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## Root morphology, anatomy and mycotrophy of the achlorophyllous *Voyria aphylla* (Jacq.) Pers. (Gentianaceae)

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**Abstract** Roots of *Voyria aphylla* only develop hairs where roots of neighboring plants or organic litter are attached. Fungal penetration occurs almost exclusively at these root-to-root attachments. The ecological significance of these immediate hyphal bridges for achlorophyllous plants is discussed. The morphological and anatomical features of *V. aphylla* roots and its Paris-type arbuscular mycorrhiza (AM) appear to be transitional between those of *V. truncata* and *V. tenella*. A hypothetical evolutionary progression of AM and its significance for the development of mycoheterotrophy is proposed.

**Key words** *Voyria* · Gentianaceae · Root structures · Arbuscular mycorrhiza · Mycoheterotrophy

### Introduction

The achlorophyllous *Voyria aphylla* (Jacq.) Pers. (Gentianaceae) is widespread in the neotropics. It thrives in rain forests and in savannas, is found in leaf mold and on decaying trees as well as in white sand, from sea level to 1800 m (Maas and Ruyters 1986). Hence, it is not surprising that *V. aphylla* is the longest known to science of its genus (Jacquin 1763; Aublet 1775; Persoon 1805) and the epiterranean parts have been well described (e.g. Lamarck 1786; Splitgerber 1840; Progel 1865; Gilg 1897; Jonker 1936; Raynal 1967; Eliás and Robyns 1975; Maas and Ruyters 1986; Pringle 1995). However, despite the interest in the mycorrhizas of achlorophyllous plants, in particular their source of car-

bon, only Johow (1889) provided a short description of the roots of *V. aphylla*. In general, data on mycoheterotrophic plants other than orchids and *Monotropa* are scarce (Hadley 1986; Leake 1994; Smith and Smith 1997; Smith and Read 1997). Recent studies on *Voyria truncata* (Standl.) Standl. & Steyerl. (Imhof and Weber 1997), *Voyria tenella* Hook. (Imhof 1997), and the Triuridaceae *Triuris hyalina* Miers (Imhof 1999) revealed remarkably distinct patterns of presumably arbuscular mycorrhizas (AM), encouraging further investigation. Since the morphology and anatomy of the epiterranean parts of *V. aphylla* suggest that it represents an intermediate stage between *V. truncata* and *V. tenella* (Welle 1986; Imhof et al. 1994), the mycorrhiza of *V. aphylla* was studied here to collect further data for genus taxonomy and to elucidate a putative mycorrhizal evolution line.

### Materials and methods

In February through April 1995, ca. 10 plants of *V. aphylla* (Jacq.) Pers. were collected at anthesis in Zanderji/Suriname from a light secondary forest south of the airport [reference specimens at the Herbariums of Paramaribo/Suriname (No. 17265) and Stephan Imhof (No. 180)]. Another 20 plants each were gathered 8 km south of Bartica/Guyana, from a pine forest on sandy soil close to the airstrip [Herbarium of Stephan Imhof (No. 179)], and from a rainforest in Estado Bolívar/Venezuela, coordinates N05°57'44"/W61°30'14", ca. 700 m above sea level (No. 175). The plants were dug out carefully, immediately fixed in formalin (37%);propionic acid:50% ethanol (0.5:0.5:9) and later transferred into 70% ethanol for storage. After dehydration in ascending butanol- or ethanol-series, root samples of ca. 5 randomly selected specimens from each location were embedded in paraffin (Merck, melting point 56–58 °C), Unicryl (British Biocell Int.), or Technovit 7100 (Heraeus Kulzer, see Igersheim and Cichocki 1995). The hardened, embedded objects were cut into 2–15 µm sections (Reichert/Jung Supercut 2065) and stained with either astrablue/safranin/auramine for color-contrasted sections (paraffin sections) or 1% toluidine blue O-solution (Unicryl, Technovit 7100 sections) after Krause (1927) and preserved in corbit-balsam as permanent slides. Suberin and cutin were detected on freehand sections of fixed material using a saturated solution of sudan IV in 70% ethanol, differentiated with glycerol (Johansen 1940).

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## Results and discussion

Roots of *V. aphylla* are 0.2–0.5 mm thick, brittle, runner-like and branched, building a more or less horizontal root net mostly within decaying litter (Fig. 1). The extent of the root net was difficult to determine but probably did not exceed a total length of 0.5 m, side roots included. Shoots develop endogenously in the axils of side roots. Clumps of radiating roots were found at the origin of such offshoots (Fig. 2). Compared to the rather extended root system of *V. truncata* (see Imhof et al. 1994), the roots of *V. aphylla* are smaller in size and extent, appearing like a miniature version of the former. On the other hand, the intensified root formation at the points where the root offshoots arise is suggestive of the morningstar-type of root system of *V. tenella* (Johow 1885; Imhof et al. 1994).

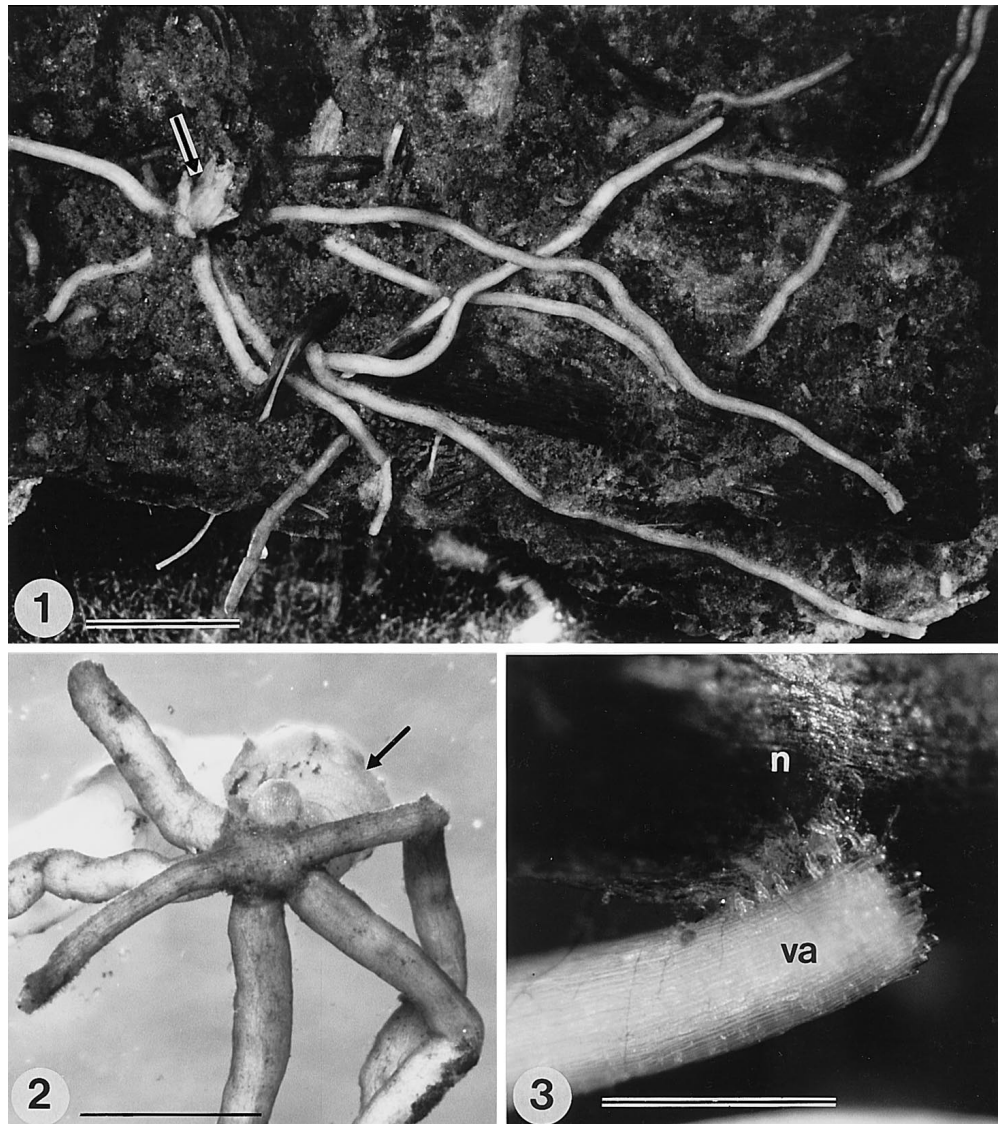
According to Baylis (1972, 1975), the lack of or reduction in root hairs is strongly correlated with plant

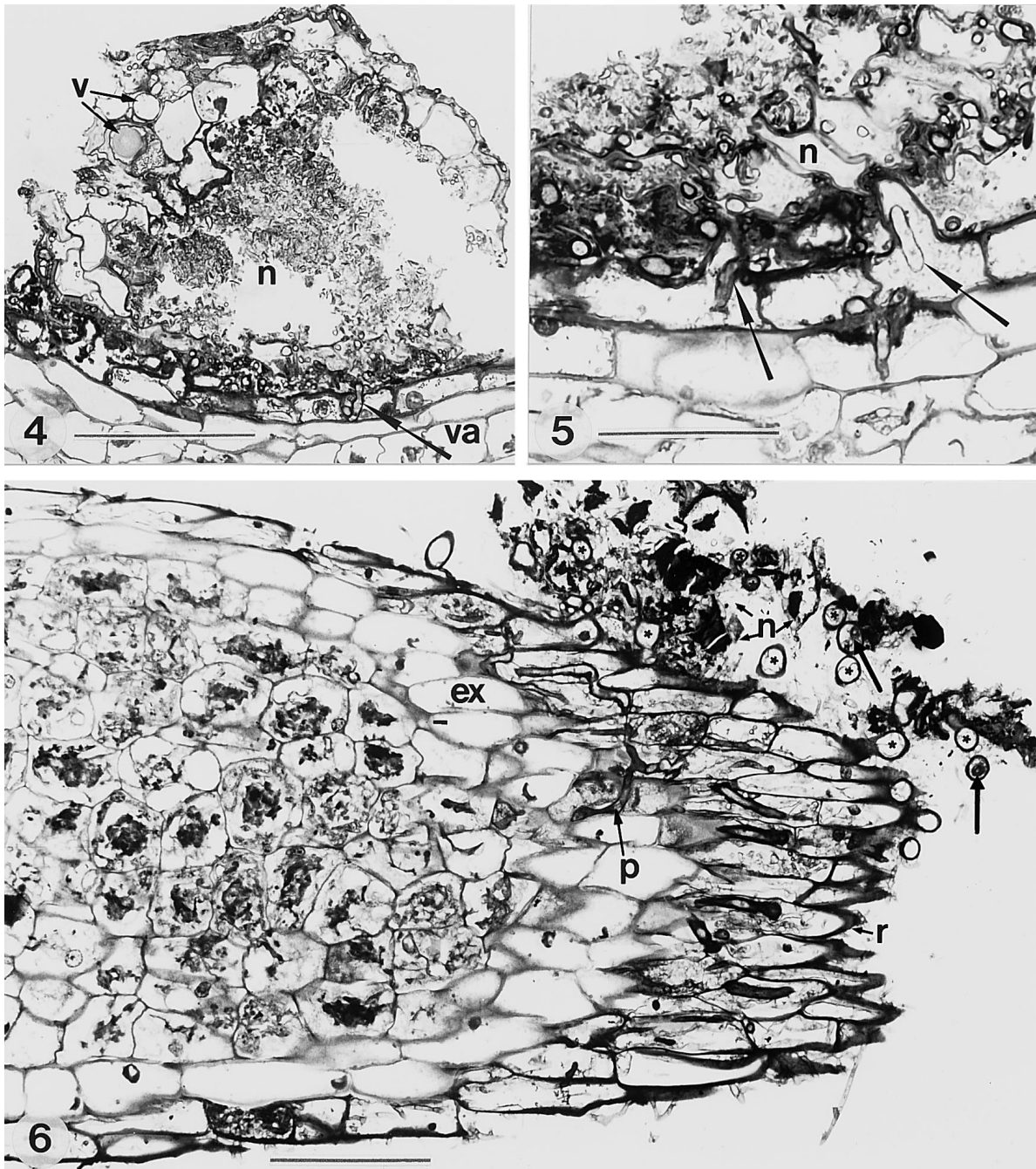
dependency on mycorrhiza. Roots of mycoheterotrophic *V. truncata* and *V. tenella* are entirely hairless (Imhof and Weber 1997; Imhof 1997). For the most part, roots of *V. aphylla* were also found to be hairless, except at the points where roots of neighboring plants or organic litter were attached (Fig. 3). Mycorrhizal penetration occurred almost exclusively at such root-to-root connections, building immediate hyphal bridges between *V. aphylla* and neighboring roots (Fig. 4). The root hairs were often used as entrance cells (Figs. 5, 6) and thus the hairs may play a role in the root attachment or penetration processes. Weber (1979, 1981) reported similar rhizome hair tufts at root connections to the rhizome of *Corallorhiza trifida* (Orchidaceae) and discussed an evolutionary pathway towards a parasitic organ (see also Imhof and Weber 1997). Newman (1988) noted the lack of evidence for hyphal links and net carbon flow between species under natural conditions, and stressed the uncertain ecological significance of mycorrhizal bridges. However, in the three *Voyria*

**Fig. 1** Root system of *Voyria aphylla* closely attached to a clump of organic material. Arrow indicates the base of a root offshoot; bar 3 mm.

**Fig. 2** Root formation close to a root offshoot (arrow) of *V. aphylla*, bar 2 mm.

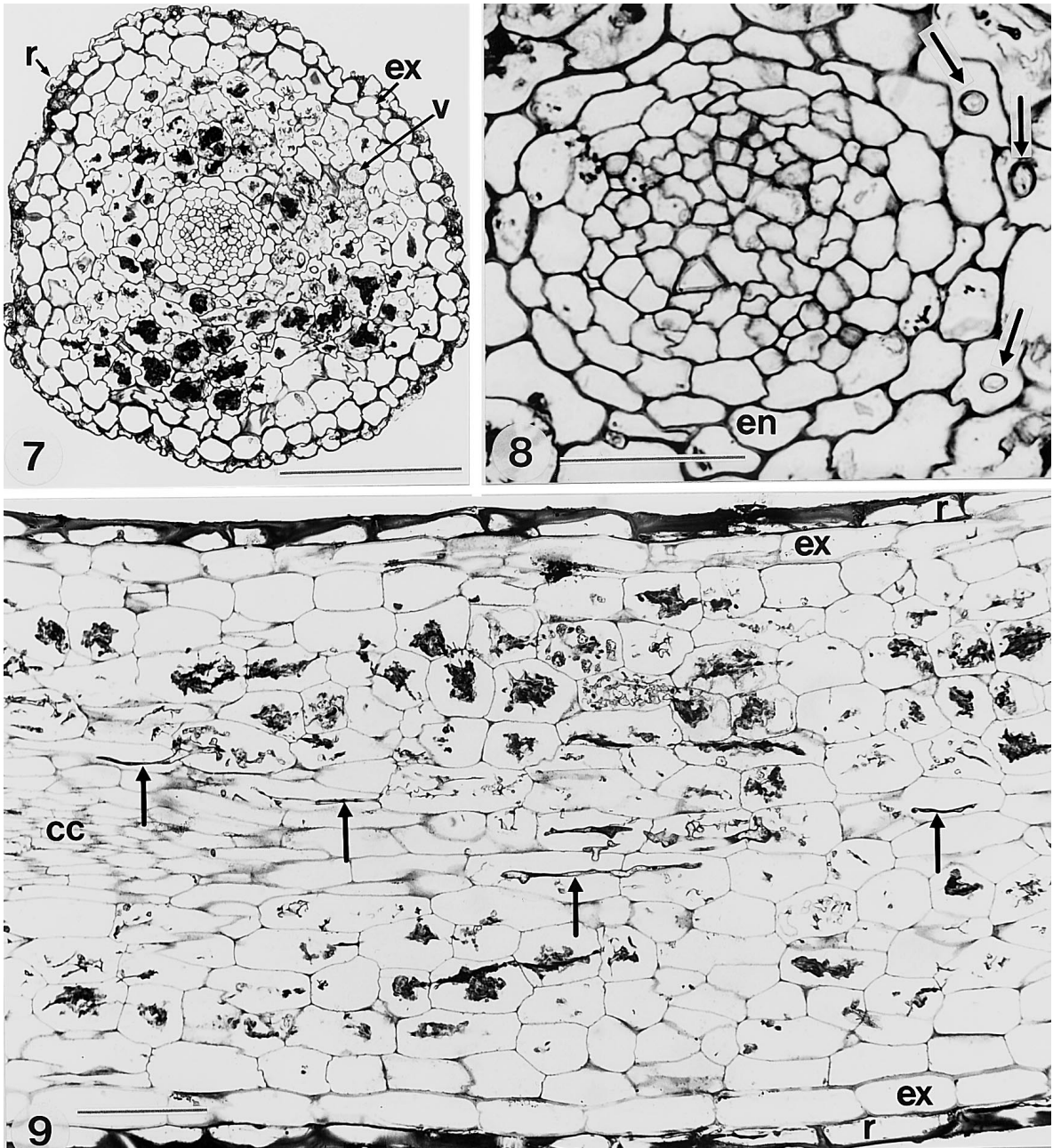
**Fig. 3** Root hairs of *V. aphylla* (va) in contact with the root of a neighboring plant (n); bar 0.5 mm





**Fig. 4** Immediate hyphal bridge (*arrow*) between a largely decomposed neighboring plant root (*n*) with vesicles (*v*) and a root of *V. aphylla* (*va*); *bar* 200  $\mu\text{m}$ . **Fig. 5** Hyphae (*arrows*) in root hairs of *V. aphylla* attached to a neighboring root (*n*); *bar* 50  $\mu\text{m}$ . **Fig. 6** Tangential section through the rhizodermis (*r*), exodermis (*ex*), and root cortex of *V. aphylla*. Note the straight, thick hyphae in the rhizodermis, and the fungus rarely penetrating the exodermis (*p*). Root hairs (\*) in cross section are seen where fragments of neighboring roots (*n*) are still present. Two root hairs contain hyphae (*arrows*); *bar* 100  $\mu\text{m}$

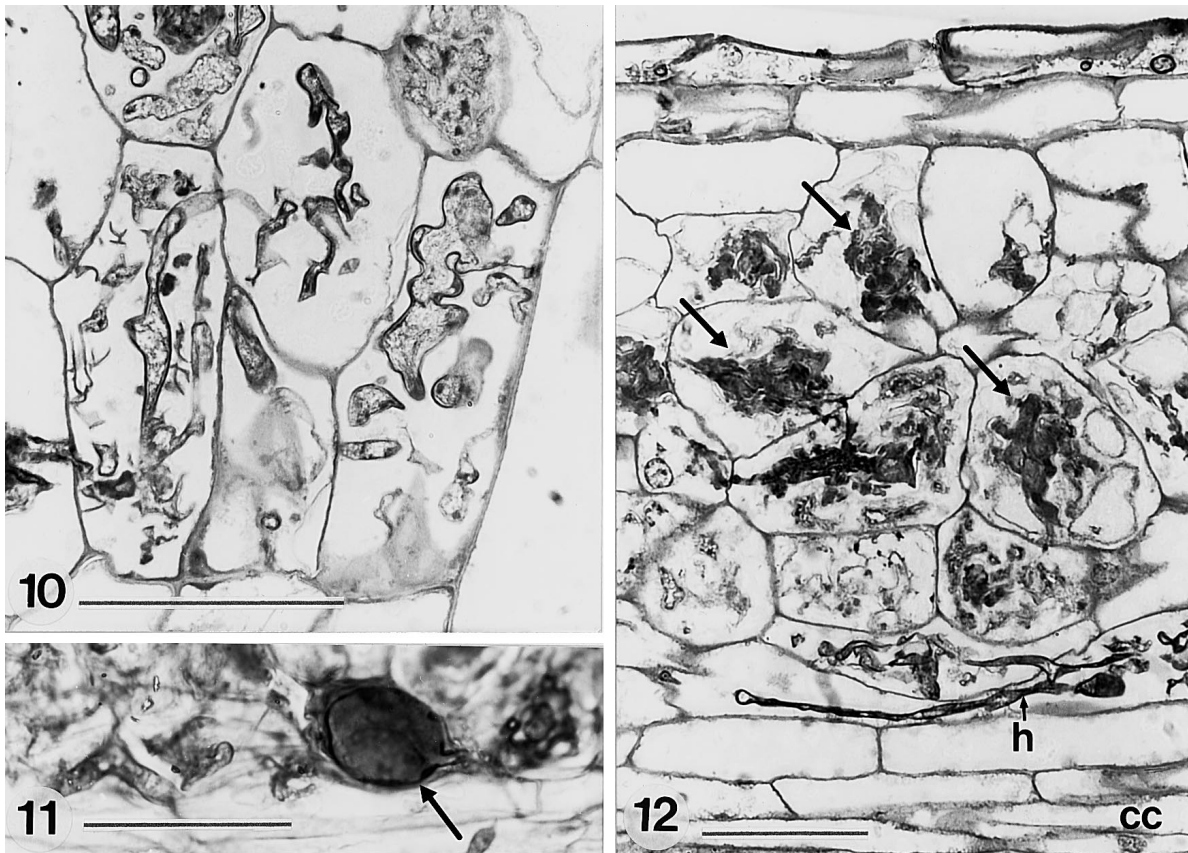
species investigated, all taken from the wild, immediate hyphal bridges were verified between *Voyria* roots and roots of neighboring plants. Because saprophytic capacity has not been detected in higher plants so far, a net carbon flow may be inferred for achlorophyllous species. A neighboring root attached to a root of *V. truncata* was shown to be decomposed only at the immediate contact area (see Fig. 11 in Imhof and Weber 1997), which suggests the possibility of carbon exchange. Because fungal penetration away from root attachments was rare, the hyphal bridge may be an essential pathway for the flow of carbon to *Voyria* species, in which case hyphal links are of ecological significance.



**Fig. 7** Cross section of a root of *V. aphylla* (*r* partly decayed rhizodermis, *ex* exodermis, *v* vesicle); bar 200  $\mu\text{m}$ . **Fig. 8** Cross section of the central cylinder of *V. aphylla* (*en* endodermis, *arrows* cross sections of straight hyphae in the inner cortex layer); bar 50  $\mu\text{m}$ . **Fig. 9** Longitudinal section of a root of *V. aphylla* with straight hyphae (*arrows*) close to the central cylinder (*cc*) (*r* rhizodermis, *ex* exodermis); bar 100  $\mu\text{m}$

The rhizodermal cells of *V. aphylla* were found to be thick-walled, ephemeral and with little or no reaction to sudan IV. The cells of the occasionally 2-layered exodermis were also relatively thick-walled (Figs. 5–7) with a suberin lamella. The cortex parenchyma consisted of 3–6 layers of more or less isodiametric cells with

only occasional intercellular spaces (Figs. 7, 9). The cell walls of the endodermis were slightly thicker than those of the parenchyma cells (Figs. 7, 8) and had a suberin lamella. The central cylinder was composed of a pericycle, phloem, xylem and some parenchymatous cells (Fig. 8). Thick-walled hyphae, with diameters of up to 10  $\mu\text{m}$  (Fig. 6), often grew straight and somewhat longitudinally along the root within the rhizodermis (Fig. 6), as observed in longitudinal sections. The exodermis was only penetrated intracellularly close to root attachments (Figs. 4–6). Penetration points were characterized by an intense yellow stain with auramine (not shown), indicating an altered composition. The penetration process resembles that in *V. truncata* (Imhof and Weber 1997), but anatomical features of specific



**Fig. 10** Cells of the root cortex of *V. aphylla* containing coils of distorted hyphae; bar 50  $\mu\text{m}$ . **Fig. 11** Vesicle (arrow) in a root of *V. aphylla*; bar 50  $\mu\text{m}$ . **Fig. 12** Hypha (h) colonizing the inner cortex. Coils in the outer cortex have already degenerated to amorphous clumps (arrows) (cc central cylinder); bar 50  $\mu\text{m}$

passage cells observed in *V. truncata*, like short cells or wall thickenings (Guttenberg 1968), were lacking. Having crossed the exodermis, the fungus proceeds deeper into the root cortex, forming hyphal coils which often showed distortions or irregular swellings (Fig. 10) and eventually became amorphous clumps (Figs. 6, 9, 12). Hyphal diameter was 5–7  $\mu\text{m}$  but greater (15  $\mu\text{m}$ ) at swellings. Hyphae in the cortex parenchyma frequently branched and the fungal infection spread directly between neighboring cortex cells (Figs. 10, 12). Vesicles were sometimes found in the rhizodermis and the root cortex of *V. aphylla* (Figs. 4, 11), but no finely branched arbuscules were observed. The endodermis was never penetrated. However, in the innermost cortex adjacent to the endodermis, hyphae became less coiled and less swollen (Figs. 8, 9, 12). This mycorrhizal pattern resembles the ‘intraradical fungus garden’ of *V. tenella* (Imhof 1997), although the distinction between inner and outer cortical hyphae is much more pronounced in *V. tenella*.

In accordance with the morphology and anatomy of stems and flowers (Johow 1889; Solereder 1908; Welle

1986; Maas and Ruyters 1986; see Leake 1994, Table 2 for a synopsis), the subterranean features of *V. aphylla* suggest an intermediate position for this species within the genus. Interestingly, this also holds for the morphological characteristics of the mycorrhiza. Penetration of the exodermis and hyphal coils in the cortex are similar to those observed in *V. truncata* (Imhof and Weber 1997), whereas the hyphal swellings and the distribution pattern of the fungus in the inner cortex are similar to mycorrhiza of *V. tenella* (Imhof 1997). The mycorrhiza of *V. aphylla* corresponds to the ‘Paris-type’ AM previously described for other species of the Gentianaceae (e.g. Jeanmougin and Gianinazzi-Pearson 1982; Weber 1984; Kühn and Weber 1986; Demuth and Weber 1990). Of the two morphological types described for AM (Gallaud 1905), the ‘Arum-type’ predominantly shows intercellular hyphal growth with intracellular arbuscule formation, and the ‘Paris-type’ develops intracellular hyphal coils. Brundrett and Kendrick (1990) suggested that the Paris-type is the best mycorrhizal strategy for plants under high-stress and low-nutrient conditions, because the slower colony formation draws less energy from the plant while still reciprocally providing nutrients. Whilst Paris-type mycorrhiza may be more advantageous to plants than Arum-type in extreme conditions, the coiled hyphae could be a sign of a major control by the plant of fungal development (see Imhof and Weber 1997). This may go as far as digestion of the fungal matter in mycoheterotrophic plants. How-



ever, since in a given plant species, genus or family, AM morphology can be either *Paris*-type, intermediate, or *Arum*-type (Smith and Smith 1997), a phylogenetic interpretation seems to be more appropriate than a purely functional one.

The *Paris*-type has been proposed to be the more advanced form of AM (Weber et al. 1995). At the end of a line of morphological/anatomical reductions within the Gentianales from woody species (e.g. Asclepiadaceae and Apocynaceae), perennial, annual, and semi-chlorophyllous herbs (e.g. Gentianaceae) to achlorophyllous plants, the most extreme genus *Voyria* exclusively has *Paris*-type AM. The *Arum*-type occurs in Asclepiadaceae (Tiemann et al. 1994a) and some Apocynaceae (Weber et al. 1995), intermediate types have been found in *Periploca laevigata* (Untch and Weber 1995) and other Apocynaceae (Weber et al. 1995), as well as in some Menyanthaceae (Weber and Krämer 1994), and the *Paris*-type exists in some Apocynaceae (Weber et al. 1995), in chlorophyllous Gentianaceae (Gay et al. 1982; Jacquelinet-Jeanmougin and Gianinazzi-Pearson 1983; McGee 1985; Kühn and Weber 1986; Heymons 1989; Demuth and Weber 1990; Demuth 1993), Loganiaceae (Tiemann et al. 1994b) and Rubiaceae (Rath 1993). *V. truncata* was found to have a *Paris*-type AM without arbuscules (Imhof and Weber 1997) whilst *V. aphylla* shows a mycorrhizal pattern closer to that of *V. tenella* (Imhof 1997). Thus, the Gentianales may serve as a model for a putative evolutionary line of AM from Asclepiadaceae to *V. tenella*, with the Apocynaceae as an important transitional family. Interestingly, the woody genera *Hedera*, *Fatsia* and the hybrid of both (*Fatshedera*) in the Araliaceae also show an intermediate type of AM, whereas the morphologically more advanced *Panax ginseng* and *P. quinquefolius* develop the *Paris*-type (Whitbread et al. 1996; Zeuske et al. 1999).

Hence, the *Arum*-type seems to be the more ancient type of AM. Fossil records indicate that intercellular hyphal growth occurred in the earliest land plants (Kidston and Lang 1921), and Remy et al. (1994) reported both intercellular hyphae and intracellular arbuscules in the early Devonian *Aglaophyton major*, also suggesting that these ancient mycorrhizas were of the *Arum*-type. In contrast, Smith and Smith (1997) doubt the advanced character of the *Paris*-type due to its frequent occurrence in lower plants; however, the prothalli of lower plants often have to contend with deep-shaded habitats, and there may be a high evolutionary pressure for an efficient mycorrhiza. Moreover, intracellular hyphal growth may have been a prerequisite for the evolution of mycoheterotrophy. In fact, it is a characteristic common to all mycoheterotrophic plant species so far investigated (orchid, monotropoid, *Paris*-type AM) (Smith and Read 1997).

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