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ON THE SYSTEM OF CLASSIFICATION OF TICKS
OF THE FAMILY ARGASIDAE CAN., 1890

BY

M. V. POSPELOVA-SHTROM

1. Two Classifications of Argasidae.

Twenty years ago a system of ticks of the family of Argasidae was proposed
in the USSR for the first time (M. V. POSPELOVA-SHTROM, 1946, Table 1). Up
to that time, as it is known, it was usual to subdivide this family into two genera,
Argas and Ornithodorus, and in America Otobius and Antricola in addition. The
system has appeared as a result of the many-year study of the morphology of
all then known Argasidae of the world, their biology, ecology, epidemiological
significance, geographical distribution. In the system the family Argasidae was
for the first time divided into 2 subfamilies, Ornithodorinae and Argasinae; three
tribes (Ornithodorini, Otobiini and Argasini) were also created, and the genera
were proposed to be understood in the narrower sense. Besides, the genera Allec-
torobius and Carios, that had been described a long time ago, were restored from
synonyms as well as the genus Alveonasus (P. Schulze) and two American genera
Otobius and Antricola have been adopted. In 1950 the Argasidae subgenera and
subspecies were established for the first time among some genera (M. V. POSPE-
LOVA-SHTROM, 1950). As a result an hierarchy system appeared in which an
attempt was made to reflect natural phylogenetic mutual relationship between
its members.

During recent years the Argasidae were thoroughly studied all over the world.
Many new species were discovered, immature stages were described (N. A. PHI-
and co-workers, 1965; Colas-Belcour and co-workers, 1962 and others). A great

1. From the Entomological Department of the Martsynovsky Institute of Medical Para-
sitology and Tropical Medicine of the USSR Ministry of Public Health (Prof. P. G. SERGIB,
Director of the Institute, Prof. V. P. UKHOVA, Head of the Department). Reported on the
I-st All-Union Acarological Conference in Leningrad on the 22-nd of December, 1966.
2. Nearly a half of species of the family Argasidae of the world fauna known at that time
were examined by us, almost all the others were studied on the basis of literature.

### Table I. — System of classification of the family Argasidae Can., 1890 by Pospelova-Shtrom, 1946.

**Fam. ARGASIDAE** Can., 1890.

1. **Subfam. I. Ornithodorinae**
   - Pospelova-Shtrom, 1946
   - Tr. I. Ornithodorini
     - G. 1. *Ornithodoros*
       - C. L. Koch, 1844
     - G. 2. *Alectorobius*
       - Pocock, 1907
     - G. 3. *Antricola*
       - Cooley et Kohls, 1942
2. **Subfam. II. Argasinae**
   - Trouessart, 1892 pr. part.
   - Pospelova-Shtrom, 1946
   - Tr. II. Otobiini
     - G. 4. *Otobius*
       - Banks, 1912
     - G. 5. *Alveonasus*
       - F. Schulze, 1941
3. **Tr. III. Argasini**
   - Pospelova-Shtrom, 1946
   - G. 6. *Argas*
     - Latreille, 1796
   - G. 7. *Carios*
     - Latreille, 1796
deal of detailed data was described in morphology, anatomy (J. S. Balashov, 1961, 1962, 1963, 1964; Roshi, 1961, 1962, 1963, 1966 and others); in karyology (J. L. Goroshchenko, 1960, 1962, 1965); in biology, ecology, epidemiological significance of Argasidae. It was found that all these data confirm the main concepts of our system, which proves its natural character. The newly described forms find their place in the system requiring only its further expansion and development. A modern expanded variant of our system is under elaboration by us at present.

The system of Argasidae proposed by us has proved to be of use both in theory and practice. So its phylogenetic conceptions made it possible to approach the disclosure of regularities in the origin of various Argasidae groups and their ancient expansion throughout the continents of the world (M. V. PospeLOVA-SHTROM, 1959). The narrower understanding of genera overcame the deadlock that had arisen in connection with the discovery of intermediate forms between the genera Argas and Ornithodoros (see below); the diagnoses of genera became more accurate, which facilitated the identification of Argasidae in practice.

In 1964 Clifford, Kohls, SonenShine, published an article in which they proposed their own classification of Argasidae (Table 2). In this classification they accept our most significant subdivision of the family into 2 subfamilies but they do not use the division of Argasidae into tribes. After Cooley and Kohls (1944) they recognize only 4 genera of Argasidae: Argas, Ornithodoros, Otobius, Antricola. The rest of genera and subgenera recognized by us (except the subgenus Theriodoros of what it is said below) are regarded by them as subgenera, besides they erect 6 additional subgenera for foreign species.

Thus at present there exist two classifications of ticks of the Argasidae family having much in common as well as principal differences between them. Our classification is older by time of origin, but it contains attempts to reflect in a greater rate the natural phylogenetic relationships among the members of the family; the classification of Clifford and co-workers is more schematic. Besides, in our opinion, many conceptions of the foreign system are weak and finally a number of mistakes and distortions were found in the cited data of the Soviet literature, which should be corrected.

The purpose of this article is to promote further development of classification of Argasidae of all the world by means of a critical comparative analysis of both classifications and to draw together the points of view on this problem of the aca-

1. The necessity in erecting the additional genera and subgenera for certain foreign Argasidae was clear to us already at the moment of working out the system of Argasidae (M. V. PospeLOVA-SHTROM, 1953, p. 116). But we were of the opinion that it was more suitable to leave the description of these taxons to acarologists of the countries from which these ticks originate.

2. The simplicity and convenience of practical identification of Argasidae with the use of our system have been confirmed by experience of multi-year training the students of the Central Advanced Training Institute for Doctors and many other persons in the systematics of Argasidae.
rologists of all the countries to a maximum possible degree, which is extremely desirable for the academic and practical utility.

2. Two Schools of Acarologists: Soviet and American.

Each classification of organisms is the result and the top of many-sided studies; therefore the two classifications regarded here reflect the traditions and possibilities of the Soviet and American schools of acarologists.

Table 2. — Classification of the family Argasidae Can., 1890 by Clifford, Kohls, Sonenshine, 1964.

<table>
<thead>
<tr>
<th>Family</th>
<th>Subfamily I. Ornithodorinae Pospelova-Shtrom, 1946.</th>
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<tbody>
<tr>
<td>Genus I. Ornithodoros Koch, 1844.</td>
<td></td>
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<tr>
<td>Subgenus 1. Ornithodoros s. str.</td>
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<tr>
<td>2. Alveonasus Schulze, 1941.</td>
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<tr>
<td>4. Ornamentum Clifford et al., n. subgen.</td>
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<tr>
<td>5. Alatorobius Pocock, 1907.</td>
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<tr>
<td>6. Reticulinasus Schulze, 1941.</td>
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<tr>
<td>7. Subparmatus Clifford et al., n. subgen.</td>
<td></td>
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<tr>
<td>Genus 3. Otobius Banks, 1912.</td>
<td></td>
</tr>
<tr>
<td>Subfamily II. Argasinae (Trouessart, 1892, pro parte), Pospelova-Shtrom, 1946.</td>
<td></td>
</tr>
<tr>
<td>Subgenus 1. Argas s. str.</td>
<td></td>
</tr>
<tr>
<td>3. Carios Latreille, 1796.</td>
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In the USSR a detailed study was carried out in the morphology of the Argasidae. A thorough study of morphology of tick immature stages, especially the study of chetotaxy of the Ixodoidea ticks has a long time ago reached an extensive development in our country (B. I. Pomeranzev, 1947; M. V. Pospelova-Shtrom et al., 1956; N. A. Philipova, 1960 and others). The anatomic and physiological research of the Argasidae is carried out on a large scale in our country (J. S. Balashev, 1957-1965 and others); here it was for the first time that the study in karyology of Argasid ticks was developed (I. I. Sokolov, 1958, J. L. Goroshchenko, 1962, 1965 and others). A deep study in the biology and ecology of the Argasidae was carried out (see the summary in the monograph by M. V. Pospelova-Shtrom, 1953). By using V. N. Beklemishev's concepts on the life schemes
of species (V. N. Beklemishev, 1956)\textsuperscript{1} and widely applying the comparative method of studying the structures of the Argasidae and their biology and ecology the Soviet authors used the only correct analytical approach to the estimation of all peculiarities of these ticks. The comprehension of the natural phenomena in their development is possible only by the use of a comparative method; this method enables us to disclose the trends and mutual relationships in the development of the Argasidae, facilitates the determination of the place of each species of these ticks in the system and sheds light on the phylogenetic relationship between them. The Soviet acarologists work a great deal at the creation of a deeply substantiated natural hierarchy system of ticks belonging to the categories of various taxonomic levels: orders, superfamilies, families (B. I. Pomeranzev, 1947; A. A. Zakvatkin, 1952; V. B. Dubinin, 1956 and others). The analysis of regularities in the origin of the fauna complexes of the Argasidae and the dispersion of these ticks throughout the continents of the world were so far carried out mainly in the USSR (M. V. Pospelova-Shtrom, 1959).

The American acarologists possess the richest collections of the Argasidae ticks not only of their own very rich fauna but also of that of the whole world. They made a detailed descriptions and drawings of the prevalent majority of species of the Argasidae of the world at various stages of their development\textsuperscript{2}, however, not using the comparative method for this purpose. There are excellent works abroad on the anatomy of the Argasidae (Robinson, Davidson, 1913, 1914; Roshdi, 1961, 1962, 1963, 1966 and others); the karyology research of these ticks is only being developed and revise the data by J. L. Goroschenko, which are to the credit of the correctness of the Argasidae system proposed by us (Oliver, 1965, 1966 and others). There are no far going zoogeographic papers on the Argasidae ticks, only reviews on the localities of their disclosure are given (Leeson, 1952, 1953, 1956). In the biological and ecological studies of foreign acarologists quite insufficient use of the comparative method is made either.

As a result the foreign authors do not see the trends in the phylogenetic development of the Argasidae ticks, they have the tendency to consider these ticks statically as something settled, separately from each other and from their surroundings. They make no attempt to approach the analysis of the structure of the Argasidae ticks (for example, their integument) as well as their mode of life, considering...

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\textsuperscript{1} "The main point of comparison in ecology is the life scheme of the species. The life scheme of a species is the whole complex of all relations of this species with all the elements of the conditions of its environment including the complex of adaptations of the species to the complex of conditions of its habitats". "... the life scheme is the mode with which each species solves the main problem of life: self preservation and reproduction". (V. N. Beklemishev, 1956, p. 1768).

\textsuperscript{2} However, even in these works there are some defects. So, in articles by one and the same authors (Clifford, Kohls, Sonenshine) published in different years one may see the non-coincidence of the number of setae of the body indicated for the larvae of one and the same species (e.g. Otobius megnini). The characters of larvae in the key to determination are not always exact (e.g. by Sonenshine, Clifford and Kohls, 1966, p. 93).
that the characters of the Argasidae ticks are simply multiform and not trying to comprehend this variety and to find any regularities or relationships in it. Besides, the foreign authors are very much bound by the adherence to the old traditions and authorities. All this prevented them from creating the system of the Argasidae ticks at the level that is dictated by the whole complex of the diverse facts being accumulated by the present time.

3. Two Ways, Two Attempts to Approach the Systematization of the Argasidae Ticks.

The system of the Argasidae ticks proposed by us (Table 1) is clearly demonstrating our conceptions regarding the phylogenetic affinity and the ways of development of the members of the family. The creation of systems of such a type are inevitably not devoid of the hypothetic character, but any hypothesis substantiated even in the slightest degree is permissible and contributes to the progress pointing to the ways and giving a basis for further investigations. Reflecting the affinities between its members the system proposed by us makes it possible to correctly foresee yet unknown features of the species so far little known with only the aid of their position in it. 1

In the classification proposed by CLIFFORD and co-workers (Table 2) the supposed mutual relationships of the Argasidae ticks are demonstrated only for groups of species by means of placing them in corresponding subgenera. Species within subgenera are placed in the alphabetic order. 2 In placing the subgenera within the genera no attempts were made to show the ideas by authors on the affinities and trends in the development of individual branches of the genus.

In two subsequent papers the same group of writers describes larvae of the Ornithodoros of the Western hemisphere (KOHLS, SONENSHINE, CLIFFORD, 1965) and of the Eastern one (SONENSHINE, CLIFFORD, KOHLS, 1963) 3. And here also the species are placed in the alphabetic order. Hardly is this order suitable since following it the most closely related species (i.e. turicata and parkeri, alactagalis and nereensis), and sometimes probably even subspecies of the same species are

1. For instance, we easily identify the American species cooleyi as a member of the genus Alveonasus and in connection with this we foresee confidently its yet non-studied biological characters, these conceptions having already been confirmed by the indirect data (see below).

2. Excluding the genus Ornithodoros where they for unknown reason are placed arbitrarily.

3. Even the method itself of carrying out the series of the work in question is hardly suitable: the classification of the Argasidae family was given in 1964 whereas the detailed investigations in the morphology of larvae of its members which evidently ought to have served for the substantiation of the system were made later in 1965 and 1966. Naturally in this series of work there is already some lack of coordination. Thus, for instance, in the paper dealing with the classification of the Argasidae ticks (1964, p. 433) it is said that the larva of the subgenus Ornamentum has no small spines on the palpal articles, but in the paper on the larvae of the Ornithodoros ticks of the Western hemisphere (1965, p. 351) it is mentioned that it has small spines on the dorsal surface of the palpal article I, and these spines are shown in Fig. 38. This feature is one of the most significant for the identification of the systematic position of the larvae of the Ornithodorinae ticks.
separated from each other and scattered among the others sometimes very distant ones. With the help of such papers one can only recognize a species using a corresponding key to the identification and find its description by alphabet; but it is not enough since it is impossible to get any idea about the position of the species among others within the subgenus, one cannot observe the relationships of the species with the other members of the subgenus, which exist in the structure as well as in the biology, ecology and generally also in the epidemiological characters.

The method of the impersonal alphabetic principle of cataloguing the species accepted by Clifford and his co-workers is probably inevitable only in groups containing a very large number of species (i.e. some insects); as for the Argasidae ticks it is not desirable and is even lagging behind the level of the old monograph of the Argasidae ticks by Nuttall, Warburton et al, 1908, in which attempts were already made to show their mutual relationships by means of the position of species. The same is seen in the monograph on the Argasidae ticks of America by Cooley and Kohls, 1944.

Thus, the method of constructing the classification in the series of papers on the problem in question by the foreign authors considerably reduces the quality of this classification and in a certain sense limits its application, whereas the system of the Argasidae ticks proposed by us is more natural and therefore more useful for the theory and practice.

4. Subfamilies, Tribes, Genera and Subgenera.

Our subdivision of the family Argasidae into two subfamilies does not give rise to any doubt to anybody and it is unconditionally assumed by Clifford and co-workers (Clifford et al, 1964, p. 430). But we and these acarologists already are of different opinion on the place of groups of Argasidae ticks in the subfamilies: in the USSR the Alveonasus and Ogadenus are placed together in the tribe Otobiini erected by us while foreign acarologists attribute the Alveonasus to the subfamily Ornithodorinae but Ogadenus following Hoogstraal (1956) to the Argasinae (Clifford et al, 1964, p. 430), i.e. they separate the co-members — in our opinion — of the same tribe (Otobiini) into two different subfamilies. For details see below.

It should be noticed that the subfamilies of Argasidae family are not easy to be characterized distinctly. This in itself is not a hindrance for recognizing the subfamilies. In our opinion the best character for distinguishing subfamilies is the one proposed by us and also used by Clifford and co-workers, the character of the chiefly radial or of non-radial pattern of disks; it corresponds to the structure of the dorsoventral muscles of the ticks. But very characteristic is also the type of the branching of the stomach, which is not used by Clifford and his co-workers. The flattened body margin is a rather stable feature in the subfamily of Argasinae; but it can be more or less developed also in certain species of Örni-
thodorinae (stageri, dunni, and according to our classification also among species of the subgenera Ogadenus and Aviaogadenus n/sg). Therefore CLIFFORD and his co-workers make a wrong statement in their diagnosis of the subfamily Ornithodorinae that the body margin of these ticks is “... never distinctly flattened”... (p. 430). The features of the presence of a sutural line and a body margin marked by a regular pattern of striations or cells have exceptions among the Argasinae too (the subgenus Chiropterargas), what is insufficiently stressed in the diagnosis of the subfamily Argasinae by CLIFFORD and co-workers. On the other hand, with some of the Ornithodorinae the structure of the integument of the body margin imitates the structure characteristic of the Argasinae (with the Alveonasus fooleyi and with the subgenera Ogadenus and Aviaogadenus). It should be mentioned by all means in the diagnosis of the subfamily Ornithodorinae, for this character already many times confused some authors. Thus the diagnoses of even the most important taxonomic category — such as subfamilies — in the classification by CLIFFORD and co-workers contain considerable defects.

As it has been already mentioned, tribes are not used in the foreign classification of Argasidae ticks under consideration. But in our opinion tribes are a very useful intermediate taxonomic category, which shows the close relations of groups of genera and the general trends of their development.

CLIFFORD and co-workers do not agree with our placing the genera Alveonasus and Otobius in the same Otobiini tribe. These authors consider that we erected the Otobiini tribe on the basis of characters of minor importance and ignored more fundamental features in the structure of ticks (“In doing so she¹ has emphasized characters of minor importance while ignoring many more fundamental features, that show that Alveonasus is more closely related to the genus Ornithodoros”, p. 430). In the course of their article the authors of the classification in question repeat four times (pp. 430, 432, 435) the assertion of the greater, in their opinion, affinity of the Alveonasus with the “Ornithodoros” (in the broad sense) than with the Otobius; but they use only proofless statements and provide no facts in the confirmation of their opinion.

Actually all the members of our tribe Otobiini differ distinctly from the species of the tribe Ornithodorini by a peculiar integument furnished with depressions and wrinkles — or depressions and granules between them (instead of the mammilliated one with the Ornithodorini) and the absence of the continuous ventral grooves. These differences are deeply principal and must be of the ancient origin. The extensive study of some representatives of the tribe Otobiini during the recent years showed in addition the peculiar branching of their alimentary canal (that of the Alveonasus by J. S. BALASHOV, 1961 and that of the Ogadenus by ROSHDI, 1966). The larvae of the Alveonasus proved to be more similar to those of the Otobius, than of the other Argasidae ticks, the nymphs of younger stages of the

¹. It refers to the placing of the genera Alveonasus and Otobius in the same tribe by M. V. POSPELOVA-SHTROM.
Alveonasus and Otobius have an integument with spines and also have some similarity in the shape of the body (compare fig. 276 by N. A. Philipova, 1966, and fig. 7 by Cooley and Kohls, 1944).

The main part of the members of the Otobiini tribe has in addition a common peculiar tendency in their life schemes that leads to the deviation from the burrow way of life of their predecessors. This is achieved by means of transition to the permanent parasitism on big vagrant animals. The ways to realize this task are somewhat different with various species of the tribe Otobiini; steps at which they are at present on the way to solve this common task are different too.

Other representatives of the Otobiini tribe — the species peusi and perengueyi (our new subgenus Aviaogadenus) look like a link connecting the subfamilies Ornithodorinae and Argasinae, as in morphology they are closely related to the Ogadenus brumpti but in their biology they are similar to the Argasinae in parasitising on birds (swallows) and living in their nests. We consider this way to be also progressive. The subfamily Ornithodorinae seems to us to be more primitive than the subfamily Argasinae as it is characterized by more primitive structure of the alimentary canal and the pattern of disks, as well as by a great number of nymphal stages and the initial mode of life in burrows usual among the Ornithodorinae (see also N. A. Philipova, 1966, p. 69).

Clifford and co-workers do not see any regularities in the biological features of the Argasidae ticks of the tribe Otobiini, attribute to them the uniform burrow mode of life and explain the deviations from this simply by the adaptation to various

1. As far as it is known, there are representatives of the tribe Otobiini still leading burrow life like their ancestors (i.e. Alveonasus eboris); but they already feed chiefly on bigger vertebrates. According to some data, Alveonasus fooliei and Alveonasus acinus, living in large shelters, parasitize on big stray visitors of the shelters. Ogadenus brumpti inhabiting caves and other large shelters often is situated in dust outside the shelters at their entrance and attack the approaching prey in no way connected with the shelter (man, big vagrant animals). The larvae of the studied representatives of the Otobiini tribe feed for a long time, sometimes for many days; nymphs often require additional feeding at the same stage (in experimental conditions). When feeding on small laboratory animals a number of species (Alveonasus fooliei, Ogadenus brumpti, as well as the Iranian Alveonasus "canestrinii", in natural conditions closely associated with sheep and goats) sometimes have a somewhat increased number of nymphal stages and the adults become dwarfs, which shows that the host did not fit for the tick (J. S. Balashov, 1961). With Alveonasus "lahorensis" (according to the terminology of Clifford and co-workers, 1964) its immature stages have already completely come over to the one-host parasitism on big vagrant mammals (sheep, goats, cattle, camels). This species even acquired similarity to the Ixodidae ticks passing, as they do, through a certain final development in the process of feeding their immature stages (J. S. Balashov, 1961). Only at the adult stage this species continues to keep to closed shelters and leads the life characteristic to its ancestors-burrow blood-suckers watching their prey. It feeds however on big animals. In laboratory conditions of rearing on small animals this tick develops worse and often leaves its host not finishing its development. The species of the genus Otobius have still further departed from the hidden burrow mode of life. The larva and nymphs of the Otobius lagophilus feed on the hare-like animals continuously for a long time whereas the adults lay eggs without feeding. The female of Otobius magnum lays eggs without having any food under the bark of trees against which vagrant ungulates come to rub themselves and so are subjected to attack by the tick larvae, which begin developing further by means of one-host way in the ears of the animals.
hosts (p. 431-432). The presence of intermediate features between the subfamilies Argasinae and Ornithodorinae is very characteristic of the representatives of the tribe Otobiini and pick them out from all the other Ornithodorinae. This is reflected in our system and was also noticed by Clifford and co-workers (pp. 430, 432).

As a result of all this we believe that the erection of our tribes was fairly well founded and necessary, and the placing of genera into different tribes was rightful.

Particularly significant difference of opinions between the authors of the two classifications is to be found in the problem of genera and subgenera. We consider as elementary that these categories, being steps of a hierarchy system, should be characterized by the features of different levels. To recognize a taxon to be a genus it is necessary that it should possess features [1] of a more general taxonomic significance as compared with the subgeneric ones. For instance, for adults it is: the type of the shape of the body, its thick or flattened margin, type of the body integument, type of the marginal integument and sutural line, the presence of some or other grooves, cheeks, hood, camerostome, some essencial anatomic differences; for larvae it is: the number and pattern of the arrangement of more constant setae, the presence or absence of respiratory apparatus, the principle of the structure of the hypostome, and in addition the type of the life scheme of species-members of the genus, a certain group of hosts, sometimes inactivity of some developmental stages, and at last, the ability or inability to transmit some causal organisms of diseases and the way of doing it etc...

On the contrary, the subgenera should have characters of more particular significance, for instance, some small differences in the structure of the entire integument or a part of it, shape of the dorsal process of the chelicerae, cheeks, grooves, sometimes in details of the structure of the rostrum, hypostome, Haller's organ (e.g. the presence of a bottle-shaped seta); with the larvae, the number and the pattern of the arrangement of less constant setae, sometimes the shape of the dorsal plate, basis capituli, hypostome, as well as the preference of a certain hosts, the association with certain causal organisms of diseases (e.g. with different groups of species of spirochaetes) and others. Due to this the number of genera and subgenera recognized cannot be set up beforehand, but it must be determined by what we find in nature. With the increase and deepening of our knowledge of the group it may be changed.

In contrast to it foreign acarologists, as far as one can judge from letters and statements of Dr. Hoogstraal when we met in Moscow, are prone to consider the recognition of a category for a genus or a subgenus to be a matter of taste. Clifford and co-workers cite as their credo Hoogstraal's opinion regarding the uselessness of recognition of a large number of genera (Clifford et al., 1964, p. 430) [2].

1. We avoid making use of the karyological features for the time being as insufficiently studied so far, though according to the data by J. L. Goroshchenko (1962, 1966), they confirm quite well the majority of concepts of the system proposed by us.

2. "Little "practical" or academic utility can be gained from tampering with present concepts of most tick genera." (Hoogstraal, 1957, p. 544).
Justifying his opinion, Hoogstraal refers to the monograph by Nuttall, Warburton and co-workers (1908). In this monograph only two genera were recognized: Argas and Ornithodoros and both with some reserve. But at that time only a little more than 20 species of Argasidae ticks were known (as compared with more than a 100 known at present), these ticks being poorly studied, and their larval and nymphal stages being generally unknown at all. Naturally, this monograph being excellent at its time, has considerably grown out of data during the past nearly 60 years, and Hoogstraal's tendency to stick to its concepts is rather unconvincing. The great variety of the forms of the Argasidae ticks known at the present time absolutely exceeds the old limits, the old genera ceased to conform to today's knowledge on the Argasidae ticks, and became artificial categories. Foreign authors being tied by traditions make attempts to preserve these categories and at the same time put in good order the whole variety of Argasidae ticks known at present. Thus Hoogstraal, in regard to the subfamily Argasinae, finds a way out in placing the variety of forms of these ticks in different subgenera. The same way is followed in their classification by Clifford and co-workers extending Hoogstraal's conception on all Argasidae ticks: they already subdivide Argasidae ticks into 13 subgenera.

But the subdivision of all the Argasidae ticks, known at present, which have various degrees of similarity or difference exclusively by subgenera brings Clifford and co-workers to the extreme non-equivalence of their subgenera, the subordination of taxonomic categories is doubtlessly violated here. Thus, Alveonasus regarded by them as a subgenus of the genus "Ornithodoros" (in a broad sense) undoubtedly represents a well established independent genus, besides belonging to another tribe than "Ornithodoros" does (see above), which means that the difference between these groups of the Argasidae ticks is at the supergeneric level. The Carios is considered by these authors as a subgenus of the genus Argas; but its differences-morphological, anatomical (see Rosidi, 1961, 1962), biological are so great that it is quite impossible not to consider it as an independent genus. Side by side with this, in the same genus Argas in the classification by Clifford and co-workers the subgenus Persicargas is placed, which differs from the typical subgenus Argas by minor morphological characters, practically almost only by the absence of a bottle-shaped seta in the Haller's organ (Kaiser, Hoogstraal, Kohls, 1964). Whereas the differences of Antricola which is recognised by Clifford and co-workers as a genus can hardly be regarded as anything more than the differences of some of their subgenera (e.g. the subgenus Subparmatus). The matter is obviously in the tradition to recognize Antricola as a genus. Our subgenus The-

1. "The genera of Ixodoidae have, in general, become well established following the monumental work of Nuttall and Warburton (1908 to 1924), species in order are few, and individual genera are quite homogeneous." (Hoogstraal, 1957, p. 544).
2. "Phylogenetic trends among ticks, especially in the genus Argas, are lucidly demonstrated on a subgeneric level." (Hoogstraal, 1957, p. 544).
3. "... we prefer to recognize only 4 genera... and to demonstrate the relationships of species groups at the subgeneric level..." (Clifford et al, 1964, p. 430).
riodoros is rejected by these authors as one based, in their opinion, on the minor features rather of the species level ("... upon very minor differences which seem to us to be more suitable for differentiation of species", CLIFFORD et al, 1964, p. 433). Actually this subgenus is characterized by good morphological differences at adult and larval stages (see M. V. POSPELOVA-SHTROM, 1953, p. 127, and N. A. PHILIPOVA, 1966, pp. 196-197), it has an original group of hosts and consists of a whole series of species but not only of 2 species as it is written by CLIFFORD and co-workers; besides, this subgenus has a definite broad geographical area. Therefore it was hardly necessary to reject this subgenus as one insufficiently grounded, if such a subgenus as Persicargas is accepted.

The genus "Ornithodoros" according to the authors of the foreign classification of the Argasidae ticks in question is treated extremely extensively (see below) and includes, in our opinion, an entire series of independent genera, one of which (Alveonasus), as it was already mentioned, we include even in another tribe. We believe that the genus Argas is also considered by them too extensively; it includes taxons of different levels — genera and subgenera — regarded at one and the same subgeneric level and one of its "subgenera" Ogadenus is considered by us, as it was already said, more suitable to be placed in the tribe Otobiini of the subfamily Ornithodorinae.

Thus, the taxonomic categories — genus and subgenus — are used by CLIFFORD and co-workers arbitrarily to a certain degree, the taxonomic levels of the features used for both of them are of mixed character and of unequal value; the authors have tendencies to keep to the small number of genera set up beforehand at the expense of the increasing number of subgenera. This is the reason why the classification discussed is not natural enough and not sufficiently suitable. And it seems to us that despite HOOGSTRAAL’s opinion it is not our treatment of genera and subgenera of the Argasidae ticks, which obscures natural relationships among groups of the Argasidae ticks, but just the way suggested by him to consider the diverse superspecies taxons at one and the same subgeneric levels. This is dealt with in the next section.

5. Deadlock Caused by Discovery of Forms of Argasidae Ticks Intermediate between Genera Argas and Ornithodoros; Advantages of Narrower Understanding of Genera of Argasidae Ticks.

The discovery of the intermediate forms between previously well differentiated genera Argas and Ornithodoros made a long time ago brought the systematics of the Argasidae ticks into a deadlock and was the reason of the appearance of incredible confusion in it. Failing to find any character for good differentiation of

1. “Previous proposals to subdivide the genus Argas into several independent genera obscure the obvious natural relationships among members of this group”. (HOOGSTRAAL, 1957, p. 544, spacing is ours).
these genera and later concluding that it was impossible to differentiate their larvae too (Sonenshine, Clifford, Kohls's opinion, 1962, p. 206), the authors practiced arbitrary reference of species furnished with intermediate characters sometimes to *Argas*, sometimes to *Ornithodoros*, sometimes back again, the characters being often used suitable for characterizing only species available though they did not fit other species of this group (flattened margin of the body, presence or absence of sutural line etc\(^1\)). All this only aggravated the confusion.

Already Neumann (1908) and Nuttall and Warburton and co-workers (1908) pondered over the necessity to unite the genera *Argas* and *Ornithodoros* in one and the same genus; Bedford (1932) did this; but up to now the matter continues to be debated (Morel and Vassiliades, 1965, Hoogstraal and Kohls, 1965 and others). We believe that it is hardly possible to speak seriously about the unification of all the Argasidae ticks in one and the same genus (single-genus concept) at present when the whole variety of these ticks became known. As early as 1946 we proposed, on the contrary, a narrower conception of genera and the erecting of independent genera for the aberrant formes. In this way the deadlock that arose in connection with the discovery of Nuttaliella namaqua — the species being intermediate between the Argasidae and Ixodidae ticks was overcome: the establishment of an independent family Nuttaliellidae for it made all the three families clearly differentiated. The same takes place at the generic level: the placing of the intermediate forms into independent genera (with subgenera) made all the genera of the subfamily Ornithodorinae clear enough and liable to fairly good diagnosis\(^2\).

1. Neumann described *Ornithodoros aequalis* in 1901, and in 1908 he transferred this species into the genus *Argas* because of its closeness to *Argas brumpti*. Warburton (1932) pointed out that *Ornithodoros franchinii* having the likeness of a partial sutural line and pattern of striations on the body margin is closely related in its morphology (and in our opinion in biology too) to *Argas brumpti* but simultaneously also to *Ornithodoros lahorensis* and *Orn. tari­catu*; therefore he placed *Argas brumpti* into the genus *Ornithodoros*. However, in doing so he aggravated the situation still more, as in this way he made away with one of the best features for differentiating the genera *Argas* and *Ornithodoros* — the presence or the absence of a sutural line and a pattern of striations on the body margin. Bedford (1932) by uniting the genera *Argas* and *Ornithodoros* in one and the same genus *Argas* placed his *Ornithodoros perengueyi* into the genus *Argas*. P. Schülze (1943) placed this species together with his new species *peusi* into the genus *Alveonasus* erected by him. Cooley and Kohls (1944) finding a flattened margin of the body in American species *Ornithodoros stageri* and *dunni* pointed out that in the conditions of America the presence or the absence of the sutural line is the best character differentiating *Argas* and *Ornithodoros*. But working with the African Argasidae ticks, Hoogstraal found the absence of a sutural line and a pattern of striations or cells on the body margin in the subgenus *Chiroptarargas* of the genus *Argas*; therefore he, on the contrary, considers a flattened body margin to be the best differing character of the genus *Argas*. On this ground he placed the species *brumpti* back to the genus *Argas*. Clifford and co-workers follow Hoogstraal in it and already quite unsuitably remove *perengueyi* and *peusi*, doubtlessly very closely related to it, from *brumpti*, though they noticed the closeness of all of these species (Clifford et al, 1964, p. 432). Thus, very closely related species found themselves in the American system in different subgenera and even genera: *Argas (Ogadenus) brumpti* and *Ornithodoros (Alveonasus) perengueyi* and *peusi*.

2. Thus, our narrow conception of genera and subgenera of the Argasidae ticks was forced on us by definite weighty reasons and considerations but it was not a result of our utilizing
Besides it was found that the intermediate species in question have much in common and they are well accommodated in the tribe Otobiini. This indicates the natural character of our subdivision of the subfamily Ornithodorinae. In the long run it seems to us that foreign acarologists are mistaken in their underestimation of our conception of a narrower understanding of the genera of Argasidae ticks and lose very much because of it.

The grounds for the genera and subgenera of Argasidae ticks recognized by us will be given elsewhere. Here only some critical remarks on certain genera and subgenera accepted in the classification of Clifford and co-workers has been given.


As it was already mentioned, the genus *Ornithodoros* in the conception of Clifford and co-workers is a clearly mixed one including many groups of the Argasidae ticks of different taxonomic categories, sometimes very distant from each other. This "genus" in fact duplicates the subfamily Ornithodorinae excluding only the genera *Otobius* and *Antricola*. In connection with this it is extremely difficult to give a good characteristics of this "genus" and Clifford and co-workers give for the adults only 4 sentences instead of the diagnosis for this "genus", which serve for differentiating the genera *Otobius* and *Antricola* from it rather than characterize the genus. But as it seems to us the authors did not succeed in this too because two of four of their sentences contain reservations to a considerable degree depreciating them ("more or less", "usually"), and the sentence of the third sentence ("Nymphal integument resembles that of adults", p. 430) is not correct, for the integument of younger nymphs of *Alveonasus* (included into the "genus" *Ornithodoros* as a subgenus) absolutely differs from that of adults. The diagnosis of the larvae is altogether bad. The characters given in four of five sentences of the larval diagnosis contain reservations or exceptions, and the presence of claws on tarsi, about which it is said in the fifth sentence ("Tarsi with claws", p. 431) is characteristic of all Argasidae ticks except larvae of some but not all species of the genus *Antricola*. That is why this feature is not suitable for differentiating the genus *Antricola* either.

In the diagnosis of larvae the best characters, e.g. the number of setae on the dorsal and ventral surfaces of the body, are quite correctly used. But the range in the number of setae for larvae of this too extensively understood genus is too wide, close to the extreme one for the Argasidae ticks: 13-50 pairs of dorsal and 7-9 pairs of ventral ones. Therefore in this case these characters have nothing typical for the genus. But in addition the reservations indicate that the number limited material (that in itself is not true to the facts) as it was written about by Clifford and co-workers: "... their concepts are based mainly on the species that occur in the USSR and thus, the limits placed on the various categories, especially the subgenera, tend to be too narrow" (Clifford et al, 1964, p. 430).
of setae of the larva of the subgenus Ornithodoros i.e. the typical subgenus of the genus does not correspond even these limits, being essential less : 7-9 pairs of dorsal setae (instead of 13-50 pairs) and 5 pairs of ventral ones (instead of 7-9) ! One may ask, if it is permissible that the typical subgenus of the genus should not correspond to the limits of the genus in its main characters? Obviously not, and hence we correctly excluded the subgenus Ornithodoros from the "genus Ornithodoros" in the broad sense, already in 1946. But together with the subgenus Ornithodoros its long ago established type, Ornithodoros savignyi, is to be excluded in this way too and so by the rule of priority the generic name "Ornithodoros" that was first proposed for the species savignyi (Koch, 1844) can by no means be applied to the "genus Ornithodoros" in the broad sense, as Clifford and co-workers understand it. And is it not the reason why these authors avoided designating the type of their "genus Ornithodoros" (in the broad sense) while for all the rest genera and subgenera the types were pointed out by them (including the subgenus Ornithodoros)?

The exclusion of a very aberrant group Ornithodoros (in the narrow sense) from the "genus Ornithodoros" (in the broad sense) slightly facilitates the characteristic of this "genus", but this genus will become clear enough only after the exclusion from it of some other distinctly different groups of the Argasidae ticks too. This will be dealt with in another paper.

The "subgenus Ornithodoros" of Clifford and co-workers (in our opinion it is a genus) is characterized satisfactorily though this characteristic could be considerably supplemented and improved. Out of two reservations of the diagnosis of Clifford and co-workers the second one may be excluded, since it is given in connection with the erroneous placing into this subgenus of the species procaviae definitely belonging to an other subgenus.


Reasons were given by us above why we do not agree with the opinion regarding this group of species as a subgenus of the genus Ornithodoros and why we consider more suitable to recognize the group as a separate genus of the tribe Oto-bini. The list of characters supporting our point of view can be considerably enlarged (see, for instance, N. A. Philpova, 1966, J.S. Balashov, 1963, J. L. Goroshchenko, 1962 and others). In recent years even many foreign authors raise the question regarding the necessity of revision of the taxonomic significance of the group under consideration (Theodor and Costa, 1960, Colas-Belcourt et Rageau, 1962, Morel et Vassiliades, 1965).

The characteristics proposed by Clifford and co-workers for adult ticks of the "subgenus" (according to their conception) Alveonasus in one essential point is not correct: protuberances on tarsi of these ticks are not "usually absent" (as they say on p. 431) but, on the contrary, are very peculiar of the majority of
species and are present also in the type of the "subgenus". The characteristics of larvae is rather vague, contains reservations, the number and the shape of setae pointed are greatly variable. This indicates to the heterogenous character of the group and the desirability of recognizing some independent taxons within it.

CLIFFORD and co-workers evidently not sufficiently well understood this group of the Argasidae ticks, for they could not determine the position in the classification of *Alveonasus cooleyi* — the proper representative of the group in question — a co-member of the American fauna: they placed it in the group "Other species" about which it is said: "It is not possible to assign these species with certainty to any of the previously described subgenera" (CLIFFORD et al., 1964, p. 435). But to assign without any doubt the species *cooleyi* to this genus and subgenus it is enough only to look at the excellent pictures and photos of this species in the monograph by COOLEY and KOHLS (1944), not to mention its description given by these authors, which completely coincides with the diagnosis of the representatives of *Alveonasus*. Besides, morphological features of the older nymph of the American species *cooleyi* are similar to those of *Alveonasus "lahorensis"* (in the conception of CLIFFORD and co-workers). Finally, the very fact of the discovery of the *cooleyi* nymph in a shipment of skins of some fur-bearing animals corresponds to the frequent finding of nymphs of *Alveonasus "lahorensis"* in the shipments of sheep skins, which is explained by a long continuous parasitism of this tick in immature stages on big mammals. Evidently the American *cooleyi* has the same life scheme so peculiar to the genus *Alveonasus*.

8. Some Other Genera and Subgenera.

A new "subgenus" of CLIFFORD and co-workers, *Ornamentum*, has good enough characteristic features and we foresaw the need of its erection in an independent genus or subgenus. Some essential characters of its adults and larvae suit the tribe Ornithodorini others tend towards the tribe Otobiini. Along with this it also has essential peculiar morphological and biological features and probably it would be better to consider it as an independent genus connecting the tribes Ornithodorini and Otobiini.

The "subgenus" *Alectorobius* of CLIFFORD and co-workers evidently includes some independent taxonomic categories by reason of which its diagnosis is vague and contains many reservations. This subgenus (in somewhat narrower sense) was first established by us (M. V. POSPELOVA-SHTROM, 1950, p. 55); CLIFFORD and co-workers evidently believe that it was they who were the first to establish it.\(^1\)

Our subgenus *Pavlovskyella* is adopted in the classification under consideration

\(^1\) "A study of the external morphology of the larvae of the Argasidae supports the concept of a group of related species resembling *O. talaje* for which the name *Alectorobius* is adopted at the subgeneric level" (CLIFFORD et al., 1964, p. 434).
also too extensively. It includes, for instance, as a synonym, our subgenus *The-riodoros* with what one cannot agree (see above). Due to all of it the diagnosis proved to be vague and having reservations. Besides, it is pointed out there, that these ticks usually have no cheek whereas they are found both in the type of the subgenus (*tholozani*) and in many other representatives of this subgenus.

In the characteristics of species *rudis* and *sparnus* assigned to the category “Other species” i.e. to an obscure subgeneric position the presence or absence of short spines on the dorsal surface of palpal article I of larvae and the presence of reticulation or its absence in their Haller’s organ were omitted (CLIFFORD et al., 1964, p. 435). The same defect can also be found in the article on the larvae of Ornithodorinae ticks of the Western hemisphere (KOHLS, SONENSHINE, CLIFFORD, 1965, pp. 359, 360). But these characters (just as some others, in our opinion) might be of help to determine the assignment of these species to a certain subgenus.

9. Some Other Defects of the Work by CLIFFORD and Co-Workers Devoted to the Classification of Argasidae Ticks.

The work under consideration, as it was already mentioned, also contains some other omissions and distortions of the data of the Soviet authors. Thus, on page 430 the use of 9 genera of Argasidae ticks was ascribed to M. V. POSPELOVA-SHTROM, whereas she used only 7 (see Table 1). On page 433 it is said that the larva of the species *cholodkovskyi* was unknown, but it was drawn in Fig. 56-57 and briefly described on page 170 in the monograph by M. V. POSPELOVA-SHTROM (1953). On page 429 of the paper by CLIFFORD and co-workers it is written: "In 1953, POSPELOVA-SHTROM published a paper on ticks of the genus *Ornitho- doros*...", while it is a monograph, as it is well known, dealing with not only the genus *Ornithodoros* but covering the whole subfamily Ornithodorinae and there is expressed just a protest in it against the too broad a conception of the genus *Ornithodoros*. In bibliography included in the paper by CLIFFORD and co-workers the monograph of M. V. POSPELOVA-SHTROM is entitled: "Ornithodorini ticks and the epidemiological significance" (CLIFFORD et al., 1964, p. 436, underlining is ours), i.e. to begin with, an error was made obscuring the meaning of the title of the book ("the" instead of "their") and, on the other hand, it was pointed out that the book deals only with the ticks of the tribe Ornithodorini, but not with the whole subfamily Ornithodorinae. Unfortunately, these bibliographic errors have been already picked up abroad and the monography by M. V. POSPELOVA-SHTROM (1953) is cited under an incorrect title, for instance, by cytologists (OLIVER, 1966).

There are also some other less important errors in the paper in question.
SUMMARY.

The system of the ticks of the family Argasidae proposed by us 20 years ago (M. V. Pospelova-Shtrom, 1946, 1953) has passed a thorough and extensive check-up by now, all its major conceptions having attained weighty support. This manifests of the natural character of this system. All the newly described forms of the Argasidae ticks find their place in it requiring only its further extension and development, which is being done by us at present.

The phylogenetic concepts of our system throw light on the mutual relationships of the Argasidae ticks and facilitate the construction of theoretical conceptions for instance about the formation of the fauna complexes of the Argasidae and about the dispersion of these ticks over the continents in the remote past. The narrower conception of genera than one, which was adopted formerly, proposed by us proved to be suitable because it overcame the deadlock arisen in the systematics of the Argasidae ticks in connection with the discovery of forms being intermediate between the genera Argas and Ornithodoros. At the same time it provided a better characteristics of genera and subgenera of the Argasidae ticks, which considerably facilitates the identification of these ticks in practice.

In their classification of Argasidae ticks Clifford, Kohls and Sonenshine (1964) accepted the subdivision of the family Argasidae, proposed by us, into two subfamilies (Ornithodorinae and Argasinae), as well as almost all of the genera and subgenera adopted by us (except the subgenus Theriodorus) but all of them were placed at the same subgeneric level. Several new subgenera were erected in addition. The grouping of genera into tribes, suggested by us, which clearly shows our ideas about the mutual relations and trends in the evolution of the Argasidae ticks, was not taken by these authors into account.

In the classification by Clifford and co-workers the phylogenetic relationships among the Argasidae ticks are designated only by means of distributing the species among the subgenera. The majority of genera is understood too extensively, the genera include remote groups of the Argasidae ticks, due to which the diagnoses of these genera are extremely vague, not exact and not good enough for practical use. The subgenera present groups of different taxonomic category because of which the subgenera are not equivalent (e.g. the subgenera Alveonasus and Persicargas). The species within the subgenera are placed in the alphabetic order and in this way the evidently closely related species are often disrupted in the list.

In the long run it seems to us that the system of the Argasidae ticks, proposed by us, advantageously differs from the classification of these ticks by Clifford and co-workers, that appeared later, by its greater validity and natural character and therefore it may evidently better meet the requirements of the theory and practice.

In the paper under consideration by Clifford and co-workers (1964) a number of omissions and distortions of the data of the Soviet authors were made that is to be corrected.

RÉSUMÉ.

Le système des tiques de la famille des Argasidae qui a été proposé par nous il y a 20 ans (M. V. Pospelova-Shtrom, 1946, 1953), a été l’objet d’une vérification approfondie et étendue, et toutes ses principales conceptions ont trouvé un sérieux appui. Ceci démontre le caractère naturel de ce système. Toutes les formes d’Argasidae récemment décrites trouvent leur place dans celui-ci, requérant simplement son extension et son développement futur, ce que nous entreprenons dès à présent.
Les concepts phylogénétiques de notre système mettent en lumière les rapports mutuels des Argasidae et facilitent l’établissement de conceptions théoriques, par exemple sur la formation de complexes dans la faune parmi les Argasidae, sur l’histoire de la formation de ces complexes et sur la dispersion des tiques sur les continents du monde entier. La conception générique plus étroite telle que nous l’avons proposée dès le début s’est révélée fructueuse parce qu’elle a surmonté la situation inextricable qui a pris naissance dans la systématic des Argasidae au moment de la découverte de formes intermédiaires entre les genres *Argas* et *Ornithodoros*. En même temps elle a fourni de meilleurs caractères des genres et des sous-genres d’Argasidae, ce qui facilite considérablement l’identification de ces tiques dans la pratique.

Dans leur classification des Argasidae CLIFFORD, KOHLS et SONENSHINE (1964) ont accepté la subdivision de la famille des Argasidae, proposée par nous, en deux sous-familles (Ornithodorinae et Argasinae), ainsi que presque tous les genres et sous-genres adoptés par nous (à l’exception du sous-genre *Theriodoros*) mais tous ont été placés au même niveau subgénérique. Plusieurs nouveaux sous-genres ont été ajoutés. Le groupement des genres en tribus, suggéré par nous, qui montre clairement nos idées sur les relations mutuelles et les tendances dans l’évolution des Argasidae, n’a pas été pris en considération par ces auteurs.

Dans la classification de CLIFFORD et de ses collaborateurs les rapports phylogénétiques des Argasidae sont désignés seulement au moyen de la distribution des espèces dans les sous-genres. La majorité des genres sont compris de façon trop étendue, les genres renferment des groupes éloignés d’Argasidae, c’est pourquoi les diagnoses de ces genres sont extrêmement vagues, et peu commodes dans la pratique. Les sous-genres contiennent des groupes de catégorie taxonomique différente, et à cause de cela les sous-genres ne sont pas équivalents entre eux (par exemple les sous-genres *Alveonasus* et *Pensesargas*). Les espèces à l’intérieur des sous-genres sont placées par ordre alphabétique, aussi les espèces ayant des relations étroites évidentes sont souvent éloignées entre elles dans la liste.

En somme, il nous semble que le système des Argasidae, proposé par nous, diffère avantageusement de la classification de ces tiques par CLIFFORD et ses collaborateurs, qui a paru plus tard. Notre classification correspond mieux par son caractère naturel et donc elle doit évidemment mieux rencontrer les exigences de la théorie et de la pratique.

Dans l’article de CLIFFORD et de ses collaborateurs (1964),] un certain nombre d’omissions et de déformations des données des auteurs Soviétiques ont été faites, et doivent être corrigées.

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