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The Xylariaceae: some ecological considerations

A. J. S. WHALLEY

Department of Biology, Liverpool Polytechnic, Byrom Street, Liverpool L3 3AF,
U. K.

Introduction

The Xylariaceae is an assemblage of sphaeriaceous genera, with obscure but apparently ancient common ancestry, which typically produce dark-coloured nonseptate ascospores in smooth perithecia embedded in stromata. Members of the family are found throughout the world and exhibit a diverse range of form including the massive sessile stromata of *Daldinia* CES. & de NOT., the erect long-stalked stromata characteristic of *Thamnomycetes* EHRENB., and the cylindrical, flat-topped form of *Camillea* FR. Although the majority inhabit wood others occur on litter and several genera are exclusive to dung. ROGERS (1979 a) recognises a central core of closely related genera consisting of *Hypoxyylon* BULL.: FR., *Xylaria* HILL ex SCHRENK, *Rosellinia* de NOT., *Poronia* WILLD., *Podosordaria* ELL. & HOLWAY, *Hypocopra* (FR.) KICKX, *Daldinia*, *Nummularia* TUL., *Kretzschmaria* FR., *Camillea*, and *Penzigia* SACC. Genera such as *Anthostomella* SACC., *Thamnomycetes* and *Entonaema* MÖLLER are accepted but their relationships with other xylariaceous genera are considered to be uncertain. ROGERS also stressed that although the family has received considerable attention in recent years, with interesting and useful data being obtained by electron microscopy, studies of cultural characteristics and anamorph form, the biological significance and ecological activities of most xylariaceous fungi under natural conditions are as obscure today as ever (ROGERS, 1979 a).

This is almost an echo of comments made concerning pyrenomycetes in general over twenty five years earlier (MUNK, 1957). It is these lesser-known aspects of the Xylariaceae which are the subject of this contribution in honour of Professor Emil MÜLLER, who is an outstanding student of the taxonomy, distribution and ecology of ascomycetes.

Distribution

It is well-known that the mapping of any fungal group is fraught with difficulties. The erratic fruiting behaviour as shown by seasonal flushes and the ephemeral nature of many species results in

scattered records often dependent on the presence of an interested party in the right place at the right time. Criticisms concerning identification, which has been suggested as throwing considerable doubt on the value of fungal mapping is a further complication (REID, 1975 a). Doubtful authenticity of many records used in the preparation of maps published under the auspices of the committee for mapping of macromycetes in Europe (LANGE, 1974) may even have resulted in misleading data (REID, 1975 b). These concerns, although partly true for the agarics, need not necessarily apply to mapping of lignicolous pyrenomycetes which are more permanent in nature and lend themselves more readily to the collection of voucher specimens for future reference. Probably of more significance is the general lack of mycological surveys in many parts of the world. BISBY (1933) stated 'mycologists have been able to map with accuracy the distribution of comparatively few fungi' and WOLF & WOLF (1947) stressed that 'vast portions of the earth's surface remain completely unexplored for fungi'. In discussing geographical distribution of fungi PIROZYNSKI (1965) pointed out that the commonly adopted approach is either to outline the occurrence of some better known species, or alternatively, to discuss the effect of various physical and biological factors on the distribution of particular fungi. In view of the scanty and incomplete records for most fungi PIROZYNSKI elected to follow the latter approach.

It is however rarely possible to dissociate these different factors since distribution of any fungal species is likely to be the result of a variety of interactions. Climate will affect host diversity and range and at a local level will influence the suitability of a particular habitat. Thus a suitable host might be present but temperature, water and other micro-environmental conditions may prevent its utilization by the fungus under consideration (BODDY, 1984).

Edaphic factors

Host selectivity

Many Xylariaceae can colonize a wide range of substrata and in relation to distribution the nutritional status of the host is probably not significant in relation to these species. *Hypoxylon rubiginosum* PERS.: FR. is truly cosmopolitan, not restricted by thermal zones, and occurs on a remarkably wide range of trees. It is apparently of limited occurrence only in the coniferous belt where it is an occasional inhabitant (MILLER, 1961). Chemical analysis of stromata suggest that the species consists of a number of different chemical races but whether these can be correlated with different host preferences is uncertain (WHALLEY & GREENHALGH, 1971). Similarly *Hypoxylon serpens* (PERS.: FR.) KICKX is found in most countries growing

on many kinds of wood, especially on old logs or stumps. *Hypoxylon sassafras* (SCHW.: FR.) CURT., although worldwide in distribution, is confined to wood of the Lauraceae, especially *Sassafras*, and is common wherever there is a suitable host. Sometimes as the geographical range of hosts decreases or as hosts become more localized so does the fungus and *Hypoxylon cohaerens* PERS.: FR., which is chiefly associated with *Fagus*, is restricted with its host to the north temperate zone. A similar pattern can be seen amongst agarics and *Oudemansiella mucida* (SCHRAD.: FR.) v. HÖHN. which usually inhabits *Fagus*, follows its host to its northern natural limit (LANGE, 1974). Surprisingly *H. cohaerens* is common in southern Norway but appears to be absent from northern England and Scotland although there is no shortage of *Fagus* there (WATLING & WHALLEY, 1977). Examples of host specificity are given in Table 1.

Certain species not only colonize highly specific substrata but do so under very exacting conditions. Thus *Hypoxylon udum* PERS.: FR., a native of the British Isles and Europe, is only found on *Quercus* and apparently only on decorticated wood which is highly rotted and usually water-sodden (WHALLEY, 1976; WHALLEY & WATLING, 1980 a). Similarly *Daldinia vernicosa* (SCHW.) CES. & de NOT. is found in Britain growing on *Ulex europaeus* L. but is invariably

Table 1: Examples of host selectivity

Fungi	Host
<i>Daldinia vernicosa</i> (SCHW.) CES. & de NOT.	<i>Ulex</i>
<i>Hypoxylon cohaerens</i> PERS.: FR.	<i>Fagus</i>
<i>H. cohaerens</i> var. <i>microsporium</i> ROGERS & CANDOUSSAU	<i>Quercus</i>
<i>H. confluens</i> (TODE.: FR.) WEST.	<i>Quercus</i>
<i>H. fragiforme</i> (PERS.: FR.) KICKX	<i>Fagus</i>
<i>H. fraxinophilum</i> POUZAR	<i>Fraxinus</i>
<i>H. investiens</i> var. <i>epiphaeum</i> (BERK. & CURT.) MILL.	<i>Magnolia virginiana</i>
<i>H. multiforme</i> FR.	<i>Betula, Alnus</i>
<i>H. nummularium</i> BULL.: FR.	<i>Fagus</i>
<i>H. rutilum</i> TUL.	<i>Fagus</i>
<i>H. udum</i> PERS.: FR.	<i>Quercus</i>
<i>H. vogesiacum</i> var. <i>macrospora</i> MILL.	<i>Salix</i>
<i>Nummulariella marginata</i> ECKBLAD & GRANMO	<i>Malus</i>
<i>Rosellinia buxi</i> FABRE	<i>Buxus</i>
<i>R. desmazieresii</i> (BERK. & BR.) SACC.	<i>Salix</i>
<i>Xylaria carpophila</i> PERS.: FR.	<i>Fagus</i> (cupules)
<i>X. longipes</i> NITS.	<i>Acer</i>
<i>X. magnoliae</i> ROGERS	<i>Magnolia</i> fruits
<i>X. oxyacanthae</i> TUL.	<i>Crataegus</i> fruits
<i>X. persicaria</i> (SCHW.: FR.) BERK. & CURT.	<i>Liquidamber styraciflua</i> fruits

restricted to bushes which have been burnt and subsequently weathered (WHALLEY & WATLING, 1980 b).

The geographical range of a fungus may be extended by a change in host preference as is shown by *Daldinia concentrica* (BOLT.: FR.) CES. & de NOT. This fungus is widely distributed throughout the world and is well-represented in Britain (CHILD, 1932). Its frequency, however, declines towards the North so that in Scotland it appears genuinely uncommon. Furthermore there is a change in host selectivity so that *Fraxinus*, the preferred host in the South, eventually becomes replaced by *Betula* in the north of England and Scotland (WHALLEY & WATLING, 1982). WINTER (1887) and VON ARX & MÜLLER (1954) reported *Fraxinus* and *Alnus* as the most common substrata in Great Britain and on the continent but in Norway *Alnus* and *Betula* are the usual host trees (ECKBLAD, 1969) whilst in Denmark *Alnus*, *Betula* and *Populus* are selected (WHALLEY & KNUDSEN, 1985 b). It is suggested that this pattern links the more southern parts of Britain with France and Germany, and Scotland with the Scandinavian countries (WHALLEY & WATLING, 1982). This ability to spread north on trees other than the most frequent host is well-known for basidiomycetes. For example *Fomes fomentarius* (FR.) KICKX is common on *Betula* in Scotland but frequents *Fagus* south of the border (WATLING, 1978) whilst *Inonotus obliquus* (PERS.: FR.) PILÁT has a wide host range in continental Europe and in Britain but although widespread in Scotland especially in the northern regions it is restricted to *Betula*, even in mixed communities (PEGLER, 1964).

Host specificity and selectivity could be explained in terms of resistance-virulence mechanisms operating between host and fungus as proposed by SHIGO & MARX (1977) and SHORTLE & COWLING (1978). RAYNER & BODDY (1985) consider this argument unconvincing and emphasized the essentially saprotrophic nutrition of many tree decay fungi and the lack of clear evidence for pathogenicity as sufficient reason to consider alternatives. They proposed that selectivity is related to a particular ecological strategy, in this case stress-tolerance. Fungi of this type are characteristic of undisturbed habitats which are relatively competitor-free because of the occurrence of 'stress' conditions unfavourable for mycelial development by the majority of potential colonists. The essential feature of these fungi is their close adaptation to a particular set of selective microenvironmental conditions and lack of competitiveness when other conditions prevail (RAYNER & BODDY, 1985). Furthermore they suggest that if stress tolerance characterizes many tree decay fungi there are several patterns of behaviour which occur with respect to alleviation or alteration of the relevant selective conditions. Thus the fungus may rapidly be replaced once the selective conditions to

which they are adapted to and therefore do not remain active for long in felled or fallen timber (HIGHLEY & KIRK, 1979). Alternatively they exhibit a latent invasion strategy when alteration in the selective conditions permits immediate mycelial extension from a previously cryptic inoculum. RAYNER & BODDY suggest that *D. concentrica* employs this strategy and that its initial competitive advantage is sustained by combative mechanisms allowing defence against or even replacement of other potential competitors (RAYNER & BODDY, 1985).

One can have considerable sympathy with these views since the rapid appearance of many xylariaceous species on apparently healthy but stressed hosts is in keeping with the general characteristics of latent invaders and is a common phenomenon in the family. Thus a number of species cause 'disease' of hosts only when there are conditions of host-stress as is seen following drought. At least ten species of *Hypoxyton* behave in this manner in relation to water-stressed tea bushes (AGNIHOTHRUDU, 1978) and cankers of oak caused by *Hypoxyton mediterraneum* (de NOT.) MILL. and *Hypoxyton atropunctatum* (SCHW.: FR.) CKE. follow similar patterns (BARBOSA, 1958; Van ARSDEL, 1972).

Although stress tolerance might well explain host specificity or preference seen in the Xylariaceae it is by no means the only reason. *Hypoxyton mammatum* (WAHL.) MILL. the causative agent of a devastating canker of aspen exhibits a number of pathogenic traits. Production of a potent toxin (SCHIPPER, 1978; STERMER, SCHEFFER & HART, 1984), and phytoalexins in response to infection (FLORES & HUBBES, 1979), the isolation of infection by callus formation (GRIFFIN & al., 1984) and the occurrence of host-orientated strains of different pathogenic capabilities (FRENCH, HODGES & FROYD, 1969) are clearly indicative of a pathogenic lifestyle; in this case host specificity can be explained in relation to host pathogen interaction imposing strong selection pressures for the development of resistance and virulence in one another's populations.

Habitat selectivity

The Xylariaceae occupy a wide range of habitats but in general can be grouped as those which frequent wood, dung and litter (Table 2). Most are wood inhabitants and here a distinction can be made between those which are associated with bark, those with decorticated wood, often well-decomposed, and those which apparently show no preference. *Hypoxyton fragiforme* (PERS.: FR.) KICKX and *Hypoxyton fuscum* PERS.: FR. are often associated with branches still attached to the parent tree. *Hypoxyton fragiforme* is a frequent early invader of *Fagus* when the trees are dead or dying from beech-bark

Table 2: Examples of habitat selectivity

Bark

- Hypoxylon cohaerens* PERS.: FR.
H. fragiforme (PERS.: FR.) KICKX
H. fraxinophilum POUZAR
H. mediterraneum (de NOT.) MILL.

Decorticated wood

- H. caries* (SCHW.) SACC.
H. confluens (TODE.: FR.) WEST.
H. quadratum (SCHW.) ELL. & EV.
H. regale MORG.
H. udum PERS.: FR.

Litter

- Xylaria carpophila* PERS.: FR.
X. magnoliae ROGERS
X. oxyacanthae TUL.
X. persicaria (SCHW.: FR.) BERK. & CURT.
H. terricola MILL.

Dung

- Poronia* WILLD.
Hypocopra (FR.) KICKX
Podosordaria ELL. & HOLWAY
Wawelia NAMYSLOWSKI

disease caused by a scale insect (SHIGO, 1964) and its appearance in this hardwood prior to basidiomycete decomposition indicates its early presence on the host tree (SHIGO, 1965). CHESTERS (1950) considered these and similar species to be primary colonists of unknown status but suggested that they may be true wound parasites or they may be aggressive, but saprophytic, organisms which are able to attack moribund or weak branches. *Hypoxylon fraxinophilum* POUZAR is not only specific to ash but grows on weak or recently dead branches still on the parent tree and once these branches are shed the fungus rapidly disappears. RAYNER & BODDY (1985) would consider this to be latent invasion where the invader lacks a combative strategy and is thus readily replaced by competitors. *Hypoxylon diathrauston* REHM might also fit here. In Europe it occurs only at high altitude in the Alps and is restricted to branches of *Pinus mugo* or closely related species. Furthermore only those trees situated in positions of extreme exposure are involved and it appears that branches subjected to wind burn provide the highly selective habitat for this species (PETRINI, pers. comm.).

After decortication the exposed wood of fallen branches is greatly influenced by external factors and tends to dry out. Upper surfaces and parts of branches clear of the ground are usually drier

than the central regions whilst the lower surface lying in contact with the ground is often close to saturation point. Thus a water gradient from the lower to upper surface becomes established and this probably exerts a major influence in the distribution of secondary colonists (CHESTERS, 1950). A large number of species can be considered secondary colonists including *H. rubiginosum*, *H. serpens* and several *Xylaria* species. *Xylaria hypoxylon* (L.) GREV. is usually associated with branches buried in the litter or in soil whilst *X. polymorpha* (PERS.: FR.) GREV. is more common on dead stumps and larger roots. *Hypoxylon serpens* has been isolated from soil (BARRON, 1968) and there is a possibility that some fungi in this category might have a soil phase. In general secondary colonists do not exhibit a distinct host preference and subsequently attack all kinds of deciduous wood. Although it is difficult to assess their importance in wood decay all xylariaceous fungi apparently have the ability to degrade cellulose and lignin (ROGERS, 1979 a). Numerically the family is important in the colonization of wood in Uganda (TALIGOOLA & WHALLEY, 1976) and SUTHERLAND & CRAWFORD (1981) have demonstrated the ability of a number of xylariaceous fungi to degrade lignin. KAARIK (1974), CARRUTHERS & RAYNER (1979) and RAYNER & TODD (1979) also draw attention to the participation of the Xylariaceae in the degradation of ligno-cellulose in nature.

Selectivity for dung is shown by the three genera *Poronia*, *Podosordaria* and *Hypocopra*. They all possess ascospores with gelatinizing outer walls which are involved in the attachment of spores to herbage (KRUG & CAIN, 1974 a, b; ROGERS, 1970) and they also adapted for dry habitats (ROGERS, 1979 a). In *Hypocopra* the ascostromata are more or less rudimentary, often with an external clypeus and the dung itself probably acts as a substitute stroma. *Poronia* and *Podosordaria* grow as stalked stromata, raising their perithecia above the substrate and thus effecting more efficient ascospore dissemination. Little is known about the activities of these dung inhabitants but *Poronia punctata* (L.: FR.) FR. and *Hypocopra merdaria* (FR.) FR., although slow growing and late colonists of cattle faeces, are both more efficient in attacking cellulose in unamended native wheat straw (WICKLOW, DETROY & ADAMS, 1980). Previously it had been shown that both species contributed to a competitive hierarchy in cattle dung in that they were antagonistic to all earlier-sporulating colonists in cultural tests (WICKLOW & HIRSCHFELD, 1979). Interestingly, *P. punctata* produces a number of antibiotic compounds, the punctatins, although surprisingly the closely related *P. oedipus* (MONT.) MONT. does not (ANDERSON & al, 1984 a, b). The little known genus *Wawelia* NAMYSLOWSKI, originally placed in the Hypocreaceae but later considered to be Xylariaceous (MÜLLER & von ARX, 1973) is also coprophilous and the two known

species are both associated with rabbit pellets. In addition *W. octospora* MINTER & WEBSTER is xerophilous (MINTER & WEBSTER, 1983) and therefore provides further evidence of adaptation by the coprophilous Xylariaceae to dry environments.

The Xylariaceae are not usually considered to be litter fungi but there are a number of reports of species which are restricted to this habitat. *Hypoxylon terricola* MILL. grows on coniferous needles and is found regularly in the Atlantic Pyrenees (CANDOUSSAU, 1977) and a number of *Xylaria* species inhabit 'fruits' sometimes with clear taxon selectivity (ROGERS, 1979 b). Thus *X. carpophila* PERS.: FR. is associated with beech cupules, *X. magnoliae* ROGERS with *Magnolia* fruits and *X. oxyacanthae* TUL. with *Crataegus* berries. REYNDERS (1983) has reported on the frequent occurrence of *X. oxyacanthae* in newly planted *Crataegus* plantations in Holland growing in situations where there is the right balance between shade and moisture once the fruits have reached a certain stage of decomposition. ROGERS (1979 a) speculates as to whether these fruits act as 'baits' for given *Xylaria* species when on the ground or if fruits are actually infected during development. The recent discovery that many xylariaceous fungi occur as endophytes on a wide range of unlikely hosts (CARROLL, MÜLLER & SUTTON, 1977; PETRINI, 1984) suggests that the latter proposal is indeed possible.

Physical factors

Climate

Climate, especially temperature, is an important factor affecting the distribution of many well-known fungi (PIROZYNSKI, 1966) and the Xylariaceae are influenced not only at the habitat level but also on a global scale. *Hypoxylon vogesiacum* var. *macrospora* MILL. exhibits an arctic-alpine distribution (WHALLEY & PETRINI, 1984; WHALLEY & KNUDSEN, 1985 a) whilst *Hypoxylon truncatum* (SCHW.: FR.) MILL. is restricted to the tropics and subtropics and has not been collected in cooler zones (MILLER, 1961). *Hypoxylon nummularium* var. *pseudopachyloma* (SPEG.) MILL. and *H. rubiginosum* var. *tropica* MILL. are tropical variants of the type varieties. *Thamnomycetes* and *Kretzschmaria* are tropical genera with *K. clavus* possibly being the tropical equivalent of *Ustilina deusta* (HOFFM.: FR.) LIND (KO, HO & KUNIMOTO, 1982).

Climatic zone may not be the only factor to consider in the restricted distribution of *Thamnomycetes* since in this genus the spores may be unfit for airborne dispersal (DENNIS, 1957).

Although some members of the family are restricted to major climatic zones few studies have been undertaken to investigate temperature requirements with geographical situation. One notable

Table 3: Examples of geographical isolation

Fungi	Region
<i>Entonaema pallidum</i> G. W. MARTIN	Panama, Trinidad
<i>E. dengii</i> J. D. ROGERS	China
<i>Hypoxyylon atropunctatum</i> (SCHW.: FR.) CKE.	North America
<i>H. bartholomaei</i> PECK	Western United States
<i>H. heterostomum</i> MONT.	Central and South America
<i>H. hians</i> (BERK.) CKE.	Australasia
<i>H. melanaspis</i> MONT.	Central and South America
<i>H. philippinense</i> (RICKER) MILL.	Philippine Islands
<i>H. pynaerthii</i> BRES.	Central Africa
<i>H. udum</i> PERS.: FR.	Europe
<i>Rhopalostroma</i> D. HAWKSW.	Africa and Asia
<i>Xylaria brasiliensis</i> (THEISS.) LLOYD	Brazil, Sierra Leone

exception demonstrated the low-temperature requirements for ascospore germination and growth of *Hypoxyylon diathrauston* (OUELLETTE & WARD, 1970). This species of the high Alps requires freezing temperatures for ascospore germination or pretreatment at -3°C prior to germination at 12°C . Growth occurs at 0°C with an optimum of $12-15^{\circ}\text{C}$ and the species is therefore well-adapted for its situation. Studies on species from different climatic belts could be useful.

Geographical barriers

Although there is evidence to show that oceans, deserts and mountain ranges can act as barriers limiting distribution in fungi (PIROZYNSKI, 1966), it is difficult to have confidence in the citation of examples of the Xylariaceae showing this type of isolation, mainly through lack of detailed surveys in many parts of the world. Even in mycologically well explored areas such as Britain new species of *Hypoxyylon* have recently been described and *H. chestersii* ROGERS & WHALLEY which was originally described from North Wales (ROGERS & WHALLEY, 1978) has subsequently been found in southern England, Switzerland, Germany and Brazil. In spite of these reservations a number of species might fit into this category (Table 3). Thus *Hypoxyylon hians* BERK. & CKE. with its distinctive cupulate perithecial projections has only been found in Australasia whilst *Hypoxyylon bartholomaei* PECK seems to be restricted to the western United States.

This attempt to relate the activities of the Xylariaceae, primarily to their distribution both on a global and on a local scale, has neglected to discuss the nutritional status of the family in relation to saprotrophy and necrotrophy. On the one hand little is known about the activities of those species which cause disease and on the other it

Table 4: Examples of diseases caused by Xylariaceae

Fungi	Principal hosts	Disease caused
<i>Kretzschmaria clavus</i> (FR.) SACC.	<i>Macadamia</i>	Black root rot
<i>Hypoxyylon atropunctatum</i> (SCHW.: FR.) CKE.	Oak	Bark slough canker
<i>H. mammatum</i> (WAHL.) MILL.	Aspen, alder, willow	Canker of aspen
<i>H. mediterraneum</i> (de NOT.) MILL.	Oak	Coal canker
<i>H. serpens</i> var. <i>effusum</i> (NITS.) MILL.	Tea, coffee, rubber	Root rot
<i>H. tinctor</i> (BERK.) CKE.	London plane, sycamore	Stem canker
<i>H. truncatum</i> var. <i>pouceanum</i> (BERK. & CKE.) MILL.	Tea, coffee	Root rot
<i>Nummulariella marginata</i> ECKBLAD & GRANMO	Apple	Nailhead blister
<i>Rosellinia arcuata</i> PETCH	Tea	Black root rot
<i>R. bunodes</i> (BERK. & BR.) SACC.	Cacao, coffee, quinine, rubber, tea	Black root rot
<i>R. desmazieresii</i> (BERK. & BR.) SACC.	Willow	Ring die back
<i>R. herpotrichioides</i> HEPTING & DAVIDSON	Hemlock, Douglas fir, Sitka spruce	Needle blight
<i>R. necatrix</i> PRILL.	Apple, apricot, cherry pear etc.	White root rot
<i>R. pepo</i> PAT.	Avocado, cacao, coffee	Black root rot
<i>Ustulina deusta</i> (HOFFM.: FR.) LIND	Beech, lime, rubber, tea etc.	Charcoal base rot of rubber, butt rot
<i>Xylaria mali</i> FROMME	Apple	Black root rot

is probable that many are saprophytic under one set of conditions but become netrotrophic under another. There are however numerous examples of Xylariaceous fungi causing disease (Table 4). In some cases, such as with *Rosellinia necatrix* PRILL., serious loss is caused over a wide range of environmental conditions and the organism is described as a plurivorous pathogen (SIVANESAN & HOLLIDAY, 1973). Other diseases only result when specific criteria are fulfilled as for example *H. rubiginosum* canker of catalpa which has been associated with the 'ritual' beating of catalpa trees by fisherman to obtain the catalpa worm for use as bait (WEIDELL, 1924). The majority cause disease following injury, drought or fire damage (ROGERS, 1979 a) and until future investigations are made, discussion of their nutritional status must remain speculative.

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Autor(en)/Author(s): Whalley Anthony J. S.

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