

UNICELL ONTOGENY AND PHYLOGENY: EXAMPLES FROM THE DIATOMS

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Introduction

Systematists have recently taken a renewed interest in ontogenetic data and its value as an estimator of phylogeny. At least two main areas of interest have become apparent in this regard. The first concerns overall correspondence between ontogenetic sequences and phylogeny, as exemplified by the work of Løvtrup (1978, 1984, 1986). The second concerns the use of ontogenetic transformations in determining polarity of particular character states. Nelson (1978, see also Nelson and Platnick 1981) has restated Haeckel's biogenetic law in Von Baerian terms. The ontogeny criterion suggests that:

“Given an ontogenetic character transformation, from a character observed to be more general to a character observed to be less general, the more general character is primitive and the less general advanced.”

(Nelson and Platnick 1981, p.332).

Much of the recent criticism of the ontogenetic criterion has centered around its applicability and generality in phylogenetic reconstruction (Rieppel, 1979; de Jong, 1980; Stevens, 1980; Brooks and Wiley, 1985; Kluge, 1985; Kluge and Strauss, 1985; Weston, 1988). The merits of these criticisms, in general, are not the topic of discussion here. Instead, we turn to a point raised by Kluge (1985), who questioned the general applicability of Nelson's biogenetic law, suggesting that prokaryotes and eukaryotic unicells “may be without ontogeny” and thus are not subject to the ontogeny criterion. To this point Nelson (1985, p. 40) has offered only that “the organs and organisms without ontogeny are irrelevant.” However, as Blackmore (1986) has recently pointed out, all organisms must have ontogenies. The purpose of this paper is to present further evidence of unicell ontogeny, and demonstrate that ontogenetic transformations can be identified during morphogenesis of the cell, as well as between states in the life cycle.

Unicell Ontogeny as Exemplified by Diatoms

The notion of ontogenetic transformations occurring in unicells is not new. Von Gelei (1950) and Hadzi (1952) understood the relationship between ontogeny and phylogeny in protists, although specific examples had been described prior to their work (Chatton 1942; Chatton and Lwoff 1935; Faure-Fremont 1950; see Corliss 1968, for a broader historical perspective and an extensive bibliography.

Gould (1977, p. 483), with reference to classical embryology, defines ontogeny as: “The life history of an individual, both embryonic and post-natal.” In general, ontogeny may be understood as the process of development at each stage of the life-cycle, and the development of one stage from its precursor. In multicellular organisms this process is largely a feature of cell division and tissue specialization and differentiation. Yet Gould's embryological definition, which essentially envisages ontogeny as the entire life cycle

of an organism, can be extended to unicells. Consider the life history of a diatom (Division: Bacillariophyta) as summarized in Figure 1. Diploid vegetative cells, composed of cytoplasm contained in siliceous, bipartite frustules undergo mitosis where mitotic division is the precursor for production of a new valve (Geitler 1963). The series of events comprising mitosis, including assembly, activity and degradation of the spindle, as well as migration of daughter nuclei, were observed and described by Lauterborn (1896) using light microscopy and recently confirmed with electron microscopy (e.g. Tippit and Pickett-Heaps, 1977; Pickett-Heaps et al., 1975, 1982, 1984; Pickett-Heaps and Tippit, 1978). Differences in the sequence of events observed during mitosis have a phylogenetic basis. For example, the taxonomic distinctions between the genera *Hantzschia* and *Nitzschia* have been shown to be the result of differences in the migration of post-mitotic daughter nuclei and subsequent morphogenesis (Pickett-Heaps et al. 1980a, b; Pickett-Heaps 1983, see below).

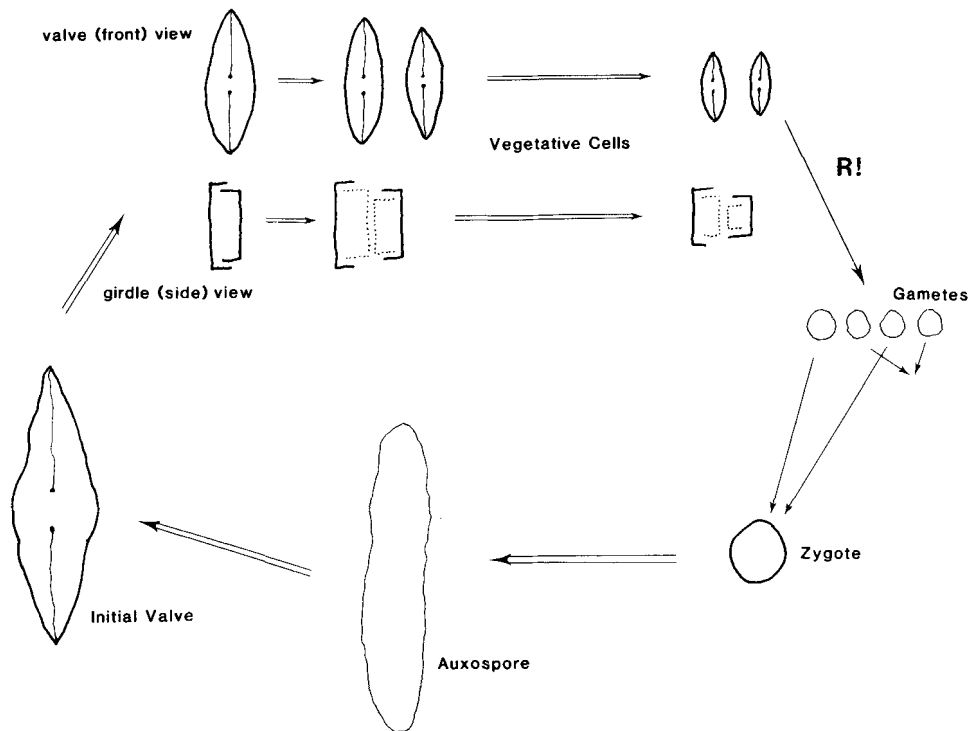


Fig. 1. Generalized life history of diatoms. Double lines indicate diploid phase, single lines indicate haploid phase. R! indicates occurrence of meiosis. See text for description.

During the "growth" cycle of vegetative cell division, daughter valves are produced that are more or less identical to those of the parent. Structure is so faithfully reproduced in the diatoms that they have served as test objects for determining the power of light and electron microscopes. The process of valve morphogenesis has been investigated in both pennate and centric types (for a recent review see Crawford and Schmid, 1986). In pennate diatoms, the silicification sequence begins with the production of a central

sternum, and is followed by the formation of transapical ribs (Chiappino and Volcani 1977; Schmid 1979, 1980; Blank and Sullivan 1983). Williams (1985) has noted that the costae found in the genera *Diatoma* and *Meridion* develop through an expansion of the more general condition of transapical ribs. In the centric diatoms, valve morphogenesis has been reported to be centrifugal (Schmid and Schulz 1979; Schnepf et al., 1980), or centripetal (Reimann 1960). The phylogenetic significance of the two morphogenetic pathways found in the centric diatoms is uncertain, as both types may occur in different species of the same genus, as well as in different genera. Also, the morphogenetic sequences involved in the formation of specialized siliceous organelles have been described (Li and Volcani, 1985b). In all cases an orderly, progressive interaction of precursor subunits has been shown to produce the complex structure of diatom valves (see also Schmid et al., 1981; Li and Volcani 1984, 1985a). The way these subunits are brought together and ordered through mitosis and cell morphogenesis is part of ontogeny. Compared to multicellular organisms, the only difference is one of scale. Instead of comparative homologies being identified at the organ/tissue level, we recognize homologies at the molecular/organelar/process level. During vegetative cell division the daughter cells are smaller than the parents, due to physical constraints imposed by rigid silica frustules. Thus, with the continued "growth" a cell line becomes progressively smaller (the MacDonald-Pfizer rule; see Hustedt, 1930; Geitler, 1932; Round, 1972). This size diminution series may be accompanied by allometric changes in structure and shape (e.g. Geitler, 1932; Stoermer and Ladewski, 1982; Stoermer et al., 1986).

During the course of size diminution, a critical size may be reached which triggers sexual reproduction (Geitler 1935; Drebes 1977). Sexual reproduction is realized in the diatoms by gametogenesis via meiosis and subsequent syngamy. The work of Manton et al. (1968, 1969, 1970a, b) has described the ultrastructural events which occur during gametogenesis. The diversity of patterns of both meiotic divisions (Steinecke 1931, Geitler 1973) and gamete migration (Geitler, 1973) have been documented for many taxa. Following syngamy, the non-siliceous, diploid zygote enlarges greatly to produce an auxospore. The auxospore restores the cell line to its maximum size. Auxospores may become encased in siliceous wrappings known as perizonia (Von Stosch, 1982), after which the first siliceous valves are laid down. In most cases the initial valves look quite unlike the "normal" frustule. Subsequent divisions and valve production return the cell line to its vegetative state. This summarizes the life history of many types of diatoms (most marine and freshwater pennates, and most freshwater centrics), but a few taxa, mostly marine centrics, may produce resting spores. Resting spores are produced with a change in environmental conditions, during the vegetative phase of the life cycle, and may or may not resemble vegetative cells (for a recent review see Hargraves and French, 1983).

The gametic life history of diatoms is not unlike the life history of many animals, so that ontogenetic transformations can be identified and treated in multicellular organisms. With regard to overall life cycle stages, gametogenesis, zygote formation, initial valve production, and, because of the siliceous valves, products of subsequent divisions can be identified. Unlike most organisms whose original cells are lost through continuous division and differentiation, siliceous valves of diatoms, and the ontogenetic precedence indicated by size (larger cells are earlier, smaller cells later), preserve a step-wise record of a cell line. The changes which occur between the zygote and smallest (oldest) cells in diatoms represent ontogenetic transformations that are totally analagous to those in "higher" organisms.

Thus, we can identify ontogenetic transformations at two levels; at the level of subcellular development at a particular stage in the life history (mitosis, morphogenesis, gametogenesis, etc.), and at a higher level between different stages in the life cycle. Information from these transformations can be applied to questions of phylogenetic relationships and polarity of character states.

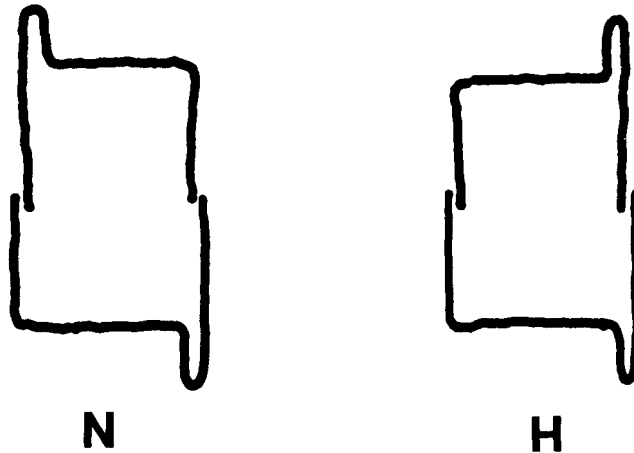


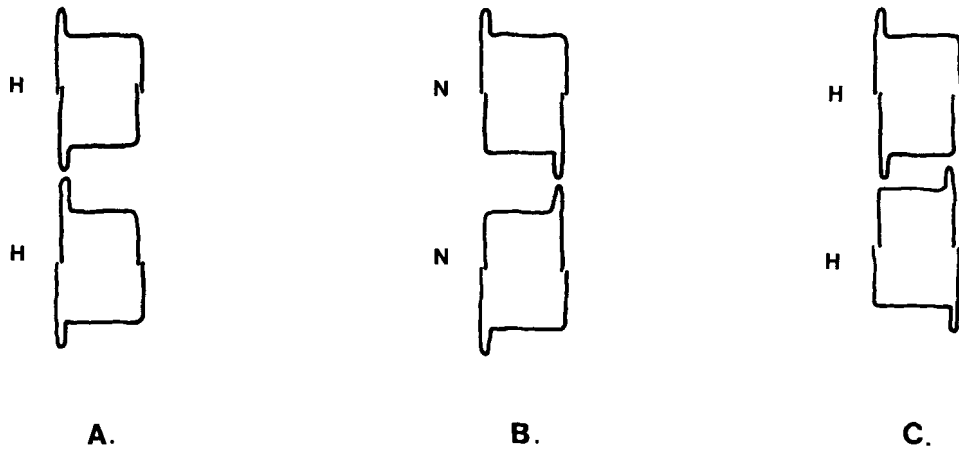
Fig. 2. Schematic representation of frustule of *Hantzschia* (H) and *Nitzschia* (N), illustrating differences in the position of the elevated keel.

Ontogenetic Data in Diatom Systematics

TAXONOMIC DISTINCTIONS BETWEEN *HANTZSCHIA* AND *NITZSCHIA*

Separation of *Hantzschia* and *Nitzschia* has been based on the position of the elevated raphe system; in *Hantzschia* the raphe system of each valve lies on the same side, while in *Nitzschia* the raphe systems lie diagonally opposed (Fig. 2). Descriptions of hantzschoid symmetry in frustules of some *Nitzschia* species (Lauritis et al., 1967; Geitler, 1968; Mann, 1980) apparently support previous doubts about the separation of the two genera (e.g. Karsten 1928). However, an elegant marriage of complimentary light and electron microscope observations has yielded a distinction between *Hantzschia* and *Nitzschia* based not on valve features, but on the fate of post-mitotic nuclei. Mann (1977; 1980) summarized work dealing with products of division in both genera, including those species of *Nitzschia* that produce hantzschoid valves. Species of *Hantzschia* always produce hantzschoid valves, with the two daughter frustules being positioned such that all four raphe systems (two per frustule) are located on the same side (Fig. 3a). In *Nitzschia* species, frustules with nitzschoid symmetry only may be produced (Fig. 3b), or in species that produce hantzschoid frustules, the daughter frustules have raphe systems positioned on opposite sides (Fig. 3c). In each of these hantzschoid frustules, the next division produces a hantzschoid and a nitzschoid frustule. Pickett-Heaps (1983) has summarized work on the genus *Hantzschia*, as well as providing additional evidence on ultrastructural features of mitosis and morphogenesis in species of *Nitzschia*. In *Hantzschia*, post-mitotic nuclei migrate from the center of the valve to the same side (Fig. 4a), while in *Nitzschia* migration of daughter nuclei is to opposite sides (Fig. 4b, c). Which of the two is the derived state, is yet to be determined. Fate of the post-mitotic nuclei determines whether hantzschoid or nitzschoid symmetry will result, since, morphogenesis of the raphe system occurs on the side of the valve containing the nucleus. From these observations two conclusions regarding the distinction of the two genera can be made. First, the hantzschoid symmetry seen in the two genera is not homologous, with the similarities in morphology being the result of different patterns of post mitotic nuclear

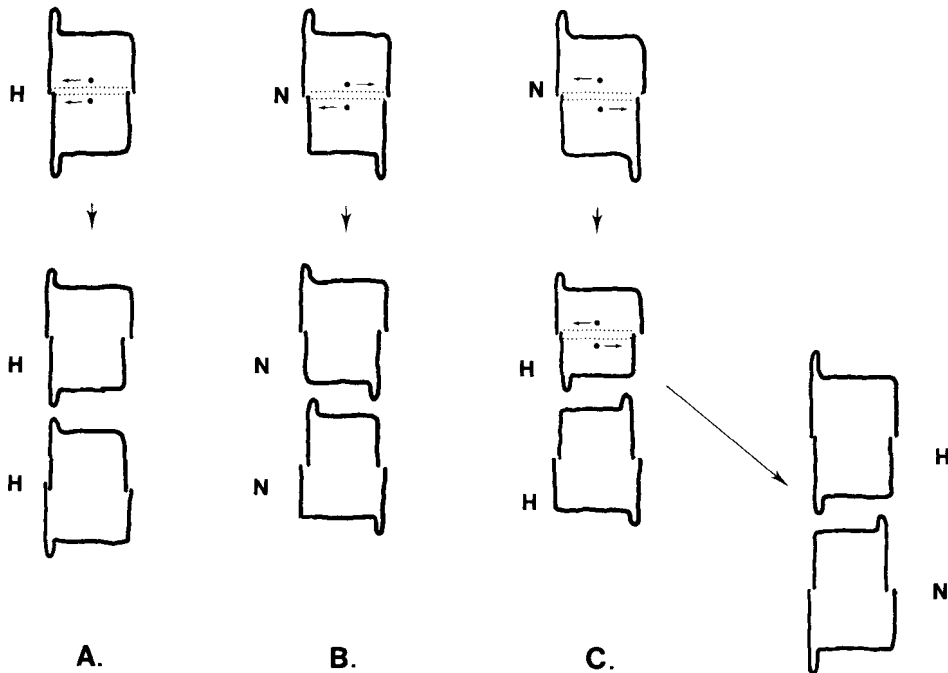
migration, and second, migration of post-mitotic nuclei appears to be a derived character state shared between the sister taxa *Hantzschia* and *Nitzschia*, with each genus distinguished by its characteristic pattern (Fig. 5).



Figs. 3a-c. Schematic representation of frustules resulting from mitotic division in *Hantzschia* (A), *Nitzschia* (B), and *Nitzschia* species that produce hantzschoid frustules (C). H=hantzschoid, N=nitzschoid.

RELATIONSHIPS OF THE MONORAPHID AND BIRAPHID DIATOMS

Within the pennate diatoms, there are two groups which are distinguished by the presence or absence of a raphe (Smith 1872). Within the raphe-bearing group, two subgroups have been distinguished; the biraphid diatoms which have raphe slits through both valves of the frustule, and the monoraphid diatoms which have a raphe on one valve, the other being rapheless (Hustedt, 1930; Patrick and Reimer, 1966). Since the raphe in these two groups is considered homologous (Mann, 1983; but see Simonsen, 1979), which of the two conditions is derived? The outgroup method of determining character state polarity (Watrous and Wheeler, 1981; Maddison et al., 1984; see also Kociolek, 1986, for its application to diatom systematics) is of little help for determining the polarity of the monoraphid and biraphid conditions, because a raphe is lacking in araphid pennate diatoms (Figs 6a, b). Ontogenetic information gathered by Mann (1982) on morphogenesis in the monoraphid genus *Cocconeis* indicates that biraphid frustules are produced initially. As morphogenesis of the valves progresses, silica is deposited in the raphe of one valve, filling the slit with silica and producing a monoraphid frustule. In biraphid types, frustules begin and remain biraphid throughout morphogenesis (Chiappino and Volcani, 1977; Schmid 1979). Considering the ontogenetic transformations with regard to raphe number, it is concluded that the biraphid condition is primitive and the monoraphid derived (Mann 1983). This interpretation helps explain both the "ghost" raphes noted on the rapheless valves of some monoraphid species (Simonsen 1979; Andrews 1981; Holmes et al. 1982), and the small holes at the apices of rapheless valves in species of the monoraphid genus *Achmanthes* (LeCohu and Maillard 1983), as incompletely filled raphe slits. Kociolek and Stoermer (1986) have analyzed evidence which supports the proposition of Cleve (1895) that the monoraphid condition has developed in several different lineages of biraphid diatoms.



Figs. 4a-c. Schematic representations of patterns of postmitotic nuclear migration and resulting frustules in *Hantzschia* (a), and *Nitzschia* species that produce hantzschoid frustules (c). Frustules resulting from a second mitotic division in this latter group are also depicted. H=hantzschoid, N=nitzschoid.

CHARACTER POLARITY OF SILICEOUS STRUCTURES AND RELATIONSHIPS OF DIATOMS AND SYNURACEAN CHRYSOPHYTES.

Of the chlorophyll-C containing algae that utilize silica in some part of their life histories, diatoms and scale-bearing Synuracean chrysophytes are thought to be sister taxa (Round, 1981; Round and Crawford, 1981; Cavalier-Smith, 1986). The Synuracean chrysophytes bear many siliceous scales on their vegetative cells, while diatoms have siliceous bipartite valves linked by girdle bands. Considering these two groups as sister taxa, and the incorporation of silica into vegetative cells as homologous, it is of interest to know the polarity of scales and valves. As in the case of the monoraphid diatoms, outgroup analysis is not helpful because potential outgroups lack siliceous scales and valves (Hibberd, 1979; Round, 1981).

In their study of the phylogeny of the diatoms, Round and Crawford (1981) noted differences in structure between stages in the life cycle of some centric species. In auxospore valves, members of the genera *Melosira* and *Biddulphia* were observed to possess silica scales very similar in appearance to those found in some species of Synuracean chrysophytes (Figs 11-20 in Round and Crawford 1981). In "normal" cells of these centrals, typical valves with girdle bands are produced. These observations suggest an ontogenetic transformation from scales to valves, and led Round and Crawford (1981) to hypothesize that the ancestral or "Ur-Diatom" was scale-bearing, and that the valves of diatoms represent evolutionary modifications of scales.

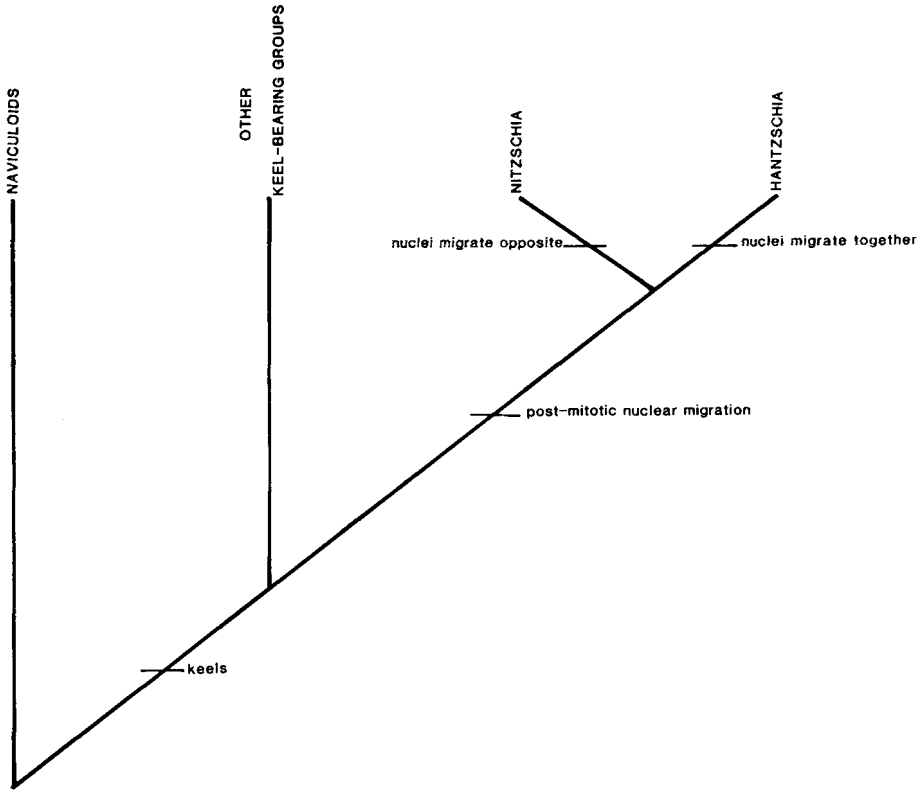
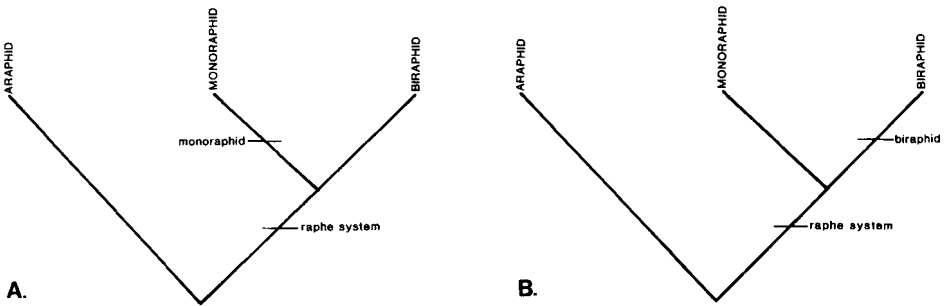


Fig. 5. Phylogenetic hypothesis concerning relationships between *Nitzschia*, *Hantzschia* and other keel-bearing diatoms. Horizontal black bars represent derived (apomorphic) conditions.



Figs. 6A, B. Alternative hypotheses concerning polarity of monoraphid and biraphid character states. Horizontal black bars represent apomorphic conditions. See text for explanation.

Conclusions

The life cycle and morphogenesis of unicells have distinct ontogenies, just as in multicellular organisms. Furthermore, in unicellular, as in multicellular life cycles, ontogenetic transformations can be identified and used in determining polarity of character states. Although some unicells may have complicated life histories that make difficult delineation of the beginning and end of an ontogeny, the process of morphogenesis, and the life histories of many unicells, make protists appropriate organisms for investigation and application of ontogenetic information.

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