Some trans-Iapetus conodont faunal connections in the Tremadocian

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ABSTRACT – Paleobiogeographical barriers within the Iapetus Ocean effectively restricted conodont faunas in Baltica from contact with those in Laurentia during Tremadocian time. Only species of Cordyloodus, Paltodus, Drepanodus, Parisistrodus and lapetognathus have been reported to occur on both sides of the Iapetus Ocean. Continued studies of faunas from deeper platform and slope settings of North America (Laurentia) and generally deeper water faunas of Scandinavia (Baltica) reveal that these faunas share a few more species. One of these taxa was first described as Oneotodus variabilis Lindström, 1955, from upper Tremadocian beds of south-central Sweden. It now has been recovered from Nevada and Pennsylvania as well. Its apparatus appears to be seximembrate, with only minor geographic variation of elements between Baltica and Laurentia. Comparison with species of the Laurentian genus Variabiloconus Landing, Barnes & Stevens, 1986, has convinced us that “O.” variabilis should be transferred to Variabiloconus. A closely related taxon, Variabiloconus transipecticus n. sp., is reported from south-central Sweden, Nevada and Colorado, strengthening the connection between conodont faunas in the two paleocontinents in the Tremadocian. Moreover, a few specimens of the North American zonal index species Rossodus manitouensis Repetski & Ethington, 1983, have been found in samples from the Paltodus deltifer Zone in Scandinavia, confirming previous correlations and demonstrating that even the strictest paleobiogeographical delimitations can sometimes be overcome.


INTRODUCTION

The North American Midcontinent (Laurentia) with its shallow, tropical sea had few conodont taxa in common with the colder, generally deeper sea that covered Baltica in the late Tremadocian (see e.g., Bergström, 1990). In uppermost Cambrian to mid-Tremadocian strata, more or less cosmopolitan species of Cordyloodus provide a firm framework for correlation (Bagnoli et al., 1987; Kaljo et al., 1988), whereas most correlations of the upper Tremadocian between Laurentia and Baltica have been inferred indirectly. The new information provided here allows direct comparison of faunas from either side of the Iapetus Ocean and reveals additional faunal connections. One taxon was described first as Oneotodus variabilis by Lindström (1955) from upper Tremadocian beds of south-central Sweden. It has now been compared with well known Laurentian taxa such as Teridontus and Variabiloconus, and we are convinced that “O.” variabilis belongs to Variabiloconus. This species, and a new and closely related one, Variabiloconus transipecticus n. sp., both seem to have a seximembrate apparatus. We also have found the North American zonal index species Rossodus manitouensis in very low abundance in a few samples from the Paltodus deltifer Zone in Baltoscandia. This discovery confirms previous correlations and emphasizes the importance of long-distance faunal connections in stratigraphy.

LOCALITIES AND MATERIAL

Variabiloconus variabilis (Lindström) has been recovered from the southwestern part of the allochthonous Hamburg klippe near Jonestown, eastern Pennsylvania, (J., unpublished USGS collection 11546-CO; Fredericksburg 7-1/2 minute toposchart quadrangle, Lebanon County); see Epstein et al. (1972) for a general description of the Hamburg klippe and discussion of faunas ca. 45 km to the east-northeast of Jonestown; see also Bergström et al. (1972) and Fail
A richer collection of \textit{V. variabilis} was found in USGS collection 11545-C0 (A.G. Harris, collector; unpublished) from the base of the limestone member of the Goodwin Formation in Ninemile Canyon, Antelope Range, Eureka County, Nevada (Merriam, 1963). This sample also yielded \textit{Variabiloconus transiapeticus} n. sp. The latter taxon has been obtained in Colorado from the Manitou Formation; in Williams Canyon in the Rampart Range near Manitou Springs and in Missouri Gulch north of Woodland Park. Both localities are in the frontal ranges of the Rocky Mountains (Maier, 1950; Berg & Ross, 1959). Another Manitou locality that has yielded this form is at Horseshoe Mountain in the Mosquito Range about 11 km southeast of Leadville, Colorado (Ethington collections; see Maier, 1950, for detailed descriptions of the Williams Canyon and Missouri Gulch localities; see Myrow et al., 1995, for location of Horseshoe Mountain).

The largest collection of \textit{V. variabilis} elements (1533 specimens) was retrieved from Scandinavia, from sample Vg84-26, upper \textit{Paltodus delifier} Zone at Brattefors, Sweden (Löfgren, 1997a). A few other samples from this locality and interval yielded this taxon, as did samples from Orreholmen which is 45 km south-southeast of Brattefors (Löfgren, 1996; see Tjernvik, 1956, for description of the Stenbrottet/Orreholmen locality). This is the same stratigraphic interval and the same general area from which Lindström’s (1955) type material of this taxon came. Additional specimens were recovered from a sample from the upper \textit{P. delifier} Zone at Ottenby, southern Öland, Sweden (see Tjernvik, 1956, for description of this locality).

\textit{Variabiloconus transiapeticus} n. sp. is present in a stratigraphically slightly higher sample (LH6) from Brattefors (reported as “Laurentian taxa” by Löfgren, 1997a). Brattefors is a unique locality, located at the foot of the hill Kinnekulle in the Province of Västergötland, south-central Sweden. The conodont samples collected at Brattefors came from an upper Tremadocian sequence that was deposited and preserved inside conical collapse structures that formed in mid-Tremadocian time. Teves & Lindström (1988) described the formation of and general stratigraphy within these structures. The stratigraphic sequence within the Brattefors “plugs” probably is more complete and less condensed than that in any other area in Sweden with beds of similar age. Löfgren (1977a) gave particulars about the rest of the conodont faunas in the Brattefors samples discussed here. Suffice it here to note that conodonts are particularly abundant in one of these samples (Vg84-26; 10,464 elements per kg of rock). One of the specimens of \textit{Rosodus manitouensis} (Pl. 3, fig. 21) was found in that sample; the abundance of this species thus is less than 0.006\% of the elements from this sample. The sample was processed in a laboratory where no sample of similar age and Laurentian origin ever had been prepared, so the presence in it of \textit{R. manitouensis} cannot be attributed to contamination.

\textit{Rosodus manitouensis} also was recovered from a sample taken at the same level as Lindström’s (1955) sample 5 from Stora Backor, Västergötland, and from a sample from the lower part of the \textit{Ceratopyge} Limestone (Björkåsholmen Formation) at Björkåsholmen, just outside the city of Oslo, Norway (Bockelie, 1982, p. 115). Both of these samples came from the \textit{Paltodus delifier} Zone. As with the sample from Brattefors, these specimens are perfectly consistent with their associated faunas in terms of CAI and details of preservation and appearance. Paleogeographic locations of these samples is shown in Text-fig. 1.

\textbf{Preservation and repository – The material generally is well to very well preserved, enabling us to study details of surface striation, distribution of white matter, etc. The figured specimens are deposited in the type collections of the Department of Paleobiology, U.S. National Museum of Natural History (USNM), Washington, D.C.}

\textbf{FAUNAL CONNECTIONS}

Studies of faunas from deeper platform and slope settings of North America and generally deeper water faunas of Scandinavia have thus revealed that these faunas share a few more species than had been assumed before.

Three localities in western Baltica (two in Västergötland, Sweden, and one near Oslo, Norway; see Text-fig. 1) have yielded extremely rare specimens of the North American zonal index species \textit{Rosodus manitouensis} Repetski & Ethington, 1983, in beds referred to the upper part of the Baltic \textit{Paltodus delifier} Zone. The Scandinavian specimens represent slightly asymmetrical coniform element types (perhaps Sb elements; Pl. 3, figs. 13, 15, 21) and fall within the limits of variation for North American populations of the species. How these specimens came to be dispersed to an area so far from the tropical main area of distribution of the species (Repetski & Ethington, 1983; Ethington & Repetski, 1984; Chen & Gong, 1986 [reported therein as “Acodus” oneotensis]; Shergold & Nicoll, 1992) is conjectural. Chance dispersal of the animals by abnormal current conditions or through ocean-crossing predators is possible.

\textit{Rosodus manitouensis} was a rare visitor to Baltica, but two species of \textit{Variabiloconus} seem to have been established as normal parts of the fauna in the upper Tremadocian of Baltoscandia. Formerly \textit{Variabiloconus} was believed to have been restricted to circumequatorial areas (e.g., Landing et al., 1986; Ji & Barnes, 1994). The two species, \textit{Variabiloconus variabilis} and \textit{V. transiapeticus} n. sp., have been found to be part of faunas...
recovered the lower to middle Tremadocian (Assemblage 2) graptolite \textit{Anisograptus richardsoni} from a level probably no more than 2 m stratigraphically separated from sample 11545-CO at this same locality.

The collections from the latter locality also produced specimens of \textit{Variabiloconus transiapeticus} n. sp. Samples yielding \textit{V. transiapeticus} n. sp. have been obtained in Colorado from the Manitou Formation in Williams Canyon near Manitou Springs, and in Missouri Gulch north of Woodland Park. \textit{Variabiloconus transiapeticus} n. sp. occurs at a slightly higher stratigraphic level than \textit{V. variabilis} at Brattefors in Sweden (sample LH6 of Löfgren, 1997a). Thus far \textit{Variabiloconus} has not been found elsewhere in Sweden, perhaps because beds of equal age have not been preserved outside the unique “plugs” of Brattefors (Teves & Lindström, 1988; Löfgren, 1997a).

\textit{Variabiloconus} is represented by other species in more typical, shallow water Midcontinent settings, but none of them is known to be represented in Baltica. It thus is highly probable that \textit{V. variabilis} and \textit{V. transiapeticus} n. sp. belonged to a \textit{Variabiloconus} stock that had slightly different environmental preferences (e.g., colder water) and also wider geographical dispersal than species belonging to the main part of the lineage. The stratigraphic interval representing times when conditions on the Baltic side of Iapetus were suitable for \textit{Variabiloconus} must have been very limited, for it is restricted to the upper part of the \textit{Paltodus deltifer} Zone. The North American ranges of \textit{Variabiloconus variabilis} and \textit{V. transiapeticus} n. sp. start in the \textit{R. manitouensis} Zone (Missouri Gulch locality in Colorado and probably the Ninemile Canyon locality in Nevada) and probably extend into the \textit{Macerodus dianae} Zone (Hamburg klippe sample). The minor morphological differences between North American and European specimens observed may be due to slight difference in their ages, but more likely they can be explained as an instance of geographical separation of populations.

**SYSTEMATIC PALEONTOLOGY**

**Genus** \textit{Variabiloconus} Landing, Barnes & Stevens, 1986

**Type species** – \textit{Paltodus bassleri} Furnish, 1938.

**Remarks** – Landing \textit{et al.} (1986) diagnosed \textit{Variabiloconus} as having a multimembrane apparatus of variously costate and sulcate, microstriated elements with albid cusps and intergradational symmetries, and their Table 3 lists up to seven different element types. All of the specimens of \textit{Ovodotoxus variabilis} illustrated by Lindström (1955) in the original description of the species were derived from the same sample, Stora Bäckor 5, from the upper \textit{Paltodus deltifer} Zone, and are part of the same apparatus. Ethington & Brand

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Text-fig. 1 - Sketch map of the Tremadocian showing the locations of finds of \textit{Roxiodus manitouensis} in Scandinavia/Baltica (filled circles) and of \textit{Variabiloconus transiapeticus} n. sp. and/or \textit{V. variabilis} in North America/Laurentia (stars). Base map from McKerrow \textit{et al.} (1991).
(1981) demonstrated that none of Lindström's specimens could be congeneric with the type species of Oneotodus, *O. simplex* (Furnish, 1938). General shape, microstriation and white matter distribution in the type species of Variabiloconus, *V. bassleri*, are similar to those in *O.* "variabilis," a fact already commented on by Landing et al. (1986, p. 1946), who tentatively assigned "O." *variabilis* to Variabiloconus. We agree with these authors that elements of *V. variabilis* have more reclined cusps and weaker costae than those of *V. bassleri*.

As reconstructed here, the apparatus of *V. variabilis* consists of six element types, the ones figured by Lindström (1955) in his text-figure 6 as a and b (=Sb), as c (=Sa), and as d (=Sc), respectively, one type with a rounded anterior and sharp posterior margin (=Sc), a short-based type represented by the specimens illustrated by Lindström’s Pl. 5, figs. 4 and 5 (=Pa), and a short-based concavo-convex type, often with a lateral costa at the base-cusp transition (=Pb).

Several of the element types also can be recognized in apparatus reconstructions of Variabiloconus bassleri (Furnish) by Landing & Barnes (1981), Landing et al. (1986), Fährus & Roy (1993) and, to a lesser extent, by Ji & Barnes (1994). *Teridontus nakamurai* (Nogami) also seems to include very similar element types according to Nicoll’s (1994) reconstruction. Some of these element types were recognized in the original description of that species (Nogami, 1967), and they may be basic to a larger group of conodonts.

**Variabiloconus variabilis** (Lindström, 1955)

Pls. 1, 2; Text-fig. 2

1955 *Oneotodus variabilis* n. sp. - Lindström, p. 582, pl. 2, figs. 14-18, 47, pl. 5, figs. 4-5, text-fig. 6.
non 1970 *Oneotodus variabilis* Lindström - Barnes & Turek, p. 90, pl. 18, fig. 3.
non 1971 *Oneotodus variabilis* Lindström - Jones, p. 60, pl. 4, fig. 10a-c.
non 1971 *Oneotodus variabilis* Lindström - Druce & Jones, p. 84, pl. 13, fig. 5a-c, text-fig. 26m.
non 1971 *Oneotodus variabilis* Lindström - Greiggs & Bond, pp. 1467-1468, pl. 1, figs. 10, 11, 13-16a.
1974 *Depnoconodina acuminata* (Pander) - Van Wamelen, p. 62-63 (pars), pl. 2, figs. 4, 5 (only).
1974 *Oneotodus variabilis* Lindström - Vira, p. 97, pl. 1, figs. 14, 15, text-fig. 118.
1975 *Oneotodus variabilis* Lindström - Abaimova, pp. 84, 85, pl. 7, figs. 11, 13, text-fig. 7 (19, 20).
non 1977 *Oneotodus variabilis* Lindström - Abaimova & Markov, p. 93, pl. 14, fig. 11, pl. 15, fig. 4.
1978 *Oneotodus variabilis* Lindström - Fährus & Nowlan, p. 460, pl. 1, fig. 20.
1983 *Schopfodina gracile* Ethington & Clark - Landing, p. 1179, text-fig. 105, U.
1983 *Schopfodina gracile* Ethington & Clark - Landing, text-fig. 106.
1988 "Oneotodus" *variabilis* Lindström - Bagnoli et al., pl. 212, pl. 40, figs. 5, 6.
1996 "Oneotodus" *variabilis* Lindström - Löfgren, fig. 8L.
non 1998 *Oneotodus variabilis* Lindström - Alabeesi, p. 127, pl. 5, figs. 31-32.

**Description** — The cusp is albid and the base hyaline, and the boundary between these regions typically is fairly sharp, making an angle of about 30 degrees with the posterior margin of the cusp. This distribution of white matter resembles that found in the older species *Teridontus nakamurai* (Nogami) as described by Nicoll (1994). In that species the line delimiting white and hyaline matter makes a greater angle with the posterior edge of the cusp than in any of the *V. variabilis* specimens investigated by us.

Interwining, rather coarse striations (each c. 1 μm wide) can be observed on well-preserved elements of *V. variabilis*, particularly on the posterior face of Sa elements. Landing et al. (1986) described elements of *V. bassleri* as being "longitudinally microstriated," while Ji & Barnes (1994) found *V. bassleri* elements "covered by faint striations." Buggisch & Repetski (1988, pl. 2, fig. 19) and Nicoll (1994, fig. 4.2e) found striations of the same size as or slightly coarser than those of *V. bassleri* in *Teridontus nakamurai* (Nogami).

**Sa element** (Text-fig. 2A-D, Pl. 2, figs. 10-17) – (Lindström, 1955, pl. 2, figs. 14, 17, text-fig. 6c). The cusp is erect to reclined; its cross-section is round distally. The basal cross-section of this symmetrical element is triangular, but the oral margin as well as the antero-lateral corners are rounded off. The lateral sides of the base carry broadly rounded carinae that end at the antero-basal corners. The carina is delimited posteriorly by a groove that fades out about half way up the cusp in most specimens. The carinae and grooves are symmetrically placed. The posterior margin of the cusp is not sharp, except for a short segment where it meets the oral margin in a few elements. This probably is the same type of element as the type specimen of *Palododus bassleri* Furnish, 1938. American Sa elements of *V. variabilis* often have deeper posterior grooves than the Swedish ones, and the grooves also begin closer to the aboral margin. The slight differences may be due to the geographical restriction of respective populations.

**Sb element** (Text-fig. 2E-L, Pl. 1, figs. 1-3, 7-10, 12, Pl. 2, figs. 1-3, 6, 9) – (Lindström, 1955, pl. 2, fig. 47, text-fig. 6b [= the holotype], pl. 2, fig. 15, text-fig. 6a). The posterior margin of the cusp and the oral margin of the base are rounded, but the anterior margin of the base is smoothly keeled; the keel is flexed to the inner side, thereby making the elements asymmetrical. Scarce elements have up to a few posterior costae where the cusp and base meet. The posterior surface in the region of strongest curvature can be scooped-out or recessed. Some Sb element have a more reclined cusp than the Sa elements, but others, like the holotype, are more erect. Some elements (see Pl. 1, figs. 8, 9, Pl. 2,
Text-fig. 2 - Camera lucida drawings of *Variabiloconus variabilis* (Lindström, 1955) from sample Vg84-26, upper *Paltodus deliser* Zone, Brattefors. All X65. A-D= Sa elements: A) same specimen as Pl. 2, fig. 15; B) same as Pl. 2, fig. 11; C) same as Pl. 2, fig. 12; D) same as Pl. 2, fig. 16. E-L= Sb elements: E) same specimen as Pl. 1, fig. 1; F) same as Pl. 1, fig. 2; G) same as Pl. 1, fig. 3; H) same as Pl. 1, fig. 7; I) same as Pl. 1, fig. 8; J) same as Pl. 1, fig. 12; K) same as Pl. 1, fig. 9; L) same as Pl. 1, fig. 10. M-P= Sc element: M) same specimen as Pl. 1, fig. 4; N) same as Pl. 1, fig. 13; O) same as Pl. 1, fig. 18. Q= Sd element: same specimen as Pl. 1, fig. 20. R= Pa element, same specimen as Pl. 1, fig. 16. S= Pb element, same specimen as Pl. 1, fig. 14.
figs. 2-3 herein; Lindström, 1955, pl. 2, fig. 15) display a slightly shorter base but otherwise are closely similar to other Sb elements.

Sb element (Text-fig. 2M-P, Pl. 1, figs. 4, 13, 18, Pl. 2, fig. 8) – (Not figured by Lindström, 1955). The cusp is slightly recurved with a rather sharp posterior edge, which continues on to the oral margin. The posterior margin of the cusp and base are rounded. A smoothly rounded anterolateral carina is present on each side. The element is slightly concavo-convex with the basal cavity opening to the inner side rather than posteriorly.

Sd element (Text-fig. 2Q, Pl. 1, figs. 17, 20, Pl. 2, fig. 7) – (Lindström, 1955, pl. 2, fig. 18, text-figure 6d). The cusp is recurved. These elements have a trapezoidal basal cross-section whose corners are rounded off as in Sa elements. In contrast with the Sa element, part of the oral margin and the posterior margin on the lower part of the cusp have a sharp edge. One or two rather sharp, posteriorly directed lateral costae are present on each side of the base; they are placed so that the elements are distinctly asymmetrical.

Pa element (Text-fig. 2R, Pl. 1, figs. 11, 16, Pl. 2, fig. 4) – (Lindström, 1955, pl. 5, figs. 4, 5). This asymmetrical element with a reclined or recurved cusp typically has a notch at the opening of the basal cavity so that it resembles Pa elements of other species of the genus. A rounded carina continues from this notch up the inner side of the base and fades out on the cusp. The cusp has a rounded cross-section. The basal cavity flares widely, particularly to the outer side.

Pb element (Text-fig. 2S, Pl. 1, figs. 5-6, 14-15, 19, Pl. 2, fig. 5) – (Not figured by Lindström, 1955). The reclined cusp has rounded anterior and posterior margins; the oral edge is short and faintly keeled. The anterior margin is smoothly carinate basally and turned inwards. An inner, often faint, posterior costa is found where the cusp and base meet in many elements.

Element ratios – The ratio between the different element types was calculated for Vg84-26, the sample yielding most of the V variabilis specimens. That sample provided 273 Sa, 750 Sb, 121 Sc, 154 Sd, 103 Pb and 121 Pb elements and 11 indeterminate specimens belonging to this taxon. The ratio which agrees most closely to these proportions is: 2 Sa: 6 Sb: 1 Sc: 1 Sd: 1 Pb.

Remarks – No template has been suggested for these kinds of apparatuses. Nicoll’s (1944) reconstruction of Teridontus nakamura had 794 S and 272 P elements which agrees better with six pairs of S elements and two pairs of P elements. It is unusual to have more than one kind of symmetrical (Sa) elements. Ji & Barnes (1994), however, found two symmetrical element types (a and c) in Teridontus and Variabiloconus, which suggests that the symmetrical elements may have had a different function or position than in other types of coniform apparatuses. The similarity of symmetrical elements of V variabilis with those of two other coniform taxa, Drepanodus arcatus and Paroistodus numarcuatus (cf. Löfgren, 1997b), makes it improbable that these elements should have had radically different functions.

EXPLANATION OF PLATE 1

Figs. 1-20 - Variabiloconus variabilis (Lindström, 1955) from sample Vg84-26, upper Palodus delusor Zone, Brattefors, Västergötland, Sweden.

1) Sb element, inner side, USNM 501091; x80;
2) Sb element, outer side, USNM 501102; x90;
3) Sb element, outer side, USNM 501103; x103;
4) Sc element USNM 501092; x100;
5) Pb element, inner side, USNM 501093; x120;
6) Pb element, posterior side, USNM 501094; x103;
7) Sb element, inner side, USNM 501104; x103;
8) Sb element, costate inner side, USNM 501095; x90;
9) Sb element, costate inner side, USNM 501096; x90;
10) Sb element, costate inner side, USNM 501105; x100;
11) Pa element, USNM 501097; x100;
12) Sb element, smooth inner side, USNM 501098; x90;
13) Sc element, USNM 501099; x90;
14) Pb element, inner side, USNM 501100; x103;
15) Pb element, inner side, USNM 501114; x85;
16) Pa element, USNM 501101; x120;
17) Sc element, USNM 501106; x133;
18) Sc element, USNM 501107; x100;
19) Pb element, inner side, USNM 501115; x90;
20) Sc element, USNM 501108; x120.
Geographic distribution – The taxon has been found previously in Sweden (Lindström, 1955; van Wamel, 1974; Löfgren, 1996) and Estonia (Viira, 1974). Previous non-illustrated reports of the taxon from Baltoscandia by Viira (1966, from Estonia) and Sergeeva (1966, from western Russia) probably are correct. The specimens figured by Bagnoli et al. (1988) from Öland, Sweden, are not typical and could belong to other taxa. Nevertheless, V. variabilis is present on Öland (van Wamel, 1974, and Löfgren, undescribed collections from Ottenby, southern Öland).

Variabiloconus variabilis also is present in deep shelf to continental slope settings in Vermont (Landing, 1983), and is reported herein from the slope deposits in both the Hamburg klippe in Pennsylvania and from Ninemile Canyon in Nevada. Of the previous reports of V. variabilis from outside Baltoscandia, those from Australia (Jones, 1971; Drue & Jones, 1971) clearly concern other Midcontinent taxa (as discussed by Landing, 1983, and Landing et al., 1986) as do those from Ontario, Canada (Greggs & Bond, 1971) and Argentina (Albanesi, 1998). The reported occurrences in the Arbuckle Group of southern Oklahoma (Mound, 1968) are too poorly illustrated to enable a definite identification, and no specimens have been found in subsequent studies of faunas from these rocks (undescribed collections of Repetski and Ethington); the location makes an attribution of the specimens to a Midcontinent taxon probable, though. Of the reports from Newfoundland, that by Barnes & Tuke (1970) definitely and that by Fähræus & Nowlan (1978) probably concerns Midcontinent taxa. In the latter case the shape of the illustrated element is similar to that of an Sb element of V. variabilis, but the cusp appears to be hyaline, which would exclude it from that taxon. The records from Antarcrica (Buggisch & Repetski, 1988), the Rocky Mountains of Canada (Ethington & Clark, 1965, p. 197) and from Siberia (Abaimova, 1975; Abaimova & Markov, 1977) are equivocal; most probably they represent some other taxa.

Material – About 2000 specimens.

Variabiloconus transiapeticus n. sp.
Pl. 3, figs. 1-12, 14, 16-20, 22, Text-fig. 3

Derivation of name – Referring to the distribution of the species on both sides of the Iapetus Ocean.


Type stratum – Approximately 2.5m above the base of limestone member of the Goodwin Formation, USGS Collection 11545-CO (A. G. Harris, collector).

Holotype – USNM 501146 (Pl. 3, fig. 20), an Sc element.

Diagnosis – The apparatus of V. transiapeticus consists of six element types; an Sa element with sharply delimited lateral “wings” and a costate posterior side, an Sb element with an inwards-flexed anterior keel on the base and often with a costate inner side, an Sc element with a flexed, slightly concavo-convex shape and costae on its base, an Sd element which is twisted and has up to four costae, and Pa and Pb elements with widely flaring bases. All elements have an erect to proclined cusp.

EXPLANATION OF PLATE 2
Figs. 1-17 - Variabiloconus variabilis (Lindström, 1955). Figs. 1-9, 13-14 from sample USGS collection 11545-CO from the base of the limestone member of the Goodwin Formation, Ninemile Canyon, Antelope Range, Eureka County, Nevada. Figs. 10-12, 15-17 from sample Vg64-26, upper Paludites delatifer Zone, Brattefors, Västergötland, Sweden.
1) Sb element, inner side, USNM 501128; x102;
2) Sb element, inner side, USNM 501129; x87;
3) Sb element, outer side, USNM 501130; x87;
4) Pa element, USNM 501131; x85;
5) Pb element, USNM 501132; x102;
6) Sb element, inner side, USNM 501133; x102;
7) Sd element, USNM 501134; x112;
8) Sc element, USNM 501135; x112;
9) Sb element, inner side, USNM 501136; x85;
10) Sa element, posterior view, USNM 501109; x100;
11) Sa element, lateral side, USNM 501110; x90;
12) Sa element, lateral side, USNM 501111; x100;
13) Sa element, oblique side view, USNM 501137; x107;
14) Sa element, posterior view, USNM 501138; x107;
15) Sa element, lateral side, USNM 501112; x75;
16) Sa element, lateral side, USNM 501113; x90;
17) Detail of right side of 10, x800.
General remarks — Six different kinds of elements are described here. The basal cavity in all of them is triangular as seen from the side, with the tip close to the anterior margin (Text-fig. 3A-H). The cusp is albid above a rather sharply delimited triangular area of hyaline material along the oral margin and the lower part of the posterior margin of the cusp. All elements have a more proclined cusp than the corresponding elements of *V. variabilis* whose cusp is erect to reclined.

**Sa element** (Pl. 3, figs. 10-12) — The cusp is erect to slightly proclined. Its anterior side is well rounded, its posterior surface is costate. One deep longitudinal furrow extends along the cusp and base on each side, delimiting the lateral "wings" from the central posterior part with its two symmetrically placed costae. The element thus is similar to a symmetrical element of *Semiacontiodus*. The element differs from the corresponding element in *V. variabilis* by its more sharply delimited lateral "wings" and the costate posterior.

**Sb element** (Text-fig. 3C-D, Pl. 3, figs. 7-9, 14) — The cusp is erect to reclined with the distal end broken in all available specimens. Its length is not known, but the cusp appears to have been longer than in the corresponding element of *V. variabilis*. The anterior keel of the base is flexed inward and fades to a rather blunt costa on the cusp. The oral edge is sharp except near the opening to the basal cavity as is its continuation on the posterior surface of the cusp. Several specimens have a costa on the inner side and close to the posterior margin; it begins on the upper part of the base and continues upward on the cusp and parallel to the posterior edge. The posterior face of the cusp is flat or concave between these edges. Minor costae are present on the outer sides of the bases and lowermost parts of the cusps of a few specimens. The basal cavity resembles an isosceles triangle in lateral view, with the shortest side at the basal cavity opening. The Sb element differs from the corresponding element of *V. variabilis* mainly in its more proclined to erect cusp.

**Sc element** (Text-fig. 3E, G, Pl. 3, figs. 19-20, 22) — The cusp is proclined and has keeled oral and posterior margins. The anterior margin is well rounded. The entire element is slightly concavo-convex due to flexing, and almost invariably displays asymmetrically distributed costae on the base. The element differs from the corresponding element of *V. variabilis* in having less distinctive anterolateral carinae.

**Sd element** (Text-fig. 3E, Pl. 3, figs. 16; 17-18) — The cusp is erect and the base can have up to four costae, two on each side, that continue on the cusp in some elements. The distribution of the costae gives the element a concavo-convex and twisted appearance. The oral margin is not keeled, and the outline of the basal

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**EXPLANATION OF PLATE 3**

Conodont elements from the upper *Palodus delicatus* Zone, Brattefors and Ninemile Canyon.

Figs. 1-12, 14, 16-20, 22 *Variablenenous transversipeticus* n. sp. Figs. 1-2, 7, 9, 10, 12, 16, 20 from USGS collection 11545-CO from the base of the limestone member of the Goodwin Formation, Ninemile Canyon, Antelope Range, Eureka County, Nevada; Figs. 3-6, 8, 11, 14, 17-19, 22 from sample LH6, Brattefors, Sweden.

1) Pa element, inner side, USNM 501133; x68;
2) Pa element, inner side, USNM 501140; x68;
3) Pa element, posterior side, USNM 501116; x105;
4) Pa element, outer side, USNM 501117; x105;
5) Pb element, outer side, USNM 501118; x105;
6) Pb element, inner side, USNM 501119; x105;
7) Sb element, inner side, USNM 501141; x102;
8) Sb element, outer side, USNM 501120; x105;
9) Sb element, inner side, USNM 501142; x112;
10) Sa element, posterior view, USNM 501143; x107;
11) Sa element, posterior view, USNM 501121; x85;
12) Sa element, posterior view, USNM 501144; x107;
13) Sb element, inner side, USNM 501122; x105;
14) Sd element, side view, USNM 501145; x102;
15) Sd element, posterior view, USNM 501123; x110;
16) Sd element, oblique side view, USNM 501124; x110;
17) Sc element, outer side, USNM 501125; x110;
18) Sc element, inner side, USNM 501146; x112 (holotype);
19) Sc element, inner side, USNM 501126; x110.


13) From Stora Backor, Västergötland, Sweden, Lindström's (1955) bed 5, USNM 501147, x185;
15) From Bjerkåsholmen, Asker, near Oslo, Norway, USNM 501148, x500;
21) From sample Vg84-26, Brattefors; USNM 501127, x135.
cavity opening approximates a square. The Sd element differs from the corresponding element in *V. variabilis* primarily by having a shorter and wider base.

**Pa element** (Text-fig. 3H, Pl. 3, figs. 1-4) — The cusp is erect. Seen from the posterior side, a few elements slightly resemble Sa elements by having two posterolateral grooves. These are asymmetrically placed, however, and the entire element is concavo-convex and slightly twisted. The base flares widely. The Pa element differs from the corresponding element in *V. variabilis* e.g. by having a wider basal cavity.

**Pb element** (Text-fig. 3A, B, Pl. 3, figs. 5, 6) — The cusp is erect to slightly proclined. This asymmetrical element has a much less flared basal cavity than the Pa element. The anterior edge is flexed far to the inner side, which also has a costa. The oral margin is short and only faintly keeled. The element differs from the corresponding element in *V. variabilis* mainly by its wider angle between the cusp and oral margin.

**Remarks** — The Sa element of *V. transiapeticus* n. sp. is less compressed antero-posteriorly than the type specimen of *Acontiodus stanfieldi* Furnish, 1938, which has a hyaline cusp (cf. Landing & Barnes, 1981, p. 1615), and probably represents the same element type of another species. Similar elements with albid cusps were referred to "Acontiodus" *iowensis* Furnish by Landing & Barnes (1981). Their taxon is of the same age as our *V. transiapeticus* n. sp., but its Sa elements seem to be more proclined and to have sharper costate. This taxon may prove to be closely related to, or even conspecific with *V. transiapeticus* n. sp., but its associated elements have not been reported as yet. Landing et al. (1986) combined it with *Oistodus mehli* Furnish, 1938, and referred to it as *Semiacontiodus iowensis*.

**Occurrence and range** — The range of *V. transiapeticus* n. sp. at the Ninemile Canyon, Nevada, section is poorly constrained at present. We recognize it unequivocally only in sample 11545-CO, taken at approximately 2.5 m above the base of the limestone member of the Goodwin Formation along this traverse. That sample is dominated by an unnamed, probably new, species of *Drepanoistodus* and a *Drepanodus* species that may be a very early representative of *D. arcuatus*. A late form of *Rosodus manitouensis* occurs at about 30 m below this sample. Samples from intervening strata have either few specimens or taxa that are not zonally diagnostic. *Laurentoscandodus aff. triangularis* (Furnish) and "*Acanthodus* lineatus" (Furnish) occur in this interval and both extend upwards for at least 25 m above sample 11545-CO; because both of these species extend only a short way into the Low Diversity Interval (e.g., see Ethington et al., 1987), it is most likely that the sample containing *V. transiapeticus* n. sp. is within the *R. manitouensis* Zone. Further support is given to this assignment by the occurrence of the Assemblage 2 graptolite species *Anisograptus richardsoni* at approximately the same horizon (Erdtmann & Comeau, 1980).

*Variabiloconus transiapeticus* n. sp. is present in an interval of approximately 30 meters in the section in

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Text-fig. 3 - Camera lucida drawings of *Variabiloconus transiapeticus* n. sp. from sample LH6, upper *Palodus delifer* Zone, Brattfors. All X90. A-B= Pb elements: A) same specimen as Pl. 3, fig. 5; B) same as Pl. 3, fig. 6. C-D= Sb elements: C) same as Pl. 3, fig. 14; D) same as Pl. 3, fig. 8. E= Sd element, same as Pl. 3, fig. 18. F= G= Sc elements: F) same as Pl. 3, fig. 22; G) same as Pl. 3, fig. 19. H= Pa element, same as Pl. 3, fig. 4.
Williams Canyon near Manitou Springs, Colorado. Its lowest occurrence is in a dolostone unit that Maher (1950) placed in the upper part of the Sawatch Quartzite for which he assumed Late Cambrian age. The species ranges upward through the interval that he identified as the Ute Pass Dolomite, also assumed by Maher to be of Late Cambrian age, and through the lowest 23 meters of dolomites and limestones that Maher identified as the Manitou Formation (Lower Ordovician) at this locality. Maher (1950) reported “Orthoceras-type cephalopods” from just above the base of the sequence he identified as Manitou, but he did not record any fossils from lower in the section. The discovery of conodonts in the purported upper Sawatch and Ute Pass demonstrates that this interval in Williams Canyon also is of Early Ordovician age. The lowest sample that produced conodonts (ca. 0.5 meter below the top of Maher’s Sawatch) has V. transiapeticus n. sp. together with Rossodus manitouensis, “Acanthodus” lineatus, and Chosonodina herfurthi. In its highest occurrence in the Manitou Formation in Williams Canyon, V. transiapeticus n. sp. is associated with Macrodus dianae Fähraeus & Nowlan.

Variabilonconus transiapeticus n. sp. is present throughout all but the lowest meter of the section of Manitou Formation in Missouri Gulch north of Woodland Park, Colorado. This locality includes the stratum typicum of Rossodus manitouensis Repetski & Ethington. The Manitou is unconformable beneath the Williams Canyon Formation (?Devonian) at this locality and does not include equivalents of the upper part of the range shown by V. transiapeticus n. sp. in the Manitou Springs area to the east. Another unconformity (Paul Myrow, personal communication, 1998) separates the Manitou in Missouri Gulch from the shaly underlying rocks which may be of Cambrian age. The evidence presented here is consistent with the biostratigraphic correlation of the Ordovician sections in this part of the Colorado Front Range provided by Berg & Ross (1959).

This species is present through 11.4 meters of Manitou Formation at Horseshoe Mountain near Leadville, Colorado. The lowest known occurrence there is in association with conodonts of the R. manitouensis Zone but the three stratigraphically higher samples from which it was recovered probably represent the Low Diversity Interval. V. transiapeticus n. sp. is not present in still higher samples from this locality that contain abundant specimens of Histiodella dianae Repetski, a species typical of the M. dianae Zone.

The occurrence in Missouri Gulch together with that in Williams Canyon indicate that V. transiapeticus n. sp. ranges in the Manitou from a level within the R. manitouensis Zone through the Lower Diversity Interval into the M. dianae Zone. Because of unconformity or unproductive lithologies, the lower limit of the range of this species cannot be established with confidence in the central Colorado sections in which it has been found. The known range is from the upper part of the Skullrockian Stage through much of the Stairian Stage of the North American Ibexian Series (Ross et al., 1997).

The range in Sweden of V. transiapeticus n. sp. is difficult to assess at present, as it has only been found in one sample in the upper P. delitfer Zone at Brattefors (Löfgren, 1997a), where it occurs together with, e.g., Drepanodus arcuatus.

Material – More than 100 specimens.

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REFERENCES


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