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ANALYSIS OF THE SPECIES CONCEPT IN THE GENUS *TABANUS* L. (*DIPTERA*) AS SHOWN BY TAXONOMIC PRACTICE

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„Enoncer clairement ses opinions sur la nature de l'espèce est pour un naturaliste l'épreuve la plus redoutable de toutes"
(A. de Candolle, 1855, p. 1068).

I. INTRODUCTION

This work is concerned with the analysis of the species concepts which have been applied in one of the fields of taxonomy, in European research on species of the genus *Tabanus* L.

The work falls into two parts – the first, the historical part, contains a discussion of a model of species in descriptive systematics and an examination of what is considered as a species by different authors, beginning with Linnaeus and continuing up to the present time. Particular emphasis has been laid on the determination of concepts which have been applied in the taxonomy of *Tabanus* L. The present state of knowledge represented by followers of the Brauer trend has been taken as a basis for comparison.

In the second part of the work data are given illustrating the morphological variability, the extent of hiatus and the specific characters of *Tabanus* L. In the light of the above, the concept of species which should properly be applied in examinations of this systematic group, is discussed in detail.

The range of problems connected with the idea of biological species is now extremely wide, but in the 18th century and the first half of the 19th, problems of species were confined to the realm of systematic problems, and continued to be discussed within it. The idea of species in this period forms an integral part of systematics (Agassiz 1869, Besnard 1864). Ever since Darwin the species has formed a basic unit, in relation to which generalisations are made by representatives of various biological fields, e.g. the evolutionists (Darwin 1858), zoo-geographers (Rensch 1929, Mayr 1947), experts on genetics (Dobzhansky 1959). The representatives of descriptive systematics are those least active in the field of the concept of species. Wheeler's statement (1939, acc. to Beckner 1959) that "taxonomy has no theory" is of great significance. It may be said that during a certain period descriptive systematics withdrew from this sphere of theoretical activity. It is obviously impossible to use a unit in everyday practice without taking into consideration what it represents. The work "The new systematics" J. Huxley (1941) forms an attempt at restoring the general biological values to research on systematics. The authors put forward in this work propositions concerning: 1) the objectivity of species, 2) population as a basic descriptive unit and 3) the significance of different criteria in the definition of species. The fundamental aim of research of systematics is, according to J. Huxley (1941) "detecting evolution at work"

Other aspects of the value of systematics are presented by Simpson (1945) in stating: 1) that it collects together for purposes of synthesis all data on species, 2) species described on the basis of morphological features are, in the majority of cases, confirmed by genetic, ecological or other research.

The situation is not at present completely elucidated. Many research workers (e.g. Gilmour 1941) question the naturalness of the natural species, considering it only as a unit in the hierarchical system with only ordinal importance. On the other hand certain other research workers (e.g. Cain 1945) assume that species distinguished by description form a different category from those distinguished by ecological or other investigation. This standpoint is dangerous from the point of view of general biology. With progressive specialisation and the increasing tendency to separateness of different biological disciplines, the establishment of common basic units becomes increasingly important. If this condition is not adhered to we exclude the possibility of transfer of any regularities of a morphological nature to ecological or genetic units and vice versa.

With taxonomy itself tendencies change as to the way in which species is understood, it being treated as a unit with either a wide or a narrow range of variation. This results in analysis of the basic unit of research in taxonomy such as is the species, being very appropriate.

The great majority of works concerned with taxonomy contain only a morphological description of the species and data on its occurrence. An explanation of the species concept applied in a given work is very rarely encountered in papers of this type. This creates the impression that a taxonomist publishing numerous detailed works is not interested in, or does not apply in his scientific activities, any concept of species. A superficial analysis of results is enough to show that the theory of species and taxonomy have developed independently of each other. In this connection it is necessary to discuss the meaning of the term used in this work "species concept", and on what principles this concept is discussed in publications, the authors of which do not express their general views on the subject of species.

The dictionary definition of "concept" is an opinion formed on the basis of an analysis of data, as to the problem to which the given concept applies. In taxonomy the species concept overlaps to a certain extent with the definition of species, but is however more detailed than the latter and more precise in the definition of the general properties of the unit, since it provides a clear reply to the question what is the biological species. The concept of species is therefore in a certain sense its model. It contains the following elements: 1) confirmation of the objectiveness or reality of species distinguished by description and, 2) definition of the range of morphological variation and the character of such variation; 3) definition of the hiatus between species; 4) definition of characters which are of essential significance in determining specific appurtenance.

These four elements differ greatly from each other as to their degree of significance. Confirmation of the objectiveness of species forms the cornerstone in the species concept, particularly important to taxonomy, since it is aimed at distinguishing units of a biological character. Morphological analysis is merely a means leading to this end. This element is as a rule constant in all concepts of species. The character of morphological variation is defined in different ways, depending on the general state of research of the group and the views held in science. Characters distinguishing the species and extent of the hiatus are established separately for each systematic group.

The species concept in taxonomy is therefore a general opinion consisting of confirmation of the objectiveness of species, and working hypotheses defining the permissible range of morphological variation within the species and of those characters of structure which are most suitable for defining the specific separateness.

Every scientific worker on systematics, using descriptive methods, has his own working opinion as to these fundamental questions. This opinion does not necessarily have to be the result of consideration of the species concept, in fact it is often assumed completely unconsciously, but however decides on the results of research work. It may even be determined on the basis of results of such work. In defining material the systematics worker must consider and decide whether the deviations in structure observed are the expression of variation within the species, or exceed the specific limits. This decision depends almost entirely on the species concept used.

The theory of species therefore forms an integral part of systematics, is its methodical implement. For systematics the discussion of general problems connected with the species concept are, as Beckner puts it (1959) "not bloodless academic questions, because the battles over both the details and the foundations of the system have been and are being fought by protagonists with only one foot firmly planted in empirical material; the other foot is placed on the infirm ground of methodology .

Theoretical and methodological questions connected with systematics do not always form an object of interest to workers on systematics, especially amateurs, but one or another species concept applied in works studied is always adopted as a means of research.

In the present work the definition and appraisal of the species concept applied by different authors arise from research on the species distinguished by them. Appraisal of the theoretical basis grounded only on general statements is dangerous in the case of species concept, since it sometimes happens that the views put forward are at variance with the principles which guided the research worker in his investigations of definite species. For instance, Meigen (1818) and Brauer (1887) define species as a biological unit, differentiated in nature, exact knowledge of which can be obtained under natural conditions. This opinion could be taken as evidence that both authors apply the biological species concept. Meigen (1820) distinguishes 40 species of *Tabanus* L. in Europe, of which 18 are the result of splitting individual species. Brauer (1880) does not split a single species in the 60 he described from Europe. As they dealt in the main with the same species, with at least one of them the condition of "biologicalness" was not respected, and the species concepts applied in descriptive research by both these authors are undoubtedly different. In order to make clear the influences of different concepts it is important to define which of them forms the true basis for research, and not to accept as the actual view one which has only the character of a declaration without foundation.

A short discussion must be made of the species concept used in this work, and the treatment of definite species arising from it, since the direct appraisal of results obtained by other authors depends on this. It was assumed that the biological species is a unit in nature, the objectiveness of which is expressed by the fact that it possesses a definite ecological niche – a specific way of making use of the habitat. From this definition it appears that:

1. Each biological species has a separate ecological niche.
2. The range of variation of the species is defined by ecological limits and can differ with different species.
3. For purposes of definition into separate species only those morphological features are of value which indicate the correlation between the morphological and the biological differences observed.

The definition of species given here is based on the biological concept of species put forward by Brehm (1856) and subordinates morphological characters to biological. The known variation in species and the morphological hiatus, which is difficult to assess, make it to a great extent impossible, especially in the case of the genus *Tabanus* L. to apply properties of structure as sole criterion of species. Confirmation of biological separateness of the group studied forms the main basis for determining to which species it belongs. This definition is justified when investigating the separateness of closely related species (Diver 1941, Trojan 1958) which are difficult to distinguish from the morphological point of view. The paper on systematics (Trojan 1959), which formed a basis for comparison of definite species distinguished by other authors, took into consideration the above results of ecological research.

When making a detailed assessment of trends in research, the method of description and material used were taken into consideration, in addition to the species concept. These three elements treated jointly provide a good basis for an assessment both of view, level of knowledge and actual treatment of species. Numerical methods were used wherever possible to obtain accurate data. These methods permit of discovering the predominating tendency in systematic solutions and comparing the effect of different concepts on the treatment of species in different works.

A correct assessment of species, in particular, of those described in the 18th and 19th centuries, presents considerable difficulties and involves an amount of work beyond the capacity of one research worker, especially in view of the lack of good and complete synonymic catalogues. On this account I limited my analysis of factual material to European species belonging to one genus only – *Tabanus* L. Considerable time was devoted to them even before Linnaeus. No other *Diptera*, with the possible exception of mosquitoes and synanthropical species, have had so much attention paid to them as has the genus *Tabanus* L. Bibliography discussing the commoner species today includes a great number of works, which is a somewhat exceptional phenomenon in the order *Diptera*. Almost all the more outstanding experts on *Diptera* have made an attempt at presenting this genus in monograph form, and at the present time a large number of specialists working in different countries in Europe are engaged on problems of the taxonomy of *Tabanus* L.

The number of species known in Europe has increased over the period of the last 200 years from four to about 90. The collections forming the basis of works have been greatly expanded during this time, but in older collections almost all the species now distinguished, which were previously not regarded as being separate, can be found. Differences are also found when comparing the results obtained by contemporary research workers. One and the same material often forms a basis for describing a different number of species. This indicates that in work on the systematics of *Tabanus* L. views on the biological species are especially important. The general concept, applied consciously or unconsciously, to a great extent decides the contents of the units distinguished.

During my processing of materials I discussed several of the problems encountered in this work with Dr. H. Kauri, cand. mag. L. Lyneborg, Professor N.G. Olsoufev, Professor K. Petrusewicz, Professor B.B. Rodendorf, Professor E.S. Smirnov and Professor A.A. Stackelberg. Our discussions enabled me to elucidate many of the doubts I had had as to general treatment, and also as to taxonomic solutions of many species of the genus *Tabanus* L.

The invitation I received from the Academy of Sciences of the USSR and the kindness of Professor A.A. Stackelberg made it possible for me to work on the collections of *Tabanus* L. in the Zoological Institute of the USSR Academy of Sciences in Leningrad. Professor N.N. Plavilscikov arranged for me to use the collections of *Tabanus* L. in the Zoological Museum in Moscow, Dr. M. Beier gave me access to the collections in the Naturhistorisches Museum in Vienna, while Professor C.H. Lindroth allowed me to work on the collections of *Tabanus* L. in the Zoological Institute in Lund.

I obtained additional material from cand. mag. L. Lyneborg, Professor N.G. Olsoufev, Professor F. Peus and Professor E.S. Smirnov. I should like to express my sincere thanks to all the above, nad to the institutes in which I worked.

I am also much indebted to Professor T. Jaczewski and dr. A.S. Kostrowicki for valuable criticism and to M.Sc. A. Straszewicz for revising the text.

My wife Bożena Trojanowa, M.Sc., took part in all the field and laboratory work and in the processing of material.

II. MATERIAL AND METHODS

The basis of the present work is formed by material provided by European species of the genus *Tabanus* L.

I examined the following collections in Poland:

1. Collection of Wroclaw University, identified by Scholz
2. Collection of the Jagiellonian University Cracow, prepared by M. Nowicki
3. Collection in the Silesian Museum in Bytom
4. Collection in the Tatra Museum in Zakopane identified by Bobek
5. Collection in the Zoological Institute of the Polish Academy of Sciences in Warsaw, containing valuable evidential material, including that prepared by O. Krober, Fr. Sintenis, G. Schroeder, O. Karl and others

In addition I worked on the following foreign collections:

1. Zoological Institute of the USSR Academy of Sciences in Leningrad – specimens identified by N.G. Olsoufev
2. Zoological Museum of M.G.U. in Moscow
3. Naturhistorisches Museum in Vienna. These collections contain valuable evidential material used in the works by J.W. Meigen, H. Loew, F. Jaennicke, A. Bergenstamm, Fr. Brauer, Z. Szilady and others
4. Zoological Institute of Lund University, containing the collections of J.W. Zetterstedt and the collection of Scandinavian *Tabanidae* prepared by H. Kauri.

The total number of specimens examined in the above collections was over 7000. In addition, for investigation, I used my own material collected in Poland, chiefly in the central region in the Kampinos Forest. The number of specimens caught there was over 15,000.

The results of my review of the collections helped me to arrive at an assessment of the level of systematics in different periods. I paid particular attention to material from earlier periods, but I was unable to trace the collections of *Tabanus* L. which formed the subject of the earliest works on this group. Linnaeus' collections (L y n e b o r g 1959) have undergone such farreaching transformations that it is today impossible to find the specimens which formed the objects of that author's descriptions. This applies to collections of other scientists of that period, for instance, those of Fabricius, which have suffered a certain amount of destruction. All conclusions as to the beginnings of the systematics of *Tabanus* L. in Europe were based entirely on an analysis of descriptions of species and the critical remarks as to their value encountered in the works of later authors. The position of collections originating from the first half of the 19th century is slightly better, as the specimens forming the subject of descriptions by Meigen, Fallén, Zetterstedt and Loe have been preserved. The collections made by Zetterstedt (1840, 1842–1848) and Scholz (1850) are those preserved in the form closest to the original of all the material to which I had access. Fragments of Meigen's collection (1804) cannot be distinguished from the subjects of his next work (1820) and even after combining these two collections the real contents of its species cannot be re-created today. In view of the above I used, in addition, the collections of less well-known experts on *Diptera* to describe the different periods. This made it possible to define the influence of the basic monographs on *Tabanus* L. on the results obtained by other scientists.

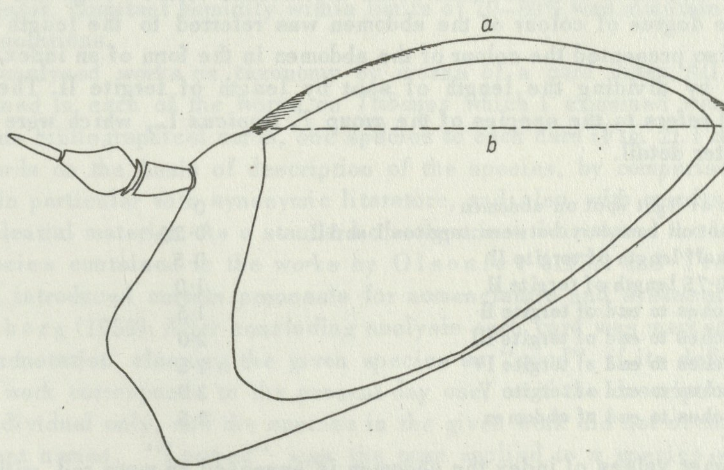


Fig. 1. Measurement of height of frons in *Tabanus* L. (diagram)

a — arc corresponding to actual height of frons; *b* — line of measurement

Pomiar wysokości czoła u *Tabanus* L. (schemat)

a — łuk odpowiadający rzeczywistej wysokości czoła; *b* — linia pomiaru

I examined morphological variations wherever possible by means of measurements. It is necessary to discuss only the measurement of the frons. When determining the height of frons the specimen was so placed that the ocellar part of the head was as clearly visible as the basal part. The measurement obtained does not give the actual lengths, as it is the chord, and not the arc corresponding to it as is formed by the frons in *Tabanus* L. (Fig. 1).

On account of the considerable variations in dimensions connected with differences in the size of individuals, I used the frons index in processing, obtaining it by dividing the height of the frons by the width of its base.

In the case of elements for which it was difficult to find numerical definition, I divided the material on the basis of agreed scales (Mayr, Linsley and Usinger 1953).

The scale of variation in colour of the third segment of the antennae is as follows:

completely red	1
basal half red, remainder brown	2
completely brown with red spot at base	3
basal half brown, remainder black	4
completely black with brown spot at base	5
completely black	6

Acceptance of this order of variation when calculating average values in a population permitted of easy definition of average colouring. The greater the average value, the darker the antennae in a given population.

In working out the scale of variation in colour of the abdomen, I measured the length of different segments and calculated the ratio between them. The least variation in dimensions during desiccation is exhibited by the longest II tergite of the abdomen, as it does not extend into the interior of the I segment. On this account the degree of colour of the abdomen was referred to the length of this tergite. I also presented the colour of the abdomen in the form of an index, which I obtained by dividing the length of spot by length of tergite II. The scale established refers to the species of the group *T. tropicus* L., which were examined in greater detail.

Absence of light spot on abdomen	0
Small spot on boundary between tergites I and II	0·25
Spot to half length of tergite II	0·5
Spot to 0·75 length of tergite II	1·0
Spot reaches to end of tergite II	1·5
Spot reaches to end of tergite III	2·0
Spot reaches to end of tergite IV	2·5
Spot reaches to end of tergite V	3·0
Spot reaches to end of abdomen	3·5

With higher values of index the abdomen is assessed as more red, with lower ones as dark.

When investigating variation I used several statistical indices, the usefulness of which for purposes of zoological systematics and definition of variation has been emphasised by Simpson and Roe (1939) and by Mayr, Linsley and Usinger (1953). I used Romanowski's methods[1] and statistical tables[2] for the calculation and estimate of these indices.

The microscopic preparations of the copulatory apparatus of males and females were made by means of the usual methods. The terminal part of the abdomen was cut off and after lixiviation was prepared under a microscope. The preparation was fixed in a mixture of glycerine and gelatine.

[1] Romanowski, W. 1951 – Zastosowanie statystyki matematycznej w doświadczalnictwie – Warszawa.

[2] Tablice statystyczne, 1957, Warszawa.

Systematic drawings were made in the following way. With the structure of the frons, antennae and palpi measurements were made of the length and breadth of each part and the distance between them. On the basis of these measurements I established the ratio of size and distance. With drawings of the frons in females I measured the height, breadth of the occelar and basal part, height of the frontal triangle and its breadth at the level of the bases of the antennae, in addition the height and breadth of the lower frontal callus, height of the central callus and, if not joined to the lower one, its distance from the lower callus.

Parts of the copulatory apparatus were projected by means of a projection microscope on to paper and the outlines of the various elements marked. Details were sketched from preparations under the microscope.

The ecological methods applied have been discussed in other publications (Trojan 1956, 1958).

In physiological experiments on longevity of the different species under different thermal conditions, the individuals brought in from field conditions were put in tens in jars covered with gauze which were then placed in the thermostat. Constant humidity within limits of 70–80% was maintained by evaporating solutions.

I analysed works on taxonomy by means of a card index. All the species contained in each of the works on *Tabanus* which I examined were entered on separate bibliographical cards, one species to each card (Fig. 2). I then analysed the cards on the basis of description of the species, by comparison with later data, in particular with synonymic literature, and also with results of a review of evidential material. As a standard of comparison I accepted the interpretation of species contained in the works by Olsoufev (1937) and Trojan (1959). I also introduced certain proposals for nomenclature and systematics made by Lyneborg (1959). After concluding analysis each card was marked with a suitable adnotation classing the given species as "good", if its definition in the given work corresponds to the present-day one, or if the description referred to one individual only, and the species in the given work did not occur under other different names. "Lumped" was the term applied to a species which I found to consist of two or more species at present considered as "good". A "split" species was one which I found to occur in a given work under two or more names.

All this analytical process was in fact a comparative examination of permissible ranges of variation in each species. I also found that the same name was often applied by different authors to a differently constructed group of individuals – the "contents" or treatment of the species by these research workers is therefore different.

In later sections of this work I have used the term "contents" of the species to emphasise the fact that I am referring to species described by many authors on the basis of other materials, by means of different methods and often on the basis of differing concepts of species. The contents of such species, despite their uniform name, do not always correspond to each other.

In addition a note was made as to whether the species was new or had been described previously. The correctness of name did not affect the assessment qualifying a given species, the chief aim was to investigate whether their distinguishing was justified. Questions of nomenclature which were both numerous and complicated were noted independently of qualitative estimates.

a

T. spodopterus Meig. — new – nowy; good – dobry

Meigen, 1820 p. 46

b

T. bromius L. — old – stary; split – rozbity; lumped – zbiorowy

Also described as:
Opisany również jako:

T. scalaris sp. nov. p. 38
T. glaucus sp. nov. p. 51

also includes:
obejmuje również:

T. maculicornis Zett.

Meigen, 1820, p. 52

c

T. tropicus L. — old – stary; lumped – zbiorowy

contains:
zawiera:

T. schineri Lyn. (1 ♂)
T. tropicus L. (1 ♂)
T. mühlfeldi Lyn. (1 ♀)
T. distinguendus Verr. (1 ♀)
T. lundbecki Lyn. (2 ♀)
T. miki Brau. (1 ♀)

Zetterstedt, 1842 coll. Inst. Zool. Lund

Fig. 2. Examples of bibliographic cards giving characters of species
a – good; *b* – split; *c* – lumped

Przykłady kart bibliograficznych zawierających cechy gatunków
a – dobrego; *b* – rozbitego; *c* – zbiorowego

Such processing yielded cards containing, in addition to names of species their characteristics, which when compared made it possible to define the number of correctly distinguished, split and lumped species, and also the number of synonymic names. I entered these data on collective cards (Fig. 3) separately for each work.

Fr. Brauer							1880
Species of *Tabanus* L. from Europe Gatunki *Tabanus* L. z terenów Europy							
Species Gatunków							
Total – Ogółem			60	New – Nowych			6
Good Dobrych	Lumped Zbiorowych	Split Rozbitych	Synonyms Synonimów	Good Dobrych	Lumped Zbiorowych	Split Rozbitych	Synonyms Synonimów
52	8	0	5	4	2	0	2
86,5%	13,5%	0%	8,3%	66,6%	33,3%	0%	33,3%

Fig. 3. Collective card – comparison of numerical data given on bibliographic cards
Karta zbiorcza – zestawienie danych liczbowych zawartych na kartach bibliograficznych

The information obtained did not always present simple connections. One species might be simultaneously split and complex, e.g., *T. bromius* L. in Meigen's work (1820) (Fig. 2) is described three times under different names, and is therefore a split species, at the same time *T. bromius* Meigen (1820) is also a lumped species, since its description and the material forming the object of this description refer to two species now considered as "good": *T. bromius* L. and *T. maculicornis* Zett. Similar examples occur in certain other works, especially in those of 19th century authors.

I used the same card index method for my work on collections but defined the contents of different species far more accurately here (Fig. 2 *c*).

Comparison of results of systematics in different periods was based on quantitative indices. I applied them both to an estimate of works on systematics, and to evidential collections. In the present work I used several such indices. They are:

1. Percentage of species correctly differentiated (*G* sp)

$$G \text{ sp} = \frac{G \cdot 100}{N \text{ sp}}$$

2. Percentage of split species (*S* sp)

$$S\ sp = \frac{S \cdot 100}{N\ sp}$$

3. Percentage of lumped species (L sp)

$$L\ sp = \frac{L \cdot 100}{N\ sp}$$

4. Index of state of systematics (Rs)

$$Rs = \frac{(N - R) \cdot 100}{N\ sp}$$

5. Increase in newly-described species (I sp)

$$I\ sp = \frac{Ng \cdot 100}{N\ sp}$$

G – indicates number of species now recognised as good, L – number of lumped species, N – number of species described as new, Ng – number of new good species, N sp – number of species distinguished by the given research worker, R – true number of species in newly-described material, S – number of split species.

Division in each case by the total number of species mentioned in a work was intended to produce relative figures, which would permit of comparison oı the results of works containing different numbers of species.

These indices make it possible to reach the opinions of the research ideas which form the basis for distinguishing species. Since they have not as yet been described in the literature to which I had access, I shall discuss the principles governing work on numerical material which enabled me to obtain information as to the species concept used.

The materials in which the number of percentage of good, lumped and split species is defined, are of significance as indices. The value of these indices is connected with the species concept applied, since from these it becomes clear whether the unit used by the scientist will be, e.g. large (variable) or small (constant). It may be assumed as a start that:

1. A large number (percentage) of species correctly distinguished indicated that the concept permits of treatment of species in practical research work in accordance with the state of knowledge we have today.

2. A large number (percentage) of lumped species is the result of using the "large species" concept. It tolerates too wide variations within the species and is the expression of lumping tendencies.

3. A large number (percentage) of split species is the result of basing work on the concept of "small species" with narrower limits of variation, and therefore forms the expression of splitting tendencies.

Low figures (percentages) do not give, in the case of the last two indices, information as to the concept of species used.

The level of methods for distinguishing of species also affects the value of these indices. In defining the concept of species both numerical data and level of knowledge in the given period and methods of research used were taken into consideration.

The importance which the different values of the index of state of systematics have for definition of the species concept require special discussion. Numerical results may be expressed in positive or negative values, or be equal to zero. Negative values of the index arise from the fact that the material actually contains more new species than the author distinguished. As an example – *T. bromius* Linnaeus (1758) contained acc. to Brauer (1880) at least two species: *T. bromius* L. and *T. maculicornis* Zett. Similarly *T. gerckei* Brauer (1880) contains two species – *T. brunneocallosus* Szil. and *T. sabulaetorum* Loew. The predominance of lumped species among those newly described leads to negative values of the index. If they are large, it is a question of lumping – a tendency to combine species. Analogically, if the number of species described as new is considerably greater than the actual figure, we have the reverse situation, over-estimation of the differences observed between the variants of variation within the species and splitting of species. In such cases the value of the index will be positive, and if large, it is a case of splitting. The state of systematics in accordance with the present-day is defined by points situated on the zero line. They correspond to those cases when the described number of new species corresponds to the true one. Incosiderable deviations from zero may be evidence of accidental errors.

III. HISTORICAL ANALYSIS OF SPECIES CONCEPT IN THE GENUS *TABANUS* L.

Preliminary remarks

Historical analysis is aimed at establishing what species concept were applied in research on *Tabanus* L., and at analysing their influence on the results of taxonomic investigations. Examination was made to see if the taxonomic solutions obtained by different scientists are close to the present state of knowledge of species, and how the present opinion on species in the genus *Tabanus* L. was established. This analysis should provide a basis for an estimate of the historical moment in which research in this systematic group stands. Comparison of the species concepts at present prevailing in research work on *Tabanus* L. and those applied in other better examined systematic groups makes it possible to foresee in what direction and from which theoretical positions research on the species of *Tabanus* L. should develop in the near future.

I set out data on species distinguished in the more important taxonomic works and collections in the form of tables (Tab. I and II). The material was arranged in chronological order and contains information as to the number of good, lumped and split species.

I compared indices calculated for different works by the same author.

Collective comparison of European species of *Tabanus* L. in outstanding works
Zestawienie zbiorcze gatunków *Tabanus* L. w ważniejszych pracach

Tab. I

Year of publication Rok wydania pracy	Author Autor	Species – Gatunki				New species – Gatunki nowe			
		total ogółem	good dobre	lumped zbiorowe	split rozbite	total ogółem	good dobre	lumped zbiorowe	split rozbite
1758	Linneus	4	1	3	0	4	1	3	0
1767	Linneus	6	2	4	0	2	1	1	0
1781	Fabricius	8	3	5	0	2	0	2	0
1794	Fabricius	11	6	5	0	3	2	1	0
1804	Meigen	17	10	5	2	5	4	0	1
1805	Fabricius	13	6	7	0	1	1	0	0
1817	Fallén	9	3	6	0	2	1	1	0
1820	Meigen	40	18	7	18	22	9	0	13
1840	Zetterstedt	11	8	3	0	5	2	1	0
1842	Zetterstedt	24	10	5	9	6	1	1	4
1858	Loew	37	27	5	5	10	9	0	1
1880	Brauer	60	52	8	0	6	4	2	0
1925	Kröber	35	28	6	2	0	0	0	0
1937	Olsoufev	54	50	2	2	3	3	0	0

Comparison of results obtained from review of collections of *Tabanus* L.
Zestawienie wyników rewizji zbiorów *Tabanus* L.

Tab. II

Year of prepared work Rok opracowania	Author Autor	Actual number of species Rzeczywista liczba gatunków	Species – Gatunki								Specimens identified Okazy oznaczone			
			distinguished in collection wyodrębnione w zbiorze *		good pojedyncze ** dobre		lumped zbiorowe **		split rozbite **		correctly dobrze		incorrectly źle	
			N	%	*N*	%	*N*	%	*N*	%	*N*	%	*N*	%
1850	Scholz	23	17	74.0	6	35.3	6	35.3	7	41.2	56	49.2	58	50.8
1873	Nowicki	27	32	118.5	10	31.2	7	21.8	11	33.3	46	46.5	53	53.5
1890	Sintenis	23	22	95.5	10	45.5	8	36.4	8	36.4	147	61.0	94	39.0
1938	Kröber	23	27	117.5	14	51.8	4	14.8	6	22.2	131	49.2	135	50.8
1910	Schroeder	19	16	84.0	13	81.4	2	12.4	1	6.2	41	85.5	7	14.5
1914	Szilady	63	61	96.7	40	65.5	13	20.6	9	14.8	2797	89.1	340	10.9
1840	Zetterstedt	15	10	66.6	6	60.0	3	30.0	3	30.0	27	52.9	24	47.1
1842	Zetterstedt	25	22	88.0	5	22.8	6	27.3	12	54.6	55	62.5	33	37.5
1848	Zetterstedt	18	13	72.2	4	30.8	7	53.9	6	46.2	64	62.0	38	38.0
1952	Kauri	27	26	96.2	21	80.8	3	11.5	4	15.4	1769	98.4	29	1.6

N – number – liczba

* – percentage calculated for actual number – procent obliczony względem liczby rzeczywistej

** – percentage calculated for number of species distinguished in collection – procent obliczony względem liczby gatunków wyróżnionych w zbiorze

Fabricius (1781) in his first work on *Tabanus* L. described 8 species, among which he distinguished 3 correctly, while the remainder are lumped species. In his next work (Fabricius 1794) of 11 species described, 6 are good, and the number of lumped species remains unchanged. In his final work Fabricius (1805) described 12 species of the genus *Tabanus* L., 6 being good and 7 lumped. In all three works taken jointly, lumped species predominate (17) over good ones (15). The percentage of the latter varies from 45.5 to 62.6. In the publications discussed distinction of species has undergone only inconsiderable changes. In relation to the results which he obtained in his first work, in the two remaining ones the percentage of species correctly distinguished is greater. There is, however, no fundamental change in the treatment of species as an unit, the species concept remains the same with Fabricius: this indicates a constant and high percentage of lumped species and absence of split species. This treatment of species is characteristic of the Linnaeus school. The species with Fabricius corresponds to the type of species called linneon (Lotsy 1916) and to lumped species (Kollektivart) of de Vries (1906). It is the unit used by workers on systematics in the 18th century, which represents the Linnaeus trend in systematics.

A different situation is revealed by an analysis of indices calculated for works by Meigen and Zetterstedt. Meigen (1804) made considerable progress in distinguishing species, if we compare his results with those of Fabricius (1794). Of the 17 described 10 are correctly distinguished. The number of lumped species has decreased also, and in this work do not exceed 30%. The second edition of this same work, however, brings fundamental changes. If in 1804 (Tab. I) split species formed 11.8% of the material, in 1820 this figure increased to 18, which forms 45% of the whole material.

Meigen in his work dated 1804 applied a concept of species similar to that of Fabricius, merely improving the means of distinguishing species. In his following work he applied a completely different approach, another working model of species – the monotypic concept reducing the range of variation (Huxley 1941). This change in concept did not involve either the liquidation of lumped species, which in Meigen's work from 1820 was 17.5%, or an increase in the number of good species, the percentage of which in comparison with his previous work (Meigen 1804) has been reduced from 58.8 to 45.0%.

We obtain similar results by comparing figures in the case of Zetterstedt also (1840, 1842), who in his first work distinguished over 72% of the species correctly on the basis of an improved method founded on the concept of linneon. In his second work (1842) the number of correctly distinguished species decreases to 41.7% as a result of the transfer to a new concept of research, in the same way as Meigen (1820) changed to the monotypic concept.

When making a preliminary examination of the working species concept in works by one author it was, therefore, found that in successive works the author either constantly used one species concept or changed it.

Great differences in the values of indices, suggesting the application of different species concepts, are found in works by scientists active during the same period, e.g. Fallén (1817) Meigen (1820). The first of them distinguished 66.7% of lumped species, the second 17.5%. Similarly large differences can be found when examining split species (Tab. I). In other cases the species concept is the same. This applies both to scientists working during the same period (Meigen 1820, Zetterstedt 1842) and to those doing research in different epochs (Meigen 1820, Kröber 1938) (Tab. I and II).

Scientists using a similar species concept were grouped by comparing the values of different indices. Data on the number of lumped and split species are of great importance here. In the comparison of data (Tab. I) zero values are found in one column only, defining the number of split species. The following scientists: Linnaeus (1758, 1767), Fabricius (1781, 1794, 1805), Fallén (1817), Zetterstedt (1840), Brauer (1880) represent a similar approach to species. In their works they do not narrow the range of variation within the species. In the majority of these works the percentage of lumped species is very high, only in two cases (Zetterstedt 1840, Brauer 1880) is it less than 50. In the first taxonomic works on *Tabanus* L., a tendency occurs to tolerate a wide range of variation within the species distinguished. This leads to the conclusion that they used the "large species" concept.

A considerable number of split species occur in works by Meigen (1820), Zetterstedt (1842) and Loew (1858a) (Tab. I). The high value of the index of split species would seem to indicate that they took the concept of "monotypic species" as a basis.

I obtained similar result when analysing evidential collections (Tab. II). Only in three cases (Schroeder, Szilady and Kauri) does the number of split species not exceed 20%, which would indicate that the correct species concept was applied. In the remaining seven cases examined we are concerned with constant distinguishing of species with an artificially narrowed range of variation, which would indicate that the monotypic species concept was applied.

Data obtained in this way are, however, only preliminary in character. When comparing the results of works which appeared at not very long intervals of time, the great differences in the values of the indices may be interpreted as resulting from the application of different concepts of species, since the level of knowledge at this time did not change greatly. When, however, a considerable lapse of time occurred between the appearance of the works such comparison is more difficult. In such cases the differences resulting from the state of knowledge of the group analysed must be taken into consideration, as the value of indices is affected both by the species concept, the prevailing state of research on the group and the methods used. The same values of indices calculated for scientists working in the 18th century will have a different significance than for research workers today.

As an approximate guide to what deviations arise from the differences in the state of knowledge, comparison was made of data concerning the three indices: percentage of 1) good species, 2) lumped species, 3) split species. These data (Fig. 4) make it possible to state that the species first described were primarily of a lumped character, since they covered two or more species today distin-

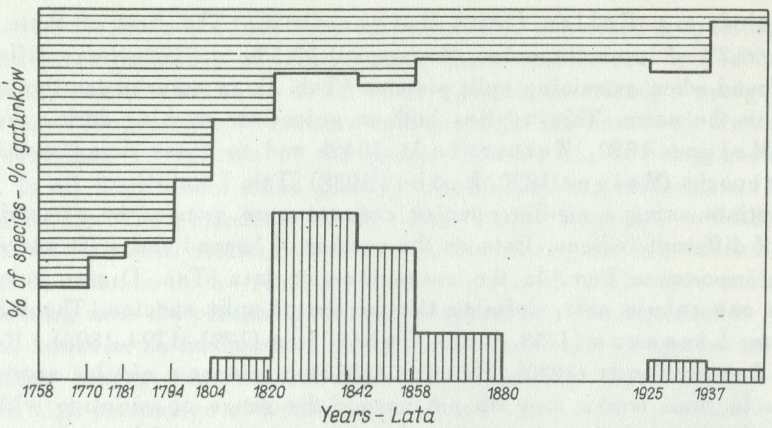


Fig. 4. Development of knowledge of species of *Tabanus* L. in Europe
Blank areas – good species; horizontal lines – lumped species; vertical lines – split species
Rozwój poznania gatunków *Tabanus* L. w Europie
Pola czyste – gatunki dobre; Linie poziome – gatunki zbiorowe; Linie pionowe – gatunki rozbite

guished as separate. The number of lumped species decreases, however, rapidly until about 1850. After that date their liquidation proceeds very slowly, they form 4–10% of the total number of species distinguished. The percentage of species correctly distinguished, fairly low in initial works on *Tabanus* L. (25%) exhibits a rapid increase until approximately 1820, from then until 1858 there is a distinct halt, or even a decrease in the distinguishability of species. It is not until after 1858 that the state of systematics begins to improve and in 1880 attains a high level. Splitting of species begins in 1804 and lasts until 1880, the appears again in the 20th century.

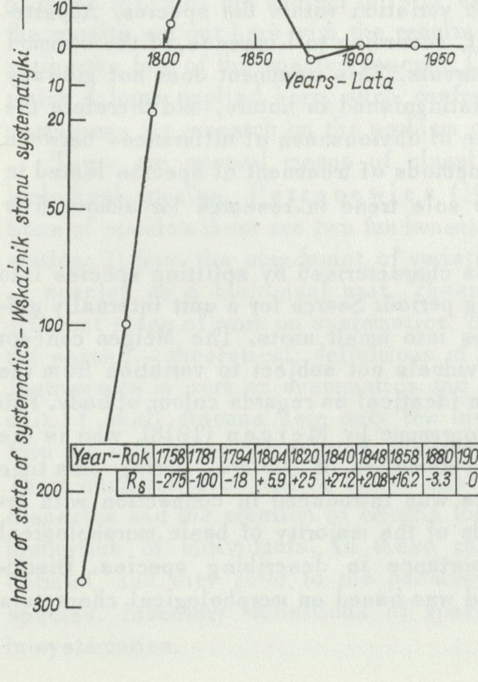
All the works and collections examined (Tab. I and II) contain a certain percentage of lumped species, i.e. including in fact two or more species now distinguished as separate. From this point of view the situation is not even today under control. Continual description and distinguishing of lumped species of *Tabanus* L. indicates that real difficulties in estimating differences between species are encountered with this genus. The greatest problem was faced by those scientists who were the first to undertake to describe and distinguish species of the genus *Tabanus* L. They were not certain what properties of structure are the expression of specific separateness, especially as no obviously apparent biological differentiation occurs here, which would make it possible to distinguish between species in another way without applying the appropriate somewhat complicated methods of research. It may therefore be assumed that during the first period the contents of the species described was decided to a greater extent by the imperfect methods of description and distinguishing than by an applied species concept; this problem will be discussed in detail later on in the present work.

Erroneous distinguishing of species must be appraised differently, now that methods are so elaborated that they permit not only of differentiation between species, but even of description of their variability. From this moment onwards, i.e. from 1800, the contents of the species has undoubtedly been decided to a greater extent by the species concept than by means of description and distinguishing used.

After taking into consideration the objections discussed above to drawing conclusions based on proposed quantitative indices, I shall begin to define the species concept which were applied for working purposes in papers on the genus *Tabanus* L. In this case the task will be combined with distinguishing between schools of research and periods in the history of research on this genus.

It is difficult to decide which of three indices (percentage of good, lumped or split species) has a decisive influence on the definition of species concept. Use of species described by preceding authors constitutes a sort of restriction on the authors of works, as they often have no access to evidential material. In addition the authority of older scientists may have had a restraining effect on the introduction of changes in the interpretation of species described previously. The author's own opinion can most clearly be described in the description of species discovered by him. Data on species described as new, processed by means of an index of the state of systematics, provides a better opportunity for defining the species concept than previous indices.

Material classed according to a time scale (Fig. 5) makes it possible to show the distinct turning points over the whole of the period examined of the systematics of European species. The first of these turning points is near 1800. It is characterised by a completely new approach to material, a change in the concept of research. We can see here a sudden move away from combining forms, often not even related to each other, into single species, to grafting new species on to units apparently possessing the rank of species. It is a transit from one extreme viewpoint to an other. About 1880 the curve approaches zero value, which is evidence that the difficulties of both the past periods have been overcome and a proper criterion obtained for defining species of *Tabanus* L.



Year-Rok	1758	1781	1794	1804	1820	1840	1848	1858	1880	1908
R_S	-275	-100	-18	+5.9	+25	+27.2	+20.8	+16.2	-3.3	0

Fig. 5. Splitting and lumping in describing new species of *Tabanus* L.

Rs – index of state of systematics

Spliterstwo i lumperstwo przy opisywaniu nowych gatunków *Tabanus* L.

Rs – wskaźnik stanu systematyki

The index of the state of systematics makes clear the regularities in the course followed by the process of recognizing species. The road leading to the present state of knowledge was not simple improvement and enlargement of the knowledge of earlier authors on the basis of one working species concept. In such case the curve would be found on one side only of the zero value and would approach zero in an asymptote. We are however, concerned with deviations on both sides, which indicate that the process of recognition follows another road, not through development and supplementation, but through rejecting the approach hitherto obtaining. This is evidence of changes in the species concept.

Deviations of the curve decrease with the passing of time, which shows that even despite considerable differences in treatment of the species, the extent of the mistakes made is increasingly smaller, and approach to reality increasingly closer. The course followed by the curve is evidence of the maintenance and decided domination of defined tendencies for a long time.

Three historical periods can be distinguished on the basis of the index of the state of systematics; in each of them a different approach to species predominates. Three sections of the curve correspond to three schools of systematics differing both as to results and to fundamental theoretical assumptions.

1. The Linnaeus period (1758–1800). In the sphere of taxonomy of *Tabanus* L. it is characterised by description of species as lumped units. The reason for this lies in the poor state of knowledge of species in this group and the application primitive macromorphological methods for distinguishing and describing. Practically speaking, the results obtained in this period do not exhibit any connection with the species concept which Linnaeus created. His definition of species is in principle indifferent to variation within the species. Appurtenance to a defined species is the result, according to Linneaus, of the common origin of individuals from one pair of parents. This treatment does not give any indication of how species should be distinguished in nature, and therefore the results obtained depended on the degree of obviousness of differences between species. The school of Linnaeus, his methods of treatment of species lasted in the systematics of *Tabanus* L., as the sole trend in research for almost fifty years.

2. The Meigen period (1800–1880) is characterised by splitting species into artificial units, in fact it is the splitting period. Search for a unit internally uniform led to splitting up natural species into small units. The Meigen concept treats this unit as a collection of individuals not subject to variation from the morphological standpoint, and even often identical as regards colour of body. This concept was introduced as part of a programme by Meigen (1818), who is the found of the splitting school in the systematics of *Diptera*. During this time a lens adapted to inspection of insects was introduced in connection with technic of description and discovery made of the majority of basic morphological characters which even today are of importance in describing species. Distinguishing of species in the Meigen period was based on morphological characters selected at random.

Meigen declared himself a supporter of the treatment of species as a unit defined by biological limits. His declaration is, however, completely at variance with the concept applied in practical research, since it is an anti-natural concept of species devoid of variation. According to it the description of each individual exhibiting any difference of structure as a separate species is justified. This treatment of species dominated in research on *Tabanus* L. for eighty years.

3. The Brauer period (1880 – up to the present), as far as the taxonomy of species of *Tabanus* L. is concerned, is characterised by the finding of appropriate measurements and ways of describing the species. The theoretical and practical bases for the species concept with *Tabanus* L. were formed by Brauer (1880, 1887). He treats the species as a unit, the limits of the variation of which are defined by natural differences. With regard to working methods on fixed material, instead of identifying single specimens, he introduces the use of a series of individuals coming from one population. The description of species drawn up by him covers the fundamental morphological features.

*

The methods used in present work made it possible to distinguish between three concepts of research in the taxonomy of *Tabanus* L. Each of them had, or has up to the present, numerous supporters. Each of the three periods of taxonomy of *Tabanus* L. is characterised by the predominance of one method of treating species, the domination of one school of research. Detailed discussion of these will form the subject of later sections in this work. I shall now compare the results set out here with the results obtained by other authors when investigating the fate of the species concept. On account of the new means of analysis which I have applied here, such confrontation makes it possible to check its usefulness for research on the problem of species in the history of systematics.

There are several means of classification of definitions and concepts of biological species. Petrusewicz (1952) states that when working of definitions of species there are two fundamental points of view to be taken into consideration: 1) from the standpoint of variation of species and 2) from the standpoint of species as a biological unit. These two points of view correspond to two different sides of work on systematics; the first – the practical (inventory work), the second – theoretical; definitions of species therefore play a double role, as instruments in work on systematics and as a theoretical picture of the biological unit. I shall discuss here only the inventory concepts analysing the species from the standpoint of variation, since only they have been applied in taxonomy. Their characteristic feature is the use of the individual as a representative of a species and the creation of criteria for distinguishing of species based on the properties of individuals. In these concepts intraspecific variation is also defined, and they refer to the permissible range of differentiation within the species. Inventory definitions of species therefore form working instruments in systematics.

Within the inventory treatment we encounter two different types of concept. The first assumes that specific separateness may be defined on the basis of investigation of similarity and of differences between individuals; the second that the limits of species are defined biologically. We have two distinct trends in research within the first type:

The first treats the species as a unit internally uniform, and acc. to B e s n a r d (1864) originates with T o u r n e f o r t (1719). In zoological research a similar opinion is represented by Tournefort's contemporary, L a n g (1722 acc. to B a c h m a n n 1906). Acc. to Tournefort (B e s n a r d 1864) "absolute identity of form" defines the species. This working assumption in systematic research leads to distinguishing as species groups of individuals which do not exhibit variation. In the initial periods of systematics, representatives of the Tournefort view altogether denied the possibility of variation within the species – this was the concept of invariable species. Later this concept changed on the basis of botanical research by J o r d a n (1873 acc. to K l e c k i 1924) to treatment of species as a small unit (petite espèce) next termed, on the basis of genetic investigations, jordanon. The same way of thinking formed the basis for the definition as a species of pure lines. In our own times the mechanical application of a single criterion of species led to the statement (D a r l i n g t o n 1941) that in certain cases the individual has the rank of species, that is, that each individual forms a separate species.

The assumption of morphological or genetic uniformity of species in systematics forms the basis for splitting activity, and is on this account harmful.

One of three species concept in *Tabanus* L., that is, the Meigen concept, has distinct connections with the Tournefort view. Representatives of the Meigen view aim in their investigations at describing species as units internally uniform, not exhibiting morphological differentiation, most often also of similar body colouring. This view is a voluntarily accepted assumption in research.

The second view accepts the existence of variation within the species. This concept originates with Linnaeus, who assumed that agreement of unvarying features defines the specific appurtenance of individuals. This definition is not very exact and in principle does not define variation within the species, but accepts, in addition to unvarying characters, the existence of characters which exhibit variation within the species. Linnaeus also defines the origin of individuals from one pair of common parents as the main criterion of specific appurtenance. With such treatment intraspecific variation is of secondary importance to the definition of appurtenance, since the main criterion is formed by origin. It cannot be applied in practical research, since the problem of variation must be solved in the first place when determining the limits of each species. An attempt was made to solve this difficulty on the basis of the Linnaeus definition by C u v i e r (1818) who proposed a practical way of estimating variation. He considers that variation within the progeny of one pairs of parents forms the norm of intraspecific variation. In practical research this condition is not as a rule complied with The basic criterion of specific appurtenance for representatives of the Linnaeus view is confirmation of similarity between individuals.

Acceptance of a wide range of variation within the species is characteristic of the research basis of representatives of this view. In his taxonomic works Linnaeus and his disciples were not, however, concerned with the description and investigation of variation. The correctness of the species described by them depends on the degree of obviousness of the differences between species and the state of practical knowledge of the species examined available at the time of describing them in taxonomic works. Linnaeus and his disciples correctly described species in well-known groups or in those in which differences between species were distinct. In groups about which practically nothing was known, the species distinguished by Linnaeus and his disciples were only good where differences were so great as to be plainly obvious, if this was not the case – they were lumped species. De Vries (1906) connects the name of Linnaeus with such lumped species; and up to the present they are still known by the name linneons.

They Linnaeus treatment of species in taxonomy is connected with the activities of this scientist himself and of his school. In particular it is in work on *Tabanus* L. that the absence of obvious differences between species and lack of knowledge of groups caused the species described to be mainly lumped, since they included several species today distinguished as separate. In all these cases, however, where separateness of species is apparent at the first glance, the species were distinguished correctly. The lumping together of species of the Linnaeus period was not therefore caused by the assumptions of concept, but by inadequate methods.

Both the trends discussed above, the Tournefort and Linnaeus have their greatest number of representatives among systematicians who use museum collections as their working basis. When applying the Tournefort or Linnaeus concept of species, the solution of taxonomic problems may be achieved by the use of museum collections only, as the estimate of similarity is usually based on morphological examination.

The second type of species concept was formed on the foundation of field work. Brehm (1856) laid down new principles for distinguishing species. He gives indices for using morphological,ethological and ecological criteria jointly. He bases this trend on the assumption that species are separated from each other by biological frontiers; and tries to get to know these frontiers by means of examining species in nature. Among the outstanding representatives of this trend is Brauer (1887) who justifies this approach from the theoretical side. Differentiation of species results in biological investigation, and the range of variation contained within the species is defined by nature itself.

The researches of Brauer and his school are most closely connected with this trend in the systematics of the genus *Tabanus* L. Evidence of this is provided by the contents of the species he distinguishes. It is true that he does not give any biological methods, but the well-known Warsaw expert on *Diptera*, Sznabl (1881) who collaborated with Brauer, writes of the unusual gift for observation of the scientist, which ensured him great success in field work. It is possible that the feeling for nature possessed by Brauer was decisive in enabling him to grasp the differences between species, since in his monograph on the genus *Tabanus* L., when distinguishing between species occurring in Austria, that is, those which he himself encountered in his field work, he made not a single mistake.

The working species concepts in the case of *Tabanus* L. discovered by investigating systematic solutions, as shown in the above review, correspond to three main theoretical trends, which either played or now play a part in inventory investigations.

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The periods distinguished in research on *Tabanus* L., exhibit a smaller connection with the development of the general concept of species. It is the result, on the one hand, of the fact that the periods proposed by different authors do not coincide, and in addition the division of concept of species applied here does not always correspond to solutions put forward by other authors.

Bachmann (1906) distinguished the period of treatment of species as an invariable unit, which according to him lasted until 1858. The next period (from 1858 to 1906) is characterised by the evolutionary treatment of species. The division of species concepts into two categories; evolutionary and non-evolutionary, was made by earlier research workers also (Besnard 1864). The authors of these treatments are clearly influenced by the Darwin theory. This division is correct from the evolutionary point of view, but is not correct as a means of treating the history of concept of species in general. Species concepts prior to Darwin were not uniform in contents and certain of them create the possibility of evolutionary analysis (Buffon 1786). The evolutionary species concept was in 1906, rather the logical consequence of Darwin's theory than a working view of systematics. For these reasons the division made by Bachmann (1906) cannot be used in investigations of the history of species concepts in systematics.

Mayr (1947) states that up to 1900 the concept of a monotypic species prevailed in systematics, then the polytypic species. He correctly defines the moment at which the polytypic concept of species arose, but the combining of all concepts of species prevailing in the 18th and 19th centuries under the name of monotypic is an undoubted simplification. Only Tournefort's treatment corresponds as to contents to what Mayr (1947) terms the monotypic concept. This condition is not complied with, from the definition of the inventory type, either by Linnaeus concept, or Brehm's, or any of the theoretical (e.g. Buffon's) species concept.

Both divisions (Bachmann 1906, Mayr, Linsley, Usinger 1953) are very tendentious, each of the authors is a supporter of one relatively "young" species concept, which he contrasts with all the remainder. The error of such a point of view arises from the fact that different definitions of species were formed on the basis of completely different initial assumptions. It is therefore almost impossible to compress them into the framework of one logical alternative, particularly when both alternatives would have been separated from each historically.

Beer and Sacchetti (1952) mention the period of the scientific activities of Linnaeus, Cuvier and J. Huxley as turning points in the history of systematics. The new attempt at dividing the history of systematics made a year later (Mayr, Linsley and Usinger 1953) contains three periods: 1) the period of investigation of local fauna, which lasted from the beginning of systematics until Darwin's times, 2) the period of evolutionary research (from Darwin until the end of the 19th century) and, 3) the period of examination of populations.

Let us make a comparison of the data given by all these authors in establishing turning points in systematics. In general all accept 1758 as the beginning of systematics based on generally accepted systematic principles. 1818 is given by Beer and Sacchetti (1952) in connection with Cuvier's works. 1858 is connected with Darwin – given by Bachmann (1906) and Mayr, Linsley and Usinger (1953), 1900 (when the polytypic concept was created) – given by Mayr (1947) and Mayr, Linsley and Usinger (1953). Beer and Sacchetti (1952) consider 1940 as a turning point in the history of systematics in connection with the appearance of the work "The new systematics".

The dates which I marked out by means of an index of the state of systematics in the history of research on *Tabanus* L. in Europe are as follows: 1758, 1800, 1880. 1758 is the formally recognised date of the beginning of modern systematics, and is connected with the appearance of the 10th edition of Linnaeus' work Systema Naturae. I too began my analysis of the genus *Tabanus* L. from this work. None of the remaining dates given in other sources agree with the results obtained when investigating *Tabanus* L. The reasons for this are twofold.

In the first place it is impossible to distinguish distinct historical periods within the inventory species concepts, as the two basic concepts (Tournefort and Linnaeus) were formed in the first half of the 18th century and exist as parallel working concepts in the 18th and 19th centuries. The biological criteria of species put forward by Brehm (1856) in the second half of the 19th century were applied only in the groups of the animal world which were better investigated from the biological aspect. Up to the present, in fact, it is only in a few cases that biological criteria form a basis for systematic works.

In the second place proposals so far made as to the division of species concepts and their history result from insufficiently thorough investigations. The definition of the influence exerted by different scientists on the development of the species concept was based on an analysis of their works and the fame surrounding their names. The influence of certain biologists on the development of species concept is somewhat mechanically assumed.

Cuvier in his scientific work exercised an undoubted influence on the development of systematics, but his definition of species is merely an attempt at methodical correction of Linnaeus definitions. He is a typical representative of the Linnaeus trend. His proposals did not, in fact, fundamentally affect the fate of the Linnaean concept, since they were not used on a wide scale in practical research work.

An analysis of work on systematics in the second half of the 19th century does not confirm the thesis that Darwin's work exercised a great influence on the fate of the species concept as Bachmann (1906), Mayr, Linsley, Usinger (1953) and Komarow (1957) suggest. "The Origin of Species" is undoubtedly connected with the concept of species, but not from the point of view of systematics. The working concept of species based on Darwin's works (Besnard 1864), (Bachmann 1906) was only a research postulate which was not used in certain systematic works until the 20th century. A real change in treatment of species arose from investigations made by Gloger (1833) and Kleinschmidt (1900); but these scientists were not evolutionists.

The influence of J. Huxley (1941) on the development of systematics (Beer and Sacchetti 1952) can not as yet be exactly determined, on account of the fact that "The new systematics" appeared comparatively recently. This work, written by numerous authors, does not, however, represent a uniform species concept and does not adopt a definite standpoint in regard to many important problems in the concept of species. For instance, with reference to the reality of species, a question forming one of the more important parts of contemporary discussion on species the above work contains many debatable statements, at variance with each other, without a clear definition of a common opinion held by the whole group of authors responsible for this work.

The differences in defining the turning points in the history of species concept in systematics result from the subjective treatment of works by different scientists. A full understanding of the fate of the concept of species is obtainable not only after detailed examination of theoretical proposals, but also after establishing their actual influence on the development of detailed research, i.e. of the sphere and time of influence.

The section of taxonomy which I examined – the history of research on the genus *Tabanus* L. – does not coincide with any of the divisions proposed. In the first case it is the result of parallel action of different species concepts in systematics. It is, however, of importance that the three fundamental species concepts used in the 18th and 19th centuries, were also used in investigation of *Tabanus* L. The order in which these three concepts occur in examinations of species in relation to *Tabanus* L. (Fig. 5) would indicate that the periods were in the following order – the lumping, splitting and biological. It is not possible to define, on the basis of investigation of one genus only, whether all three concepts must follow on after each other in a similar way. It is certain that in other systematic groups the splitting period began considerably earlier than in the systematics of *Diptera*. The first attempts at the splitting treatment of birds (Gmelin 1788) were made as early as in "Systema Naturae" Gmelin (1788) introduces the Tournefort concept to a work, the author of which was Linnaeus. Hence it is probable that certain authors (Mayr 1947) gained the impression that the creator of the monotypic concept was Linnaeus and not Tournefort. It must here be emphasised that the Polish scientist Jundziłł (1807) criticised Gmelin for this treatment of species, and not Linnaeus, as Mayr did 140 years later.

The difficulties of the splitting period in the systematics of birds were overcome and transition to the new polytypic concept of species took place considerably earlier than was the case with the systematics of *Tabanus* L., in which Brauers (1887) concept, corresponding more or less to Brehm's concept (1856), has cominated up to the present.

The polytypic species concept has not been used as yet in the systematics of *Tabanus* L. It is impossible today to make an exact comparison of the time of appearance and prevalence of different species concepts in research work. Only material processed from the quantitative aspect could form a basis for more accurate analysis. Material processed in this way could be used as a basis for thorough consideration of the history of the species concept in systematics.

The Linnaeus trend and period (1758–1800)

Representatives of the genus *Tabanus* L., were known as long ago as in ancient Greece. One of the correlative generalisations made by Aristoteles stating that insects with a proboscis at the front of their bodies always have two wings, is the result of anatomical examination of the structure of *Tabanus* L. and *Culex* L. No material has been preserved from pre-Linnaean times which would make it possible to determine what treatment was used by various authors. Research on species may therefore be considered as starting with Linnaeus. His work on *Tabanus* L., in "Systema Naturae" was such a revolution for those times that none of the later authors has quoted works previous to him. With Linnaeus we encounter elements of systematic work which are today in common use, such as the general species concept, methods of description and identification and preservation of the insects forming the subject of description. The problem of species as a working question examined using *Tabanus L.* as material, does therefore actually begin with Linnaeus. His system and principles for forming names has frequently been analysed and described, but an appraisal of his views is very difficult today, and opinions expressed are often contradictory. Komarow (1957), Mayr, Linsley and Usinger (1953) and many other biologists define Linnaeus as an outstanding theoretician, creator of the species concept. Ramsbottom (1938) disagrees with this view, and maintains that Linnaeus was only an experimenter and published general opinions in so decided a form for didactic purposes only.

The principles created by Linnaeus, on which the system of the living world is based, and among them the species concept, evoked a far-reaching echo in the taxonomic research of that period. His views, regardless of the reason for which they were published, should therefore be carefully considered.

Linnaeus' treatment of species has been very differently understood:

1. Mayr, Linsley and Usinger (1953) state that Linnaeus in general differentiated species correctly.

2. De Vries (1906) and Lotsy (1916) are of the opinion, however, that the species described by him are too large, not uniform, and even propose separate names for them – de Vries "Kollektivart", and Lotsy "linneon".

3. Kleinschmidt (1900) holds an opposite view to this problem. He asserts that the species distinguished by Linnaeus are too small and are the result of splitting true units, termed by Kleinschmidt "Formenkreise".

These contradictory treatments of species in Linnaeus' work do not permit of forming an initial opinion as to the actual attitude of Linnaeus in this matter. His definition of species contains confirmation of constancy and common origin from one pair of parents. There is no exact guide in it to a practical means of differentiating species – no criteria of species or assumptions as to the range of variation within the species. Discussion on the theoretical plusses and minuses in treatment of species by Linnaeus would therefore in principle serve no useful purpose. This appraisal can only be made from the aspect of results, without losing sight of the needs and interests of research predominating in Linnaeus' time. Biology was then faced with the task of setting in order and describing the diverse living world in the "System of Nature". This task was carried out on the basis of newly prepared principles of systematics and nomenclature. The most important task was to allocate species to their proper place in the system, there was not enough time to make investigations of each species, they had first to be described and set in order. For these purposes the morphological criterion of species was the easiest to use. Similarity formed the only gauge of specific separateness. The results obtained in the works of systematicians during this period differed greatly.

Species of birds then well known to hunters were on the whole correctly differentiated by Linnaeus, while the results of investigations in other groups were dependent to a great extent both on the obviousness of morphological differences between the species, and on the degree to which investigation had been carried out.

In the genus *Tabanus* L. Linnaeus initially distinguishes only four species, of which three are lumped. This to a considerable extent is due to the means of description and division into species used. Linnaeus rather put material in order on the basis of features which were immediately apparent than differentiated between species. In the beginning he mentions the largest form – *T. bovinus* L. "T. oculis virescentibus, abdominis dorso maculis albis trigonis longitudinalibus". This description includes two Swedish and two further species from Central and Southern Europe: *T. bovinus* L., *T. sudeticus* Zell., *T. spodopterus* Meig, and *T. eggeri* Schin. It is impossible, on the basis of features given by Linnaeus, to distinguish between any of these four species, all of which without exception fit the diagnosis quoted above. Then follow small, grey horse-flies, which are the most numerous – *T. bromius* L., then the golden *T. tarandinus* L., which manifests its specific separateness almost by the parts of its body. Finally there are black horse-flies with red spots on the sides of the abdomen, a nuisance both to animals and humans on hot days; Linnaeus termed them *T. tropicus* L. In only one collection made by Zetterstedt (1842) containing many split species, of eight specimens identified as *T. tropicus* L., seven species can easily be distinguished. The actual number of species covered by the common name *T. tropicus* L. includes, during this period, more than ten separate forms.

Not the weaknesses, however, but the advantages of a method decides its success. Directly after the appearance of "Systema Naturae" Linnaeus' methods were applied by other biologists working in different countries of Europe. With regard to research on *Tabanus* L., in addition to Linnaeus (1758, 1767) mention must be made first and foremost of the continuer of his work in the sphere of entomology – Fabricius (1781, 1894, 1805). Other scientists, such as for instance, Harris (1782), Herbst (1787), Gmelin (1788) Geoffroy (1762), Scopoli (1763), Rossi (1790) and Panzer (1793) for the main part use the material contained in the works by Linnaeus and Fabricius. Some of them described, on the basis of the Linnaean method, new good species such as, for instance, *T. ater* Rossi, *T. autumnalis* L., *T. barbarus* Coq., *T. gigas* Herbst., *T. nigritus* Fabr., chiefly those which were obviously different from each other, and which could not be included in species previously described. This indicates that the reason for combining species by representatives of the Linnaean school was to a great extent the lack of proper means of description, and not the accepted species concept.

The Linnaean method was more extensively applied in works by Fabricius. In them we encounter attempts at developing description, attempts which were, however, inconsequent. The considerable amount of material at his disposal enabled him to distinguish a far greater number of species. Here, however, the technic of description which he used begins clearly to restrict the possibilities of his work. It may be assumed that Fabricius saw more species in his material than he was able to describe, examples of this being *T. paganus* Fabr. and *T. borealis* Fabr., which he described with greatest emphasis on the colour of the eyes and abdomen. It never proved possible to identify these species in material on the basis of these descriptions, despite the fact that at least the second of them most certainly at the time of description formed a new species, but today it is unknown which species of several possible ones. As a result many species described by authors of the first period were later included in catalogues as undefined forms and problematical synonyms of species described later on.

The reasons for the difficulties experienced in recognising species described n the first period are two-fold. In the first place such features as "black abdomen with red maculae on sides" was too general a description and the range of possible variation was accepted as very wide, or in any case undefined. In the second place the features used were, in the majority of cases, not specific; "green eyes with three purple bands" occur in a very large number of paleoarctic species of *Tabanus* L., and therefore such features are naturally not suitable for describing species. These weaknesses in the Linnaean method of description in relation to species of *Tabanus* L. caused the methods to be not only insufficient for the description of species, but also quickly to lose their significance as a means of putting material in order.

The poor results obtained in the first period of systematics of *Tabanus* L. are not, however, the result of applying an erroneous species concept. In the systematics of *Diptera* of this period no means of description was worked out which would make it possible to grasp differences between species. This was to some extent due to the fact that the material itself was difficult to work on. The Linnaean method applied during that same period to work on spiders permitted of correct distinguishing of species, and of the systematics of this group being put in good order for those times.

The exhaustion of the possibilities of research of this primitive technic of description caused the downfall of the Linnaean school in Dipterology. In the systematics of *Tabanus* L. the Linnaean period lasted about fifty years, and is characterised by the small number of species described. Only 11 were distinguished in Europe, the majority of them being lumped units. Their number initially forms 75% of the whole of the forms described, but towards the end of this period, chiefly owing to the efforts of Fabricius, this was reduced to 45%. There is not one split species during this period and the number of synonymous names is very small. The re-description of known species as new ones did not in fact take place at all.

The method of distinguishing between species based on the Linnaean method lasted longer than period mentioned above. After the publication of Meigen's (1804) work, the last work of Fabricius on *Diptera* appeared. Fallén (1809. 1817), who in his first work on *Tabanus* L. in Sweden gives only six species described by Linnaeus, may be regarded as a continuator of the Linnaean trend in the systematics of *Tabanus* L. In the monograph on the *Diptera* of Sweden (Fallén 1817) lumped species form 66% of the total number. Certain influences of Linnaeus' treatment (lack of split species, 27% lumped species) can also be found in the paper "Insecta Lapponica" (Zetterstedt 1840) (Tab. I).

The difficulties with which we are faced today, in understanding what material formed the subject of description of each species distinguished in the first period, became apparent almost immediately after the publication of the above works. Meigen (1818) emphasises that Fabricius' species are artificially differentiated and that it is difficult to identify them from material. The work by Brauer (1880) contains a detailed discussion and attempt at interpretation of these species. The Linnaean treatment of species in *Tabanus* L. arouses a faint echo even today. Starcke (1954) in the list of horse-flies of the Oberlausitz (Germany) district mentions species from the group *T. tropicus* L. under the joint name of *T. tropicus-fulvicornis*, as though emphasising in this way that he is concerned with the joint treatment of all the forms belonging there. It is, however, a stand-point completely isolated and it is only referred to here as an interesting example of the fact that working opinions which have been out of date for a century and a half may still have their supporters.

The results of the activities of a large group of research workers during the Linnaean period are not satisfactory, the species as treated by them remained in practice the sum of individuals complying with the requirements of an unspecified diagnosis, and the unformed feeling of similarity made it impossible to give even a rough systematic picture of the genus *Tabanus* L. The species remained in principle beyond the grasp of these investigators. Practical solutions in the systematics of *Tabanus* L. remain far behind the views put forward. They were not natural units, only a mixture of extremely varied forms, often not in any way related to each other. This was not due to deficiencies in theory. Linnaeus' species concept was not a poor one, as it considered objectiveness essential, but did not provide any guide to methods of differentiating between species, and the weaknesses in technic of description already referred to did not permit of the realisation of the accepted theoretical postulates.

Meigen trend and period (1800–1880)

At the beginning of the 19th century a somewhat difficult situation arose in research on *Tabanus* L. in Europe. Identification of species on the basis of inadequate description was difficult, and further systematic work using the old methods was practically impossible. This was brought about to a great extent by the universality of the works of their predecessors. "Systema Naturae" was a work covering the whole of the then known living world, and merely on account of its enormous range must have been inexact. The constantly increasing number of species described led to specialisation by scientists in different systematic groups, and as a result processing became more accurate. Fabricius still worked on all insects and certain groups of spiders, while Meigen limited his activities to the *Diptera* order only. In 1800 he published his first attempt at a systematic revision of this order, and four years later his first work on species based on new methods of description. An appraisal of the results obtained by that author show that in practical research he used a completely different species concept than Linnaeus. He published his views on species (Meigen 1818) in a new issue of his monograph on the *Diptera* of Europe. In the introduction he strongly criticised the treatment of species used by his predecessors. He stated that many species had been distinguished artificially, and that it was only possible to arrive at a correct definition of species by painstaking observations under natural conditions, as each species has its own specific way of living in nature.

In Meigen's case, therefore the species concept was combined with the previous conviction as to the objectiveness of the existence of species in nature. The debatable problems are who differentiates species correctly, which species are true ones, and which artificial. This attitude in the discussion of species is repeated in many works, but is usually expressed less clearly. Every research worker is of the opinion that it is his method of distinguishing of species which reflects the natural reality.

Meigen (1818) also undertakes to define more exactly the range of variation, as is partly shown by his criticism of the treatment of species by Linnaeus and Fabricius. He writes that where they distinguish one or a few species only, he sees far more. He states his attitude even more decidedly in the following principle: "Formen ändern bei derselben Art wenig oder gar nicht ab. Wo also Artverschiedenheit auf abweichende Form gegründet ist, da steht sie ungleich fester".

Meigen's attitude is therefore defined, the species (apart from cases of pathological changes) is a group of individuals almost identical as regards structure. Each morphological deviation from normal forms grounds for distinguishing a good species. This principle grew up from the rejection of the wide range of variation implicit in the descriptions of the Linnaean period. Meigen's treatment is, however, just as extreme and is at distinct theoretical variance with the principle of the natural separateness of species. If indeed species differ as to their way of life in nature, then it is that property and not morphological differences which define the specific separateness of the group of individuals examined. In practical research it turned out, however, that even the principles of morphological difference proved to be too restricting. Meigen described very few species differing as to structure, and even inconsiderable deviations in colouring of body were sufficient for him to regard an individual as a representative of a new species.

The treatment of species by Linnaeus was indifferent to the range of variation of the species, while Meigen's concept is most decidedly based on the small species, consisting of individuals morphologically identical. This is a return to the Tournefort (1719) definition of species, best characterised by Huxley (1941) as the monotypic concept.

Meigen also supplemented work on systematics by technique, using a specially conctructed magnifying glass to inspect specimens. This instrument enabled him to improve description to a considerable extent, especially as regards the small elements of body structure, and as a result the way of describing species underwent a marked change.

Differences between the methods of Fabricius and Meigen can best be shown by comparing description of one of the species, especially species about which it is certain that both scientists handled a large number of specimens and were able to catch the insects themselves. This species is *T. bromius* L.

Fabricius gives the following diagnosis: "T. oculis fascia purpurea, corpore cinereo". Meigen (1804) gives for this species "abdomine cinereo lineolis obliquis nigrofuscis". This description is even shorter than that of their predecessors, but it is followed by a description of the colour of the head, the mouth apparatus, antennae and frons of the female. Information is even supplied that there is a black spot above the antennae, to which a "line" runs (frontal spots). He gives in detail the colouring of the eye, thorax, upper and undersides of the abdomen and wings; the description occupies eight lines of print in all.

The further volumes of the work begun in this way were not published on account of the Napoleonic Wars. Meigen waited fourteen years for the opportunity of publishing them, and throughout this time he perfected his technic. The fame he achieved enabled him to publish the work straight away as a whole, so that it is possible to compare the old and new descriptions. The principle of diagnosis and description has been maintained, but diagnosis and description have altered slightly. He describes the same *T. bromius* L. as follows: "Nigricans, thorace albido lineato; abdomine trifariam flavicante maculato; antennis testaceis; fronte femine callo quadrato; lineaque nigris". The following have now been introduced into the diagnosis: description of mesonotum, detailed description of spots on the abdomen, antennae and frons of the female. The description occupies 22 lines of print and is far more exact in defining each feature than previously.

The reaction to Meigen's way of describing was almost immediate. The majority of experts on *Diptera* greeted it with enthusiasm, and many of them offered their own collections for him to work on. Fabricius (1805) is probably the only one to pass over in absolute silence all the new species of *Tabanus* L. described by Meigen, but quotes him scrupulously wherever Meigen's work confirms nis own investigations. Fallén (1809, 1817) also applies the old way of differentiating between species. These were, however, the final attempts at defending the Linnaean technic of description in Dipterology. In this way at the beginning of the 19th century division of the genus *Tabanus* L. into small oı large species, black or red, comes to an end, and description of material begins. Meigen's method provided ample opportunity for obtaining fresh knowledge, which resulted in the rapid development of the taxonomy of *Tabanus* L. during this period. The old working methods could not stand the competition with the more exact methods of Meigen, which in addition constituted a novelty. Together with them, almost imperceptibly, the Tournefort concept with its splitting ettects enters the sphere of dipterology. A whole generation of scientists arises who accept the new style of work with enthusiasm. The most decided application of the concept of small species was that of Robineau-Desvoidy (1830, 1863) in the taxonomy of *Diptera*. Every deviation in structure or colour of body was to him proof of specific separateness. When making a detailed investigation of individuals of the parasite fly *Phryxe vulgaris* (Fall.) He describes, within this one species, as many as 246 separate "species". This treatment forms an excellent example of the absurdity of the assumptions of the Tournefort and Meigen concept of species, which in consequence led to placing an "equals" sign between individual and species.

Until 1880 Meigen's concept formed the basis for practical work on the systematics of *Diptera*. The genus *Tabanus* L. is the subject of numerous works, and about fifty publications appeared on this subject during this period. Many research workers in different European countries published numerous systematic and faunistic works based on Meigen's monograph. Among the most outstanding representatives of the Meigen school in the systematics of *Tabanus* L. are Egger (1859), Jaennicke (1866), Schiner (1862), Wahlberg (1849), Wiedemann (1830), Walker (1848) and Zetterstedt (1840, 1842–1848).

The number of species described grows rapidly and towards the end of this period there are over four times as many as in the previous period. As many as 46 well differentiated species of *Tabanus* are known from Europe. In addition the number of lumped species undergoes even further decrease, never exceeding 20% of the whole material. The number of correctly distinguished species does not, however, increase, it is only in the first work on *Tabanus* L. by Meigen (1804) that they reach 50%. The Meigen period lasted about 80 years. The stagnation in the development of knowledge of species over the period of so many years, with the simultaneously considerable development of research methods, forms the best index to an estimate of the Meigen school, and stagnation in the differentiation of good species forms the best proof of the falseness of the species concept. In addition it indicates that even the best methods of research do not ensure good results if the research assumptions and the theory by which we are guided in assessing natural phenomena are erroneous.

The application of the splitting species concept during the Meigen period brought about the appearance of a new phenomenon split species, which are most characteristic of this period. In the beginning their number formed scarcely 6% of the whole material, but in later works, chiefly those of Meigen and Zetterstedt, the split species form about 40%. Improvement of the situation does not take place until the work by Loew (1858a), who is not, however, a typical representative of the Meigen school.

A practical assessment of the results of this trend are provided in the first place by a review of the contents of Meigen's species, or those of other research workers during this period, which forms a gauge of the actual correctness of distinguishing. The difficulties, already discussed, in tracing the complete material which Meigen used for his descriptions make it difficult now to state what the species distinguished by him actually looked like. Greater possibilities of dealing with this task are afforded by examing the collections of Scholz (1850) and of Zetterstedt (1840, 1842–1848). Material for the first was collected from Lower Silesia and as the condition of the collection kept in the Zoological Institute of Wroclaw University indicates, the specimens there today have not been moved from their original places. During that period Wroclaw was an important centre of entomological research, with outstanding dipterologists working there, hence Scholz's collection is rather the reflection of the high level of the systematics of *Tabanus* L. at that time General data (Tab. II) concerning the species distinguished by him permit of estimating the possibilities of identification by means of the descriptions of the Meigen period. Of the 114 specimens in this collection only 56 are well defined, which is about 50%. The possibility of correct identification is therefore very small. Over 35% of the 17 species distinguished by Scholz are lumped ones, and contain two or more species now considered as separate. At the same time the split species form over 41% of the material. Of the 23 species in the material he distinguished only 17 – and of these only 26% well. Everyone who has worked on old collections refers in general terms to a similar situation.

Zetterstedt's collection consists of three parts corresponding to his three works – 1) Insecta Lapponica (1840), 2) Diptera Scandinaviae (1842), 3) Supplementa (1848). I worked on each of them separately (Tab. II). In all three collections the number of species is lower than the true figure, the percentage of species correctly distinguished by Zetterstedt is low, in the case of Insecta Lapponica 40% and 20% for Diptera Scandinaviae. The considerable percentage of lumped and split species combined with the foregoing data are evidence of poor differentiation of species. Simultaneously the identification of specimens on the basis of the Meigen method and descriptions is very difficult (52.9 – 62.5% of correctly identified specimens). This state of affairs and the results of systematic research as seen from examination of the collection of one of the most eminent entomologists of that period is evidence that the species concept applied, the way in which they were ditinguished and possibly description as well, did not provide and adequate instrument for solving the taxonomic problems of *Tabanus* L.

Apart from such features as hairiness of the eyes or shape of the ocellar tubercule which were later included as fundamental features in the systematics of *Tabanus* L. we encounter in Meigen's description nearly all the features used today to describe species Of course the description of the frons is today done far more accurately, nevertheless certain of Meigen's descriptions referring to the frontal calli undoubtedly make correct determination of the species possible. The cause of failure in the practical application of methods of description does not, therefore, lie in the features themselves which are used, but in how they are used. I made a comparison (Tab. III) of all characters in tum used for the description of four species with black body colouring, described at the beginning of Meigen's monograph (1820). The characters occurring in the description of the given species I marked +, and those which did not use, I marked –. I maintained the order of succession of the characters used, and put the new characters occurring in descriptions of further species, under them. Of the 18 characters used for description in all species, only three are repeated. Four are repeated in three species. Two are repeated in four species, seven are used by Meigen once only. Those taxonomic features may be termed good ones which are differentiated and discussed in all species. Characters about which we have no information as to how they appear in near species, have low working value regardless of whether they are specific or not. After working on the first four species it became clear that they form 39%. Since at the same time the sole means of identification was to compare specimens with the description, and descriptions with each other, it is not strange that so many errors are to be found in old collections. The exactitude of description introduced by Meigen, and the attention paid to many morphological details led to the discovery of the majority of anatomical features which have since been applied in the systematics of this genus. There was a lack of consequence, however, in the descriptions of the Meigen period they were not given comparative treatment to an extent which would have made exact identification possible. Poor description combined with a poor concept are two of the sources of error in this period.

The situation is similar in the case of results obtained by other research workers who used Meigen's methods. Certain species described over 100 years ago, e.g. *T. plebeius* Fall. and *T. sublunaticornis* Zett. were not correctly defined until quite recently (Collin 1945, Kauri, 1951).

The third source of errors in the Meigen period is to be found in the method used. The basis subject of analysis is the individual placed in a collection and classified on the basis of the structure of certain parts of the body. As a rule it is not labelled with the time and place of capture. When using large collections this rules out the possibility of combining material in series of uniform origin. The research workers of that period examined and analysed different individuals, Characters used by Meigen (1820) for description of four species of *Tabanus* L.

Cechy użyte do opisu czterech gatunków *Tabanus* L. przez Meigena (1820)

Tab. III

No Nr	Character Cecha	*T. ater* Rossi	*T. aterrimus* Meig.	*T. micans* Meig.	*T. anthracinus* Meig.
1	colour of body – zabarwienie ciała	+	+	+	+
2	colour of edge of eye – zabarwienie brzegu oka	+	+	–	–
3	structure of frons of female – budowa czoła samicy	+	+	+	+
4	structure of antennae – budowa czułków	+	–	+	–
5	hair on thorax – owłosienie tułowia	+	–	+	+
6	distribution of spots on abdomen – rozmieszczenie plam na odwłoku	+	–	+	+
7	colour of wings – zabarwienie skrzydeł	+	+	+	+
8	colour of face – zabarwienie twarzy	–	+	+	–
9	colour of halteres – zabarwienie przezmianek	–	+	+	+
10	colour of squamula – zabarwienie łuski tułowiowej	–	+	+	+
11	colour of copulatory apparatus – zabarwienie aparatu kopulacyjnego	–	+	–	–
12	structure of legs of male – budowa nóg samca	–	–	+	–
13	colour of palpi – zabarwienie głaszczków	–	–	+	–
14	colour of eye – zabarwienie oczu	–	–	+	–
15	colour of pleurae of thorax – zabarwienie boków tułowia	–	–	+	–
16	colour of underside of abdomen – zabarwienie spodu odwłoka	–	–	+	–
17	colour of legs – zabarwienie nóg	–	–	+	+
18	hair on face – owłosienie policzków	–	–	–	+

and on the basis of their appearance decided to which species they belonged. This working method is in principle a contradiction of the biological way of approach to species. It is also the cause of differentiating a large number of split species. The authors of the Meigen period used European material, including in the case of *Tabanus* L. mostly sympatric forms, well separated from the biological aspect.

During this period new species were described almost always as the result of splitting local populations of one species into several apparently separate forms. The practical consequence of the principle of limited variation within the species is therefore the artificial splitting of variation in the local population, separation of small sections forming part of the whole species, and endowing the group separated in this way with the rank of species. This is splitting treatment at most complete variance with the biological treatment of species, but this kind of treatment of species in the case of *Tabanus* L. is not without its imitators even today. Let us take a concrete example of this way of investigation and solution of problems.

Large series of specimens suitable for research on variation in local populations are fairly seldom encountered in museums, even in the case of common species, and this caused a further difficulty when investigating individual populations.

Material collected in a certain area is usually segregated into species as the first step in work on then. When this is being done differences between specimens from the same place, as though between groups of specimens belonging to different populations, are especially easily perceived. Such groups were formerly distinguished chiefly as varieties or species, and today also as subspecies. Classic examples of splitting treatment in the case of *Tabanus* L., are the sympatric units within the species, e.g. in *T. aterrimus* Meig. This species has finally been split into the "foms" or "varieties" as follows: *aterrimus* Meig., *auripilus* Meig., *lugubris* Zett., *jacobi* Bouv., *palpalis* Kröb. In almost every population individuals are encountered which may be considered as belonging to these units. As this species supplies a good illustration of the use of superficial methods of analysis when examining variation within the species, I shall discuss it in detail.

T. aterrimus Meig. was described in one work only split into four species (Meigen 1820), and was given the following names: *T. aterrimus* Meig., *T. signatus* Meig., *T. auripilus* Meig. and *T. austriacus* Meig. The same year it was also described from Scandinavia as *T. aethiops* Ljungh. *T aterrimus* Meig. was further described as new species as follows: *T. nigerrimus* Zetterstedt (1842) and *T. heydenianus* Jaennicke (1866). Only three of the above names survived to pass on to the continued history of research on *T. aterrimus* Meig: *aterrimus*, *auripilus* and *lugubris*. This last name was accidentally connected with the species *T. aterrimus* Meig. as the result of an erroneous interpretation of a description of another species: *T. lugubris* Zetterstedt (1840) which referred to a form completely unrelated to the group of black coloured species within the sub-genus *Tylostypia* End. Apart from one attempt at differentiating yet another species on the basis of the old name – *T. nigerrimus* (Enderlein 1931), only those three names corresponding to three varieties mentioned above are encountered for almost one hundred years in European literature on *T. aterrimus* Meig. They are distinguished differently – completely black hairy individuals are always *T. lugubris* Loew 1858a (nec Zetterstedt 1840), the completely golden, *T. auripilus* Meig. T. *aterrimus* Meig. comes in between, closer to one or the other fom, or so combined with it that we have only two very slightly differing varieties. In 1938 Kröber within var. *aterrimus* Meig. distinguished a new form (f. *palpalis* Kröb.) with yelow palpi. In 1945 Bouvier, among the specimens near var. *lugubris* Loew, distinguished a new variety – var. *jacobi*

Bouv. The present state of taxonomv of units within the species of *T. aterrimus* Meig. may be summed up in the following key:

1. Abdomen and femora thicklv covered with golden hair
   a. palpi black, covered with black hair
   T. aterrimus var. *auripilus* f. *auripilus* Meig.
   b. palpi yellow, covered with golden hair
   T. aterrimus var. *auripilus* f. *palpalis* Kröb.
2. Abdomen slightly covered with golden hair
   T. aterrimus var. *aterrimus* Meig.
3. Abdomen covered with black hair, one edges of tergites and sternites silvery hairs. Mid tibia has silvery and black hairs.
   T. aterrimus var. *jacobi* Bouv.
4. Abdomen and legs completely covered with black hair
   T. aterrimus var. *lugubris* Loew

The above key and means it supplies of distinguishing these pseudo-varieties form an example of the superficial treatment of material, using characters which are accidentally very apparent. I examined over 200 individuals of this species in an endeavour to segregate them according to the above key, and the following observations occurred to me:

Varieties var. *aterrimus* Meig. and var. *auripilus* Meig. cannot be distinguished in a large amount of material. All stages of transition between the two forms are present, the more so that they are defined far from precisely, as strongly or weakly covered with golden hairs. Both varieties taken jointly form 58.7% of the material. Both former and present-day attempts at giving these forms the rank of species (Surcouf 1924, Olsoufev 1937) are therefore unjustified.

The second form which can be distinguished in the material is var. *lugubris* Loew, covering 41.3% of the specimens. Differentiation of var. *jacobi* in the material I examined is very dubious. Only two individuals could be classed under the definition of this form, but have not silvery but platinum hairs. In fact Bouvier himself (1945) admits that it is a rare variety.

It is however possible to use other features which have the same value as those given above, for the division of the same material. When segregating, for instance, according to colouring of palpi in the material, the following categories of individuals may be found:

1. palpi black
   a. hair on palpi black only – 43 individuals
   b. hair on palpi mixed black and golden – 23 individuals
2. palpi -brown
   a. hair on palpi black only – 25 individuals
   b. hair on palpi mixed, black and golden – 28 individuals
3. palpi yellow
   a. hair on palpi black – 55 individuals
   b. hair on palpi mixed, black and golden – 55 individuals

After examining 178 individuals with undamaged palpi it was found that their colouring in the case of *T. aterrimus* Meig., treated here in its widest sense with all varieties as one species varies from black to yellow. Within each variant of colour of palpi we encounter both pure black hairs and mixed black-golden ones. Generally speaking black hair is more common (123 cases), then the mixed black-golden (55 cases). Other surface characters may be searched for, e.g. colouring of hairs at the basal part of tibia, and from this aspect also two forms may be distinguished, one with black hairs, the other with golden ones. A very large number of such divisions may be formed from each material and all the differentiated forms named as is done with the splitting treatment. I should like to draw attention here not to the purposelessness of multiplying this kind of taxonomic stock, but to an assessment of this same material from another point of view. Included in *T. aterrimus* Meig. thus distinguished are two species clearly separate from each other, which cannot be mistaken if attention is paid to the three fundamental taxonomic characters of *Tabanus* L. – structure of frons, antennae and palpi. I did not give a comparison of variants of colouring of palpi divided into three variants, but it is within var. *lugubris* Loew that two different forms occur, one with narrow and black palpi almost right-angled in cross section, and the other with light yellow ones, wide at the base, covered with black hair and distinctly oval in cross-section. These forms also differ as to the structure of the frons and frontal spots, antennae and, exceptionally distinctly, the postabdomen of males and females. The form with yellow palpi was described in 1914 from the Caucasus as *T. tetricus* Szil. Among the 79 specimens of *T. aterrimus* var. *lugubris* Loew which I had in my hands, 52, that is, almost 68%, belong to the above species. I found specimens of *T. tetricus* Szil. in many European collections, with the exception of those from Scandinavia. The material forming the basis of the above discussion all reached my hands identified as *T. aterrimus* Meig or its variants. The specialists who had to do with this species include such names as J.W. Meigen, R. Schiner and O. Kröber.

The example given above presents a characteristic picture of the method of systematical analysis used by representatives of the Meigen school. In the period directly connected with Meigen the unit distinguished was in the principle a species. Zetterstedt gives several varieties with each species, but he is an exception. In more recent times the representatives of the splitting trend mainly use varieties as units.

Of the two assumptions, 1) as to the biological character of species and 2) of the morphological homogeneity of species, only the second formed the basis of systematic research during the Meigen period. The criticism of results obtained by the Linnaean school was not evoked by accepting correct concepts in research and working methods.

The recognition of the objectiveness of species proved during this period to be a principle for the sake of principle, not justified by the results of research. Several research workers (Allen 1908, Bessey 1908) assumed that the Darwin's concept overthree the reality of natural species. This, however, occurred even earlier than Darwin, in fact on the grounds of systematic investigations. The Tournefort's species concept led, as shown by the example of Robineau-Desvoidy (1830, 1863) to describing each individual as a separate species.

This treatment is not only extreme, but is contrary to what is understood by the term species, which regardless of what definition we use, is always a collective unit consisting of many individuals. If we use the equals sign between individual and species, in this very way we reject the possibility of treating the species as a collective unit. In this way the application of the Tournefort concept led to the overthrow of the view held by the systematicians of the Linnaean period, according to which the species is real.

Towards the end of the Meigen period the systematics of *Tabanus* L. was in a very difficult situation. A fairly large number of species had been described and their number was further multiplied. The technic of description worked out permitted of describing, with a certain amount of effort, each individual, and the Meigen concept enabled it to be recognised as a separate species, if only some sort of difference was contained in the description. Investigation of the species of *Tabanus* L. changed into a hunt for differences between individuals and the description of new species. The impossibility of comparing these descriptions resulted in its being possible to fit several descriptions found in different works to one specimen. Under such conditions identification of species was rendered extremely difficult. The number of synonymous names increased greatly, which also added to the confusion prevailing. A crisis occurred in the systematics of *Tabanus* L. which could only be overcome by a theoretical revision of views on the species and methods of distinguishing it.

The Brauer trend and period (1880 up to the present)

Investigations of species which were developed in the 19th century were chiefly descriptive in character. The morphological definition of species was of predominant importance during this time. The estimate of similarities and differences was based chiefly on anatomical examination. A somewhat specific category of research workes was formed during this period, who were biologists only in name, and were not engaged in research on species in nature. They used only material already prepared and kept in collections. It even happened that these systematicians never saw the species on which they were working under its natural conditions. Such research workers made the greatest number of mistakes in distinguishing between species, as they used exclusively morphological criteria. The Linnaean species concept narrowed down to the morphological similarity of individuals, was in many disciplines of science replaced by the Tournefort definition sanctioning splitting.

The first blow to this way of thinking was struck by Gloger (1833) when he stated that the name of a species is a collective term understood as covering a certain number of common features encountered in animals. Some of the naturalists of this period realised (Besnard 1864) that according to the morphological species concept, the species is only an abstract total of characters. In statements on the subject of species he often referred to biological treatments in concrete research work and put forward as desirable a change in the definition of species. It was during this period also that B r e h m's (1856) definition appeared, which for the first time contained definite instructions as to the use to be made of joint criteria: morphological, ethological and ecological, as a basis for distinguishing species.

The animated discussion in progress did not fail to include the systematics of *Diptera*. The first attempt at a revision of views on the contents of species of *Tabanus* L. was undertaken by the eminent observer and field worker Z e l l e r (1842) who is among the lesser known European experts on *Diptera*, despite the fact that his work exerted a considerable influence on the drawing up of new working methods in the systematics of *Diptera*. B r a u e r (1880) describes him in fact as a discoverer of features which are most applicable to the differentiation of species of *Tabanus* L. The actual work he did on definite species did not, however, come up to the demands which he himself made. The material which he had available, in addition, was too scanty to permit of his applying his own method on a wider scale. This was not done until L o e w (1858a) did so in his review of European species of *Tabanus* L. Loew begins his work with the significant statement: "Die Arten der Gattung *Tabanus* sind ziemlich schwer sicher zu unterschieden und noch schwerer ist es sie zu beschreiben" and further "... nicht nur die Beschreibungen der älteren Autoren, sondern such Meigen's, so wie die in seinem Werke mitgetheilten Beschreibungen Wiedemanns zu vielfältigen Zweifeln Veranlassung geben, welche dadurch noch vermehrt werden, dass beide Autoren in der Bestimmung un Benennung einiger Arten offenbar nicht im Einklang gewesen sind".

Both Zeller and Loew, however, are reluctant to express general views. Meigen's authority dominates unquestioned during this period as regards the systematics of *Diptera*, and therefore in their statements (Loew's letters acc. O s t e n - S a c k e n 1903) they are very restrained in their criticism of the view held by their "master", and in relation to Meigen himself are almost obsequious. This attitude is, however, at variance with their viewpoint as research workers. The discussion on morphological features defining the species of *Tabanus* L. which L o e w (1858a) makes in relation to almost every detail of structure in question, contains remarks as to the range of variation. His treatment is widely divergent from the Meigen-Tournefort concept of species.

When discussing features which form the greatest differences between species L o e w (1858a) gives as the most useful, the shape of the palpi and the third segment of the antennae. He states, however, that too much importance should not be attached to deviations in this latter feature, as they often occur within the species. According to Loew similar variation is exhibited by another feature – the frontal calli. He mentions several taxonomic characters which are of importance when identifying and describing species, e.g. differentiation in the size of the lens in the eye of males, their hairy covering etc. He also emphasises the great importance of the colour of the abdomen, while indicating the possibilities of its modification by different factors. The shade of colour of the abdomen is of far greater importance to him than the distribution of spots, and he considers colour and pattern of dusting as the most constant character. Loew almost entirely rejects the possibility of treating differences in colour as specific characters, and the range of morphological variation which he considers acceptable is in many cases even too wide, causing the combination of several different species. These errors of Loew's are chiefly due to his lack of skill in field observations (Osten-Sacken 1903). His work contains almost all the elements which we now use to describe species of *Tabanus* L. He omitted only the colour of the notopleural plates, hair on the basal segments of the antennae and the ocellar tubercule, characters which are today used to describe species or even sub-genera.

The systematic part of Loew's work contains an innovation in comparison with the works of Meigen, that is, the putting of species in order according to the formation of homological characters, i.e. a key. He groups species on the basis of the hairiness of the eyes, colour of the legs, abdomen, wings, eyes, antennae and structure of the palpi. His keys do not always lead to species, most often they lead to groups of species. These groups often include closely related forms, but often completely separate ones, on account of the random nature of the characters used. In the groups containing forms systematically distant from each other Loew found no difficulty in finding one or more characters distinguishing the species from each other. In the case of closely related species however, e.g. the group *T. tropicus* L. or *T. aterrimus* Meig., not only does he not give distinguishing characters, but in addition he has no formed opinion as to whether the forms described are species or variants of variation within the species.

The value of descriptions of different species given in Loew's work (1858a) is also not uniform. Descriptions of new species are far more precise than those of old species. These last descriptions are shorter and do not contain exact information as to the appearance of the animal.

An appraisal of Loew's work was made by research workers contemporars with him, on *Tabanus* L., such as Osten-Sacken (1903) and Brauer (1880). The first of them expressed himself somewhat sarcastically about the results of Loew's work, the other clearly critically. Negation of Loew's results was based on the statement that he was not able to distinguish between species of larger *Diptera* (Osten-Sacken), and also on the criticism of work on species described earlier, many of which were omitted (Brauer). It is very difficult today, 100 years later, to establish to what extent this criticism arose from real defects in Loew's work, and to what extent from personal antagonisms between these scientists. It is, however, well known that he was unable to overcome the difficulties in the interpretation of older species, since his access to old material was very limited and he worked in almost complete isolation (Osten-Sacken). Among the Polish *Diptera* experts contemporary with him, Sznabl and Nowicki must be mentioned, as they held very high opinions of his authority in matters connected with Dipterology and made use of his advice and assistance. The genus *Chrysops* Meig. (Loew 1858b), described by similar methods, attained a very favourable rating in Szilady's work (1917). When Loew's work (1858a) is considered from the point of view of results for the taxonomy of *Tabanus* L., it forms an important contribution to the task of setting in order the principles of systematic work on the genus *Tabanus* L.

Apart from the few specimens I had, I was unable to find the materials identified by Loew. I can, therefore, take only the collection of *Tabanus* L. of Nowicki (1873) on which his work on the *Diptera* of Southern Poland is based, as the foundation for an appraisal of the results of his work. I do not know to what extent identification in this collection may be referred to Loew himself, who was staying with Nowicki in 1872 as the latter's guest, but in any case identification of material was based on the work by Loew (1858a) and the later work by Schiner (1862). The number of incorrectly identified specimens in Nowicki's collection is over 53% (Tab. II) and is therefore very large. At the same time, however, the percentage of correctly distinguished species increases in comparison with the majority of the collections in which identification was based on works written before 1858. Difficulty in identifying resulted in differentiation of species improving only very slightly. Part of the errors made by Nowicki are undoubtedly caused by his tendency to distinguish the largest possible number of species, and many of them are therefore split species (Tab. II). Similarly Schiner (1862) obtained far from the best results on the basis of Loew's method. A further improvement in the situation occurred after the proper and consequent application of specific criteria defined by Loew and Zeller.

Loew went so far in his restrained treatment of the work of his predecessors that, probably not wanting to liquidate several of the Meigen species, he passed over them altogether in his monograph on *Tabanus* L., and gave part of them without expressing any view as to their specific separateness. A general attempt at putting the taxonomy of *Tabanus* L. in order had therefore to be postponed until later, and in fact this was done by Brauer (1880), who at the same time initiated a new period and biological trend in the systematics of *Tabanus* L.

Among the characteristic features of this period are the high percentage of correctly distinguished species and the almost complete liquidation of split species. They still appear in greater or lesser amounts in different works, but do not constitute a phenomenon indissolubly bound up with working methods and the way of thought of that epoch. The number of lumped species decreases more slowly than the number of split species, as a result of the difficulties involved in the description and assessment of the extent of morphological difference between species. The number of correctly differentiated species is initially 53, but later increases considerably, chiefly owing to the description of new forms from the hitherto little-examined areas of South-Eastern Europe.

The improvement in the state of the taxonomy of *Tabanus* L. is connected with the acceptance of a new species concept, which was worked out on the basis of research made by Zeller, Loew and Brauer. The last of these expressed very decided views on species. He writes (Brauer 1887, p. 13): "Die Art setzt sich aus Individuen der nähsten Verwandschaftsgrades zusammen, aus

Individuen, welche sich gegenseitig aufsuchen und als zusammengehörig erkennen". On the page 16 he states: "... in der Natur objective Arten existiren, d.h. Individuenreihen, welche nicht nur durch viele Merkmale scharf charakterisiert sind sondern auch sich gegenseitig aufsuchen und sich von anderen Individuen derart trennen, dass zwischen denselben meist eine gewisse Scheidewand besteht, die bei niederen Thieren oft eine mechanische, bei höheren aber meist psychische zu sein scheint".

The decisive importance of biological criteria in defining the boundaries of species is emphasised in other parts also of the work referred to. Brauer states quite clearly there, that the biological units of the species, and not morphological properties of individuals, decide the objectiveness of species in nature. Correct recognition of species is only possible in one way, by the discovery of definite biological groups. In his deliberations on the objectiveness of biological species Brauer (1887) uses the method of comparing different units of the living world with each other; an individual, a swarm of bees etc., indicates how complicated are the implications of this concept. Species for him is therefore one of such whole units of nature.

In addition to general deliberations on the species concept he devotes a great deal of attention to problems of method. For instance, he introduces the idea of the systematic individual. This as understood today is a group of arithmetical means of the values of different characters for each species. In comparing an actual individual with the systematic one he writes: "Die Erscheinung eines Thieres gibt uns daher nicht das Bild eines systematischen Individuums, sondern etwas viel allgemeineres, das eines conkreten Individuums" – as each individual contains many deviations in different directions from average values established for the whole species. In speaking of the possibility of defining the species on the basis of one individual he writes: ". . . Allerdings kann in obigen Fällen nur ein Individuum sichtbar gewesen sein, aber die Beobachtung und Untersuchung lehrt uns gewisse Charaktere an einen gegebenen Individuum nicht als individuelle, sondern als solche einer Art. . .".

These deliberations contain a concrete methodical view on the species as a collective unit. The subject of description and knowledge is not a definite individual, but a systematic individual – the species itself. In the morphological sphere – they are simple average values together with a definite range of variation of the given character. It must be admitted that in his monograph on the genus *Tabanus* L. Brauer (1880) fully satisfied this requirement.

Yet another remark throws a light on Brauer's view (1887) when he discusses the working methods of systematicians. He writes: "Die Fähigkeit solche Charaktere in einem gegebenen Falle herauszufinden ohne eine grosse Anzahl von Individuen vergleichen zu können, wird durch die vorhergegangene Uebung im Untersuchen verwandten Individuenreihen erklärlich". It is therefore quite clear that examination of a series of individuals is referred to here.

In Brauer's opinion the subject of description is the systematic individual, and a series of closely-related individuals constitutes the representative of the species in examinations of museum material. Collections of *Tabanus* L. amassed.

during Brauer's activities in Austrian territory, and in particular in the Vienna district, are evidence that this methodical principle formed the basis for his real work.

Brauer did not (1887) altogether avoid mistakes, however, he believed, for instance in the existence of invariable characters, but this viewpoint is at distinct variance both with his later arguments and with his practical research work. Information on variation, particularly of taxonomic features, was extremely scanty during the period when Brauer did his work, and therefore one of the old formulations of systematic principles crept into his text: "Die Aufgabe der Systematiker ist jene charaktere bei einer Thier oder Pflanzenform zu erkennen, welche wie man annimt keiner Individuellen Veränderung unterliegen". It was this attitude in research workers such as Brauer which led to its being demonstrated that invariable characters do not exist in nature.

I comparison with the previous concept of specie with *Tabanus* L. the matter contained in Brauer's statement and in his works on actual species differs considerably. Species as Brauer understood it was variable and possessed biological characters proper to it. The range of variation is in his view defined by biological limits – the real limits of species.

All the features which are proper to the species as Brauer sees it are based on data concerning another biological unit-population. Today it is easier for us to define the features of species by means of population properties, nevertheless neither of these units overlap the other, at least not in space. Brauer's species is not a unit possessing a geographical measurement. He gives abundant information on the occurrence of species known to him within the paleoarctic region, but species with Brauer are not split up into local populations or subspecies. He extends the properties of local populations, accurately observed, to the whole species. With this kind of treatment there is no room for discussion of the geographical differentiation of the species. From the point of view of the development of the general concept of species and also from the systematic group elaborated by Brauer (insects) statements on the geographical differentiation of species would, however, have been premature. The application of new working principles and the biological treatment of the definition of species form a considerable step forward in relation to the state of knowledge which had existed up to that time.

Brauer combines in himself characteristics rarely found together; a tendency to profound philosophical analysis of nature and enormous exactitude in the working out of results. He also may be considered as the creator of the principles of proper description of the species *Tabanus* L. It is he who for the first time gives a separate description of male and female. He discussed each systematic character according to an established plan: first the head, with detailed discussion of the properties of the frons, the structure and colour of the antennae and palpi. Then follow the various parts of the thorax and attachments (wings, halteres, legs) and a description of the abdomen. This order is generally observed for all the species. We sometimes encounter a changed order in the description of the wings in place of the description of the abdomen. Many properties of structure, chiefly the head and its attachments, are illustrated. Several drawings, e.g. the profiles of the head of males, form proof of Brauer's special kind of mastery in drawing.

In Brauer's monograph (1880) there is no discussion of the biological properties of the species of *Tabanus* L. There are no indications that he used biological features to differentiate them. It is probably that he did not carry out a precise elaboration of the biological criteria of species. Sznabl (1881) states that Brauer possessed unusually well developed capacity for observation in field conditions. It is possible that this enabled him to grasp biological differences between species without making detailed analyses. It is significant here that in distinguishing between species occurring in Austria, with which he was most often concerned, he made only one mistake.

It proved possible to trace the influence of Brauer's method on the improvement in the ability to differentiate species and identify specimens in the collection of Sintenis and G. Schroeder (1910) (Tab. II). The former worked independently and collected material from the Dorpat district. His collection is determined on the basis of Brauer's work (1880). Schroeder worked in an entomological centre in Szczecin, in which there were extensive collections and which had its own established traditions. In both collections a considerable increase in the percentage of correctly identified specimens can be observed. The results of Brauer's method can be seen particularly clearly when considering the distinguishing of species, which in the case of Schroeder, were brought to a very high level. Sintenis mistakes are caused partly by inadequately thorough examination of specimens for identification. Investigation of the materials of Brauer himself might supply more interesting data, but in the collection made by this scientist, kept in the Naturhistorisches Museum in Vienna, specimens bearing an identification label with Brauer's name are less numerous than specimens from Winthem's collection from the 18th century. Either there are not labels on the whole of the material, or they bear the name of Bergenstamm, a close collaborator with Brauer. As the whole collection was later on re-positioned and agglomerated, it is difficult today to discover what really constituted the contents of Brauer's species, the more so that it is often extremely difficult to find individuals forming material for description in his monograph. In this case also it was only possible to define the influence of Brauer's investigations on the improvement in the state of systematics of *Tabanus* L., which in any case is the most important for the purposes of this work.

Brauer's methods and views carried with them a revolution in the systematics of *Tabanus* L., similar to that caused 80 years earlier by Meigen's work. Meigen's method opened the way to unrestrained descriptive research. Brauer's method was an attempt at creating a system of rules for research in descriptive work. A large proportion of research workers contemporary with Brauer (Bigot 1880, 1892; Pandellé 1883; Gobert 1881) chiefly French systematicians, ignored his works and used Meigen's method as a basis for their own work. Brauer's contribution to setting the systematics of *Tabanus* L. in order was, however, to great to pass over in silence. This is clearly shown by the history of research on the genus *Tabanus* L. in the 20th century.

Biological sciences in the 20th century exhibit a flowering of experimental research. New disciplines arise, experimental technique is worked out with precision. General biological problems are increasingly frequently attacked from the point of view of experimental data. During this period working methods of systematics and the character of the results obtained by taxonomic research undergo great changes. The result of this situation is that an increasing lead in general biological discussions is taken over by representatives of other trends, in the sphere of the problems of species, in particular by geneticists. These attempts, as I showed previously, led on the basis of individual genetics to a continuation of the splitting treatment of species originating with Tournefort's concept. On the other hand, certain representatives of genetics (Lotsy 1931) propose the complete deletion of the idea of "species" from biological terminology.

Within systematics itself the situation is also critical. On the basis of discussion begun as early as halfway through the 19th century on the objectiveness of the biological species, a series of systematicians (Allen 1908, Bessey 1908) and of dipterologists (Williston 1908) reach the conclusion that species is an agreed unit, useful only for setting biological material in order. Plate (1914) considers that the best criterion of appurtenance to a species of an individual is its possession of features detailed in the description and diagnosis of species. At the same time Kleinschmidt (1900) endeavours on the grounds of systematics to overthrow the idea of species and introduce a different term "Formenkreis".

In this situation, when many eminent biologists have tried to overthrow the idea of species or to reduce it to the category of an agreed unit, the majority of systematicians withdrew from general considerations and engaged only in work on definite taxonomic problems. Research on *Tabanus* L. followed this path in the 20th century.

Brauer published the final and full discussion of the problem of species in 1887. From that time on there was, in fact, not a single statement made putting the question of species in the case of *Tabanus* L. openly. Such escape from theoretical reasonings is not, however, possible. Each definite systematic solution is the result of a definite species concept applied consciously or unconsciously.

In investigations of the genus *Tabanus* L. this departure from general consideration of the problem had somewhat serious consequences during this period. In the 20th century a return to the Tournefort's species concept is evident in the work of several scientists, and consequently a return to the splitting trend.

Development of research on the genus *Tabanus* L. in the 20th century took place in three directions – the faunistic-systematic, the methodical, which during this period covers only the means of description and the nomenclature.

Faunistic and systematic research

After the appearance of Brauer's (1880) monograph it became very desirable to carry out systematic and faunistic research, as the results of previous works could not be referred to the existing state of knowledge.

Before the first World War the *Tabanidae* of Denmark had been worked on by Lundbeck (1907), of great Britain – by Verrall (1909). In 1914 Szilady published his first work on *Tabanus* L. in the Paleoarctic Region. All these scientists used the Brauer concept of species and put their own materials in order from the systematic aspect on the basis of Brauer's method. The last two of the authors mentioned above also try to develop Brauer's method further and introduce supplements and corrections to his monograph.

During the inter-war period Szilady (1923) continued to work intensively, publishing material from the lesser known and investigated regions. Among the best known of the authors of monographs and faunistic work during this period is Kröber (1923, 1924, 1925, 1928, 1932, 1935, 1938). The *Tabanidae* of France were twice given treatment in monograph form (Surcouf 1924, Séguy 1926). Among some of the most interesting works those by the following authors must be mentioned: Shannon and Hadjinicolaou (1936), Drensky (1929), Olsoufev (1937), Ghidini (1937) and Oldroyd (1939).

After the second World War the following territories were worked on from the systematic and faunistic aspects: Switzerland (Bouvier 1945), Belgium (Leclerq 1952), Italy (Leclerq 1956), Spain (Leclerq 1957a), France (once again) (Leclerq 1957b). Czechoslovakia (Moucha and Chwala 1958–1959) Sweden (Kauri 1951, 1954) Roumania (Dinulescu 1958), Hungary (Aradi 1958), Poland (Trojan 1959).

Development of methods of description

Continued development of methods of description during the present century have been based on Brauer's methods. The first interesting attempt at developing this method is given in the work by Verrall (1909). He used an enlarged description of different species extending in certain cases to over seven pages of small print. This method, although it made an exact description of material available to the research worker, is not universally applicable in practical work on systematics. Verrall's successors in Great Britain, who include Oldroyd (1939) in their number, did not follow in his steps but shortened descriptions of species considerably.

Szilady (1914, 1923) exhibited a varied approach to description and discovered a very large number of new species from the Paleoarctic Region. He used Brauer's method to describe some of them, setting out in drawings a comparison of the three main taxonomic features, i.e. structure of the frons, antennae and palpi. In many cases, however, e.g. in that of *T. mixtus* Szil., his description is not a description at all, only consideration of the differences between near species and statement of a name for the intermediate form. Despite this, this short discussion made it possible later on to differentiate this species with certainty from a group of others closely related. Szilady had therefore considerable intuition regarding the fundamental feature in a given group of species and had the gift of defining it in a few words. In addition in the work of this author we encounter many unjustified attempts at splitting species into apparent units within the species. I was able to obtain a close knowledge of Szilady's working methods when reviewing the collection containing 3137 individuals with his identification labels The percentage of incorrectly identified specimens is 10.8%. If, however, we deduct from the total number of incorrect identifications the 189 individuals of *T. apricus* Meig. identified by him as *T. graecus* var. *apricus* Meig. in which case the name and definition are correct, apart from the species having been reduced to a variety, then the material contains only 4,8% of incorrect identifications. It is of interest here that these mistakes most often refer to species described by Szilady himself, the types or single specimens of which are contained in the same box. The difference lies only in the fact that Szilady's types come from Siberia or the southern part of the Paleoarctic Region, and the incorrectly identified specimens from Europe.

Szilady evidently did not believe in the possibility of finding these species in Europe and did not distinguish them in the material. Among the unsuccessful attempts we may also include the majority of the variants (varietas) differentiated by him from Europe. His *T. bromius nigricans* Szil. consists of two species, one of which is actually very dark – *T. maculicornis* Zett. The second variant *T. bromius flavofemoratus* Str. according to Szilady is the species already described previously, *T. regularis* Jaenn. The extraordinary intuition with which he was endowed in relation to material originating from unexamined areas deserted him almost entirely when he was confronted by collections from Central Europe.

Olsoufev's (1937) services to the development of description of species of *Tabanus* L. are very great, on account of the enlargement of Brauer's description, the application of a logical and constant order in descriptions of all species and the illustration by at least three drawings of each species to which he had access, thus combining the drawing of the three main features from Szilady's description with exactitude not hitherto encountered in the description of whole insects. In that part of the systematic collection of *Tabanus* L. identified by Olsoufev which I was able to see (chiefly materials from the *T. tropicus* L. group) I was left in no doubt as to the unambiguous distinguishing of each species, apart from one case of a lumped species.

Collin (1940) made use of new characters: the structure of the cerci and the final sternite – to differentiate between closely related species. I obtained very good results from the extensive material which I examined by means of this method, and the differences discovered between near species are often more distinct than when other methods are used.

The features now used to describe and distinguish species of *Tabanus* L. cover in principle all possible combinations of the elements of external structure. Each of them in the definite group of species may take on, in comparison with others, primary importance. The following elements included in the structure of the various parts of the body were used:

Head

1. Shape of head (especially when distinguishing males)
2. Structure, colour, pattern and hair on eyes
3. Structure of ocellar tubercule

4. Breadth and hair on lists behind the eyes
5. Structure of frons, its proportions, spots and dusting
6. Height and dusting of frontal triangle
7. Dusting and hair of face and cheeks
8. Structure, colour and hair of antennae
9. Structure, colour and hair of palpi

Thorax

1. Colour, dusting and hair of mesonotum
2. Colour of notopleural plates
3. Hair on scutellum
4. Hair and dusting of pleural plates
5. Structure and use of wings
6. General colour of wings and distribution of spots on their surface
7. Colour and hair on calyptrae
8. Colour of halteres
9. Colour and hair of legs

Abdomen

1. General shape
2. Structure of genitals of males and the ovipositor of females
3. Colour, dusting and hair of abdomen and distribution of these elements on its surface (pattern)

This review is not very detailed and it can be extended considerably. Not all of the features mentioned are ot equal importance. It is possible to mention several of such features from the list given above, which in the case of *Tabanus* L. are of fundamental importance: if omitted this would render any description of the species of no use whatsoever. In the case of females these are: structure of frons, antennae and palpi and structure of postabdomen; with males: structure hair and colour of antennae, structure of eyes and colour of abdomen. An important feature, not as yet properly examined, is the structure of the cerci, in particular their final segment. In certain cases other features also become important, but they do not lend themselves to application to all species or their variability is too great for them to constitute a reliable basis for defining differences between species.

A perfected means of description constitutes a great achievement in research on *Tabanus* L. in the 20th century. Verrall (1909) attained the greatest degree of exactitude. His descriptions make it possible to find the individuals in the collection which formed the subject of his work. Extended description. despite the increased exactitude, is of little use for systematic purposes on account of its prolixity. The subject of systematic investigation is not the individual, but the species, which is always an agglomeration of individuals. The features expressed by adjectives in the classic description used in the systematics of *Tabanus* L. should be fundamentally changed, and achieve a quantitative expression. When describing a collective unit it is not sufficient to state that the antennae are yellow, sometimes brownish. Such words as "seldom", "sometimes", "longer", etc. which imply the definition of the quantitative character of a given phenomenon are now replaced by indices making it possible to represent more extractly the actual relations and variation in the population. The first attempts as formulating indices permitting of representing materials in a quantitative way were undertaken by Kauri (1958) in his work on holoarctic species of the genus *Tabanus* L. The preparation of a whole series of such indices is essential for the continued development of research on variations in *Tabanus* L.

Questions of nomenclature

Questions of a technical nature are chiefly those connected with nomenclature. In the first place there is the question of synonymics. Distinguishing and naming of new species is not always connected with correct recognition of their contents, and this is particularly true of species described some time ago. This leads to an increase in the number of names in relation to the actual number of species. This phenomenon, traced over a period of time, makes it possible to discover the considerable decrease in the number of species possessing one name. During a period of approximately 100 years their number fell from 100% to 31% (Fig. 6). The greatest decrease in non-ambiguous naming of species and the increase in the number of erroneous names connected with it took place during the Meigen period. Over 60% of European species of *Tabanus* L. were described then under different names, as pseudo-new species twice or even many more times.

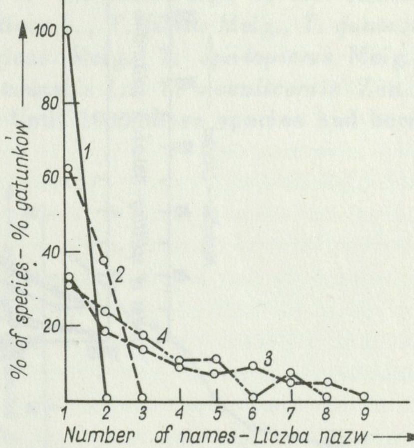


Fig. 6: Structure of synonymy of European species of *Tabanus* L.
1 – 1758 year; *2* – 1800 year; *3* – 1850 year; *4* – 1909 year
Struktura synonimiki europejskich gatunków *Tabanus* L.
1 – 1758 r.; *2* – 1800 r.; *3* – 1850 r.; *4* – 1909 r.

Confrontation of descriptions and materials forming the basis for synonymic works (Kertesz 1900, Bezzi 1903, Verrall 1909) makes it possible to trace in time the phenomenon of repeated naming of species already described; some of them were described as many as eight times. The development of synonymics in time (Fig. 6), presented in the form of curves describing the moment in time, show that in the first period the percentage of species described several times was very small. From the point of view of users of systematics this state of affairs was very favourable, since in literature we encounter considerable lack of ambiguity in specific names. The Meigen period was one of mass description and repeated naming of species previously described. It is only now that a certain constant relation has been established between correct and incorrectly differentiated new species. The number of species with one name is established on a level of about 30%; with two names – about 20%; with three 15%; with four or five about 10%; 12% of species have 6 to 8 names.

This state of nomenclature renders it difficult to make use of the results of systematics works, if only on account of the fact that the synonymisation of the species is as a rule subjective. It is therefore never certain whether the synonymised names do in fact refer to one species. The acceptance of some sort of system of synonyms is usually the result of confidence in its author. Synonymics is also evidence of the usefulness of systematics. The increase in the number of names in *Tabanus* L. shows that if each distinguishing of a good new species corresponded until 1800 to the creation of 1.4 names, from 1850

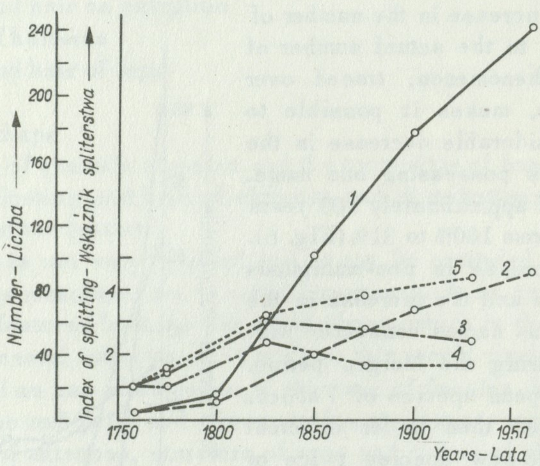


Fig. 7. Development of splitting trend in the genus *Tabanus* L. in Europe
1 – number of names; *2* – number of species. Splitting: *3* – all Europe; *4* – Southern Europe; *5* – Central and Northern Europe

Rozwój spliterstwa w rodzaju *Tabanus* L. na obszarze Europy
1 – liczba nazw; *2* – liczba gatunków. Spliterstwo: *3* – cała Europa; *4* – Europa południowa; *5* – Europa środkowa i północna

to 1900 this index increased to 2.5. The number of names increases therefore 2.5 times more quickly than the true number of species recognised. These effects are most often obtained by splitting up previously described species the so-called splitting tendency, which systematicians have endeavoured to counteract for a long time now. This can be clearly expressed in figures. The index of the splitting tendency exhibits a constant and considerable increase in Central and Northern Europe. The situation in South-Eastern Europe is better (Fig. 7). Geographical differentiation of this index reveals the causes of the splitting tendency, which depends on four factors:

1. The degree to which the area from which the material originates has been examined. The activities of the majority of systematicians working on the genus *Tabanus* L. are confined to the areas of Central and Northern Europe. The materials forming the basis of their work came from two sources. The basic part (from the aspect of number of specimens) was formed by materials from the country in which the given scientist worked. Specimens from other areas were obtained as a rule in small numbers only, chiefly by means of exchange or during expeditions to regions not investigated to the same extent. It is for this reason that during the first period of development of systematics of *Tabanus* L. we observe the index 1.4 in Central Europe, which is evidence of the very small degree of splitting of species. During this same period we do not find a single repeat description of species from South-Eastern Europe (index equals 1.0).

2. The amount of material used by the research worker. The most numerous species from Central and South-Eastern Europe are those most frequently described. The largest series of specimens in the Naturhistorisches Museum in Vienna consists of the following species: *T. aterrimus* Meig., *T. ater* Rossi, *T. umbrinus* Meig., *T. gigas* Herbst., *T. rusticus* L., *T. fulvus* Meig., *T. quatuornotatus* Meig., *T. graecus* Fabr., *T. apricus* Meig., *T. spodopterus* Meig., *T. sudeticus* Zell., *T. bovinus* L., *T. autumnalis* L., *T. maculicornis* Zett., *T. glaucopis* Meig., and *T. cordiger* Meig. Until 1900 these species had been given on an average 3.77 names each, while the remaining European species in this same period had on an average 1.65 names each. Of course these figures increased later on.

3. The research methods in use at the given moment. Not every means of distinguishing species yields good results. In the first period of the systematics of *Tabanus* L. (1758–1800) the method of diagnosis provided no practical possibilities of describing the species, as the characters used were not specific. In the 19th and 20th centuries the means of description made it possible to distinguish species.

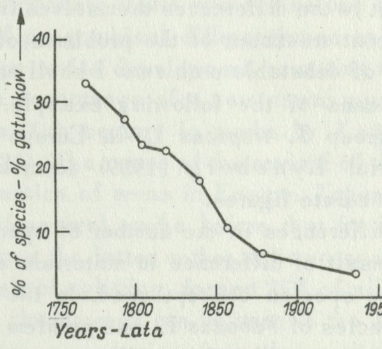


Fig. 8. Increase in new species in Europe
Przyrost nowych gatunków w Europie

4. The attitude of the research worker. This is formed both by the species concept accepted and talent for observation, as well as prestige factors.

The action of all these factors must be taken into consideration when attempting to assess the development of systematic research. They decide on the possibilities and prospects for development of research on a given group. The increase of freshly-described "good" species in the given area is an index of the degree of knowledge of the systematic group. This increase in Europe over the last 200 years is normal in pattern (Fig. 8). The possibility of describing new good species decreases with the passing of time. Good species described in more recent times mainly come from less thoroughly investigated areas lying on the extreme fringes of Europe. At the present time for one "good" newly-described species there are three attempts at splitting old species into artificial units. These data from a different side indicate that under present conditions consideration should be given to ways and means which would enable the systematics of *Tabanus* L. to be protected from an increase in the ballast of unnecessary names. Each of them creates considerable difficulty with nomenclature after the lapse of fifty or more years.

Against the background of the research on *Tabanus* L. described above, a conflict arose in the 20th century between two systematic tendencies based on different species concepts. Its source must be sought for in the '20s when, after the end of the First World War, work was begun on *Tabanus* L. by a new generation of research workers, while the influence of Brauer's work (1880) is far weaker, if only on account of the lapse of time. In addition to the prevailing Brauer concept of species of *Tabanus* L., the Meigen concept of species is revived. A characteristic feature of this discussion is that it takes place solely on the plane of definite research solutions, and none of the representatives of either trend makes any open statement on general problems. There is therefore no attempt at criticism of trend or justification of one or other of the two scientific attitudes. Research workers do not perceive, or do not want to perceive, that it is the differences themselves in view on species which lead to completely different treatment of the problems of specific systematics and differing solutions of debatable problems. I shall endeavour to illustrate the situation created by means of the following example. Olsoufev (1937) differentiates within the group *T. tropicus* L. in Europe six species, and in practically the same material Lyneborg (1959) describes 12 species. Many other authors give intermediate figures.

Differences in the number of species in this and in other examples are not the result of difference in materials and the actual number of species, but only in the species concept used. In the discussion taking place on the taxonomy of species of *Tabanus* L. one problem is raised – species distinguished by whom are to be considered "true" ones – while the real basis of this differentiation – the Brauer or the Meigen concept, does not enter into the subject of discussion. When those taking part in the discussion adopt such an attitude it cannot lead to an explanation of the fundamental question – in what way should the species concept in the light of our present knowledge of the variability of *Tabanus* L. form a working basis? Until a final solution of this problem is arrived at there can be no question of a rapid solution of definite taxonomic problems. The Brauer concept formed the only working view in the taxonomy of *Tabanus* L. before the first World War. Verrall Szilady and others use it as the basis for their work. After the first World War Séguy, Olsoufev and Oldroyd follow their lead, as do Moucha and Chwala, Kauri and others after the second World War.

The crisis prevailing in systematics at the beginning of the present century was overcome chiefly by introducing the polytypic species concept. In investigations on the genus *Tabanus* L. work on local fauna has hitherto been the rule, and as a result the possibility of grasping geographical differentiation of species in considerably limited. The polytypic species concept has not so far been applied on a large scale in practical work. Nevertheless when comparing descriptions of species Olsoufev (1934, 1936) a difference can be found between the formation of taxonomic characters in individuals from different parts of its range. The means of description used by Olsoufev did not, however, permit of making the difference between populations really clear; this was not in fact the aim of the works referred to. Many interesting data on differences in the formation of morphological features in different local populations of two species of *Tabanus* L. were given by Kauri (1958). An assessment of the present situation of the taxonomy of species of *Tabanus* L. was given by Oldroyd (1954) in his introduction to the monograph on Ethiopian species of *Tabanus* L. "... we seem to be approaching a stage in the classification of this tribe (*Tabanini* – my note) when we can recognise complexes of races, genetical forms or subspecies". In this way the supporters of the Brauer concept are now arriving in their investigations at confirmation of differentiation of species within an area and the necessity for investigating this differentiation. The polytypic species concept elaborated by bio-geographers may best serve this purpose. In this case the application of a new theoretical view in examination of species does not lead to an overthrow of what has hitherto been established on the basis of the Brauer concept, which as I showed previously treats species as one large population. The introduction of the idea of geographical differentiation to this concept can only form a logical continuation of its development, resulting from present day needs in research, and not the acceptance of a new starting-point.

The splitting trend was revived in the 20th century in works by Kröber (1923, 1924, 1932, 1938) and Surcouf (1924). The cause of the revival of these tendencies lay partly in the faunistic exhaustion of areas in Europe. *Tabanidae* in France had already been the subject of several works before that by Surcouf (1924), and in his search for new forms the latter author split up species artificially. Such forms, created as the result of splitting, formed 35% of all the species distinguished in his work. A similar phenomenon can be seen in the works referred to by Kröber, which make no new contribution from the methodical aspect. Description of species given by him are often insufficient and the drawing not exact. A check on 266 of the specimens identified by him (Tab. III) makes it possible to establish by means of several indices, that the results of his works may be compared to the Meigen period in the systematics of *Tabanus* L.

After the second World War the Tournefort concept of species is revived in works by Leclercq (1956, 1957a, 1957b) and Lyneborg (1959).

Splitting in the 20th century has a slightly different character from that during the Meigen period. In cases of examination of local fauna, especially when the areas had been investigated before, the application of the splitting species concept presents apparent opportunities for discovering new "forms" or species. A new tendency appears, to describe as new species or variants of different geographical populations of one species. This is evident in the examples of split species in the 20th century, e.g. *T. lunatus* Fabr., in which case, out of 6 differentiated geographical variants only two really have separate ranges. A similar situation arose in other cases. *T. glaucopis* Meig. and *T. sudeticus* Zell. were split into several units which were given different ranks – from form to good species. Differentiation within the species in *Tabanus* L. is shown by means of different units. The idea "form" which approximately corresponds to the idea "varietas" used by scientists of the Meigen period, is that most seldom used. In the 20th century "form" defines individual deviations in variation within the population. The term "variety" (varietas) indicates in the systematics of *Tabanus* L. both different individuals or groups of individuals within the population, and also differing geographical populations. These latter are usually termed "subspecies" (subspecies), but the consequent application of this term to geographical units within the population in the case *Tabanus* L. is encountered only in Olsoufev's work (1937).

Investigation of geographical differentiation with *Tabanus* L. followed a different road from analogical research on other systematic groups (Rensch 1929). Adherents of the splitting tendency, who where the authors of the geographical forms described, were responsible for the greatest part of the confusion. During this same period the supporters of the Brauer concept did not make distinguishing of the geographical variation they observed part of their programme, but postponed more thorough investigation of the problem until later (Oldroyd 1954), but did as did Olsoufev (1937) already referred to, in using two precisely defined units: "subspecies" for definition of a geographical unit and "form" to define a variant of inter-population variation.

Continued correct development of research on geographical variation in *Tabanus* L. will depend to a great extent on whether the species concept is set in order and on the use of proper descriptive units.

IV. VARIATION IN TAXONOMIC CHARACTERS AND THE SPECIES CONCEPT IN *TABANUS* L.

Choice between current species concept in *Tabanus* L. should result from examination of variability in species and the determination of which theoretical model of species most closely corresponds to the properties of the material examined. Systematic research so far carried out on *Tabanus* L., which the exception of the work referring only to part of the problem, but carried out with great exactitude by Kauri (1958) supplies practically no material which permits of assessing the variations in populations or of the species within its natural range. The greater part of the remarks made on the variation of species is based on impressions gained from firsthand observations of individuals, and not on measurements of the characters examined. Such a situation is not favourable to the development of useful discussion on the extent of variation of the species and does not permit of settling the questions as to which of the concepts is applicable in research on *Tabanus* L. The solution of this question is of considerable significance from the aspect of continued development of the taxonomy of this group. At the present time representatives of the Brauer and

Meigen trends use units of completely different values in their works. The same names often lead to error. With Lyneborg (1959) species implies something quite different to that implied by Kauri (1958) or Trojan (1959) species as used by Moucha and Chvala (1958–1959) does not correspond to the treatments given it by Leclercq (1957a and b). A decision must therefore be reached as to what extent of variation of taxonomic features in *Tabanus* L. is intraspecific and what exceeds the limits of species.

A correct solution of systematic problems, in view of the considerable geographical variation of the species and the occurrence of numerous local populations cannot be based on material collected at random, and referring to single individuals. Series of specimens should be sufficiently large to make quantitative description possible. It is also essential to know whether the given form is in fact the only representative of the species in the given area. Definition of the conditions which must be complied with by material used for taxonomic diagnosis in the case of *Tabanus* L. is therefore of fundamental importance among systematic problems.

Variation of taxonomic characters in very numerous populations

Populations of panmictic species in which the numbers are very great constitute a basis for the correct genetic and ecological reactions which shape their variation. It is assumed that such populations exhibit established relations between each genotype and a considerable extent of variation (Wright 1941), which is expressed in the form of a normal curve.

All these populations of species of the genus *Tabanus* L. in which the numbers are high should in principle comply with these conditions.

Variability in taxonomic features in such populations was examined for several species of *Tabanus* L. In the first place analysis was made of the variation of the frontal index in three forms fairly widely distant from each other from the systematic aspect. Series of 100 individuals chosen at random from large populations were used for the purpose of measurements. The first of them was the commonest and most thoroughly investigated European species – *T. bromius* L. The range of variation of the frontal index of this species was determined previously (Kröber 1925) as 4–5 and by Olsoufev (1937) as 4–4.5. The measurements made of individuals in the Kampinos Forest showed that even the average frontal index in one population exceeds the value given by Olsoufev (op. cit.). Determination of the extent of variation of a definite character in a population is possible on the basis of the value of the arithmetical mean (M) and standard deviation (σ). Mayr, Linsley and Usinger (1953) state that 99.72% of the variation of a given character in a population comes within values $M - 3\sigma$ and $M + 3\sigma$. This formula makes it possible to calculate the theoretical extent of variation. Its value for the frontal index (Tab. IV) does not greatly deviate from those obtained on the basis of the material examined. The upper limit of the extent of variation, calculated theoretically, was however exceeded

Numerical values of index of frons in *Tabanus* L. in three large local populations

Charakterystyka ilościowa wskaźnika czoła *Tabanus* L. w trzech dużych populacjach lokalnych

Tab. IV

Species – Gatunek	N	Range of variation Przedział zmienności		$M \pm m$	σ	V	Degree of agreement with normal distribution Stopień zgodności z rozkładem normalnym
		observed zaobserwowany	theoretical teoretyczny				
T. bromius L.	100	3.98 – 5.91	3.64 – 5.72	4.68 ± 0.035	0.346	7.38	2.24
T. distinguendus Verr.	100	3.86 – 6.15	3.70 – 6.00	4.85 ± 0.038	0.383	7.89	2.18
T. quatuornotatus Meig.	100	2.75 – 4.38	2.64 – 4.41	3.52 ± 0.030	0.295	8.36	1.35

N – number of individuals in sample – liczba osobników w próbie

M – arithmetical mean – średnia arytmetyczna

m – standard error of average – błąd standardowy średniej

σ – standard deviation – odchylenie standardowe

σ^2 – variance – wariancja

V – coefficient of variation – wskaźnik zmienności

t – difference between given population and that based on sample consisting of 100 individuals – różnica między daną populacją, a opartą na próbie ze 100 osobników

p – probability of identity of samples – prawdopodobieństwo identyczności prób

Explanations to Tab. IV–IX

Objaśnienie do tab. IV–IX

Dependence of numerical values of index of frons of several species of *Tabanus* L. on size of sample

Zależność charakterystyk ilościowych wskaźnika czoła kilku gatunków *Tabanus* L. od wielkości próby

Tab. V

Species Gatunek	N	M ± m		σ	V	t	p
T. quatuornotatus Meig.	5	5.56 ±	0.17	0.377	6.78	4.01	0.0001
	10	5.00	0.07	0.214	4.28	1.21	0.2301
	25	4.84	0.07	0.365	7.54	0.52	0.6171
	50	4.76	0.05	0.377	7.92	1.50	0.1392
	100	4.85	0.04	0.383	7.89	–	–
T. distinguendus Verr.	5	3.74	0.06	0.129	3.45	1.394	0.1615
	10	3.61	0.07	0.213	5.90	0.929	0.3681
	25	3.57	0.07	0.347	9.72	0.725	0.4839
	50	3.48	0.04	0.329	9.45	0.749	0.4588
	100	3.52	0.03	0.295	8.36	–	–
T. bromius L.	5	4.56	0.08	0.182	3.96	0.617	0.8414
	10	4.88	0.09	0.297	6.08	1.758	0.0805
	25	4.67	0.06	0.298	6.37	0.1315	0.8926
	50	4.64	0.06	0.348	7.52	0.660	0.5097
	100	4.68	0.03	0.346	7.38	–	–

in the case of *T. bromius* L., as also happened in the case of the next species – *T. distinguendus* Verr. (Tab. IV). A greater degree of agreement between the theoretical extent and that obtained from material occurs in the case of another species – *T. quatuornotatus* Meig. (Tab. IV). Comparison of these indices for one population with the data found in literature for the whole range of these species, e.g the frontal index for *T. distinguendus* Verr. 5–5.5, and for *T quatuornotatus* Meig., 3.5–4 or 4–4.5 (Kröber 1925, Olsoufev 1937) shows that in these cases in which the variation of a given taxonomic feature has not been thoroughly examined, the range of variation may be erroneously determined. The length of the range of variation given for the majority of species as 0.5 is actually in the cases examined always greater than 2.0. At the same time both the standard errors, and the standard deviations of each mean are not great, and the index of variation (v) of this feature is similarly formed in the case of all the species, and does not exceed 9. The importance of this index for an assessment of variation in populations is the subject of numerous discussions. Its same values for different material and different values of arithmetical mean do not always point to uniform variation. In the case of mammals variation. the index of which comes between 5 and 6, is considered as small, and higher values rather indicate that the material was not uniform (Simpson and Roe 1939), e.g. from the aspect of age of individuals. In other cases (Philiptschenko 1927) the coefficients of variation prove to be far higher.

Curves of variation of the frontal index (Fig. 9) of the three species of *Tabanus* L. referred to, in accordance with the assessments of variation obtained, have one peak only, and steeply sloping sides. This is an additional indicator of the slight variation of the feature examined in large populations. These curves correspond to normal curves calculated for arithmetical averages and accepted divisions of variation. The variation of the frontal index is therefore from every aspect similar to its typical course which is observable in numerous biological materials.

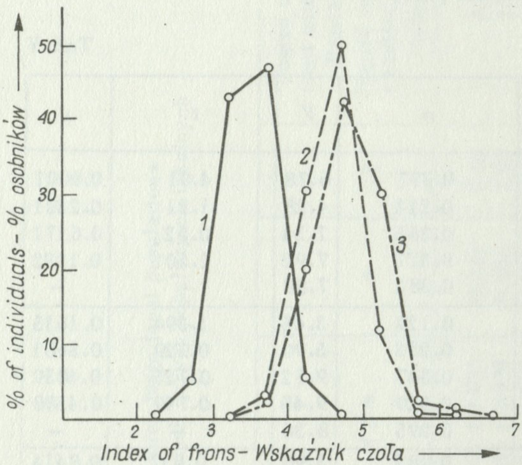


Fig. 9. Variability in index of frons of *Tabanus* L. in large local populations

1 – *T. distinguendus* Verr.; 2 – *T. quatuornotatus* Meig.; 3 – *T. bromius* L.

Zmienność wskaźnika czoła *Tabanus* L. w dużych populacjach lokalnych

1 – *T. distinguendus* Verr.; 2 – *T. quatuornotatus* Meig.; 3 – *T. bromius* L.

The index of the callus, use of which is not very general in the taxonomy of *Tabanus* L., is also connected with the frons. In principle the height of the actual callus is usually given in comparison with the height of the frons. What is necessary here, however, is the joint length of both frontal calli (lower and middle) which are joined together in the group of species *T. solstitialis* Meig. I calculated the index of callus by dividing the height of the frons by the joint length of both calli. The results obtained from the measurements of 100 specimens of *T. distinguendus* Verr., similarly to the case of the frontal index, give a curve with one peak only on the graph (Fig. 10) with fairly steep sides. However the numerical characteristics of variation of this index coefficient of variation ($v = 13.6$) worked out similarly make it possible to establish that this variation is almost twice greater in comparison with the frontal index. It is difficult to assess by how much the numerical result is caused by a low mean for the frontal index, and how much by actual variation, which is not shown by the graph. On the basis of the structure itself of the frontal callus, the shape of which depends on the extent to which the shiny portion in the middle of the frons is covered by matt dusting, it may be assumed that in this case it is far easier simply to wipe off the dusting and so enlarge the frontal calli, and in this way to change the value of the index of the calli, which in the case of the frontal index can only take place if changes occur during the development period of the pupa. These causes may result in the index of callus having a really greater variation than the index of the frons.

A good example of the difference between the judgment of variation by eye only, and its estimation by means of quantitative indices is proved by examination of the structure of the antennae in *T. solstitialis* Meig. The quantitative treatment of variation in the antennae is somewhat difficult. Mayr, Linsley and Usinger (1953) propose that each form of structure should be treated as a variant and their numerousness defined in the population. From the point of view of taxonomy the fundamental property of the material examined is the breadth of the antennae. Its correct assessment will therefore be the definition of the ratio of length to the breadth of the third segment. With a series of 43 individuals from the Kampinos Forest a set of antennae (Fig. 11) was obtained which considerably exceed the limits of variation usually shown in systematic descriptions of this species. The differences between extreme forms is so striking that in the event of allopatricity of these forms of the occurrence of differences during the period of appearance, they would have to be considered as belonging to separate species. This population, however, complies with all other requirements, and thus permits of their being one species. The differences shown are very distinct. The curve of frequency of each variant (Fig. 12) forms a single-peak curve, but in comparison with graphs of the previous characters it has a fairly extended base, which would point to the far greater variation in the index examined. The range of variation in this feature (1.3–1.7) observed is in agreement with the theoretical one (1.21–1.75) and does not exceed it, as happened in the case of the frontal index. Other values characterising this material ($M \pm m$ = 1.48± 0.014; σ = 0,09; V = 6.08) indicate the far smaller variation of this index in comparison with the foregoing ones. The basic feature of variation in the structure of the antennae in the series shown is that they become narrower, as shown by the index used. The eye perceives small differences in the sketch of the antenna, which might be assessed in different ways, often not paying attention to the chief phenomenon – regular variation exhibited by the given feature.

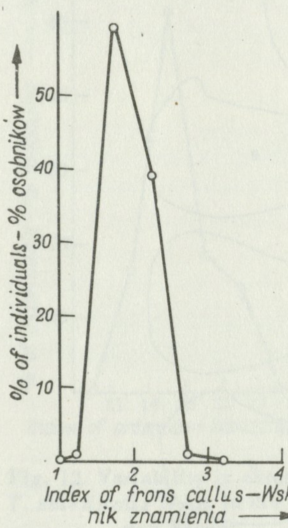


Fig. 10. Variability in index of frons callus of *T. distinguendus* Verr. in the Kampinos Forest

Zmienność wskaźnika znamienia *T. distinguendus* Verr. w Puszczy Kampinoskiej

A similarly distinct variation can be found in the structure of the palpi of this species. We encounter both individuals with narrow palpi and those with very much thickened ones, which are termed swollen ones. Within the range of variation of this characters (Fig. 13) all intermediate forms of transition in the structure of the palpi can be seen within this same population from Kampinos

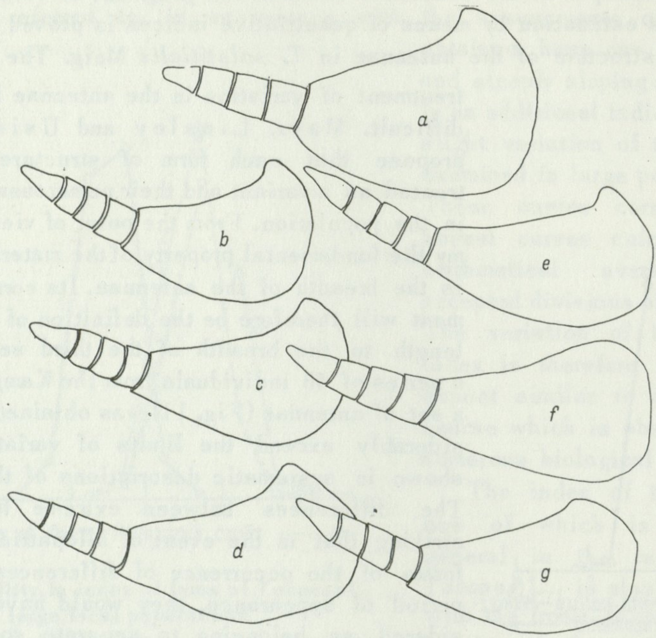


Fig. 11. Variability in structure of antennae of *T. solstitialis* Meig. in the Kampinos Forest

Zmienność budowy czułków *T. solstitialis* Meig. w Puszczy Kampinoskiej

Forest. The curve of variation in the structure of die palpi, formed similarly to that in the case of the antennae, based on the index of ratio of maximum length to maximum breadth, constitutes a single-peak curve of regular structure (Fig. 14). Indices characterising variation in the structure of the palpi ($M \pm m = 2.45 \pm 0{,}034$; $\sigma = 0{,}225$; $V = 9.2$) point to the greater variation of this character than of all those previously examined. In connection with this the theoretical range of variation of the feature examined is also slightly broader (1.78 – 5.13) and greater than that observed (2.14 – 2.88). These data permit of determining the suitability of the characters referred to for distinguishing species. Those characters are most useful which have the lowest index of variability, therefore the use of the index of palpi to differentiate species, especially those in the group *T. solstitialis* Meig. (Leclercq 1957b) is not the best means of achieving that end from the point of view of the data given here.

Examination of variability in the colour of the abdomen supplies other information. Two species of the sub-genus *Tylostypia* End., that is, *T. solstitialis* Meig. and *T. distinguendus* Verr., will be considered here. I include all forms from the species *T. solstitialis* Meig. which have a short, blunt-ended final segment to the cerci and mushroom-shaped subgenital plate (Collin 1940), frontal callus right-angled and distincly striped transversely, and whitish dusted abdomen. The description is given in this place as at the present time the contents of this species is given varying treatment, sometimes being split into several species – chiefly according to the colour of the abdomen. Forms are encountered with a completely black abdomen and also those with red spots reaching from the beginning of the 1st, to the end of the 3rd, and even to the beginning of the 4th tergite. In the drawing of the abdomen of a representative of this species (Fig. 15) the spots are marked with numbered lines which may be found in different individuals. These spots may be arranged in order of increasing length and by comparing their length with the length of the 2nd tergite the index of colour of the abdomen may be obtained. The series of figures obtained in this way for the specimens in the Naturhistorisches Museum in Vienna gives a good picture of the graduation of transition in colour of the abdomen, and in addition permits of calculating the index of variability ($V = 16.1$), which proves the considerable variability of the character examined. In this species individuals predominate with spots coming within

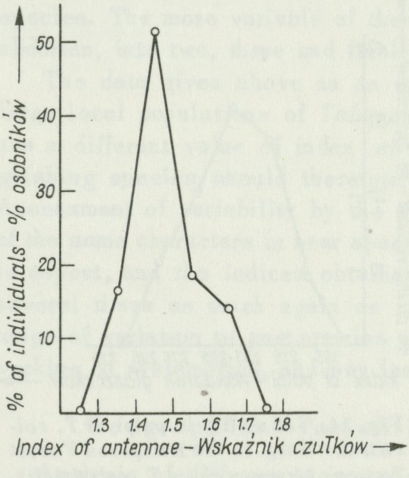


Fig. 12. Variability in antennae of *T. solstitialis* Meig. in the Kampinos Forest

Zmienność czułków *T. solstitialis* Meig. w Puszczy Kampinoskiej

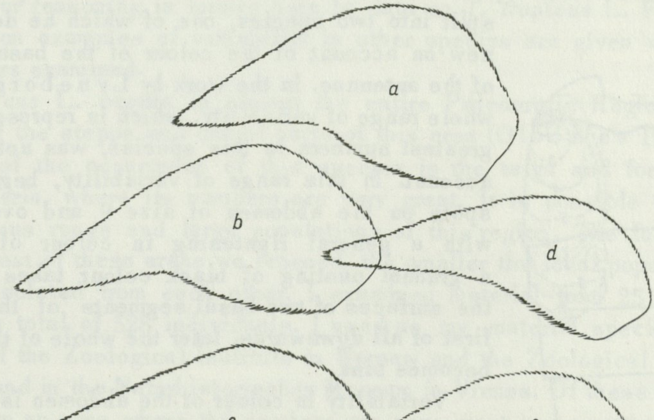


Fig. 13. Variability in structure of palpi of *T. solstitialis* Meig. in the Kampinos Forest

Zmienność budowy głaszczków *T. solstitialis* Meig. w Puszczy Kampinoskiej

categories 7 – 11 (Fig. 15). However in certain areas. e.g. in Great Britain, the commonest forms are those in categories 1 – 3 (Oldroyd 1939). Similarly at the opposite extreme end of the area, in the Ussuri Region (Olsoufev 1937) black forms, or forms with small spots on the boundary between tergites I and II, predominate. In the remaining parts of its range this species exhibits only slight tendencies to melanism. I found confirmation of this both in material from the Kampinos Forest and from other scattered stations in Europe. During one season it proved possible to catch individuals which complete the whole range of variability of the species. If, however, the local population is not numerous, as appears from the data contained in the work by Lyneborg (1959), who on the basis of several collections obtained 76 individuals of this species, then gaps appear in the range of variability of the species *T. solstitialis* Meig. On the basis of Lyneborg's data (1959) and of the materials belonging to the species *T. bisignatus* Jaenn. and *T. collini* Lyn. identified by him, I established that from the whole range of variability of abdominal spots (Fig. 15) he distinguished the section 0 – 5 as *T. bisignatus* Jaenn., while individuals with a type 6 spot he identified as *T. bimaculatus* Macq. He did not find type 7 – 10 in his material at all, and type 11 – 12 he split into two species, one of which he described as new on account of the colour of the basal segments of the antennae. In the work by Lyneborg (1959) the whole range of variability, which is represented in the greatest numbers in this species, was not taken into account. In this range of variability, beginning with spots on the abdomen of size 9 and over, together with a general lightening in colour of the body, a gradual ousting of black colour takes place from the surfaces of two basal segments of the antennae, first of all downwards, later the whole of their surface becomes pink.

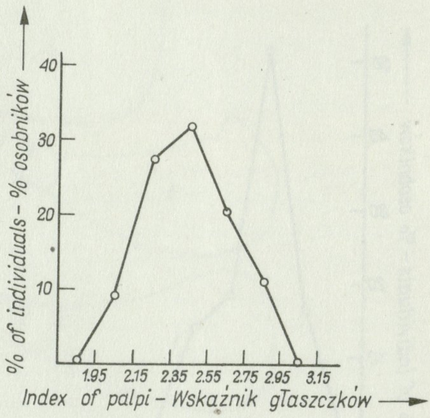


Fig. 14. Variability in palpi of *T. solstitialis* Meig. in the Kampinos Forest
Zmienność głaszczków *T. solstitialis* Meig. w Puszczy Kampinoskiej

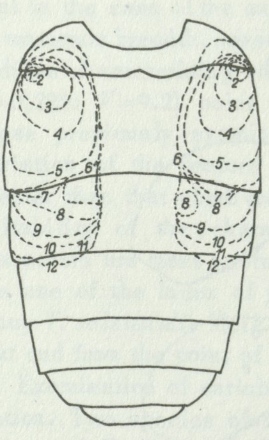


Fig. 15. Shapes of spots on abdomen of *T. tropicus* L. (Explanations in text)
Kształty plam na odwłoku *T. tropicus* L. (Objaśnienia w tekście)

Variability in colour of the abdomen is completely different in the case of *T. distinguendus* Verr., which belongs to the same group of species in the sub-genus *Tylostypia* End., as the previous one. This species occurs in large numbers in the Kampinos Forest. We have only three different variants in colour of abdomen here. The spot stretches: 1) to the end of the 3rd tergite – index 2.8, 2) to the end of the 4th tergite – index 3.19, 3) to the end of the 5th tergite

¬ index 3.68. The variability of this character, calculated by a similar method to that used for *T. solstitialis* Meig., is v = 3.72 (for a figure of individuals equal to 100). It is therefore over four times less than for the previous species.

Variability of this same taxonomic character differs in two closely related species. The more variable of them was split, on account of the colour of the abdomen, into two, three and finally (Lyneborg 1959) even into four species.

The data given above as an example show that variability is not great in large local populations of *Tabanus* L. Each character in the given population has a different value of index of variability. Choice of characters for distinguishing species should therefore be preceded by an analysis of variability. Assessment of variability by the eye only is often misleading. The variability of the same characters in near species may differ considerably from the systematic aspect, and the indices obtained of variability in variable species may be several times as much again as in a related species. The application of the range of variation of one species to others is a dangerous simplification when working on systematics, and may lead to erroneous taxonomic solutions.

Geographical variability of species of *Tabanus* L.

Analysis of differences in variability between different populations within the range of the species form one of the fields of systematic work in which we are faced with the greatest difficulties. Data are given below concerning variability of taxonomic characters in *Tabanus* L. in different populations; I described them for those European species, the range of which covers almost the whole of the Paleoarctic Region. This provides a fairly wide comparative scale. The basis for reasoning is formed here by data on *T. tropicus* L. For purposes of comparison examples of variability in other species are given with each of the characters examined.

T. tropicus L. occurs in almost the entire Paleoarctic Region, with the exception of the steppe and desert parts of this area (Olsoufev 1937). A typical place of the occurrence of this species is the taiga and forest land of Eastern Siberia, where its numbers are very great. It is possible to speak of the continuous range and large populations of this region. The further to the south and west of these areas we proceed, the smaller the local populations and the better isolated from each other. I examined material from 25 populations containing a total of 528 individuals. I used as my material specimens in the collection of the Zoological Institute in Warsaw and the Zoological Institute in Leningrad, and in the Naturhistorisches Museum in Vienna. Of these populations 11 come from an area where the numbers are very great and occurrence more or less continuous, while the remaining 14 contain specimens from places where this species is not very common or even very rare. I examined the six fundamental characters distinguishing this species from the related group, which are as follows: 1) structure of antennae, 2) colour of antennae, 3) index of frons, 4) colour of notopleural plates, 5) colour of abdomen, 6) structure of postabdomen of the female. The variability of these characters will be discussed in turn.

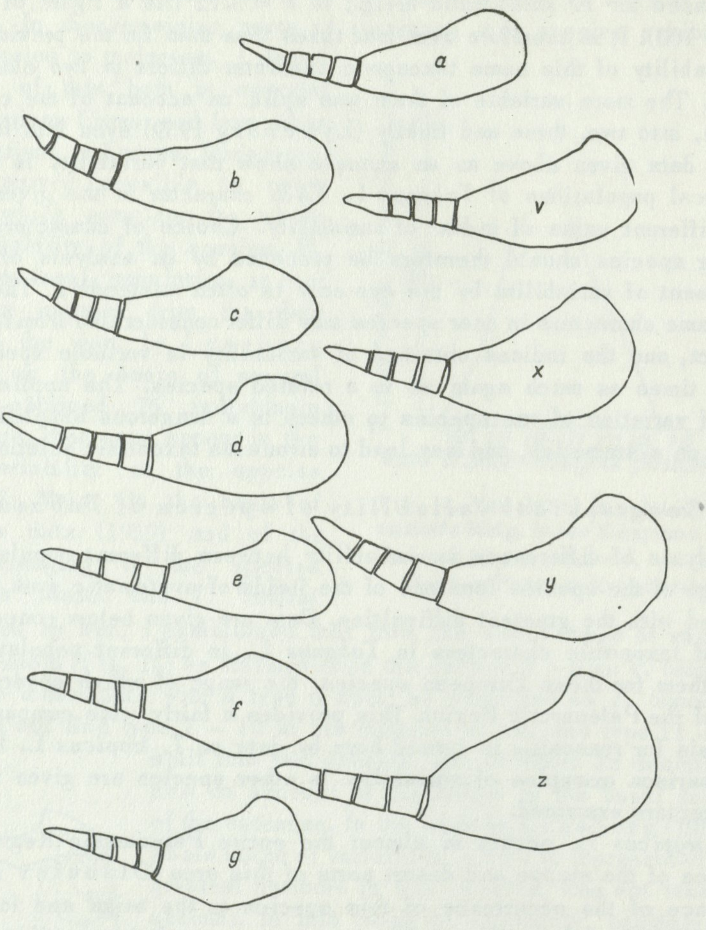


Fig. 16. Variability in structure of antennae of *T. tropicus* L.
a, b — Leningrad; *c* — Murmansk; *d* — Finland; *e* — Strassbourg; *f* — Cresta-Auers; *g* — Leningrad; *v* — Ussuri; *x* — Leningrad; *y* — Baikal district; *z* — Zabaikale

Zmienność budowy czułków *T. tropicus* L.
a, b — Leningrad; *c* — Murmańsk; *d* — Finlandia; *e* — Strassburg; *f* — Cresta-Auers; *g* — Leningrad; *v* — Ussuri; *x* — Leningrad; *y* — okolice Bajkału; *z* — Zabajkale

Structure of the antennae. 11 types of antennae (Fig. 16) were distinguished in the whole material, and the percentage of each type determined in each local population. Certain difficulties are encountered in putting the variants in order according to variability, taking their shapes into consideration. The narrowest antennae are clearly included in the range of variability of the related species *T. nigricornis* Zett., the widest are similar to the antennae of *T lundbecki* Lyn., and in any case cover the whole range of variability of *T tuxeni* Lyn. This species differs from the first two species, i.e. *T. nigricornis* Zett. and *T. lundbecki* Lyn., as to several characters previously defined (Olsoufev

1937, Trojan 1959) and as to the morphology of the postabdomen of the female. *T. tuxeni* Lyn. was combined here with *T. tropicus* L. Correct determination of specific appurtenance of individuals with extreme types of structure of antennae is therefore possible in the case of *T. tropicus* L. on the basis of other characters.

All the variants of the antenna found may be arranged in two ranks, which would provide a picture of the divergence in shape of antenna in this species, if we take as our basis the property, important from the taxonomic aspect, that is, the formation and situation of the frontal tooth. Variant *A* may be taken as a starting point (Fig. 16). This is the narrowest antenna, with a very weakly marked tooth. A left rank may be drawn out from it, having a flat tooth near the central part of the segment, and a right rank, having extremely protruding tooth situated near the base of the third segment of the antennae. The first rank leads to the typical forms *T. tropicus* L. described by authors on the basis of material from Western Europe, the second from T. *tuxeni* Lyn to T. *lundbecki* Lyn. Investigation of the variability of antennae on the basis of this plan of divergence both in large and in small populations does not permit of showing any evolutionary regularity which could express itself in the shifting of the range of variability in certain populations towards the rank *T. lundbecki* Lyn., and in the second – towards *T. tropicus* L. Each of the populations examined contains variants of both these ranks. In the Baikal district, for instance, 19% of the specimens had type *B* antennae (Fig. 16), type *Y* about 36%, type *A* over 28% etc. The situation is similar in other local populations. Divergence in the structure of the antennae on a geographical scale is not the case here.

In order to put the variants in order I therefore used another character, that is, the index of breadth of antennae, previously discussed, measurements being made along line *a* and *b* (Fig. 16g). On this basis I obtained a scale of variability, from very narrow antennae with an index of 2.18 to very broad ones, with an index of 1.49. The narrowest antennae, with an index value of over 2, I compared according to their participation in each population. Material compared in this way forms the following geographical picture. In the northern and central parts of the range (first zone) the narrowest antennae form the chief variant of variability (Fig. 17) and over 50% of the individuals in each population. These areas surround, going from the east, the second zone, made up of: Sakkhalin, Primorie, Amur, Mongolia, the Baikal district and probably also the central part of the Russian lowlands and Esthonia. In the remaining parts of its range (zone three) narrow antennae are encountered only sporadically and they form only a minute percentage of variability; the chief variant occurring in populations are broad antennae, which also form an important part of variability in the second zone. Specimens from Poland are similar to populations from the Leningrad district and Altai as regards structure of the antennae, despite the fact that they are within the belt of reduced frequency of narrow antennae. There are, however, no specimens among them from the lowlands of Poland, they are either individuals from mountain populations or from marshy district, somewhat similar to the taiga.

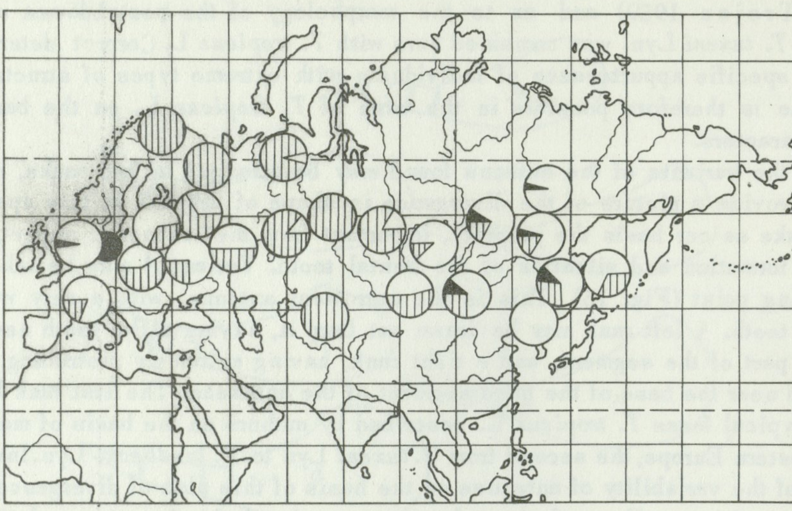


Fig. 17. Percentage of three variants of antennae in three populations of *T. tropicus* L. Lined areas – index of antennae greater than 2; blank area – index of antennae from 1.5 to 1.8; black area – index of antennae less than 1.5

Udział trzech wariantów czułków w trzech populacjach *T. tropicus* L. Pola zakreskowane – wskaźnik czułków większy od 2; pola białe – wskaźnik czułków od 1,5 do 1,8; pola czarne – wskaźnik czułków mniejszy od 1,5

The extreme variant, the broadest antennae, requires separate discussion (Fig. 16 z). They were found in 6 specimens only. They occur as single variants in populations of the second and third zones in Asia. Their presence was established in 5 populations represented in collections by a fairly large series (12 – 41 individuals). In these populations they form only a very inconsiderable percentage of variability.

The actual outline of the antennae is connected with the situation of the tooth near the base or nearer the middle of the third segment and also with the height of this tooth. The tooth itself is also variable, but does not exhibit so regular a connection with the distribution of the species as the ratio of length of segment to its breadth. The further the place of capture of the specimens lies from the first zone of occurrence of this species, the more often we encounter separate variants of structure of the antennae, admittedly coming within the limits of the average breadth of the antennae, but with different shapes. Among them we must include specimens from the Ussuri Region (Fig. 16v) with narrow antennae, but projecting tooth, specimens from Finland with a flat tooth (Fig. 16d) protruding forwards and specimens from Strassbourg (Fig. 16 *f*) and Cresta-Auers in Switzerland (Fig. 16 *g*). With the exception of Finland, this species occurs in the places mentioned only in populations composed of small numbers, and hence establishment of variants of the structure of antennae may take place which are not encountered in a typical area of occurrence for this species. A particularly interesting example is supplied by the differentiation of the species in question in Denmark. In the area formed by the Danish islands, a form occurs with broad (1.4 – 1.5) antennae, while Jutland and southern Sweden are inhabitated almost entirely by forms with antennae of average breadth (1.5 – 1.8). This case may be considered as resulting from the joint effect of isolation and small population numbers.

In the case of *T. distinguendus* Verr., a near species from the systematic standpoint to the species *T. tropicus* L., differences may also be observed in the structure of the antennae (Fig. 18). The ranges of both forms are, practically

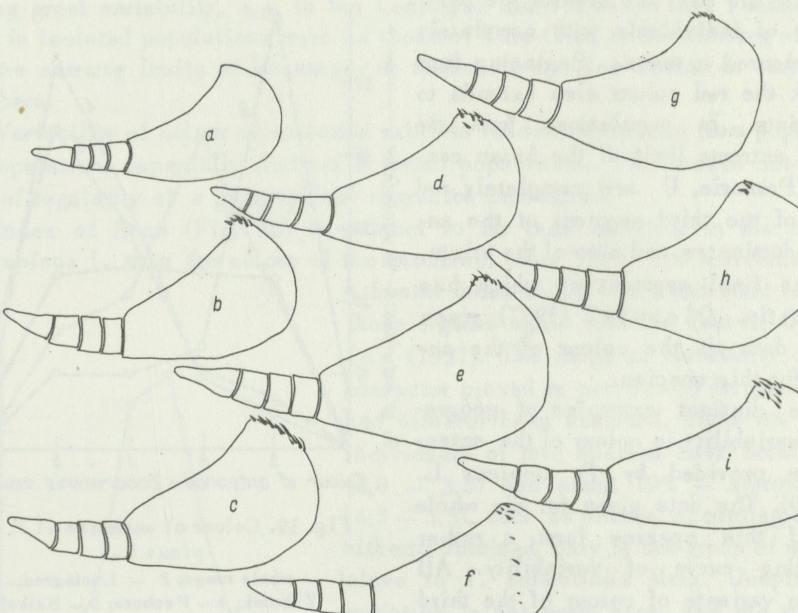


Fig. 18. Variability in structure of antennae of *T. distinguendus* Verr.
a – Hungary; *b* – Leningrad; *c* – Sverdlowsk; *d* – Chkalov; *e* – Semipalatynsk; *f* – Tomsk; *g* – Irkhutsk; *h* – Yakutsk; *i* – Ussuri

Zmienność budowy czułków *T. distinguendus* Verr.
a – Węgry; *b* – Leningrad; *c* – Świerdłowsk; *d* – Czkałow; *e* – Semipalatyńsk; *f* – Tomsk; *g* – Irkuck; *h* – Jakucja; *i* – Ussuri

speaking, the same, but the proportions of the antennae on a geographical scale with *T. distinguendus* Verr. are subject to smaller changes (1.35 – 1.61) and in the majority of cases deviate only slightly from the average index (1.51). The same can be said of the outline of the antennae. The situation of the antenna tooth in this species is more or less constant (in the basal 1/3 part of the antennae). More distinct differences occur only in the incision of this tooth and cause in it certain individuals, e.g. those from the Leningrad district or Semipalatynsk to be protruding, while in others, e.g. those from the Tomsk or Orenburg district it is flatter. Different variants of antennae in this species may be encountered in every larger population, their occurrence does not exhibit any connection with the geographical position.

The colour of the antennae of *T. distinguendus* Verr. exhibits little variation. The typical colour is an even dark red of the third segment and a dark brown or black arista. In Western and Central Europe such individuals form a small percentage of the general variability of the species. Forms predominate in these area with brownish upper surface and end to the third segment. A good example is provided by the population from the Kampinos Forest, where 9% of the individuals exhibit completely red colour, 62% a brownish surface, and in 29% of the individuals the whole distal part of the third segment is brown. The further to the east the greater the percentage of individuals with completely light-coloured antennae. Beginning from Irkhutsk the red colour also extends to the arista. In populations from the eastern extreme limit of the Asian continent (Primorie, U uri) completely red colour of the third segment ot the antennae dominates, and also of the arista, only the final segment of which has a black tip. Olsoufev (1937) gives similar data on the colour of the antennae for this species.

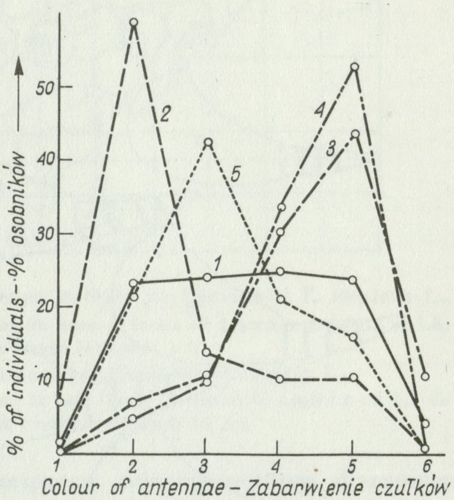


Fig. 19. Colour of antennae of *T. tropicus* L.
1 – whole range; *2* – Leningrad; *3* – Yakutsk; *4* – Pechora; *5* – Baikal
Zabarwienie czułków *T. tropicus* L.
1 – cały zasięg; *2* – Leningrad; *3* – Jakucja; *4* – Peczora; *5* – Bajkał

More distinct examples of geographical variability in colour of the antennae are provided by *T. tropicus* L. (Fig. 19). The data given for the whole area of this species form a rather interesting curve of variability. All possible variants of colour of the third segment of the antennae are exhibited by this species, from light red to completely black without even a brown spot at the base. The curve of variability for this character is trapezoid in form, which is evidence of the considerable deviation from the normal curve. Apart from extreme variants all the others occur similarly frequently in this species and constitute 20 – 25% of the variability of the character examined. Such a curve is evidence of great inter-population variability. The range of variability may be similar in their case, but the frequency of each variant is different and maxima are often at different points on the scale of variability. In the Leningrad district red colour with a brown distal part of the third segment of the antennae predominates, while on the Pechora and in Yakutsk black antennae, with a brown spot at the base, predominate. The population from Baikal is transitional from this aspect, as over 15% of all intermediate variants occur, although brown antennae with a red spot at the base dominate. In the populations which examined from other places, the maximum frequency of this variant occurs in the Jaroslav and Irkhutsk districts. Brown antennae with a red spot at the base predominate in the western part of Siberia and on the Amur. Antennae with black tips and brown at the base predominate in Esthonia, on the Solovietskie Islands, Murmansk, Sverdlovsk, Mongolia and Sakkhalin. The third segment of the antennae, completely black. with a brown spot near the base, is predominant, not only in the places mentioned, but also in the Alps, is common in Poland and in Altai. The completely black colour, like the completely red one, is encountered in populations exhibiting great variability, e.g. in the Leningrad district, Altai and Yakutsk, and also in isolated populations such as those of Kara-Chau or Strassbourg situated on the extreme limits of its range, or where the species occurs in very small numbers.

Variability of colour of antennae exhibits random deviations from population to population, especially distinct in small populations. This makes determination of regularity of a geographical character impossible.

Index of frons (Fig. 20) is subject to far less variation in the case of *T. tropicus* L. than the colour of the antennae. Over 70% of the individuals has a frontal index of 3.5 – 4.5 and what is more, these figures agree with the data of Olsoufev (1937). The range of variability of this character proved in practice to be greater than had hitherto been assumed, since 8% of the individuals of this species have broad frons (3.0 – 3.5) and about 19% – narrow frons (4.5 – 5.5), such as occurs, according to data hitherto obtained, only in the group of species close to *T. solstitialis* Meig. Despite this variation is not great here, and the majority of the curves of variability of the 29 populations investigated from this aspect in different parts of the Paleoarctic Region exhibit maxima within the limits of the index of the average calculated for the whole species. A tendency to narrowing of the frons greater than that observed for the whole species (index 4.6 – 5.0) is exhibited only by populations from the Irkhutsk and Jaroslav districts. In the material examined 12 series came from different places, chiefly Central Europe. The series were small, the maximum number of specimens being 5. Of the total number of 26 individuals from small local populations, measurements of which were made, 19 had an index coming within the limits of the main variants of variability for this character of the species. The remaining 7 individuals had so-called nontypical frons, either narrower or wider. It is interesting to know that even in such scanty material coming from local populations in which the numbers were small. regularity occurred more or less the same as it

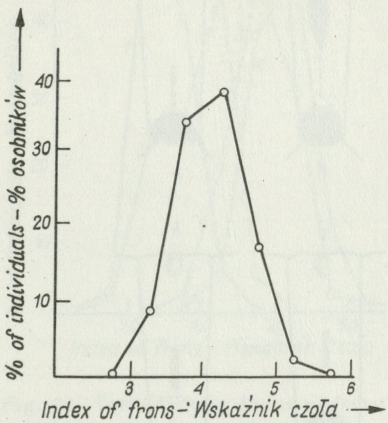


Fig. 20. Variability in index of frons of *T. tropicus* L.
Zmienność wskaźnika czoła *T. tropicus* L.

does within a whole species. If, for instance, within large populations the empirical probability of occurrence of the typical from is $p = 0.72$, in the combined material from small populations this is expressed by a similar figure ($p = 0.73$). This does not, of course, rule out the possibility that in small populations the structure of the frons will reveal considerable differences, which have sometimes been interpreted as proof of specific or subspecific separateness, especially if differences in dusting of the frons were also present, varying from greyish to golden- or if variability occurred in the formation of the frontal calli. Varying types of frontal structure are shown in drawings for purposes of illustration (Fig. 21).

There is also an additional differentiation, more difficult to grasp by measurement, in the actual structure of the frons within this species. Differences occur both in the proportions and in the shape of the frontal calli. The most

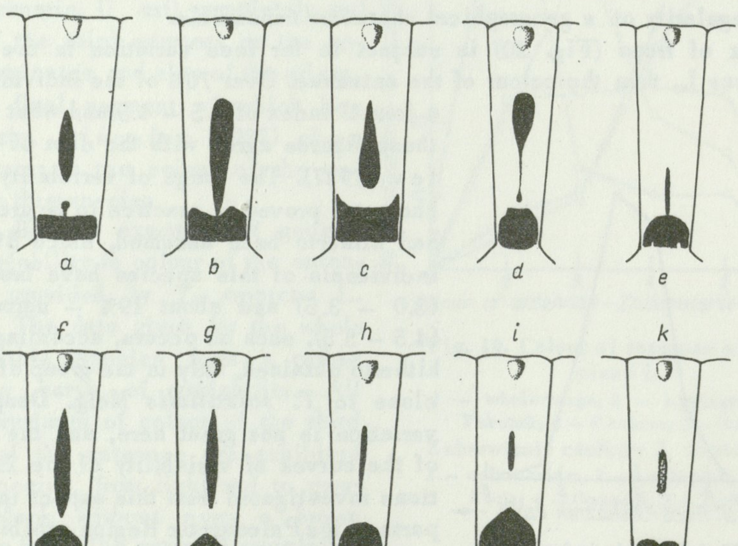


Fig. 21. Variability in structure of frons of *T. tropicus* L.
a, b, c, — Murmansk; *d* — Cresta-Auers; *e* — Kara-Chau; *f* — estuary of Chuna; *g* — Jaroslav, *h* — Yakutsk; *i* — Ussuri; *k* — Mongolia

Zmienność budowy czoła *T. tropicus* L.
a, b, c, — Murmańsk; *d* — Cresta-Auers; *e* — Kara-Czau; *f* — ujście Czony; *g* — Jarosław; *h* — Jakucja; *i* — Ussuri; *k* — Mongolia

typical shape is shown in Fig. 21*g*. Deviations can, however, be seen which in the structure of the central callus tend in the direction of the stronger formation of this character (Fig. 21*b, c, f*). This form is commonly encountered in northern populations and in certain European populations. In the southern part of the Paleoarctic we encounter the reverse phenomenon, the reduction of the central callus (Fig. 21 *h, i, k*). The lower callus takes on various forms: triangular, pentagonal, rectangular and semi-circular. Additional deformations often occur here. Different variants of the frontal structure are met with either in the case of single individuals, or predominate in whole populations. Considerable local variability indicates that extreme variants should also be treated as part of the inter-population variability, and not as new species, subspecies or forms, the more so that numerous transitional forms can be found among them if more thorough examination is made.

For the sake of comparison I examined differences in the index of the frons in two other species belonging to this group: *T. distinguendus* Verr. referred to above, and *T. lundbecki* Lyn. In this case I took a population from Poland (Kampinos Forest) as a basis for comparison, and also one from the taiga region. In both these species a similar tendency can be observed to narrowing of the frons the further one progresses from west to east (Fig. 22). This is most distinctly evident in the populations of *T. lundbecki* Lyn. from Leningrad, Zabaikal and the Ussuri Region. Other populations from Siberia (the Pechora and Spaskoje districts) and from Kamchatka are rather characterised by great variability of the frontal index without a distinct maximum, as far as this could be established on the basis of the somewhat scanty material at my disposal.

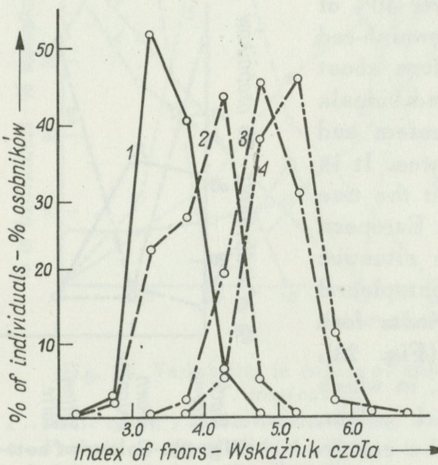


Fig. 22. Variability in index of frons of *T. lundbecki* Lyn. *1* – Poland; *2* – Eastern Europe and Western Siberia; of *T. distinguendus* Verr; *3* – Poland; *4* – Eastern Europe and Western Siberia

Zmienność wskaźnika czoła *T. lundbecki* Lyn. *1* – Polska; *2* – Europa wschodnia i Syberia zachodnia; *T. distinguendus* Verr. *3* – Polska; *4* – Europa wschodnia i Syberia zachodnia

The differences between the index of the frons in the population from the Kampinos Forest and the material, treated as a whole, from the taiga, as regards *T. distinguendus* Verr. are not so great as in the case of the previous species. In different Siberian populations differences may also be found (e.g. in the series from Irkhutsk and Yakutsk), in which this index is formed similarly to that in the population from the Kampinos Forest.

Notopleural plates. In descriptions of *T. tropicus* L. they are usually given as yellowish-brown, distinctly separating in colour from the dark mesonotal plate. In fact not much over 71% of the specimens in the material examined satisfies this condition. Of the remaining number over 25% have black plates and in 3% I found a colour of a transitional nature; most often there was a brown spot in the middle or in the posterior part of the notopleural plate. Non-typical colour occurs in some populations fairly frequently, while in Northern Siberia and certain mountain populations 30 – 100% of the individuals have it. I found this to apply to other populations in the following areas: the Alps, the Solovietskie Islands, Murmansk, Tobolsk, Altai, Yakutsk and Sakkhalin. Darkening of the notopleural plates occurs in a geographical pattern similarly to that of structure of antennae.

With *T. distinguendus* Verr. the colour of the notopleural plates exhibits a similar variability of the other taxonomic characters, discussed previously, of this species. Black is usually mentioned as a typical colour, although certain scientist (Olsoufev 1937, Lyneborg 1959) confirm in addition the occurrence of a different colour of these plates. Typical colour is most clearly evident in the example provided by the population from Leningrad, where 80% of the individuals have black notopleural plates. The largest of the series so far examined from Central Europe (Kampinos Forest) has slightly over 40% of black forms and the same amount with brownish-red plates. Yellowishbrown notopleural plates form about 10% of this material. The majority of the individuals collected single in different parts of Western and Central Europe have black notopleural plates. It is difficult on these grounds to estimate what the true variability of this character is in Western European populations. To the east of Irkhutsk the situation changes radically, and yellowishbrown notopleural plates dominate, while the remaining variants form only an inconsiderable admixture there (Fig. 23).

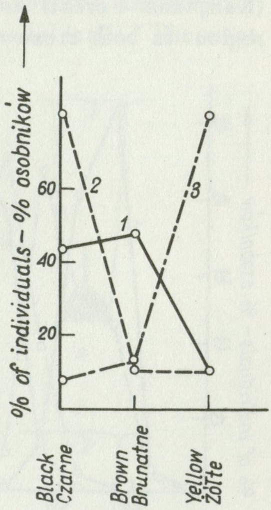
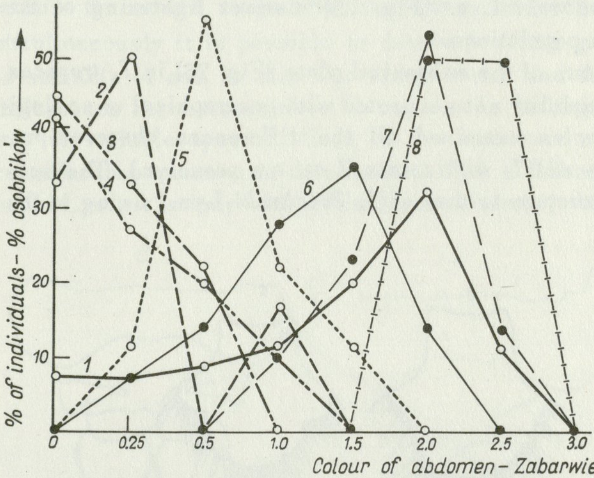


Fig. 23. Colour of notopleural plates of *T. distinguendus* Verr.
1 – Kampinos Forest; *2* – Leningrad; *3* – Eastern Siberia

Zabarwienie płytek notopleuralnych *T. distinguendus* Verr.
1 – Puszcza Kampinoska; *2* – Leningrad; *3* – Syberia Wschodnia

The third species – *T. lundbecki* Lyn., in which the notopleural plates have a typical black colour, do not exhibit a lightening in colour in the eastern part of the area, as was shown in the case of *T. distinguendus* Verr. In Poland about 10% of the individuals of this species have light-coloured notopleural plates, and over 20% transitional. As a whole, however, this character reveals great constancy over the whole of the range of this species.

Abdomen. *T. tropicus* L. provides the best examples of geographical and ecological variability. The curve of variability of this character is similar to the curve described for *T. solstitialis* Meig. The diagram drawn up for *T. tropicus* L., treated jointly, exhibits a higher level of left branch, which is evidence of a fairly strong tendency to darkening of the abdomen in this species. In addition the range of variability observed in *T. tropicus* L. is greater than that of *T. solstitialis* Meig., since it includes forms ranging from completely black ones to those in which the red spots on the sides reach to the end of tergite V. In different populations curves do not, as a rule, cover the whole range of variability. Populations from the Solovietskie Islands, from Murmansk and from Pechora consist in the majority of completely black individuals (Fig. 24), and those in which the light spot does not reach the end of tergite II. The second and most numerous group is formed by populations in which the spot reaches to the end of tergite III. The curve of variability for series from Yakutsk supplies an example of such populations. Series from Sverdlovsk and Esthonia have intermediate curves. I found a far greater shift



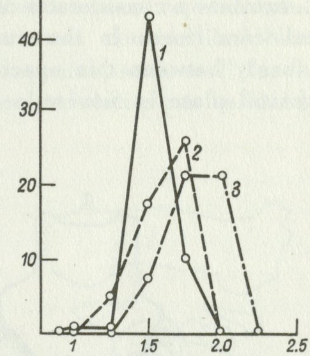


Fig. 24. Variability in colour of abdomen *T. tropicus* L.

1 – whole range; *2* – Solovietskie Island; *3* – Murmansk; *4* – Pechora; *5* – Sverdlovsk; *6* – Esthonia; *7* – Yakutsk ; *8* – Mongolia

Zmienność zabarwienia odwłoka *T. tropicus* L.

1 – cały zasięg; *2* – wyspy Sołowieckie; *3* – Murmańsk; *4* – Peczora; *5* – Świerdłowsk; *6* – Estonia; *7* – Jakucja; *8* – Mongolia

Fig. 25. Variability in colour od abdomen of *T. lundbecki* Lyn.

1 – Poland; *2* – Zabaikale; *3* – Ussuri

Zmienność zabarwienia odwłoka *T. lundbecki* Lyn.

1 – Polska; *2* – Zabajkale; *3* – Ussuri

in the direction of red abdomen only in specimens from Mongolia. This character also reveals a certain zoning, beginning with black forms connected with the northern extremes of the range of this species, and ending with almost red ones, occurring on the southern and eastern limits. Certain mountain populations occurring in Central Europe e.g. in the Iser Mountains, exhibit a similarity to the northern forms, although incomplete, in the darkening of the abdomen. They occur in mountains or marshy areas. Data referring to the geographical variability of this species may be interpreted as geographicoecological variability. The more difficult their living conditions, the darker the colour of the body. This principle failed to find confirmation with *T. tropicus* L. only when inspecting the colour of antennae.

The two remaining species of the group under discussion present a different picture from this aspect. The colour of the abdomen with *T. distinguendus* Verr.. exhibits great constancy. In 60% of the individuals the light spots reach to the end of tergite IV. The percentage of individuals with longer spots (to the end of tergite V) is greater only in material from Irkhutsk and Orenburg. A darker abdomen is rarely encountered (spots to the end of tergite III) not more than in 8% of the population. This species, from the aspect of colour of other parts of the body, exhibited lightening of colour the further to the east one progressed, but the colour of the abdomen does not clearly confirm this.

With the species *T. lundbecki* Lyn. (Fig. 25) distinct lightening of the abdomen was found in eastern populations.

Postabdomen. The structure of the subgenital plate (Fig. 26) in *T. tropicus* L. exhibits a considerable variability not connected with geographical or ecological conditions. In the examples examined all the differences observed previously between this species and *T. nigricornis* Zett. are preserved. The subgenital plate is similar in structure to that of *T. lundbecki* Lyn., owing to the

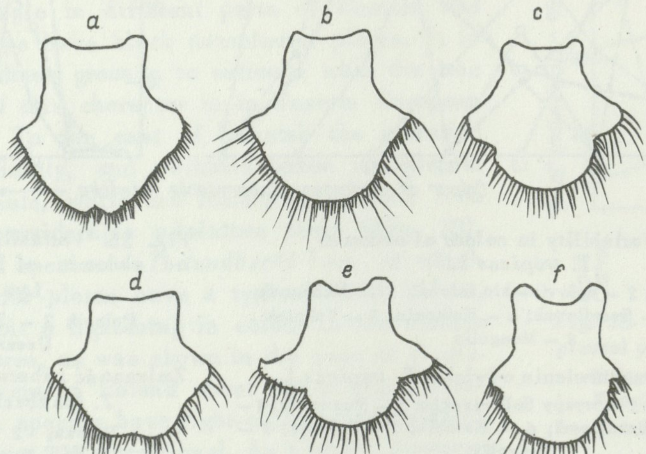


Fig. 26. Subgenital plates of *T. tropicus* L.
a, b, c — Leningrad; *d* — Les Grisons; *e* — Sverdlovsk; *f* — Kampinos Forest

Płytki subgenitalne *T. tropicus* L.
a, b, c — Leningrad; *d* — Les Grisons; *e* — Świerdłowsk; *f* — Puszcza Kampinoska

loss of the incision in the distal part of the plate and the shift to the centre of the basal part. The greatest variability is exhibited by the side processes, which are extended sideways to a considerable extent, e.g. in an individual from Les Grisons (Fig. 26 *d*) or almost completely reduced, as in the individual from the Kampinos Forest (Fig. 26 *f*). The final tergite is subject to reduction, the incision of which is often deeper than in typical individuals. It never narrows, however, in the same way as in the case of *T. nigricornis* Zett. The final segment of the cerci (Fig. 27) varies in *T. tropicus* L. from semi-circular with an even edge to ones in which part of the oval is cut off straight or diagonally (Fig. 27). Similar shortening of the cerci as in the case of *T. lundbecki* L. is not, however, encountered here.

Other species exhibit far less variability from this aspect.

The materials described above concerning geographical variation make it possible to expand the conclusions obtained by means of an analysis of large populations. One character may be very variable or exhibit decided constancy within the whole range. By comparing the variability of several characters simultaneously it is possible to determine if the group of taxonomic characters is variable or not. In this way also we can find the existence of considerable differences between species. *T. tropicus* L. belongs to the typical representatives of variable species. Each of the taxonomic characters examined exhibits considerable variation in this species. With a different species, such as *T lundbecki* Lyn., it is only with difficulty that interpopulation variability can be found.

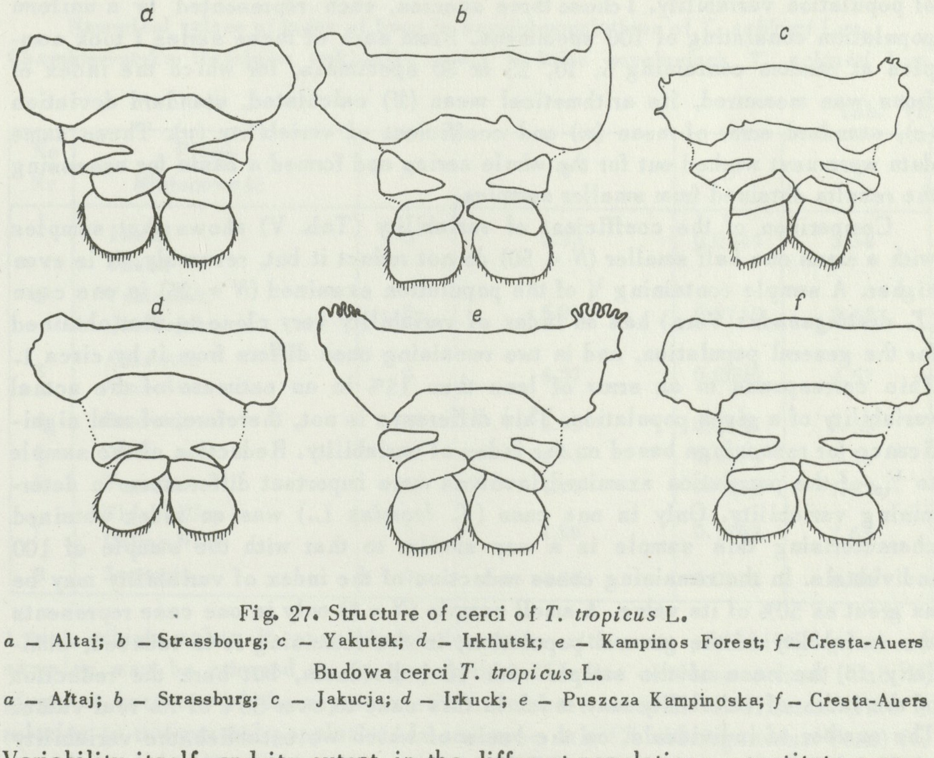


Fig. 27. Structure of cerci of *T. tropicus* L.

a – Altai; *b* – Strassbourg; *c* – Yakutsk; *d* – Irkhutsk; *e* – Kampinos Forest; *f* – Cresta-Auers

Budowa cerci *T. tropicus* L.

a – Ałtaj; *b* – Strassburg; *c* – Jakucja; *d* – Irkuck; *e* – Puszcza Kampinoska; *f* – Cresta-Auers

Variability itself, and its extent in the different populations, constitute a property of the species which in a certain way characterises it as a collective unit.

The extent of variability of a character established for one population may coincide completely with the extent of variability in another. Frequently, however, we are concerned both with shifts in extent and average values, and also with a completely different course followed by curves. Formation of characters in different populations may therefore differ so considerably that the extents of variability (Fig. 24) of a given character do not coincide at all.

When such variability is encountered in material, especially in cases of somewhat scanty material, the result is the splitting of species on the grounds of these distinct hiatuses between extents of variability; such hiatuses can also exist within the same species. The fundamental problem lies, therefore, in comparison of variability and assessment of the extent to which the material under consideration is representative.

Comparison of variability

The series of specimens of *Tabanus* L. in museums are often small, consisting of a few individuals only. I made several tests in order to form an idea of what series in the case of *Tabanus* L. yields a sufficiently correct picture of population variability. I chose three species, each represented by a uniform population consisting of 100 specimens. From each of these series I took samples at random containing 5, 10, 25 or 50 specimens, for which the index of frons was measured, its arithmetical mean (M) calculated, standard deviation (σ), standard error of mean (m) and coefficient of variability (v). These same data were next worked out for the whole series and formed a basis for assessing the results obtained from smaller samples.

Comparison of the coefficient of variability (Tab. V) shows that samples with a mass one half smaller (N = 50) do not reduct it but, reversely, it is even higher. A sample containing ¼ of the population examined (N = 25) in one case (*T. distinguendus* Verr.) has an index of variability very close to that obtained for the general population, and in two remaining ones differs from it by circa 1. This corresponds to an error of less than 15% in an estimate of the actual variability of a given population. This difference is not, therefore, of real significance for reasonings based on the index of variability. Reduction of the sample to $^1/_{10}$ of the population examined involves more important differences in determining variability. Only in one case (*T. bromius* L.) was an index obtained characterising this sample in a way similar to that with the sample of 100 individuals. In the remaining cases reduction of the index of variability may be as great as 50% of its value. A small sample (N = 5) only in one case represents the variability of the general population, in the remaining it is reduced, similarly to the case of the sample with 10 individuals, but here the reduction of the index of variability may reach in this case to over 50% of its real value. The number of individuals, on the basis of which we establish the variability of the character examined in a local population, should not be lower than 25.

It is usually necessary to use only the smaller number of individuals to determine the average values of the character examined. Comparison of arithmetical means obtained from samples of different size was based on the Student

Numerical values of index of frons in several populations of *T. mühlfeldi* Lyn.
Charakterystyka ilościowa wskaźnika czoła w kilku populacjach *T. mühlfeldi* Lyn.

Tab. VI

No Nr	Place Miejscowość	N	$M \pm m$	σ^2	V
1	Sverdlovsk Swierdłowsk	7	5.65 ± 0.09	0.0542	4.13
2	Leningrad	10	5.65 ± 0.01	0.1983	7.88
3	Western Siberia Zachodnia Syberia	10	5.11 ± 0.01	0.1842	7.94
4	Kampinos Forest Puszcza Kampinoska	100	5.85 ± 0.09	0.2564	8.66
5	Białowieża Forest Puszcza Białowieska	9	5.76 ± 0.08	0.0574	4.17

Numerical values of index of frons in several populations of *T. schineri* Lyn.
Charakterystyka ilościowa wskaznika czoła w kilku populacjach *T. schineri* Lyn.

Tab. VII

No Nr	Place Miejscowość	N	M	σ^2	V
1	Izmail Izmaił	5	5.23	0.0344	3.54
2	Yeniseisk Jenisejsk	8	5.09	0.0755	5.42
3	Alma-Ata Ałma-Ata	6	4.57	0.0603	4.57
4	Borowsk	10	5.08	0.2336	9.53
5	Omsk	10	4.93	0.1674	8.26
6	Węgorzewo	15	4.97	0.1281	7.22
7	Nida Valley Dolina Nidy	5	4.86	0.1703	7.65
8	Szczecin	9	4.85	0.0885	6.14

t test, which makes it possible to determine with wnat probability (p) these samples may be reterred to one population. The list of these values (Tab. V) gives an estimate of the representativeness of the samples of different size in relation to the general population. In one case only (*T. distinguendus* Verr.) for a small sample ($N = 5$) was a result obtained not representative of the general population, in all the others deviations are random in character. The arithmetical mean and other indices obtained from the samples are similar in samples and in the general population. In investigations of *Tabanus* L. the average values from small series can correctly determine the actual relations of a whole population.

In order to establish the usefulness of such materials, the index of the frons was examined for five populations of *T. mühlfeldi* Lyn. (Tab. VI) taken from different places in its range. They exhibit a fairly inconsiderable variability in the value of arithmetical means, which fluctuates between 5.41 and 5.85, that is, within the limits of the so-called narrow frons. The difference between averages is not random only in the case of the differences between the population from Western Siberia and the Kampinos Forest. None of the remaining populations exhibit significant differences as regards the index of frons.

Material of *T. schineri* Lyn. (Tab. VII) comes from eight places scattered over the whole northern part of the Paleoarctic Region. From a total of 28 possibles, 21 comparisons are evidence of the uniformity of the species, as regards formation of index of frons, only in 6 cases (over 25% of all comparisons) do the observed values attain such a size that the differences between means are statistically probable and in one case the difference (between populations from Western Pomerania and Alma-Ata) is statistically significant.

T. distinguendus Verr. (Tab. VIII) forms the final example of comparison of the index of variation in frons between populations of one species. The material

Numerical values of index of frons in several populations of *T. distinguendus* Verr.
Charakterystyka ilościowa wskaźnika czoła w kilku populacjach *T. distinguendus* Verr.

Tab. VIII

No Nr	Place Miejscowość	*N*	*M*	σ^2	*V*
1	Leningrad	10	5.17	0.0638	4.86
2	Orenburg	11	5.55	0.1204	6.27
3	Yakutsk Jakucja	10	4.69	0.0394	4.23
4	Primore Primorje	9	5.33	0.1130	6.31
5	Irkhutsk Irkuck	9	4.79	0.1330	7.67
6	Ussuri	10	5.08	0.0312	3.48
7	Kampinos Forest Puszcza Kampinoska	100	4.82	0.1827	8.89
8	Altai Ałtaj	5	5.23	0.1006	6.04
9	Tomsk	5	5.25	0.0156	1.92

is taken from 9 populations coming from different parts of the Paleoarctic. Twenty-four comparisons out of 30 possible ones showed that the material examined is not statistically uniform. The index of frons is different in almost all populations.

Further similar examples of differences between the formation of taxonomic characters in *Tabanus* L. could be given. This is illustrated, but without giving detailed results of statistical comparisons, by materials on the variability of characters in different local populations. The three examples given here exhaust, however, on the basis of only one index, all obtainable results of such comparisons. The first of them presents the situation when the formation of the systematic character of the species is more or less stable throughout the whole area. The species exhibits more or less similar extents of variability and arithmetical means in all populations (*T. mühlfeldi* Lyn.).

The second possibility is the situation in which the character under examination is formed similarly within the whole range, but considerable deviations occur in several cases, which when compared statistically are revealed as significant differences between means (*T. schineri* Lyn.).

The last possible result is the differentiation of the systematic character so that in almost all populations considerable deviations and small probabilities of uniformity of material are found as regards the character examined (*T. distinguendus* Verr.)

Numerical values of index of frons in species from group of *T. solstitialis* Meig.
Charakterystyki ilościowe wskaźnika czoła gatunków z grupy *T. solstitialis* Meig.

Tab. IX

Species – Gatunek	*N*	*M*	*σ*	*V*
T. distinguendus Verr. (with narrow frons) (o wąskim czole)	50	5.28	0.1467	7.26
T. distinguendus Verr (with wide frons) (o szerokim czole)	119	4.81	0.1681	8.54
T. schineri Lyn.	68	5.03	0.1481	7.66
T. solstitialis Meig.	44	4.96	0.2375	9.83
T. mühlfeldi Lyn.	66	5.73	0.2118	8.03

On the basis of the materials described comparison of the index of frons can also be made between species of this group. As the greatest differences occur in the case of *T. distinguendus* Verr. material consisting of this species was divided into two groups, the first, with a wide frons, including populations marked nos. 3, 5 and 7 (Tab. VIII), and the second with a narrow frons, which comparises the remainder of the populations. Five groups were therefore used for purposes of comparison (Tab. IX). *T. distinguendus* Verr. (group with narrow frons) and *T. mühlfeldi* Lyn. are separate forms. *T. solstitialis* Meig. does not differ from these populations of *T. distinguendus* Verr., which have wide frons, nor from *T. schineri* Lyn.

Statistical analysis of the index of frons makes it possible to state that single characters compared between species may exhibit considerable and significant differences with, however, inter-population variability of this index (as in the case of *T. distinguendus* Verr.) similar or even greater differences may be obtained for interspecific variability. In other cases the differences observed between indices of frons in different species are slight and no significant differences can be found in their formation. Comparison of material as regards index of frons indicates that incorrect distinguishing of species of *Tabanus* L. on the basis of one character may be possible, and may lead to erroneous systematic conclusions. Even when a considerable difference is found there is no guarantee of the specific separateness of the series examined. In investigations of *Tabanus* L. the rule is to search simultaneously for differences in several characters.

Simultaneous comparison between several properties of two populations is neither easy nor exact, and quantitative methods have not been worked out. There are three methods so far known of comparing populations in respect of several characters (Olekiewicz 1956), of which the simplest and most graphic is the method of comparing shapes of plants worked out by Jentys-Szaferowa (1951). This method may also be applied to an analysis of differences between taxonomic characters in cases in which they are converted to measurable units. Such comparisons were made for several species from the group *T. solstitialis* Meig. In the case of *T. mühlfeldi* Lyn. a population coming from Finland was used as a comparative unit. The four taxonomic characters analysed (index of frons, length of spots on the abdomen, colour of antennae and colour of notopleural plates) belong to characters so far analysed which exhibit the greatest variability and at the same time constitute characters composing the fundamental morphological definition of the species. A graph of quotients (Fig. 28) shows the considerable aggregation of curves in the regions corresponding to the values of the characters

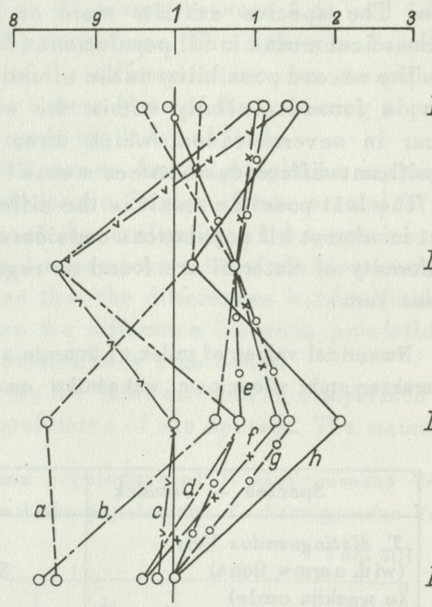


Fig. 28. Deviations of systematic characters in several populations of *T. müchlfeldi* Lyn., compared with a population from Finland

I – index of frons; *II* – length of spots abdomen; *III* – colour of antennae; *IV* – colour of notopleural plates; *a* – Alma-Ata; *b* – Chkalov; *c* – Kampinos Forest; *d* – Białowieża Forest; *e* – Leningrad; *f* – Sverdlovsk; *g* – Akmol; *h* – Pskov

Odchylenia cech systematycznych w kilku populacjach *T. müchlfeldi* Lyn. w porównaniu z populacją z Finlandii

I – wskaźnik czoła; *II* – długość plam na odwłoku; *III* – zabarwienie czułków; *IV* – zabarwienie płytek notopleuralnych; *a* – Ałma-Ata; *b* – Czkałow; *c* – Puszcza Kampinoska; *d* – Puszcza Białowieska; *e* – Leningrad; *f* – Świerdłowsk; *g* – Akmol; *h* – Psków examined in the population serving as a basis for comparison. All the deviations come within the limits 0.8–1.2, which indicates the existence of inconsiderable differences in the formation of each character, regardless of the place within the range of the species from which the material for comparison was taken. From this graph it will be seen that in the majority of cases the index of frons is slightly greater, and therefore the narrow frons predominates; also that colour of the abdomen predominates in which the spots usually extend slightly beyond the limit seen in the population from Finland, although we also encounter considerable deviation in the direction of shortening of the spots on the abdomen. Similarly the antenna are on the whole slightly lighter in colour, and the notopleural plates in the majority of the individuals are light in colour or have a transitional colour. It is probable that comparison of this same material with the mean values of these characters calculated for the whole species would give even greater aggregation of curves round value 1.

The results of the comparison are affected to a considerable extent by the unit used as a basis for comparison, as Jentys-Szaferowa (1951) has already pointed out. Differences in the results obtained are shown by means of the example of *T. distinguendus* Verr. (Fig. 29), which as has already been established on the basis of data given previously, exhibits considerable variability in the formation of the index of the frons. Two comparisons were made for this species. In the first case the population from the Kampinos Forest was used as a basis for comparison. Marked aggregation of values of indices are exhibited by the populations studied in the case of the first two characters. The considerable differences observed when examining the frontal index are not very great when compared with those exhibited by other characters. The greatest deviations are shown by points corresponding to the quotients of colour of antennae, notopleural plates and hair on tergite II. It is not essential in this case to discuss the variability of these characters within the species, as it does not exceed the examples already discussed, e.g. the colour of the abdomen in *T. tropicus* L. This graph on the other hand reveals a new phenomenon, the parallelism of deviations in many populations. Half of the curves on the graph run parallel. Within the range of this species these populations form a sequence with begins in the west in the region of Irkhutsk and ends in the eastern extreme limit of the Asiatic continent. These five populations exhibit deviations in three of the five characters examined. Other populations also exhibit considerable deviations but they are as a rule haphazard and unrepeatable.

A greater degree of connection is exhibited by these deviations with the abundance of the species. *T. distinguendus* Verr. occurs commonly only in the eastern parts of the range. If we accept this area as the basis for comparison, we then obtain (Fig. 30) a group of curves also deviating, but differently than before, which correspond to populations situated to the west of Irkhutsk. The series from the eastern part of Siberia exhibit only haphazard deviations from the value 1, under which the data for the population from Ussuri was entered in this comparison. On the basis of the material described above it may be assumed

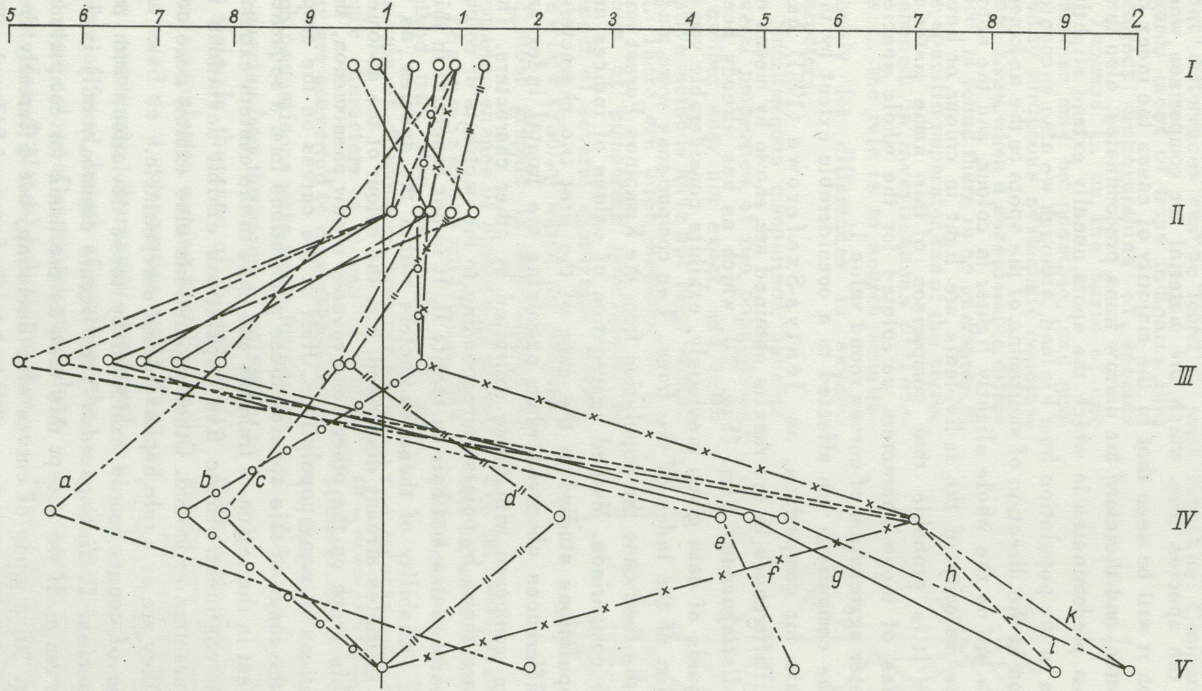


Fig. 29. Deviations of systematic characters in populations of *T. distinguendus* Verr. compared with a series from the Kampinos Forest
I – index of antennae; *II* – length of spots on abdomen; *III* – colour of antennae; *IV* – colour of notopleural plates; *V* – hair on second tergite; *a* – Tomsk; *b* – Leningrad; *c* – Altai; *d* – Chkalov; *e* – Irkhutsk; *f* – Sverdlovsk; *g* – Ussuri; *h* – Primorie; *i* – Yakutsk; *k* – Amur

Odchylenie cech systematycznych w populacjach *T. distinguendus* Verr. w porównaniu z serią z Puszczy Kampinoskiej
I – wskaźnik czułków; *II* – długość plam na odwłoku; *III* – zabarwienie czułków; *IV* – zabarwienie płytek notopleuralnych; *V* – owłosienie drugiego tergitu; *a* – Tomsk; *b* – Leningrad; *c* – Ałtaj; *d* – Czkałow; *e* – Irkuck; *f* – Świerdłowsk; *g* – Ussuri; *h* – Primorje; *i* – Jakucja; *k* – Amur

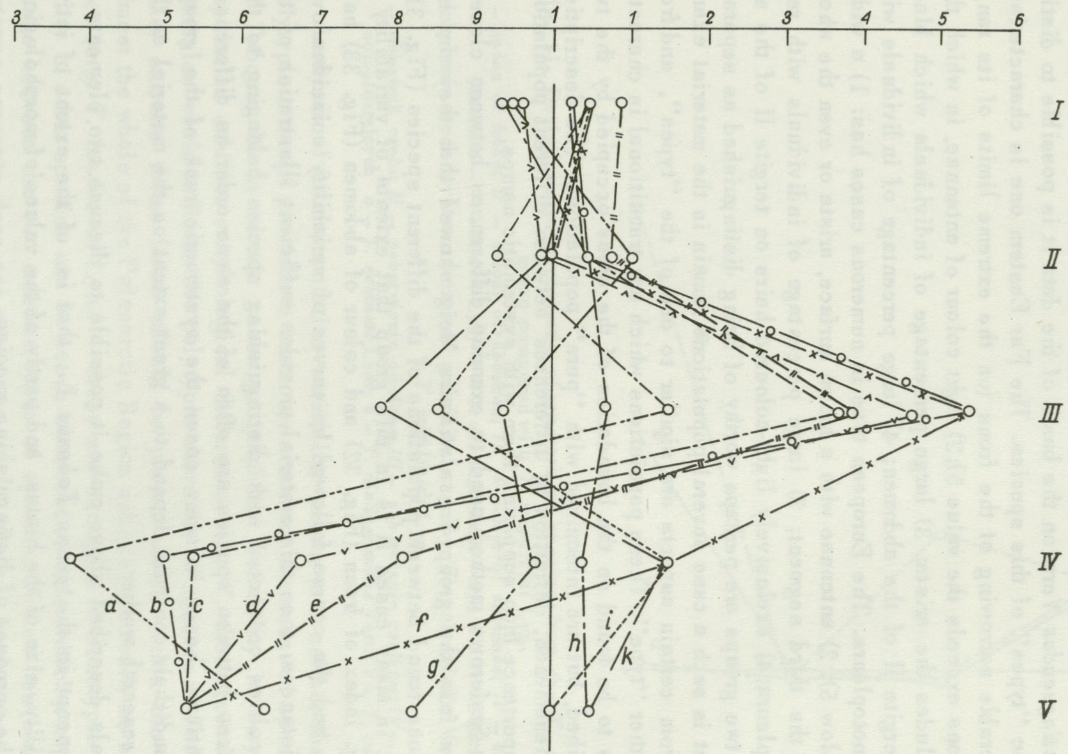


Fig. 30. Deviations of systematic characters of *T. distinguendus* Verr. in different populations compared with a population from Ussuri
I – index of frons; *II* – length of spots on abdomen; *III* – colour of antennae; *IV* – colour of notopleural plates; *V* – hair on second tergite; *a* – Tomsk; *b* – Leningrad; *c* – Altai; *d* – Chkalov; *e* – Kampinos Forest; *f* – Sverdlovsk; *g* – Irkhutsk; *h* – Yakutsk; *i* – Primorie; *k* – Amur

Odchylenia cech systematycznych *T. distinguendus* Verr. w różnych populacjach porównanych z ussuryjską
I – wskaźnik czoła; *II* – długość plam na odwłoku; *III* – zabarwienie czułków; *IV* – zabarwienie płytek notopleuralnych; *V* – owłosienie drugiego tergitu; *a* – Tomsk; *b* – Leningrad; *c* – Ałtaj; *d* – Czkałow; *e* – Puszcza Kampinoska; *f* – Swierdłowsk; *g* – Irkuck; *h* – Jakucja, *i* – Primorje; *k* – Amur

that *T. distinguendus* Verr. in areas in which it occurs abundantly, reveals a relative stability in the formation of systematic characters and a similar variability in different populations. In areas where the numbers of this species are low and stricter isolation of local populations is possible, especially in Europe, the inter-population differences are greater.

With *T. distinguendus* Verr. on the basis of the data it is possible to distinguish two basic "types" of this species. The Far Eastern one is characterised by: 1) considerable narrowing of the frons (on the extreme limits of its range the index of frons exceeds the value 5); 2) light colour of antennae, in which the red colour includes the arista; 3) large percentage of individuals which black hairs on the tergite II of the abdomen; 4) large percentage of individuals with light-coloured notopleura. The European type in numerous cases has: 1) a wider frons (index below 5); 2) antennae with a brown surface, arista or even the whole distal part of the third segment; 3) large percentage of individuals with red-coloured notopleura; 4) exclusively light-coloured hairs on tergite II of the abdomen. These two groups are perhaps worthy of being distinguished as separate subspecies, but in such a case several populations remain in the material examined, which from certain aspects are similar to one of the "types", and from others to the other "type" These populations which are transitional in character are not always to be found on the boundaries of the areas occupied by the two "types" described, but are intermixed with "pure" populations. The description itself of the phenomenon, definition of differences between different populations is of greater importance than supplying them with systematic names.

The Jentys-Szaferowa method used to examine differences between closely related species from the group *T. solstitialis* Meig. showed that they are not greater than those found between populations of the different species (Fig. 31). If we add that in many cases it is in this group that extents of variability in characters, e.g. index of frons (Fig. 32) and colour of abdomen (Fig. 33) have similar values, and the course followed by curves of variability coincides over considerable distances, then this material provides sufficient illustration of the very real difficulties connected with distinguishing species belonging to this group. Differences between species are often of the same order as differences between populations, hence in many cases the systematic rank of the groups distinguished and their contents depend to a great extent on the material at the disposal of the research worker.

The materials described above make it possible to discuss two elements of the species concept in the genus *Tabanus* L., that is, of the extent of intraspecific variability, size of the hiatus, and partly of the values of morphological characters for the purposes of distinguishing species.

Ranges of intraspecific variability of taxonomic characters in species of *Tabanus* L. assessed by numerical means are considerably wider than supposed by other authors. Inter-population variability is, however, similar to that found in average zoological material. This indicates that neither the solution of the Linnaean school (application of too wide a range of variability) nor of the Meigen school (narrowing of the range of variability) find justification in the data on variability of local populations of species of *Tabanus* L.

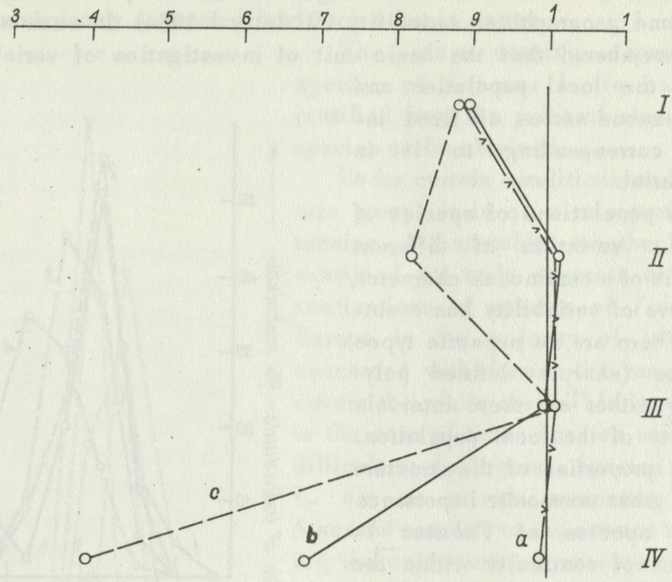


Fig. 31. Deviations of systematic characters of species from the *T. solstitialis* Meig. group compared with *T. mühlfeldi* Lyn.

I – index of frons; *II* – colour of abdomen; *III* – colour of antennae; *IV* – colour of notopleural plates. *a* – *T. schineri* Lyn; *b* – *T. distinguendus* Verr.; *c* – *T. solstitialis* Meig.

Odchylenia cech systematycznych gatunków z grupy *T. solstitialis* Meig. w porównaniu z *T. mühlfeldi* Lyn.

I – wskaźnik czoła; *II* – zabarwienie odwłoka; *III* – zabarwienie czułków; *IV* – zabarwienie płytek notopleuralnych *a* – *T. schineri* Lyn.; *b* – *T. distinguendus* Verr.; *c* – *T. solstitialis* Meig.

Analysis of inter-population variability shows that neither the monotypic nor polytypic concept provides a basis for a correct treatment of species in the case of *Tabanus* L. In certain cases geographical variability is very distinct, each population exhibits morphological difference (e.g. *T. distinguendus* Verr.). Such examples would indicate the polytypic character of species in *Tabanus* L. On the other extreme those forms should be placed which within the range including almost the whole of the Paleoarctic Region exhibit practically no such differentiation (e.g. *T. lundbecki* Lyn.) – these are examples of monotypic species. Variability of other species can be set in consecutive order which completely fills the space between the two extreme types of species. Choice between one of the two extreme concepts does not serve any useful purpose in the case of *Tabanus* L. as neither of them makes it possible to interpret the real relations existing in nature. Heterogeneity of forms of variability of species is today a phenomenon taken as a matter of course by an unprejudiced scientist, and hence a choice between two concepts of species is unnecessary.

Analysis of variability of species does not have to be based on the conviction that geographical variability is large or small. What is essential in the stage on which research on *Tabanus* L. is entering is the discovery and analysis of inter-population and geographical variability (Oldroyd 1954). In such a situation it must be remembered that the basic unit of investigation of variability in the species is the local population and the homogeneous series of fixed individuals corresponding to it in museum material.

In local populations of species of *Tabanus* L. variation of different characters is of a continuous character, and the curve of variability has a single peak. There are no separate types of structure (sharply defined polymorphism), neither are there intervals in variability of the local population. Many of the properties of the structure possessing great taxonomic importance exhibit in species of *Tabanus* L. decided lack of continuity within the area. Different populations have different maxima of curve of variability and even extens of variability of the same character may not coincide. It is easy to discover in many species considerable intervals between the variability of different populations The inter-population hiatus is often as great as the intraspecific hiatus, and on this account assessment of specific separateness on the basis of the morphological hiatus is difficult and determination of even great morphological differences between two allopatric populations does not necessarily constitute proof of their specific separateness.

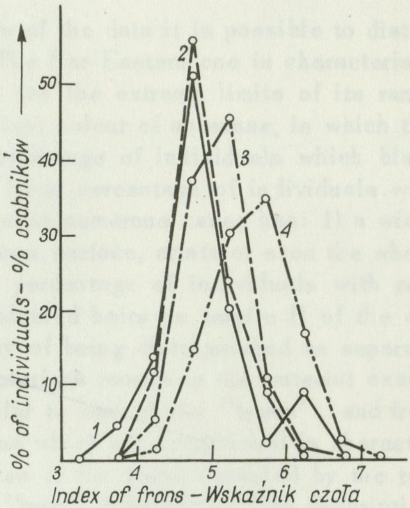


Fig. 32. Variability in index of frons
1 – *T. solstitialis* Meig.; 2 – *T. mühlfeldi* Lyn.; 3 – *T. distinguendus* Verr.; 4 – *T. schineri* Lyn.

Zmienność wskaźnika czoła
1 – *T. solstitialis* Meig.; 2 – *T. mühlfeldi* Lyn.; 3 – *T. distinguendus* Verr.; 4 – *T. schineri* Lyn.

Those elements of structure were used for an analysis of variability which are of fundamental taxonomic importance, since species of *Tabanus* L. are distinguished on the basis of such characters as structure of frons, antennae, palpi, colour of abdomen etc. The joint use of a group of taxonomic characters makes it possible to distinguish different groups, which if sympatric as a rule possess the rank of species, and if allopatric often constitute only the expression of differentiation within one species.

Criteria of species in *Tabanus* L.

The difficulties we encounter in attempts at dividing up species of *Tabanus* L. by morphological means have led to certain authors to making statements on the lack of boundaries between species in nature. Among them is, in the first place, Surcouf (1924) who stated that certain groups of species in the sub-genus *Ty-*

lostypia End. are in the initial stages of evolutionary divergence and on this account are not clearly separated from each other in nature.

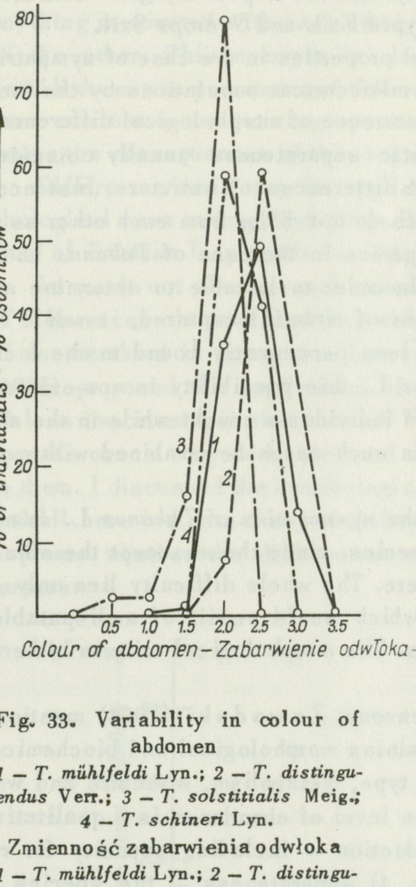


Fig. 33. Variability in colour of abdomen

1 – T. mühlfeldi Lyn.; *2 – T. distinguendus* Verr.; *3 – T. solstitialis* Meig.; *4 – T. schineri* Lyn.

Zmienność zabarwienia odwłoka

1 – T. mühlfeldi Lyn.; *2 – T. distinguendus* Verr.; *3 – T. solstitialis* Meig.; *4 – T. schineri* Lyn.

The view denying separateness of species of *Tabanus* L. in nature is not justified from the point of view of data on species so far obtained.

Under certain conditions and in systematic groups it is as a rule possible to determine indisputably whether the units examined are truly separate or not. In investigations of species of *Tabanus* L. in Europe in the majority of cases we are concerned with forms, the range of which covers the whole area. This is at least true in the case of those species which are most difficult to distinguish. Species of *Tabanus* L. are as a rule sympatric in Europe. A second property of importance in establishing the objectivity of species is their way of reproduction, which in this case is sexual, and the coupling of individuals of different sexes free. Species of *Tabanus* L. in Europe are therefore sympatric and panmictic.

The status of such species in local fauna belonging to one section of time is exactly defined (Dobzhansky 1959). Under such conditions related species not completely separated from each other in nature cannot occur. Barriers making cross-breeding impossible usually exist between panmictic species, and any breaking down of these barriers must involve the rapid uniting of hitherto separate groups in one species. In such cases the existence of transitional forms is also very unlikely. Grounds for these general statements are to be found in the biology of species of *Tabanus* L. Sympatricity is not limited here to occurrence in one area, species of *Tabanus* L. as a rule occur in the same biotopes, and as far as European species are concerned their way of using the habitat involves co-occurrence in space. Many species are caught simultaneously by the same bait. If there were no distinct barriers between them separating them from each other, mixing of their contents must inevitably ensue fairly rapidly. Consideration of transitions existing between species is more the result of objective difficulties in distinguishing species than proof of the existence of evolutionary joining up of co-occurrent species. The difficulty lies in the fact that morphological differences between species are both small and inconstant. Two species in one area may differ as to different characters of structure than in another. Search over a period of many years for "large" differences between species of *Tabanus* L. did not give satisfactory results. Especially great difficulties still exist today in the sub-genera *Tylostypia* End. and *Ochrops* Szil.

Definitions of species based in biological properties in the case of sympatric forms describe the specific independence of co-occurrent populations by the lack of reproduction between these groups. The occurrence of morphological differences is not in general essential, although genetic separateness usually coincides with the occurrence of more or less distinct differences of structure. Instances of cryptic species are, however, known, which do not differ from each other as to structure. The possibility of finding such species in the case of *Tabanus* L. is very doubtful on account of their biology. In order to be able to determine appurtenance to a cryptic species on the basis of material captured, it would be necessary for the individuals to be more or less permanently bound to the local habitat, e.g. to the host plant. With *Tabanus* L. this possibility is non-existent as the research material is taken chiefly from individuals caught while in the air. Any distinguishing of forms must therefore in such cases be combined with morphological differences.

The difficulties hitherto encountered in the systematics of *Tabanus* L. do not therefore arise from lack of definitions of species, since these accept the objective existence of those species belonging here. The whole difficulty lies only in searching for and applying suitable criteria which would permit of undisputable and relatively easy distinguishing of species. The morphological criteria hitherto applied do not promise to fulfil these hope.

Criteria of species are fairly heterogeneous. Zawadski (1954) mentions 10 of them, as follows: 1) organisation containing morphological and biochemical properties of species expressed in unity of type, metabolism, structure and way of life of the individuals; 2) abundance – the level of abundance is a qualitative character describing the species; 3) reproduction – including capacity for reproduction within the group and fecundity; 4) separateness – the species is a group separated from others and closed; 5) space – range of the species is a fundamental element of its characteristics; 6) vital niche – the species occupies a definite place in the turnover of matter in nature; 7) history – the species arises, exists, changes and disappears giving birth to new species; 8) permanence – the species lasts a long time in time; 9) heterogeneity – the species contains different forms, biological types, populations, strains etc; 10) integrality – the species is not a simple total of individuals.

Other authors (Cuenot 1936) treats criteria of species more from the aspect of their applicability to defining and limiting species. Such criteria are supplied by genetics, physiology, ecology, ethology and geography. We have now a sufficient number of examples to illustrate the usefulness of applying these criteria. If, however, we accept as the fundamental principle in determining specific separateness in sympatric forms the necessity for genetic isolation of two populations, we shall not commit an error by naming as separate species two co-occurrent populations not differing from each other as to any particular, but which in nature do not interbreed. In practice apart from similarities, neither of these groups has anything in common with each other, each of them has its own history independent of the other. This example is abstract, isolation involves the occurence and establishment as permanent of differences between groups, but it is not they which form the basis for defining specific separateness in sympatric forms, they are rather the consequences of this separateness.

Different criteria may be applied in the systematics of *Tabanus* L. the morphological ones taking first place. Investigations of structure must always in the case of *Tabanus* L. precede investigations from any other standpoint.

As we do not always reach unambiguous solutions in this way, the assessment of differences obtained together with morphological analysis by means of criteria of another kind is important. Semenov-Tian-Szansky (1910) and Cuenot (1936) proposed the application of joint criteria. The geographical criterion is of less importance in the case of *Tabanus* L. A considerable number of species spreads over a very wide area and co-occurs with the forms most closely related to them. I discussed the morphological properties of species of *Tabanus* L. above, I shall here indicate the possibility of applying data which make it possible to estimate whether the differences of structure observed conceal biological difference.

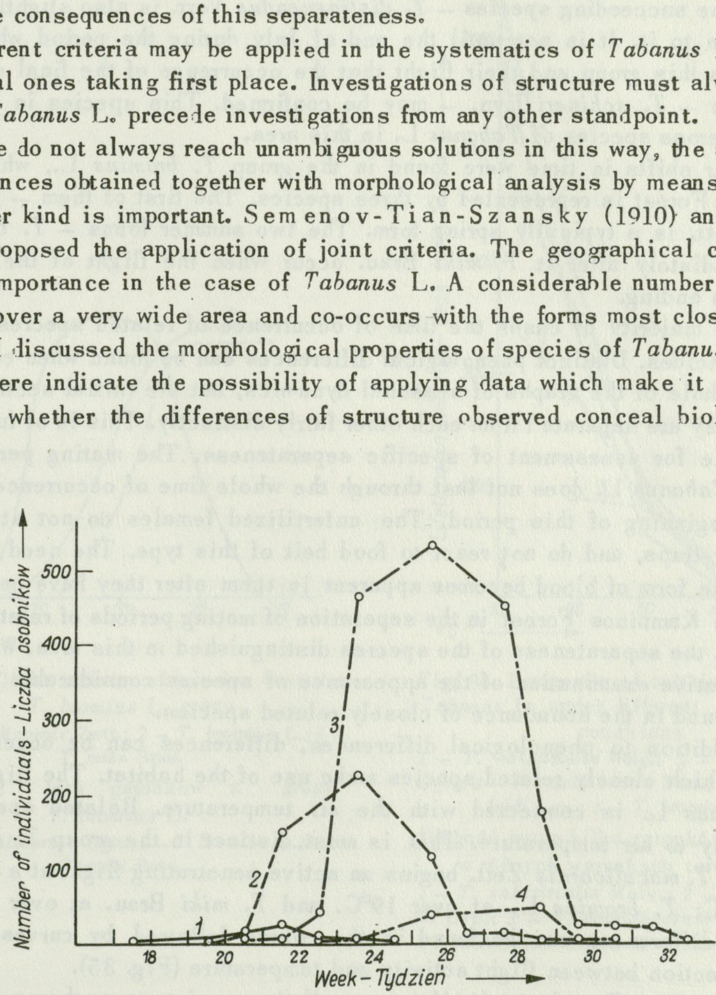


Fig. 34. Seasonal changes in numbers of closely related species of *Tabanus* L.

1 – *T. nitidifrons* Szil.; *2* – *T. solstitialis* Meig.; *3* – *T. mühlfeldi* Lyn.; *4* – *T. distinguendus* Verr.

Dynamika sezonowa blisko spokrewnionych gatunków *Tabanus* L.

1 – *T. nitidifrons* Szil.; *2* – *T. solstitialis* Meig.; *3* – *T. mühlfeldi* Lyn.; *4* – *T. distinguendus* Verr.

The first category of these data is formed by phenological material. Closely related species of *Tabanus* L. frequently have shifted periods of occurrence. In the group *T. solstitialis* Meig. in the Kampinos Forest (Fig. 34) *T. nitidifrons* Szil. occurs in the spring, and immediately after it *T. luridus* Fall., which hovewer differs considerably from it as regards structure. The abundance of neither species is great, and they can only be caught on warm spring noons. The next species is *T. solstitialis* Meig. – at the moment when its numbers attain their maximum *T. mühlfeldi* Lyn. appears in the study area. The beginning of the flight of the succeeding species – *T. distinguendus* Verr. is also slightly delayed in relation to it. It is not until the end of July during the period when all the species in this group end their flight that the occurrence of the final species in this group – *T. schineri* Lyn. – may be confirmed. This species is among the least numerous species of *Tabanus* L. in this area.

Similar shifts in time were found in the group *T. bromius* L., which in the Kampinos Forest is represented by three species. The first of them – *T. maculicornis* Zett. is a typically spring form. The two summer forms – *T. bromius* L. and immediately after it *T. miki* Brau. occur when the flight of the preceding species is ending.

In the majority of cases the time of occurrence of related species only partially coincides. Distinct phenological differences can be found when considering not the whole of the graphs of seasonal dynamics, but the initial sections of the curve. They are separated from each other fairly distinctly. This is of fundamental importance for assessment of specific separateness. The mating period in the case of *Tabanus* L. does not last through the whole time of occurrence. but only at the beginning of this period. The unfertilized females do not attack either people or traps, and do not react to food bait of this type. The need for finding food in the form of blood becomes apparent in them after they have been fertilized. In the Kampinos Forest in the separation of mating periods of related species indicates the separateness of the species distinguished in this area. When making a quantitative examination of the appearance of species considerable differences can be found in the abundance of closely related species.

In addition to phenological differences, differences can be observed in the way in which closely related species make use of the habitat. The flight activity of *Tabanus* L. is connected with the air temperature. Related species react differently to air temperature. This is most distinct in the group *T. bromius* L., in which *T. maculicornis* Zett. begins an active penetrating flight at a temperature over 17°C; *T. bromius* L. at over 19°C. and *T. miki* Brau. at over 21°C. Also distinct differences can be found in the course followed by curves describing the connection between flight activity and temperature (Fig. 35).

In the group *T. solstitialis* Meig. not all the species were thoroughly investigated from this aspect, but similar differences were found in flight activity. *T. solstitialis* Meig. begins flight at over 14°C. The related species. *T. mühlfeldi* Lyn. – at temperatures over 16°C. *T. lundbecki* Lyn. attains its greatest activity at 18–19°C., while the optimum conditions for *T. mühlfeldi* Lyn. are at temperatures over 22°C. Investigation of the connection between flight activity and atmospheric moisture vields similar data (T r o i a n 1958).

Data on the vitality ot individuals belonging to different species provrue yet further information as to their separateness. The life span of individuals in different thermal conditions. with a constant, high relative atmospheric moisture, was used as an index. From this aspect also (Fig. 36) closely related species

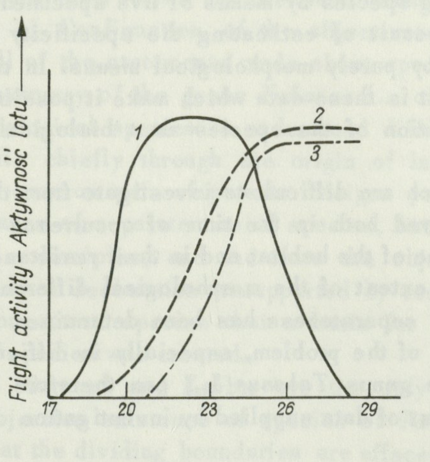


Fig. 35. Flight activity of species from the *T. bromius* L. group

– *T. maculicornis* Zett.; 2 – *T. bromius* L.; 3 – *T. miki* Brau.

Aktywność lotu gatunków z grupy *T. bromius* L.

1 – *T. maculicornis* Zett.; 2 – *T. bromius* L.; 3 – *T. miki* Brau.

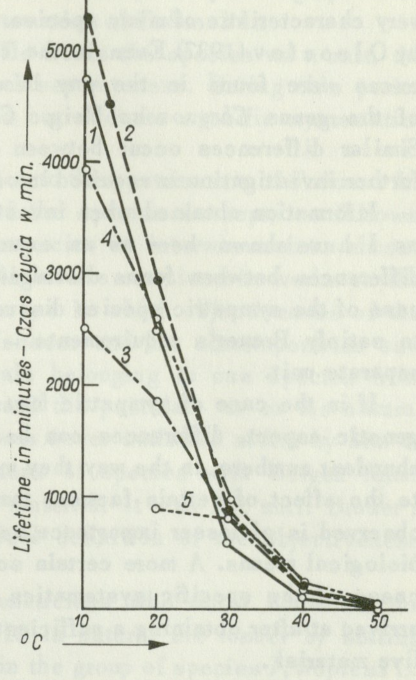


Fig. 36. Longevity of certain species of *Tabanus* L. under different temperature conditions

1 – *T. solstitialis* Meig.; 2 – *T. lundbecki* Lyn.; 3 – *T. maculicornis* Zett.; 4 – *T. mühlfeldi* Lyn.; 5 – *T. bromius* L.

Długość życia kilku gatunków *Tabanus* L. w różnych warunkach termicznych

1 – *T. solstitialis* Meig.; 2 – *T. lundbecki* Lyn.; 3 – *T. maculicornis* Zett.; 4 – *T. mühlfeldi* Lyn.; 5 – *T. bromius* L.

exhibit considerable differences. A species which appears earlier (*T. solstitialis* Meig.) is far more resistant to low temperatures (+ 10°C.) than the summer species (*T. mühlfeldi* Lyn.) The situation alters with higher temperatures, when *T. solstitialis* Meig. gives place to *T. mühlfeldi* Lyn., its lifetime at such temperatures being almost half shorter.

Species from the group *T. bromius* L., are less resistant to low temperatures than the group discussed previously. The least resistant is *T. bromius* L. When higher temperatures are used than normally occur in the habitats of these species, the differences in resistance rapidly diminish and at 50°C are very slight in the case of all the species.

Simple attempts at making use of ethological data to determine differences between sympatric species are also known. When collecting material from domestic animals (Terterjan 1954) it was found that the choice of place for feeding is very characteristic of many species. Similar information is given in certain cases by Olsoufev (1937). Even in the case of artificial bait (the Skufjin trap) differences were found in the way in which the trap was attacked by two species of the genus *Chrysozona* Meig.: *Ch. pluvialis* (L.) and *Ch. hispanica* (Szil.). Similar differences occur between closely related species of *Tabanus* L. but further investigation is required in order to determine them exactly.

Information obtained when investigating species by means of live specimens, as I have shown here as an example, permit of estimating the specificity of differences between forms distinguished by purely morphological means. In the case of the sympatric species discussed, it is these data which make it possible to satisfy Brauer's requirements – definition of the species as a biologically separate unit.

If in the case of sympatric forms, which are difficult to investigate from the genetic aspect, differences can be observed both in the time of occurrence of abundant numbers, in the way they make use of the habitat and in their resistance to the effect of certain factors, then the extent of the morphological difference observed is of lesser importance, as their separateness has been determined by biological means. A more certain solution of the problem, especially in difficult cases of the specific systematics of the genus *Tabanus* L., can therefore be arrived at after obtaining a sufficient amount of data supplied by investigation of live material.

V. CONCLUSIONS

The aim of this work was to examine the species concept in taxonomy, using the genus *Tabanus* L. as an example. The starting point for our reasonings was the statement that in research work on the contents of distinguished units, it is the accepted species concept and methods of description used which are decisive.

Investigations were made on the basis of proposed quantitative methods by means of which comparison was made of results contained in works on the systematics of this genus over a period of 200 years.

Three schools of research and three periods can be distinguished in the systematics of *Tabanus* L.:

1. The Linnaean (1758–1800). The characteristic feature of this school was the treatment of species as a large and variable unit. The lack of suitable means of describing and distinguishing species during this period caused the majority of the species of *Tabanus* L. described to be lumped. This was caused by the

state of knowledge at that time and not by theoretical errors in the Linnaean species concept.

2. The Meigen (1800–1880). It is based on the Tournefort species concept. This school introduces the treatment of species as a unit morphologically invariable, and led to the splitting treatment of species of *Tabanus* L. and to many of them being split into units apparently possessing the rank of species. During this period the majority of morphological characters of considerable importance to taxonomy were discovered, but errors in the actual way of describing specimens resulted in a failure to throw light on the systematics of *Tabanus* L.

3. The Brauer (1880 up to the present). He treats the species as a unit, the limits of which are determined by biological separateness. During this period correct methods of description were worked out and the specific systematics of *Tabanus* L. set in order.

These three schools of research, in relation to the systematics of *Tabanus* L., state their views on the basic elements of the species concept, as follows:

1. Confirmation of the objectiveness of species is interwoven into almost all of the statements made about species which were examined in works on the taxonomy of the genus *Tabanus* L., only the way in which objectiveness of the biological species is understood differs. Linnaeus and his contemporaries saw this chiefly through the origin of individuals belonging to one species from a common pair of parents. Meigen put forward the postulate as to the natural bases of separateness of species, but this was never satisfied either by him or his disciples, and therefore the objectiveness of species with Meigen forms only a declaration unsupported by research material. It was not until Brauer's concept of species that a basis for biological definition of the objectiveness of species was created.

Surcouf and Kröber are the only systematicians who throw doubt on the objective existence of species of *Tabanus* L. in nature, the former by stating that the dividing boundaries are effaced within the group of species *T. tropicus* L. and the latter by constant changes in the status of each group which he now endows with the rank of species, and again merely that of a variant, and sometimes even of other units.

Doubt as to the objectiveness of biological species in systematics is connected with the application of the Tournefort species concept, which permits of considerable freedom in distinguishing species and leads to conventionalism — the treatment of the biological species as a conventional unit. This is not, as many systematicians at the turning point of the 19th century assumed, the result of Darwin's theory, since it was not this which undermined the objectivity of natural species. The activities of the systematicians themselves led to the overthrow of the objectiveness of the natural species.

2. The range of variability accepted for the species forms the second element in the species concept. The Linnaean school did not investigate intraspecific variation, but from its practical reasonings it is clear that, during that period, a wide range of variability was accepted for species. This state was only to

a slight extent the result of conscious research theories, its chief cause being the poor level of knowledge of species and macroscopic methods of distinguishing them. The Meigen school holds firmly to the standpoint that intra-specific variability is very slight, especially as far as structure is concerned. As shown in extreme cases (Robineau-Desvoidy 1830, 1863) this leads to almost each individual being described as a new species, which constitutes a dangerous tendency in systematics, at variance with the theory defining species as a collective unit. The Brauer school accepts a range of variability which defines the biological limits of the material.

3. Size of hiatus. The Linnaean period is characterised by a search for considerable differences between species. Only a few species of *Tabanus* L. exhibit large morphological differences from those species closest systematically to them. The Meigen school accepts that each morphological difference forms proof of specific separateness, while Brauer, contrary to both the previous schools of thought, holds that it is not the size of the morphological difference which decides specific separateness, but its agreement with the biological separateness of the groups examined.

4. Morphological characters distinguishing species of *Tabanus* L. were discovered by research workers of the Meigen period. They were initially set in order by Loew (1858a) and systematized by Brauer (1880). The means of description are continually being improved up to the present time. The assessment of morphological differences, based on biological criteria of species, is of fundamental importance.

In an analysis of the species concept in the genus *Tabanus* L. three basic elements of scientific work were taken into consideration: the theory of species, methods and factual material. They are closely connected with each other, and a change in one of these elements involves a change in the remainder. Species of *Tabanus* L. did not meet the requirement of objectiveness in Linnaeus' works. The reason for this was the lack of a proper means of description. Together with increasing specialisation and improvement of instruments of research, work on material became increasingly exact. Starting from differentiation of material Meigen overthrew the Linnaean means of description and large species concept. The Meigen concept of small species made it possible to describe innumerable new species, without providing any possibility of distinguishing them in material. Opposition to the Meigen trend began from the aspect of methods. Loew did not allow himself to criticize the theoretical views of Meigen, but he undermined the whole basis of description of species, introducing the principle of ranking them according to the formation of homological characters. The only principle directly opposed to the Meigen concept was the acceptance of considerable variation, even from the morphological aspect, for species. Brauer developed Loew's line of thought even further and created the biological concept of species of *Tabanus* L., introducing at the same time new principles of description.

The Linnaean definition is in principle indifferent to the contents of the species, and leaves it to the scientist to solve the question as to whether the species is a large or small unit. Its place has finally been taken by the two remaining concepts, treating as part of their programme the species as an invariable (Meigen) and variable (Brauer) unit. Both concepts have adherents in research on *Tabanus* L., even up to the present time.

Research methods in each period have had a considerable influence on the units distinguished, but the new, more perfect means of descriotion sooner or later oust the out-of-date methods from research work. Today representatives of both trends use the new methods worked out on the basis of Brauer's proposals.

Material – the natural reality – is a very active element in the development of our knowledge of species. Examination of material leads to the breakdown of both methods of description and the research concepts. It is, of course, possible to compress it, by means of different means of segregation and description, into a framework dictated by a given view on species, but each fresh examination of material, if only it was not classified in accordance with the actual state of the species, leads to the old concepts being rejected and a new one introduced. Despite the fact that in different periods we find larae deviations in the direction of combining of species, or their being split into apparent units, in each successive period systematic knowledge approaches increasingly closer to reality.

The present state of knowledge of species of *Tabanus* L. in Europe indicates that possibilities of discovering new species have been considerably exhausted, nevertheless many research workers representing the Meigen trend continue to describe new species. The results of this splitting activity are disturbing. In historical development considerable increase is found in the number of proposed new names for species, in relation to the real number of new species discovered. This causes an increase of synonymics and many difficulties in work on them, on account of the names being ambiguous. Synonymisation is fundamentally of a subjective nature, so that the integration of species carried out does not give reliable results, as an attempt may always be made to restore apparents units to the rank of species.

Development of technic of description in research work on *Tabanus* L. has not tended to the working out of methods which would permit of investigating the species as a complex unit. There are no correct quantitative methods or indices defining the morphological properties of a population or species. At present the classic description is used – of a typic individual, sometimes giving deviations observed. No attempts were found at connecting systematic research on the genus *Tabanus* L. with the polytypic species concept.

Investigation of several fundamental morphological properties of certain species of *Tabanus* L. determined the applicability of quantitative indices and the size of samples which should be used when establishing quantitative characteristics. It was found that differences between populations are greater than between species, that species exhibit within their range of variability – accidental or geographical, or even ecological, variability. Each population has fundamental taxonomic characters formed in a way characteristic of itself. In certain cases it proved possible to find the combination of differences between variability in different places within the range with the abundance and degree of isolation of local populations.

Species of *Tabanus* L. have extremely differing variability. We encounter here examples of polytypic and monotypic and also intermediate forms of geographical differentiation. Choice between these two alternative species concepts is not justified by the properties of species of *Tabanus* L., and a choice should not be made between two extreme alternatives, since they usually do not give a true picture of natural reality.

The following contents of four elements of the species concept are in my opinion justified at the present stage of research on the genus *Tabanus* L.:

1. Species of *Tabanus* L. exist objectively in nature. This is not the result of general biological indications only. Their objectiveness may and should be proved by biological means and not, as has hitherto been the case, by morphological ones.

2. The range of intraspecific variability is defined by the character of variability of the species themselves. In the genus *Tabanus* L. different types of intraspecific variability are realised. Variability itself may be accepted as a property better characterising the species than characters on the basis of which it was distinguished. The subject of research and description should be variability within and between populations.

3. and 4. Species of *Tabanus* L. can be distinguished on the basis of the morphological hiatus found, which is correlated with biological differences. The size itself of the morphological hiatus, especially in the case of allopatric populations, is of slight importance for distinguished species.

The debatable problem of whether the species distinguished by systematicians and the species concept itself in systematics are of general biological significance requires discussion.

The species is at present treated as an objective unit of nature. It has a geographical dimension, defined range within which it divides up into populations, which often differ considerably from the morphological aspect and which form a defined link in the economics of nature by being closely bound by ecological ties to the biocenosis.

The way in which species is treated as a dynamic and evolving unit is particularly characteristic. Evolutionary processes within the species take place on two planes – on the first by the historical variability of the species in time, and on the second by its differentiation in space.

The general biological species concept contains two elements in common with the systematic one. These are: the statement of the objectiveness of species and the treatment of species as a variable unit in space. Investigations of systematicians based on the biological and population concept have provided data here. As will be seen, the work of systematicians, if based on correct theoretical assumptions, does not lead only to the creation of a „species museorum" or as Cain (1954) wishes – to „morpho-species" – units which are of significance only for themselves, but permits of a knowledge being obtained of objective units of nature, which have a common meaning for all biologists.

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ANALIZA KONCEPCJI GATUNKU W RODZAJU *TABANUS* L. (*DIPTERA*) W ŚWIETLE PRAKTYKI TAKSONOMICZNEJ

Streszczenie

Niniejsza praca zawiera analizę koncepcyj gatunku w systematyce opisowej przeprowadzoną na przykładzie rodzaju *Tabanus* L. Stwierdzono, że problematyka gatunku została stworzona przez systematykę i stanowi integralną jej część. Badanie koncepcyj gatunku stanowi obecnie ważny odcinek działalności naukowej w systematyce ze względu na ponawiane ciągle próby obalenia koncepcji gatunku oraz odmawianie gatunkom wyróżnianym w badaniach systematycznych wartości ogólnobiologicznych.

Koncepcja gatunku w systematyce opisowej składa się z czterech elementów: 1) twierdzenia o obiektywności gatunków w przyrodzie, 2) określenia zakresu i charakteru zmienności wewnątrzgatunkowej, 3) określenia hiatus między gatunkami, 4) określenia cech, które dla rozróżniania gatunków mają znaczenie zasadnicze.

Każde opracowanie systematyczne oparte jest na określonej koncepcji gatunku, można ją poznać poprzez zbadanie konkretnych gatunków jakie ono zawiera. W badaniach własnych autor operował koncepcją gatunku według której każdy gatunek posiada odrębną niszę ekologiczną, sobie właściwy sposób korzystania ze środowiska. Granice biologiczne określają zakres zmienności wewnątrzgatunkowej. Granice te można poznac poprzez wykrywanie korelacji między różnicami biologicznymi i morfologicznymi.

Przy omawianiu zastosowanych metod autor podaje sposób przeprowadzenia pomiarów, zastosowane skale zmienności oraz sposób wyciągania wniosków przy operowaniu skalami umownymi, jakich używa się dla jednostek trudno mierzalnych. Badania porównawcze nad wynikami uzyskanymi przez poszczególnych autorów oparto na pięciu wskaźnikach ilościowych; są to: 1) procent gatunków dobrze wyodrębnionych, 2) rozbitych, 3) zbiorowych, 4) wskaźnik stanu systematyki oraz 5) rzeczywisty przyrost nowoopisywanych gatunków. Szczegółowo opisano sposób operowania materiałem przy wyliczaniu tych wskaźników.

Przebadano wartości wskaźników w różnych pracach tego samego autora oraz porównano je dla prac różnych autorów. Okazało się, że we wszystkich pracach stosowana jest jedna koncepcja gatunku (np. Fabricius), bądź też autorzy zmieniają ją (np. Meigen czy Zetterstedt). Badacze pracujący w jednym okresie stosują tę samą lub całkiem odmienne koncepcje gatunku.

Zmiany ujęcia gatunku u *Tabanus* L. w czasie przedstawiono w oparciu o zmiany zawartości gatunków w pracach systematycznych i zbiorach. Stwierdzono, że w latach 1758–1800 przeważały gatunki zbiorowe, w skład których wchodziło po dwa lub więcej gatunków wyróżnianych obecnie. Dobrze wyodrębnione gatunki stanowiły w tym okresie mały, wzrastający z czasem procent. W latach 1800–1880 panuje tendencja do rozbijania gatunków, wyraźna przewaga gatunków dobrze opisanych i wyodrębnionych rozpoczyna się od roku 1880.

Zmiana sposobu ujmowania gatunków uwidoczniła się najostrzej po przeanalizowaniu zawartości gatunków opisywanych jako nowe. Na przestrzeni 200 lat można stwierdzić trzykrotną zasadniczą zmianę koncepcji gatunku w badaniach *Tabanus* L. Pozwala to na wyodrębnienie trzech szkół badawczych, każda z tych trzech szkół nawiązuje do innego z trzech kierunków teoretycznych jakie powstały w XVIII w. Pierwszą z nich można wiązać z nazwiskiem Linneusza, drugą – Tourneforta, trzecią – Brehma i Brauera.

Koncepcja gatunku Linneusza (poza propozycjami Cuviera) nie określała w zasadzie zakresu zróżnicowania gatunku. Dzięki temu rzeczywista zawartość gatunków u Linneusza zależna była od ówczesnego stopnia ich poznania. W rodzaju *Tabanus* L. 75% gatunków na początku tego okresu to gatunki zbiorowe, każdy z nich składał się z kilku a nawet kilkunastu wyróżnianych dziś gatunków. Sytuacja ta uległa poprawie dzięki pracom Fabriciusa. Wyodrębnianie gatunków zbiorowych jest w tym okresie głównie efektem niewystarczających metod opisu, który był zbyt ogólny, a stosowane cechy niespecyficzne, na ich podstawie nie można było wyodrębniać gatunków. Wyczerpanie możliwości dalszej pracy badawczej w oparciu o metody Linneusza stanowiło główną przyczynę rewizji poglądów na gatunek i metody jego wyodrębniania.

Już w okresie linneuszowskim obserwujemy wzrost specjalizacji, coraz więcej prac obejmuje wąskie grupy świata zwierzęcego. Pierwszym człowiekiem, który poświęcił się wyłącznie pracy nad muchówkami był Meigen. Opracował on teoretycznie i metodycznie zasady pracy nad gatunkiem u muchówek. Przeprowadza on krytykę rozwiązań systematycznych Linneusza i Fabriciusa oraz proponuje nowe ujęcie gatunku – jako jednostki małej, niezmiennej pod względem morfologicznym, nawiązuje on w ten sposób do koncepcji

Tourneforta. Ujęcie takie jest sprzeczne z założeniem o biologicznej odrębności gatunków. Meigen wprowadza do badań nad muchówkami skonstruowaną przez siebie lupę, która pozwala na rozwinięcie metody opisu. Obok krótkiej charakterystyki gatunku podaje on również opis owada. Przy opisywaniu budowy *Tabanus* L. Meigen wykrywa większość tych właściwości budowy, które dziś mają zastosowanie przy pracy nad systematyką *Tabanus* L. Nowe propozycje teoretyczne i metodyczne trafiły na podatny grunt i szybko zyskały Meigenowi licznych zwolenników. W okresie jego działalności i następnych latach pojawia się wiele prac na temat systematyki *Tabanus* L. Koncepcja Meigena dominuje przez dłuższy czas, co pozwala na wyodrębnienie okresu meigenowskiego (1800–1880) w systematyce *Tabanus* L. Charakteryzuje go obniżenie liczby gatunków zbiorowych do 20% oraz wysoki procent gatunków rozbitych, który waha się w różnych pracach tego okresu około 40. Dzięki temu liczba gatunków dobrze wyodrębnionych jest mała. Szczegółowe zbadanie zbiorów z tego okresu wskazuje również na to, że oznaczanie gatunków było wtedy bardzo utrudnione.

Poziom ówczesnej systematyki *Tabanus* L. mimo postępu w metodyce badań był bardzo niski. Wynika to z kilku przyczyn. Sposób opisu był w rzeczywistości zły, ponieważ nie był konsekwentny. Do opisu pokrewnych gatunków używano dla każdego innych cech, co utrudniało prawidłowe wyróżnianie ich w materiale. Okazy w zbiorach zwykle nie były etykietowane, co uniemożliwiało łączenie materiału w serie jednakowego pochodzenia. Opis oparty był z reguły na jednym osobniku. Populacje lokalne jednego gatunku rozbijano na jednostki pozornie odrębne, nadające im rangę gatunkową. Przeprowadzona analiza na przykładzie *T. aterrimus* Meig. wskazuje na to, że przyczyny spliterstwa leżą również w powierzchownym traktowaniu materiału.

Rozwój spliterstwa w pierwszej połowie XIX w. będący konsekwencją zastosowania monotypowej koncepcji gatunku wywołał sprzeciwy u wielu badaczy i spowodował powstanie biologicznej koncepcji gatunku w systematyce. Teoretyczna dyskusja poglądów na gatunek odbiła się również w systematyce *Tabanus* L. Zeller i Loew w swych pracach poddali krytyce spliterskie potraktowanie gatunków *Tabanus* L. i zaproponowali nowe zasady wyróżniania gatunków. Stwierdzają oni znaczną zmienność wielu cech morfologicznych i przeprowadzają rewizję zasad opisu. Wpływ koncepcji meigenowskiej nie został jednak całkowicie przezwyciężony. Właściwe rozwiązanie podstawowych problemów związanych z rozumieniem i opisem gatunku znajduje dopiero Brauer, którego można uważać za twórcę biologicznej koncepcji gatunku u *Tabanus* L. Propozycje Brauera idą w kierunku opanowania żywiołowego sposobu pracy nad gatunkiem. Początkowo spotkały się one z przyjęciem negatywnym, szczególnie badaczy francuskich, jednak w XX w. metody jego zyskały powszechne uznanie i zastosowanie w pracach nad gatunkami *Tabanus* L. w Europie.

Na przełomie XIX i XX w. wraz z załamaniem się koncepcji gatunku daje się odczuć u systematyków niechęć do dyskusji nad problemami ogólnymi związanymi z pracą badawczą. W zakresie systematyki *Tabanus* L. nie powstają już nowe koncepcje gatunku. Do dziś dominuje koncepcja Brauera, jednak zdarzają się próby powrotu do koncepcji gatunku monotypowego, pozbawionego zmienności. W XX w. metody opisu rozwijane są dalej w pracach Verralla, Szilady'ego, Ołsufijewa i Collina. Nie stworzono jednak dotąd takich metod, które by pozwoliły na badanie zmienności wewnątrzpopulacyjnej i międzypopulacyjnej.

Po 200 latach działalności systematyków liczba gatunków *Tabanus* L. posiadających tylko jedną nazwę jest bardzo niewielka. Stosunki procentowe między gatunkami posiadającymi 1, 2, 3, 4 ... 8 nazw są stałe i w ciągu ostatnich 100 lat ulegają tylko nieznacznym zmianom. W okresie linneuszowskim na wykrycie jednego dobrego gatunku przypadło przeciętnie 1,4 nazwań. W okresie meigenowskim – 2,5, obecnie liczba ta bliska jest 3. Sytuacja taka powstała w wyniku działalności spliterskiej. Wskaźnik spliterstwa u *Tabanus* L. jest zróżnicowany pod względem geograficznym, większy w Europie środkowej i północnej niż południowo-wschodniej. Rozmiary spliterstwa uwarunkowane są czterema czynnikami: 1) stanem zbadania obszaru z którego pochodzi materiał, 2) wielkością materiału jakim badacz operuje, 3) metodami badawczymi, 4) umiejętnością i postawą badacza.

Zdawanie sobie sprawy z aktualnej wartości tych czynników wydaje się istotne przy badaniu określonych grup systematycznych. Opisywanie nowych gatunków *Tabanus* L. z obszarów Europy jest niebezpieczne, ponieważ obserwujemy stałe wyczerpywanie się możliwości odkrycia rzeczywiście nieznanych na tym terenie gatunków.

Dokładne przebadanie zmienności cech taksonomicznych w populacjach o dużej liczebności wskazało, że zakresy zmienności podawane dla gatunków *Tabanus* L. w dotychczasowych opracowaniach są niedokładne, nie wykazują bowiem stosunków rzeczywistych. Różne cechy taksonomiczne dają się uszeregować pod względem ich wzrastającej zmienności. Wartość wskaźnika zmienności określa zarazem ich przydatność dla celów wyróżniania gatunków. Wiele cech szacowanych wzrokowo wykazuje znaczną zmienność (wskaźnik czoła, budowa czułków czy głaszczków), jednak zbadanie tej zmienności za pomocą metod statystycznych wskazuje, że leży ona w granicach ustalonych dla przeciętnych materiałów biologicznych. Szereg błędów powstałych w systematyce *Tabanus* L. wynikło na skutek przyrównywania zakresu zmienności jednych gatunków do drugich. Wykazano to na przykładzie zmienności odwłoka *T. solstitialis* Meig. i *T. distinguendus* Verr. Sztuczne rozbijanie zaobserwowanej skali zmienności wynika często z braków metod badawczych i zastosowania monotypowej koncepcji gatunku a nie luk w materiale przyrodniczym.

Zmienność geograficzną zbadano głównie w oparciu o dane dotyczące *T. tropicus* L. Budowa czułków u tego gatunku wykazuje znaczne zróżnicowanie. Wszystkie warianty można ułożyć w dwa szeregi różniące się między sobą położeniem zęba na trzecim członie. Każda z przebadanych populacji zawiera warianty obu tych szeregów, pozwala to na stwierdzenie braku geograficznej dywergencji tej cechy. Po uporządkowaniu wariantów względem wskaźnika szerokości czułków uzyskano wyraźny obraz geograficzny. Najwęższe czułki występują u ponad 50% osobników każdej populacji w północnej i centralnej części zasięgu (strefa I). Strefę tę otacza pas (strefa II) w którym przeważają czułki o średniej szerokości. W innych częściach zasięgu czułki wąskie spotyka się sporadycznie i to w określonych warunkach ekologicznych. Czułki najszersze spotyka się tylko w dużych populacjach pochodzących spoza pierwszej strefy. Zarys czułków jest również zmienny. Nie wykazuje on jednak wyraźnych prawidłowości geograficznych. Im dalej od strefy pierwszej (największa liczebność populacji lokalnych) tym częściej spotykamy warianty czułków odrębne. Ich występowanie można traktować jako efekt małej liczebności i izolacji populacji lokalnych. U pokrewnego gatunku *T. distinguendus* Verr., który ma podobny zasięg, zmienność budowy czułków wykazuje minimalne zróżnicowanie.

Zabarwienie czułków *T. distinguendus* Verr. wskazuje na to, że przy posuwaniu się z Europy środkowej na wschód czułki ulegają stopniowemu rozjaśnieniu (w Kraju Ussuryjskim żółte zabarwienie obejmuje niemal całą wić). *T. tropicus* L. wyczerpuje niemal wszystkie możliwe warianty zabarwienia czułków. Zmienność tej cechy wykazuje przypadkowe odchylenia z populacji na populację i jest szczególnie silna przy małej liczebności gatunku w danym miejscu.

Wskaźnik czołowy u *T. tropicus* L. wykazuje zmienność wykraczającą poza dane spotykane w piśmiennictwie. Daje się to zaobserwować we wszystkich większych seriach. W przypadku małych populacji lokalnych spotyka się często osobniki wykraczające swymi wskaźnikami poza wartości przeciętne. Często połączone są z tym również znaczne różnice w zabarwieniu czoła i wykształceniu znamion czołowych. Po przebadaniu szeregu niedużych serii pochodzących ze strefy małej liczebności i izolowanych populacji lokalnych stwierdzono, że prawdopodobieństwo występowania osobników i serii wykazujących odchylenia od przeciętnej wartości wskaźnika czoła jest tu takie samo jak w populacjach dużych. Bez zbadania zmienności danej cechy w obrębie gatunku nawet duże różnice zaobserwowane w populacji lokalnej nie mogą stanowić podstawy do opisu odrębnych gatunków.

U *T. lundbecki* Lyn. i *T. distinguendus* Verr. występują znaczne różnice między wartościami wskaźnika czołowego między populacjami środkowoeuropejskimi a syberyjskimi.

Płytki notopleuralne u *T. tropicus* L. wykazują znaczne ściemnienie na obszarach o ostrzejszym klimacie. U *T. distinguendus* Verr. ustalono, że zmienność tej cechy dotychczas ustalana była błędnie. Osobniki o jasnym zabarwieniu stanowią w Europie stały wariant (20% i więcej) zmienności, natomiast w populacjach dalekowschodnich dominującą większość. Największą stałość pod tym względem wykazuje w obrębie całego zasięgu *T. lundbecki* Lyn., u którego przynajmniej 70% osobników ma notopleury czarne.

Zabarwienie odwłoka u *T. tropicus* L. wykazuje również zróżnicowanie geograficzne. Na północy zasięgu występują formy czarne, na południowym wschodzie niemal całe czerwone. Na ściemnienie odwłoka wpływają również ostrzejsze warunki ekologiczne. Zabarwienie odwłoka u *T. distinguendus* Verr. wykazuje minimalną zmienność zarówno w poszczególnych populacjach jak i w obrębie całego zasięgu. Natomiast u *T. lundbecki* Lyn. populacje wschodnie mają wiele jaśniejszy odwłok.

Przeanalizowanie materiałów dotyczących zmienności geograficznej cech taksonomicznych pozwala na dalsze rozszerzenie wniosków wyciągniętych przy analizie populacji o dużej liczebności. Poszczególne cechy zmieniają się na ogół niezależnie. Zdarza się, że ta sama cecha u gatunków pokrewnych bądź wykazuje stałość w obrębie całego areału, bądź jest bardzo zmienna. Ogół cech gatunkowych wykazuje bądź stałe przedziały zmienności i maksima, bądź zmieniają się one z populacji na populację. Samą zmienność czasem lepiej charakteryzuje poszczególne gatunki niż cechy, jakie różnią go od grupy pokrewnych. Nie ma ani jednego gatunku, który by nie wykazywał zmienności geograficznej przynajmniej pod względem jednej cechy.

Przyczyny spliterstwa leżą często w niewystarczającej reprezentatywności materiału użytego do opisu rzekomo nowych gatunków. Zbadano związek podstawowych wskaźników statystycznych charakteryzujących zmienność w sposób ilościowy. Porównano ze sobą próby o różnej masie (N = 5, 10, 25, 50, 100). Przy określaniu zmienności gatunków *Tabanus* L. masa próby nie powinna być mniejsza niż 25 osobników w serii. Przy operowaniu wartościami średnimi nawet mniejsze serie dają charakterystyki podobne do uzyskanych na większym materiale (N = 100).

Porównanie średnich wartości wskaźnika czoła za pomocą metod statystycznych w różnych populacjach lokalnych trzech gatunków pozwoliło ustalić, że przy badaniu statystycznym spotykamy się tu z takimi sytuacjami, że wykształcenie cechy taksonomicznej jest podobne w obrębie całego zasięgu lub też jednorodność materiału widoczna jest tylko na niewielkim obszarze. W innych miejscach spotykamy się ze znacznymi odchyleniami. Porównanie średnich pozwala również wykryć niejednorodność w wykształceniu cechy.

Przeprowadzone porównania między gatunkami bliskimi pod względem systematycznym wskazują, że różnice między poszczególnymi populacjami bywają czasem większe, niż między gatunkami. Porównanie jednocześnie wielu cech przeprowadzone metodą Jentys-Szaferowej pozwoliło stwierdzić, że nawet przy operowaniu zespołem cech taksonomicznych różnice między gatunkami są tej samej wielkości, co różnice między populacjami jednego gatunku.

Przedstawione materiały naświetlają możliwość rozwiązania kwestii związanych z systematyką gatunków *Tabanus* L. na drodze morfologicznej. Wykrycie nawet poważnych luk morfologicznych między dwoma badanymi grupami nie stanowi wystarczającego dowodu ich odrębności. Dowody takie można uzyskać na drodze badań biologicznych.

Gatunki *Tabanus* L. w Europie należą w większości do form panmiktycznych i sympatrycznych. Przypadki takie z punktu widzenia obecnego stanu rozwoju koncepcji gatunku nie powinny nastręczać trudności. Tak w rzeczywistości przedstawia się sytuacja. Trudności jakie spotykamy, leżą nie w braku odrębności gatunków, lecz w braku odpowiednich metod. Przebadanie zmienności *Tabanus* L. pozwoliło stwierdzić, że ani koncepcja politypowa ani monotypowa nie ilustrują poprawnie zmienności gatunków *Tabanus* L.

Przy badaniu różnic międzygatunkowycn u *Tabanus* L. można stosować kryteria łączone. Przedyskutowano zastosowanie wskaźników fenologicznych, ekologicznych i fizjologicznych. Dane uzyskane na tej drodze pozwalają na ocenę wartości różnic zaobserwowanych w trakcie badań morfologicznych.

Na zakończenie autor proponuje następującą treść koncepcji gatunku u *Tabanus* L.:

1) Gatunki *Tabanus* L. istnieją w przyrodzie obiektywnie. Obiektywność ta może i winna być przedmiotem dowodzenia na drodze biologicznej.

2) Zakres zmienności gatunku określonv jest granicami biologicznymi i zależnie oa gatunku może być duży lub mały.

3 i 4) Odrębność gatunków *Tabanus* L. można stwierdzić w oparciu o wykazaną korelację między różnicami biologicznymi a morfologicznymi.

Przedstawiona koncepcja gatunku stanowi próbę rozwinięcia modelu brauerowskiego i adaptowania go do aktualnych zadań systematyki opisowej. Na obecnym etapie polegają one na badaniu i porównywaniu między sobą zmienności wewnątrz i międzypopulacyjnej.