Spore Form and Phylogeny of Entolomataceae (Agaricales)

By D. N. PEGLER [1]) & T. W. K. YOUNG [2])

Résumé. Douze types des spores existent chez les Entolomatacées mis en évidence dans ce travail par le microscope électronique à balayage. L'importance phylogénétique de la morphologie des spores est discutée, ainsi que les incidences sur la classification.

FAYOD (1889) was the first to recognise the regular arrangement of polyhedral facets of the spores which characterize genera of Entolomataceae (= Rhodosporés). He concluded that, although both spore quotient and facet number are variable, all spores can be reduced to a basic geometrical form consisting of a prism surmounted by a tetrahedron, with the hilar appendix at one of the angles at the base of the prism (Fig. 1). Any comparison with geometrical forms can only be approximate as the facets are often concave or convex, and inflation of the spore which always occurs abaxially results in bilateral rather than radial symmetry. All morphological variations were explained by FAYOD on the basis of either hypertrophy, reduction or doubling of edges and corners. KÜHNER & BOURSIER (1929), who studied a large number of European species representative of all genera, attempted a systematic survey of spore types in which none corresponded to the FAYOD schema. They concluded, correctly, that the hilar appendix always subtends a single adaxial (= dorsal) facet and never a pair of adaxial facets. FAYOD's observations were limited to a comparison of spore outlines whilst KÜHNER & BOURSIER examined spores allowed to rotate in lactophenol under an oil-immersion objective. Their preliminary results indicated that a basic symmetry prevailed even in the most complicated spores, although abnormal spores were frequent in any sample. Further, the basal region of the spore was less variable than the apex owing the to presence of the hilar appendix. Significantly, they noted that the spore base always comprised one of two forms, which allowed spore types to be initially grouped. In the first type, the hilar appendix is positioned mid-way along the edge where the single basal facet and the adaxial facet join. This type was found to be less variable and more common, and the simplest in this category was recorded as *Nolanea staurospora* BRES. In the second type three edges

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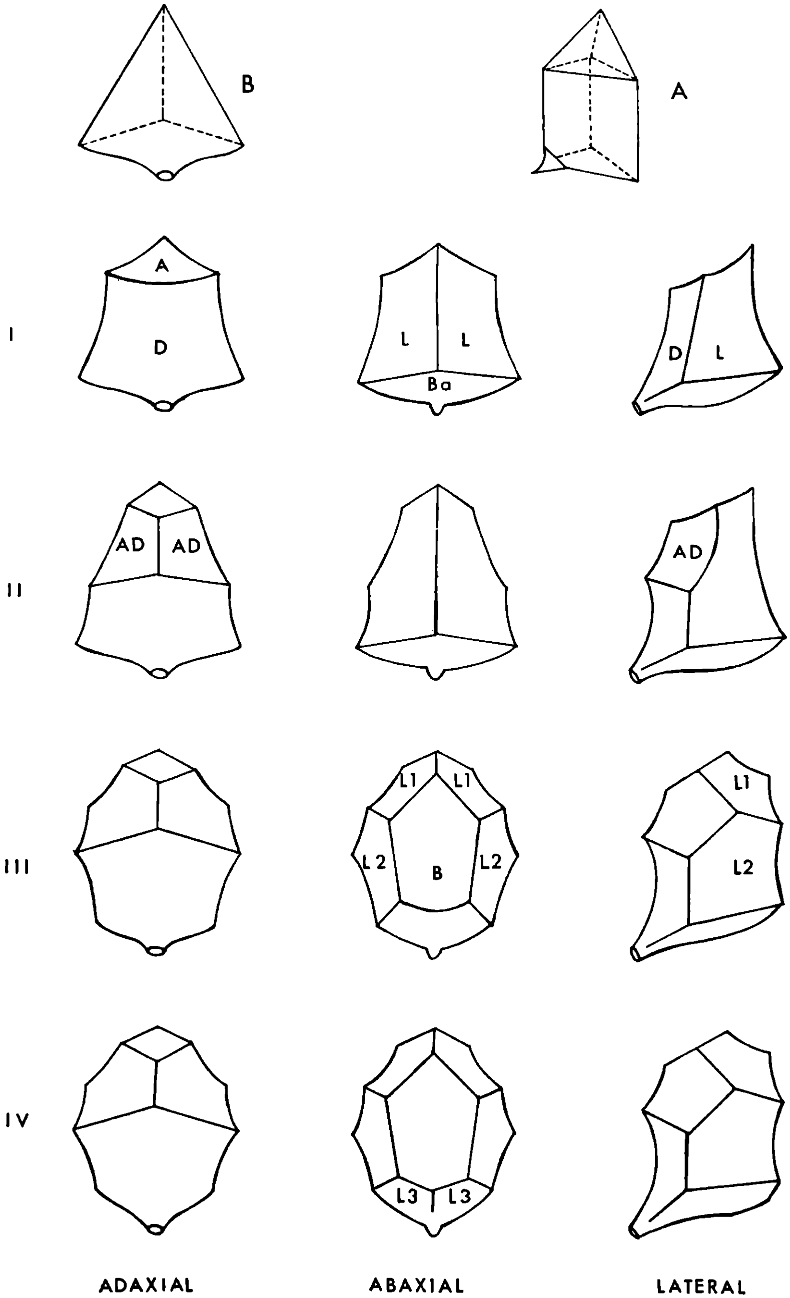

Fig. 1. Spore types of Entolomataceae. — A. Basic schema according of Fayod. — B. Archetypal tetrahedron. — I. Prismatic type. — II. Simple Base type. — III. Common type. — IV. Incomplete Dihedral Base type.
A, apical facet; AD, apico-adaxial facet; B, abaxial facet; Ba, basal facet; D, adaxial facet; L, lateral facet

are involved, with a dihedral pair of facets forming the spore base, as in *Leptonia rhombispora* KÜHN. & BOURS. The dihedral base was, however, regarded as very variable. Subtypes were postulated to result from apical modification and the introduction of additional facets. No attempt was made at this stage to recognize a "primitive" type and the two series were considered independently. ROMAGNESI 1932, 1933) expanded on these results by introducing the terms "isodiametric" and "heterodiametric" to distinguish differences in spore quotient, and also renamed the first type of spore base as "prismatic" (or "asymmetric") and the second as "cuboid" (or "symmetric"). The terms "simple" and "complex" were also used to reflect apical variation. A survey of the results of KÜHNER & BOURSIER and ROMAGNESI has been provided by EINHELLINGER (1966). The form of the mature spore was also related to ontogenetic development, in order to suggest possible phylogenetic relationships. Spores of the Hymenogastraceous fungus, *Richoniella leptoniispora* (RICHON) COST. & DUFOUR, were compared with those of the agaricoid genera, in which several intermediate spore forms were observed. ROMAGNESI concluded that evolutionary and ontogenetic development could be interpreted on the basis of three laws relating to spore form. First, the development of sporal volume is determined by successive transformation of an apico-adaxial facet. Secondly, the originally triangular apico-adaxial facet becomes quadrangular, then divides vertically to form a dihedral pair. Thirdly, this developmental sequence occurs once in the symmetric spores but up to three times in the asymmetric spores. ROMAGNESI's hypothesis, derived only from light microscope observation, is not supported by results obtained with the scanning electron microscope. Triangular facets are not to be found, other than in a tetrahedral primordial state or in a prismatic spore type.

The first taxonomic revision of Entolomataceae (= Rhodophyllaceae) based on spore structure was presented by ROMAGNESI (1937) and this system was largely accepted by SINGER (1943). A revised classification, which attempted to link spore form with basidiocarp morphology, was undertaken by ROMAGNESI (1941) when considering the tropical flora of the Malagasy Republic, and in a reassessment of the European flora (KÜHNER & ROMAGNESI, 1953) the combined characters of form of the spore base, basidiocarp pigmentation and presence of clamp-connexions were emphasized.

Utilisation of the form of the spore base as a taxonomic character suffers from two major disadvantages. First, the extreme difficulty of correctly interpreting the structure of the spore base under the light microscope has led to limited acceptance of ROMAGNESI's classification. Secondly, the precisely faceted Entolomataceous spores are unique within the Basidiomycotina and the probability of such regularly faceted structures arising on more than one occasion would presumably be very low. It is difficult to accept the notion of two parallel series of asymmetric and symmetric spore types, which appear in taxa at virtually every level and the possibility could be that the prismatic spore and the cuboid spore either arose initially one from the other or alternatively, and more probably, originated from a common ancestral type.

The present scanning electron microscope investigation was undertaken in order to clarify spore structural relationships and to elucidate possible phylogenetic relationships. When the survey is complete, spores from about one hundred and sixty species will have been analysed, a sample in which all the recognized genera and subgeneric sections are represented. A summary of the spore types. together with possible taxonomic and phyletic implications, is given below.

Materials & Methods

Specimens were obtained from the Herbarium, Royal Botanic Gardens, Kew (K), the Royal Botanic Garden, Edinburgh (E), the Laboratoire de Cryptogamie, Muséum National d'Histoire Naturelle, Paris (PC), and the Institut für Systematische Botanik, ETH, Zürich (ZT). Spore samples were prepared by the critical point technique (Pegler & Young, 1974) and examined with a scanning electron microscope. Care was taken to differentiate mature from immature spores as the latter may not bear the full complement of facets. The interpretation of European species is according to Dennis, Orton & Hora (1960).

Nomenclature of Spores and Sporal Facets

The overall form of the spores is determined by the length/width ratio i. e. the quotient ,expressed as Q. Isodiametric spores are defined as having a quotient ranging from 1.0—1.24, heterodiametric-ovate spores as Q = 1.25—1.5, and heterodiametric-elliptic spores as Q = 1.6 or more.

To facilitate discussion of and comparison between spores it becomes necessary to use a system of nomenclature when referring to a particular facet. The following terminology has been adopted for this purpose. Adaxially the spore surface is formed by a large single, depressed facet, termed the adaxial facet (D), formerly referred to as the inner or dorsal facet. The apical region is typically formed by a single, often small facet, termed the apical facet (A), although this is absent from cuboid spores. In all spores, apart from the simplest types, a pair of facets which join to form a dihedron is introduced between the adaxial and apical facets, these are termed the apico-adaxial facets (AD), formerly referred to as apico-dorsal facets. The base of the spore is formed by a single facet, the basal facet (Ba), although in certain spore types this facet is wanting and the basal region is occupied by a dihedral pair of lateral facets. In most spore types a single facet termed the abaxial facet (B), occupies the central region of the outer, abaxial surface. In the more complicated, heterodiametric spores, the abaxial facet may be accompanied by a second, single facet situated below the first. The rest of the spore surface is formed by up to three pairs of lateral facets. Lateral-I pair (Ll) commonly meets abaxially to form a dihedron immediately below the apical facet and above the abaxial facet. Lateral-II pair (L2) is always truly lateral in position, mostly remaining separated and only meeting abaxially in spores which lack the abaxial facet. Lateral-III pair (L3) is situated towards the spore base, either remaining separated or joining abaxially below the abaxial facet to form a dihedron. This third pair of lateral facets is present only in more complex spore types. In spores with a dihedral base, the true basal facet is lacking and the basal region is occupied either by the lateral-II pair or the lateral-III pair. The full complement of facets is developed in the *Pouzaromyces* spore type described below.

As the spores are bilaterally symmetrical, the terms "asymmetric" and "symmetric" are confusing, and it is proposed to replace them with the terms "simple base" and "dihedral base" respectively.

Principles of Spore Formation

The development of facets follows a definite sequence enabling relatively simple spore types with few facets to be related to more complex spores by a series of prescribed stages. Sporogenesis proceeds as follows:

1. The spore initial is globose and smooth but soon after inflation the facets are formed by production of ridges of the epicorium above the pseudocorium but below the enveloping pseudotunica.
2. The basal region is predetermined in the primordial stage.
3. The first stage in development is the formation of a single facet in the apical region.
4. Next, an apico-adaxial pair of facets develops.
5. A single facet always alternates with or is subtended by a pair of facets.
6. The final stage in any postulated development series is the establishment of a three facet configuration forming the basal region.

Spore Types

A systematic survey of agaricoid members of Entolomataceae and related gasteroid species placed in Hymenogastraceae and Secotiaceae has led to the recognition of twelve spore types:

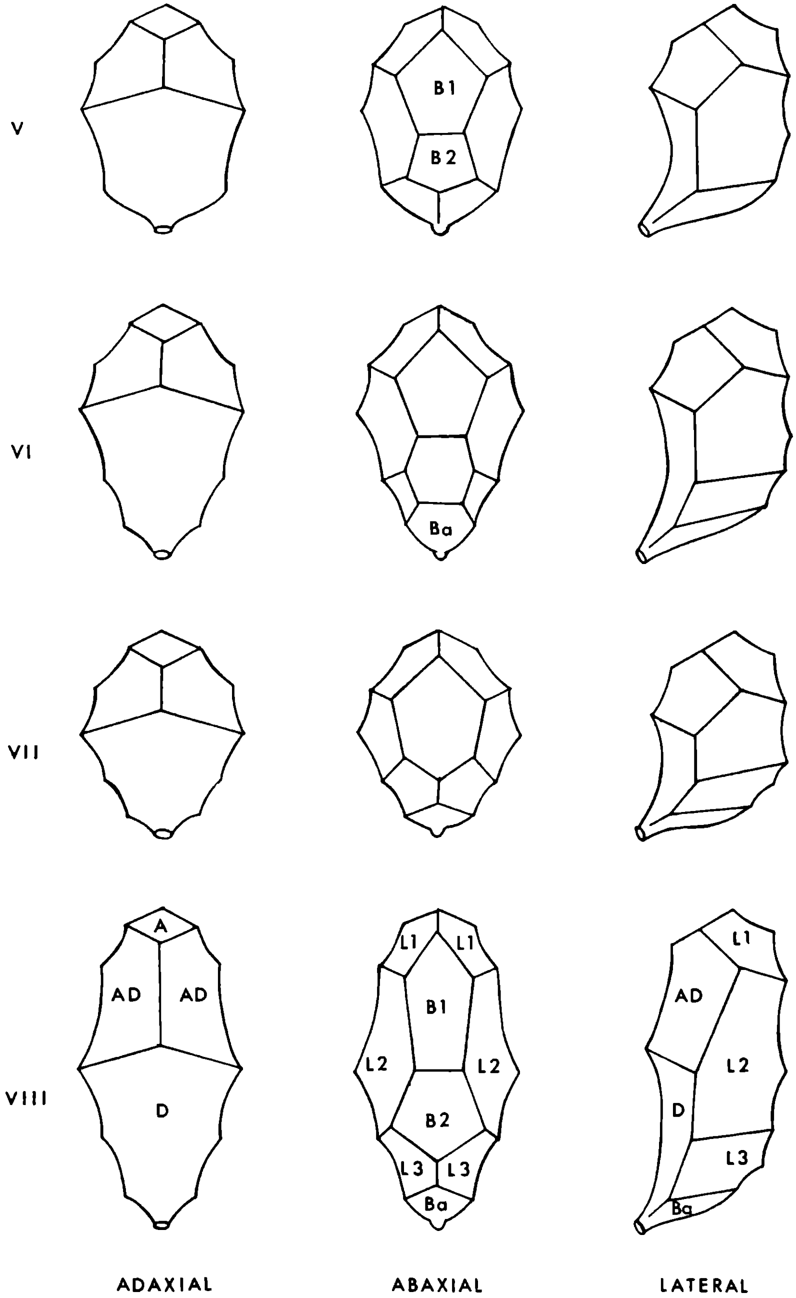

Fig. 2. Spore types of Entolomataceae. — V. Double Abaxial type. — VI. Nigella type. — VII. Y-Base type. — VIII. Pouzaromyces type

Type I. Prismatic (Fig. 1/I). This is essentially a truncatet tetrahedron, comprising a large depressed, quadrangular adaxial faced a triangular apical facet, a pair of quadrangular facets joining abaxially along the midline, and a large basal facet. All facets tend to be strongly depressed and the corners, especially the apico-abaxial corner, may be extended to appear winged e. g. *Entoloma procerum* STEV. All are isodiametric, Q = 1.13—1.24, although extension of the corners can result in a more elongated form e. g. *Nolanea xylophila* (J. LANGE) P. D. ORTON. Under the light microscope prismatic spores can be confused with type IX, cuboid spores, as both are quadrangular in face and lateral view, however the end-view is triangular. A prism can be formed by the formation of an apical facet which replaces the pointed apex of a tetrahedron, and immature spores attached to the sterigmata often appear tetrahedral in form. This is particularly noticeable in the tropical species, *N. pinna* (ROMAGN.) DENNIS. It is suggested that the tetrahedron, being the simplest geometrical solid, could represent the archetypal form for all spore types with a simple base. All prismatic-spored species are probably closely related and best placed in *Nolanea* (FR.) KUMMER sect. *Staurospori* (ROMAGN.) LARG. & THIERS. An-exception is *Rhodogaster chilensis* HORAK (Pl. 1/5), a South American secotioid species. Other species include: *N. staurospora* BRES. (Pl. 1/3), *E. nothofagi* STEV. and *Leptonia intermedia* F. H. MØLLER.

Type II. Simple Base. (Fig. 1/II). This resembles the prismatic spore in lacking an abaxial facet but the introduction of a dihedral pair of quadrangular facets in the apico-adaxial region gives a spore with seven facets. The apical facet is quadrangular, whilst the adaxial and lateral facets are pentagonal. Although facet number and arrangement is relatively simple, there is nevertheless a degree of variation in the overall form of the spore. Most spores are isodiametric and either obtusely angular to appear almost subglobose e. g. *Rhodophyllus rhodellus* ROMAGN. or very angular e. g. *E. sericatum* (BRITZ.) SACC. Others are heterodiametric-ovate e. g. *L. leptonipes* (KÜHN. & ROMAGN.) P. D. ORTON. In *Eccilia paludicola* P. D. ORTON (Pl. 1/1) ,a small proportion of spores develop an abaxial facet thus being indistinguishable from type III which could indicate a phyletic relationship between the species showing these spore types. Most species with spores of type II also tend to have an unspecialised basidiocarp typical of *Eccilia* (FR.) KUMMER sect. *Undati* ROMAGN.; *Nolanea* sect. *Minuti* ROMAGN. e. g. *N. minuta* P. KARST., *N. solstitialis* (FR.) P. D. ORTON; *Nolanea* sect. Nolanea e. g. *N. mammosa* (L. ex FR.) QUÉL.; *Nolanea* sect. *Papillati* e. g. *N. clandestina* (FR. ex FR.) KUMMER; *Entoloma* sect. Nolanidei FR., e. g. *E. sericatum* (BRITZ.) SACC.

Type III. Common (Fig. 1/III). As the name implies this is the most common spore type, having ten facets constituting the full

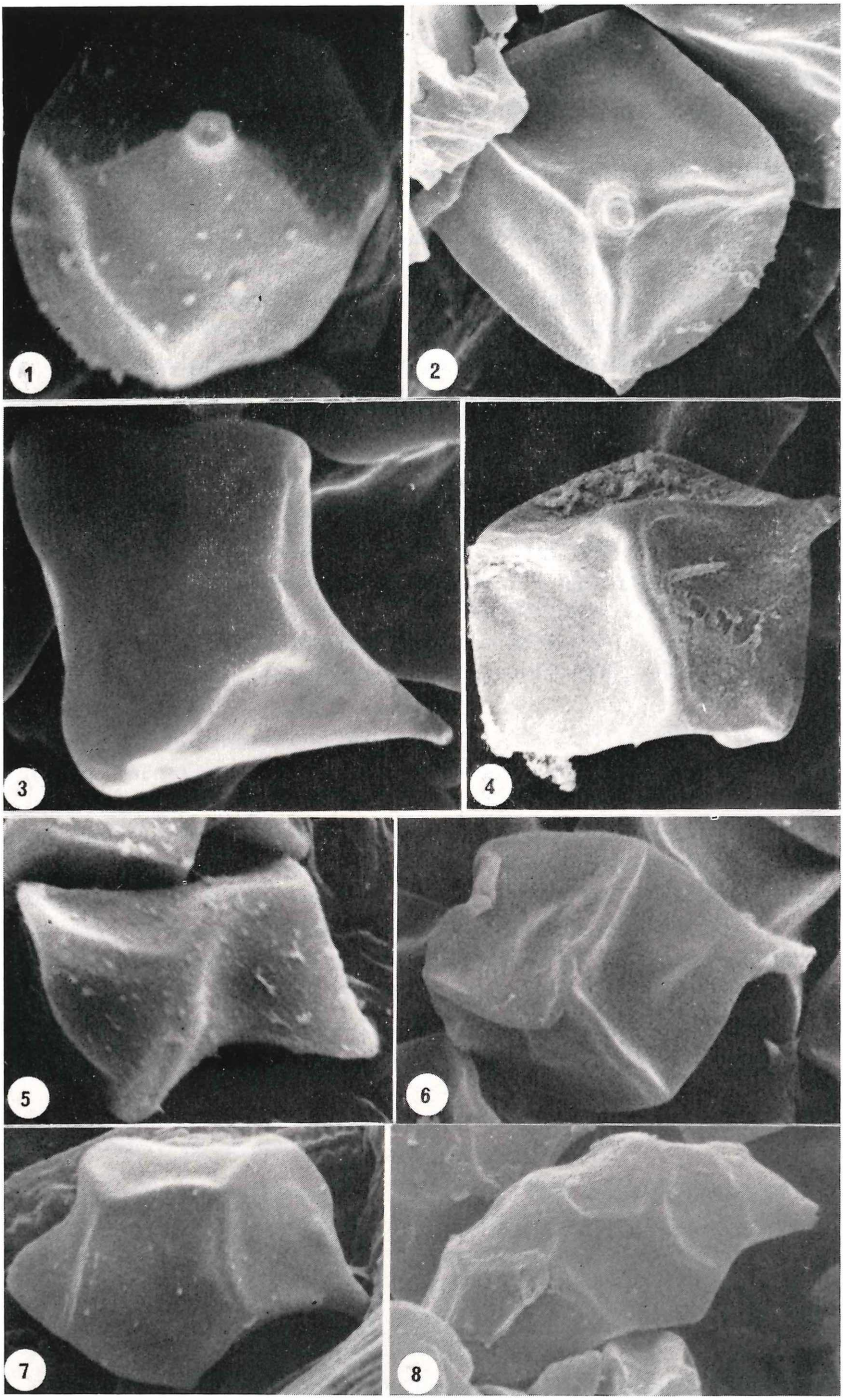

Fig. 1. *Eccilia paludicola* with simple base ×7450. — Fig. 2. *Entoloma brunneum* with dihedral base ×4950. — Fig. 3. *Nolanea staurospora*, prismatic spore ×6200. — Fig. 4. *Entoloma brunneum*, cuboid spore ×4500. — Fig. 5. *Rhodogaster chilensis*, prismatic spore ½4500. — Fig. 6. *Richoniella afra*, cuboid spore ×4200. — Fig. 7. *Leptonia anatina* common type spore ×3750. — Fig. 8. *Leptonia babingtonii*, Pouzaromyces-type spore ×4000

complement of basic types of facet. Much of the abaxial surface is occupied by a pentagonal abaxial facet, separating the lateral pair found in types I and II. An additional dihedral pair of lateral facets separates the apical from the abaxial facet. A wide variation in overall form is encountered, many species have isodiametric spores, sometimes with very obtuse angles e. g. *Eccilia rhodocylix* (LASCH) KUMMER, *Entoloma convexum* STEV., and *E. cystidiophorum* DENNIS, but more often the spore is angular as found in *Nolanea sericea* (BULL. ex MÉRAT) P. D. ORTON, *E. nitidum* QUÉL., and *E. sinuatum* (BULL. ex FR.) KUMMER. Heterodiametric-ovate spores are also common e. g. *Encilia cancrina* (FR.) RICKEN, *Claudopus byssisedus* (PERS. ex FR.) GILLET, *Nolanea papillata* BRES. and *Entoloma porphyrophaeum* (FR.) KARST. Occasionally a Common Type spore may occur in association with other spore types. Of particular interest in this respect are *Entoloma abortivum* (BERK. & CURT.) DONK, *L. anatina* (Pl. 1/7) and *Rhodophyllus bisporus* HONGO with spore forms equally divided between types III and IV In *Eccilia sericeonitida* P. D. ORTON, type III spores are to be found with type VII, and in *Rhodophyllus pulcherrimus* ROMAGN. with spores of type VI. Species with Common Type spores are frequently found in *Eccilia* sect. Undati, *Nolanea* sect. Cosmeoexonema LARG. & THIERS, *Entoloma* sect. Entoloma and Apriles (KÜHN. & ROMAGN.) ROMAGN., and *Leptonia* (FR.) KUMMER sect. Paludocybe LARG.

Type IV Incomplete Dihedral Base. (Fig. 1/IV). This is similar to the Common Type spore but with a vertically orientated ridge extending from the base of the abaxial facet to form a dihedral pair of facets. Normally, however, this division remains incomplete. All spores of this type are elongate, mostly heterodiametric-ovate e. g. *Leptonia sarcitula* KÜHN. & ROMAGN. ex P. D. ORTON, *Rhodophyllus ater* HONGO, although occasionally also heterodiametric-elliptic e. g. *L. anatina*, *L. aethiops* (SCOP. ex FR.) GILLET. The incomplete division of the basal region suggests that this type might be less stable than other spore types with which it is often found to be associated. *Rhodophyllus ater*, *L. sarcitula* and *L. lampropus* (FR. ex FR.) QUÉL. have type IV spores associated with type VII, and *L. mougeotii* (FR.) P. D. ORTON with Type V Most species with spores of the Incomplete Dihedral Base type occur in *Leptonia* sect. Leptonia.

Type V Double Abaxial. (Fig. 2/V). This is similar to type IV but with a second abaxial facet introduced below the first and above the dihedral basal region. Such spores are always heterodiametric-ovate and angular. A few species with spores of this type are restricted to *Leptonia* sect. Leptonia e. g. *L. caerulea* P. D. ORTON, *L. mougeotii* and *L. serrulata* (PERS. ex FR.) KUMMER.

Type VI Nigella (Fig. 2/VI). These spores differ from type V in having a well defined basal facet joined to the base of the lower abaxial facet so that the dihedral pair of facets is separated being truly lateral in position. This is a variant of type VIII but spores in this group are heterodiametric-ovate and less elongate e. g. *Eccilia nigella* QUÉL., *Rhodophyllus pulcherrimus* ROMAGN. and *Leptonia inocybeoides* P. D. ORTON.

Type VII. Y-Base. (Fig. 2/VII). This resembles the Incomplete Dihedral Base type, with the addition of a small basal facet. The basal region of the spore is formed by a single basal facet plus a dihedral pair of lateral facets. It possibly represents the most stable form of base to be found in the faceted spores, which could be reflected by the large number of species distributed throughout a wide range of taxa. Further, the overall form shows considerable variation. Isodiametric spores occur in *Entoloma aprile* (BERK.) SACC., *E. clypeatum* (L. ex FR.) KUMMER and *E. prunuloides* (FR.) QUÉL. In *Nolanea farinolens* P. D. ORTON, the obtuse angles result in an almost globose spore. Many species have heterodiametric-ovate spores with a Y-base, including *E. helodes* (FR.) KUMMER, *Leptonia euchroa* (PERS. ex FR.) KUMMER, *L. fulvostrigosa* (BERK. & BR.) P. D. ORTON, *L. incana* (FR.) GILLET, *N. cetrata* (FR. ex FR.) KUMMER and *N. hirtipes* (SCHUM. ex FR.) KUMMER. Heterodiametric-elliptic spores exist in *E. jubatum* (FR.) KARST. and *L. xanthochroa* P. D. ORTON. The Hymenogastraceous species, *Richoniella macrospora* CRIBB, from Australia, has spores of this type which are the largest observed for faceted spores, measuring $15.5-19 \times 9.5-12$ $(17 \pm 0.97 \times 11 \pm 0.75)$ µm. Species with this type may be found in *Nolanea* sect. Nolanea and Cosmeoexonema; *Eccilia* sect. Cancrini ROMAGN.; *Entoloma* sect. Entoloma, Apriles and Leptonidei (FR.) KONR. & MAUBL.; and *Leptonia* sect. Leptonia and Cereicaules LARG. It may be pertinent, from a phylogenetic standpoint, to indicate that the Y-Base spore can also be derived from type XII by the addition of a dihedral pair of facets in the apico-abaxial position.

Type VIII. Pouzaromyces. (Fig. 2/VIII). This is the most complicated form combining the double abaxial facet of types V and VI with the Y-base structure of type VII. All spores are heterodiametric-elliptic, very angular and the quotient exceeds 2.00 e. g. *Pouzaromyces strigosissima* (REA) HORAK and *L. babingtonii* (BLOX.) P. D. ORTON (Pl. 1/8).

Type IX. Cuboid. (Fig. 3/IX). The spore form is determined by six quadrangular facets, comprising a depressed adaxial facet, a dihedral pair of lateral facets meeting in the apico-adaxial position, a large abaxial facet, and a dihedral pair of lateral facets which form the spore base. There is no differentiated apical facet. All spores are isodiametric. It is difficult to see how a cuboid form could have been derived from either a prismatic form or a regular tetrahedron, owing to

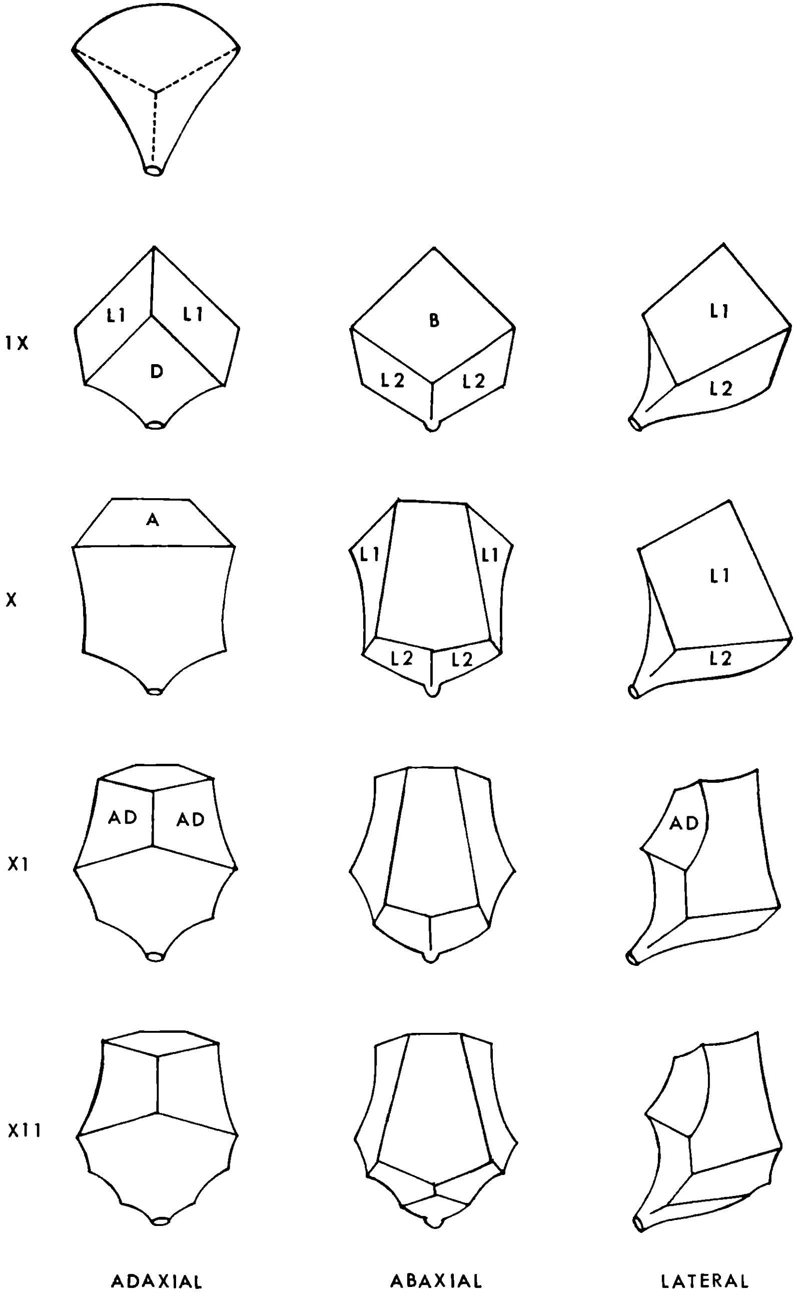

Fig. 3. Spore types of Entolomataceae. — IX. Cuboid type. — X. Dihedral Base type. — XI. Alboleptonia type. — XII. Rhodopolium type

the dihedral nature of the spore base. However, an inverted tetrahedral archetype (Fig. 3) could be postulated from which a cuboid spore might easily be reached by the addition of a dihedral pair of facets in the apico-adaxial position. It appears that all truly cuboid spores are found in species occurring in equatorial or south temperate regions, with the exception of the North American species, *Nolanea murrayi* (BERK. & CURT.) DENNIS. No cuboid-spored species are known to occur in Europe. All agaricoid species are best placed in *Nolanea* sect. Psittacini ROMAGN., and include *Rhodophyllus holocyaneus* ROMAGN., *R. incertus* ROMAGN., *Entoloma brunneum* PETCH (Pl. 1/2, 4) and *E. colensoi* STEV. Two Hymenogastraceous species, *Richoniella pumila* G. H. CUNN., from New Zealand, and *R. afra* PEGLER (Pl. 1/6), from Ghana, also produce cuboid spores.

Type X. Dihedral Base. (Fig. 3/X). This type is characterized by the European species, *Leptonia rhombispora* KÜHN. & BOURS. The isodiametric, angular spore might be described as a truncated cube where the edge formed by the apicoadaxial facets of the cuboid spore has been replaced by a quadrangular apical facet. The majority of *Richoniella pumila* spores are also of this type.

Type XI. Alboleptonia. (Fig. 3/XI). This is similar to the Dihedral Base spore of type X but with the addition of an apico-adaxial, dihedral pair of quadrangular facets which results in a pentagonal apical facet. Spores may be either isodiametric e. g, *Entoloma nidorosum* (FR.) QUÉL., *E. rhodopolium* (FR.) KUMMER. *E. turbidum* (FR.) QUÉL., or heterodiametric-ovate e. g. *Leptonia catalaunica* SINGER, *L. chalybea* (PERS. ex FR.) KUMMER and *L. gnophodes* (BERK. & BR.) SACC. It is the characteristic type of *Alboleptonia sericella* (FR.) LARG. & BENED., and it is also found in the pantropical relative, *L. stylophora* (BERK. & BR.) DENNIS. Species with this spore type may be found in *Entoloma* sect. Nolanidei and Turfosi (KÜHN. & ROMANGN.) ROMAGN.; *Leptonia* sect. Leptonia, Cereicaules and Roseicaules LARG.

Type XII. Rhodopolium. (Fig. 3/XII). This is a subtype of type XI and the two forms are always found together. It differs from type XI only in the structure of the basal region of the spore, where an additional facet gives the three facet arrangement characterizing types VII and VIII. It has been observed in a minority of spores in both *Entoloma rhodopolium* and *Alboleptonia sericella*.

Spores form and Phyletic Classification

Although it has never been difficult to assess the individual characteristics of basidiocarp structure, such as the presence of specialised hymenial structures, a differentiated pileipellis, the formation of surface hairs and squamules, pigmentation, hygrophany, and lamella attachment, the fundamental problem seems to lie in the assumption of different rates of phylogenetic development of the structures which has hindered attempts to provide a satisfactory phyletic classification of Entolomataceae. ROMAGNESI (1941) enumerated the advanced or specialized characters for each of the genera (as subgenera) but subsequent attempts to associate these with spore characteristics have only resulted in the establishment of additional subgenera, such as *Hygropilus* ROMAGN. (1941), *Inopilus* ROMAGN. (1974), *Paraleptonia* ROMAGN. (1941), *Paranolanea* SINGER (1951) and *Romagnesia* SINGER (1943). Spore form ranges from the simple, five-faceted structure of the prism to the complex thirteen-faceted structure of the *Pouzaromyces*-type. These facets are shown to be precise both in arrangement and order of development, and all spore types can be derived geometrically either from the prism or the cube. It is reasonable to imply that some of the simple spore types might be the more primitive and that facet arrangement could offer a guide towards clarifying phylogenetic relationships.

Spore form is perhaps particularly relevant when consideration is given to the possible progressive or retrogressive trends thought to exist between agaricoid species and those gasteroid forms arbitrarily grouped in Secotiaceae and Hymenogastraceae. Such relationships have been exhaustively discussed and documented by SINGER (1958) and HEIM (1971). Two genera, *Richoniella* COST. & DUFOUR (Hymenogastraceae) and *Rhodogaster* HORAK (Secotiaceae), are known to produce pink, faceted spores identical in form to those of Entolomataceae. The uniqueness of this form of spore probably confirms a phylogenetic relationship and, indeed, ROMAGNESI (1937) proposed subfamilies Richoniellae and Rhodogoniosporae under the single family, Rhodogoniosporaceae HEIM (= Entolomataceae). The prismatic spores of *Rhodogaster chilensis*, from South America, are largely comparable with those of *Nolanea* sect. Staurospori, probably the most widely distributed of all agaricoid sections. Species of *Richoniella* produce spores which are cuboid, types IX and X, indicating the probability of a different line of development from *Rhodogaster*. *Richoniella macrospora* from Queensland, Australia, produces spores of the Y-base type which could, on the basis of facet arrangement, equally have been derived from cuboid or prismatic prototypes. In all the gasteroid species, the spores have a depressed adaxial surface, an adaxially inclined hilar appendix, and are never radially symmetrical. It could be assumed that they are either produced by autobasidia or of ballistosporic ancestry, which would support the degradation theory of gasteroid forms representing reduced agarics. Nevertheless, it is also possible that Entolomataceae have been derived from another agaricoid family, such as Hygrophoraceae or Tricholomataceae, the evolutionary line passing through stages comparable to the genera *Clitocybe* with smooth hyaline spores, *Clitopilus* with longitudinally ridged spores, and *Rhodocybe* with regularly ridged spores. The unusual spore-wall structure, found in *Clitopilus*, *Rhodocybe* and the Entolomataceous genera, was shown by KÜHNER (1948) and BESSON—ANTOINE & KÜHNER (1972a, b) to be similar, which could support a possible relationship, although the wall structure of *Clitocybe* species is quite distinct and does not support any suggested phylogenetic sequence.

The simplest spore forms in Entolomataceae tend to belong to species with specialized or advanced basidiocarp characters, such as the bright pigmentation, presence of cheilocystidia, free and ascending lamellae, and a highly differentiated pileipellis of sections Psittacini and Callidermi ROMAGN. of *Nolanea.* A difficulty lies in phyletically linking such species with the unspecialized gasteroid species. Conversely, species with undifferentiated basidiocarps, such as the sections Undati and Cancrini ROMAGN. of *Eccilia,* frequently produce the more complex spore types.

Genera of Entolomataceae, as currently accepted, cannot be defined by spore types alone since in each genus spores with a single faceted base i. e. "asymmetric" and spores with a dihedral base i. e- "symmetric" occur. In any case, this classification does not account for the very common spore type with a Y-base or that with an incomplete dihedral base (type IV). A possibility in evolutionary terms is that once the regularly faceted spore state was attained, variations of increasing or decreasing complexity could have occurred several times, resulting in the present-day complicated situation.

Current generic limits contain species which have attained a common level of morphological development but do not necessarily reflect a linear phylogenetic relationship. Many taxonomists have attempted to overcome this problem by placing all species under a single generic name, either *Rhodophyllus* QUÉL. or *Entoloma.* At the infrageneric level, however, the value of analysing spore types becomes greater. In general terms, the simpler spore types occur in sections of *Eccilia* and *Nolanea,* moderately complex spore types, such as types II, III, X and XI, occur in sections of *Nolanea* and *Alboleptonia,* and the most complicated spores are to be found in sections of *Leptonia, Entoloma* and *Pouzaromyces.*

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