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BRIEF COMMUNICATION

# SEM STUDIES ON VESSELS IN FERNS. 9. *DICRANOPTERIS* (GLEICHENIACEAE) AND VESSEL PATTERNS IN LEPTOSPORANGIATE FERNS[1]

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Ferns in which vessels have been demonstrated to date are phylogenetically relatively specialized and characteristic of habitats with marked extremes in temperature and water availability. These specifications do not apply to the Gleicheniaceae, which indicates that vessels may occur in a range of more primitive ferns, including those from more nearly mesic habitats. Vessels in *Dicranopteris* have perforation plates (both lateral and terminal) with morphology similar to that of lateral wall pitting as seen with light microscopy. Scanning electron microscopy (SEM) is therefore necessary to demonstrate presence of perforations. Vessel presence in *Dicranopteris* is important in forming a picture of vessel presence and specialization in ferns, the phylogenetic and ecological distribution of which may differ from the patterns found in monocotyledons and dicotyledons. We believe that presence of vessels may not be a reliable indicator of phylogenetic position among ferns.

**Key words:** *Dicranopteris*; ecological plant anatomy; ferns; Gleicheniaceae; perforation plates; vessels; xylem.

In a series of papers, we have shown that vessels are much more extensive in ferns than had hitherto been realized (Carlquist and Schneider, 1997a, b; in press; Carlquist, Schneider, and Yatskievych, 1997; Carlquist, Schneider, and Kenneally, in press; Schneider and Carlquist, 1997, 1998, in press). Although vessels had been reliably reported in *Pteridium* (Russow, 1873; Bliss, 1939) and *Marsilea* (White, 1961; Loyal and Singh, 1978), only Gwynne-Vaughan (1908) had claimed vessels in several more genera, a claim discounted by several workers (see White, 1962). White (1962) suspected vessels might be present in some species of *Woodsia*, because of the morphological difference between end walls and side walls of tracheary elements, but the transparency of pit membranes in light microscopy prevented White from confirming this suspicion. Scanning electron microscopy (SEM) can readily demonstrate the presence of pit membranes or remnants of pit membranes in perforation plates and thus proves to be the ideal tool for demonstrating perforation plates not obviously seen by light microscope by virtue of marked differentiation between end wall and lateral walls.

In searching for possible instances of vessel presence in ferns, we began with *Woodsia* not only because of White's (1962) observations, but because the *Woodsia* species with more marked differentiation of tracheary element end walls occupy habitats with more extreme fluctuations in moisture availability (Carlquist, Schneider, and Yatskievych, 1997; Carlquist and Schneider, in press; Schneider and Carlquist, 1998). After we had demonstrated vessels in these species of *Woodsia*, the search for vessels progressed to other ferns of extreme habitats. We had noted that *Pteridium* and *Marsilea* grow in areas that range from very dry to very wet, and in other vascular plants, evolution of vessels seems to parallel entry of phylads into progressively more seasonal habitats (Carlquist, 1975). *Phlebodium* (Schneider and Carlquist, 1997) occurs in humid but dry tropics, both as an epiphyte and on rocky surfaces; *Polystichum* (Schneider and Carlquist, 1997) survives winter freezing; *Microgramma* is a tropical epiphyte (Schneider and Carlquist, in press); and *Platyzoma* is a ‘‘resurrection plant’’ of highly seasonal tropical Australian habitats (Carlquist, Schneider, and Kenneally, in press). The selective value of vessels in these ferns is presumably facilitation of more rapid conduction during brief periods of water availability.

If one compares the abovementioned genera of ferns to phylogenetic systems, one finds that Aspidiaceae (*Polystichum*), Dryopteridaceae (*Woodsia*), Polypodiaceae (*Microgramma*, *Phlebodium*), Marsileaceae (*Marsilea*), and Pteridaceae (*Astrolepis*, *Pteridium*, and very likely *Platyzoma*) occur in families ranked as specialized among leptosporangiate ferns, either in traditional schemes based on macromorphology (Copeland, 1947; Tryon and Tryon, 1982) or macromorphology combined with molecular data (Pryer, Smith, and Skog, 1995) or molecular data alone (Wolf, 1997). Therefore, a reconnaissance among more primitive families more of leptosporangiate ferns seemed necessary in order to discriminate between the roles of phylogenetic specialization and ecological extremes in the evolution of vessels in ferns.

The Gleicheniaceae are ranked in a near-basal position in most systems (Copeland, 1947; Tryon and Tryon, 1982; Pryer, Smith, and Skog, 1995). The species of this family do not characteristically grow in areas where frost occurs, nor do they occur in sites where drought is frequent or pronounced. Therefore, the occurrence of vessels in Gleicheniaceae and other primitive ferns of mesic areas might signal that vessels are widespread in ferns, although more specialized vessels are to be expected in ferns of habitats with greater ecological extremes.

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The traditional basis for recognition of vessels as opposed to tracheids has been the absence of pit membranes in the perforations of end walls, whereas pit membranes are present in pits of lateral walls. The assumption that this differentiation could be detected with light microscopy has been implicit until very recently, especially where primary xylem is concerned. By using SEM, we have found vessels with relatively little difference in secondary wall patterns between perforation plates without pit membranes and lateral walls (e.g., *Phlebodium, Polystichum*); thereby, the difference between end walls and lateral walls is no longer a usable criterion except where SEM can be employed to demonstrate the presence or absence of pit membranes. The fact that perforation plates can be like lateral walls in all respects other than pit membrane presence is underlined by our discovery that some ferns can have perforation plates on lateral walls as well as on end walls (e.g., *Microgramma, Platyzoma, Polystichum, Pteridium*). *Dicranopteris* is a fern in which no differentiation between end walls and lateral walls can be detected with light microscopy alone.

As our studies of fern vessels with SEM have proceeded, we have found distinctive features in particular genera, such as alternating narrow and wide pits (*Plebodium, Platyzoma*), pit membranes with porosities of various sizes, etc. *Dicranopteris* has yielded such features. The diversity of morphology of fern tracheary elements as seen with SEM leads us to extend our studies with this technique into xylem of a wide range of ferns. The questions of ecological and phylogenetic relationships of vessel occurrence in ferns are critical in this regard, and the degree to which vessels in ferns may be polyphyletic is another significant question. We view *Dicranopteris* as a genus of special significance in assessing these questions because of its ecology and phylogenetic position.

## MATERIALS AND METHODS

Roots and stem portions of *Dicranopteris linearis* (Burm. f.) Underw. were collected near Volcano, Hawaii Island, in September 1997, by Edward L. Schneider. Fixed root and stem portions were macerated in Jeffrey's fluid, mounted on aluminum stubs, dried, sputter-coated, and examined with a Bausch and Lomb Nanolab SEM. Care was taken to distinguish true perforations from damaged pits. Perforations were identified only if a continuous strip of wall, forming a cohesive unit, bore porose membranes or no pit membrane remnants at all. Lateral walls mostly bear intact pit membranes after maceration, but on some, torn and displaced membranes permit one to identify pits. Our observations with macerated material correspond to designation of perforation plates and lateral wall pitting in those ferns with clear difference between perforation plates and lateral walls (*Astrolepis, Pteridium, Woodsia*). Thus, we believe our interpretations of macerated material as viewed with SEM in *Dicranopteris* are reliable.

## RESULTS

Portions of vessels from roots are shown in Figs. 1–5. Pit membranes are absent from most of the walls shown. Striate pit membranes may be seen in three pits in Fig. 1 (bottom center) and a wall portion to the left of that wall portion), and in Fig. 5 (far left and two pits at bottom, left of center). We believe that the remaining structures must be termed perforations and that therefore, perforation plates are abundant. One must keep in mind that fern tracheary elements can have more than one end wall—several end wall facets per tracheary element are typical and each of these may be a perforation plate. Some end walls are quite elongate, extending down much of the length of a tracheary element. In addition, lateral perforation plates are present on tracheary elements of *D. linearis,* as they are in other ferns (e.g., *Pteridium*; Carlquist and Schneider, 1997). Tracheary elements are mostly rather wide with many facets. We did not observe any tracheids.

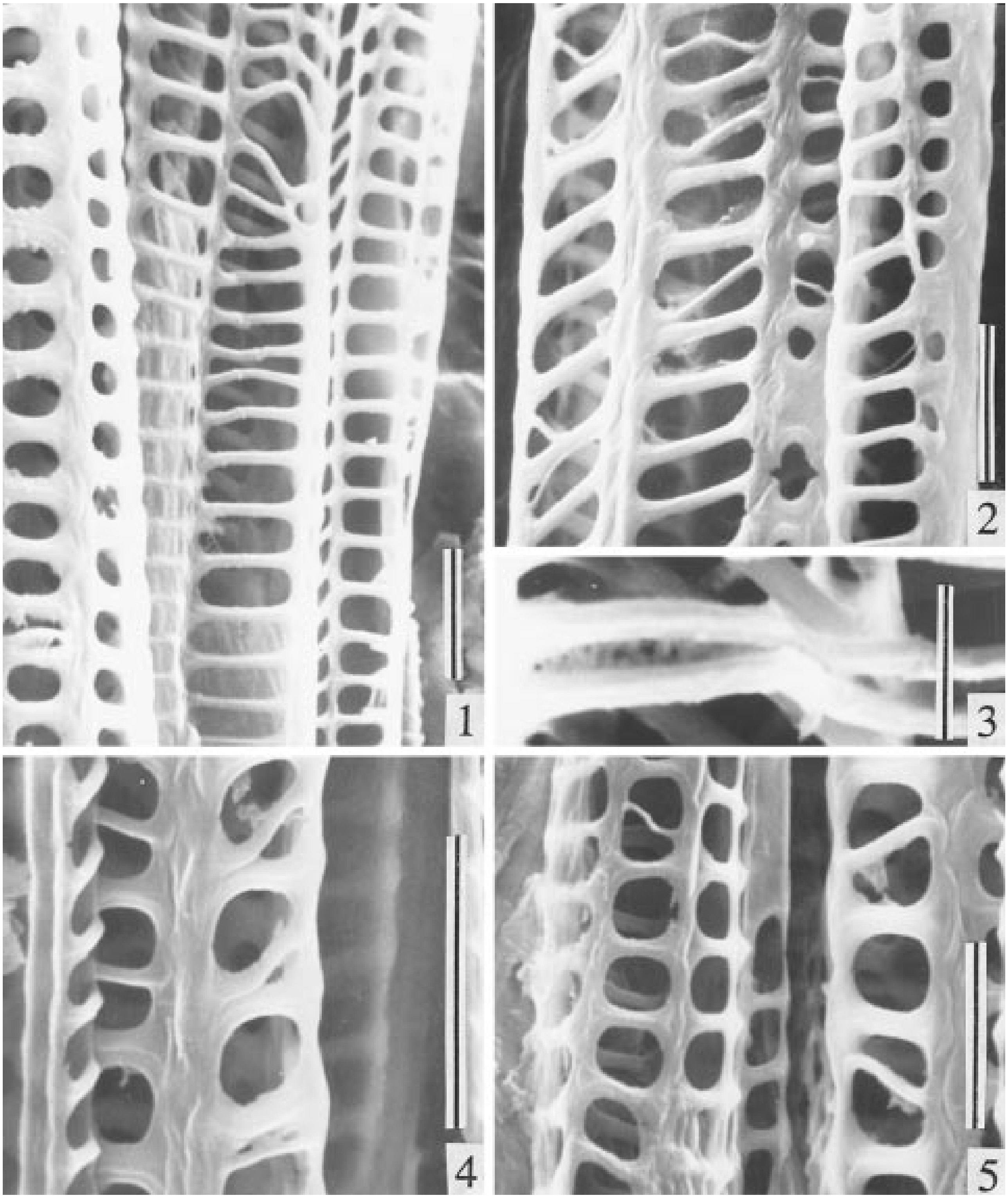
We would like to call attention to perforations that are diagonally traversed by strands of secondary wall material. Such slender strands may be seen in Fig. 2, as well as in Fig. 5 (upper left). Diagonal strands that are thicker traverse perforations in Figs. 4 and 5 (right). We have neither observed nor seen in the literature instances in other fern species of perforations subdivided in this manner. Pit membranes with porositites can be seen in some narrower perforations (Fig. 3).

Tracheary elements from rhizomes are shown in Figs. 6–10. Figure 6 represents a vessel element portion that we interpret as having poorly differentiated lateral perforation plates. A well-differentiated perforation plate is seen in Fig. 7 (center); pit membranes cover the file of lateral wall pits at the left edge of the photograph. In Fig. 8, a portion of one perforation (and a small piece of another, top) are illustrated to demonstrate the presence of very delicate pit membranes in which porosities occur; a greater degree of lysis of pit membranes occurred in adjacent pits. In Fig. 9 (center) there is a well-defined lateral perforation plate. We counted 192 bars in this perforation plate, which was clearly delimited at its top and bottom by lateral wall pits in which torn pit membranes were uniformly present. At the top of the photograph are five perforations in which adjacent bars fuse in a curious fashion. In Fig. 10 (left of center) are two facets that represent perforation plates in the upper two-thirds of the photograph, but the lower third of the two facets bears pit membranes. As a generalization, we find that perforation plates in rhizomes of *D. linearis* are less common than they are in the roots, and one finds that perforation plates are narrower (compare Figs. 1–4 with Figs. 7, 9, and 10) and, in some cases (Fig. 8), contain porose pit membranes.

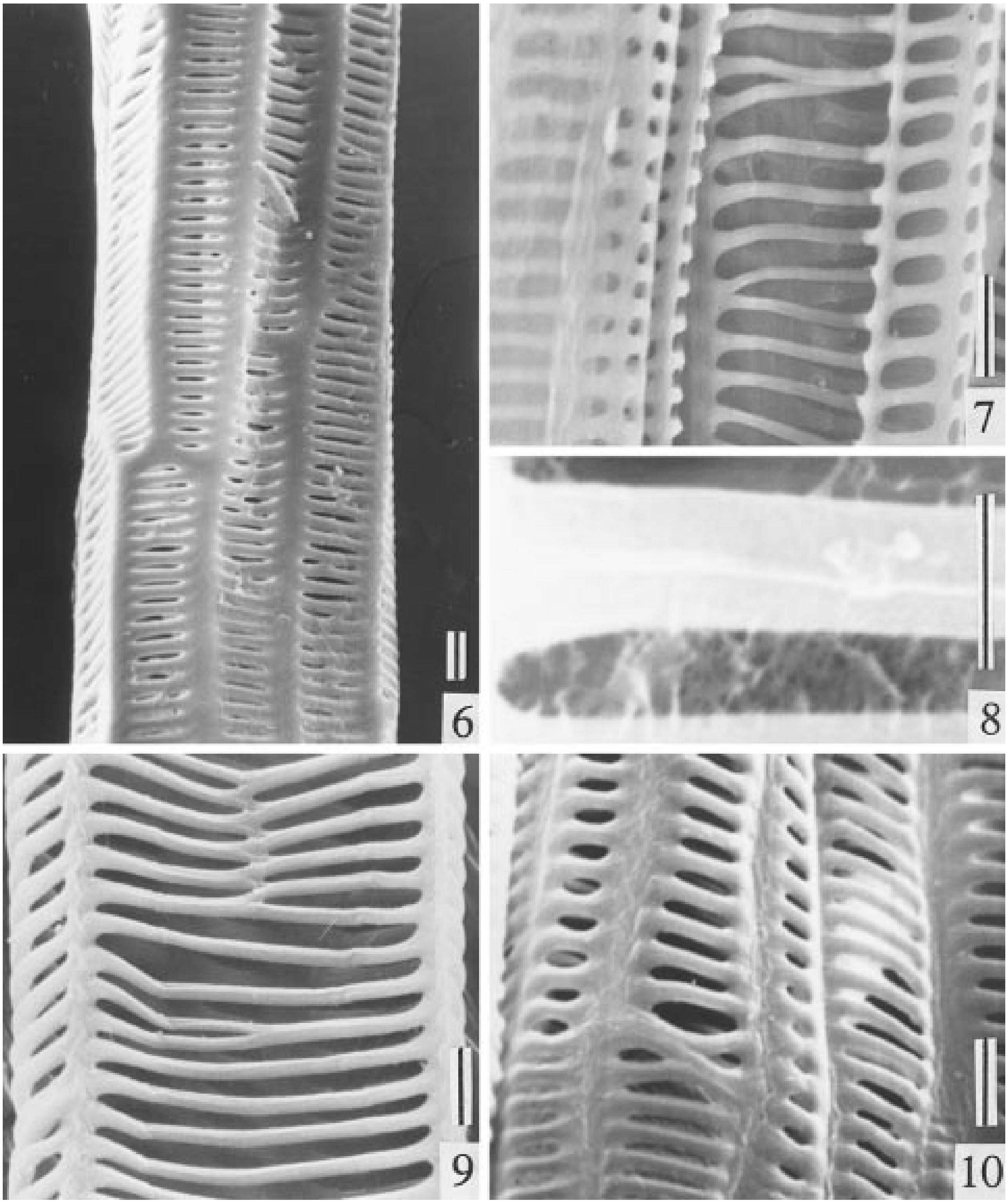
## DISCUSSION

*Dicranopteris linearis* roots and rhizomes have vessels with numerous perforation plates and apparently lack tracheids, a pattern we have seen in other ferns. The perforation plates are similar to lateral wall pitting except in the presence of perforations. As in some other ferns we have studied (e.g., *Phlebodium, Polystichum*; Schneider and Carlquist, 1997), the perforations resemble lateral wall pits in morphology, and thus would not be evident without examination by means of SEM. *Dicranopteris linearis* supports our generalization that vessels in ferns have more clearly developed perforation plates in roots than in stems.

The Gleicheniaceae are placed in a near-basal position among leptosporagiate ferns by various workers (see introduction), yet its vessels are just as clearly present as




Figs. 1–5. Vessel elements of *Dicranopteris linearis* roots. **1.** Perforation plates of vessels; pit membranes of lateral walls are visible below the perforation plate, center, and to the left of the perforation plate. **2.** Perforations traversed by slender diagonal strands of secondary wall material. **3.** Narrower perforation (left) in which a remnant pit membrane containing porosities is present. **4.** Vessel with perforations traversed by wide diagonal bars of secondary wall material. **5.** Vessels with a few lateral wall pit membranes (below, left of center; axial striations visible in pit membranes) and a few perforations traversed by diagonal bands of secondary wall material. Scale bars in Figs. 1–2, 4–5 = 10 μm; bar in Fig. 3 = 3 μm.




Figs. 6–10. Vessel elements of *Dicranopteris linearis* stems. **6.** Central portion of a vessel element; lateral walls have numerous facets and weakly differentiated perforations. **7.** Perforation plate (center); lateral walls with pit membranes at left. **8.** Portions of perforations with thin porose pit membrane remnants. **9.** Central portion of a lateral perforation plate; fusion among bars at top. **10.** Vessel element (left) in which two facets show lateral wall pits (below) plus perforations (upper two-thirds). Scale bars in Figs. 6–7, 9–10 = 10 μm; bar in Fig. 8 = 3 μm.

those of Polypodiaceae or Pteridaceae. We believe that the presence of vessels may not be a reliable indicator of phylogenetic position among ferns. Ferns in habitats with ecological extremes do appear to have greater specialization of vessel elements, as shown by *Marsilea* (White, 1961), *Pteridium* (Carlquist and Schneider, 1997a), and *Woodsia* (comparisons within the genus; Carlquist and Schneider, in press). Presence of vessels in *Dicranopteris* indicates that vessels have evolved in ferns in habitats with only moderate degrees of seasonality. Thus, ferns will provide significant comparisons to dicotyledons and monocotyledons, in which origin of vessels and degree of specialization of vessel elements are closely keyed to shifts from mesic habitats into more highly seasonal habitats (Carlquist, 1975).

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