THE CLASSIFICATION OF THE HYPHOMYCETES

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ABSTRACT

The classification of the Hypomycetes is discussed with special reference to spore types, conidiophore behaviour and initiation and development of spores. Eight basic morphological spore types are recognized: the blastospore, the gangliospore, the phialospore, the porospor, the arthrospore, the meristem arthrospore, the spiculospore and the chlamydospore. No taxonomic significance is attached to the chlamydospore. It is pointed out that the forms now placed in the Mucidiaceae, the Dematiaceae, the Tuberculariaceae and the Stilbaceae of Saccardo may be placed in six Families as suggested by the author earlier: (i) the Torulaceae (Type genus, Torula Pers. ex Fr.) for those producing blastospores; (ii) the Bactridiaceae (Type genus, Bactridium Kunze ex Fr.) for those producing gangliospores; (iii) the Tuberculariaceae (Type genus, Tubercularia Tode ex Fr.) for those producing phialospores; (iv) the Helminthosporiaceae (Type genus, Helminthosporium Link ex Fr.) for those producing porospor; (v) the Geotrichaceae (Type genus, Geotrichum Link ex Sacc.) for those producing arthrospores; and (vi) the Coniosporaceae (Type genus, Coniosporum Link ex Fr.) for those producing meristem-arthrospores. The Families are subdivided into Sections on the basis of characters of the conidiophore related to spore initiation and development, the presence or absence and nature of "sporogenous cells", the presence or absence of "separating cells" and certain distinct modes of spore formation which are outlined. Twenty-four Sections are delimited and tentatively keyed out: thirteen in the Torulacea, four in the Bactridiaceae, two each in the Tuberculariaceae, the Helminthosporiaceae and the Geotrichaceae, and one in the Coniosporaceae. A separate Section is provisionally suggested for forms producing spiculospores. Typical examples of genera for each Section are given together with illustrations. Some of the difficulties still requiring solution are mentioned, including those relating to speculations about the classification of the Hypomycetes general types inadequately or imperfectly understood are an urgent necessity.

Although Saccardo's (1880, 1886) classification of the Hypomycetes has been in wide use ever since it was first proposed and later elaborated in the Sylloge, there has been much general dissatisfaction with it. It is now generally agreed that the primary criteria on which the Mucidiaceae, the Dematiaceae, the Tuberculariaceae and the Stilbaceae of Saccardo were separated by Saccardo are not sufficiently reliable (see Hughes, 1953a; Subramanian, 1958). In the search for better criteria for classification, which are a pre-requisite for good taxonomy, significant approaches have been made by Vuillemin (1910a, 1910b, 1911; see also Langeron & Vanbreuseghem, 1952), by Mason (1933, 1937, 1940, 1941), by Hughes (1953a, 1958) and by Tubaki (1958). Of these, the most outstanding and original contributions came from Vuillemin and Mason: the former initiated sound thinking about the different morphological categories of spores aimed at serving as a sound basis for a good classification; the latter extended these ideas further to include the biological spore types—the "slimy spore" and the "dry spore"—and made the first serious attempt to fix generic concepts based on non-nominal spore types. It is no exaggeration to state that Mason also inspired much critical work aimed at a solution of the pressing problem of classification of this important group, of which the most notable has been that of Hughes, paving the way for the scheme later proposed by him (Hughes, 1953a). The concepts of the "slimy spore" and the "dry spore" (= the Gloeosporaceae and the Xerosporeae respectively of Wakefield & Bisby, 1941) and the "aquatic spore" (Ingold, 1942), although very significant biologically, may not provide a more satisfactory basis for classification than the morphological features that are seen in the twin processes of initiation and development of spores. I have indicated elsewhere (Subramanian, 1962) the need to apply Hughes' system, suitably modified where necessary, to those genera of the Hypomycetes whose nomenclatural types are adequately known. I believe that an analysis of the spore types seen in the Hypomycetes should be the first step towards arriving at an arrangement of these genera.

What then are the basic spore types which may be recognized for purposes of classification? I believe that the following six distinct morphological categories of spores (see Subramanian, 1962) may be recognized:

1. the blastospore, formed as a blown-out end from any cell on a fertile hypha or, where spores develop in acropetal chains, from the previously formed spore as well;
2. the gangliospore, developed by the transformation of the swollen tip of a hypha into a spore: a spore initial may or may not be delimited;
3. the phialospore, derived from the tip of a phialide in succession, exogenous or endogenous, sometimes grouped in false heads at the tips of the phialides, sometimes forming basipetal chains. The phialospores are usually thin-walled. The phialide is a unicellular structure which is usually terminal on simple or branched conidiophores and is oval to sub-cylindrical to flask-shaped or subulate, often
with a distinct basal swelling and a narrow distal neck, with or without a terminal collarette;

4. the porospor, formed through minute terminal or lateral pores on the wall of the conidiophores: such spores are usually rounded at the base and even in contour except for a basal pore corresponding in position to its point of attachment to the conidiophore;

5. the arthrospore, formed as a result of septation and breaking up of simple or branched hyphae;

6. the meristem-arthrospore, formed at the tip of the conidiophore which remains meristematic, and differentiated in basipetal succession: such spores may or may not form chains. The conidiophore is sometimes poorly differentiated and its tip imperceptibly merges with the chain of conidial initials which exhibit a gradual maturation towards the distal end of the chain.

A seventh spore type, the spiculospore (Subramanian, 1962) may also be delimited: such a spore is formed at the tip of a pointed structure often elongate and so resembling a spike, as in Hirsutella and Anataphomycetes. Further work appears necessary, however, before this spore category can be accepted for any formal taxonomic grouping. Besides these, an eighth spore type, the chlamydospore (Fig. 39), may also be recognized. The chlamydospore is a thick-walled thallospore formed from pre-existing elements of the vegetative hyphae (and sometimes of spores) and biologically serving for perpetuation and not meant for dispersal. In contrast to the other seven spore types delimited here, which are "dispersal spores" the chlamydospore is a "sedentary spore" (Gregory, 1952); it is found in all groups of fungi and is of particular taxonomic significance even in the delimitation of genera.

It has been suggested (Subramanian, 1962) that, on the basis of spore types, the Hyphomycetes may be divided into six families as follows:

1. Torulaceae: Hyphomycetes producing blastospor. Type genus Torula Pers. ex Fris.
5. Geostrichaceae: Hyphomycetes producing arthrospore. Type genus Geostrichum Link ex Sacc.

The main purpose of this paper is to present the further classification of the Hyphomycetes at the subfamily level.

Although the basic spore types already referred to have been delimited on the basis of their mode of initiation and development, certain well-defined differences in spore development within each of these spore types can be recognized. Thus, there can be:

1. production of a single solitary spore, terminating the growth of the conidiophore;
2. production of successive solitary spores by
   (a) meristem activity of a sporogenous cell such as a phialide;
   (b) proliferation of the conidiophore through scar of fallen spore;
   (c) sympodial growth of the conidiophore and formation of spores repeatedly from new growing points produced sympodially;
3. production of successive spores in chains by
   (a) acropetal budding (acropetal chains):
   (b) meristem activity of the conidiophore tip or sporogenous cell such as a phialide (basipetal chains);
   (c) sympodial growth of the conidiophore and formation of spores repeatedly from new growing points: basipetal chains different in ontogeny from those of 3(b).

Although in 3(a) the spores are formed in acropetal chains and the younger spores are usually found towards the tips of the chains, in some Hyphomycetes the spores in the chain may mature from the apex of the chain backwards. It may be noted that these different modes in spore formation are primarily derived from two components: (i) the behaviour of the conidiophore, and (ii) the presence or absence of sporogenous cells and their behaviour when present. The growth of the conidiophore may be terminated by the production of a solitary spore or spore chain formed by acropetal budding. In the formation of these acropetal chains, the conidiophore is not involved except for the formation of one primary spore which is the oldest and the lowest in position in the chain. However, in the formation of basipetal chains of spores, continued activity of a conidiophore or a sporogenous cell is always involved. In the same way, production of successive spores, either solitary or in chains, is made possible only by the meristem activity of the conidiophore tip or of a sporogenous cell such as a phialide, or the proliferating behaviour or sympodial growth of conidiophores except, of course, for the formation of acropetal chains of spores already referred to. The term "sporogenous cell" can be applied to any spore-bearing cell, but it is better to restrict its application to a spore-bearing cell which is morphologically distinguishable from other ordinary sporiferous cells of conidiophores or hyphae. Their presence may be significant. Sporogenous cells may be simple or may be formed in acropetal chains. In the case of species of Arthri- nium and Dictyothalasmum the conidiophore may be interpreted as producing a chain of sporogenous
cells in basipetal order although it can be interpreted also as a conidiophore with a basal elongating region. In the latter case it would be a basauxic conidiophore as suggested by Hughes (1953a). This is yet another feature of the conidiophore which is significant, although apparently not very common. These are some of the characters of the conidiophore which appear to be of value in classification since they are closely connected with features in the development of spores which are suggested here as a basis for classification. Characters of the conidiophore such as their arrangement or aggregation to form sporodochia or synnemata, and their branching in various ways, both of which are not closely connected with the initiation of spore development, and also the arrangement of sporogenous cells on conidiophores are perhaps of subsidiary importance in the subdivision of the Families into groups. These and other characters would, however, be of value in classification at the level of the genus and subgeneric taxa.

Yet another character which is important is the mode of insertion of the spore on the conidiophore. It is noteworthy that Costantin (1888) attached importance to this in a classification he proposed for over one hundred genera now placed in the Mucorinae and the Dematiaceae of Saccardo. The presence of a separating cell separating the spore from the conidiophore is a feature seen in some Hyphomycetes. Such separating cells may be seen in forms producing blastospores and gaugliosporos. Although their significance is not clear, their presence would be of taxonomic value. Spores may be acrogenous or acropleurogenous; they may be exogenous or produced endogenously. The endogenous type of development may be seen in many forms classified in the Tuberculariaceae and in some of the Geotrichaceae, as defined here.

I believe that all these characters may be usefully employed in classification of the Families delimited here into Sections, of which a summary is given below with suitable examples and illustrations. No formal taxonomic groups are proposed, but only an attempt is made to delimit a number of Sections which I believe would permit suitable disposition of the majority of the genera adequately known.


The family is divided into 13 Sections:

**Section I:** The main feature of the forms placed in this Section is the presence of a "separating cell" separating the spore from the conidiophore. The spores may be solitary, e.g. *Beltranella* Penzig (Fig. 1). *Beltranella* Subram., or in simple or branched acropleurogenous chains, e.g. *Bahusathadika* Subram. (Fig. 3). These spores may be terminus spores (Hughes, 1953a) as in *Cosoplas* Pers. ex Fries (Fig. 2). They may be acrogenous or acropleurogenous. When in chains, the spores are separated from each other by distinct separating cells.

**Section II:** The hallmark of this Section is the production of spores in basipetal chains which are the result of the sympodial growth of the conidiophore and repeated formation of spores, e.g. *Trichothecium* Link ex Fries (Fig. 4).

**Section III:** The spores are terminus spores that are mostly solitary and are produced at the tip of the conidiophore and its sympodially formed successive growing points; they are pointed or apiculate at their point of attachment to the conidiophore, e.g. *Harpographium* Sacc., *Drumopama* Subram., *Thoropama* Subram., *Trirachitum* Limber, *Beauveria* Vuill. (Fig. 5).

**Section IV:** Similar to Section III except that, instead of being pointed or apiculate at the base, the spores have a distinct flat basal scar, e.g. *Pleurophragmium* Cost. (Fig. 6). *Polythriuncium* Kunze & Schm. ex Fries. The scars on the conidiophores are also flattened.

**Section V:** The spores are borne on sporogenous cells which may or may not be vesicle-like, e.g. *Draulomala* Subram., *Nigrospora* Zimm. (Fig. 7). *Zhysosporum* Mont. (Fig. 8). The sporogenous cells may sometimes be formed in acropleurogenous chains, e.g. *Sadasavinia* Subram. (Fig. 9).

**Section VI:** The spores are developed acrogenously or acropleurogenously in simple or branched acropleurogenous chains and mature in acropetal order, e.g. *Torula* Pers. ex Fries (Fig. 10). *Septonema* Corda, *Cladosporium* Link ex Fries, *Lacellilza* Subram., *Lacinopsis* Subram.

**Section VII:** The spores are formed in acropetal chains as in Section VI, but mature from the apex backwards in the chains, e.g. *Fernonia* Tode ex Schw. (Fig. 11). *Draulomala* Subram.

**Section VIII:** The spores are produced in acropleurogenous chains, without any sympodial growth of the conidiophore as in Section II, e.g. *Scopulariopsis* Bain. (Fig. 12). The conidiophores (annellophores) show annellations.

**Section IX:** The spores are produced successively from the tip of the conidiophore by proliferation, but do not form chains; the conidiophores are annellophores showing typical annellations, e.g. *Annellophora* Hughes (Fig. 13). *Sigmia* Sacc., *Septidium* Arnaud.

**Section X:** Similar to Section IX except that the conidiophores do not show typical annellations, but repeated proliferation of the conidiophore often gives it a beaded appearance, e.g. *Sporidesmium* Link ex Fries (Fig. 14). *Deightonella* Hughes, *Edmundiaspora* Subram., *Endophragmia* Duv. & Maire.

**Section XI:** The spores are produced acropleurogenously on conidiophores. Some of the forms classified in Section VI may also show this type of development; however, the spores of Section VI form chains, whereas those of Section XI are solitary.
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Section XII: The diagnostic feature of the forms classified here is the characteristic basal elongation of the conidiophore. These conidiophores are termed basausic conidiophores by Hughes (1933b). The conidiophore may arise from a flask-shaped or barrel-shaped basal cell; the basal cell may bear a terminal, often atypical, spore prior to the elongation of the conidiophore. The spores are solitary and are borne apically and in whorls laterally between characteristically thickened septa of the conidiophore. The oldest conidia are usually produced at the apex and the youngest near the base of the elongating conidiophore, e.g. Arthrinium Kunze ex Fries, Dictyoarthrinum Hughes (Fig. 17).

Section XIII: The salient feature of the forms placed here is the characteristic development of an inverted funnel-like cell wall within the funnel-shaped apex of the conidiophore, resulting in a characteristic, conspicuous scar which is typically cupuliform, as in Hansfordiella Hughes (Fig. 18). The spores are solitary; a succession of these may sometimes be produced sympodially or by proliferation of the conidiophore.


The family is divided into 4 Sections.

Section XIV: The spores are subtended by separating cells, e.g. Balamium Wallr. (Fig. 20), Anguillospora Ingold (Fig. 21), Tetrachaeum Ingold.

Section XV: The growth of the conidiophore is determinate and is terminated by the production of a solitary apical spore. The spore initial is invariably cut off early from the parent cell or conidiophore and the wall of the spore is continuous with that of the conidiophore on which it is attached, e.g. Bactridium Kunze ex Fries (Fig. 24), Dictyodermium Hughes (Fig. 19), Petalakia Sydow, Articulospora Ingold.

Section XVI: Similar to Section XV, but in contrast, the spores are seldom deciduous. They are always terminal. Mostly they remain attached to the hypha on which they are borne and, if detached, part of the hypha on which they are borne remains attached to them, e.g. Aegerita Pers. ex Fries, Chlamydozymes Bain., Monodictys Hughes (Fig. 22), Pithomyces Berk. & Br. (Fig. 23).

Section XVII: The spores are ishmosospores (see Hughes, 1933b), e.g. Ishmospora Stevens (Fig. 23).


The family is divided into 2 Sections.

Section XVIII: All spores are endogenous, e.g. Thielaviopsis Went, Sporochisma Berk. & Br., Chalara (Corda) Rabenh. (Fig. 26). Endosporostilbe Subram.

Section XIX: Usually only the first-formed spore is truly endogenous, e.g. Tuberculata Tode ex Fries (Fig. 27), Memmuniella Hocnuc (Fig. 28) Fusarium Link ex Fries, Cephalosporium Corda.


The family is divided into 2 Sections.

Section XX: The spores are produced acrogenously and acropleurogenously, e.g. Helminthosporium Link ex Fries (Fig. 29). The conidiophore may proliferate through scar of fallen spore and produce further spores at successively higher levels, e.g. Stemphylium Wallr., Corynespora Giussow (Fig. 30). Sometimes they may be formed in acropetal chains, e.g. Corynespora.

Section XXI: Similar to Section XX, but the spores are always acrogenous and successive production of spores is by sympodial growth of the conidiophore. Thus the spores are terminus spores. The spores may be solitary, e.g. Drechslera Ito, Curturala Boedijn, Dendryphiosis Hughes (Fig. 31), or may form simple or branched acropetal chains, e.g. Dendryphion Wallr. (Fig. 32), Alternaria Nee ex Wallr.


The family is divided into 2 Sections.

Section XXII: The spores are differentiated endogenously within the outer wall of the hyphae; the hyphae then fragmenting into units; each unit carries at either end a projecting frill formed by the hyphal wall, e.g. Coremiella Bubak & Krieger (Fig. 33), Bhusakala Subram. (Fig. 34).

Section XXIII: The spores are not formed endogenously, but by septation and simple fragmentation, e.g. Geotrichum Link ex Sacc. (Fig. 35).


Only one Section is recognized.

Section XXIV: The spores are developed basipetally usually from poorly differentiated conidiophores which have a meristemetic region towards the tip so that the conidiophore merges imperceptibly with the spore initial. The spores may be solitary or, more usually, in chains, e.g. conidial Erysiphe (Fig. 39), Coniosporium Link ex Fries (Fig. 37).

Apart from the twenty-four Sections classified in the six Families, a separate Section (XXV) is tentatively provided to accommodate forms producing spiculospores, e.g. Insecticola Mains (Fig. 38), but these require further study.

A tentative Key to the Families and Sections is given below.
Key to Families and Sections

**Producing hlastospores**

Conidiophores of the basauxic type

Section XII

Conidiophores not of the basauxic type

Section I

Separating cells present

Section XIII

Separating cells absent

Section II

Conidiophores with characteristic cupulate scars

Section XIV

Conidiophores without characteristic cupulate scars

Section X

Spores in acropetal chains

Section XVI

Spores moving acropetally

Section XVII

Spores maturing from the apex backwards in the chains

Section XVIII

Spores not in acropetal chains

Section XV

Spores borne on distinct sporogenous cells

Section XX

Spores not borne on distinct sporogenous cells

Section XXI

Spores produced aerogenously

Section XXII

Spores in basipetal chains

Section XXIII

Chains formed by sympodial growth of conidiophore

Section XXIV

Chains formed by meristem-arthrospore growth of conidiophore

Section XXV

Spores formed by prolification of collidiophore through scars of fallen spores

Section XXVI

Spores not in acropetal chains

Section XXVII

Spores produced acropetogenously

Section XXVIII

**Producing blastospores**

Separating cells present

Section XII

Separating cells absent

Section II

Spores athrospores

Section XIII

Spores not athrospores

Section XIV

Spore initial usually not cut off early

Section XV

Spore initial cut off by septum early

Section XVI

Spores produced by proliferation of conidiophore through scars of fallen spores

Section XVII

Successive spores usually produced by sympodial growth of conidiophores

Section XVIII

Spores differentiated endogenously within the outer wall of the hypha

Section XIX

Spores differentiate endogenously within the outer wall of the hypha

Section XX

Producing arthrospores

Section XXI

Producing spiculospores

Section XXII

Notwithstanding what has been proposed, the problem of classifying certain Hyphomycetes producing spores of more than one basic type would remain. There does not appear to be an ideal solution for this problem (Subramanian, 1962). The scheme proposed here is tentative and will doubtless have to be amended to include examples not known to me and not covered by the Sections or to reclassify those which have probably been misinterpreted by me. There is no pretense of having aimed at the elucidation of natural relationships either. Tubaki (1938) has discussed critically the possibility of ascertaining the real relationships of the members of the nine Sections which he recognized amongst the Hyphomycetes with members of the various Families of the Ascomycetes and the Basidiomycetes. However, while correlations between the nature of the Hyphomycete imperfect stages with the Perfect stages with which they are known to be connected at first sight may be interpreted to convey certain relationships, an analysis of the distribution of the various basic Hyphomyceteous spore types in the different Orders of the Ascomycetes and the Basidiomycetes (see Table I), for instance, would soon dispel hopes of a satisfactory solution of the taxonomic problem of the Hyphomycetes by this approach. It is also significant that in ascomycetous or basidio-mycteous fungi which are considered to be closely related and are therefore classified together in a system of classification, different Hyphomyceteous spore types are seen (Table II). Blastospores, gangliospores, Phialospores and arthrospores are seen in

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**TABLE I**

Occurrence of the different basic types of Hyphomyceteous spores in the Ascomycetes and the Basidiomycetes

| Blastospores | ASCOMYCETES: Endomycetales, Eurotiales, Hymenochaetales, Hysteriales, Dothideales, Sphaeriales, Pezizales, Helotiales, Dothideales, Hypocreales, Sphaeriales, Pezizales, Ustilaginaceae, Polyporaceae, Thelephoraceae |
| Gangliospores | ASCOMYCETES: Eurotiales, Hymenochaetales, Hysteriales, Sphaeriales, Pezizales, Dothideales, Hypocreales, Sphaeriales, Pezizales, Dothideales, Hypocreales, Sphaeriales, Pezizales, Ustilaginaceae, Polyporaceae, Thelephoraceae |
| Phialospores | ASCOMYCETES: Eurotiales, Hymenochaetales, Hysteriales, Sphaeriales, Pezizales, Dothideales, Hypocreales, Sphaeriales, Pezizales, Dothideales, Hypocreales, Sphaeriales, Pezizales, Ustilaginaceae, Polyporaceae, Thelephoraceae |
| Meristematic arthrospores | ASCOMYCETES: Eurotiales, Hymenochaetales, Hysteriales, Sphaeriales, Pezizales, Dothideales, Hypocreales, Sphaeriales, Pezizales, Dothideales, Hypocreales, Sphaeriales, Pezizales, Ustilaginaceae, Polyporaceae, Thelephoraceae |

**TABLE II**

The Sections into which the Hyphomycete imperfect stages of the Ascomycetes and the Basidiomycetes may be classified, as far as is known

| Endomycetales | Blastospores (Sections 4, 6) |
| Eurotiales | Blastospores (Sections 4, 11) |
| Conidiospores (Sections 19) | Phialospores (Section 19) |
| Arthrospores (Section 22) | Blastospores (Sections 6, 24) |
| Erysiphales | Meristematic arthrospores (Section 24) |
| Hymenochaetales | Blastospores (Section 17) |
| Hysteriales | Blastospores (Section 6) |
| Dothideales | Blastospores (Sections 3, 4) |
both the Ascomycetes and the Basidiomycetes. While it is interesting to note that porospores and meristosporus arthrospores are so far known to be associated only with Perfect stages in the Ascomycetes, similar clear-cut correlations are not available in the majority of connections known. Imperfect forms corresponding to those classified in Section XVI for example, are seen in such widely separated groups as the Eurotiales, the Hypocreales, the Pezizales and the Thelephoraceae. Other similar examples would be apparent from the data presented in Table II. It is obvious that any arrangement of the Hyphomycetes based on speculations regarding their probable relationships to Perfect stages would be beset with serious difficulties, especially in view of the fact that we do not yet have a satisfactory “phylogenetic” classification of the Perfect forms. Our knowledge of the interrelationships of the forms classified in the Ascomycetes and the Basidiomycetes is not such as would permit generalizations regarding the interrelationships of the Hyphomycetes as a whole. For the present we shall have to be content with an artificial arrangement of the genera of the Hyphomycetes in which those which are basically similar in certain features which are considered significant are brought together. Even if it were possible to evolve a perfect classification of the Ascomycetes and the Basidiomycetes, it may still be that we may never be able to predict the likely niche of any Hyphomycete in a Perfect classification. All the same, we have a good deal yet to do towards the detailed study of generic types in this group which, if carried out with precision and thoroughness, would provide the basis for a complete and improved classification of the Hyphomycetes which is urgently needed.

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Fig. 1-9
Figs. 10-17.
Figs. 18-25
(18 after Deighton; 19, 22, 24, 25 after Hughes; 20 after Hughes and Hennebert; 21 from Barnett; 23 from Ellis).
Figs. 26-32


(26 from Barnett; 27 after Booth; 29, 30 after Ellis; 31 after Hughes; 32, 32 after Subramanian.)
Figs. 33-39
(Section 25). 39. Chlamydospores of Fusarium. (33, 35, 37 after Hughes; 36 after Yarwood; 38 from Barnett; 34, 39 after Subramanian)