COMMENTS ON THE FIRST RESULTS OF THE
INTERNATIONAL COOPERATIVE WORK ON CRITERIA
USED IN CHARACTERIZATION OF STREPTOMYCETES

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SUMMARY. In the characterization of the taxonomic criteria of Streptomyces species, or so-called "species groups," the property in question is to be defined considering the extreme polymorphism of these organisms, and taking into account all sources of error, and problems which may arise in the course of identification. Based upon their own investigations and analysing the summarised data of the cooperative work, the authors came to the conclusion that the properties assigned by the Subcommittee to be studied can be separated with certainty only according to the following scheme:

Morphology of sporophores: 1, Rectus flexibilis. 2, Spira. 3, Verticillatus rectus flexibilis. 4, Verticillatus spira.

Colour of substratum mycelia: 1, Yellow-brown. 2, Yellow-brown + red. 3, Yellow-brown + blue (blue or violet or red-blue with indicator-character). 4, Yellow-brown + green.

Colour of aerial mycelium (more precisely that of spores): 1, Niveus (snow-white). 2, Griseus (yellowish to greenish-grey). 3, Venetus (blue-grey to blue-green to green-grey). 4, Cinereus (ash-grey). 5, Cinnamoneus (light carmine to brownish). The possible confusion of the spore-colours "griseus" and "venetus" may be eliminated by the simultaneous study of four other properties (i.e. structure of sporophores, melanin-reaction, habits of the aerial mycelium, spore surface), as the latter occur in characteristic combinations with these spore colour-groups.

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The results of the first international cooperative work (10,15) organized by the International Subcommittee on Taxonomy of Actinomycetes in 1960, proved to be extraordinarily instructive with regard to the usefulness of the most important characteristic properties used up to now in the identification of ray fungi. It is a fact that the summarized results of this cooperative work show, in many respects, the most considerable divergence of opinions, and the question is raised whether several of the studied characteristic properties (structure of sporophores, colour of substratum mycelia, etc.) can be used at all in the further taxonomic work. Krasil'nikov et al. (8) have pointed out that one substantial source of differences of opinion, and of the dubious or rather improper morphological- and colour-typifying might be the fact that the concept of the characteristics to be examined had not been clearly and finally determined.

The strict, conceptual definition of characteristic properties is of the utmost importance in the taxonomic work. Thus, for example, those studies which gave a real basis to the colour-group determination of spores (2,5,6,11), exhibited the decreased dependence of spore-colours on the composition of culture media, and abolished all spore-colour determinations based upon the colour of the substratum mycelia, or that of the soluble pigments, greatly promoted the advance of our knowledge in taxonomy. The summarised results of the cooperative work show that we are still in debt for the generalised conceptual definition of many properties. On the other hand, the data obtained from numerous investigators render possible the performance of simplifications and separations in the field of typifying of substratum mycelium- and spore colour-groups, of the structure of sporophores, etc. which may in time contribute to the more precise and unequivocal determination of these properties, and cancel the differences of opinion as well.

The Colour of the Substratum Mycelia

The colour of the substratum mycelia or colonies is one of the oldest characteristics which have been used in the identification of ray fungi. Undoubtedly, the colour of the endopigments of the substratum mycelia is a very striking property, and quite often the experienced taxonomist may be directed by it—with the simultaneous consideration of

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some other properties—in the search for relationship. Some authors (1, 3, 4, 12, etc.) take this property for the basis of separation of subspecies, groups, sections, and series; moreover, it is taxonomically preferred by them to the colour of spores. Others (2), however, found it to be so variable that they did not use it in the identification of groups or of species. Table 1 shows a few colour-scales recommended by different authors for the determination of species or "species-groups." Considering the abundance of colour of most of these scales, and the colour changes depending on the age of cultures and the composition of culture media, one can understand the difficulties to be overcome if a "precise" colour-determination is required.

In the course of our investigations we came to the conclusion that the accuracy of colour-determination of the substratum mycelia can be increased only by taking into account the following:

1. No species or species group can be characterized by colourless or white substratum mycelia.

2. The substratum mycelia of strains of Streptomyces, no matter to which species or species-group they belong, exhibit a yellowish or brownish hue at least in a certain period of their growth.

3. The yellowish and brownish hues either cannot or only slightly be discriminated in a way characteristic of species or species-groups. Differences which occur cannot serve as a basis for accurate identification.

4. Only certain species are able to produce further red, or blue, or blue-red with indicator character or green endo-pigments which on certain diagnostic culture media and at least in a certain period of growth entirely suppress the "yellow-brown" ground-colour endowing the substratum mycelium with uniform red, or blue, or green colour.

5. An indispensable requirement is at every colour identification the distinct determination of the degree of grey-scale, and the application of the latter at the colour-group ranging.

Considering the above criteria, the colour-determination of the substratum mycelia of actinomycetes may be made, in our opinion, only according to the following scheme.

- a) Yellow-brown: The colour of the substratum mycelium exhibits different hues of yellow and brown in all diagnostic culture media and in all periods of growth.

These "yellow-brown" colours may be shaded by grey in all degrees—from almost colourless light grey through dirty white to black.

- b) Yellow-brown + red: The substratum mycelium produces, at least on one diagnostic culture medium and in a certain period of growth, red or pink endopigments to such extent that both yellow-brown ground colour and grey shade are entirely submerged, and the mycelium becomes pronouncedly red.
- c) Yellow-brown + blue: Like in b) except that the endopigment is not red but blue or violet, or blue-red with indicator character.
- d) Yellow-brown + green: Like in b) but the endopigment is green.

Using these colour groups the following observations have been made. First, the colour typifying of strains can be carried out with the greatest certainty. Secondly, such deviations in the composition of diagnostic culture media, caused, for example, by variable trace element content of tap water (the control of which involves great difficulties) do not affect the determination of these colour-groups.

Taking the above into account, let us examine the summarized data of the cooperative work. The data of colour analysis obtained from the participants in the cooperative work are grouped according to the described principles in Table 2. It is to be noted that we do not intend to deal with data of strain No. 5, as this organism is somewhat variable in certain properties, probably a heterokaryon. In addition strain No. 22 proved to be a *Nocardia*, therefore its treatment was omitted from this paper. In the second subcolumn of the table the data for the grey-scale have been united ("colourless," dirty white, white, light grey, grey, dark grey, black). It should be seen that one of the degrees of the grey-scale is represented in the substratum mycelium of all strains. On the other hand, the grey-colour is not exclusively characteristic of any strain, i.e., it has no independent diagnostic value. In the third subcolumn the summarized data of the yellow and orange colour determinations are presented. In the fourth subcolumn the number of the brown colour determinations can be seen. The data of the last two subcolumns firmly demonstrate that the hardly distinguishable hues of yellow and brown are undeniably present in the substratum mycelium of almost all strains.

Table 1. Colour-scales for the determination of colour of the substratum mycelium presented by different authors.

Krasil'nikov 1949	Gauze et al. 1957	Flaig et Kutzner 1960	Baldacci 1959	Waksman 1961	Szabó et Marton 1962
Colorless	Colorless	Colorless	Colorless	Colorless	Yellow-brown
Yellow	Yellow	Brownish to dark brown	Yellow to yellow-brown	Colorless to yellow	Yellow-brown + red
Lemon-yellow	Yellow-brown	Brown	Yellow to green-yellow	Yellow	Yellow-brown+blue (violet, blue or blue → red)
Red-yellow	Brown	Brownish-gray		Yellow to orange	
Yellow-orange	Brown-black	Brownish to rose-red	Yellow with green and pinkish spots	Colorless to olive buff	Yellow-brown + green
Brownish-yellow	Red-brown			Dark gray to black	
Orange	Red	Reddish			
Brown	Orange	Orange	Brown to black	Orange	
Black	Blue	Pink to dark red	Brown to green-brown	Red	
Black-violet	Blue-violet	Orange-brownish	Brown	Red to blue	
Violet	Violet	Violet	Orange	Green	
Red		Red or blue violet	Flesh-rose	Brownish to green	
Blue		Blue-purple	Red	Brown to black	
Blue → red		Bluish-green	Violet-blue-red		
Green		Yellowish-green to green	Lemon-yellow- creamy colored		
Blue-green		Greenish Greenish-gray			

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Table 2. The colour of Streptomyces colonies (substratum mycelium) of the international collection based upon data from various laboratories and according to our typifying scheme.*

Strain No.	Grey-scale ("colourless," dirty white, white, light grey, grey, dark grey, black)	Yellow + orange	Brown	Red + orange (red)	Violet	Green	Blue
1	55	37	29	--	--	--	--
2	10	45	47	--	--	1	--
3	56	44	21	1 (1)	--	31	--
4	78	16	19	25 (19)	--	--	--
6	2	75	12	9 (1)	--	2	--
7	50	44	13	9 (3)	--	2	--
8	73	44	6	--	--	--	--
9	39	66	27	--	--	--	--
10	57	23	28	17 (8)	1	--	--
11	59	29	34	6 (1)	4	1	--
12	42	12	55	9 (5)	4	1	--
13	77	--	31	--	--	43	3
14	2	91	--	76 (27)	3	--	--
15	72	4	11	--	--	2	3
16	65	26	14	--	--	6	--
17	28	58	21	--	--	2	--
18	46	10	30	3 (3)	23	--	4
19	5	1	--	51 (51)	44	--	--
20	17	65	27	10 (1)	--	2	--
21	56	--	39	--	2	27	3
23	5	26	60	--	--	--	--
25	21	27	14	65 (41)	--	--	--

* 1. Table 2 contains the summarized results of the first experiment of the international cooperative work organized by the "International Subcommittee on Taxonomy of Actinomycetes" in 1960 with regard to the colour of the substrate mycelium from the point of view of the disciplines established in our paper. The data include those obtained in our laboratory as well.

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Table 2. (continued)

Strain No.	Colour-group	Inestim- able data
1	Yellow-Brown (66)	-
2	Yellow-brown (92)	1
3	Yellow-brown + green (65 + 31)	1
4	Yellow-brown + red (29 + 25)	-
6	Yellow-brown (87)	3
7	Yellow-brown (57)	5
8	Yellow-brown (50)	-
9	Yellow-brown (93)	-
10	Yellow-brown (51)	9
11	Yellow-brown (63)	6
12	Yellow-brown (67)	10
13	Yellow-brown + green (31 + 43)	3
14	Yellow-brown + red (42 + 76)	3
15	Yellow-brown (15)	5
16	Yellow-brown (40)	6
17	Yellow-brown (79)	2
18	Yellow-brown + violet (40 + 30)	-
19	Yellow-brown + violet (0 + 95)	-
20	Yellow-brown (92)	3
21	Yellow-brown + green (39 + 27)	5
23	Yellow-brown (86)	-
25	Yellow-brown + red (17 + 65)	-

2. At the beginning of the collective experiments the board of the International Subcommittee on Taxonomy of Actinomycetes announced the participating investigators the eleven membered colour scale which should be taken into account in the determination of the colour of the substrate mycelium. In this way the possibility of the use of an infinite number of colour varieties has been eliminated.

3. The 32 laboratories participating in the collective investigations studied the colour of the strains in three experimental periods. Theoretically this would provide 96 results of analysis for every strain. In fact the number of results of the summarized analysis is extremely different. The cause of this may reside in two facts: (a) the prescribed observations were not performed by every investigator with all strains at every time interval, (b) in some cases the colour of the substrate mycelium of the strains examined was found to be characterizable by the use of more than one colour of the scale. In the latter case every colour indication was regarded by the subcommittee as the result of a separate analysis.

In only two strains, Nos. 19 and 15, may doubt be cast on this fact. Strain No. 15, however, has grown very poorly and atypically on glycerol-asparagine-agar prescribed by the Subcommittee, while in the substratum mycelium of strain No. 19 the red-violet pigment was predominant during the whole period of observation. The determination of colour is carried out in practice not only on a single culture medium, but by the application of a series of diagnostic media. Inoculating the latter with strain No. 15 and No. 19, one can easily be convinced that their substratum mycelium becomes a yellow-brown in many cases.

In the next four subcolumns of Table 2 the analysis data for red, violet, green and blue colours are given. So-called pure-blue Streptomyces was not encountered in the collection of strains. The summarized data of red + orange are given for those strains which exhibited red pigmentation. In case of orange, there exists a source of error by confusing this colour, either with a hue of yellow (yellow and orange are united in subcolumn 3 for this reason), or with a fainter yellow-shaded tone of red pigmentation. In this way orange may be present twice in our table. The validity of our considerations may be supported by the following: In strain No. 25, red and orange colours are indicated by 41 and 24 data, respectively. It is obvious that the substratum mycelium of this strain contained, besides its yellow-brown ground-colour, red pigment too, which under certain circumstances, in combination with the ground-colour, appeared to be "only" orange. In fact, orange means in this case a hue of red. Different is the situation with strain No. 10. The red, orange and yellow-brown colours are indicated by 8, 9 and 51 data, respectively. In this case the strong tendency of the substratum mycelium towards colourless and white colour (28 + 21), in a certain period of growth, should be taken into account, when the pronounced red colour of the aerial mycelium penetrating through the substratum mycelium, may suggest a false red or orange colour, etc.

It is to be seen from Table 2 that in case of 8 strains the yellow-brown ground-colour is supplemented by further pigments. This, with strains No. 3, 13 and 21 green, with strains No. 4, 14 and 25 red, with strains No. 18 and 19 violet. In the last subcolumn the summarized data of colour-indications contradictory to the grouping are given.

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Strains No. 18 and 19 belong essentially to the yellow-brown + blue group, together with species producing violet and blue-red, with indicator character, mycelia. It should be noted that colour groupings given in Table 2, concerning these strains, are based upon data obtained only on glycerol-asparagine agar, prescribed by the Subcommittee. As has been mentioned before, determinations must be made in practice on several culture media, for the sake of more accurate separation of blue, red and green colour groups.

Taking into account the data of colour analysis (2572) concerning the studied 22 strains, the following calculation can be made. Twenty-five hundred ten data (97.6%) could be arranged according to our scheme, while 62 data (2.4%) were inestimable. Examples of inestimable data were the following: 1 green in strain No. 2, 1 red in strain No. 3, 1 red and 2 green in strain No. 6, etc.

Considering these highly favourable statistical figures we can establish that the colour of the substratum mycelium may serve as first-class characteristic property, and the considerable difference of opinions existing between the participants in the cooperative work may almost entirely be eliminated by application of the methods described herein.

Morphological Properties

The summarized data of the cooperative work also fail to show a uniform picture with regard to the morphological properties. The differences of opinion involved not only in the typifying of sporophores but also of the judgement of branching type of the aerial mycelium. As for us, we are in agreement with the statement of Krasil'nikov et al. (8) that first of all the concepts of types of sporophores are to be cleared up, and a strain should be regarded as spiral-producing even if only a minor part of its sporophores shows real spiral turning.

Studying the collection of strains of our Institute for several years we came to the conclusion that with the strains of Streptomyces (Actinomyces) four well-defined types of sporophores and branching could be separated.

1. *Rectus flexibilis*: The sporophores are straight and wavy, the number of hooks forming complete turns is small, the occurrence of real spirals is very rare, though possible with every strain.

2. *Spira*: The sporophores are in open or compact spirals. In several cultures the number of straight sporophores may outdo the spiral ones. In extreme cases the number of spirals is fewer in comparison to straight sporophores, but never very rare (sporophore types 1 and 2 exhibit monopodial or sympodial branching of the aerial mycelium, but sporadic occurrence of verticillate branchings is also possible with all species).

3. *Verticillatus-rectus flexibilis*: Like type 1, but aerial mycelium has branching verticils. Besides the verticils, sympodial and monopodial branchings may also be observed to some extent.

4. *Verticillatus-spira*: Like type 3, but with branching verticils.

Figs. 1 to 23 show the morphological relationships of strains examined in the cooperative work on starch-agar prescribed by the Subcommittee demonstrating all observed cases of variability. In our opinion, this culture medium was suitable in the great majority of strains, though not in all cases, for morphological typifying. Not a single verticillate strain has been found. In fact, only *spira* and *rectus flexibilis* strains have been observed in the following ratios:

Spira: Strains No. 1, 4, 5, 7, 8, 9, 10, 11, 12, 13, 16, 19, 20, 21, 23, 25.

Rectus flexibilis: Strains No. 2, 3, 6, 14, 15, 17, 18.

The tendency of strain No. 1 towards spore formation is poor. Although the occurrence of spiral sporophores is not rare in this strain, its diminished frequency may be connected with the insufficiency of spore formation (considerable part of the hypha-threads and spirals remains sterile). Strain No. 2, which belongs to the *Streptomyces griseus* (*Actinomyces globisporus*) group, very rarely produces forms similar to primitive spirals. Likewise, the presence of spiral-like sporechains can be detected very rarely with strain No. 6. It is worthwhile to mention that while the preponderant majority of sporophores is of the spiral type in strain No. 20, in strains No. 9 and 23 the number of *rectus flexibilis* sporophores increases, in strains No. 11 and 12 the amount of spirals significantly diminishes, and strain No. 10 represents that type of species in which the number of spirals is few but still enough to relate this organism to the spiral group.

Naturally, this typifying refers only to starch-agar,

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prescribed by the Subcommittee. It is possible that by increasing the number of culture media, the frequent occurrence of spirals could be observed even in those strains which showed "only" *rectus flexibilis* type on starch-agar. Having no reliable knowledge concerning the nutritional factors which influence the formation of spiral sporophores, the typifying must always be referred to well-defined culture media. At present, theoretically it may be presumed that a great enough number of culture media do not exist to exhaust all the possibilities of induction of spiral-formation. On the other hand, the observance of 1 or 2 spiral sporophores cannot be decisive in typifying. In fact, in some cases it is very difficult to differentiate between a "real spira" and a "spiral-like turning." It is well known from the history of taxonomy of ray fungi that some species, described as spiral-producing on the basis of a few spiral-like sporophores observed, later proved to be *rectus flexibilis* with regard to the sporophore formation (e.g. *Streptomyces californicus*: 14, etc.).

Colour Determination of Aerial Mycelium or Spores

In spite of the fact that according to the data of literature (2, 5, 6, 11, 12) the colour of spores is a characteristic property of *Streptomyces* which exhibits great stability independently of the composition of culture media, it should be emphasized that the determination of the colour of spores requires the greatest experience and caution and may be the source of most disagreements.

Ettlinger *et al.* in 1958 (2) published a practical "colour-grouping" scheme for the determination of the colour of spores of the *Streptomyces* strains, which was completed by Hütter (6) with a new colour-group in 1962. Accordingly, the following spore colour-groups are to be discriminated: *niveus*, *cinereus*, *cinnamomeus*, *griseus*, *prasinus*, *azureus* and *glaucus*. Based on our own observations, these colour-groups proved to be very useful for practical purposes. Some modifications are, however, to be initiated by reason both of the results of the cooperative work and the requirements for reliable identification. Thus strains No. 13, 20 and 21 are ranged in the "azureus" spore-colour category by us as well as by Hütter (6). The summarized data of Küster (10), however, show that the aerial mycelium of these three

strains has been characterized by grey, blue and green colours approximately to the same extent by the participants in the cooperative work. Similar problems may arise rather with *glaucus* (blue-green) and partly with *prasinus* (green-greyish-green) spore-colours. It seems therefore advisable to unite these three colour-groups, which have been established by Pridham *et al.* in 1958 (11). In addition, the more precise definition of the concept of spore-colour "*niveus*" is thought to be necessary. Taking into account all the above the following spore-colour-groups are suggested:

1. *Niveus*. The colour of the mature aerial mycelium (i.e. that of spores) is white at least on one diagnostic culture medium and in a certain period of growth.

2. *Cinereus*. The mature aerial mycelium is ash-grey.

3. *Cinnamoneus*. The main component of the spore-colour is red. Shaded with grey, it may result in a brown tone.

4. *Griseus*. The colour of spores is a variable mixture of yellow, green and grey.

5. *Venetus*. The colour of spores is a variable mixture of grey, blue and green. (The discrimination between "*griseus*" and "*venetus*" can be facilitated by simultaneous examination of other properties. The spore-colour "*griseus*" combines with *rectus flexibilis* sporophore, melanin negativity, smooth spore-surface and "*pulverulentus*" aerial mycelium. The spore colour "*venetus*" is always accompanied by spiral sporophores, melanin-positivity, "*lanatus*" aerial mycelium and with few exceptions, by structured spore surface.)

As for us, we group the strains of the cooperative work as follows:

1. The colour of spores cannot be determined on glycerol-glycine-agar: Strains No. 7, 9, 15, 16.

2. *Niveus*: Strains No. 1, 14, 19.

3. *Cinereus*: Strains No. 3, 4, 5, 6, 8, 11, 12, 18, 23, 25.

4. *Venetus*: Strains No. 13, 20, 21.

5. *Cinnamoneus*: Strain No. 10.

6. *Griseus*: Strains No. 2, 17.

Strain No. 17 usually forms white, sterile aerial mycelium and does not produce spores on glycerol-glycine-agar. After prolonged cultivation, however, it produced the characteristic "*griseus*" spores in spots and in sector-like fashion.

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The determination of the "niveus" spore colour in strain No. 14 and chiefly in strain No. 19 was greatly disturbed by the red or red-violet colour of the substratum mycelium and by the soluble exopigment. Strain No. 2 represents the sort of "griseus" spore colour which contains no or the slightest shade of green. The "cinereus" aerial mycelium of strains No. 11 and 12 exhibited a transient weak red shade during maturation. On the contrary, the red hue of the aerial mycelium of strain No. 25 was due to the substratum mycelium.

Strain No. 16 should also be mentioned in brief (Streptomyces sulphureus). This organism produces intensive yellow, greyish-yellow aerial mycelium on certain culture media. That is to say, it belongs to the "griseus" colour group. (Strain ATCC 3007 of Streptomyces sulphureus is regarded by Ettlinger *et al.* (2) as identical with the very species of S. griseus). As has been shown, however, the sporophores of strain No. 16 have been qualified as spiral, which contradicts the fact of stable property-combination concerning "griseus" spore-colour and rectus flexibilis sporophore. It is interesting that Krasil'nikov *et al.* (8) qualify the sporophores also of strain No. 2 as spiral and range this strain in the globisporus group, although this group is otherwise characterized by straight sporophores. It is fact, however, that the real spirals are not frequent in the cultures of Strain No. 16 either, and we are facing here an organism which stands on the critical borderline of being susceptible to typification. This is reflected by the results of summarized analysis of the cooperative work: rectus 14.6%, flexibilis 26.0%, retinaculum 44.0%, spira 15.6%. In reality, there are exceptions to all seemingly stable combinations of properties, and therefore the progress of taxonomical investigations in the future will depend on increasing the number of properties to be studied.

The importance of accurate conceptual determination of the terminology used in taxonomy cannot be emphasized sufficiently. In our opinion, the results of this cooperative work have provided rich empirical material and contributed greatly to the elucidation of certain concepts and to the solving of seemingly extreme differences of opinion.

Strain 1

Strain 2

Strain 3

Strain 7

Strain 8

Strain 9

Strain 10

Strain 11

Strain 12

Strain 13

Strain 14

Strain 15

Strain 16

Strain 17

Strain 18

Strain 19

Strain 20

Strain 21

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