella* populations and their evolutionary relationship. For some Norian epigondolellids a new generic name Mockina was introduced by Kozur; it corresponds to "Epigondolella" sensu Budurov & Sudar (1988) without "E": *echinata* (Hayashi) and platformless forms. The principal distinction of these two genera is in the different ornamentation of the platform margins: "Epigondolella" is distinguished by node development while Mockina bears long denticles" (Kozur, 1990b). At present, generic name Epigondolella is retained in accordance with the gradual
evolutionary changes noted by Orchard (1983). Further development of Norian epigondolellids included forms lacking platforms. Such individuals are assigned to the genera "Parvigondolella". "Parvigondolella" evolved from E. bidentata. Transitions from the youngest representatives of E. bidentata with platform reduced to a single denticle on both sides of the element to forms with a single denticle on one side only (or platformless) "Parvigondolella" have been observed (Kozur 1990a). In a chapter on the apparatus of gondolellid conodont and its evolution Kozur (1990b, 427-429) states that Mockina and "Parvigondolella" have similar apparatuses but certain elements differ in form at the genus level. Evolutionary changes affected whole apparatuses: they are manifested in complete platform reduction in P-elements while other elements underwent only slight evolutionary modifications. It is evidently that in taxonomy of final platformless members of evolutionary lineage discussed morphological criteria prevailed. Clark et al.(1981) regard "Parvigondolella " as merely the ultimate stage in the evolution of Epigondolella, not as separate genus. Sharing the opinion of Clark et al.(1981) platformless gondolellid elements from Sija are here identified as E.andrusovi.

Acknowledgments
I wish to thank Dr.Stanko Buser (University of Ljubljana) who kindly provided trial sample, valuable information about the locality and for his kindly accompanying me in the field. I am especially grateful to Drs.David L.Clark (University of Wisconsin, Madison) and Leon Krystyn (University of Vienna) for critical reading of the manuscript and offering useful advice for its improvement. The linguistic correction by Dr.David L.Clark is gratefully acknowledged as well.

References


PLATE 1.

Figs.1-4 Epigondolella bidentata Mosher. Bidentata-R.Z. Samples 4 (2453); figs. 1, 2 and 5 (2452); figs. 3, 4, (150x).

Fig. 5 Epigondolella andrusovi (Kozur & Mock). Hernstein-A.Z. Sample 6 (2452), (150x).

Figs.6a,b Miskella hernsteini (Mostler). Hernstein-A.Z. Sample 6 (2452), (150x).

Figs.7,8 Epigondolella cf.humboldtensis Meek. Bidentata-R.Z. Sample 4 (2481), (150x).

Figures 9, 10 Dicerobairdia bicornuta Kollmann, hernstein- A.Z., sample 6 (2452), (50x).
EVENTS RELATED TO THE PERMIAN / TRIASSIC BOUNDARY IN TETHYS AND BIARMIA

G.V. Kotlyar and G.N. Sadovnikov, VSEGEI, Sredniy prospect 74, St Petersburg, Russia

Introduction
A presumed gap in the top beds of the Permian section in the Tethys Realm has not been confirmed by new data. Therefore, the Lyudyanza horizon in south Primorye, which is subdivided into two zones, *Iranites* sp. (lower) and *Linchengoceras melnikovi* - *Colaniella parva* (upper), apparently represents the full range of the Dorasham stage. In addition to index species, abundant *Colaniella* occur: *C. leei*, *C. pulchra*, *C. sikouensis*, *C. cylindrica*, *Pseudocolaniella xufulingensis* and fusulinids- *Reichelina* spp., *Shindella* wp. A, *Staffella zisonghengensis*, St. ex gr. *orientalis*, *Eonankinella cf. humanensis* (Vuks and Chediya, 1986). Most species are characteristic of the Dorashamian and Changxingian in southern China, the southeast Pamirs, the Upper Toyoma Series of Japan, Greece, Malaysia, and Thailand.

New Biostratigraphic Data
New information on conodonts from middle Asia facilitates the recognition of Dorashamian deposits (Davydov et al., 1991). Conodonts were found in the Takhtabulak suite of the southeast Pamirs, crowning the section of Permian deposits. They were previously applied to Dzhulfian (Kotlyar et al., 1989) or even to Midian (Kotlyar et al., 1983). *Gondolella subcarinata* occurs in the middle part in the Igrimjuz section and *Gondolella planata* was found in the top of the Korteke section at the boundary with the Triassic. In addition to these conodonts, brachiopods similar to north Caucasus brachiopods (Grunt and Dmitriev, 1973; Kotlyar et al., 1983), a fusulinids assemblage of the Shindella pamirica-Sh. simplicata Zone, and smaller foraminifers, similar to Lyudyanza assemblage of south Primorye (Kotlyar et al., 1983) occur in abundance. *Reichelina, Shindella, Nankinella, Staffella, and Colaniella (C. parva, C. media, C. lepida, C. etalis)* occur most frequently, single *Palaeofusulina* also occur. A number of species are known from Changxingian of southern China (Rui and Sheng, 1981) and also from Upper Permian deposits of the northern Caucasus and Japan. Obtained data agree well with paleomagnetic data (Davydov et al., 1982; Kotlyar et al., 1984).

In the northern Caucasus, Nikitin-Urushenian deposits, which are facial analogues, include diverse highly developed *Palaeofusulina-P. nana, P. sinensis, P. wangi, P. ellipsoidalis, Parananlingella labensis*, abundant highly developed *Colaniella, C. nana, C. media, C. parva, C. densecamerata, C. cylindrica* in addition to abundant brachiopods and single *Claraia caucasica* Kluk et Tkach. The foraminiferal assemblage is undoubtedly Dorashamian and almost identical to the Upper Changxingian assemblage of southern China (Rui and Sheng, 1981). The Dorashamian age of the Takhtabulak suite of the southeast Pamirs, and Nikitin-Urushenian deposits of the northern Caucasus, is presently disputed only by Y.D. Zakharov (Kotlyar et al., 1983) on the basis of ammonoid determinations.

In spite of the completeness of the Permian section in the various regions studied, the character of the Permian/Triassic boundary cannot be established because lower Triassic horizons are obscure. The most complete continuous Permian/Triassic section in the southern part of the USSR within the Tethyan Realm is known only in the Transcaucasus. Complex study of transitional Permian/Triassic sections and reliable correlation of zonal succession according to various groups of fauna (especially ammonoids and conodonts), facilitates the tracing of detailed changes in faunal associations at the boundary and gives evidence as to its preferable orientation.
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Of particular interest are new occurrences of rich assemblages of marine fish (or ichtyoliths) remains, collected from the upper part of the *Paratirolites* beds in a stratotype of the Dorashamian. M.G. Minikh and A.V. Minikh, who examined this collection, noted the presence of shark teeth (*Hybodus of. sasseniensis* Stensio and *H. cf. microdus*, Stensio) previously described in the Lower Triassic of Spitsbergen (Kotlyar, 1991). Taking into consideration the insufficient study of Late Permian and Early Triassic ichtyofauna of the Tethys and its relation to ichtyofauna from continental deposits of the East European Platform, the complex age is estimated to be no older than Early Triassic.

The full succession of Upper Permian and Lower Triassic deposits at the Permian/Triassic boundary in Iran and in the Transcaucasus can hardly give rise to doubt. Occurrence of an assemblage of smaller foraminifers, similar to Upper Changxingian foraminifers of southern China, in *Paratirolites* beds (Pronina, 1989), Upper Changxingian ammonoids in the lower part of red clays (Zakharov, 1985), continuous succession of conodont Subcarinata-Parvus-Isarcicella Zones in transitional beds indicate both completeness of the section and occurrence of analogues of the Otoceras Zone in red clays. All specialists who studied these sections in detail (Gakharov, 1985, 1988; Pyatakova, 1983; Grigoryan, 1990; Kotlyar, 1991) came to similar conclusions. Analogues of the Otoceras woodwardi zone were established in the stratotype section based on conodonts, possessing a similar succession to the type section of the woodwardi Zone. It is interesting to note that the Permian character of the biota is preserved in the Parvus Zone of the Transcaucasus in spite of scarce organic remains (Bando et al., 1980; Sheng et al., 1984; Bhatt and Arora, 1984; Broglio Loriga et al., 1988). Permian conodonts-*Gondolella orientalis* and *G. subcarinata, H. typicalis*, brachiopods-*Araxathys minor*, and ostracods-*Healdinella dorashamensis* and *H. splendidia*, continue to exist here. Simultaneous appearance of abundant *Claraia, Ophiceras (Lytophiceras)* sp., *Isarcicella isarica* occur at the base of the Karabaglyar suite above algal limestones. The only representative of smaller foraminifers, *Nubeculinella* genera, occur 0.5 m higher. A similar conodont succession occurs in most transitional Permian/Triassic sections in the southern Alps, Iran, the Himalaya, the Salt Range, southern China and Tibet.

Direct correlation of Upper Permian sections of the Tethys with continental deposits of western and eastern Europe is impossible. Paleomagnetic data, however, indicate approximate correspondence of the upper boundary of the Tatarian to the middle part of the Dzhulfiyian. Information on miospores, vertebrate fauna and conchostracans confirms this conclusion. In particular, Novozhilov correlates the Upper Tatarian stage on the basis of conchostracans with the Upper Newcastle Series and the lower Narrabeen Group of eastern Australia, which, in turn, are correlated by Foster (1979) on the basis of palynological data with the Chidru Formation of the Salt Range (Dzhulfiyian). Similar correlations were proposed by Anderson (1977) on the basis of vertebrates and by Balmr (1979) and Gomankov (1988) on the basis of palynological data. Miospore assemblages from eastern Greenland, which are quite similar to those from the Russian Platform, enable a direct correlation of the Upper Tatarian stage with the Posidonia shales, and Productus and Martinia limestones of Greenland, which correspond to the upper Midian or lower part of Dzhulfiyian in the Tethyan scale (Gomankov, 1988). Gomankov places the section interval from the Dzhulfiyian to the middle of the Otoceras woodwardi Zone, which is poorly characterized by spores and pollen all over the world, as the Paleozoic/Mesozoic boundary. The palynological characteristics of this interval in the Salt Range and eastern Greenland show that the Permo-Triassic elements are mixed. Gomankov presumes that it is with this interval and, thus, to the break between the Tatarian and Vetluga deposits of the Russian Platform, that the volcanogenic sedimentary sequence of Central Siberia corresponds. These deposits occur on the palynologically well-characterized Upper Permian sediments, correlated with the Tatarian stage of the Russian Platform, and yielding mixed "Permian" and "Triassic" elements. A peculiar Tunguska palynological assemblage, which has no equivalents outside Siberia, is characterized by a mass development in its upper part of typical Permian pollen, including *Lueckisporites virkkiae* Pot. et Ul., a high content of *Protohaploxypinus* pollen, and appearance of
Indospora and Triquiritites spores. Since the above-mentioned stratigraphic interval represents a significant range, and only the small, uppermost part belongs to the Triassic, there is no reason to assign the entire volcanogenic sedimentary strata of central Siberia to the Triassic. Sadovnikov is of a similar opinion regarding the age of volcanogenic sedimentary deposits of central Siberia. He believes that the Gagary, Ostrov and Tutonchan horizons correspond to the Upper Tatarian. The overlying Lebedev, Hungtukun, Putoran, and Marinin horizons have no equivalents in the Russian Platform; they will, most likely, correspond to a break between the Upper Tatarian and Vetluga-deposits (Sadovnikov, 1991). Sadovnikov correlates only the Ustkelter horizon with the Vetluga Series.Otoceras Zone, recorded on the eastern side of the Verkhoyanye Ridge can, in his opinion, correspond to the upper Marinin or lower Ustkelter horizons. The presence of abundant Lueckisporites in volcanogenic deposits of the Tunguska Basin, indicated by Kozur (1989), as well as in Zechstein, Dzhulfian, to a certain extent, confirms the Permian age of the Siberian volcanogenic-tarrogenous formations. At any rate, if it is presumed that the Permo-Triassic sedimentation in central Siberia was continuous, a certain part of the deposits, above the Upper Tatarian Gagary Ostrov horizon, corresponding to a break in sedimentation on the Russian Platform or the Dzhulfian Dorashamian deposits of Tethys, should be assigned to the Permian. These data are also confirmed by the presence of the Permian megaspores in the lower parts of the Bundsandstein (Fuglewicz, 1987; Virgili, 1991) and the Werfen Formation (Visscher et al., 1988).

As to the position of the boundary in marine facies, the traditionally used boundary at the base of the Otoceras woodwardi Zone does not seem good because of a rare occurrence of index-species in the sections of the Tethyan Realm. In Biarmi (Boreal) Realm the O. boreale Zone corresponds with the Otoceras woodwardi Zone, whereas the O. concavum Zone is synchronous to the upper part of the Dorashamian or Changxianian and is, doubtless, Permian (Sweet, 1979; Kozur, 1981). While drawing the boundary at the base of the concavum Zone, shall we be able to draw it in the Tethyan sections. The boundary at the base of the Hindeodus parvus Zone, proposed by some specialists (Ji et al., 1988; Grigoryan, 1990), will be drawn in the middle part of the Otoceras woodwardi Zone in the Tethyan sections and the O. boreale Zone in Biarmia. Despite an extensive occurrence of parvus Zone in the Tethyan Realm, where it is rather easy to choose the boundary stratotype in the complete Permo-Triassic section and in a continuous phylogenetic lineage, in Biarmia its determination, due to an almost complete lack of conodonts, will be extremely difficult.

Proceeding from the criteria for drawing the boundary in continuous monofacies sections between easily recognized zones of one or several orthostratigraphic groups of fauna, most preferable is the level at the base of the Isaricella isarica Zone coinciding with the base of the Ophiceras tibeticum Zone, with the mass appearance of diverse Claraia, and associated with a major restructuring of biota and a total extinction of the Permian elements. This boundary has the highest correlation potential and is easily recognized ubiquitously.

Extinction of stenohaline organisms near the Permo-Triassic boundary should probably not be associated with any catastrophic events. High iridium concentrations have not been confirmed either in the Transcaucasus or in southern China. The above volcanic processes have a purely local significance. The analysis of spherules from the boundary beds shows that they are predominantly composed of phosphate and calcite, which does not confirm an extraterrestrial origin. The available data indicate that the extinction of organisms was the consequence of an abrupt lowering of sea level and aridization of climate.

References


TRIASSIC TRANSGRESSIVE-REGRESSIVE CYCLES OF SVALBARD AND OTHER ARCTIC AREAS: A MIRROR OF STAGE SUBDIVISION

A. Moerk, Continental Shelf Institute (IKU), 7034 Trondheim, Norway

Abstract
Transgressive-regressive (T-R) cycles have been recognized and compared throughout the Arctic (Sverdrup Basin, Embry 1988; Sverdrup Basin and the Barents Sea area, Moerk et al. 1989; Svalbard and East Siberia, Moerk and Egorov in prep.).

"Simultaneous transgressions" (as defined by Moerk et al. 1989) are transgressions which fall within the same one or two ammonoid zones in various basins; i.e. within a time span of two million years or less. Four "simultaneous transgressions" are recognized throughout the Arctic and were initiated in the earliest Griesbachian, earliest Smithian, earliest Anisian and earliest Carnian. These transgressions which are recognized in the Sverdrup Basin, Svalbard and East Siberia, all areas which were located on the AmEurAsian Plate during the Triassic, suggest a common mechanism for the transgressions; i.e. eustasy.

The other transgressions recognized are less precisely dated, or are confirmed as NOT being contemporaneous within either one basin or between several basins. These transgressions may be controlled by tectonism (c.f. Cloetingh 1986, 1988, Embry 1990).

Introduction
Scientists have for years worked in individual areas on the Arctic margin of the AmEurAsian plate (Fig. 1). The later years joined efforts have shown great similarities in the sedimentary development of the different areas. This contribution summarizes some of the similarities in stratigraphical and sequence geological development; the aim is both to present our results and to stimulate discussions and compare our findings with other areas in different plate tectonic setting (e.g. Tethys).

Ammonoid-based biostratigraphical zonation for the Triassic succession in the Arctic was first established in the Sverdrup Basin (Arctic Canada) by Tozer (1961, 1963). This zonation was extended to Svalbard by Tozer and Parker (1968), and improved by Korchinskaya (1970, 1972a,b, 1982, 1986), Weitschat and Lehmann (1978, 1983) and Weitschat (1986). Recently ammonoid zonation of Svalbard and Eastern Siberia were compared by Weitschat and Dagys (1989).

The ability to define the synchronocity of a geological process, such as a transgression, is dependent on the precision of the dating method available for the rocks involved, and the duration of the geological process. Proof of synchronocity or non-synchronocity of transgressions depends on our ability to date the oldest beds deposited during the transgression. Uncertainty in dating is due both to the resolution level of the involved fossils, as well as to the abundance of fossils in the transgressive beds.

According to the Subcommission on Triassic Stratigraphy (Visscher, 1985) the duration of the Early Triassic is 6 Ma and the Middle Triassic is 10 Ma. For this time span the number of recognized ammonoid zones varies from area to area being 13 in Svalbard, 15 in the Sverdrup Basin and approximately 20 in Siberia. Assigning equal time span for each zone gives a mean duration of 0.8 to 1.2 million years for an individual zone. One individual zone will thus be approximately in the range of 1 million years.
Nature of the Transgressions

Moerk et al. (1989) recognized three groups of synchronicity of transgressions (simultaneous, possibly simultaneous and independent) based on both biostratigraphical and lithostratigraphical data from the Svalbard - Barents Sea region and from the Sverdrup Basin.

Simultaneous transgressions - These transgressions occur in various Arctic basins and fall within the same one or two ammonoid zones. Transgressions in this group took place in a time span of two million years or less (shaded in Fig. 2).

Independent transgressions - These transgressions are also well dated and pegged to one or two ammonoid zones. In contrast to the above group they occur only in one basin and biostratigraphic and lithostratigraphic control is sufficient in other basins to document their absence.

Other transgressions have less precise age control and are only dated to substage level. They occur in various basins, but due to the lack of precision in dating it is not known if they represent simultaneous or independent transgressions.
Fig. 2 Triassic ammonoid zonation (from Moerk et al. in press), based on Korchinskaya (1970, 1972a,b, 1982, 1986), Moerk et al. (1989), Silberling and Tozer (1968), Tozer (1980) and Weitschat and Dagys (1989). Shaded areas represent "simultaneous transgressions" for the involved areas.
Of the ten transgressions recognized along the northern margin of the Euro-American Plate during the Triassic, all ten have been reported from the Sverdrup Basin (Embry 1988, Moerk et al. 1989, A.F. Embry pers. comm. 1990). Four have been well dated (i.e. inside two ammonoid zones) and appear to be simultaneous in several areas from Canada (both British Columbia and the Sverdrup Basin) to Svalbard and to Eastern Siberia. These four transgressions occurred in the earliest Griesbachian, earliest Smithian, earliest Anisian and earliest Carnian.

These simultaneous transgressions can be followed all along the northern margin of the AmEurAsian Plate and all of them start very early in a stage. Possibly the base of stages, as first defined outside the Arctic, were defined where significant faunal "episodes" took place. The "significant faunal episodes" that occurred in the areas where the stages were first defined may thus correlate with the transgressive episodes that can be correlated circum Arctic.

Such synchronous transgressions thus had a much wider geographic extension than the northern areas of the AmEurAsian plate. This suggests a common mechanism for the transgressions in all the areas; i.e. eustacy.

Eustacy was the traditional explanation for synchronous transgressive development following the Exxon school (Vail et al. 1977), however, in a series of papers in later years describing such cycles in the Arctic (Embry 1988, 1989, 1990, in press,a,b, Embry and Podraski 1988, Johannessen and Embry 1989, Moerk et al. 1989, Moerk and Egorov in prep.) there has been an increased interest to attribute transgressive - regressive development to intra plate stress phenomena as described by Cloetingh (1986, 1988). Such intra plate stress (Cloetingh 1986, 1988) may provide a mechanism producing variable transgressive-regressive development in one basin, while more extensive tectonic episodes naturally may incorporate also an eustatic effect. In comparing the Sverdrup Basin, Svalbard and East Siberia examples of synchronous transgressive development, and of independent transgressions will be given. All these examples are from the high Arctic areas, and it is hoped that discussion may be stimulated for comparing such T-R cycles worldwide. The fact that also in the Arctic the three-partite subdivision into the Early, Middle and Late Triassic correspond to the classical German Buntsandstein, Muschelkalk and Keuper indicate inter-regional extent of the episodes controlling the T-R cycle development.

**Triassic Transgressions**

Below the development of the different transgressions recognized in the Arctic areas will be briefly summarized. Only major transgressive developments are discussed, while minor cycles as para-sequences (fourth order or higher) are omitted. Examples of the sedimentological development in the different areas are given in Fig. 3.

**Base Griesbachian transgression**

The base of the Triassic system is regarded as below the *Otoceras* ammonoid zone (Tozer 1988), and this zone fossil is present in the Sverdrup Basin, Svalbard and East Siberia. In the Sverdrup Basin (Plate 1, fig. a) and Svalbard extensive hiatus occur along the basins margins, while continuous sedimentation may have taken place central in the basins (Plate 1, fig. b)(Moerk et al. 1989). On Svalbard such continuous sedimentation is not proved neither by macrofossils nor by palynology and no verified Tatarian beds have been recognized. The Permian - Triassic transition is associated with an extensive change in sedimentation pattern across the present Arctic, where spiculitic well cemented shales of the late Permian are being replaced by softer claystones in the Triassic. In Eastern Siberia a marked hiatus occur over most part of the basin. However, the lowermost beds of the Verkhoyansk mountains Triassic deposits contain *Otoceras* (i.e the lowermost ammonoid zone) (Moerk and Egorov in prep.).
Fig. 3 Interpretative sections giving examples of sedimentological development with localization of transgressions (arrow). The section from the Sverdrup Basin is from Moerk et al. (1989), and the section from East Siberia is modified from Egorov et al. (1991). Legend in Fig. 4. Capitals letters represent the early Griesbachian (G), early Smithian (S), early Anisian (A) and early Carnian (C) transgressions.
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Fig. 4 Legend to Figure 3.
Dienerian transgression

Sediment of Dienerian age are present throughout the Arctic, but a clear transgressive development is only recognized on Bjoernoeoya (Moerk et al. 1990) and on southernmost Spitsbergen (Worsley and Moerk 1978, Nakrem and Moerk 1991). In east Siberia transgressive development continued from the Griesbachian into the Dienerian (Moerk and Egorov in prep.).

Early Smithian transgression

The early Smithian (Olenekian) transgression is one of the most widely recognized in the Arctic; Sverdrup Basin (Plate 1, fig. c) (Embry 1988, Moerk et al. 1989), Svalbard (Plate 1, fig. e) (Moerk et al. 1989), East Siberia (Moerk and Egorov in prep.). The excellent *Eusferlingites* fauna in Svalbard is probably associated with the maximum flooding surface and the underlying (transgressive) beds contain an unidentified arctoceratid fauna below the ammonoid dated beds (Weitschat and Dagys 1989).

Late Smithian or earliest Spathian transgression

A transgression of this age have been recognized in the Sverdrup Basin (Plate 1, fig. c) by Embry (1988). On Svalbard it has not been recognized, however in the southwestern Barents Sea, in the Svalis Dome, it is clearly present and correspond with the transition from organic poor to organic rich sedimentation (Moerk and Elvebakk in prep.). In Eastern Siberia an Upper Spathian transgression is also reported by Moerk and Egorov (in prep.).

Early Anisian transgression

The transition from the Lower to Middle Triassic successions is recognized all over the Arctic (Plate 1, fig. c,d,e), and on most places a clear transgression is noted. In the Sverdrup Basin subaerial erosion took place during the regressive development of the late Spathian and organic rich transgressive sediment was deposited at the base of the Anisian (Embry 1988, Moerk et al. 1989). On Svalbard a marked lithological change from sandstones to organic rich shales took place along the basins margin in the earliest Anisian, corresponding to a transition from siltstone to shale with increased organic content in the basin (Moerk et al. 1989, Moerk and Bjoroeq 1984). Locally there is a limestone at top of the underlying unit marking the change from regressive to transgressive development. In Eastern Siberia continuous sedimentation occurred in the central part of the basin and the lowermost ammonoid zone are represented by a hiatus along the basin margin, but all areas were transgressed before the end of the early Early Anisian (Moerk and Egorov in prep.). In some of the areas in Eastern Siberia three cycles are recognized, each being more pronounced than the underlying (Moerk and Egorov in prep.). These cycles may however represent higher order cycles; five such cycles has recently been reported within the Anisian sediment from the Svalis Dome (Rasmussen et al. in press).

Early Ladinian transgression

This transgression can also be recognized over large part of the Arctic. In the Sverdrup Basin the transgression initiating the second Middle Triassic cycle is not very well dated; actually the transgression may be of late Anisian age (Moerk et al. 1989). In Svalbard Weitschat and Lehmann (1983) described ammonoids of the lowest Ladinian ammonoid zone, but the relations to a transgression is not clear. Sediments of this part of the Middle Triassic succession are clearly of transgressive nature, although clear transgressive beds have not been pinpointed, and going eastward on the archipelago (i.e. to eastern Spitsbergen, Barentssoya and Edgeoya) deep shelf sedimentation
prevailed throughout the Ladinian. In eastern Siberia transgressive development can only be followed along the basins margin (Moerk and Egorov in prep.).

Early Carnian transgression
In the Sverdrup Basin a limestone of early Carnian age was deposited on the basin margin during transgression while shale deposition took place in the basin (Emby 1988, Moerk et al. 1989). On Svalbard a nonsequence, or a period with very low sedimentation, separate the organic rich shales and siltstones of Middle Triassic age from overlying grey sideritic shales now regarded as of Late Triassic age (Korchinskaya 1982, Weitschat and Dagys 1989). On the main islands of Svalbard a Carnian fauna occur in basal transgressive beds (Weitschat and Dagys 1989), however higher in the succession biostratigraphical control is poor, but the presence of Upper Triassic sediments in mixed marine and marginal marine settings are indicated by palynology (Hochuli et al. 1989). On Bjørnøya sandstones (overlying rocks are eroded) are overlying a thin shale unit and are interpreted by Moerk et al. (1990) as representing an earliest Carnian transgression. In Eastern Siberia an early Carnian transgression, marked by a polymict conglomerate, is recognized in the Verkhoyanskiy area (Plate 1, fig. f), however overlying part of the T-R cycles is partly eroded (Moerk and Egorov in prep.).

Mid-Carnian, earliest Norian, late Norian and Rhaetian transgressions
In the Sverdrup Basin mid-Carnian, earliest Norian, latest Norian and Rhaetian transgressions are recognized (Emby 1988, pers. comm. 1991, and Moerk et al. 1989). Beds of late Carnian to mid Jurassic age are developed in shallow to marginal marine and continental environments. On Svalbard there are extensive (probably several) hiatus, but due to this problematic data quality, and poor biostratigraphical resolution, correlatable transgressions can not be recognized. Note that the base Norian is an important sequence boundary in the Barents Sea (Johannessen and Embry 1991). The basal conglomerate of the Wilhelmoeeya Formation (Moerk et al. 1982) may serve as a candidate for the late Norian transgression. In East Siberia four transgressions are recognized by Moerk and Egorov (in prep.), however, complete T-R cycles are not at present recognized.

Discussion
From the data presented four Triassic transgressions are regarded as simultaneous through the studied part of the Arctic. Improved dating may include also other transgressions in this group. Assignments of independent transgressions are more problematic as it is needed to show that a transgression is not taking place in an area at a given time. This imply that both a possible transgressive episode need to be recognized, and that this episode need to be confidently dated.

In Eastern Siberia the resolution in ammonoid zonation is much better than in the other areas (Fig. 2). Three T-R cycles in the Anisian of East Siberia as recognised by Moerk and Egorov (in prep.) seems to have no counterparts on Svalbard or in the Sverdrup Basin, however they may possible be correlated with some of the five cycles recently described from the central Barents Sea area by Rasmussen et al. (in press).

Embry (1990) point out that the T-R cycle use the transgressive surface for delineating cycles, whereas the depositional sequence of Vail et al. (1987) use the correlative surface of the subaerial unconformity. Both the depositional sequence and the T-R cycle use the same boundary in exposed areas, but going basinward the sequence boundary of the depositional sequence concept will be located in the upper part of the regressive part of the T-R cycle. This imply that the basal beds of a depositional sequence (of Vail) are deposited under low sea level conditions during the final part of a regression. In the T-R cycle model the basal beds of a cycle are deposited during the initialization of
a transgression. Going away from the sediment source towards the central parts of depositional basins the transgressive surface will nearly coincide with the maximum flooding surface produced during maximum transgression, commonly being separated by thin highly fossiliferous beds (condensed interval). High number of pelagic fossils, as ammonoids, are often found in the lower part of a T-R cycle and may thus be a result of the slow sedimentation during the transgression as the transgressive and maximum flooding surfaces nearly coincide. Reduced fossil content for the remainder part of the cycles may reflect higher sedimentation rate during the regressive part of the cycle.

In the Arctic there is clearly fossil achmes in the lower part of T-R cycles. In central Spitsbergen, however, the achmes often occur some metres above the transgressive surface. These areas represent basin margin environments and the beds with fossil achmes may reflect the maximum flooding, while underlying fossil poor beds represent the transgressive system. In more central parts of the basin abundant ammonoid faunas occur at the base of the cycle (i.e. earliest Carnian, eastern Spitsbergen, Weitschat and Daggs 1989), possible reflecting very low sedimentation rate when transgressive and maximum flooding surfaces coincide.

The stratotypes for the Lower Triassic are situated in the Canadian Arctic with exception of the Namalian (Dienerian and Smithian) which is defined in the Himalayas. Stratotypes for the Middle and Upper Triassic are, however, located to the Alps (Tozer 1984). The correspondence of dating of the basal Triassic (Griesbachian) transgression with the base of the stage is thus logic, although uncertainties exist as the underlying (?Permian) beds are not properly dated. The apparent correspondence between other transgressions and the base of stages defined outside the Arctic realm has important consequences. In the Arctic it is indicated above that the concentration of ammonoids may be a response to deposition during the transgressive system often connected to beds located between the transgressive surface and the maximum flooding surface. The base for defining the stratotypes may also have suffered the same mechanism; i.e. stages has been erected with transgressive systems at base. Following this line of concluding it may imply that T-R cycles that are initiated close to base of stages represent real widespread synchronous episodes like a common increase in sea level. 'Eustacy' as a term has widely been used for such widespread sea level changes (Exxon school), however, as all the localities considered in the present contribution are located on or around the same megaplats a tectonic mechanism may have controlled the sea level. One should, however, have in mind that it may be a psychological bias towards having common bases for geological features as stages and cycles or sequences.

The critical parameter for regarding transgressions in different areas as simultaneous will be the ability to regard ammonoid zones as simultaneous when they are based on different zonal species. None of the lowermost ammonoid zone has the same zone fossil throughout the Arctic, however there are several examples of the second ammonoid zones being present in all areas. Examples of such zones is the Griesbachian *Otoceras* boreale zone and the Anisian *Lenotropites* caurus zone. Possibly the presence of these zones in such extensive areas reflect that they occurred during maximum flooding. When discussing synchronicity in remote areas it is essential that paleontological evidences show acceptable correlations also when the principal zonal fossil changes. The proof of real synchronicity thus needs the documentation that ammonoid zones that are correlated between different areas firstly in the Arctic realm are synchronous, and secondly that this correlation can be carried further to other realms.

Another problem of synchronicity is the actual duration of a geological process as a transgression and the ability to date such an event with biosratigraphical methods. It is earlier argued that 'synchronous' transgressions are transgressions taking place within the period of a maximum of two million years. Whether such a time period in geological terms is justified as synchronous is debatable. Similarity in sedimentological development may, however, indicate that there is similarities in
geological development taking place as response to similar processes in large areas.

Candidates for eustatic processes based on this study are the early Smithian, early Anisian and early Carnian and possibly also the early Ladinian. The early Griesbachian transgression, although it need to be verified outside the Arctic, is also a probable candidate as there seems to be general acceptance that a major transgression took place at the Permian - Triassic boundary (Tozer 1988). The published "global"sea level curve of Haq et al. (1987, 1988) do, however, not show any marked increase in the sea level on the Paleozoic - Mesozoic boundary, although they mark the boundary as a transgressive surface.

The independent transgressions are restricted to single basins or parts of basins. Such transgressions may have more local origin, possible due to tectonic activity (i.e. intra plate stress; c.f. Cloetingh 1986, 1988). Possible joined conclusions may be inferred when tectonic activity trig eustatic sea level changes.

Conclusions

Four T-R cycles present in Arctic Canada, Svalbard and East Siberia are interpreted to have been initiated by synchronous transgressions close to the base of stages. These transgressions took place in the earliest Griesbachian, earliest Smithian, earliest Anisian and earliest Carnian. The recognition of transgressive development at the base of these stages in the Arctic as well as in the stage stratotypes imply a common control on sea level; i.e. eustacy; whether controlled by tectonic mechanisms or not. Independent transgressions in single basins or locally in basins are indicated to be a response to tectonic processes.

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Fig. 5 Summary of transgressions marked by arrows. Capitals letters represent the early Griesbachian (G), early Smithian (S), early Anisian (A) and early Carnian (C) transgressions, all here regarded as 'simultaneous'.
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PLATE 1

Photos showing important transgressive beds marked by arrows.
a) Permian - Triassic boundary (arrow) in east-central Sverdrup Basin (photo A.F. Embry).
b) Permian - Triassic boundary (arrow) at Festningen, western Spitsbergen on Svalbard.
c) Three T-R cycles in the Lower Triassic succession of the northwestern Sverdrup Basin. 1, Griesbachian-Dienerian; 2, Smithian; 3, Late Smithian-Spathian; 4, Lower part of the Anisian with a Cretaceous sill at top. Arrows indicate transgressive beds in the early Smithian (S), late Smithian (LS) and Anisian (A) (photo A.F. Embry).
d) Spathian - Anisian boundary at the Tas-Ary island in Eastern Siberia. The arrow marks the conglomerate formed by the early Anisian (A) transgression.
e) The Lower and Middle Triassic succession at Barentsoeya, Svalbard. Arrows marks the early Smithian (S), early Anisian (A) and early Carnian (C) transgressions.
f) Ladinian - Carnian boundary at the Tas-Ary island in Eastern Siberia. The arrow marks the conglomerate formed by the early Carnian (C) transgression.
TRIASSIC BIOSTRATIGRAPHY OF JAPAN BASED ON VARIOUS TAXA

K. Nakazawa (Kyoto University), T. Ishibashi (Kyushu University), T. Kimura (Institute of Natural History), T. Koike (Yokohama National University), D. Shimizu (Kyoto University), and A. Yao (Osaka City University)

Abstract

Two different faunas belonging to two different lithofacies are distinguished in the Triassic of Japan. The one belongs to the shelf facies composed of terrigenous clastic rocks, and is characterized by ammonites, bivalves, and less amount of brachiopods and gastropods. The zonation of the lower half of the Triassic is mainly based on ammonoids, while the upper half is founded on bivalve fossils.

The other one belonging to the oceanic facies consists of chert, limestone, pelagic shale, and greenstone, and yields abundant conodonts and radiolarians. Molluscan fossils are also common in pelagic limestones. The zonation of the oceanic sequence is made by mainly conodonts and radiolarians. The comparison of the two different zones is difficult, because the two faunas do not occur in association.

Reviewing the various zonation, it becomes clear that the lower Eo-Triassic Induan strata are missing both in the shelf and oceanic facies. The latest Triassic "Rhaetian" is probably lacking in the shelf facies, but developed in the oceanic facies.

The shelf facies faunas are related to those of Primorye and Siberia. On the contrary, those of the oceanic facies have typical Tethyan aspects. It is worthy of note that the land plants belong to the Dictyophyllum-Clathropteris floristic province of warm climate. The present distribution of the two quite different assemblages is well explained by the plate tectonics theory.

Introduction

Recent studies, especially micropaleontological and paleomagnetic researches, reveal that the Japanese Islands consist of various terranes or structural belts of different origin, characteristic of the active continental margin (Fig. 1). The results of the Pre-Cretaceous terranes are recently summarized (Ichikawa et al., eds., 1990). The structural units in Japan can be classified into two different groups based on the different lithological and paleontological associations. The one is the shelf facies group primarily formed on the epicontinental or island arc shelf, and the other one is the oceanic facies group originally formed under the oceanic condition far from the continent. The first group is composed of sandstone, shale, and conglomerate of terrigenous clastic materials, and volcanogenic rocks are negligible. The oceanic group is constituted by chert, limestone, pelagic shale and basic volcanic rocks. Biofacies of the two rock groups are also different. The oceanic facies group is characterized by such microfossils as radiolarias and conodonts. Molluscan fossils are also common in some limestones. The shelf facies group is characterized by ammonites, bivalves, and less amount of brachiopods and gastropods, radiolarians and conodonts are very poor, if present. Furthermore, it has recently been clarified that the molluscan assemblages of the two groups are distinct from each other (Tamura, 1987 and 1990; Nakazawa, 1991). Accordingly, the zonation of the two is different, and the accurate correlation of the two is not easy. The present status of the Triassic zonation in Japan and the problems will be reviewed in this paper.
1: Hida Terrane (gneiss, X-line schist, granite)
2: Hida Marginal Belt (Sil.-Dev., Carb.-Perm., X-line schist)
3: Chugoku Belt (composite terranes)
4: Maizuru Belt (Perm., Trias, ophiolite complex)
5: Ultra-Tamba Terrane (End-Permian accretionary complex)
6: Tamba-Mino-Ashio Terrane (Late Jura.-Earliest Cret. accretionary complex)
7: Ryoke Belt (High T/P metamorphic rocks)
8: Sambagawa Belt (Low T/P metamorphic rocks)
9: "Chichibu Belt" (Jur.-Cret. accretionary complex with Korosegawa Terrane)
10: Korosegawa Terrane (Sil.-Dev., Carb.-Perm., Mesoz., gneiss, X-line schist, Serpent.)
11: Shimanto Terrane (Cret.-Palaeog. accretionary complex)
12: Abukuma Terrane (gneiss, X-line schist)
13: Southern Kitakami Terrane (Sil.-Dev., Carb.-Perm., Mesoz.)

*: Shelf facies Triassic
* : Oceanic facies Triassic

Figure 1. Index map showing Triassic localities cited in the text and the geological division of Japan.
Zonation of Shelf Facies Group

The Triassic strata of the shelf facies are distributed in the following areas (Fig.1).

1) Southern Kitakami Terrane, Northeast Japan: The Lower to Middle Triassic Inai Group, and the Norian Saragai Group.

2) Maizuru Belt, Inner Side of Southwest Japan: The Lower to Middle Triassic Yakuno Group, the Lower Carnian Arkaura Formation, and the Carnian-Norian Nabae Group.


4) Kurosegawa Terrane, Outer Side of Southwest Japan: The Upper Anisian Ussurites Bed, the Upper Ladinian Zohoin Group, the Carnian-Norian Kochigatani Group in Shikoku and Takagochi Formation in Kyushu.


Representative animal fossils are ammonites and bivalves, brachiopods are not common, and gastropods are rare in this facies. Ammonites occur commonly in the lower half of the Triassic, and bivalves were flourished in the upper half.

Ammonite zones

The Lower to Middle Triassic ammonite zones are established in the Inai Group. The Inai Group, 2,000-3,000m thick, is divided into five formations, the Hiraiso, Osawa, Fukkoshi, Isatomae, and Rifu Formations, in ascending order (Fig. 2) (Ichikawa, 1951; Onuki & Bando, 1959). The Rifu Formation is distributed separately from the main Inai Group, and the lower part is considered to overlap the upper part of the Isatomae Formation. Seven ammonite zones are distinguished as follows in descending order (Bando, 1964, 1967, 1970; Bando & Shimoyama, 1974).

Protrachyceras reitzi Zone of the Upper Rifu Formation: Protrachyceras reitzi (Boechk), Monophyllites wengensis (Klipstein), *Ptychites* compressus Yabe & Shimizu, Japonites cf. urga (Diener), etc.

Paraceratites Zone of the Lower Rifu and Upper Isatomae Formations: Paraceratites cf. trinodosus (Moj.s.), P. orientalis Yabe & Shimizu, Monophyllites cf. wengensis (Klipstein), Ussurites yabei Diener, etc.

Hollandites Zone of the Middle Isatomae Formation: Hollandites japonicum (Moj.s.), H. haradai (Moj.s.), Balatonites gottschei (Moj.s.), Danubites naumannii (Moj.s.), etc.

Leiophyllites Zone of the Lower Isatomae and Fukkoshi Formations: Leiophyllites cf. pseudopradyymna (Welter), Gymnites watanabei (Moj.s.), etc.

Arnauctocelites Zone of the Upper Osawa Formation: Arnauctocelites sp., Prenkites cf. timorensis Spath, Dalmatites sp., etc.

Subcolumbites Zone of the main Osawa Formation: Subcolumbites perrinsmithi (Arthaber), Columbites parisianus Hyatt & Smith, Eophyllites dieneri (Arthaber) etc.

*Glyptophiceras* cf. gracile Zone of the Hiraiso Formation.

Founded on these ammonite zones, the Osawa Formation is considered to range from Owenitan to Prohunagarian of Spath (1934) or Smithian-Spathian of Tozer (1965), the Fukkoshi, Isatomae, and Lower Rifu Formations are Anisian, and the Upper Rifu Formation is Early Ladinian. The lower part of the Hiraiso Formation provided with Glyptophiceras was referred to as Otoceratan of Spath (Bando, 1970), because G. gracile occurs from Otoceratan in Greenland.
Figure 2. Schematic columnar section of the Triassic System in the Southern Kitakami Terrane, Northeast Japan. (Prepared by Nakazawa)
Figure 3. Composite range chart of fossils of the Nabae Group in the Nabae-Matsunooodera area, Maizuru Belt, Southwest Japan, based on Nakazawa Fig.5) with emendation of species name. Asterisk indicates the occurrence of the name or intimately related species in Primorye and/or Siberia. (Prepared by Nakazawa)
Tozer (1971) pointed out that the type species of *Glyptophiceras, Xenodiscus aequicostatus* Diener, from Pastannah in Kashmir, differs from *Ophiceras* in having strong peripheral projection of growth-lines. One of the authors (K.N.) examined the Kitakami specimen, and confirmed that it is more similar to *G. aequicostatus* of Smithian age than to *gracile* in having peripheral projection. Therefore, the Hiraiso Formation is here considered to be Smithian. This is supported by the bivalve fossils as will be discussed later.

Ammonoids are rather rare in the lower part of the Yakuno Group in the Maizuru Belt. They are identified as *Pseudosageceras* aff. *multilobatum* Noetling, *Meekoceras* sp., *Keyserlingites* sp., and *Xenoceltites* aff. *spitsbergenensis* Spath, which suggest Late Eo-Triassic age (Bando, 1968).

The Yakuno Group in Yakuno yields Anisian ammonites, such as *Hollandites, Danubites*, and *Balatonites* in its upper member, but left undescribed.

The *Ussurites* Bed in Shikoku is compared to the *Paraceraites* Zone in Kitakami (Nakazawa, 1964).

The Late Ladinian ammonite zone is represented by *Proachyloceras* aff. *archelaus* (Laube), *P. pseudarchelaus* (Boeckh) and others of the Zohoin Group (Shimizu, 1930a), and was named the *Proaechyloceras* aff. *archelaus* Zone (Bando, 1967).

In the Upper Triassic formations, ammonites have been reported from various places, but few in number and the preservation is not good.


2) Arakura Formation (Nakazawa, 1958a): "*Mojsvarites*" *arakurensis* (Nakazawa) and *Monophyllites* sp.

3) Nabaer Group (upper part of N3 Formation) (Nakazawa, 1958b): *Cyrtopleurites* cf. *sakawanus* (Mojs.), *Cyrtopleurites* sp., and *Dimorphites* sp. from the *Tosapecten-Pseudolinae* Zone (identified by Ishibashi)


7) Tanoura and Takagochi Formations (Ishibashi, 1972): *Buchites kumamotoensis* Ishibashi, *Arcestes* (*Proarcestes*) cf. *asseaenus* (Hauer), etc. from the lower member of the Tanoura Formation and *Placites* aff. *oxyphilus* (Mojs.) from the middle member of the Takagochi Formation. Ishibashi considered that the former member is Late Carnian and the latter member as Early Norian.

**Bivalve zone**

The Lower to Middle Triassic bivalves were examined in detail in the Yakuno Group of the Maizuru Belt (Nakazawa, 1958, 1961, etc.). The Lower Triassic part of the Yakuno Group changes its lithofacies from northern coarse-grained facies to southern muddy facies through middle medium-grained facies (Nakazawa, 1958b). The bivalve fauna of the coarse- and medium-grained facies is represented by the association of *Neoschizodus* cf. *laevigatus* (Zieten), *Bakevellia* (Maizuria) *kambei* Nakazawa, *Eumorphotis* sp., etc., and that of the fine-grained facies is by the association of small shells of *Palaeonello, Niculana, Entolium*, and others. The lower Triassic part of the Yakuno Group belongs to the *Neoschizodus-Bakevellia or Palaeonello-Niculana Zone*. In some places, this zone can be divisible into the *Claraia (=Pseudocharaia)* Subzone, below and the *Niculana nogamii yakunoisens*
Subzone, above. The bivalve assemblage of the Yakuno Group is very similar to that of the Hiraiso Formation of the Inai Group in Kitakami. The Anisian beds of Kitakami and Maizuru yield poor bivalves, which are not useful for zonation.

The Ladinian bivalves are represented by species of *Daonella*, namely, *Daonella multistriata* Yabe & Shimizu, *D. densissulcata* Yabe & Shimizu of the Rifu Formation (Yabe & Shimizu, 1927), and *D. alta* Yabe & Shimizu, *D. subquadrata* Yabe & Shimizu, *D. indica* Bittner, etc. of the Zohoin Group (Kobayashi & Tokuyama, 1959). Onuki and Bando (1959) recognized the *Daonella multistriata* Zone above the *Protrachyceras reiti* Zone in Rifu.

The Upper Triassic zonation by means of bivalves was first attempted by Kobayashi and Ichikawa (1950, etc.) for the Kochigatani Group, then by Nakazawa (1950b, 1957) for the Nabae Group.

The Kochigatani Group is classified into four beds (or zones), the *Oxytoma-Mytilus, Halobia-Tosapexten, Myoconcha, and Monotis* Beds, in ascending order. Due to complicated geologic structure, however, the stratigraphic succession of these beds is not clear in the field. But this succession is verified in the Takagochi Formation in Kyushu excepting the *Myoconcha* Bed, of which fauna could not be found (Tamura & Murakami, 1985). Characteristic species are listed in the followings.


**Myoconcha** Bed: *Oxytoma subzittelli* Kob. & Ich., *Myoconcha trapezoidalis* Kob. & Ich., *Asoella aff. spitsbergensis* (Bohm), *Tosapexten suzukii* (Kob.), etc.

**Monotis** Bed: *Monotis ochotica, M. zabaikalica*, etc.

In the Nabae Group, three bivalve zones are discriminated, *Palaeophrasus-Lima yataensis* Zone, *Tosapexten-Pseudolimea* Zone, and *Pleuromya-Neoschizodus* Zone in ascending order (Fig.3).

Common species in each zone are as follows.


In some places, this zone is divisible into two subzones, the *Minetrigonia hegiensis* Subzone and the overlying *Halobia* Subzone.

**Tosapexten-Pseudolimea** Zone: This zone is characterized by long-ranging species, such as, *Tosapexten suzukii* and *Pseudolimea naumannii* and common occurrence of brachiopods. Ammonites, *Cyrtolepturus* and *Dimorphites* were collected from this zone as already mentioned.

**Pleuromya-Neoschizodus** Zone: This zone is distributed only in Nabae area. Characteristic species are *Pleuromya wakasana* Nakazawa and *Neoschizodus semicostatus* Nakazawa.

The thick Upper Triassic beds developed in the westernmost area of the Chugoku Belt are collectively called the Mine Group. It is divided into four formations in the type area, that is, the brackish Takiguchi, neritic Hirabara, limnic Momonoki, and paralic Aso Formations, in ascending order, reaching 4,000–4,800 m in total thickness. Bivalves are commonly found in the Hirabara and Aso Formations. Coal seams are developed in the Momonoki and Aso Formations. The Hirabara fauna is similar to that of the *Oxytoma-Mytilus* and *Halobia-Tosapexten* Beds of the Kochigatani Group and especially to the *Palaeophrasus-Lima yataensis* fauna of the Nabae Group, in having *Bakevellioides hekiensis, Minetrigonia katayamai, Palaeophrasus oblongatus, Oxytoma subzittelli, Halobia
kawodai, Paralleloodon monobensis Nakazawa and others (Tokuyama, 1960, etc.).

The Monotis beds are distributed in the Southern Kitakami Terrane (Saragai Group), the Chugoku Belt (Nariwa Group), the Kurosegawa Terrane (Upper Kochigatani Group), and the "Chichibu Belt" (Monotis bed). The zonation based on Monotis species were discussed by several authors (Ichikawa, 1954a; Onuki & Bando, 1958; Nakazawa, 1964; Tamura, 1965). Ando (1987) made a detailed paleobiological study of the Japanese Monotis, and proposed four Monotis zones of scutiformis, ochotica multistriata, ochotica ochotica, and zabaikalica or mabarica, in ascending order. Monotis is sometimes discovered from muddy rocks within an accretionary complex, for example, Mukaihata Monotis bed in Western Chugoku, and Monotis from the Tamba Mino Terrane.

Shells of Monotis usually occur crowdedly making fossil bank with a few associating species. They are: Halobia aff. fallax Mojs., H. cf. obruchevi Kiparisova, Otapira sp. from the scutiformis Zone in Kitakami.

Oxytoma cf. subzelteli and Tosapecten suzuki from the ochotica ochotica Zone of Nariwa, "Especten" infrequense (Kob. & Ich.) from the Upper Kochigatani Group.

Other marine fossils

Except for ammonites and bivalves, other fossils are not common. Among them, brachiopods frequently occur from the Upper Triassic Nabae and Mine Groups. Gastropods are rare throughout the Triassic. The occurrence of brachiopods is listed in the followings including undescribed species with asterisk (*).

Lingula sp. and Orbiculoidea sp. from the Osawa Formation (Murata, 1973).

Spiriferina cf. fragilis Schlotheim*, S. sp.*, and Terebratulid from the Fukkoshi Formation (Ichikawa, 1951).


Spiriferina sp.* from the Saragai Group.

Lingula sp.*, Rhynchonella cf. pupula Bittner*, and "Adygella" cf. himalayana (Bittner)* from the Lower Triassic Yakuno Group (identified by Shimizu).

Clavigera cf. cuneiformis (Trechmann)* and Rastelligera elongata Thomson from the Arakura Formation (identified by Shimizu).

Rastelligera cf. diomedia Trechmann*, Mentzeliospis cf. spinosa Trechmann* and Spiriferinoides cf. sakawurus Kobayashi & Tokuyama* from the Tosapecten-Pseudolinea Zone of the Nabae Group (identified by Shimizu).

Sakawaihynchia katayamae Tokuyama and "Rhincheonella" hirabareasis Tokuyama from the Hirabara Formation (Tokuyama, 1957a,b).

"Rhincheonella" subflabellata Tokuyama and "R." asoensis Tokuyama from the Aso Formation (Tokuyama, 1957b).

Spiriferinoides sakawurus Kobayashi & Tokuyama, S. yeharae Kob. & Tok., Sakawaihynchia tokomboensis Kob. & Tok., etc. from the Kochigatani Group (Tokuyama, 1957a).

It should be added that Ulatatusaurus hatii Shikama et al. (1978), the oldest ichthyosaurid in the world, has been discovered from the Spathian Osawa Formation in Kitakami.

Land plants

Plant remains are poorly known from the Lower Triassic through the Lower Ladinian in Japan. Kon’no (1973) first reported Pleuroemia hataii and Neocalamites muratae from the Osawa Formation.
of the Inai Group. *Pleiromeia* first described from the Buntsandstein in Central Europe is now known from North China and Southern Primorye. The occurrence of *Neocalamites* cf. *hoerenis* (Schimper) is also reported from the Anisian Isatome Formation (Igo, 1952). On the other hand, abundant plant fossils are yielded in the Upper Ladinian Tsubuta Formation, the coal-bearing Momonoki and Asa Formations of the Mine Group, Norian Nariwa Group, and Carnian-Norian Nabae Group, all are located in the Inner Side of Southwest Japan. The paleobotanical study of the Mesozoic plants was advanced by Oishi 1940, etc.) and other workers, and summarized by Kimura (1980). Oishi referred the floras as Rhaeto-Liassic flora, but interbedded marine fossils indicate Ladinian to Norian age. No "Rhaetian" evidences have been found yet.

In East Asia, two paleofloristic provinces are recognized, that is, northern *Danaeopsis-Symopteris* Province and southern *Dictyophyllum-Clathropteris* Province (Kimura, 1985, 1987). The former includes the Yanchang flora distributed in Ordos, Shanxi, and Shaanxi in North China. Dipteridaceae plants, such as, *Dictyophyllum* and *Clathropteris*, which show a warm climate, are missing in this flora, while those plants are abundant in the latter province. Japan, Korea, and Northeast China constitute the Eastern Subprovince of the *Dictyophyllum-Clathropteris* floristic province.

**Discussion on the Triassic Shelf Facies**

**Lower and upper boundary of the Triassic**

The Early to Middle Triassic Inai and Yakuno Groups lie disconformably on the latest Permian Toyama and Maizuru Groups, respectively. The lowermost part of the Inai Group was once considered as the earliest Triassic Otoceratan or Griesbachian age, but is now concluded as late Eo-Triassic, Smithian in age, because the ammonite of the Hiraiso Formation of the Inai Group identified as *Glyptophiceras* (= *Xenodiscus*) cf. *gracile* Spath is revealed to be more allied to Smithian *Glyptophiceras aegricostatum* (Diener). The associating bivalves have not been described, but are very similar to those of the Yakuno Group, which are, in turn, closely related to the fauna commonly yielded in the late Eo-Triassic beds of Primorye (Zakharov, 1968). Accordingly, the Triassic strata in Japan lack Griesbachian and probably Dienerian, too.

The Upper Triassic flora in Japan was once considered as Rhaeto-Liassic in age, but marine fossils obtained from the alternating beds with the plant beds indicate Carnian or Norian age. The youngest fossil from the plant-bearing strata is *Monotis zabaiakalica*. The genus *Monotis* is not found from the Rhaetic in the sense of Krystyn (1980). The uppermost Triassic is probably missing in the shelf facies of Japan.

**Correlation of the Upper Triassic zones and their age (Fig. 5)**

The *Oxytoma-Mytilus* and *Halobia-Tosaspecten* Beds of the Kochigatani Group, the *Palaeopharus-Lima yataensis* Zone of the Nabae Group, and the Hirabara Formation of the Mine Group are correlated with each other based on the similarity of bivalve assemblages. The *Myoconcha* Bed of the Kochigatani, the *Tosaspecten-Pseudolimea* Zone of the Nabae, and the Momokuni and Aso Formations of the Mine are stratigraphically comparable, but their faunas are not so similar. The Kochigatani Group excepting the *Monotis* Bed is generally considered as Carnian in age by some alliance of the bivalve fauna with the St. Cassian fauna of the Alps and also by the occurrence of *Paratrachyceras* and *Arcestes* (Proaccestes) from the *Halobia-Tosaspecten* Bed. The Nabae Group as a whole was also included in the Carnian. The Aso Formation was referred to range from Carnian up to lower Norian judging from the presence of Norian-type brachiopods (Tokuyama, 1960). It should be mentioned, however, that *Cystopleurites sakawanus* was reported from the *Halobia-Tosaspecten* Bed in Shikoku and *Placies aff. oxyphilus* was described from the middle part of the Takagochi Formation together with *Otapiia dubia* (Ichikawa), *Palaeoneilo iwaiensis* Ichikawa, and *Halobia*.
spp. *Cystopleurites* is a Norian genus (Tozer, 1980) and *Placites oxyphyllus* is a Norian species of Alps and Sicily (Mojisovics, 1873). *Placites aff. oxyphyllus* was once reported from the *Monotis scutiformis* Zone in Kitakami (Shimizu & Mabuti, 1932). Furthermore, many species of the "Carnian" in Japan occur from the *M. scutiformis* Zone of Primorye and Siberia. The examples are *Oxytoma mojsisovici*, *O. ziteli*, *Tosapeten suzuki*, *Pseudolimea naumannii*, *Chlamys mojsisovici*, *Otapiira dubia*, *Halobia aotii* etc. (Kiparisova et al., 1966; Kiparisova, 1972). The *scutiformis* Zone was once considered as Carnian in USSR, but is now referred to as the Middle Norian (Rostovtsev & Zamoida, 1984; Payevskaya, 1985). Therefore, as to the age of the *Halobia-Tosapeten* Bed and its correlatives in Japan, the further examination will be needed. In the present paper, the *Myoconcha* Bed of the Kochigatani, the *Tosapeten-Pseudolimea* and *Pleuromeia-Neoschizodus* Zones of Nabae, and the Aso Formation of the Mine Group are tentatively treated as early Norian in age.

The latest Triassic fauna of Japan is represented by fossils of the *M. zabikalica* Zone, the highest *Monotis* zone. Several ammonites have been found from the *Monotis* beds in Japan as previously stated, but these are usually poor in preservation to be determined specifically, and not useful for exact age determination. Conodonts have not been detected from the *Monotis* beds. The Norian-Rhaetian problem is still in controversy in the world, but genus *Monotis* did not survive into either the upper *Rhabdoceras suessi* Zone or *Choristoceras marshi* Zone.

**Zonation of Oceanic Facies Group**

The oceanic facies group consists of chert, siliceous shale, limestone, and greenstone accompanied by terrigenous clastic rocks of off-shore origin. They are distributed in a very complicated manner and it was very difficult to establish the stratigraphy. But the recent progress of micropaleontological study, especially of conodonts and radiolarians, makes it possible to reconstruct the original stratigraphical succession. Generally speaking, greenstones occupy the basal part of the succession, limestone is intercalated in the greenstone or lies on it, and chert overlies greenstone and/or limestone. These oceanic rocks are covered by terrigenous shale and sandstone, and muddy conglomerate or olistostrome. The zonation of the oceanic facies is based on radiolarians of chert and muddy rocks, and conodonts of chert, limestone, and siliceous shale. Molluscan fossils are sometimes contained in the pelagic limestone.

**Conodont zones**

The occurrence of conodont fossils in Japan was first announced by Muller (1964) from the Taho (correct pronunciation is Tao) Limestone in Shikoku, and they were described by Nogami (1968). Since then, conodonts have been reported from various places throughout Japan and contributed very much to analyse the geologic development of the Japanese Islands. Detailed biostratigraphy of conodonts in carbonate rocks were studied in the Taho Limestone by Koike (1979) and the Kamura Limestone in Kyushu by Watanabe et al. (1979).

In the Taho Limestone, about 40m thick, seven conodont zones are recognized, the *dieneri-conservativus*, *triangularis*, *homeri*, *timorensis*, mixed, *nodosa*, and *spatulata* Zones, in ascending order, covering the Smithian-early Norian interval. The disconformity between the latest Smithian-earliest Anisian *timorensis* Zone and the early Norian *nodosa* Zone is shown by the mixed zone of limestone conglomerate containing various conodont species of Anisian, Ladinian and Carnian.

The Kamura Limestone, about 40m thick, lies disconformably on the latest Permian *Palaeofusulina-bearing* Mitai Limestone. Eight conodont zones are distinguished in it. The presence of several disconformities or diastems is proved by the absence of conodont zones beneath limestone conglomerates.
<table>
<thead>
<tr>
<th>Lower Triassic</th>
<th>Middle Triassic</th>
<th>Upper Triassic</th>
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Neospathodus dieneri
Ns. wageni
Ns. conservativus
Furnishius triserratus
Platyvilloso costatus
Ns. triangularis
Ns. homeri

Icriospathodus collinsoni
Neogondolella timorensis
Ng. regale
Ng. bulgarica
Ns. kockeli

G. malayensis
Ng. foliata
Ng. polygynathiformis
Ng. tadpole
Ng. nodosa
Ng. primitia
Epigondolella abneptis
E. spatulata

Ng. navicula
E. postera
Ng. hallstattensis
E. multidentata
Ng. steinbergensis
E. bidentata
Misikella hernesteini
M. posthernesteini

Figure 4. Triassic conodont zones and vertical distribution of pectiniform species in Japan. (Prepared by Koike)
Figure 5. Correlation chart of various Triassic zones in Japan.
The conodonts of chert and siliceous shale have been studied by many workers since the study of the Adoyama Chert Formation in Northern Kwanto Mountainland by Hayashi (1968). A detailed conodont biostratigraphy was established in about 45m thick chert and siliceous shale of the Kanoshima Group in west Chugoku by Tanaka (1980). The following conodont succession has been recognized, the *homeri, timoensis, bulgariaca, excisa, hungaricus, nodosa, spatulata,* and *bidentata* Zones, ranging in age from Spithian to Norian.

The conodont biostratigraphy was summarized by Koike (1981). Now sixteen conodont zones are established as illustrated in Fig.4. It is a noticeable fact that the Early Eo-Triassic zones have not been detected both in chert and limestone as in the case of the shelf facies group. However, the Rhaetian conodont zone characterized by the *Miskella posthemsteinii* assemblage without *Epigondolella bidentata* was confirmed in the top of the Triassic chert in Kyoto and in the continuous Triassic-Jurassic bedded chert at Inuyama, Central Japan (Isozaki & Matsuda, 1982), both situated in the Tamba-Mino Terrane, Inner Side of Southwest Japan.

**Radiolarian zone**

A study on the Mesozoic radiolarian fossils by means of scanning electronic microscope (SEM) in Japan was first developed by Yao and Ichikawa (1969) and Yao (1972). Radiolarians occur commonly not only in chert, but also in muddy rocks, and furthermore they are not limited to Triassic and many papers have been published concerning the Mesozoic radiolarian biostratigraphy. Comparing with the zonation of Jurassic and Cretaceous, the Triassic one is less accurate and under development.

Yao (1982) distinguished three assemblage zones covering Anisian to Rhaetian interval in the bedded chert at Inuyama. These are the *Triassocampe deweveri, Triassocampe nova,* and *Canoptum triassicum* Zones (Pl. 2). The age of these zones can be determined by associating conodont fossils as shown in Fig. 5. Sato et al. (1986) recognized five interval- and range-zones in the Triassic-Jurassic chert beds in Kyushu, namely, the *Archaeospongounum compactum, Emiluvia? cochleata, Capnuchosphaera triassica, Capnodoce, Betricium deweveri, Parahsuum sp. A,* and *Parahsuum directiporata* Zones, in ascending order. The first zone is considered as Anisian, and the last two zones belong to Early Jurassic. The unnamed zone beneath the first zone may go down to Early Triassic.

**Molluscan zone**

The Lower Triassic molluscs have been discovered in the following limestones of the Outer Side of Southwest Japan (Nakazawa, 1971) (Fig.1).

*Eumorphotis-Unionites* assemblage of Shionosawa Limestone in Kwanto Mountainland, Kurotaki Limestone in Shikoku, and Kamura Limestone in Kyushu.

*Anasibrites-Meeoceras* assemblage of Tafo Limestone.

The *Eumorphotis-Unionites* assemblage is composed of *Eumorphotis multiformis* (Bittner), *Unionites canalensis* (Catulo), *U. fassaensis* (Wissmann), *Pteria ussuriaca yabei* Nakazawa, *Leptochondria minima* (Kiparisonova), etc. Most species are rather widely distributed in the world, and not limited to the limestone facies but also found from the shelf clastic rock facies. The coexisting ammonites determined as *Cypites japonicus* Kambe, *Aspenites kamurenensis* Kambe, etc. from the Kamura Limestone and *Wyomingites sp.* from the Kurokami Limestone suggest Smithian age.

The *Anasibrites-Meeoceras* fauna consists of *Anasibrites onoi* (Yehara), *A. pacificus* (Yehara), *Meeoceras japonicum* Shimizu & Jimbo, *M. orientale* Shimizu & Jimbo, *Hemiphrionites katoi* (Yehara), etc. All species show Smithian age, too. Above ammonite and bivalve horizons of the Kamura and Tafo Limestones, Middle and Upper Triassic conodont zones are ascertained as already mentioned.
Occurrences of Upper Triassic Ammonites and Bivalves

The Upper Triassic ammonites and bivalves are found from other limestone bodies distributed along the southern border of the "Chichibu Belt" (Sambosan Belt) as enumerated in the followings.


The Nakijin Formation is composed mostly of limestone accompanied by basaltic lava and siltstone. Three ammonite zones are established in it.

Juvavites cf. kelleyi Zone: Juvavites cf. kelleyi Smith, J. cf. dacus (Mojs.), Arcestes (Proarcestes) carpenteri Smith, etc.

Sandlingites aff. oribasus Zone: Sandlingites aff. oribasus (Dittmar), Anatomites cf. toulai (Mojs.), Tropigastrides cf. columbianus (McLearn), Discotropites cf. laurae (Mojs.), etc.

Syrenites cf. nanseni Zone: Syrenites nanseni Tozer, Hannanoceras nasturtium (Dittmar), Trachyckeras (Paratrachyckeras) sp. etc.

In addition, Halobia stylriaca (Mojs.) was reported from the lower ammonite zone. All these fossils are closely related to Tethyan and North American Carnian species.

Konose Group in Kyushu

Tamura (1972) reported bivalve fossils with Tethyan affinity from limestone boulders derived from the Konose Group. They are Myoporia cf. intermedia (Schlotheim), Costatoria goldfussi (Alberti) (later emended as Palaeocardiida sp.), Gruinwardia decussata (Münster), Elegantinia cf. elegans (Dunker), etc., most of which occur in Middle and Upper Triassic in Europe.

Megalodont Limestone

The so-called Megalodont limestone yielding Triadomegalodon cf. tofnae (Hoernes) and Dicerinocardium kawagataforme Tamura has been discovered from Kyushu and Shikoku (Tamura, 1983), and later even in Kwanto Mountainland and Hokkaido. Tamura concluded that the Megalodont limestone was formed under reefal, lagoonal environment of the tropical region. The age was estimated as Norian-Rhaetian.

Buko Limestone in Kwanto Mountainland

The Buko Limestone situated westward from Tokyo has the Upper Ladinian-Carnian bivalves of typical Tethyan aspect as listed below (Tamura, 1981).

Palaeoneilo elliptica (Goldfuss), Gervillia (Cultriopsis) angulata Münster, Entolium subdetinissum Münster, Gruinewaldia wöhrmanni (Bittner), etc.

All these bivalve fossils mentioned above belong to Tethyan fauna and are distinct from the contemporaneous shelf facies faunas, which are allied to those of Primorye and Siberia. Certainly, limestones provided with the Tethyan fauna were migrated from the lower latitudinal region and amalgamated with Japan (Tamura, 1990; Nakazawa, 1991). A small limestone block in the Tamba Terrane near Kyoto yielding Halobia cf. talauana Wanner, H. aff. superbescens Kittl and other Halobia and conodonts is also considered to have a same origin (Nakazawa, 1967).

Concluding Remarks

1) There are two different Triassic faunas recognized in Japan. The one is the shelf facies fauna and the other one is oceanic facies fauna. The former resembles the Primorye and Siberian fauna, while
the latter is closely related to the Tethyan fauna. The two faunas are distributed side by side at present. This is due to the migration of the oceanic rocks from the tropical region by plate movement.

2) The shelf facies fauna is characterized by ammonites and bivalves. Ammonites are common in the lower half of the Triassic, and bivalves were flourished in the upper half of the Triassic. Accordingly, zonation of the Lower and Middle Triassic is based on ammonites, and of the Upper Triassic is based on bivalves.

3) The oceanic facies fossils are represented by conodonts and radiolarians in chert, siliceous shale, and limestone, and molluscs in limestones. The zonation of the oceanic rocks is made by means of conodonts and radiolarians.

4) The Early Eo-Triassic fossils are not found from both the shelf and oceanic facies. The Induan strata are most probably lacking in Japan. The "Rhaetian" fossils have not been discovered in the shelf facies, but the Rhaetian conodont zone of Misikella posternsteini is confirmed in bedded cherts of the oceanic facies.

5) The Upper Triassic flora is distributed in the Inner Side of Southwest Japan. It belongs to the eastern subprovince of the Dictyophyllum-Clathropteris floristic province of East Asia.

6) The oceanic facies zonation and the shelf facies zonation are difficult to correlate, because two different faunas of the two facies do not coexist. This is a problem to be solved in the future.

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PLATE 1

All figures x60 except Figs. 3, 8, 19, 21, 33 x50; 31 x70; 32 x35. Prepared by Koike.

Fig. 1. Neospathodus conservativus (Müller), Tahoe Limestone, Loc.1116, YNUC-15670.
Fig. 2. Neospathodus dieneri Sweet, Tahoe Limestone, Loc.1119, YNUC-15671.
Fig. 3. Neospathodus waageni Sweet, Tahoe Limestone, Loc.1176, YNUC-15672.
Fig. 4. Neospathodus homeri (Bender), Tahoe Limestone, Loc.1185, YNUC-15673
Fig. 5. Neospathodus triangularis (Bender), Tahoe Limestone, Loc.1185, YNUC-15674.
Fig. 6. Neospathodus kockeli (Tatge), Tahoe Limestone, Loc.1118, YNUC-15675.
Fig. 7. Neogondolella timorensis (Nogami), Tahoe Limestone, 7 Loc.1194, 8 Loc.1191, YNUC-15676,15677.
Fig. 8. Neogondolella cf. jubata Sweet, Tahoe Limestone, Loc.1192, YNUC-15678.
Fig. 9. Neogondolella bulgarica (Budurov and Stefanov), Tahoe Limestone, Loc.1201, YNUC-15679,15680.
Fig. 10,11. Neogondolella mombergensis (Tatge), Tahoe Limestone, Loc.19.
Fig. 13,14. Neogondolella foliata (Budurov), 13 Kuzuun, Loc.1205-14, 14 Kamura Limestone, Loc. II.
9a-5, YNUC-15681,15682.
Fig. 15. Neogondolella tadpole (Hayashi), Kuzuun, Loc.1109-4, YNUC-15683.
Fig. 16. Neogondolella polygnathiformis (Budurov and Stefanov), Tahoe Limestone, Loc.1205, YNUC-15684.
Fig. 17. Neogondolella nodosa (Hayashi), Tahoe Limestone, Loc. 22.
Fig. 18,19. Neogondolella navicula (Huckriede), Tahoe Limestone, 18 Loc. 1209, 19 Loc. 1210,
YNUC-15685, 15686.
Fig. 20,21. Epidigondolella primitiva Mosher, 20 Tahoe Limestone, Loc.1205, YNUC-15687, 21 Kuzuun,
Loc. 03-10.
Fig. 22 Epidigondolella abneptis (Huckriede), Tahoe Limestone, Loc.1141, YNUC-15688.
Fig. 23,24. Epidigondolella spatulata (Hayashi), Tahoe Limestone, 23 Loc.1143, 24 Loc.1209, YNUC-15689, 15690.
Fig. 25,26. Gladigondolella tethydis (Huckriede), Tahoe Limestone, 25 Loc.1201, 26 Loc.1202, YNUC-15691, 15692.
Fig. 27. Gladigondolella malayensis Nogami. Tahoe Limestone, Loc.1203, YNUC-15693.
Fig. 28. Budurovignathus hungaricus (Kozur and Végh), Kuzuun. Loc.1110-4.
Fig. 29,30. Icriospathodus collinsoni (Solien). Tahoe Limestone, 29 Loc.1170, 30 Loc.1113.
Fig. 31,32. Platylvilosus costatus (Staesche), Tahoe Limestone, 31 Loc.1173, 32 Loc.1114.
Fig. 33. Furnishius triserratus Clark, Iwai, YNUC-15694.
PLATE 2

Magnification: Figs. 1-3 and 8-21 x140, Figs. 4 and 6 x150, Figs. 5 and 7 x200. Prepared by Yao.
Locality: all specimens are from the CH-2 bedded chert, Unuma, Kagamigahara, Gifu Prefecture.

Figs. 1-7 Triassocampe deweveri Assemblage
Fig. 1 Triassocampe deweveri (Nakaseko and Nishimura)
Fig. 2 Pachus(?) sp. A
Fig. 3 Yeharaia elegans Nakaseko and Nishimura
Fig. 4 Pouulpus aff. curvispinus Dumitrca, Kozur and Mostlerv
Fig. 5 Pentactinocarpus fustiformis Dumitrca
Fig. 6 Eptingium cf. manfredi Dumitrca
Fig. 7 Pseudostylophera japnicum (Nakaseko and Nishimura)

Figs. 8-14 Triassocampe nova Assemblage
Figs. 8 Triassocampe nova Yao Triassocampe sp. C
Figs. 9 Triassocampe sp. C
Fig. 10 Syringocapsa batodes De Wever
Fig. 11 Canesium aff. lentum Blume
Fig. 12 Capnuchosphaera theloides De Wever
Fig. 13 Kozuasterum sp. A
Fig. 14 Capnodoce crystallina Pessagno

Figs. 15-21 Canoptum triassicum Assemblage
Fig. 15 Canoptum triassicum Yao
Fig. 16 Dictyomitrella(?) sp. C
Fig. 17 Syringocapsa sp. A
Fig. 18 Livarella gifuensis Yoshida
Fig. 19 Squinabolella(?) sp. C
Fig. 20 Dreyericyrtium sp. A
Fig. 21 Kozurastrum aff. quinquespinosa (Kozur and Mostler)
CONODONT BIOCHRONOLOGY AROUND THE EARLY-MIDDLE TRIASSIC BOUNDARY: NEW DATA FROM NORTH AMERICA, OMAN AND TIMOR.

M.J. Orchard, Geological Survey of Canada, 100 West Pender, Vancouver, V6B 1R8, Canada

Abstract

Spathian and Lower Anisian conodonts are reported from Canada, the USA, Oman, and Timor. Most of these are calibrated with ammonoid faunas. Several new conodont species are recognized informally, and the taxonomic scope of several key taxa is reviewed and found to be in need of revision. Several Neogondolella species occur within the Spathian of North America, although most are presently submerged in N. jubata; Neospathodus homeri and N. triangularis have also been broadly interpreted in the past. The Spathian fauna from Oman contains common Gladiozondolella but no Neogondolella. Key Neospathodus species and some ramiform elements are common to Spathian faunas from Oman and North America. Conodonts from the Subrobustus Zone in Canada are similar to those from the Haugi Zone of Nevada, but contain many more neogondolelliids, including Neogondolella ex gr. regale. Chiosella timorensis appears in the basal Anisian Japonites weteri beds in Nevada, with many Neogondolella ex gr. mombergensis and fewer N. ex gr. regale. The latter species is far more common throughout the remainder of the Lower Anisian in North America, and is accompanied first with Nicoraella? n. sp. A in the Pseudokeyserlingites gueri beds, and then with Nicoraella germanica in the Silberlingites mulleri Zone. Lower Anisian samples from both Oman and Timor contain Chiosella timorensis and Gladiozondolella tethydis.

Introduction

This report summarizes progress on the study of Triassic conodont successions of the Spathian and Lower Anisian, emphasizing the intercalibration of conodont and ammonoid biochronologies. This has largely been possible through the recovery of conodonts from the matrix of ammonoid faunas collected by E.T. Tozer and H. Bucher, whose role in making this contribution possible is gratefully acknowledged. New data on this interval is reported from western and Arctic Canada, western USA, Oman, and Timor. Taxonomic studies of these collections is underway.

Conodonts from Spathian and Lower Anisian strata have been known for over 30 years, but our knowledge of many taxa remains inadequate. Similarly, although some of the earliest accounts of these conodonts were from ammonoid bearing beds, the intercalibration of ammonoids and conodont zonations is generally poor. In this paper I summarize the records of Spathian-Lower Anisian ammonoid-conodont associations in North America, Oman and Timor and introduce some conodont taxonomic refinements that impact on conodont zonation and boundary definition.

Important conodont species that feature in current zonation of the Spathian and Lower Anisian were originally described from Timor (Nogami, 1968), Chios (Bender, 1970), and the Salt Range (Sweet, 1970). Solien (1979) added one pectiniform index species from Utah. Other useful species are known from Mangyshlak (Kozur & Mostler, 1976) and Siberia (Dagis, 1984), although they are not considered in the zonal scheme compiled recently by Sweet (1988). Clark (1959) and Staesche (1964) described new but relatively restricted lower Spathian species from Nevada/Utah and Italy respectively, but these are not considered further here. Other potentially useful conodont elements have also been reported from successions in North America (Mosher, 1968), Spiti (Goel, 1977), Primorye (Buryi, 1979), Anhui Province in east-central China (Ding, 1983), Nepal and Svalbard (Hatteberg & Clark, 1984), and the Pamirs (Dagis, 1990). Several other species have been recorded
from the Spathian and Lower Anisian, but their holotypes originated at higher stratigraphic levels and the specimens from the present interval are probably not correctly identified.

**Western and Arctic Canada**

**Spathian conodonts**

Mosher (1973) recorded conodonts from the matrix of ammonoid bearing beds in Canada provided by Tozer. Spathian conodonts were recovered (but not illustrated) from two samples of the Subrobustus Zone of British Columbia (Mosher, 1973, p. 184-5). Additional conodont collections have now been recovered from other Subrobustus Zone samples provided by Tozer, but none are yet known from the older Pilaticus Zone.

A single conodont fauna is known from the Subrobustus Zone in the type area of the Spathian in the Canadian Arctic, and eight others are currently known from the Subrobustus Zone of northeastern British Columbia. The B.C. collections are characterized by variable associations of the pectiniform elements *Neospadodus ex gr. homeri* Bender (e.g. Mosher, 1973, pl. 20, fig. 14), high-bladed neogondolellids here referred to *Neogondolella ex gr. regale* Mosher, and other neogondolellids assigned by Mosher (1973) to *N. jubata* Sweet, but here provisionally referred to *N. ex gr. mombergenisis* Tatge. Only the latter species is recorded from the Arctic collection. *Chiosella timorensis* (Nogami) does not occur in any of the Subrobustus Zone collections from Canada.

The type material of *Neospadodus homeri* was originally described from the Marmarotrapezakalk (6 m above the base, section CM II, north slope of Marathovuno) in Chios, Greece (Bender, 1970). The species characterized a long-ranging *homeri* Zone which was regarded as both late Early Triassic and Early Anisian in age. The level of the holotype is now fixed at 4.5 m below the base of the Anisian Stage (Assereto, 1974, p.36), but its precise age range remains uncertain. *N. ex gr. homeri*, broadly interpreted morphologically, has since been reported from Spathian sections throughout the world. The species has been reported to occur with *Chiosella timorensis* at its type locality (Bender, 1970; Assereto et al., 1980; Gaetani et al., 1991), and also in the Salt Range (Sweet, 1970), western Australia (McTavish, 1973), Nevada (Collinson & Hasenmueller, 1978), Primorye (Buryi, 1979), Kashmir (Chhabra & Sahni, 1981; Chhabra & Kumar, 1989), Japan (Koike, 1981), and Guizhou, China (Ding & Huang, 1990). However, *C. timorensis* and *Neospadodus homeri* have not been found together in any North American collection studied by the author, and it is assumed that they overlap in an interval between the latest Spathian and earliest Anisian ammonoid faunas reported here (see below).

*Neogondolella* specimens from the Subrobustus Zone are superficially similar to *N. regale* and *N. mombergenisis* which were originally described from, respectively, the Middle Anisian of British Columbia (Mosher, 1970), and from the German Muschelkalk (Tatge, 1956). However, neither name is regarded as strictly appropriate for elements found in the late Spathian and Lower Anisian. Similar neogondolellids have also been identified by some authors (e.g. Matsuda, 1984) as, respectively, *N. jubata* Sweet and *N. elongata* Sweet, but the holotypes of those Lower Triassic taxa from the Salt Range (Sweet, 1970) are clearly different from the neogondolellids of the Subrobustus Zone. The long range attributed to *N. jubata* beyond the Spathian zone of that name (e.g. Sweet et al., 1971; Sweet, 1988) probably obscures the value of *Neogondolella* in the uppermost Lower Triassic. Pending revision of the neogondolellids of this interval, I refer specimens with a high fused carina to *N. ex gr. regale*, and those with a low medial carina to *N. ex gr. mombergenisis*. 
Lower Anisian conodonts

The Lower Anisian strata of Canada were formerly classed as the Caurus Zone (Tozer, 1967). This interval is now subdivided into the Mulleri Zone and an overlying Caurus Zone of restricted scope, which itself is further divided into lower and upper subzones (Tozer, this volume and in press). No conodonts have as yet been found in the Mulleri Zone of Canada. Mosher (1973, p.184) recorded a single Caurus Zone faunule on the Alaska Highway which contained equal numbers of the generalized "Neogondolette mombergensis" and "N. regale"; this collection originated in what is now referred to the lower subzone of the Caurus Zone. Additional conodonts have been recovered by the author from this locality, and from both Caurus Zone subzones on Liard River, and a further five undifferentiated Caurus Zone collections in northeastern British Columbia. These collections are generally dominated by N. ex gr. regale sometimes associated with subordinate N. ex gr. mombergensis. Neither Chiosella nor Nicoraella species occur in any of the Caurus Zone collections from Canada, although Chiosella timorensis is now known from otherwise undated strata in the accreted terranes of the western Cordillera (Orchard and Bucher, 1992).

Western USA

Conodont collections from Spathian and Lower Anisian ammonoid bearing strata in western USA have been reported by Mosher (1968), Sweet (1970), Nicora (1977), and Collinson & Hasenmueller (1978). Solien (1979) described Spathian conodonts that occurred above Smithian ammonoids. There are many occurrences of Spathian ammonoids in Idaho, Utah, Nevada, and California, many of which were described by Kummel (1969). Conodonts have been recovered in samples from Idaho (Tozer collections), Nevada (Bucher collections), and California (Stone et al., 1990; plus new collections). The Idaho Spathian sequence, from which only small conodont faunules have so far been obtained, comprises, in ascending order, the Tirolites hartii beds, Columbites beds, "Procolumbites" bed, and Prohungarites beds. The stratigraphy of all these beds, except the "Procolumbites" (discovered by Tozer in 1964), is described in Kummel (1954).

The Nevada sequence has two Spathian ammonoid faunas, that of the Prohungarites-Subcolumbites beds followed by the faunas of the Haugi Zone. These are followed by a Lower Anisian sequence first described by Silberling & Wallace (1969) and Silberling & Nichols (1982). Bucher (1989) has presented the most recent account, and a significant refinement of the Lower Anisian succession, which was formerly correlated with the Caurus Zone by Silberling & Tozer (1968). A four-fold subdivision of the interval is now recognized by Bucher (op. cit.): Japonites welteri beds, overlain by Pseudokeyserlingiis guexi beds, Silberlingiis mulleri Zone, and then the Lenotropites caurus Zone (of restricted scope). Large conodont collections have been recovered from the matrix of each of these ammonoid levels.

Spathian conodonts

Collinson & Hasenmueller (1978, p. 187) reported a conodont fauna (assigned to their Zone 7) from the Columbites beds of southeastern Idaho, and from other Spathian ammonoid beds in the Confusion Range of Utah and the Medicine Range of Nevada (see Collinson, 1968, p. 35). This conodont fauna (Zone 11 of Sweet et al., 1971) is reported to consist of Icriopspathodus collinsoni (Solien), N. homeri, N. triangularis Bender, and Neogondolette jubata. Apart from a Icriopspathodus collinsoni from the Columbites beds of Webster Canyon, Idaho (Sweet et al., 1971, pl. 1, figs. 12,13), illustrations of these elements from Nevada and Idaho have not yet been published and cannot be evaluated. Illustrations provided by Solien (1979) from Utah and by Clark et al. (1979) are of specimens from undated or unspecified stratigraphic levels. A single collection recovered by the author from the Columbites parishianus beds of Idaho contains, in my interpretation, Icriopspathodus
collinsoni, Neopathodus n. sp. B, N. ex gr. spathi Sweet, and Neogondolella aff. elongata.

Two small conodont faunas from the "Procolubrites" beds in Idaho differ from those of the Columbites beds in lacking Icriopathodus collinsoni, and including rare Neogondolella ex gr. regale. Because they lack I. collinsoni, these collections fall within Zone 8 of Collinson & Hasenmueller (1978, p. 187), and the jubata Zone of Sweet et al. (1971, p. 454), which was formerly recorded from the Prohungarites beds in southeastern Idaho, and the Subcolumbites beds in the Tobin Range in northwestern Nevada. However, conodont collections recovered by the author from Prohungarites beds in both Idaho and Nevada differ significantly from those of both the Columbites and "Procolubrites" beds.

The Prohungarites fauna is associated with the conodonts Neopathodus ex gr. homeri, N. ex gr. triangularis, Neogondolella n. sp., and 'Oncodella' n. sp. A, all of which require definition. The fauna contains many new elements and marks a natural break in North America. 'Oncodella' n. sp. A (a ramiform-coniform apparatus) also occurs in Oman (see below), Primorye (Buryi, 1979), Malaysia (Koike, 1982), and Nepal (Hatleberg and Clark, 1984). Neopathodid species from the Prohungarites fauna are similar to some, but not all, of the elements that have been assigned to N. homeri and N. triangularis previously.

Conodonts from the Haugi Zone in the Lower Prida Formation of the Humboldt Range in Nevada have been recorded by Collinson & Hasenmueller (1978, p. 187). They report Neopathodus homeri and Chiosella timorensis from an ammonoid locality documented by Silberling and Wallace (1969, locality USGS M2823). The author has studied Collinson's collections and two large faunas from matrix samples of the upper part of the Haugi Zone (Yatesi beds) in the same area. These are dominated by N. ex gr. homeri, with some elements approaching Chiosella gondolelloides (Bender); a single immature Neogondolella ex gr. monbergensis occurs in one collection, and 'Oncodella' n. sp. A in a second. Samples from the type locality of the Haugi Zone in the Union Wash Formation in the Inyo Mountains of California have not yielded conodonts, although Neopathodus homeri is recorded below it, and Chiosella sp. cf. C. timorensis is found at a presumably higher stratigraphic level in a second section (Stone et al., 1991).

Lower Anisian conodonts

Lower Anisian conodonts from the Prida Formation in Nevada were studied by Nicora (1977), who found Chiosella timorensis both below and within the Caurus Zone sensu lato (Nicora, 1977, p. 95, 97). In one sample from the Coyote-Bloody Canyon section, and in all but the lowest of four samples from the Star Canyon Section, the species occurred with "N. regale". The range of Chiosella timorensis into the Caurus Zone sensu stricto, suggested by Nicora's data (1977), has not been confirmed in the present study. In the Lower Anisian sequence established by Bucher (1989), only the fauna of the oldest level, the basal Anisian Japonites welteri beds, includes Chiosella timorensis. Collections from the Prida Formation below the J. welteri beds, and above the Haugi Zone, have yet to be examined. Both Neogondolella ex gr. monbergensis and far less common N. ex gr. regale are associated with Chiosella timorensis in three collections from the J. welteri beds.

Chiosella timorensis was originally described from north of the Laco River in the Manatuto District of Timor (Nogami, 1968, p. 117, loc. 041). The locality corresponds to the Leiophyllites/Procamites-bearing ammonoid locality of Nakazawa (Nr.91006, in Nogami, op. cit.), originally regarded as latest Scythian. However, the holotype of C. timorensis is not well dated, as discussed by Nicora (1977, p. 96, 97). Reliably constrained occurrences of the species from the USA appear to be exclusively from the Japonites welteri beds of the Lower Anisian, with the exception of the questionable record reported by Collinson & Hasenmueller (1978, see above). C. timorensis has a worldwide occurrence and appears to be a suitable index for the base of the Middle Triassic, as has been suggested by several authors (e.g. Assereto et al., 1980).
In both Nevada and Chios (Nicora, 1977; Gaetani et al., 1991), "N. regale" is reported to first occur slightly higher than the first Anisian ammonoids. This has led to the suggestion that the species developed from Chiosella timorenensis (Nicora, 1977), and was in fact the forerunner of all later Triassic neogondolellids (Bender, 1970; Kozur, 1980, p. 754; 1990, p. 395). However, both Neogondolella ex gr. regale and other neogondolellids of the late Spathian provide an alternative root stock. Until the taxonomy of the N. regale group has been revised, no particular biochronologic significance is attached to records of "N. regale" from the Spathian and Lower Anisian.

A possible derivative of Chiosella timorenensis, provisionally assigned to Nicoraella? n. sp. A, characterizes one collection from the Pseudokeyserlingites gueri beds. This new species may account for some of the published records C. timorenensis and Neospathodus homeri, above the basal Anisian. Nicoraella? n. sp. A is a relatively small species with similar blade proportions to Chiosella timorenensis, but with a different posterior basal configuration. It is the probable precursor of younger, relatively short Nicoraella species. Neogondolellids in the P. gueri beds are almost exclusively examples of Neogondolella ex gr. regale.

In the conodont collections from the overlying Mulleri (2 collections) and Caurus zones (3 collections) of Nevada, Neogondolella ex gr. regale is again far more common than N. ex gr. mombergensis, which is rare or absent in most collections. Nicoraella germanica (Kozur) occurs in both collections from the Mulleri Zone, but has not been recovered from the Caurus Zone.

Oman

Ammonoid bearing Hallstatt facies limestones from Oman have been described by Tozer & Calon (1990) who reported ammonoids of Early, Middle and Late Triassic age. Smithian, Spathian and Anisian faunas are preserved in red limestone olistoliths that originated northeast of the Arabian platform and which now lie within the structurally stacked Hawasina nappes.

Conodont faunas have been recovered from the Oman blocks (Orchard, 1992) at both Jabal Safra and Wadi Alwa (Tozer & Calon, 1990). In this paper, I outline the Spathian and Anisian data with reference to the localities described in Tozer & Calon (op. cit.). Spathian collections have been recovered from Jabal Safra in blocks 1 and 3, and from Wadi Alwa 1 where a Spathian fauna is followed by Lower Anisian fauna.

The Oman conodont faunas differ in some significant respects from North American faunas of Spathian and Early Anisian age. In particular, Gladiogondolella is common in all the Oman collections, whereas 'typical' Neogondolella species are absent. Neospathodus species are common in all Lower Triassic collections, and provide the best correlative tool. Non-pectiniform elements are also well represented and some distinctive, stratigraphically restricted Spathian forms are recognized. Anisian conodont collections from Oman are of low diversity.

Conodonts were recovered from two levels within the 1 m thick Block 1 (=104) at Jabal Safra, which contains indeterminate ammonoids (Tozer & Calon, 1990). The conodont faunas from the two levels are very similar, comprising common elements of Icriospathodus collinsoni, Neospathodus ex gr. spathi, N. ex gr. homeri, N. n. sp. aff. triangularis, Gladiogondolella carinata, and the apparatus of the peculiar coniform Aduncodina unicosta Ding, which has previously been recorded only from the Biandanshan Formation of Chaoxian, Anhui Province, China. The presence of Icriospathodus collinsoni in Block 1 suggests correlation with the North American Columbites beds, but the presence of N. ex gr. homeri implies a younger age based on its first occurrence in North American (Prohungarites beds).

Three conodont collections from the base, at 2 m, and at the top of the 3.5 m thick Block 3 (=103) at Jabal Safra (Tozer & Calon, 1990) yielded conodont fauna that is dominated by Gladiogondolella carinata Bender (not present at the base), Neospathodus ex gr. spathi, N. n. sp. B, and N. ex gr.
homeri, rare N. ex gr. triangularis, and 'Oncodella' n. sp. A (not present at the top). The top level of Block 3 contains the Spathian ammonoid Procarinates kokeni Arthaber (Tozer & Calon, 1990, p. 205), as does a comparable collection from Wadi Alwa I (118B).

The conodonts from Block 3 permit broad correlations with the Spathian of North America. In particular, the presence of Neosphathodus ex gr. homeri, N. ex gr. triangularis, and 'Oncodella' n. sp. A are suggestive of an age close to the Prohungarites beds. Some other elements suggest a slightly older age.

Tozer & Calon (1990, p. 206) record Japanites subacutus Welter, dated as Lower Anisian, from a bed (118C) about 15 m above the level (118B) at Wadi Alwa I with Spathian Procarinates kokeni and the conodonts mentioned above. Conodonts from the Anisian bed are Chiosella timorensis and the long ranging Gladiogondolella tethydis Huckriede. This is essentially the same low diversity association that occurs in the Japanites beds of the Chios section (Bender, 1970; Nicora, 1977, p. 96). Broad correlation of these faunas with the basal Lower Anisian J. welleri beds of Nevada is suggested on the basis of Chiosella timorensis.

**Timor**

A block of Hallstatt limestone containing both Keyserlingites angustecostatus Welter and a new species of Pararochodiceras has been under study by E.T. Tozer (this volume) who interprets this as condensation of latest Spathian Subrobustus Zone and an earliest Anisian fauna. Several samples of the red, pink and buff, multi-generation matrix from both within and around the ammonoid specimens has been processed for conodonts. Faunules recovered from all samples are similar: Chiosella timorensis is the most common species, with fewer Gladiogondolella tethydis. A single specimen of Neogondolella ex gr. regale occurs in one collection.

As shown in the discussion of both North American and Oman collections, the Timor conodont fauna is consistent with an Early Anisian age, the age of the younger ammonoid (Tozer, this volume). The conodont collection is very similar to that from the Lower Anisian of Oman and Chios. There is no evidence that the conodont fauna includes both Lower and Middle Triassic elements as interpreted for the ammonoids, although this cannot be absolutely ruled out. One scenario for the genesis of the Timor block is that older sediment was largely or wholly winnowed away from the large Keyserlingites prior to slow accumulation of Lower Anisian sediment within and around a mixed ammonoid fauna. Alternatively, some or all of the conodonts may date from the uppermost parts of the Subrobustus Zone. This possibility must be weighed against the fact that Chiosella timorensis does not occur in any of the nine conodont collections from the Subrobustus Zone of Canada.

**Conclusions**

Spathian conodont zonation is likely to improve with taxonomic revisions that are clearly necessary within Neosphathodus and Neogondolella. For example, neogondolellids of the Columbites beds are quite different from those of the Subrobustus Zone, although both have been referred to Neogondolella jubata.

Neosphathodus ex gr. homeri is characteristic of the Prohungarites beds and the Haugi Zone in the western USA, and the Subrobustus Zone in British Columbia. Examples have not yet been found from older or younger ammonoid levels during this study, although faunas from Oman suggest that it may range lower.

At least two Spathian conodont faunas and one Anisian fauna are recorded from Oman. At present, the Spathian faunas can be correlated broadly with the Columbites through Prohungarites interval in western USA. The Oman collections contrast biogeographically with low latitude North American equivalents in the occurrence of Gladiogondolella and the absence of Neogondolella. Some non-
pectiniform Oman species like *Aduncodina unicosta* are also unknown in North America, whereas others like 'Oncodella' n. sp. A occur also in Nevada and Idaho.

In Nevada, *Chiosella timorensis* has only been found in the lowermost Anisian *Japonites welters* beds of Bucher (1989) during the present study. The species is absent in both American and Canadian collections from the Mulleri and Caurus zones. Occurrences of *Chiosella timorensis* suggest that the *Japonites* occurrences in Oman and Chios, and the *Paracrochordiceras*-bearing block in Timor are broadly correlative with the *J. welters* beds. Furthermore, correlation is suggested with the top part of the Salt Range sequence wherein Sweet (1970) established the *timorensis* Zone above the *jubata* Zone. The Spathian ammonoids described by Kummel (1966) and Guex (1978) occur below the *timorensis* Zone.

The appearance of *Chiosella timorensis* provides a suitable datum for defining the Lower-Middle Triassic boundary. On the basis of Canadian and Nevedan data, this level is probably close to the disappearance of *Neospathodus homeri*, but post-dates the appearance of *Neogondolella ex gr. regale*.

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**References**


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Figs. 1-10, 12-14. Chiosella timorensis Nogami: Different growth stages showing variable flange development.

Figs. 1, 2. Upper and lateral views, x70. Fatoc Nifockoko, Toeboclopo, Timor. From matrix of specimen of Keyserlingites augustecostatus (Welter) collected by G.A.F. Molengraaff Expedition, 1911 (label mentions Kampong Soeli). Repository is the Museum of the Delft University of Technology, the Netherlands.


Figs. 5, 6. Lateral and upper views, GSC 95355, x80. C-176327, as Figs. 3, 4.

Fig. 7. Upper view, GSC 95356, x80. C-176327, as Figs. 3, 4.

Fig. 8. Lateral view, GSC 95357, x80. C-176327, as Figs. 3, 4.

Figs. 9, 10. Upper and lateral views, x80. As Figs. 1, 2.

Fig. 12. Upper view, GSC 95358, x70. C-176327, as Figs. 3, 4.

Fig. 13. Lateral view, GSC 95359, x70. C-176327, as Figs. 3, 4.

Fig. 14. Upper view, GSC 95360, x. C-158458, near summit of ridge north of Wadi Alwa, about 50 km south of Muscat, Oman. Topmost of three ammonoid beds exposed at south end of large outcrop of red Hallstatt limestone about 25 m thick, and at least 100 m wide. Tozer collection, 1984 (TE-118C).

Figs. 11, 15-18. Neospathodus ex gr. homeri Bender.

Figs. 11, 18. Upper and lateral views, GSC 95361, x80. O-56179, Nabesche River map area (94B/6), north side of Needham Creek, SW of junction with Graham River, British Columbia. Toad Formation, about 124 m above top of Fantasque Formation. Tozer collection, 1963 (207A). Subrobus tus Zone.

PALEOECOLOGICAL, BIOSTRATIGRAPHIC AND PALEOBIOGEOGRAPHIC FINGERPRINTS OF BRACHIOPOD FAUNAS: CASE STUDIES FROM THE ANISIAN OF HUNGARY

J. Pálfy, Department of Geology and Paleontology, Hungarian Natural History Museum, Budapest, Pf. 330, H-1370, Hungary

Abstract
Temporal and spatial distribution of Anisian brachiopods in three regions of Hungary is assessed. Even though there is commonly an interaction of paleoenvironment, evolution, bioprovincialism and paleogeography, selected cases demonstrate the independent effect of primarily paleoecological, biostratigraphic or paleobiogeographic control.

Introduction
Temporal and spatial distribution of brachiopod taxa is controlled by paleoecological, biostratigraphic and paleobiogeographic factors. Apparent distribution patterns are the result of the often complex interplay of environmental conditions, evolutionary processes and bioprovincialism. It may be tempting to emphasize one particular aspect governing the brachiopod distribution in a given case. However, special care should be given to assess the overprint of the other factors.

In order to help determining the effect of any one of the three major factors, case studies are presented where only one variable controls the difference between assemblages from two or more localities. Ecological causes are demonstrated in coeval faunas originated from the same tectonostratigraphic unit (terrane). Evolutionary change, the result of stratigraphic difference, is illustrated by successive faunas from similar environmental setting within the same terrane. Endemism and bioprovincialism is assessed in coeval assemblages from similar facies but different terranes.

The case studies selected among the Anisian faunas of Hungary serve as references to facilitate the understanding of more complex cases.

The Anisian Brachiopod Faunas of Hungary
The Anisian brachiopod faunas of Hungary provide a suitable basis for a study outlined above. Reasonably well-known assemblages are available from three different terranes: the Bakony Unit (Balaton Highland), Silicicum (Aggtelek-Rudabánya Mts.) and Tisza Unit (Mecsek and Víllány Mts.) (Fig. 1). Brachiopods were collected from a wide spectrum of lithofacies representing different carbonate environments. In several cases excellent ammonite biostratigraphic control provides high-resolution age dating.

A Case for Predominantly Paleoeological Control
In the Balaton Highland 4 localities (Kőveskál, Aszófő, Felsőörs and Iszkaszentgyörgy) along a 70 km section yielded rich brachiopod faunas of Pelsonian age. Brachiopod-bearing strata are assigned to the Balatonicus Zone at Aszófő (Vörös 1987) and Felsőörs (Szabó et al. 1980). A similar age is supposed for the localities of Kőveskál and Iszkaszentgyörgy. Nonetheless the assemblages are significantly different due to their respective paleoenvironmental setting. Diversity, distribution of higher rank taxa, ratio of disarticulated shells and size frequency of some common taxa along with the
host rock lithology and the composition of the associated macrofauna differs from one locality to the other (for a detailed discussion see Pálfy 1991). Variable energy level and substrate conditions are interpreted as the main control over the brachiopod distribution. The *Mentzelia mentzeli-Tetractinella trigonella* association of Köveskál developed on the foreslope of a carbonate platform. The *Caucasorhynchia altapecta-Trigonirhynchella attilina* association of Felsőörs was preserved in a small local basin with lime mud substrate. The *Coenothyris vulgaris-Lingula tenuissima* association of Iszkaszentgyörgy represents high-stress environment of marginal shallow water. The high diversity assemblage of Aszófő records the faunal mixing from different habitats in a slope environment (Fig. 2).

Fig. 1: Location and tectonostratigraphic position of the regions yielding Anisian brachiopods. (Base map after Brezsnyánszky and Haas 1986)

Fig. 2: Palaeoenvironmental reconstruction for the Late Anisian in the Balaton Highland based on brachiopod associations. (After Pálfy 1991)
A Case for Predominantly Biostratigraphic Control

A younger counterpart of the Pelsonian (Balatonicus Zone) brachiopod fauna of Aszófő was found at another locality in the Balaton Highland, in a section near Vászoly (Vörös and Pálfy 1989). The brachiopod-bearing beds here are assigned to the top of the "Parakellnerites" Zone and the base of the Reitzi Zone (Vörös et al. 1991). The relatively high diversity, the frequently disarticulated shells, the dominance of spiriferids with fair representation of other higher taxa as well as the similarity of the bioturbated limestone lithofacies suggest a palaeoenvironment comparable to that of Aszófő. Intense reworking on a slope resulted in a mixing of faunal elements from different habitats.

There are only 3 common elements among the 12 species of Vászoly and the 26 Pelsonian species of Aszófő. On the other hand, each of the 9 genera represented in the Vászoly section was also found at Aszófő. Most of the congeneric species of the two sections are seen as successive members of evolutionary lineages. Some prominent examples are plotted on Fig. 3. The duration of two and a half ammonite zones is reflected in the brachiopod assemblages by a marked species turnover. The resolution of brachiopod biostratigraphy therefore reaches approximately the substage level.

A Case for Predominantly Paleobiogeographic Control

According to widely accepted paleogeographic reconstructions, the distance between the Triassic sedimentary basins of the Balaton Highland, Aggtelek and Rudabánya Mts., and the Mecsek and Villány Mts. was exceeding their present-day distance (e.g. Dercourt et al. 1990). Our study is concerned with the possibility of demonstrating the displacement and different affinities by means of brachiopod paleobiogeography. Since reliable ammonite biostratigraphic control is lacking in most sections of the Aggtelek and Rudabánya Mts. as well as the Mecsek and Villány Mts., composite assemblages are compared from the Anisian of the three regions. This method offsets possible stratigraphic biases and also compensates for local ecological differences of individual sections. All the three regions are characterized by predominantly shallow water carbonate facies.

The sources of the faunal data are Pálfy (1986) and Vörös and Pálfy (1989) for the Balaton Highland; DeCret (1970, 1974), Pálfy and Török (in press) and unpublished data of Török for the Mecsek and Villány Mts.; Scholz (1972) and the author's unpublished data for the Aggtelek and Rudabánya Mts. Binary coefficients were used to assess the affinities quantitatively. Both Simpson and Dice coefficients were calculated. The first is better suited to emphasize similarities while the latter is more sensitive to the dissimilarities (Archer and Maples 1987, Maples and Archer 1988). Simpson coefficient values indicate remarkable similarities between the three regions (Fig. 4). A rather low Dice coefficient value, however, suggests significant difference between the Balaton Highland and the Mecsek and Villány Mts. The composition of the Balaton Highland and Mecsek faunas are even more strikingly different (Fig. 4). The less diverse brachiopod assemblages of the Mecsek are dominated by the overwhelming abundance of Coenothyris vulgaris. These features are characteristic of German-type faunas (Pálfy and Török in press). Nevertheless the Mecsek fauna contains no endemic element not known from the Balaton Highland or Northeast Hungary. This corroborates the view that in the Middle Triassic the Western Tethys did not support distinct brachiopod provinces; the German-type assemblages are only impoverished derivatives of the rich Alpine faunas (Dagis 1974).

Conclusions

The Anisian faunas from three regions of Hungary allow the assessment of paleoecological, biostratigraphic and paleobiogeographic factors controlling brachiopod distribution in space and time. Several cases can be selected where only one of the three factors is primarily responsible for the differences between the faunas compared.
Fig. 3: Biostratigraphic distribution of selected brachiopod taxa in the Vászoly and Aszófő sections of the Balaton Highland.

Fig. 4: Comparison of the brachiopod faunas of three regions of Hungary using Simpson and Dice coefficients. Number of species shown in the circles. Pie charts based on combined total specimen numbers of selected representative localities.
Conclusions

The Anisian faunas from three regions of Hungary allow the assessment of paleoecological, biostratigraphic and paleobiogeographic factors controlling brachiopod distribution in space and time. Several cases can be selected where only one of the three factors is primarily responsible for the differences between the faunas compared.

Brachiopods provide valuable paleoecological information due to the restricted habitat, substrate or energy regime preference of some taxa. Brachiopod taphonomy also helps enhancing paleoenvironmental models.

Species turnover rate allows a substage level resolution of brachiopod biostratigraphy.

In the Anisian there was no marked brachiopod bioprovincialism in the Western Tethys. The impoverished German-type faunas derived from their richer Alpine counterparts but do not contain significant endemic forms.

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PROBLEMS OF GLOBAL CORRELATION OF THE CONTINENTAL TRIASSIC ON THE BASIS OF TETRAPODS

M.A. Shishkin, Paleontological Institute, Academy of Sciences of the USSR, Moscow; V.G. Ochev, Saratov State University, Saratov, USSR

Introduction

As is well known, the evolution of land vertebrates provides a good basis for correlation of the Triassic continental deposits (Romer, 1970; Cox, 1973; Anderson and Cruickshank, 1978; Benton, 1983; Ochev and Shishkin, 1989, etc.). In spite of the regional peculiarities of this evolution, some principal faunal changes are traceable over most of the continents and reveal the most important biostratigraphic boundaries. The latter in turn may be used as a framework for a more detailed comparison of the regional faunal sequences.

According to the scheme put forward by Ochev and Shishkin (1989) the global history of the Triassic tetrapods includes three principal successive phases, which roughly correspond to three main divisions of the Triassic and are named by their dominant reptilian groups as the proterosuchian, kannemeyeroid and dinosaur epochs. This scheme is typified by the faunal sequence from the Triassic of eastern and central Europe dominated by amphibians. The proterosuchian and kannemeyeroid epochs are most fully documented here by the faunal assemblages from the Cis-Uralian Triassic. The record of the proterosuchian epoch known from this region is particularly important for several reasons: 1) in the northern hemisphere, the Early Triassic was a time of explosive tetrapod radiation, which gave rise to a number of short lived groups or genera with a limited vertical range, thus providing opportunity for a detailed stratigraphy of the fossil-bearing sections, and 2) the tetrapod zonation established for the Scythian of the Cis-Urals may be directly correlated with the marine scale, due to expansion of some of the Early Triassic labyrinthodont amphibians into the nearshore marine basins.

Discussion

In Europe the proterosuchian epoch includes two faunas composed mainly of amphibians. The earlier ("neorhachitome", or Wettugsaurus-Bentosuchus) fauna comes from the Wetlugian Series of Cis-Urals and includes three subdivisions. The oldest one belongs to the Vokhmian horizon: it is equated with the Induan (Griesbachian-Dienerian) of Greenland (Wortley Creek Formation) by the occurrence of two labyrinthodont genera, the brachyopod Tupilakosaurus and lydekkerinid Luzocephalus. The middle subdivision corresponds to the Rybinskian horizon: it is dominated by the early trematosaurid labyrinthodont Bentosuchus. Its age is defined by the presence of the closely related Bentosphenus in the Lower Oleneckian (Smithian) of the Russian Far East. The latest member of the sequence, which comes from the Sludkian horizon, is the Wettugsaurus subdivision. It also belongs to the Lower Oleneckian.

The succeeding Early Triassic fauna belongs to the Yarenskian horizon and is dominated by the capitosaurid Parotosuchus and the advanced trematosaurids. These fauna provide a correlation with the Upper Oleneckian (Spathian) coastal deposits of the Caspian Depression and Mangyshlak Peninsula and, on the other hand, with the Middle Buntsandstein of central Europe where the same forms are known.

The record of the following (kannemeyeroid) epoch, which belongs to the Middle Triassic, begins (in the Cis-Uralian sequence) with the Eryosuchus fauna coming from the Donguz Formation. The
labyrinthodont *Eryosuchus* is here a dominating form. The reptiles are represented mostly by kannemeyeronid dicynodonts and pseudosuchians accompanied by rare gomphodonts and bauriamorphs. In central Europe the equivalent of this fauna is the assemblage from the topmost part of the Upper Muschelkalk (Grenzolomit). Like the Donguz assemblage, it includes the primitive plagiosaurids (a group of short-headed aberrant amphibians) and, possibly, *Eryosuchus*.

The latest phase of the kannemeyeronid epoch is represented in the Cis-Urals by the *Mastodonsaurus* fauna coming from the Bukobay Formation. A wide occurrence of the mastodontsaurid labyrinthodonts together with the advanced plagiosaurids of the Plagiostoma group justifies the correlation of this fauna with that of the Lettenkeuper in central Europe. From invertebrate evidence, both Upper Muschelkalk and Lettenkeuper are usually equated with the Ladinian of the Alpine section, and the same dating may definitely be accepted at least for the Cis-Uralian *Mastodonsaurus* fauna. On the other hand, it should be taken into account that the actual lower time limit of the Upper Muschelkalk tetrapod fauna is unknown because of the predominance of marine conditions in the Germanic basin during most of the Middle Triassic. For this reason, it is quite possible that both the Upper Muschelkalk fauna and its Cis-Uralian equivalent (*Eryosuchus* fauna) came to rise as early as the Late Anisian. As a whole, we still have no clear idea about the composition of the land tetrapod assemblages that existed in Europe during most of the Anisian, the only exception being the Early Anisian represented by the *Eocyclotosaurus* fauna.

The *Eocyclotosaurus* fauna is known from the Upper Buntsandstein, the Voltzia Sandstone of France and their equivalents, including the Holbrook member of the Moenkopi Formation in the USA. In the Cis-Urals, this fauna is not recorded with certainty. As its reptilian components are very poorly known, it is not clear to which faunal epoch it should be assigned (i.e., proterosuchian or kannemeyeronid).

The faunas of the dinosaur epoch are lacking in the Cis-Uralian sequence but they are known from the Middle to Upper Keuper of central Europe. Amphibians are represented here by cyclotosaurids, toposaurs and plagiosaurids. Among the reptiles, the most common are phytosaurs (a group of crocodile-like archosauromorphs) and pseudosuchians. Dinosaurs appear at the Stubensandstein level (i.e., from the Middle Norian).

This sequence of principal biotic changes established in Europe may be followed more or less clearly over other continents. For the proterosuchian epoch, most of the available data are related to the Gondwanan land masses, where the epoch is mainly represented by the *Lystrosaurus* fauna. It is known extensively from South Africa. In contrast to the European Early Triassic biota, that fauna is dominated by reptiles (mainly synapsids) and shows no evidence of evolutionary changes which could help to subdivide it into subsequent members. The dicynodont *Lystrosaurus* is the most common form of this fauna. The amphibians are dominated by lydekkerinids, and no true capitosaurids are known. Outside of South Africa, the *Lystrosaurus* fauna in Gondwana is reported from Antarctica, India and possibly South America (Sanga do Cabral Formation, Brasil). In Laurasia, it is known from China (Singkiang). In addition the genus *Lystrosaurus* occurs in the Induan member of the Cis-Uralian faunal sequence and in the Tunguska Series of northern Siberia (Shishkin et al., 1986). The presumable equivalent of *Lystrosaurus* fauna, represented mostly by the endemic amphibians, is known from Australia.

The typical assemblages of the kannemeyeronid epoch outside of Europe include the faunas from the Yerapalli Formation of India, the Ermay Wallet Formation of China, the Manda and Ntwere Formations of East Africa and the Chataeres and Lower Santa-Maria Formations of South America. In contrast with the European Middle Triassic biota, all these assemblages are dominated by reptiles. Here, the kannemeyeroids are mostly accompanied by pseudosuchians and gomphodonts. The detailed correlation of these faunas with each other and also with the European faunas is complicated by the almost total lack of common genera in them.
The dinosaur epoch is best represented by faunas of the Laurasian type which are peculiar due to the presence of the metoposaur amphibians and the phytosaurs. This type is particularly widespread in North America, where it is mostly known from the Chinle formation (Arizona), Dockum Formation (Texas) and from the basal members of the Newark Group (Atlantic coast). The detailed zonation within these faunas made for the Southwest of the United States (Lucas and Hunt, 1989) is based on the change of the archosaur genera. The boundary between the Carnian and Norian is suggested based on evidence from the palynomorph complexes.

Outside Europe, North America and Southeast Asia, this type of biota is also known to spread into the northern Gondwana where it is recorded in northern Africa (Argana Formation) and India (Malery Formation). The assemblages found in these areas are comparable with the Carnian tetrapod complexes of Europe and North America. Much more difficult is to typify the composition of the Late Triassic faunas in the southern Gondwana. For this area, the best known is the faunal succession from the Ischigualasto and Los Colorados formations of Argentina. The metoposaurs and phytosaurs are absent there, while the role of theriodont reptiles (in the lower unit) is much more important than in the northern faunas.

The transition from the Late Triassic to the Jurassic communities, both dominated by dinosaurs, is very gradual and that is why the actual age of many so called Rhaeto-Liassic faunas (for example, from the Lufeng Formation in China and Elliot Formation in South Africa) is still a matter of debate. In a framework of the discussed threefold division of the Triassic tetrapod history, a more detailed correlation of the local faunas with the European reference sequence is still biased both by the incompleteness of the fossil record and the zoogeographical differences. One of the most important problems concerns the boundary between the Lower and Middle Triassic in the faunal sequences of Laurasia and Gondwana (as typified by eastern Europe and South Africa).

In South Africa, the Lower Triassic has long been believed to include two faunal members, the already mentioned Lystrosaurus Zone and the succeeding Cynognathus Zone, the latter being also known from South America and Antarctica. Both these zones are dominated by therapsids. The Lystrosaurus Zone is usually compared with the European "neorhachitome" fauna and the Cynognathus Zone with Parotosuchus fauna. In terms of marine scale, the Cynognathus Zone is assigned to the Spathian, while the range of the Lystosaurus Zone now tends to be reduced to the Griesbachian.

However, this correlation is at variance with the above conclusion on the global pattern of the tetrapod faunal change during the Triassic. It was demonstrated that the transition between the proterosuchian and kannemeyerid epochs marked by the extinction of the Parotosuchus fauna falls in Europe at the Scythian-Anisian boundary. On the other hand, in South Africa, the beginning of the kannemeyerid epoch corresponds to the Cynognathus Zone and so should be placed in the Spathian if we accept the current dating of this zone. That discrepancy poses a dilemma: either the kannemeyerid epoch actually began earlier in Gondwana than in Europe or the dating of the Cynognathus Zone should be reevaluated.

We prefer the second solution (Shishkin and Ochev, 1989). The idea of the Lower Triassic age of the Cynognathus Zone was advocated mainly on the basis of its amphibians said to include the trematosaurids and the Scythian genera of capitosaurids and brachyopoids. But in reality, two latter families are represented in the Cynognathus Zone by more advanced members than those known from the Spathian Parotosuchus fauna, while the importance of trematosaurids as an indicator of the Scythian age is far from certain. On the other hand, the reptiles of the Cynognathus Zone are dominated by the most common groups of the Middle Triassic, primarily by kannemeyerioids and gomphodonts. Moreover, a number of typical forms of the Cynognathus assemblage like Batrachosuchus, Kannemeieria, gomphodonts Diademodon and Triachodon are known from the Middle Triassic faunas of East Africa (Lower Ntawe Formation and Manda Formation). In
addition, the Upper Fremouw Formation of Antarctica containing the equivalent of the *Cynognathus* fauna is now suggested to be of Anisian age based on palynomorph evidence (Farabee et al., 1990). This reappraisal brings us back to the problem of the age of the earlier Lystrosaurus Zone. As previously noted, the recent workers reduce it to the base of Induan (Anderson and Cruickshank, 1978) obviously proceeding from the position of *Lystrosaurus* in the European faunal sequence. It would imply a great gap between two South African zones, which would increase still more if we assign the Cynognathus Zone to the Anisian. This stimulated the idea that a sort of intermediate Early Triassic fauna should have existed in Gondwana and attempts were made to identify it with some Scythian assemblages from Australia and Tasmania.

We propose instead the alternative solution suggesting that the faunal record in the Lower Triassic of Gondwana is not strongly disjuncted and that the *Lystrosaurus* fauna lasted there during all or most of the Scythian. In other words, it may correspond to both the "neorhachitome" and the *Parotosuchus* faunas of Europe. The principal evidence for this viewpoint is given by the composition of the *Lystrosaurus* fauna, which looks like a mixture of forms indicative of different levels. Amongst its typical components, *Lystrosaurus* and the lydekkerinid amphibians are known to be confined to the Induan in Europe. On the other hand, the *Lystrosaurus* fauna includes the rhytidosteids, a family indicative of the Smithian (Lower Olenekian) in every place where it is known together with the marine invertebrates (Middle Sakamena Group of Madagascar, Sticky Keep Formation of Spitsbergen, Hedenstroomia beds of northern Siberia). Its type member, the genus *Rhytidosteus*, described from the South African Lystrosaurus Zone has been recently recorded as a member of the *Parotosuchus* fauna in the Spathian of the Cis-Urals. The procolophons (lizard-like cotylosaur reptiles) known from the Lystrosaurus Zone, correspond by the evolutionary level of their dentition to the Smithian-Spathian forms of Europe.

The idea of such a wide stratigraphic range of the Lystrosaurus Zone seems to be indirectly supported by the composition of its presumed equivalents from the Australian region. They come first of all from the Arcadia Formation of Queensland, the Blina Shales of western Australia and Knocklofty Formation of Tasmania. These faunas are peculiar for being dominated by the endemic amphibians and are devoid of *Lystrosaurus*. Like their South African correlative they also demonstrate the strange combination of groups which are known to differ in their age in Laurasia. The "Induan-looking" elements are represented by lydekkerinids and dissorophids, and the "Lower Olenekian (Smithian)" by rhytidosteids, while the evolutionary level of brachyopoids and the possible presence of plagiosaurids suggests a Spathian age. The latter possibility seems also to be indicated by the presence of the erythrosuchid reptile (*Tasmaniosuchus*) in the Arcadia Formation and the dicroidean flora in the sediments facially replacing the Blina Shales.

**Conclusions**

To summarize, both the South African and Australian Lower Triassic assemblages demonstrate the coexistence of forms or groups expected to indicate quite different ages from Induan to Upper Olenekian in the areas outside of Gondwana. This suggests that during the Scythian the tetrapod evolution proceeded much more slowly in Gondwana than in Laurasia, where the Lower Triassic may be calibrated by tetrapods with a high degree of resolution (revealing four stages of biostratigraphic changes within two faunas). The presence of *Lystrosaurus* and lydekkerinids, which characterized the whole Scythian in Gondwana, did not extend in Laurasia over the Induan-Olenekian boundary. By contrast, the Middle Triassic *Cynognathus* fauna constituting the initial and very distinctive stage in the development of the Gondwanan kannemeyeroid biota is not detected, so far, in Laurasia. However, it may possibly be correlated with the *Eocyclotosaurus* fauna of the Upper Buntsandstein and its equivalent in North America.
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STRATIGRAPHIC RANGE OF TRIASSIC BOREAL NAUTILOIDEA

E.S. Sobolev, Institute of Geology and Geophysics of the Siberian Branch of the USSR Academy of Sciences, 630090, Novosibirsk, USSR.

Introduction
Nautiloids were not applied until recently to the subdivision and correlation of the Boreal Triassic. Detailed examination of a number of stratigraphic sections in Taimyr, Verkhoyansk Ridge, in basins of the Olenek, Indigirka, and Kolyma rivers and at the Okhotsk coast have shown that although nautiloid deposits are relatively scarce, they occur almost throughout the Triassic (Fig. 1). Siberian material revised by the author revealed the rather high taxonomic diversity of nautiloid evolution (Sobolev, 1989). It became evident that nautiloids can be successfully used in zonal stratigraphy.

Fig. 1. Map of occurrences of Triassic nautiloids in northeastern Asia.
Fig. 2. Differentiation of nautiloid genera structure in Triassic paleoaquatoriums.
Nautiloid Zonation

The Triassic zonal scheme for Siberia developed by Dagys et al. (1979) and Dagys (1986) is used in this article as the reference scale. Two major stages can be recognized in the history of development of Triassic nautiloids. The first stage comprises Early and Middle Triassic and is characterized by the dominance of three families, Tainoceratidae, Grypoceratidae and Liroceratidae, transient from the Upper Paleozoic. Many of the genera from these three families originate in the Triassic. The second stage comprises Late Triassic and is marked by a burst of new forms originating. There appear Clydonautilidae typical of Late Triassic, which are characterized by strongly dissected suture lines. The first representatives of the suborder Nautilina, which continue into the Jurassic, appear at this stage. Within the two stages, nautiloids were irregularly developed. Although development within the stages differs, these are not significant systematic changes, but rather relate to dynamics of genera development (Fig. 2). In the Tethyan and Boreal realms they were developed more or less synchronously, showing less systematic diversity in the Boreal realms.

During the late Triassic burst of new genera varieties, nautiloids migrated from the Tethyan realm to the Boreal realm. Some of these migrants gave rise to the start of endemic phyletic lineages, which developed in the Boreal realm for long periods. The proposed chart is developed based on the evolution of such long-existing phyletic lineages of nautiloids.

Lower Triassic

In the Induan nautiloids are scarce in all aquatoriums. The Tethyan is characterized by grypoceratids with subventral and ventral siphuncles. In the Boreal realm common at that time were liroceratids (genus Tomponautilus, which is represented by species T. setorymi Sobolev), probable descendants of the Upper Permian genus Permonautilus, and a few representatives of the Upper Permian genus Tainonanautilus (Fig 3). This assemblage of nautiloids is distributed in the Lower Induan Zones, such as Concavum, Boracale and Nielsen and may be recognized as an independent Zone of Tomponautilus setorymi.

In all Upper Induan and Lower Olenekian (Hedenstroemi Zone) Boreal regions, nautiloids are absent. However, in the Early Olenekian of Siberia widely distributed are forms with straight conchs, which immigrated from the Tethyan at the beginning of the Kolymensis phase. Based on these orthocones there was recognized a Trematoceras boreale Zone, which was subdivided into Pseudotemperoceras pulchrulm and Trematoceras boreale subzones precisely corresponding to the Kolymensis and Tardus ammonoid standard Zones.

In Upper Olenekian the burst of new genera occur in the Tethyan basins, among nautiloid assemblages dominated by tainoceratids, which prevail in nautiloid fauna until the beginning of the Upper Carnian. Coiled nautiloids migrated to Boreal regions. In the Boreal Realm throughout the Olenekian distinctly dominant was the endemic line of the Phaedrysmocheilus genus from tainoceratids on whose evolution the zonal chart has been developed.

The main phylogenetic sequence of the genus in Siberia consists of the following species: Phaedrysmocheilus ornatus - P. evolutus - P. subaratus (Fig. 3). Phaedrysmocheilus ornatus Sobolev is an initial species. It is characterized by moderately evolute conch with angular outline and many prominent transverse ribs on the first two whorls. This species made its first appearance in the Euomphala phase and initiated a phylogenetic sequence that evolved in the direction of intensification of the conch involution and a weakening in its ornamentation.

The next species in the sequence Phaedrysmocheilus evolutus Sobolev (Contrarium phase) is characterized by moderately evolute conch, showing a roundish outline and fewer ribs.
Fig. 3. Regularities of the development of Boreal Nautiloids and Triassic zonal stratigraphy (Lower Triassic).
Fig 4. Regularities in the development of Boreal Nautiloids and Triassic zonal stratigraphy (Middle Triassic).
Fig. 5. Regularities in the development of Boreal Nautiloids and Triassic zonal stratigraphy (Upper Triassic).
The Grambergi phase yields Phaedrysmochelitus subaratus (Keyserling), showing moderately involute conch and badly developed ribs. Originating from it in the Spiniplicatus phase are Phaedrysmochelitus velilulus Sobolev and Phaedrysmochelitus involutus Sobolev. The latter species is characterized by the most involute conch in this genus and barely evident ribs, which are only developed on one-and-a-half initial whorls. Origin of Phaedrysmochelitus nestori (Shimansky) species is not quite clear. Probably this species, having a well-sculptured moderately involute conch appeared as a branch of the single generic stock in the Grambergi phase.

The Phaedrysmochelius ornatus Zone is the oldest and contains index-species and a new species from the genus Anopluceras. It corresponds to the Euomphala ammonoid Zone. The next zone, Phaedrysmochelius evolutus, comprises Contrarius and a greater part of the Grambergi ammonoid Zones. For the upper part of the Grambergi Zone, Parasibirites efimovae Bytschkov is a characteristic and very specific assemblage of nautiloids. The Phaedrysmochelius nestori Zone is identified by index-species as well as on the first appearance of representatives of Phaedrysmochelitus subaratus, which are characteristic of the uppermost zone. The Phaedrysmochelius involutus upper Zone includes index-species, Phaedrysmochelius subaratus and Ph. velilulus. The presence of similar species from Phaedrysmochelius and Anopluceras genera suggests a strong similarity between the assemblage from Ornatus and Evolutus Zones in Siberia and nautiloid assemblages from the Columbites parisiianus Zone of Idaho (Kummel, 1953) and Mangyshlak (Schastlivtseva, 1988).

Middle Triassic

The Early and partly Middle Anisian nautiloids are relatively monotypic both in the Tethyan and Boreal realms. The nautiloid endemic phyletic lineage continues to develop in the Boreal realm (Fig. 4). Genus Arctonautilus being most characteristic of the Anisian deposits in Siberia, appears to be a direct descendant of the Early Triassic genus Phaedrysmochelius.

Within the genus Arctonautilus outlinea is a certain phylogenetic sequence which is represented by the species of Arctonautilus ljubovae (Schastlivtseva) - A. svetkovi Sobolev - A. egorovi Sobolev the range of which coincides with that of the Anisian substages. The representatives of the sequence which constantly retained a large convex discoidal conch with radial ribs on one-and-a-half initial whorls and deep narrow ventral lobe in the suture line are characterized by a steady increase in the height of whorls at the late stages of ontogeny, deeper annular lobes in the suture line and the disappearance of the siphuncle toward the dorsal side. During the evolution of the genus Arctonautilus there appeared forms that lost some generic characters. For example, the Middle Anisian species Arctonautilus migayi Sobolev, unlike the other species of the genus, shows the suture line on the ventral side to be almost straight. Two Arctonautilus zones (A. ljubovae and A. migayi) are established, which correspond to the Lower and Middle Anisian.

Nautiloid taxonomical diversity increases sharply in the Upper Anisian Tethys, when another migration of the group to Boreal aquatoria occurred. Endemic genus Arctonautilus continues to evolve. Typical species Arctonautilus egorovi Sobolev gave the name to the zone that corresponds to the Upper Anisian. The genera of Paranautilus and Syringonautilus immigrated from the Tethys and allowed this zone to be subdivided into two subzones, which are consistent with the Rotelliformis and Nevadanus Zones on the ammonoid scale. The Arctonautilus egorovi Zone correlates quite well with the Meeki and Occidentalis ammonoid Zones from Nevada due to the presence of the species Paranautilus smith Kummel.

In the Ladinian stage in major world aquatoria taxonomic diversity decreases in nautiloids as well as in other cephalopods (Shevyrev, 1986). This decrease in diversity affects also the Boreal fauna. Rare representatives of the cosmopolitan genera of Sibyllonautus, Syringonautilus and "Gryponautus" are represented here by local species. It is currently proposed to distinguish "Gryponautus" kegalensis Zone for almost all the Ladinian stage. Forms similar to zonal index-species and described as
"Indonautilus" awadi Kummel and "Nautilus" sp. ex aff. N. griesnachi Diener are known from the Fassan of Israel, Arabia (Parnes, 1986) and the Himalaya (Diener, 1895).

The boundary between the Ladinian and Carnian stages is confined to one of important reconstructions in systematic composition of nautiloids, that was discussed above. After retardation of nautiloid evolution tempo in all realms during the Ladinian age, the beginning of the Carnian age is marked by a burst of new forms.

Upper Triassic

In Boreal regions the appearance of two major groups of nautiloids (Clydonautilia and Nautilina) is confined to the beginning of the Carnian. Upper Triassic zones recognized by nautiloids in the Boreal realm are based on clydonautilians development (Fig. 5). The oldest among clydonautilians in the Boreal realm is considered to be the species Procydonautilia anianiensis (Shimansky) which probably is derived from endemic species "Gryponautilia" kegalensis Sobolev with its similar conch shape. Saltation in this phyletic line resulted in the appearance in descendants of a narrow and deep ventral lobe in the suture line and disappearance of the annular lobe. The species "Cosmonautilia" polaris Sobolev is a direct descendant of Procydonautilia anianiensis. In this phylogenetic sequence the development proceeded in the direction of changing in conch outline from discoidal with a narrow and flattened ventral side and narrow ventral lobe in the suture line to phacoidal with a convex ventral side and wide ventral lobe in the suture line.

The oldest Carnian deposits, referred to as the Procydonautilia anianiensis nautiloid Zone, yield, apart from index-species, the first representatives of the genus of Cenoceras, which may be descendants of the local lineages of Syringonautilia, which evolved in the direction of intensification of the conch involution (Dagys and Sobolev, 1989). In addition, the last representatives of the genus Sibyllonautilia occur in deposits of this zone.

The boundary between the Ladinian and Carnian stages, adopted currently by ammonoids is not consistent with the range of Nautiloidea. The Procydonautilia anianiensis Zone confidently known from stratigraphic intervals to be equal to the Tenuis ammonoid Zone, comprises also the upper part of the Macconnelli Zone in modern interpretation.

The "Cosmonautilia" polaris Zone is identified by the first appearance of index-species. The zone is subdivided into two subzones ("Cosmonautilia" polaris and Procydonautilia goniatites). The upper subzone is characterized by the appearance in Boreal Nautiloid assemblages of first clydonautilians with reticular ornamentation of the species of Procydonautilia goniatites (Hauer) which migrated from the Tethys realm at the beginning of Seimkanense phase. This species is also known from the Julian substage of the eastern Alps, Afghanistan, Tibet and Timor Island.

The species Procydonautilia goniatites marked the beginning of a new phylogenetic sequence for clydonautiliids with reticular ornamentation, which occurs in the Late Carnian and Early Norian of Siberia. This sequence includes the following species: Procydonautilia goniatites (Hauer) - P. pseudoseimkanensis Sobolev - P. seimkanensis Bytschkov. The evolution proceeded here in the direction of conch outline changing from subspherical in the initial species to phacoidal with a convex ventral side poorly expressed in intermediate species to discoidal conch clearly expressed in intermediate species to discoidal conch with a clearly expressed, flattened ventral side in the latter species.

In Siberia the first representatives of the genus Germanonautilia, widely distributed in low latitudes in the Middle and beginning of the Late Triassic, appear in the upper part of the "Cosmonautilia" polaris Zone. The "Cosmonautilia" polaris Zone in its range corresponds to Omkuchanicum and Seimkanense ammonoid Zone and to the lower part of Pentasticus Zone.

In Late Carnian the retardation of evolution tempo occurs at the generic level in both realms. In
Boreal regions Late Carnian nautiloids are represented by two genera: Protoclydonaulus and Germanononaulus. However, specific diversity increases at that time. The Protoclydonaulus pseudoseimkanensis Zone corresponds in its range to the upper part of the Pentastichus Zone and the Zone of Yakutens in ammonoid standard and is characterized, apart from index-species, by the following species: Protoclydonaulus sinekensis Popov, Germanononaulus sibiricus Sobolev and G. popovi Sobolev.

The Carnian-Norian boundary is not clearly delineated by nautiloids. In the Boreal realm the Protoclydonaulus seimkanensis Zone is identified at the base of the Norian stage. It correlates with the Obrucevi ammonoid Zone. The assemblage from this zone is poor, not diverse, and includes index-species and Germanononaulus popowi.

The nautiloid assemblage is greatly renewed in the Tethyan and Boreal realms at the lower and Middle Norian. In Siberia this level (Ussurienis Zone) yields the first endemic family Siberionaulidae, represented by two genera (Siberionaulus and Yakutionaulus), which show the most complete suture line for nautiloids. Family Siberionaulidae originated in Usurienis phase from Siberian representatives of the genus Protoclydonaulus with reticular ornamentation (possibly from P. seimkanensis). Saltation is expressed in a more complex suture line due to appearance of additional lobes between the ventral and lateral lobes. The genus Siberionaulus is probably the first representative of the new family. The family evolved very fast, the evolution proceeding by further complications of the suture line. In the same phase the genus Yakutionaulus is characterized by a denticulate saddle in the suture line, which separates it from Siberionaulus.

The stratigraphic interval comprising the Usurienis Scutiformis and Ochotica Zones in the northern standard and characterized by the species Siberionaulus multilobatus Popow, Yakutionaulus kavalerovae Arkhipov et Barskov, Y. angulatus (Popow), Protoclydonaulus natosini McLearn and Germanonaulus kyotanii Nakazawa is thought to identify the Yakutionaulus kavalerovae nautiloid Zone. In the future a more detailed division of the Triassic deposits of the interval composed by this group will be possible due to progress in the study of suture lines. The correlation of the Middle and Upper Norian in Tethyan and Boreal realms based on nautiloids is somewhat difficult because of maximum endemic forms in nautiloid fauna from both regions. Protoclydonaulus natosini appears to be the single species common to Siberia and mid-paleolatitude fauna of British Columbia (McLearn, 1946).

At the Norian-Rhaetian boundary (according to Dagys and Dagys, 1990) a Siberian Efimovae Zone is interpreted as Rhaetian stage for the present article) almost all nautiloid genera and families die out in all aquatoria of the globe. In Siberia only one species (Grypoceras bytschkovi Sobolev) is known from terminal Triassic deposits. Only the family Cenoceratidae crosses the Triassic-Jurassic boundary. The oldest Jurassic deposits in Siberia contain the only representatives of this family. In the Lower Hettangian beds Psiloceras species of the genus Cenoceras are common.

Nautiloid Zonation

A nautiloid-based zonation including 19 biostratons suggests a rather detailed subdivision of Triassic deposits. The zones mostly have wide ranges and in many cases suggest detailed correlations within the entire Boreal realm (Figs. 6, 7). Wider correlations are ordinarily hampered, because of the lack of thorough studies of the Tethyan nautiloids. However, there are some datum levels (Phaedrynomochilus ornatus and P. evolutus Zones in the Upper Olenebian, Paranaulius smithi subzone in the Upper Anisian and Protoclydonaulus goniatites subzone in the Lower Carnian), due to recurrent waves of nautiloid immigration to Boreal regions from the Tethys, which allow wide correlation of Boreal and Tethyan charts to be made.
**Fig. 6. Geographic distribution of the characteristic nautiloid zonal assemblages in various structural-facial provinces of Siberia.**
<table>
<thead>
<tr>
<th>Stages</th>
<th>Ammonoid zones</th>
<th>Nautiloid zones</th>
<th>Nautiloid Fauna</th>
</tr>
</thead>
<tbody>
<tr>
<td>Russian</td>
<td>Efimovae</td>
<td>Grypoceras bytchkovii</td>
<td>Grypoceras bytchkovii Sob.</td>
</tr>
</tbody>
</table>
| | Ochotica | Yakutionaulius kavalerovae | Yakutionaulius kavalerovae Archipov et Barsk  
Siberonautilus multidobatum Popov, Yakutionaulius angulatus Popov, Yakutionaulius angulatus Popov, Germanonautilus kyotai Nakaz., Procyldonautilus natosini Mc Lean. |
| | Scutiformis | kavalerovae | |
| | Usuriensis | Procyldonautilus semikanensis | Procyldonautilus semikanensis Bytsch., Germanonautilus popowi Sob. |
| | Obrucevi | | |
| Cenomanian | Pentastichus | | |
| | Seimkanense | Procyldonautilus goniatis | C. polaris |
| | Omkutchanianum | | |
| | Tenuis | Procyldonautilus anianiensis | Procyldonautilus anianiensis (Shim.), Sybillyonautilus sp. nov., Ceanoceras boreale Dagg et Sob. |
| | | C. polaris | C. polaris |
| | Mcconnelli | Gryponautilus | Gryponautilus kavalerovii Sob., Sybillyonautilus artius Sob., Syringonautilus aff. nordskjoeldii (Lindstr.) |
| | Krugi | kegalensis | K. polaris |
| | | | K. polaris |
| | Omoloyensis | | |
| | Oleshkoi | | |
| | Nevadanus | Arctonautilus egrovi | Arctonautilus egrovi Sob., Trematoceras e. laticepsetatum (Huer), Arctonautilus orthoculus Sob., Sybillyonautilus orientalis Sob., Syringonautilus nordskjoeldii (Lindstr.), Papatacitus smiti Kumm. |
| | Rotelliforme | Paranauutilus smithi | |
| | Arctonautilus egrovi | A. egrovi | |
| | Kharaulakhensis | Arctonautilus migayi | Arctonautilus migayi Sob., A. vvedenski Sob., Trematoceras aff. spinosum Diter |
| | Decipiens | | |
| | Caurus | Arctonautilus ljuovae | Arctonautilus spissiensis Sob., A. ljubovae (Schasti), A. dolganensii Sob. |
| | Taimyrensis | | |
| | Spiniplicatus | Phaedrysmocheiulus involutus | Phaedrysmocheiulus involutus Sob., P. veliolus Sob., P. subaratus (Kyes.), Trematoceras subcampanile Kipar. |
| | Grambergi | Phaedrysmocheiulus nestor | Phaedrysmocheiulus nestor (Shim.), P. subaratus (Kyes.), Trematoceras subcampanile Kipar. |
| | Contrarium | Phaedrysmocheiulus evolutus | Phaedrysmocheiulus evolutus Sob., Anoploceras taimyrense (Schasti). |
| | Euomphala | Phaedrysmocheiulus ornatus | Phaedrysmocheiulus ornatus Sob., Anoploceras sp. nov. |
| | Tardus | Trematoceras boreale | Pseudotenoperoceras pulchrum |
| | Kolymensis | T. boreale | Pseudotenoperoceras pulchrum Schasti, Trematoceras clarum Schasti, T. boreale Schasti. |
| | Hedenstroemi | | |
| | Compresaus | | |
| | Turgidus | | |
| | Decipiens | | |
| | Nielsen | Tomponaulius setorymi | Tomponaulius setorymi Sob. |
| | Boreale | | |
| | Concavum | | |
The main changes in systematic composition of Triassic Boreal ammonoids and nautiloids coincide in time, consequently many boundaries also coincide, however, this coincidence is not complete. For example, the boundary between the Phaedrysmocheilus evolutus and P. nestori Zones is placed in the upper part of the Grambergi Zone, the boundary between the "Gryponautillus" kegalensis and Proclydonautillus anianicensis Zones is placed in the upper part of the Macconnelli Zone, among others. A zonal chart based on nautiloids allows considerable correction of the divisions and correlations of the sections from Boreal regions.

References


SYNCHRONEITY OF PALYNOLOGICAL EVENTS AND PATTERNS OF EXTINCTION AT PERMO-TRIASSIC BOUNDARY IN TERRESTRIAL SEQUENCE OF INDIA

R.S. Tiwari and Vijaya, Birbal Sahni Institute of Palacobotany, 53, University Road, Lucknow - 226007, India.

Abstract
There is no marine control for Permo-Triassic boundary on the Indian peninsula; therefore, palynology remains the only parameter for delineation of this systemic boundary. Other fossil groups have limitations because of taphonomic factors. The palynocladogram reveals that the end Permain extinction is preceded by arrays of diversification, particularly in striate disaccate pollen. Across the boundary several lineages have suffered set-back; nevertheless, some of them continue to survive with attenuating trends in taxonomic abundance and diversity. The origination of several non-striate disaccate as well as taeniatae pollen, along with cavate spores, is recorded just before this boundary. Nine palynocaravnets have taken place along the transit from uppermost Permian to lowermost Triassic in the type area. The correlation of events amongst the basins of peninsula provides a comprehensive model depicting uniform sequential trends in the spectrum of palynological transformations. The climatic change that accompanied the boundary event was not catastrophic and abrupt but, at the same time, it was deciding and definitive; and so was the change in vegetation. These happenings could be linked with great regression of sea and resetting of tectonic movements on peninsula which were the causal factors for change in geomorphology, ecology, and the climate. The higher degree of background extinction followed by enhanced evolution in flora in the stratigraphic vicinity of systemic boundary does not qualify for mass extinction in morphos. It is a case of high turnover. The situation in marine domain was different where definite mass extinction has occurred. Such a differential response, of land and sea life, to the causal factors supports the view that environmental stress triggered by geological readjustment, rather than the impact of bolide, was the cause of high turnover. It did not bring catastrophe to the terrestrial life at Permo-Triassic boundary.

Introduction
The sequence encompassing Permo-Triassic systemic boundary on the peninsular India comprises only terrestrial sedimentary suites. Therefore the tagging of this span with chronostratigraphic scale poses problems. Although animal and plant fossils provide useful parameters for biostratigraphy, yet they lead only to a coarse calibration because of the taphonomic bias and paucity of occurrences in closely spaced levels in sections of Gondwana basins. In such a situation, the palynofossils have been effectively utilised for event stratigraphy because of their high preservation potential due to their inherent resistance to decay, and also their production in enormous numbers. Further advantage is added by the fact that the Permo-Triassic transition on Indian Peninsula is represented by Raniganj-Panchet formation which mostly makes a continuous sequence in the type area, i.e. Damodar graben, and contains coal-shale-sandstone units which are the best suited lithofacies for palynomorph preservation. Thus closer sampling, high yield and good preservation have made a strong data-base. It has also been possible to link the available palyno-daturn planes with those of contemporary marine sequences of P/Tr transition in the Salt Range and Western Australia. The sequence homology amongst the palynoassemblages of these regions supports the correlation. The homotaxy does not contradict the equation because of the great influence of Glossopteris flora during this time on the eastern Gondwana land.
Thus on the basis of multiple evidences, the Raniganj-Panchet formational boundary has been identified as the Permo-Triassic boundary (Vijaya and Tiwari 1991). The present article deals with the identification of palynoevents and degree of origination as well as extinction of lineages in morphos; such episodes have been primarily identified in Damodar Valley which is the type area for Upper Permian Raniganj Formation and Lower Triassic Panchet Formation. The synchronicity of these events in other basins (Map 1) has also been traced and a model of extinction pattern at the P/Tr boundary has been built.

Map 1: Gondwana basins on Indian Peninsula
Palynoevents

The palynoevents are identified cumulatively on the basis of generic assemblages, species range zones, steady or unsteady FADs and LADs of morphos (given in Table 1) and diversification and extinction of lineages in view of their cladistic relationship (Tiwari and Singh, 1986; Tiwari and Tripathi, 1991; Vijaya and Tiwari, 1987, 1991). Thus the characteristic episodes of wider spatial occurrence, with diagnostic features of non-niche nature are graded as palynoevents. The unsteady First Appearance Datum (FAD-U) is that incidence where extremely rare, inconsistent and highly sporadic specimens of a morphos are recorded, whereas steady First Appearance Datum (FAD-S) are marked when (could be) rare but consistent presence is marked. So also the LAD-U and LAD-S are defined. Nine such events are identified across the span encompassing latest Permian and earliest Triassic in the Damodar Valley (Text-figs 1,2). Each palynoevent triggers a new phase of composition which lasts till the occurrence of the next palynoevent. The phase between two palynoevents is termed here as palynoevent passage --- abbreviated as PAS and named after the immediately preceding event, e.g. PAS-I is the zone which follows the Palynoevent - I.

Palynoevent - I

At the advent of Late Permian Raniganj Formation, striate disaccate Striatopodocarpites-Faunipollenites rich assemblage dominates the scene which continues monotonously through about three-fourth of the run of this formation; Palynoevent - I is identified on the top of this assemblage by the appearance of morphos (disaccate pollen) with transitionary morphography in having striate type of groves on the body (Tiwari and Ram-Awatar, 1991) viz., cf. Lunatisporites- Trabeulosporites (Text-fig. 1). These striate forms lead to unquestioned typically multitaeniate pollen at the level of Palynoevent - IV. Vertually the taeniate pollen are the characteristic components of Triassic palynoflora where they are abundant. Their sporadic, unsteady and inconsistent appearance at this level, in the lithological suite of shale and sandstone, foreshadows the change in palynoflora which occurred later in the sequence. Except for this morphos, the PAS-I basically remains a continuum of the Striatopodocarpites-Faunipollenites - rich assemblage which started at the beginning of the Raniganj Formation (Text-fig. 2).

Palynoevent - II

Not much deposition has taken place after the Palynoevent-I when the Palynoevent - II is documented by the rapid radiation of the cavate, zonate form Gondisporites (Text-fig. 1). The duration of PAS-II is short- lived. It is generally located in the carbonaceous shales within the sandstone unit (Text-fig. 2). In rest of the morphos, the monotony of the Lower Raniganj assemblage continues. This is the significant level for successive palynofloral changes which take place in the uppermost Raniganj and continue up to the beginning of Panchet.

Palynoevent - III

At this level, the enveloping monosaccate organisation represented by Densipollenites (Text-fig. 1) records its maximum abundance while Gondisporites declines (Text-fig. 2). The PAS-III persists in the coal-shale-sandstone cyclic unit till the last coalseam, in the closing phase of the Raniganj Formation.
Text-fig. 1: Illustrates the marker spore-pollen and diagnostic incidences at each palynoevent. Numbers indicate the Morphos Index Number as given in table 1.
Text-fig. 2: Range diagram showing distribution pattern, FAD and LAD of important spore-pollen taxa through transit zone of Late Permian Raniganj Formation and Early Triassic Panchet Formation in Raniganj Coalfield, Damodar Basin. Generic and species assemblage zones (after Tiwari and Singh, 1986 and Tiwari and Tripathi, 1991, respectively) correlated with the generalized lithological sequence, depicting average thicknesses based on bore-hole data. Identification of nine palynoevents and their characteris- tics is based on totality of compositional pattern, advent of new morphos and the nature of assemblage zones. The phenomenon of regression is represented by broad curved line. Other indices: ...Straddlers; ---unsteady occurrence; straight line: consistent continuity and relative abundance; small horizontal bar indicates LADs, solid circle represents FADs. Numbers at lower margin represent "morphos" as given in table 1.
Palynoevent - IV

At the close of PAS-III, above the top of the last coalseam, in a shale and sandstone unit, several morphographies, viz., Playfordiaspora, Lundbladispora, Goubinispora, etc., record their first unsteady appearance (FAD-U). The definite multi-taeniate morphography is also exhibited in this group of morphos (Text-fig. 1). Evidently there is a major change at this datum indicated by the trickling appearance of the palynofloral elements of Early Triassic. The Palynoevent-IV triggers the beginning of high turnover in the lineages, because the straddler elements as well as new entrants continue up to the base of the last sandstone unit of the Raniganj Formation. The acutal line of major qualitative change is denoted at this event, although background taxa of long standing still continue to be impressively present in PAS-IV (Text-fig. 2).

Palynoevent - V

The steady first appearance (FAD-S) for most of the morphos which are the main elements of Triassic is recorded at this level (Text-fig. 1). Beside this, the straddlers of long geological history with evolutionarily exhausted morphographies, viz., those of the girdling monosaccate pollen group, die out at this plane. This event is also characterized as the terminating phase for most of the apicate triletes and other forms which qualify the Permian assemblage (Gondisporites, Indospora, Microfoveolatispora, etc.). Evidently the degree of extinction is also high at this level. The sequence of sediments between the topmost coalseam and the base of khaki-green shale consists of carbonate shale, sandstone intercalated with shales, and the sandstone units. The advent of khaki-green shale demarcates the inter-formational boundary. Generally the upper part of the sandstone unit with shale intercalation, or the base of the uppermost sandstone unit in Raniganj Formation records the Palynoevent-V (Text-fig. 2). A far degree of floral continuity is evidenced by the representation of some striate disaccate pollen (e.g., Striatopodocarpites, Faunipollenites) across this event into the PAS-V. On the other hand, the change in flora is assertive because of the consistent and high percentage of the taeniates (Lunatisporites), small non-striate disaccates (Klausipollenites) and cavit spores (Lundbladispora). The definitive changes in lineages (Text-fig. 3) and qualitative pattern-shifting make this event a singular episode.

Palynoevent - VI

Persistent steady occurrence of the Lower Triassic morphos (Ringsporites, Vernucosisporites, Lundbladispora, Densoisporites, Playfordiaspora, Klausipollenites, Goubinispora) as well as their quantitative diversity is recorded at this level (Text-fig. 1). The lithofacies containing this kind of change are typical khaki-green shales and sandstone units, in which seldom streaks of carbonaceous matter may be present; such change in sedimentary suites during PAS-V is associated with the interformational changes (Text-fig. 2).

Palynoevent - VII

A definite diminishing phase of striate disaccates of very long standing history begins at this datum. So also, along with Lunatisporites and Klausipollenites, the typical population of Vernucosisporites and Callumispora (Text-fig. 1) becomes prominent. The trilete apulate spores of Permian also vanish from the stage. The kind of change - over, a transitional nature of lithofacies, from khaki-green shale to the chocolate shales has also been observed. A relatively increased degree of extinction in morphos lines is also revealed at this level (Text-fig. 2).
Text-fig. 3: A simplified sketch showing span of basic lineages (hatched lines) in diagnostic spores and pollen through Permian and Triassic sequences. The nature of extinction and innovation at P/Tr boundary demonstrated by change in morphos. The relative occurrence is represented by ...straddler; ---unsteady; straight line: steady; parallel lines: established behaviour pattern.
Text-fig. 4: Proposed trees for the morphologically related spores and pollen (Dashed lines) established on the basis of cladistic analysis (Vijaya and Tiwari, 1991). The known stratigraphic range of each clad is represented by its height and relative occurrence by the width of balloons (not to the scale).
Palynoevent - VIII

The radiant prominence of Verrucosisporites and Callumispora makes a new compositional set-up of the morphos in which important older lineages of long standing (e.g. Densipollenites, of Late Permian) have lost their identity (Text-fig. 1). The dominant chocolate nature of the lithounit containing these varied morphos reflects the continuation of constant condition in the depositional set-up with reference to the immediately older strata. (Text-fig. 2).

Palynoevent - IX

The establishment of the caveate, cingulate spores (Lundbladispora, Densoisporites) and the taeniate pollen (Lunatisporites) is indicative of the completion of the change over which started at Palynoevent-V (Text-figs.1,2). The singular features of this plane are the commanding recurrence of Lunatisporites prominence and disappearance major Permian clades.

Synchronicity of events

Taking the calibration of palynoevent sequence in Damodar Valley as a scale for tagging, various tie-points have been located in other basins of peninsular India. The available data provides useful material for comparisons with Son and Godavari Valley basins where Late Permian-Early Triassic palynoassemblages are recorded in close proximity of different palynoevents (Tiwari and Ram-Awatar, 1990; Srivastava and Jha, 1990). In Rajmahal, Mahanadi and Satpura basins although solitary or few levels are known yet they are significant as reference points (Tripathi, 1986, 1989; Tiwari et al., 1991; Bharadwaj et al., 1978).

The term "Palynoevent" is used here exclusively for the qualified episodes recorded only in the Damodar Valley basins whereas "tie-points" are the comparable reference-assemblage-points in other basins which have a bearing with palynoevents of Damodar Basin. The exact matching of palynoevents with tie-points is not feasible in certain cases because the data is incomplete and does not make a continuous sequence of closely sampled lithounits or contiguous PASs. Inspite of these limitations, the prime criterion for correlatability of tie-points is their sequential order of superimposition with reference to the palynoevents. The term "younger elements" is used for those palynomorphs which are characteristic for Early Triassic palynofloras but make their appearance individually or collectively at an older level, in the closing phase of Late Permian, viz., Lunatisporites, Klausipollenites, Lundbladispora, Goublinispora, Playfordiaspora, etc.

The analysis of data (Tables 2 and 3) reveals that the order of succession in tie-points in Rajmahal, Son, Godavari and Mahanadi valley basins corresponds with the palynoevents of Damodar valley, although it may be that some of tie-points are missing or the run between the two tie-points may vary in its extent. Inconsistency in occurrence of Gondisporites phase in other basins seems to be related with its short span of existence. Hence, the chances of identification of a tie-point comparable to Palynoevent-II are lessened. The genus Densipollenites shows stretched phase of prominence in its last segment and may enter into the Crescentipollenites phase, or even overshadow the latter, reaching up to the P/Tr boundary; such is the case observed in Son and Godavari valley basins. In Son Valley the prominent occurrence of unique Trabeulosporites - a taeniate- striinate disaccate pollen, at the boundary transition makes a characteristic episode which is not yet located in other basins; yet the steady occurrence of younger elements at this level determines that the position of this tie-point is at P/Tr boundary.

The tie-points assignable to Palynoevent-IV or PAS-IV have been located in almost all the basins of peninsula. This is the phase where Densipollenites/Crescentipollenites occurs in high percentage and, at the same time, younger elements start trickling on the scence. This phenomenon is indicative of a close proximity to Permo-Triassic transition. Subsequently, up in time, the younger elements become
steady and consistent which incidence makes the base line for earliest Triassic.

**Mass Extinction or High Turnover of Clades**

The term mass extinction is used to denote extinction of large and diverse portion of biota, which has taken place at a particular time in geological history. The turnover is the total sum of extinction and origination of lineages at a time plane or a short span of time representing a transition in evolution. The latest Permian extinction is generally considered as one of the five mass extinctions of the marine life (Hoffman, 1989). On terrestrial regime, however, the story seems to be different as the extinction at this level may not be qualified as mass extinction (Benton, 1989).

With relation to Permo-Triassic boundary on Indian peninsula, the palynoevents identified in the present work play an important role to decipher the sequence of alterations in assemblages which reflect a change-over in vegetational composition across this time span. It has been established that the beginning of Raniganj Formation has witnessed the continuity of species acme-zones which stretch across from the older strata. The genera with maximum number of species are *Verticipollenites* and *Densipollenites* (Tiwari and Tripathi, 1991). This diversification continues throughout the Raniganj Formation. In addition, the epiboles of number of species in the genera *Crescentipollenites* and *Striatopodocarpites* appear at the level of Palynoevent-III. Such trends support the view that there has been a substantial diversification in morphos at the end Permian phase. The proposed phylogenetic relationship among the organisations based on cladistic analysis (Vijaya and Tiwari, 1991) also decipher that the Upper Permian was a time of radiation and diversification in striate and non-striate (*Scheuringipollenites*, etc.) disaccate pollen. Similar analysis, based on ancestral and derived character states linked with stratigraphy, has been done in case of certain significant spores as depicted here in Text-fig. 4. The great multiplication in morphos makes the latest Permian a period of cladogenesis in spores and pollen.

The monosaccate lineages have almost disappeared in the Upper Permian (Text-fig. 3). These evolutionarily exhausted clades of long geological history apparently contribute to the phenomenon of "great" extinction at the Permo-Triassic boundary. Beside this, several other morphos, viz., *Microfoveolatispora*, *Didecitrites*, *Indospora*, *Acanthotriletes*, *Navalesporites*, *Striatosporites*, *Cycloganisporites*, *Verticipollenites*, also extinct at this level (Text-fig. 2). These terminations obviously project a high degree of extinction but they are counter-balanced by the appearance of several new branches from the older clades, depicting an evolutionary shift in the population. Such new-comers are taeniatae pollen, small-winged simple disaccate pollen and cavate as well as sculptured spores. Thus, an equilibrium of existence has been established and a high turnover has resulted (Text-fig. 4).

The analysis further reveals that in Raniganj Formation of Damodar Valley basins Palynoevent-I occurred at the level of Coalseam VIII in the Raniganj Coalfield where taeniatae pollen grains make their sporadic appearance. This is followed by the Palynoevent-II in the next younger coalseam (VIII A) where *Gondisporites* proliferates in number. In the shale unit underlying the Coalseam IX (Kajora seam), the *Densipollenites*-rich phase begins which may run concurrently with the proceeding phase of *Crescentipollenites*. Just above the splits of Coalseam X (Bharatchak seam), heralds the singular episode of first unsteady appearance (FAD-U) of new morphos of younger affinity which become steady at Palynoevent-V, coinciding with the Raniganj-Panchet boundary (Vijaya and Tiwari, 1987). The Panchet Formation is identified by different set of lithology comprising khaki-green shales and sandstone units. This is associated with steadiness and sprouting in morphos of Palynoevent - V.

The extinction pattern of spore-pollen species through Raniganj-Panchet transition has been deciphered by the finding that about three-fourth of the existing species perish at the top of Raniganj (at Palynoevent - V), while one-fourth of the total population continues to exist in the lowest Panchet (Tiwari and Tripathi, 1991). It is interesting to note that this design of distribution emerges when the
steady first appearance (FAD-S) is taken into account. However, if the unsteady occurrence datum (FAD-U) of species is considered, the apparent high degree of extinction gets smothered and a mode of high turnover is relieved. In other words, FAD-S projects the impressions that a drastic change had taken place at the P/Tr boundary whereas FAD-U reveals that extinction and innovation had occurred hand in hand. There are definite differences between latest Permian palynoflora and that of the earliest Triassic, but many forms of the former horizon continue to thrive into the latter (Text-figs 3.4). At the same time, the origination of new forms (Triassic elements) predates the termination of several older forms (Permian elements), that means - an overlapping of end-lines and new-lines. On the basis of these observations it is derived that the span encompassing Permian-Triassic boundary shows high turnover, rather than catastrophic mass extinction in the spore-pollen lineages.

What Causes the Episode of Palynoevent V?

Palynoevent-V is not as simple an episode as it appears. It is a combination of several trends exhibited by the changes in lithological features, megafaunal components (*Glossopteris* flora to *Dicroidium* flora), palynological assemblage, estheriid population and other faunal association (Vijaya and Tiwari 1991).

The vegetational changes as evidenced by megaflores and reflected in palynofloras, could have been caused by the shifting in evolutionary pathways which were primarily guided by tectonic of the peninsula. The Upper Permian Raniganj sediments were deposited by meandering streams which were flowing towards northwest and west. The process of deposition was rapid and the subsidence was continuous and quick. At the beginning of Lower Triassic Panchet Formation new incidence of tectonic uplift and readjustment of palaeoslope have occurred. Thus, the palaeodrainage was readjusted toward west and southwest and the deposition has taken place largely by braided streams which became sinuous in the down current direction (Casshyap and Tewari, 1988). The tectonic movement was more pronounced in Damodar Valley basins during most of the Raniganj sedimentation but began to lose its intensity at its closing phase. The processes of subsidence further slowed down during Panchet sedimentation. On the peninsula, although the different basal belts have varying tectonic setting which are reflected in the arrangement of lithic fills (Ghosh, 1975), the broad correlation of palynoevents and tie-points based on their sequence of super-imposition is remarkable (Table 2).

This changing set-up of the geological dynamics in the transitional zones of latest Permian and earliest Triassic must have caused faster and substantial alteration in the ecological environment on the peninsula. The pressure generated by forces of newer geomorphology and resultant ecology, and the fluctuating climate persuaded the floral lineages to perish in large number as well as to originate newer branches from the basic lineages during this time. The chain of environmental episodes at faster rate during this time span is also reflected in the form of palynoevents I to IX (Text-fig. 2).

There is a difference of opinion regarding the cooling during the end of the Permian (Waterhouse, 1973; Stanley, 1984,1988). On Indian peninsula although there are no evidences which support an intensive lowering of temperature at the Permian-Triassic passage, nevertheless, there are indications that the warm humid climate of the late Lower Permian and most of the Upper Permian had become moderately cool during the close of Raniganj Formation, where the incidence of girdling monosaccate lineage shows a fair recurrence. This cooling seems to have contributed to the floral changes at the systemic boundary. A similar condition appears to be continued into the Lower Panchet where *Callumspora* is recorded in high number. After the Palynoevent-VIII the warming up of the climate has been envisaged.
Conclusions
The causal mechanisms for the extinction of marine life have been postulated to be the regression, trace elements, poisoning of environment, cosmic radiation, salinity fluctuations, etc. (see Maxwell, 1989). No such phenomenon appears to be responsible for the change in floristic component during the Permian-Triassic passage on Indian peninsula, because the extinctions were not calamitous or unsparing. The regression of the ocean which occurred, could have added to the climatic changes during this time. The increased continentality could have triggered drier conditions. The sequence of palyneoevets are strong indicators of faster changes during short interval of time which fact corroborates with the palaeogeomorphographical rearrangements inducing the new ecological conditions. On terrestrial regime no mass extinction has taken place in plant life at or in the stratigraphic vicinity of P/Tr boundary. The rate of extinction is accentuated but gradual shifting in composition with origination of new branches in basic lineages is remarkable.

Acknowledgements
The authors are grateful to the Organisers of the Symposium on Triassic Stratigraphy, Lausanne, Switzerland for granting us financial support to attend this deliberation. Our special thanks are due to Prof. A. Baud, Chairman of the Subcommission on Triassic Stratigraphy for his keen interest and kind help in materializing our participation in the Symposium. To the past Chairperson of this Subcommission, Prof. C. Virgili, Collegio de Espana, Paris our gratitude is extended for her encouragement to us to be the active contributor of this specialised group for Triassic Stratigraphy. To Dr. B.S. Venkatachala, Director, B.S.I.P., Lucknow, we are thankful for his help and permission to communicate this paper at the STS.

References


1. Potoniopsis Bharad, 1964
2. Distriromonasites Bharad, 1962
4. Virkkipollinities Lele 1964
5. Barakarites Bharad. and Tiw. 1964
6. Divartiacus Venkatch. and Kar 1966
7. Vesicaspora Schemal 1951
8. Circumstrialetes Lele and Makada 1972
10. Tiwariaspors Matoshw. and Kar 1967
12. Vesigispores Balme and Henn, emend. Tiw. and Singh 1984
15. Kamitiusacites Sriv. and Jha 1986
17. Densipollinities Bharad, 1962
20. Striatopodocarpites Sedova 1956
22. Cuneatiporites Lesch. 1955
23. Piatysaccus Pot. and Kr. 1954
24. Scheuringipolinities Tiw. 1973
25. Luukispores Pot. and Kl. emend. Kl. 1963
26. Placipolitinities Lele 1964
27. Parasaccites Bharad, and Tiw, 1964
29. Playfordipora Maheshw. and Baner. 1975
31. Satsangaacites Bharad. and Sriv. 1969
32. Vitreiporites Lesch, emend. Jans. 1962
33. Klauspollinities Jans. 1962
34. Gouhinipora Tiw. and Rana 1981
35. Chordiporites Klaus 1960
38. Acantarotyrites Naum. emend. Pot. and Kr. 1954
39. Apiculatiporites Ibr. emend. Pot. and Kr. 1956
40. Cyclograniporites Pot. and Kr. 1954
41. Distromonocolpites Bharad, and Sinha 1969
42. Ephedripites Bolkhovit. ex Pot. 1958
43. Gondisporites Bharad, 1962
44. Henneleiporites Tiw. 1968
45. Indospors Bharad, 1962
46. Lacinireites Venkatch. and Kar emend. Tiw. and Singh 1981
47. Laevigatiporites Ibr. emend. Schopf, Wils. and Benda 1944
49. Navalesporites Sarate and Ram-Awatar 1984
51. Striatiporites Bharad. 1954
53. Cyclobaculiporites Bharad, 1955
54. Horniditreites Bharad and Sal. 1964
55. Lophotyrites Naum. ex Pot. 1954
56. Microbaculipora Bharad, 1962
57. Callumipora Bharad, and Sriv. 1969
58. Ginkgoceadophytus Samoilov. 1953
59. Indothripites Tiw. 1964
62. Lundbladipora Balme emend. Playf. 1965
63. Inaperturapolinities Thoms, and Pflug emend. Pot. 1958
64. Osmaninacladites Couper 1953
65. Weylandites Bharad, and Sriv. 1969
66. Peiricoipolinitides Danze-Cor. and Lav. 1963
67. Guttaiporites Visscher 1966
68. Simeonipora Balme 1970
69. Rengiporites Tiw. and Rana 1981

TABLE - 1 Morphos Index Number of spore-pollen taxa, given for photos in text-fig.1 and at the base line in text-fig.2.
<table>
<thead>
<tr>
<th>Basin Tie-point</th>
<th>Location of tie-point in the Assemblage</th>
<th>Position of tie-points relative to Palynoevents in Damodar Valley basins</th>
<th>Basis of tagging</th>
<th>References</th>
<th>Reasons for placements</th>
</tr>
</thead>
<tbody>
<tr>
<td>Son Valley</td>
<td>Striatopodocarpites Lunatisporites</td>
<td>within PAS-VI</td>
<td>diversified state of Lunatisporites in association of strataes</td>
<td>Mahadevas, Gopad River; Tiwari &amp; Ram-Awatar, 1991</td>
<td>stratigraphic position of the samples suggestive of younger level within PAS-VI</td>
</tr>
<tr>
<td>#6</td>
<td>Striatopodocarpites Klausipollenites</td>
<td>in PAS-V, at the close proximity of Palynoevent-VI</td>
<td>establishment of morphs of Palynoevent-V</td>
<td>Nidpur beds Tiwari &amp; Ram-Awatar, 1990 (MB, NID-10, 8)</td>
<td>proliferating trends of Lunatisporites, Goubinispora, Klausipollenites; indicative of younger aspect within PAS-V</td>
</tr>
<tr>
<td>#5</td>
<td>Striatopodocarpites Trabsculosporites</td>
<td>matched with Palynoevent-V</td>
<td>FAD-S of morphs of Palynoevent-IV</td>
<td>Gopad River section, Tiwari &amp; Ram-Awatar 1990 (GPD-83-88)</td>
<td>proliferation of strinate morphs</td>
</tr>
<tr>
<td>#4</td>
<td>Densipollenites</td>
<td>above Palynoevent IV</td>
<td>proliferation of Densipollenites, FAD-U of morphs of Palynoevent-IV</td>
<td>Dargaoon, Jothila River section, Tiwari &amp; Ram-Awatar, 1987 (C-7-C-71)</td>
<td>last segment of Densipollenites, younger element trying to be steady</td>
</tr>
<tr>
<td>#3</td>
<td>Densipollenites</td>
<td>just above the Palynoevent-III</td>
<td>proliferated phase of Densipollenites, but absence of younger morphs</td>
<td>UKD-8, Korai Coalfield; Gopad River, Nidpur beds; Tiwari &amp; Ram-Awatar, 1987b, 1990</td>
<td>lower limit of sequence not known</td>
</tr>
<tr>
<td>#2</td>
<td>Faunipollenites</td>
<td>matched with Palynoevent-I</td>
<td>FAD-U of strinate forms</td>
<td>Sehra naia, Mathhas; Ass.1, UKD-8, Korai Coalfield; Tiwari &amp; Ram-Awatar, 1986, 1987b, 1990</td>
<td>sudden appearance of strinate group within Striatopodocarpites-Faunipollenites phase</td>
</tr>
<tr>
<td>#1</td>
<td>Lunatisporites Verrucissporites</td>
<td>in PAS-IX</td>
<td>radiation of Lunatisporites</td>
<td>Melaram area (GAM-7, Ass.5) Sriv. &amp; Jha, 1990</td>
<td>lower limit of sequence uncertain</td>
</tr>
<tr>
<td>Godavari Valley</td>
<td>Lunatisporites Verrucissporites</td>
<td>in PAS-IX</td>
<td>radiation of Lunatisporites</td>
<td>Melaram area (GAM-7, Ass.5) Sriv. &amp; Jha, 1990</td>
<td>lower limit of sequence uncertain</td>
</tr>
<tr>
<td>#3</td>
<td>Densipollenites</td>
<td>near top of PAS-IV</td>
<td>FAD-U of morphs of Palynoevent-IV</td>
<td>in 6 bore-holes (Ass. 5) Sriv. &amp; Jha, 1988</td>
<td>last segment of Densipollenites blooms with with inconsistent younger elements</td>
</tr>
<tr>
<td>#2</td>
<td>Faunipollenites</td>
<td>base of PAS-IV</td>
<td>FAD-U of morphs of Palynoevent-IV</td>
<td>Sriv. &amp; Jha, 1988 (Ass. 4); 1990 (Ass. 4)</td>
<td>depleted Densipollenites, inconsistent younger elements may be present</td>
</tr>
<tr>
<td>#1</td>
<td>Faunipollenites</td>
<td>base of PAS-I</td>
<td>FAD-U of taeniate pollen</td>
<td>Sriv. &amp; Jha, 1988 (Ass. 4); 1990 (Ass. 2)</td>
<td>appearance of taeniate group within Striatopodocarpites-Faunipollenites phase</td>
</tr>
<tr>
<td>Mahanadi Valley</td>
<td>Striatopodocarpites Crescentipollenites</td>
<td>Top of PAS-II</td>
<td>Proliferated Densipollenites along with Crescentipollenites</td>
<td>Malda River section, Talcher Coalfield, Tiwari et al., 1991 (Ass.4)</td>
<td>significant presence of Crescentipollenites and absence of younger elements</td>
</tr>
<tr>
<td>#4</td>
<td>Densipollenites</td>
<td>matched with Palynoevent-III</td>
<td>Densipollenites proliferation begins</td>
<td>-do- (Ass.3)</td>
<td>closer yielding samples in sequence and the palyno-composition assert the positioning of the Tie-points</td>
</tr>
<tr>
<td>#3</td>
<td>Gondisporites</td>
<td>matched with Palynoevent-II</td>
<td>radiation of Gondisporites</td>
<td>-do- (Ass.2)</td>
<td></td>
</tr>
<tr>
<td>#1</td>
<td>Faunipollenites</td>
<td>in pre-strinate phase</td>
<td>absence of strinateae</td>
<td>-do- (Ass.1)</td>
<td></td>
</tr>
<tr>
<td>Rajmahal Purnea</td>
<td>Lundbladispora Densisporites</td>
<td>equivalent to P-IV Zone of Tiwari &amp; Singh, 1986</td>
<td>dominance of cavate, taeniate morphs</td>
<td>Purnea Well; Venkatatalaya &amp; Rawat, 1979</td>
<td>due to graphic limitations Tie-point 2 is placed in PAS-IX; it is important reference point for sequence</td>
</tr>
<tr>
<td>#2</td>
<td>Striatopodocarpites Crescentipollenites</td>
<td>in lower part of PAS-I</td>
<td>FAD-U of morphs of Palynoevent-IV</td>
<td>B.H.RJNE-8,9,16; Tipathi, 1986, 1989</td>
<td>occurrence of younger elements; lower limit not known</td>
</tr>
<tr>
<td>Satpura Valley</td>
<td>Striatopodocarpites Densipollenites</td>
<td>just above Palynoevent-IV</td>
<td>FAD-U of morphs of Palynoevent-IV</td>
<td>Sukhtawa sect. Bharadwaj et al., 1978</td>
<td>last segment of Densipollenites with younger elements</td>
</tr>
</tbody>
</table>

**TABLE 2:** To illustrate the position of known tie-points in various basins of peninsular India, with reference to the Palynoevents and PASs of Damodar Valley basins in Text-fig.2.
<table>
<thead>
<tr>
<th>Basin</th>
<th>Mahanadi S.E. Son Valley Basins</th>
<th>Rajmuhal Purnea Basins</th>
<th>Damodar Valley Basin</th>
<th>Son Valley Basins</th>
<th>Satpura Basin Valley</th>
<th>Godavary Valley Basins</th>
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<tbody>
<tr>
<td>Lower Triassic</td>
<td></td>
<td>(*)</td>
<td>IX</td>
<td></td>
<td>*4</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>PAS VII</td>
<td></td>
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<td>VI</td>
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<td>PAS VII</td>
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<td>I PAS VI</td>
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<td>VI</td>
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<td>PAS V</td>
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<tr>
<td>Upper Permian</td>
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<td>*1</td>
<td>PAS IV</td>
<td>*3</td>
<td>*1</td>
<td>*2</td>
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<td>IV</td>
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<td></td>
<td></td>
<td>III</td>
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<td></td>
<td></td>
<td>*4</td>
<td>PAS III</td>
<td>*3</td>
<td>*1</td>
<td>*1</td>
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<td>*2</td>
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<td>*1</td>
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</table>

**TABLE 3:** Synchronicity of tie-points(*) in various basins showing correlation with the palynoevents calibrated with I - IX palynoevents of Damodar Valley basins; PAS- passage in two palynoevents. Refer to table 2 for other details.
SIGNIFICANCE OF TRIASSIC STAGE BOUNDARIES DEFINED IN NORTH AMERICA

E.T. Tozer, Geological Survey of Canada, 100 West Pender Street, Vancouver, British Columbia, V6B 1R8, Canada.

Abstract
New data on ammonoid faunas at and near the Permian-Triassic, Spathian-Anisian, and Anisian-Ladinian boundaries are reviewed. The question of the status of the Rhaetian is discussed. Justification is given for continued application of the boundary positions defined in North America. Use of Rhaetian as the ultimate Triassic stage is not recommended. Proposed new taxa of Triassic Ammonoidea are: Inyoceras n. gen., Subhungarites n. gen., Pseudacrochordiceras n.gen., and Paracrochordiceras welerti n.sp.

Introduction
Twenty five years ago a biochronology for the Trias with about 35 divisions (standard zones) was recognized from the sequence of ammonoid and bivalve faunas preserved in North America (Tozer, 1967; Silberling and Tozer, 1968). Representatives occur of nearly all ammonoid and pelagic bivalve faunas known elsewhere, except for most in the Muschelkalk facies of Europe. The Lower Triassic biochronological divisions were grouped into new stages defined in Arctic Canada (Griesbachian, Dienerian, Spathian). For the Middle and Upper Trias the zones were grouped in the Anisian, Ladinian, Carnian, Norian and Rhaetian stages, all of which were originally defined in the Mediterranean region - Tethys.

Comparisons between the North American zonal scheme and the classical zones of Tethys revealed serious shortcomings and errors in the Tethys scheme. Some zones were shown to be arranged in the wrong sequence, others were based on condensed faunas of more than one age. It was also clear that some intervals of time shown by the North American data to have distinct faunal characteristics were not accommodated in the Tethys scheme.

Particularly ill-defined in the classical scheme for Tethys was the boundary between the Lower and Middle Triassic (i.e. the base of the Anisian), the Carnian-Norian boundary, and the Norian-Rhaetian boundary. Anisian-Ladinian and Ladinian-Carnian boundaries also lacked precise definitions.

It was found possible to identify world-wide correlatives of nearly all the zones defined in North America. Correlatives were recognized wherever marine Trias is found: in Tethys, around the Pacific and throughout the Arctic. The zonal scheme appeared to have the potential for application in the marine Trias everywhere, even in parts of the Muschelkalk.

Knowledge of Triassic successions has greatly improved in the last 25 years, significant discoveries having been made in North America, Tethys and the Arctic. Table 1 gives the zonal scheme presently recognized in North America. Its foundation is Tozer (1967), and Silberling and Tozer (1968). There have been some additions and changes. The Upper Norian classification, which eliminated the Rhaetian, was introduced by Tozer (1979a, 1980). Silberling and Nichols (1982) documented much of the Nevada Anisian sequence and now important new discoveries by Bucher (1988, 1989) have led to the introduction and placement of two new zones, the Silberlingites mulleri and Nevadisculites taylori Zones. A correlative of the Mulleri Zone is now recognized in Canada, as will be noted below. The Middle Anisian, formerly one zone (Varium) in British Columbia (Tozer, 1967, p. 24) is now three zones (Tozer, 1971, p. 1017; Dagys and Tozer, 1989, p. 6).
<table>
<thead>
<tr>
<th>Triassic Period</th>
<th>Uppermost Substage</th>
<th>Lowermost Substage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper Norian</td>
<td>Crickmayi</td>
<td>Desatoyense</td>
</tr>
<tr>
<td></td>
<td>Amoenum</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Cordilleranus</td>
<td></td>
</tr>
<tr>
<td>Middle Norian</td>
<td>Columbianus</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Rutherfordi</td>
<td></td>
</tr>
<tr>
<td>Lower Norian</td>
<td>Magnus</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Dawsoni</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Kerri</td>
<td></td>
</tr>
<tr>
<td>Upper Carnian</td>
<td>Macrolobatus</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Welleri</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Dilleri</td>
<td></td>
</tr>
<tr>
<td>Lower Carnian</td>
<td>Nanseni</td>
<td></td>
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<tr>
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<td>Obesum</td>
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<th>Triassic Period</th>
<th>Uppermost Substage</th>
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<tr>
<td>Ladinian</td>
<td>Sutherlandi</td>
<td>Subasperum</td>
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<td>Maclearni</td>
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<td></td>
<td>Meginae</td>
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<tr>
<td></td>
<td>Poseidon</td>
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</tr>
<tr>
<td>Upper Anisian</td>
<td>Chischa</td>
<td></td>
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<tr>
<td></td>
<td>Deleeni</td>
<td></td>
</tr>
<tr>
<td>Middle Anisian</td>
<td>Minor</td>
<td></td>
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<tr>
<td></td>
<td>Hayesi</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hagei</td>
<td></td>
</tr>
<tr>
<td>Lower Anisian</td>
<td>Caurus</td>
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<th>Triassic Period</th>
<th>Uppermost Substage</th>
<th>Lowermost Substage</th>
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</thead>
<tbody>
<tr>
<td>Spathian</td>
<td>Subrobustus</td>
<td>Mulleri</td>
</tr>
<tr>
<td></td>
<td>Pilaticus</td>
<td></td>
</tr>
<tr>
<td>Smithian</td>
<td>Tardus</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Romunderi</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hedenstroemi</td>
<td></td>
</tr>
<tr>
<td>Dienerian</td>
<td>Sverdrupi</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Candidus</td>
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</tr>
<tr>
<td>Upper Griesbachian</td>
<td>Strigatus</td>
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<tr>
<td></td>
<td>Commune</td>
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</tr>
<tr>
<td>Lower Griesbachian</td>
<td>Boreale</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Concavum</td>
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</tr>
</tbody>
</table>

**Table I: Triassic Time Scale Based on North American Data**
Zones in left column have type localities in Canada, in right column in western U.S.A. Details in Tozer (1967), Silberling and Tozer (1968), Tozer (1979a), Silberling and Nichols (1982) and Bucher (1988, 1989).
In the Triassic, as in the other Mesozoic systems, faunal provincialism had posed correlation problems at several levels. North American occurrences occur over a latitudinal range of nearly 50 degrees. The faunas have been interpreted as representative of Lower, Mid or High paleolatitude (LPL, MPL, HPL) (Tozer, 1982). Some of these faunas, in classical terminology, had been designated Boreal or Tethyan, e.g. in Dagys (1988a). Whatever one chooses to call them, Table I shows that correlation and contemporaneity of most LPL, MPL and HPL faunas can be demonstrated from occurrences in North America. Full details of the Canadian sequences will soon be published in a monograph now in press. The chronology proposed in the monograph is more refined than that of Table I, with the introduction of subzones for most of the zones. An indication of the level of refinement that will be attained is indicated by the zonal tables in Zapfe (1983, pp. 10,11).

Many of the questions concerning the world-wide significance of the North American zonal scheme have been discussed in previous reviews (Tozer, 1971, 1974, 1978, 1980, 1981, 1984). This paper considers some of more recent discoveries and contributes a few new data. In particular it addresses four controversial matters:

1. the Permian-Triassic boundary; 2. the Spathian-Anisian boundary; 3. the Anisian-Ladinian boundary; 4. the status of the Rhaetian.

1. Permian-Triassic boundary.

This is a subject on which there is a voluminous literature. There are two controversial issues: the definition of the boundary and the correlation of the boundary beds. A summary, with references to much of the literature, has been provided by the writer (Tozer, 1988b). Until recently the base of the Otoceras woodwardi Zone, defined in the Himalayas, was universally accepted to define the Permian-Triassic boundary. Around the turn of the century there were advocates for treating the Otoceras beds as Permian but for about 50 years, from 1920 to 1970, the issue was considered settled. Most of the alternative views were reviewed recently (Tozer, 1988b). The case for continuing to define the base of the Trias at the base of the Otoceras beds was defended, not for the first time (Tozer, 1988a). Views that the Otoceras beds should be regarded as Permian, as by Newell (1988), for example, were opposed, and still are. Most workers concerned with marine invertebrates continue to treat the Otoceras beds as earliest Triassic (Dagys and Dagys, 1988; Wang et al., 1989; Zacharov and Rybalka, 1987; Shevyrev, 1990; Teichert, 1990). The main problem regarding correlation of the Otoceras and other boundary beds stems from the fact there are few, if any, places where beds regarded as youngest Permian (Dorashamian, Changshingian) are overlain by beds with unquestioned Otoceras. This has led some workers (e.g. Sweet, 1979, 1988a, 1988b; Yin et al., 1988) to suggest that the Otoceras and Dorashamian beds are at least partly correlative. The faunas are entirely different but they suggest that the differences reflect provincialism or facies control, not a difference in age. From the rarity of Otocerataceans in the youngest Permian deposits, in contrast to their undoubted presence (as Araxoceratidae) in the somewhat older Dzhulfian deposits, it has been suggested that beds with Otoceras follow closely in age the Dzhulfian beds with Araxoceratids. The writer has completed a study of the morphology, classification and stratigraphic distribution of the Otocerataceae. Representatives of nearly all the named taxa have been examined, and the distribution of many has been investigated in the field. The results have not yet been published. For the Permian otocerataceans, the proposed classification is a drastic revision. From examining type and other specimens it is the writer's opinion that the published classifications (Ruzhencev, 1959, 1962, 1963; Zhao et al., 1978; Bando, 1973, 1979, 1980) are unnecessarily elaborate, with far too many genera. Also, some of the morphological data are suspect. In the case of the material described by Ruzhencev, original specimens have been restored with plaster before being photographed, with misleading or false morphological implications. From the literature one is led to believe that many Araxoceratidae have flat venters. My own collections lead to the suspicion that the flat venters are the
result of syn-sedimentary corrosion, injudicious preparation, or both. Probably the most reliable indication of what an araxoceratid venter was really like is provided by the illustration of Araxoceras varicatum Rzhencov (1962, pl. 4, fig. 2b). The mid-line of the venter has a rounded siphonal ridge. This interpretation is confirmed by a specimen from Kuh-e-Ali Bashi, Iran, collected by the writer in the company of K.Seyed-Emami and F. Golshani.

A significant section covering the Permian - Triassic boundary occurs at Shah Reza, south of Isfahan, Iran. This section is briefly described by Zahedi (1973, p. 97-99). It was visited by the writer in 1972. In the time available it was not possible to obtain specimens exactly in situ. The sequence is much like that of Kuh-e-Ali Bashi, 1000 km to the NW, described by Stepanov et al. (1969) and Teichert et al. (1973). Dorashamian Paratroilites is present, followed, as at Kuh-e-Ali Bashi, by Triassic "Calcaire vermiculé". Other ammonoids from this locality include Pseudotoceras djoufensis (Abich) and Pseudogastrioceras sp. Although it is not possible to say that the three kinds of ammonoid are from exactly the same level, they are certainly not widely separated stratigraphically. At Kuh-e-Ali Bashi Araxoceras and Prototoceras certainly underlie Paratroilites. These data indicate a succession of Permian otocerataceans in which the older, of Dzhulfian age, are Araxoceras and Prototoceras, and the younger, Dorashamian in age, is Pseudotoceras. Some of the data presented by Bando (1979, 1980) conform with this interpretation. The Dorashamian otocerataceans he has described, like the specimens described by Toumanskaya (1966), are certainly not Triassic Otoceras. Contrary to Kozur (1980a, p. 753), Otoceras does not occur in the Dorashamian. Prototoceras and Araxoceras have simple suture lines, with few divisions; Pseudotoceras has a more divided suture line; Otoceras, of Griesbachian age has a suture line more divided than that of Pseudotoceras. Although Otoceras is nowhere known to overlay Pseudotoceras, if the morphological series be regarded as a phylogenetic sequence, the Otoceras beds fall into place as younger than the Dorashamian beds with Paratroilites and Pseudotoceras. These findings are taken as a further justification for regarding the Griesbachian Otoceras beds as younger than Dorashamian, and for treating them as earliest Triassic.

2. Spathian-Anisian boundary.

In the last 25 years many discoveries have been made relating to ammonoid faunas at Spathian-Anisian boundary. The most significant ammonoid faunal sequences covering this interval described until now are from the Humboldt Range, Nevada (Silberling and Tozer, 1968; Silberling and Wallace, 1969; Bucher, 1989), Siberia (Dagys, 1988b) and Qinghai, China (He, Wang and Chen, 1986). New data and collections have been obtained from the Himalayas by Leopold Krystyn (personal communication) but the results have not yet been published. Sequences in Arctic Canada, and British Columbia (Tozer, 1967), Svalbard (Tozer and Parker, 1968; Korchinskaya, 1982; Weitschat and Dagys, 1989) also have both late Spathian and Lower Anisian ammonoid faunas.

Sequences in Chios (Assereto,1974) and Oman (Tozer and Calon, 1990) may have earliest Anisian but evidently lack latest Spathian. Sequences in Primorye (Zacharov and Rybalka, 1987) and Iran (Tozer, 1972) have Spathian and Anisian faunas but lack certain indicators of both latest Spathian and earliest Anisian.

The position of the Spathian-Anisian boundary on Table I, between the Neopopanoceras haugi and Silberlingites mulleri Zones is based on the sequence in the Humboldt Range, Nevada, which has recently been revised by Bucher (1989). Previously (Tozer, 1967; Silberling and Tozer, 1968) the base of the Anisian was drawn at the Lenotropites cauris Zone, but it is now clear, from the sequences in Nevada and Siberia, that Lenotropites makes its appearance above the base of the Anisian. A unique fauna, from locality 68226 in British Columbia (Tozer, 1967, p. 69), formerly treated as the basal assemblage of the Caurus Zone, is now correlated with the Mulleri Zone. The scope of the Caurus Zone on Table I is thus more restricted than as originally defined.

In the older literature the Haugi Zone (Parapopanoceras Zone of Smith, 1914, p.5) was classed as
basal Anisian (e.g. in Spath, 1934, p.35). The position of this zone in relation to the Lower Anisian was first established by Silberling and Wallace (1969). Silberling and Tozer (1968, p. 39) gave reasons for correlating the Haugi Zone with the Subrobustus Zone, which nearly everybody regards as latest Lower Triassic (e.g. Dagys and Tozer, 1989, p.4). Correlation of the Haugi and Subrobustus Zones, and their treatment as latest Spathian is maintained (Table I). Kozur (1980b) treated the Subrobustus Zone as basal Anisian but his view does not seem to have attracted adherents.

Support for the Haugi-Subrobustus correlation is given by Bucher (1989, p. 950) who records *Keyserlingites subrobustus* (Mojsisovics) and *Metadagnostoceras pulchrum* Tozer from the Haugi Zone of Nevada. Judging from type and topotype material, *Tirolites pacificus* Hyatt and Smith from the Haugi Zone of California is a species of *Keyserlingites. Acrochordiceras inyoense* Smith, also from the Haugi Zone of California, does not resemble true Anisian *Acrochordiceras*. It provides no basis for regarding the Haugi Zone as Anisian. It is now proposed as type species of a new genus - *Pseudacrochordiceras*. The fauna of the Haugi Zone includes two more new genera: *Inyoceras*, and *Subhungarites*. These new genera are described in an appendix. Although at present they do not contribute to the correlation of the Haugi Zone they do serve to emphasize the distinctive character of its fauna.

Tozer (p. 10) discussed the morphology and stratigraphic significance of *Keyserlingites*. It was concluded that *Keyserlingites* (based on a species from Siberia) is a synonym of *Durgaites* (type species *Ceratites dieneri* Mojsisovics from the Himalayas). It was suggested that the *Keyserlingites* beds of the Arctic, correlate with the so-called *Durgaites* beds of the Himalayas and Timor, contrary to the traditional view in which the beds from the Himalayas and Timor were regarded as Anisian. This correlation is still maintained.

Dagys and Ermakova (1986, p. 22) considered that the external suture lines of *Keyserlingites* and *Durgaites* are indistinguishable. I agree. In spite of this, they give *Keyserlingites* such a restrictive diagnosis that it includes only the type species - *K. subrobustus* (Mojsisovics). In a later paper, Dagys (1988b, p. 6) gives morphological data which he asserts justify the recognition of *Keyserlingites* and *Durgaites* as separate taxa. This is given to support his belief that there is a difference in age, with *Keyserlingites* being Spathian, *Durgaites* Anisian. *Durgaites* is said to have an external saddle which is narrow and high compared with that of *Keyserlingites*. It is said that this saddle may acquire phylloid outlines, a suggestion based on a figure given by Welter (1915, p. 109) for *Keyserlingites angustecostatus* Welter. He also believes that the inner whorls are different. At a small diameter, before the appearance of marginal tuberculation, *Keyserlingites* is said to have weak ventral ribbing compared with that of *Durgaites*. I have studied the type specimens of all the relevant species. None of these differences can be defended. The external saddles of *Keyserlingites subrobustus, *Ceratites dieneri*" and *Keyserlingites angustecostatus* were accurately illustrated by Mojsisovics and Diener (See Spath, 1934, p. 355, 357) and Welter (1915, pl. 5, fig. 3). They are essentially similar. None are phylloid. Welter (1915, p. 108) thought that the suture line of *K. angustecostatus* differed from that of both "C." *dieneri* and *K. subrobustus* but I agree with Spath (1934, p. 359) that the differences are trivial. Data for comparing inner whorls are insufficient. The type specimen of "C." *dieneri* does not show them. Nor are there any topotypes that do so.

In the writer's interpretation at least 4 species are referable to *Keyserlingites: K. subrobustus* (Mojsisovics), *K. dieneri* (Mojsisovics), *K. angustecostatus* Welter and *K. pacificus* (Hyatt and Smith). Assignment of *K. dieneri* and *K. angustecostatus* to a different genus - *Durgaites* - is not justified on morphological grounds. Close morphological similarities, particularly between *K. subrobustus* and *K. angustecostatus*, are taken to justify the conclusion that they are the same age. It is most unlikely, as held by Wang (1984) and Dagys (1988, p. 6), that *K. angustecostatus* is Anisian, particularly as *Keyserlingites* has never been found in the undoubted Lower Anisian deposits of Nevada, British Columbia, Svalbard and Siberia.
Reexamination of the specimens of *Keyserlingites angustecostatus* from Timor described by Welter (1915, p. 108), housed at the Delft University of Technology, has led to some new discoveries. They are in blocks of Hallstatt limestone facies from an olistostrome. The blocks with *K. angustecostatus* also provided ammonoids that indicate an Anisian age, as recognized by both Welter (1915, p. 102) and Spath (1934, p. 359). One large block described by Welter (loc. cit.) was discussed by Tozer (1965, p. 12) leading to the suggestion that it preserved the Spathian-Anisian boundary. The writer has now examined a small block, with stratification and geopetal features that permit its orientation at the time of deposition. The lower part is an incomplete phragmocone of *Keyserlingites angustecostatus*, 140 mm in diameter (Plate I, figures 2a-c). Resting in its umbilicus, on the upper side, is a specimen now described as *Paracrochordiceras weltleri* n.ssp. (Plate I, figures 1a-d, figure 2c). *P. weltleri* indicates a Lower Anisian age. Also on the upper side, adjacent to the specimen of *P. weltleri*, is an ammonoid identified as *Leiophyllites* cf. stocklini Tozer (Plate I, figures 3a-b; figure 2c), which also suggests an Anisian age. Some might consider that this association indicates that *Keyserlingites angustecostatus* is Lower Anisian but I prefer an interpretation in which the block contains ammonoids of two zones, one, with *Keyserlingites*, being top Spathian, the other, with *Paracrochordiceras* and *Leiophyllites*, basal Anisian. Beds containing ammonoid faunas of more than one zone are a common phenomenon in the Mesozoic. Ranges of genera and discrimination of zones are best established in sections like those of Nevada, British Columbia and the Arctic where the possibilities of condensation or redeposition are reduced to a minimum in preference to sequences in the Hallstatt facies where these possibilities are always present. This occurrence in the Hallstatt facies does not warrant overturning conclusions on the ranges of *Keyserlingites* and *Paracrochordiceras* determined from sequences in Nevada and British Columbia.

Conodonts have been obtained from the block with *Keyserlingites*, *Paracrochordiceras* and *Leiophyllites*. They have been studied by M.J.Orrchard (this volume).

An important new *Keyserlingites* locality is now known in Qinghai, China (Wang, 1984; He, Wang and Chen, 1986). The beds are between undoubted Spathian with *Subcolumbites* and *Amautoscelites* and undoubted Anisian with Beyrichitidae. Associated and immediately below *Keyserlingites* are ammonoids which are referred to Anisian genera (*Lenotropites*, *Grambergia*, *Grenelandites*, *Peyrandites*, *Arctohungarites*). These identifications and the Anisian dating have been discussed and rejected, on good grounds, by Bucher (1989, p. 958-959). The *Keyserlingites*, however, appear to be correctly identified. He et al. (op. cit. p. 202) agree that *Keyserlingites* and *Duragna* are synonyms but regard the *Keyserlingites* beds of the Arctic as Spathian; those of Qinghai, the Himalayas and Timor as Anisian. *Japonites*, indicative of Anisian, is also recorded from the beds with *Keyserlingites*. If *Keyserlingites* and *Japonites* are from exactly the same level the association is presumably yet another instance of condensation of two zones into one bed.

Referring to Table I, it is important to note, as established by Silberling and Wallace (1969, p. 17), that beds in Nevada with *Subcolumbites* (and *Prohungarites*) are older than the Haugi Zone. This is taken to justify rejecting zonal schemes in which the *Subcolumbites* faunas are regarded as latest Spathian (Zacharov, 1978, Table 6; Wang, 1984, p. 531; Rostovstev and Dagys, 1984, p.188; Dagys,1988b, p.5). Zacharov goes so far as to consider the Subrobustus Zone to be older than the *Subcolumbites* beds. In making this interpretation he was evidently influenced by the occurrence of "*Keyserlingites*" miroshnikovi Burij and Zharnikova at a level (*Neocolumbites insignis* Zone) below the *Subcolumbites* beds of Primorye. "K." miroshnikovi does not closely resemble *Keyserlingites*, neither in the very restricted interpretation of Dagys and Ermakova (1986), nor in the broader interpretation advocated here. Dagys and Ermakova (op. cit.p. 23) assign "K." miroshnikovi to their genus *Olenekoceras*, which appears to have a longer range than *Keyserlingites*.

In conclusion, it is maintained that the Haugi and Subrobustus Zones are late Spathian, at least approximately correlative and are particularly characterized by a cosmopolitan genus - *Keyserlingites* -
which is known from Siberia, Svalbard, British Columbia, Nevada, California, Timor and the Himalayas.

3. Anisian-Ladinian boundary

In North America the base of the Ladinian is drawn at the Subasperum Zone, for which the type locality is in Nevada (Silberling and Tozer, 1968, p. 12; Silberling and Nichols, 1982, pp. 4,10). Correlative beds in British Columbia are marked by the appearance of *Eoprotarachyceras*. The underlying Occidentalis Zone is characterized by *Nevadites*.

Correlation between North America and Europe is not yet firmly settled. Brack and Rieber (1986, p.210) have recognized an Anisian-Ladinian boundary in the Brescian Prealps and Giudicarie which they correlate with the boundary as defined in North America. In contrast, Krystyn (1983, p. 245), Zacharov and Rybalka (1987), and Voros and Palfy (1989) favour placing beds in Europe with ammonoids identified as *Nevadites* in the early Ladinian, i.e. they assign the Occidentalis Zone to the Ladinian.

Although a firm decision on the question of this boundary should await full descriptions of the critical sections and faunas from Italy, Greece and Hungary, it is still maintained that definition of the Ladinian base at the Subasperum Zone at its correlatives is more useful than any other for worldwide correlation. A Ladinian base at the Occidentalis Zone would be unrecognizable in British Columbia and the Arctic (Tozer, 1981, p. 415) whereas the boundary at the Subasperum Zone can be recognised with fair confidence in Svalbard (Tozer and Parker, 1968; Weitschat and Dagys, 1989), and Siberia (Arkadiev and Vavilov, 1989; Dagys and Tozer, 1989).

4. The Rhaetian question

The Rhaetian, traditionally the ultimate Triassic Stage, does not appear on Table I. Rhaetian is not there because at least three different interpretations for the stage are in the contemporary literature (Tozer, 1990). In the face of these ambiguities Rhaetian has not been used in North America for more than a decade (Tozer, 1979a, 1980; Palmer, 1983; Taylor et al., 1983; Carter et al., 1989). Instead, the latest Triassic biochronology is expressed in terms of the Cordilleranus, Amoenum, and Crickmayi Zones which are clearly and unambiguously defined. On Table I these zones are grouped as the Upper Norian Substage.

The three different definitions of the Rhaetian, which make it so ambiguous, are as follows. The most comprehensive Rhaetian (Rhaetian s.I) embraces all three Upper Norian zones. This is advocated by most of the authors in Wiedmann et al. (1979) and Tollmann (1985). Less comprehensive is a Rhaetian (Rhaetian s.m) encompassing the Amoenum and Crickmayi Zones, advocated by Dagys and Dagys (1990). Most restricted is the Rhaetian (Rhaetian s.s) of Krystyn (1980, 1988) and Golebiowski (1986) which includes only the Crickmayi Zone and its correlatives.

Considering the bearing of ammonoid faunas on this question, Rhaetian s.l can be defended as being characterized by the only Triassic heteromorphs, the Choristocerataceae. However, a disadvantage to interpreting Rhaetian in this way is that it would include many beds, particularly those with *Rhabdoceras* and *Monotis*, which have always been regarded as Norian.

Rhaetian s.m. has some merits. It provides as biochronological division of useful scope to express the age of the late Triassic Suparmonotis beds in Siberia, the Caucasus and New Zealand which are demonstrably younger than the Cordilleranus Zone but which owing to the absence of Choristoceratidae cannot be differentiated as Amoenum or Crickmayi (Tozer, 1980, p. 852, 856). The Otatirian Stage of Marwick (1953), defined in New Zealand, is a synonym of Rhaetian s.m.

Krystyn (1988), in a preliminary report, has proposed an elaborate subdivision of Rhaetian s.s. recognizing two zones (Stuerzenbaumi and Marshi) with both divided into subzones. His divisions are
based on the sequence from the Zlambach Beds, not from the Koessen Beds, which constitute the original Rhaetian stratotype. All the zonal and subzonal ammonoids are Choristoceratidae. The zonal sequence may be correct but at present it is inadequately documented, no new material from any locality, let alone the Zlambach Beds, having been described or illustrated. Type locality for *Vandaites stuerzenbaumi* (Mojsisovics) is Drnava, Czechoslovakia. At present the only described specimens are from that locality (Mojsisovics, 1893; Kollarova-Andrusovova, 1973). Type locality for *Choristoceras* marshi Hauer is in the Koessen Beds. No examples from the Zlambach graben have been described. Thus no specimens of the index species, *Choristoceras marshi* and *Vandaites stuerzenbaumi*, have been described from Zlambach Graben. The present taxonomy of Choristoceratidae is not very satisfactory for two reasons. First, well preserved, complete, undistorted specimens are exceedingly rare. Second, variability has not been adequately described and assessed. Coiling in Choristoceratidae appears to by highly variable. In *C. marshi*, for example, the detached part of the whorl varies in length between less than half a whorl to more than one whorl (Tozer, 1980, pl. 63, fig. 9a). A zonal scheme based on these ammonoids must take these problems into account. This has not yet been done.

Whether or not Krystyn's subdivisions are justified, in my opinion Rhaetian s.s. cannot be defended as a stage in terms of ammonoid faunas. Most of the salient facts of ammonoid distribution that bear on this question have already been summarized (Tozer, 1980). The only certain candidates as exclusively Rhaetian ammonoids are Choristoceratidae (*Choristoceras*, *Vandaites*). In several places, notably Nevada, Vancouver Island and Austria, Choristoceratidae occur with ammonoids that have been regarded as Norian by nearly everybody. They include *Arecestes* of the *galeait* group, *Rhabdoceras*, and probably also *Pinacoceras metternichii* (Hauer). This is one of the principal reasons that induced me to remove the Rhaetian from the hierarchy of Triassic stages, and to consider the Norian as the ultimate Triassic stage.

In addition to the work of Krystyn, there have been recent contributions concerning the distribution and occurrence of *Choristoceras* in Nevada (Laws, 1982; Guex, 1982); Queen Charlotte Islands, British Columbia (Carter et al., 1989), Peru (Frinz, 1985) and Chile (Chong and Hillebrandt, 1985; Hillebrandt, 1990). In the chronology of Table I these occurrences are Crickmayi Zone; in the chronology of Krystyn, Rhaetian.

Guex (1981, 1982) and Donovan et al. (1989) have described material which suggest that the typically Hettangian ammonite family Psiloceratidae may be represented in the latest Triassic faunas.

The material described by Guex is from beds Z2 and Z3 of the New York Canyon Section. Z3 is less than a metre below the start of the Hettangian, Z2 about one metre below. *Choristoceras crickmayi* Tozer and *Psiloceras* sp. indet. are recorded from both beds (Guex, 1981, p. 247; 1982, pl. 1, figs. 6-10). All the specimens are crushed so the identifications are not wholly convincing.

The single specimen described by Donovan et al., from the Penarth Group (formerly Rhaetic) of England, is a smooth serpentine, 3.8 mm in diameter, with asymmetrical suture lines. Identification of the specimen as a psiloceratid seems justified.

*Palaeonoriceras diversai* D'Aversa (1982), from the Dolomia Principale of Valredola, Italy, which appears to be a smooth serpentine with a simple suture line presumably represents another addition, as yet imperfectly known, to the Upper Norian ammonoid fauna.

In conclusion: Rhaetian s.s. has too small a scope, and a fauna too similar to that of the underlying beds to be useful. Rhaetian s.m. is a useful division, for which the name Otapirian is available. Upper Norian is also a useful division, justifiably a stage rather than a substage. Rhaetian s.l. is synonymous with Upper Norian but cannot be accepted as a substitute because it would necessitate treating many traditionally Norian beds as Rhaetian. Division of the Norian into the three substages of Table I remains the best compromise.
5. Appendix

Descriptions of new genera of Ammonoidea from the Neopopanoceras haugi Zone and of Paracrochordiceras welteri, new species, from Timor.

Family XENOCELTITIDAE Spath

INYOCERAS new genus. Type species Xenodiscus bittneri Hyatt and Smith, 1905, p. 123).

Diagnosis. Xenoceltitid with ventral projection of growth lines and ribbing much like that of Glyptophiceras Spath. Differs in having less uniform ribbing which is coarse and distant on the inner whorls and relatively faint and dense on the outer. Ribbing denser compared with that of Kashmirites Diener and Xenoceltites Spath.

Composition of genus: Xenodiscus bittneri Hyatt and Smith, Xenodiscus multicameratus Smith.

Family LONGOBARDITIDAE (Spath)
Subfamily LONGOBARDITINAE Spath.

SUBHUNGARITES new genus. Type species Hungarites yatesi Hyatt and Smith, 1905, p. 129.

Diagnosis. Longobarditin with both inner and outer whorls smooth. Venter narrowly and neatly tricarinate with both the ventral and ventro-lateral keels sharply angular, becoming slightly blunted at the aperture. Suture line with about two auxiliary lobes.

Composition of genus: type species only.

Resemblance to Hungarites Mojsisovics, a much younger genus, is probably superficial. Morphologically Subhungarites, like all Longobarditinae, differs from Hungarites in having an occluded umbilicus.

Family ACROCHORDICERATIDAE Arthaber

PSEUDACROCHRODICERAS new genus. Type species Acrochordiceras inyoense Smith, 1914, p. 40).

Diagnosis. Acrochordiceratid with thick phragmocone formed of depressed whorls. Ribbing strong on flanks and venter on both inner and outer whorls, somewhat elevated, almost bullate, on the flank. Suture line ceratitic with rounded unindented saddles and a narrow external lobe.

Eaacrochordiceras Wang differs in having ribs stronger on the flanks than on the venter; Acrochordiceras Hyatt and Proacrochordiceras Korchinskaya differ in having lateral nodes; Paracrochordiceras Spath differs in having more serpentine coiling. Suture lines of both Acrochordiceras and Epacrochordiceras differ in having saddles which are moderately to deeply indented.

Composition of genus: type species only.
PARACROCHORIDICERAS WELTERI new species. (Plate 1, figures 1-4).

Material. Known only from the holotype (Plate 1, figures 1-4) from Fatoo Nefakoko, near Kampong Soeli, collected by the G.A.F. Molengraaf Timor Expedition, 1911, and housed in the collection of the Delft University of Technology. It was discovered in the umbilicus of a specimen of Keyserlingites angustecostatus identified by Welter (1915, p. 109). When Welter studied the specimen the Paracrochoridiceras was completely buried by matrix.

Diagnosis. Paracrochoridiceras about 35 mm in diameter, whorl height about 40 percent of diameter, whorl width about 48 percent, umbilical width about 40 percent. Inner whorls depressed ovoid in section, somewhat wider than high, with dense simple ribs on the flank and an almost smooth venter. On the outer whorl the ovoid whorl section is retained but with the acquisition of faint ventral shoulders, some ribs bifurcate on the inner flank and most can be traced across the venter, although with diminished strength.

Remarks. On the inner whorls the shell is preserved. On the outer whorl there is some shell material but preservation is mostly as internal mould. Septa and sutures are not visible. At the start of the last whorl there is an abrupt change in the style of ribbing, from dense to distant. There are about 6 whorls. The abrupt change on the last whorl may indicate that the specimen was mature and complete. A quarter whorl from the aperture, as preserved, there is a discordance in the ribbing. This probably indicates a feature similar to the transitional mouth borders described by Diener (1895, p. 104) for Sibirites pandya, which is a species of Paracrochoridiceras (Tozer, 1971, p. 1017). The exact nature of the ribbing on the new species cannot be determined because the part in question is preserved as internal mould.

The most closely comparable species is Paracrochoridiceras americanum McLearn which may differ only in having stronger ribbing on the inner whorls. P. pandya differs in having ribs that branch on the outer part of the flank, P. anodosum (Welter), P. plicatum Bucher and P. silberlingi Bucher have stronger ribbing, P. macleami Bucher has weaker ribbing.

References


Spath, L.F. (1934): Catalogue of the fossil Cephalopoda in the British Museum (Natural History), part 4, the Ammonoidea of the Trias. London.


PLATE 1

All illustrated specimens are from one small Triassic olistolith from locality Nifockoko, Toeboelopo, Timor, collected by the G.A.F. Molengraff Expedition, 1911. Repository is the Museum of the Delft University of Technology, the Netherlands.

Figs. 1a-d. *Paracrochordiceras welteri* n.sp. Holotype. All figures X 2. 1a, coated with ammonium chloride. 1b-d not coated. No sutures are visible.

Figs. 2a-c. *Keyserlingites angustecostatus* Welter. Topotype. All Figures natural size. 2a, side; 2b, venter; 2c, sectional view. Specimen is wholly septate. 2c is oriented as at time of deposition, as indicated by stratification and geopetal features. Left arrow indicates part of the holotype of *Paracrochordiceras welteri* remaining in the umbilicus. Right arrow is part of specimen of *Leiophyllites cf. stoecklini* (Figs. 3a, b).

Figs. 3a,b. *Leiophyllites cf. stoecklini* Tozer. Both figures X 2. Specimen is septate except for last quarter whorl.
PERMIAN-TRIASSIC CEPHALOPOD FACIES AND GLOBAL PHOSPHATGENESIS

Y.D. Zakharov and E.L. Shkolnik, Far-Eastern Geological Institute, Far-Eastern Branch, USSR Academy of Sciences, Vladivostok, 690022 USSR.

Abstract
Ammonoid ecology, the formation of phosphatic concretions and the peculiarities of P\textsubscript{2}O\textsubscript{5} distribution in the main cephalopod facies during the Late Paleozoic and Mesozoic are discussed. Nodules with a high P\textsubscript{2}O\textsubscript{5} content, which reflect the terminal stage in phosphate diagenesis, are preferentially formed while ammonoids with tissue remains are sporadically localized within the sediments saturated in organic matter. The phosphatogenesis peaks within the Late Paleozoic and Mesozoic occur during periods of humid climate partially connected with transgressions. Therefore, the data on phosphatogenesis (with ammonoid participation) can be used in palaeogeographic reconstructions.

The Cephalopoda is one of the most widely distributed group of marine invertebrates in the Late Paleozoic and Mesozoic. Their remains are often found in phosphorites, especially in nodules, therefore the analysis of cephalopod facies is of interest to problems of phosphatogenesis. The present work is an attempt to analyse the role of ammonoids in this process by examining original material from the Permian-Triassic of the Far East, Siberia, Pamirs, Urals, Mangyshlak, Transcaucasia, the Upper Cretaceous of Sakhalin (Yu. D. Zakharov’s collection), the Lower Triassic of North America (B. Kummel’s collection), and the Jurassic of western Europe (U. Lehmann and W. Weitchat’s collections).

Ammonoid Ecology
Ammonoids (or at least some of their representatives) may be compared with the present day nautilus, species of which are distributed between the Fiji Islands, Australia, and the Philippines. The role of hydrostatic apparatus in all cephalopods with an external skeleton is known to be played by the phragmocone (Shimansky, 1948; Zakharov, 1978; Lehmann, 1990; Doguzhaeva, 1991). Like the recent nautilus, the ammonoids made regular, apparently vertical, daily migrations. The nautilus ascends to shallow depths at night, while staying near the seafloor at a depth of 200-570 m during the day (Shimansky, 1948; Reyment, 1958; Lehmann, 1990). Westermann (1982) has shown, based on the thickness of cephalopod siphons, the depth limits for recent nautilus is about 600-800 m, and for ammonoids is between 300-500 m (Ancyloceratina) and 800-900 m (Phylloceratida and Lytoceratida orders). It is likely that below these depths the carbonate cephalopod shells would be crushed. Therefore, the preferable depths for ammonoid life were, obviously, limited to the outer continental shelf and upper slope.

Judging from peculiarities of muscular imprints, which were recognized in the living chambers of ammonoids, the basic function of their locomotor apparatus was, evidently, realized by a funnel (Doguzhaeva, 1991). Taking into account the large dimension of ventrolateral muscular imprints in some oconoceratine representatives (e.g., Aciconoceras), it may be assumed that at least these ammonoids were comparatively good swimmers. But it seems highly likely that the majority of ammonoids, just like recent nautilus, were slow animals living near the seafloor. This is partly explained by concentrated food sources on the seafloor. Having a thin-walled shell, ammonoids avoided locating near reefs, because of the risk of being destroyed in storms.
The food for juvenile cephalopods is plankton, but adults also consume bentonic and nectonic animals (Philippova, 1973). Recent nautilus feed on decomposed animals on the seafloor. The cutting edge of the ammonoid jaw was calcified, therefore they could eat hard-shelled animals (crustaceans, etc.). Ammonoid locomotion comparatively close to the continents seems to be connected with concentrations of phyto- and zooplankton in some part of outer shelf and upper slope (possibly due to upwelling) that provided the stable trophic connections.

Present-day cephalopods usually live in waters with normal salinity. At the same time, in western Baltic waters with lower salinity, *Allotteuthis* and *Loligo* are common, but they are not reproduced there. The fresh waters of Canada are populated with only rare species of the *Octopus*. It is believed that ammonoids, like recent nautilus, were stenohaline animals. But the results of studying boron and absorbed bases concentrated in Mesozoic sediments of the Boreal basins (Gramberg and Spiro, 1965; Ivanovskaja, 1967), which were populated with cephalopods, and also oxygen isotopic composition in the Lower Triassic ammonoid shells (Zakharov et al., 1975) and Jurassic belemnite rostrums (Naidin, 1973) of these regions seem to be evidence of the inhabitation of the Boreal cephalopods in more or less fresh waters during the early Mesozoic. The absence of the Dzhulfian and Dorashamian ammonoids in the Boreal realm may be caused by significant addition of fresh water to the boreal basins by the end of the Permian.

During Permian and Triassic time, ammonoids were usually spread in both the Tethyan and Boreal realms, reaching maximum taxonomic diversity near the equatorial zone. From stable isotopic analyses, the water temperature in the Triassic Boreal basins seems to be lower (average about 14.5°C) (Zakharov et al., 1975) than in the western Tethyan (about 21.5°C or higher) (Kaltenegger, 1967). Comparative data show that the late Cretaceous (Santonian-Campanian) ammonoids lived at temperatures of about 8.4° to 11.1°C (Zakharov et al., 1984). All data are from the analysis of ammonoid shells. The lowered temperatures of the Cretaceous near bottom waters within the South Sakhalin shelf, which were populated with the abundant ammonoids and some other mollusks, appear to be related to upwelling.

Cephalopods are characterized by variably expressed sexual dimorphism. Sexual characteristics of the ammonoids are shown in sculpture peculiarities of the mouth edge in the living chamber, and by relative dimensions, thickness and evolutionary degree of their shell. The juveniles had the primitive hydrostatic and locomotor apparatus and therefore likely led a planktonic life.

Nesis (1973) showed that reproduction of present day cephalopods takes place in well-protected bays. The localities with mass accumulation of the fossil cephalopods probably had such conditions (Artinskian locality in the southern Urals, Oleneckian locality in Arctic Siberia, some Jurassic and Cretaceous localities in Europe, Siberia, Sakhalin, etc.) (Plate 1).

Recent nautilus often undergoes post-mortality drift, fainting its body during the process. Therefore, one can find representatives from Fiji near Japan. But nothing like this has been described for ammonoids.

**Formation of Phosphatic Concretions**

The most widespread type of cephalopod facies in the Upper Paleozoic and Mesozoic are clay sediments with variably phosphatized concretions. Concretions containing cephalopod remains seem to be formed in reducing surroundings. According to Week (1957), the rapid formation of carbonate sediments as concretions took place because of the rotting, which provoked an increase in alkalinity. The decomposed material (the soft tissue in ammonoid living chambers) can be a centre for the gathering and precipitation of concretion substance.

Formation of the phosphorite material in some concretions, in contradiction to Kazakov (1939), is connected with the early stage of diagenetic changes in diffusive character. Conditions for the
concretion-type of phosphatogenesis seem to be the following (in addition to the presence of the strictly local gathering of fresh soft tissue at the bottom of shelf or upper slope): (1) the intensive sedimentation of mainly fine deposits promoting a rapid conservation of soft tissue that prevents their rotting and destruction. At present this is achieved usually at about several centimetres below the seafloor; (2) absence of intensive bioturbation prevented the preservation of somatic tissue; (3) increase in the common alkalinity surrounding places of concretion formation (as mentioned above, because of rotting organic materials); (4) elimination of sulfate-ion from the pore solution of adjacent deposits (its presence in amounts corresponding to those of normal marine water makes phosphatogenesis impossible); and (5) intensive saturation of silts because of the remains of phytoplankton and some other organisms containing biogenic phosphorus.

When a buried ammonoid was affected by diagenesis, the phosphatic material seemed to be concentrated mainly inside the shell (inner phosphatic nucleus) (Plate 2A); but when we have a compact ammonoid assemblage, some surrounding space in addition to the inner part of ammonoid shells undergoes the process of phosphatogenesis (phosphatic nodule). This means that the gathering of phosphorus from adjacent sediments and its concentration within the limited spaces containing abundant organic remains and subsequent conservation took place (Shkolnik, 1989). In spite of this, the hydrostatic chambers of some fossil cephalopods originally were not filled by sediments. Eventually these cavities were filled by calcite, which, naturally, is not phosphatized now.

Several stages of early phosphatogenesis were recognized using paleontological data. In connection with it, at least two types of phosphatic nodules can be recognized (Shkolnik et al., 1984). In concretions of the first type, from the Lower Triassic of Olene river, for instance (Zakharov, 1978), a concentration of phosphorus was recognized only in the central concretion; it is known that the carbonate elements of shells are not phosphatized. Nodules of the second type are characterized by very high concentrations of P₂O₅ which occurred in both organism elements (sometimes soft tissue ones) and surrounding concretion material. Some examples are concretions from the Middle Anisian of Spitsbergen (Weitschat, 1986) (Plate 2B), Upper Triassic of the northeast USSR (Bychkov, 1975; Polubotko and Repin, 1975; Dagys et al., 1979), and Upper Cretaceous of the Atlantic Ocean (Blake Plateau) (Shkolnik et al., 1988). The examination showed that the second type of nodule was formed, firstly, when the adjacent deposits were saturated with organic substance, probably, because of the plankton concentration (the nodules of such type are often found in high carbonaceous shales), and secondly, when abundant ammonoid remains were distributed sporadically within the deposit strata. The mass compact ammonoid assemblages that compose the beds and lenses make impossible the effect of significant phosphorite concentration. The form of the concretions depends on the character of the shell disposition which were the centers of phosphatogenesis. The mechanical concentration of phosphatic nodules and nuclei by erosion, with the formation of the original conglomerates, favors the production of commercial reserves of phosphorites.

**Phosphorus Distribution within Cephalopod Facies**

**Carbonate Facies**

In widespread reef facies of the Late Permian (Zakharov and Pavlov, 1986), Late Triassic (Dagys, et al., 1979) and Late Cretaceous (Pojarkova et al., 1988) cephalopod shells are rare. In the deposits of Midian age in the Primorye region (Nakhodka Reef) no signs of phosphatisation have been recognized. A typical example of shallow carbonate facies (not reefogenic) are some Artinskian beds in the Urals, some Dzhulfian, Dorashamian and Induan sequences in Trans-caucasia, and also some Lower Triassic strata in Nevada. In the west Urals, the Upper Artinskian limestones of the Sterlitomak Mountains are richest in P₂O₅. The phosphorite horizon (0-3 m) is represented by a phosphatic seam or lens (less than 34.2% P₂O₅) interbedded with less phosphate-rich rock (about 7.0% P₂O₅) and sometimes dolomitized limestones, containing *Medlicottia*, *Parapronorites*, *
Paragastrioceras, etc. (Bezrukov and Vorozhez, 1937). Directly in the phosphorites, abundant fossils such as radiolarians, foraminifera, porifera, sponges, fish, and plant remains were recognized immediately adjacent to rare ammonoids.

Lower concentrations of phosphorus (0.68-1.61% P_2O_5) were found by the authors in the Lower Artinskian aphanitic limestone (0-0.2 m) in the southern Urals Aktasy River, characterized by ammonoid Neopronorrites, Paragastrioceras, Uraloceras, etc. and other groups of cephalopods, orthoceratids, nautiloids, and bactritoids. Very high phosphorus concentrations in the Sterlitomak Mountains may be provoked by the extremely high saturation of deposits with microorganisms (plankton). In our opinion, it was a main cause of the formation of seam or lens-like concretions. However, Bezrukov and Vorozhez (1937), suggest that chemical phosphate sedimentation took place in this region.

In the Transcaucasia, visible phosphorus contents were recognized in both pinkish grey limestone of the zone of Araxoceras latissimum in Ogbin (less than 2.2% P_2O_5) and grey clay-calcareous rocks of the same zone in Karabaglar (about 1.67% P_2O_5). Signs of phosphorus were expected also in light grey sandy limestone of the same level in Akhura. Overlying sediments of the uppermost Permian (reddish brown and greyish brown limestones and argillites and the Lower Triassic basal beds (greyish green, reddish brown, greyish yellow marls, limestones and argillites), containing abundant ammonoid remains, are practically unphosphatized. The most probable cause of relatively low P_2O_5 content in the red coloured Permian-Triassic boundary sediments in Transcaucasia is an original oxidizing character of these facies.

In Nevada, the Lower Triassic carbonate cephalopod facies were established within the zone of Meekoceras gracilitatis at Crittenden Spring. The Lower Triassic sequence consists of the following: a) limestone, light grey, with limonite flecks (5.2-10.1 m); b) covered, occasional beds of limonitic limestone (3.7 m); c) limestone, light grey with limonite stains (6.3 m); d) limestone, grey, with slabby partings (4.6 m); e) limestone, light grey, contains Lingula (13.7 m); f) limestone, light grey, massive (14.6 m); and g) limestone, grey (3.7m) (Kummel and Steele, 1962). In seven specimens of Kummel’s collection of limestones from beds “a” and “d” (characterized by ammonoid Pseudosejacecers, Meekoceras, Arctoceras, Owenites, Juvavites and Aspenites) a high phosphorus content (0.6-6.0% P_2O_5) has been determined. The increase of P_2O_5 content in this locality may be connected with original conditions of sedimentation.

Sandy-Carbonate Facies

In south Primorye, the sequence of Lower Triassic greyish green sandstone with numerous lenses (0-0.3 m) of sandy limestones (Russian Island) is representative of sandy-carbonate facies (Zakharov, 1968, 1978). Characteristic of these sediments (Hedenstroemia bosphorensis zone) is the presence of numerous ammonoid Meekoceras, in contradiction to more deep water clay facies of the same level characterized by Prosphingites domination. Ammonoids of sandy-carbonate facies in south Primorye are usually associated with numerous bivalves and conodonts.

Phosphorus concentrations in the shells of Russian Island are low (less than 0.28-0.40% P_2O_5). No phosphorite signs were recognized in adjacent sandstones with the exception of the places where Lingula remains were expected. Sandy carbonate facies is an example of relatively low concentrations of phosphorus. In this case, it may be connected with the uninterrupted mass burial of macrofossils.

Black-Clay Shale Facies

As mentioned above, this is one of the more widespread types of cephalopod facies of the Carboniferous, Permian, Triassic, Jurassic and Cretaceous.

In the black shales (70 m) within the gandinian in southeast Pamirs, no concretions have been found.
Diverse ammonoids (Bamyaniceras, Gaetanoceras, Parapronorites, Propinacoceras, Agathiceras, Prostachooceras, Medlicottia, Sicanites, Sundaites, Neogoceras, Epiglyphioceras, Pseudovidioceras, Neocrinites, Sosiocrinites, Ariococeras, Palemites?, Adrianites, Tauroceras and Paraceltites?) were collected in calcareous argillite bands (~1.5-2.5 m thick). No visible phosphorus concentrations were recognized in sediments of either the stratotype of the Kubergandinian stage (Kubergandy River) or the Kutil River sequence.

In Japan, judging from the work of Eanisawa and Ehiro (1986), P₂O₅ contents in concretions from black shales of the Toioma Series range from 0.40 to 17.73%. The richest content (17.73%) falls within the Upper Sunuzaki Formation. These beds seem to be characterized by rare ammonoids, such as Vescotoceras, Araxoceras, Timorites, etc. Somewhat lower P₂O₅ contents were recognized in the Middle Senatsu Formation (9.19-12.81%) and Middle Tanoura Formation (about 13.42%) where some Late Midian (Cyclolobus) and, apparently, Dorashamian (Medlicottidae) ammonoids associated with bivalves and foraminifers were collected.

In south Primorye, concretions among black shales of the Ludjanza Formation characterized by Late Midian Cyclolobus and Dzhulian Eusanyangites and some other ammonoids (these strata correspond to the Tojoma Series), high P₂O₅ contents were not observed. In addition one phosphatic nodule was found in the Lower Triassic basal conglomerate (side by side with pebbles of Paleozoic rocks, including Upper Permian limestones).

Lower Triassic black shale facies are known in both the zone of Hedestromia bosphorensis (about 10.0-12.0 m) on the east coast of Ussuri Gulf and the Russian stage (about 72.0 m) on Russian Island. No show of phosphatization was found in bands of sandy limestones with numerous ammonoid remains (Hedestromia, Arctoceras, Owenites, etc.) among black shales and alueorolites of the zone of Hedestromia bosphorensis. The P₂O₅ contents in concretions and lenses of overlying sediments of the Lower Triassic (Neocolumbites insignis and Subcolumbites multiformis Zones) are extremely low (less than 0.20-0.26%). Isolated phosphatic concretions in the Triassic black shale facies in Primorye regions were found only in Ladinian argillite (20% P₂O₅).

In Mangyshlak no P₂O₅ concentration was found in concretions or lenses of calcareous marl characterized by abundant Lower Triassic Tirolites, Stachoceras and many other ammonoids (which were observed within black shales and alveorolites of the Tartalinskian Formation). The previous explanation given for the Lower Triassic of Primorye may be used for this case.

Verkhojansk area black shales (14-20 m) at the base of the Induan in Setorym River yield chert-calcareous concretions with large shells of ammonoid Otoceras boreale Spath associated with small bivalves and gastropods. P₂O₅ content in the central part of concretions is about 0.6-3%.

The numerous calcareous marly septarian concretions among black shales (250 m) in the Olenekian stratotype in Arctic Siberia attract attention in three respects: (1) their central parts are usually overcrowded with ammonoid shells; (2) the shells, as a rule, are composed of aragonite, which is rarely preserved in fossils; (3) some ammonoid living chambers contain the remains of ammonoid jaws. The latter testifies, apparently, to rapid burying of shells that favours the preservation of soft tissues for a long time and the rapid phosphatization of some ammonoid elements and concretion substance. It is remarkable that in some concretions, the adult and juvenile representatives of the Olenekites spiniplicatus (Mojsisovics) dominate, but in other concretions dominant ammonoids include Olenekoceras middendorfi (Keyserling), Prosphingites czekanowskii Mojsisovics, Nordophiceras schmidti (Mojsisovics) Svalbardiceras sibiricum (Mojsisovics) or Sibrites eichwaldi Mojsisovics (adult and juvenile individuals) (Plate 3). All these species are contemporaneous. Associations like these seem to be real, and did not form during post-mortality mechanical sorting. Of other cephalopods, some rare remains of orthoceratids, nautiloids and belemnoids were collected in this sequence. Benthonic remains (bivalves) are usually absent in these deposits. P₂O₅ contents in the central parts of the concretions range from 0.76 to 1.74%.
Much higher phosphorus contents in Arctic Siberia were found in the Anisian black shale facies. P$_2$O$_5$ contents in concretions with Arctohungarites, Grambergia and some other ammonoids (5-10 m) found in black argillites and aleurolites in the Olenek Bay sequence fluctuate from 0.54 to 1.86%, but in one case (in association with Popanoceras) reaches 21.78%.

Many phosphatic nodules of the same facies type were collected from different levels in the regions of the northern USSR and Spitsbergen: (1) Middle Carboniferous argillite, Tiksi Formation in delta of Lena River (3.5-8% P$_2$O$_5$) (Tuchkov, 1966); (2) Induan sandy-aleurolite measures in Anabar-Olenek interstream (12-27% P$_2$O$_5$) (Mishin, 1975); (3) Olenekian bituminiferous argillite in Levy Eedon and Russkaya rivers basin (about 29.25% P$_2$O$_5$) (Polubotko and Repin, 1975); (4) Olenekian argillite of Lena River basin, Ogner Yurjak (Tuchkov, 1966); (5) Upper Anisian and Ladinian argillite in Omolon Massif, Dzhugudzhak River (17.92-31.0% P$_2$O$_5$) (Polubotko and Repin, 1975); (6) Anisian and Ladinian aleurolite-clay deposits in Jana-Kolyma region (about 32.28% P$_2$O$_5$) (Bytchkov, 1985; Shkolnik et al., 1984); (7) Middle Anisian argillite, Anagymnotoceras varium Zone, in Spitsbergen (P$_2$O$_5$ content is high, but not determined) (Weitschat, 1986).

The following strata are close to the black shale type facies: (1) Pliensbachian clay sediments of Lower Lena and Omolon Massif contain about 20.93% P$_2$O$_5$ in phosphorite nodules (Tuchkov, 1966; Polubotko and Repin, 1975); (2) Toarcian clay sequences in the Omolon Massif (about 19.41% P$_2$O$_5$); (3) Bajocian argillite of the Lena River left bank (about 14.6% P$_2$O$_5$) (Tuchkov, 1966); (4) apparently Callovian aleurolite of the Lower Lena (about 0.4-1.44 P$_2$O$_5$) (Tuchkov, 1966); (5) Valanginian argillites of the Lower Lena (about 23.97% P$_2$O$_5$) (Tuchkov, 1966).

In England some specimens with ammonoid Dactylioceras commune (Sowerby) and Grammoceras striatum (Sowerby) from the Toarcian Bifrons and striatum Zones contain 0.3-1.45% P$_2$O$_5$.

In Sakhalin, some argillite members (50-200 m) of the Upper Cretaceous Bykov Formation contain calcareous concretions with numerous ammonites. Their shells are usually composed of calcite (recrystallization) and rarely of aragonite. Ammonoids are associated with more rare gastropods, bivalves (including inoceramids) and crustaceans. These sediments also contain coniferous remains. In concretions from the Middle Bykov Formation (member 7) where the Gaudryceras tenuiliratum Yabe dominates, P$_2$O$_5$ content reaches 3.4%.

Sandy-Clay Shale Facies
The Anisian deposits of the Far East (Birobidzhan region, south Primorye and Japan) are a typical example of the sandy-clay shale facies. They are represented by spotty sandy-clay rocks with large septarian concretions. The concretions contain in their central parts abundant ammonoid shells and occasional remains of ammonoid jaw apparatus. The thickness of the Far East Anisian is about 150 m. The distribution of concretions is irregular (they were expected only within some measures).

Noticeably higher phosphorus concentrations are marked in Anisian sequences in comparison with the Lower Triassic ones. The Lower Anisian Ussuriphyllites amurensis Zone in south Primorye contains crumbly sandstone bands characterized by ammonoids, brachiopod and bivalve detritus. About 0.78% P$_2$O$_5$ was measured in the sandstone (in adjacent sediments of basal Anisian represented by calcareous clay and chert clay rocks on Russian Island, not more than 0.35% P$_2$O$_5$ was expected). In the overlying sediments (Phyllocladiscites basarginensis Zone) of Basargin Peninsula P$_2$O$_5$ reaches 6.0% (in large septarian concretions) and 2.8% (in some lenses of sandy clay rocks).

Environmental Implications of Phosphorite Formation
The analysis of the Late Paleozoic and Mesozoic material made it possible to assume that different P$_2$O$_5$ contents have been expected in concretions with ammonoids from different stratigraphical
levels (our attention was concentrated on their limited values). Some high levels of phosphatogenesis can be recognized within the Late Paleozoic and Mesozoic: (1) Lower to Middle Carboniferous (limited value P₂O₅ is about 29.2%); (2) Lower Permian (about 34.2% P₂O₅); (3) Murgabian (about 26.4%); (4) Upper Midian - Lower Dzhulfian (about 17-73%); (5) Middle Induan (?) (about 27.0%, only in the Boreal realm); (6) Lower Russian (about 10.00-29.25%, only in the Boreal realm); (7) Middle Anisian (about 21.78%); (8) Ladinian (about 32.28%); (9) Lower Carnian (about 21.88%); (10) Lower Norian (about 17.64%); (11) Pliensbachian (about 20-93%); (12) Toarcian (about 19.41%); (13) Bajocian (about 14.6%). In general, they fall on the time of expansion of humid climate zones partly connected with maximum transgressions (Plate 4).

Another peculiarity of phosphatogenesis at least for the Early Mesozoic is its prominence within the Boreal realm rather than in the Tethyan realm. On the basis of the first group of facts, concerning cephalopod facies, some global processes most probably play an important role. The local events provoked the rapid destruction of soft cephalopod tissues in some basins (because of storm erosions or mass episodic development of some preditory animals, for instance), and are believed to be the reason for the extremely irregular distribution of phosphorus-bearing provinces. At the same time, it becomes obvious that in such reconstructions, a role of phyto- and zooplankton is not adequately appreciated. It is difficult to judge the character of change of their biomass in different geological epochs. It is known only that an abrupt global change is observed in carbon isotope composition (decrease in delta ¹³C values) in carbonate rocks at some main boundaries in the Phanerozoic (Holser, 1984; Baud et al., 1989; Zakharov, 1985). This global change, in accordance with Holser's (1989) idea, testifies in particular to a decrease of biological productivity by the beginning of the Mesozoic and the beginning of the Cenozoic.

Phosphatogenesis and Paleoenvironments

Some factors seem to favour intensive bio-diagenetic phosphorite formation. Most significant of them during the Late Paleozoic and Mesozoic are, obviously, both the active erosion of phosphorus from the continents and the biological evolution of marine organisms (including phytoplankton), having the ability to assimilate dissolved phosphorus. The intensity of delivering phosphorus to the marine basins and the peculiarities of the biotic evolution considerably depend on climate and hydrodynamic conditions. It seems likely that the significant lowering of sea level and climatic aridization within extensive parts of some continents provoke a double effect in this respect.

First, it favours the decrease in abundance and taxonomic diversity of many terrestrial and marine organisms. Lowering sea level leads to the drainage of most parts of the continental shelf, which destructively influences many marine communities and also organisms having feeding connections with them. Secondly, climatic aridization increases the difficulty of delivering phosphorus to the ocean by rivers. Thus, the degree of phosphatization of global marine sediments as a process connected with the natural accumulation of phosphorus-containing organisms seems to be an indirect indicator of the paleoenvironments during some geological epochs. Inferiority of the offered method is explained by the specificity of environments in the different parts of marine basins, the absence of trustworthy evidence of the role of upwelling in organic matter ascent from deep parts of the ocean by the end of Paleozoic and Mesozoic, and some other factors. Information on reworking phosphate sediments, naturally, cannot be used for this purpose without special analysis.

Judging from data on phosphorus distribution it is suggested, on the one hand, that an arid climate existed at least during the significant part of the Lower and Middle Permian, Permian-Triassic boundary time, significant part of the Early Triassic, Anisian-Ladinian boundary time and Middle Norian. On the other hand, it is proposed that the development of humid climate on the extensive territory (accompanied by the rise of sea level) during the Artinskian, Murgabian, Middle Midian, Early Dzhulfian, Middle Dorashamian, Middle Induan?, Early Russian, Middle Anisian, Ladinian,
Early Carnian, and Early Norian. Humid climate was especially expressed in this time, most likely, during the Artinskian and Ladinian when the intensive accumulation of phosphorus took place in the Northern Hemisphere.

Our conclusions agree with most palaeobotanical data (Vakhrameev et al., 1970; Dobruskina, 1982; Burago, 1986; Parrish, 1990), according to which, (1) during the Permian (in contrast with Carboniferous) the arid zone was extended leading to the disappearance of the humid tropical forests in the Euro-American realm (within Cathasian existed during Late Paleozoic to earliest Triassic time); (2) Early Triassic is the time of maximum expansion of the belt of arid climate (regions with humid climate are recognized only within local territories of the Gondwana province); (3) next stage of the expansion of hydrophilous flora corresponds to the Middle Triassic; (4) in the Early Jurassic, the strongly pronounced arid belt appeared again in the Northern Hemisphere. Data on Late Paleozoic and Mesozoic phosphatogenesis seem to be useful for the detailed paleogeographic reconstructions, however, the material on phosphatogenesis is still poorly known.

Summary

The results obtained through the investigation of Late Paleozoic and Mesozoic cephalopod facies are summarized as follows:

1. Among the remains of the Late Paleozoic and Mesozoic macrofauna recognized in phosphorite concretions (nodules), only ammonoids prevail; this is caused by coincidence of the main places of living and burial of the ammonoids and the zone of optimal phosphatogenesis (external shelf - upper slope).

2. Nodules with high $P_2O_5$ contents (product of terminal stage of phosphatogenesis) were formed under conditions of strictly sporadic distribution of ammonoids in sediments intensively saturated with organic remains (usually planktonic). Small ammonoid assemblages or single ammonoids with preserved soft tissues, located several meters from each other, in this case seem to play a role of the centre of local concentrations of phosphorus, which migrates by diffusion from adjacent phosphorus-containing deposits (in connection with alkaline surroundings, as a result of decomposition of the soft tissues).

3. In the case of mass accumulation of ammonoid remains forming continuous beds (or elongate lenses) or ammonoid location in many concretions with very close grouping, high concentrations $P_2O_5$ in general did not appear because of more limited conditions for the local phosphorus accumulation.

4. The subordinate role of ammonoids in the facies characterized by extremely intensive planktonic sedimentation is proposed. A striking example of this sort of facies, rare for the Late Paleozoic and Mesozoic, is the Upper Artinskian limestone of the Sterlitomak Mountains (seam to lens-like concretions). No large ammonoid concentrations were recognized in this type of phosphorus-bearing sediment.

5. The epochs with the most intensive phosphatogenesis during the Late Paleozoic and Mesozoic, when the ammonoid biological evolution took place, generally fall within the time of expansion of the zone of humid climate. Thus, data on phosphatogenesis can be used in paleogeographic reconstructions.

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PLATE 1

Ammonoid sexual dimorphs, from concretions of the Olenikites spiniplacatus Zone, Lower Triassic, Arctic Siberia, Olenek River, Mengiljakh, x1.

A and B: the dimorph pair in *Nordophiceras schmidtii* (Mojsisovics) A: involuticonch, EPI 674/802, B: evoluticonch, 7BPI 137/802.
E and F: the dimorph pair in *Svalbardiceras asiaticum* Yu.Zakharov; E: involuticonch, BPI 235/802; F: evoluticonch, EPI 226/802.
K and L: the dimorph pair in *Xenoceltites glacialis* (Mojsisovics); K: evoluticonch, BPI 18/802, L: involuticonch, BPI 267/802.
M and N: the dimorph pair in *Olenikites spiniplacatus* (Mojsisovics); M: involuticonch, BPI 363/802, N: evoluticonch, BPI 352/802.
O and P: the dimorph pair in *Subolenikites altus* (Mojsisovics); O: evoluticonch, BPI 649/802, P: involuticonch, BPI 647/802.
Q and R: the dimorph pair in *Sibirites eichwaldi* Mojsisovics; Q: involuticonch, BPI 666/802; R: evoluticonch, N BPI 665/802.
S and T: the dimorph pair in *Olenekoceras middendorffi* (Keyserling) S: involuticonch, EPI 675/802, T: evoluticonch, BPI 682/802.

PLATE 2

A: Megaconch of *Olenekoceras middendorffi* (Keyserling) in large concretion (inner phosphatic nucleus), from the Olenikites spiniplacatus Zone, Lower Triassic, Arctic Siberia, Olenek River, Mengiljakh; 94/802. Scale bar: 10cm.
B: Ammonoid *Amphipopanoceras* cf. *medium* (Mclearn) with phosphatized shell from the Middle Anisain Spitzbergen (W. Weitschat's photo), x 450.

PLATE 3

Some finds in the central parts of some concretions from the Olenikites spiniplacatus Zone, Lower Triassic, Arctic Siberia, Olenek River, Mengiljakh.

A: the *Olenikites spiniplacatus* (Mojsisovics) dominant, BPI 652/802, x1.
B: the *Nordophiceras schmidtii* (Mojsisovics) dominant, BPI 676/802, x1.
C: single shale of *Nordophiceras schmidtii* (Mojsisovics), BPI 107/802, x1.
D: *Sibirites eichwaldi* Mojsisovics dominant, BPI 673/802.
E: jaw apparatus from the living chamber of *Olenikites spiniplacatus* (Mojsisovics), BPI 251/802, x46.

PLATE 4

Phosphatogenesis and environment during Late Paleozoic-Early Mesozoic time.
A: The hypothetical world stages of the Late Paleozoic and Early Mesozoic phosphatogenesis based on data of limited values of $P_2O_5$ in some localities. B and C: Climatic changes.
B: Based on paleobotanical data.
C: Based on data on phosphatogenesis and palaeobotany ($H$ = humidization, $A$ = aridization)
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