A REVIEW OF THE SYSTEMATICS OF THE TICK FAMILY ARGASIDAE (IXODIDA)

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ABSTRACT — The tick family Argasidae is a complex and diverse assemblage of about 190 species. Taxa within the Family Ixodidae had received considerable attention by contemporary researchers, but currently there is no consensus about the relevant morphological features for the determination of argasid species nor there is consensus on the appropriate genus for about 130 species. As a result, many species of Argasidae have not been yet adequately described. The generic and subgeneric arrangements are still a matter of discussion and currently there is no strict description of supraspecific systematics of this group. In this review, we introduce the competing proposals for the systematics of the family Argasidae, together with an overview of prominent morphological, ecological and behavioural features, which are of interest in a synthesis of the family. Special attention is paid to previous attempts to systematize the group based on cladistic analysis, outlining the possible pros and cons of such a method. We also present the largest phylogenetic tree of the family in terms of the number of species resolved by molecular biology based on 16S rDNA. This tree provides support for some of the previously proposed systematic arrangements based on morphology alone, and shows no basic differences with other previously published trees using either nuclear or mitochondrial, coding or non-coding genes. Our main conclusion is that we are still far from an accurate view of the main evolutionary lines of the family. There is thus an urgent need to obtain additional material to, first, explore the relative position of the different species in the phylogenetic arrangement of the family, and second, to capture adequate morphological features which could support a systematic key, necessary for any kind of faunistic or epidemiological studies.

KEYWORDS — Argasidae; phylogenetic relationships; morphology; ecology; cladistics; 16S sequences

INTRODUCTION

The tick superfamily Ixodoidea Banks contains three families (Keirans, 2009). The family Ixodidae, or hard ticks, has gathered copious attention because of its role in the transmission of pathogens. Although some aspects of the family Ixodidae continue to be a matter of discussion, adequate knowl-edge is being accumulated at present about the phylogenetic relationships of this family (summarized by Nava *et al.*, 2009). Another line is represented by the rare *Nuttalliella namaqua* Bedford, found in semiarid areas of Namaqualand (South Africa) and Tanzania. The external surface of *N. namaqua* is like an argasid tick with some generalized ixodid-like characters and other structures unique to *Nuttal-*

liella (Oliver, 1989). Hoogstraal (1985) considered it a relict evolutionary line of ticks. The situation is different with the Argasidae, the third family in Ixodoidea, including around 190 species. Competing taxonomies for Argasidae have very different genus-level groupings, as developed by the eastern school of taxonomists (i.e. Pospelova-Shtrom, 1946; Filippova, 1966; Pospelova-Shtrom, 1969) or by the sometimes radically different opinion of the western school (Clifford *et al.*, 1964; Hoogstraal, 1985). A third group of researchers (Camicas and Morel, 1977; Camicas *et al.*, 1998) also developed a different approach to the systematics of the family, rearranging some genera and suggesting new subgenera in conflict with previous proposals. A cladistic analysis by Klompen and Oliver (1993a) proposed a radically different view of the whole family. A further molecular taxonomic study (Nava *et al.*, 2009) did not solve the main problems in the existing classifications because of the poor representation of different alleged natural groups.

The genus-level taxonomy of the family Argasidae is much more uncertain than that of the Ixodidae, as is at the species level. There are two factors related to such as incertitude. First, the lack of adequate guidelines based on stable morphological features for a reliable determination. Second, the high biodiversity of Argasidae, which has been much underestimated regarding the compilation of taxonomic keys. In example, Venzal *et al.* (2008) provided evidence of inadequate knowledge of some species so deeply established as *O. puertoricensis* or *O. talaje*, demonstrating that the former is more geographically restricted than previously reported and than the latter may be actually more than one single species. The point here is that we are unable to assess how much morphological variability is associated with intra- or inter-specific variations, since we miss genetic data for most of the species. Therefore, we have few support to define some conflicting generic arrangements. Another example is *O. erraticus* and *O. sonrai*, two argasids distributed in parts of the Mediterranean basin. Although a detailed study has been never performed, the adults of these species share many morphological features and larvae are hardly differentiated. The morpho-

logical and molecular details of the isolated pockets of distribution of these two species, or how they are sympatrically distributed in some areas like Morocco, are still a matter of discussion (Chabaud, 1954).

In this paper we will review the different approaches to the classification of Argasidae. Later, we will show the different problems associated with the systematics of the family, as derived from morphological, biological and ecological features. We will discuss also the insights recently obtained by means of molecular biology, and how they support (or fail to) the proposed classifications.

A TALE OF TWO TRIBES

We will review herein the point of view of different schools of researchers regarding the systematics of Argasidae. The eastern school is mainly represented by Pospelova-Shtrom (1946, 1969) together with contributions by Filippova (1966). The contributions from the western school were provided in several papers by Clifford, Sonenshine, Keirans and Hoogstraal. They also provided numerous reports about the ultrastructure of several body portions with taxonomic interest. The French school is based primarily on the works by Morel, Camicas, and their co-workers. In this review we adhere to the denominations of the genera and subgenera as commonly used in the papers by the western school. This is not an endorsement of any systematic approach, but only an homogenization of the nomenclature of the taxa along this paper. The name of the authors for each genera and subgenera are included in the list provided as supplementary material, and full references are included in the corresponding section.

Both eastern and western workers recognized groups largely by overall similarity, with the taxonomic rank determined by the degree of phenetic differentiation. The differences among schools of taxonomists are not a matter of the use of different morphological characters, but in the interpretation of the importance of those characters as to provide coherent systematic clusters among genera and/or species. Therefore, a given character (i.e. cuticu-

lar foldings in adults) may be considered as of importance in delineating the phylogenetic relationships of the family (eastern school) or not (western school). However, at the infra-subfamily level, Argasinae and Ornithodorinae may not even be distinguishable based on larval characters alone (Sonenshine *et al.*, 1966). Whereas eastern scientists considered that larval features are more specific than adult or nymphal ones, the western school based the classification mainly on adult features but there may not be *a priori* reason to assume that data from a life stage have primacy over those from another stage (Kluge and Strauss, 1985). In summary, both eastern and western classifications are mainly focused towards identification of the species, but they do not reflect the natural system of relationships between genera and subgenera.

Pospelova-Shtrom (1946) reviewed the classification of the Argasidae and divided it into the subfamilies Ornithodorinae and Argasinae. In Argasinae, she created a single tribe, Argasini, while in Ornithodorinae she created two tribes, Ornithodorini and Otobiini (see supplementary material). The genera *Ornithodoros*, *Alectorobius* and *Antricola* were place in Ornithodoriini, and the tribe Otobiini had two genera, namely *Otobius* and *Ogadenus*. The tribe Argasini retained two genera, *Argas* and *Carios*. In 1950, Pospelova-Shtrom further revised her classification dividing the genus *Alectorobius* into three subgenera: *Alectorobius s. s.*, *Theriodoros* and *Pavlovskyella*, and reduced *Ogadenus* to a subgenus of *Alveonasus*, which had been erected by Schulze (1941). Filippova (1961) further reduced *Alectorobius* to a subgenus of *Ornithodoros*, but she retained *Alveonasus* as a separate genus. Pospelova-Shtrom later pointed out the need of an additional subgenus (*Aviaogadenus*) to accommodate some species. However, *Aviaogadenus* is a *nomen nudum* because it lacks description (art. 13a of the International Code of Zoological Nomenclature) and lacks a type species (art. 13b). The species in that subgenus were later included into *Proknekalia* (see below). The two Tribes in Ornithodorini were thus erected based on the integument structure, on which Pospelova-Shtrom was deeply interested as a method to understand the

natural history and the "natural arrangement" (*sic*) of the Argasidae (Pospelova-Shtrom, 1969) because "these differences are deeply principal and must to be of ancient origin" (*sic*). However, both western and French schools (see below) rejected the idea of the Tribes.

The point of view of the western school about the systematic arrangements within the Argasidae was radically different. Clifford *et al.* (1964) proposed several differences at the generic level, recognizing the well-supported subfamilies, with one genus in Argasinae, *Argas* (subgenera *Argas s. s.*, *Persicargas*, *Microargas*, *Carios*, *Chiropterargas*, *Secretargas* and *Ogadenus*), and four genera in Ornithodorinae, namely *Ornithodoros* (subgenera *Ornithodoros s. s.*, *Alveonasus*, *Pavlosvkyella*, *Ornamentum*, *Alectorobius*, *Reticulinasus*, and *Subparmatus*) *Otobius*, *Antricola*, and *Nothoaspis*. By the time of development of classification by eastern workers, *Nothoaspis* was still unknown. We include in the supplementary material the arrangement of genera and subgenera as considered by the western school in the supplementary material. The erection of two tribes in Ornithodorinae (Ornithodorini and Otobiini), based on the modifications and the structure of the integument, was rejected in the paper by Clifford *et al.* (1964) and subsequent works by the western school, an opinion which was deeply criticized by Pospelova-Shtrom (1969). Additional studies on the fine structure of the Haller's organ in different species by scanning electron microscopy, as well as on the isolation of viruses from a wide number of species have been reported as reinforcing such a classification system. It is interesting that Keirans (2009) continued to adhere to this proposal of nomenclature and systematic arrangement.

Morel (1965) proposed the erection of Argasidea Schulze, including the family Argantidae Agassiz, 1848 (=Argasidae Murray, 1878) and Nuttalliellidae. Morel (1965) justified the support of such a superfamily Argasidea because of "the numerous differences in the biology and ecology as compared with Ixodidea" (*sic*). However, this remains a matter of speculation, since little is known about the apparently intermediate tick family Nuttaliellidae, a monotypic family that has been the subject of con-

jectures for over 50 years. Morel considered the subgenera *Carios s.s.* and *Chiropterargas* as included within the genus *Carios*, mentioning that "ventral fossae" (*sic*) in nymphs and adults clearly separate them from *Argas*. However, he did not consider them as near *Ornithodoros s.l.* Morel considered *Secretargas* as a separate genus, in the midline between *Argas* and *Carios*. Camicas *et al.* (1998) revised these works and erected *Secretargas* as a subgenus of *Ogadenus*. It is interesting to mention that in a further cladistic approach to the systematics of Argasidae (Klompen and Oliver, 1993a, see below), *Secretargas*, *Ogadenus* and *Proknekalia* were grouped together, closely related to *Argas* and *Alveonasus*.

Camicas and Morel (1977) and Camicas *et al.* (1998) proposed different schemes in two further approaches to the problem. However, generic arrangements are sometimes not justified (see below), new subgenera have been never defined, and only a list of species is included. In an attempt to group species of Argasidae, these authors used numerous sub-genera that may be considered unjustified by some workers. The French authors ranked *Carios* (with the subgenera *Carios* and *Chiropterargas*) and *Ogadenus* (with the subgenera *Ogadenus*, *Aviaogadenus* and *Secretargas*) to full genera into the Argasinae. Other major changes were produced in the Ornithodorinae as the inclusion of *Microargas* into the Ornithodorinae, the ranking of *Alectorobius* to full genus, the rejection of the subgenera *Ornamentum* and *Pavlovskyella*, the rise of the subgenus *Theriodoros* Pospelova-Shtrom, 1950 to a full genus, and the creation of the subgenus *Reticulibius* Morel (in Camicas *et al.*, 1998) within the genus *Alectorobius*. *Theriodoros* (*sensu* Morel) was redefined to accommodate the species in Ornithodorinae that cannot be placed neither in *Ornithodoros s.s.* nor *Alveonasus*. Morel emphasized that the bat-parasitizing species in the New World cannot be easily accommodated in the classification of Ornithodorinae, and that they should be closer to *Reticulinasus*. The name *Reticulibius* first appeared without definition in Camicas et al (1998) to accommodate some bat-parasitizing species previously accounted into *Alectorobius*. No definition of the subgenus is provided and no further references have been published. According

to the rules of Zoological Nomenclature, *Reticulibius* should be considered a *nomen nudum*. In all these taxonomical proposals the landscape of the systematics of Argasidae was composed by a variable number of genera and subgenera, with a high number of species that cannot be adequately accommodated into any of the existing taxonomic arrangements. Indeed, most species of Argasidae can be assigned to more than one genus; there is currently no agreement on the best genus for 130 of the 190 species of Argasidae.

Klompen and Oliver (1993a) proposed a phylogenetic analysis of relationships at the generic and subgeneric level in the family Argasidae, including 80 morphological characters and 3 more based on development and behaviour for most of major lineages. Before such a report, the few comparative analysis on Argasidae dealing exclusively with larval characters (Edwards, 1975; Klompen, 1992) did not provided strong support for either one of the existing classification schemes reinforcing the notion that existing classifications did not reflect natural relationships. Most characters used by Klompen and Oliver (1993a) were derived from chaetotactic features of the larvae, since they are considered to be a stable feature, able to track evolutive history of the involved taxa. The set of characters further included data on the Haller's organ, the post-larval stages, development and behaviour. A total of 53 species were included. The reader is referred to the original reference for an adequate description of every species, characters, and coding used. The results by Klompen and Oliver (1993a) lead to a radically new view of the family Argasidae (see supplementary material). However, in the same paper it is accepted that 71% of the studied species had a poor support for the best taxonomic tree. The genus *Ornithodoros* is therein diagnosed by the presence of small dorsal spines on the palp trochanter of the larva, rapid or no feeding of larvae, reduction in the development of larval hypostomal denticles, the insertion of the fine setae of the anterior pit of Haller's organ in deep sockets, and the presence of a dorso-ventral groove in the adults. The cladistic analysis included the subgenera *Ornithodoros s.s.*, *Pavlovskyella*, *Ornamen-*

tum and *Microargas*, into *Ornithodoros*, without support for a well defined group. The previously recognized subgenera *Ogadenus* (*sensu* the eastern school), *Proknekalia*, *Alectorobius*, *Subparmatus*, *Reticulinasus*, and *Alveonasus* were removed from *Ornithodoros*. The sister group of *Ornithodoros* would be a lineage containing the genera *Otobius* and *Carios*, the latest raised from *Argas* (*Carios*) and including the subgenera *Chiropterargas*, *Alectorobius*, *Reticulinasus* and *Subparmatus*, as well as the genera *Antricola*, *Parantricola* and *Nothoaspis*. According to that study, *Ornithodoros sparnus* is placed near the genus *Otobius*, since all three species in this group share some diagnostic features. Interestingly, these critical characters shared by *Otobius-O. sparnus* are also present in the larvae of the *O. moubata* group (4 species) which according to the cladistic analysis are far from the "*Otobius-Carios*" lineage. The rest of the previously recognized subgenera would fit into Argasinae, in the single genus *Argas*. The two widely accepted subgenera *Argas* and *Persicargas*, were proposed to be shrunk into the single genus *Argas*, with five subgenera, including *Persicargas* as a synonym of *Argas* (Klompen and Oliver, 1993a). It should be stated that the only accurate character used by previous workers for the separation of both subgenera is based on the presence of a trumpet-shaped sensillum in the tarsus I of *Persicargas* larvae.

The current generic divisions proposed by Hoogstraal (1985), Klompen and Oliver (1993a) and Camicas *et al.* (1998) have taxonomic arrangements characterized by a genus that contains most of the species of Argasidae, namely *Ornithodoros* in Hoogstraal (1985), *Carios* in Klompen and Oliver (1993a) and *Alectorobius* in Camicas *et al.* (1998). It is now known that *Ornithodoros* as presented by Hoogstraal (1985) is paraphyletic (Klompen and Oliver, 1993a; Nava *et al.*, 2009). This statement is supported by both morphological and limited genetic data. Therefore the use of *Ornithodoros* for several species of Argasidae appears to be unjustified. However, the monophyly of the genus *Carios* as presented in Klompen & Oliver (1993a) has a low support as recognized by the authors, meaning that species included currently in *Carios* will prob-

ably change their genus in the future. The arrangement by Camicas *et al.* (1998) need studies to confirm the extent to which their proposal is valid, but probably species currently considered belonging to *Alectorobius* will not be kept there. Any choice for a given generic arrangement has controversies impossible to be settled with our current knowledge of the family.

Morphological characters in Argasidae: ancestral or derived?

The morphological features of the different taxonomic arrangements in the family have been adequately described. We will not repeat herein every single proposal, since our purpose is to show the lack of adequate morphological characters to define these arrangements, and to reflect the phylogenetic relationships of the family.

Morphological features have undoubtedly a role for specific determination, but they may play only a secondary role in delineating the evolutive lines of the species, because we ignore what is a primitive character and what is a derived one. We observe Argasidae as a very diverse group with ancestral characters largely unknown. Existing classifications considered both morphological and biological characters, to reinforce the notion of solid taxonomic arrangements. In example, classic classifications considered larval *Reticulinasus* as having 14 pairs of dorsal setae, 8 pairs of ventral body setae, an hypostome with 3/3 or 4/4 dentition and all the life stages (including adults) feeding on bats. In contrast, larval *Otobius* have 7-10 pairs of dorsal setae, 5 pairs of ventral body setae, hypostome with 2/2 dentition and larvae and nymphs feed on mammals as one-host ticks. This is an example of the customary set of morphological and behavioural characters that commonly apply to the systematics of Argasidae.

The structure of the integument is one of the characters commonly used for the separation of the adults in the genera of Argasidae. It is generally described as mamillate, granulate, wrinkled, or striate. These terms are not well defined, which makes comparisons based on the literature prob-

lematic. Regarding how the structure of the integument should be considered, as ancestral or derived, the outgroup conditions for cuticle structure are not obvious. The dorsum in both Holothyrida and Mesostigmata, which are considered as representative of the ancestral state of this character for ticks, is almost completely covered by a well-developed opisthonotal shield (Van der Hammen, 1983) exposing little or not cuticle. We simply cannot capture if the evolution of the bizarre forms in the cuticle of Argasidae have a positive selection or appeared by genic derive. In example, the structure of the marginal cuticle differs distinctly from that of the remaining integument by unusual patterns of cells, dense striation or tubercles. In *Antricola* and *Parantricola* there is a unique modification consisting of modified mamillae with tufts of setae, even in the only species that lacks large portions of dorsal mamillae (*A. delacruzi*). Among the taxa with cell differentiation or striation, it is pronounced in most *Argas*, all *Persicargas* and all *Carios*, with some differentiation found in the remaining genera but *Secretargas* (Hoogstraal *et al.*, 1967).

Another morphological feature commonly used for the classification of Argasidae is the transverse postanal groove, which extends in a more or less straight line posterior to anus. It is distinct in *Ornamentum*, *Reticulinasus*, *Pavlovskyella*, *Alectorobius*, *Subparmatus*, *Parantricola*, *Antricola*, *Nothoaspis*, *Microargas*, and some species of *Ornithodoros*. It is poorly developed in *Otobius*, *Carios* and *Chiropterargas*, and absent in the remaining Argasidae. Absence is considered the ancestral condition in Argasidae. Cladistic analysis deeply involves this character at a very basal level, being one of the main characters in the separation between Argasinae and Ornithodorinae (Klompen and Oliver, 1993a).

Larval characters have been deeply investigated looking for more coherent patterns in the systematic arrangements of Argasidae. The determination of main groups of larvae proposed by Clifford *et al.* (1964) used the presence/absence of dorsal plate, chaetotactic features of the dorsal plate, and setal arrangements on body surface. The dorsal shield or scutum is absent in the postlarval stages of nearly all members of the family Argasidae, which is con-

sidered a modern or derived character. The arrangement of dorsal setae, while adequate to separate the genera according to the concepts raised by the western school, cannot be used to draw any conclusion about the phylogenetic relationships of the genera, other than obvious groups of related species.

The cladistic analysis by Klompen and Oliver (1993a) was partially based on previous works by Klompen (1992) and extended by further publications (Klompen and Oliver, 1993b; Klompen *et al.*, 1996). That study proposed morphological features to separate both subfamilies as described below (larval setal nomenclature follows Klompen and Oliver, 1993a). The subfamily Ornithodorinae Pospelova-Shtrom, 1946 is diagnosed in the larva by the loss of seta pd1 on the palp femur, the reduction of the setal complement on the proximal two-thirds of the palp tibiotarsus to two setae, the presence of seta dm on tarsi II-III, the insertion of setae pd2 II-III distal to the dorsal lyrifissure, and presence of setae ad2 II-III. Most important, as stressed by the same authors, such a combination of characters is unique for, and not reversed within, this subfamily. However, the subfamily Argasinae (Trouessart, 1892, *pro parte*) is diagnosed in the larvae by the presence of a well-developed respiratory system, the insertion of tarsal seta ad3 I at the level of setae d2 and the loss of setae pd3 on tarsus II-III. The point herein is that some of these characters are reversed in some proposed lineages within Argasinae, which render problematic the phylogenetic interpretation. Further on this, the loss of one or several setae is considered a derived character, but the insertion of a given seta at a definite position carries no phylogenetic argument yet.

One of the most important results by Klompen and Oliver (1993a) based on the interpretation of these morphological characters is that *Ornithodoros* is not monophyletic. A monophyletic group is formed by a clade of organisms, meaning that it consists of an ancestor and all its descendants (Enval, 2008). The alignment of the *Ornithodoros* resulting from this proposal would include species with or without dorsal plate and with eyes present or absent. Other characters would be more or less vari-

able among the different species in this assemblage. However, another conclusion drawn from this systematic approach based on cladistic analysis of morphological features is the inclusion in the genus *Carios sensu* Klompen and Oliver 1993a of several formerly separated genera. Such a group of species is allegedly supported by the presence of the characters of the subfamily Ornithodorinae *sensu* Klompen and Oliver (1993a) together with the presence of respiratory apparatus in the larvae. These are the former genera *Alectorobius*, *Reticulinasus*, *Subparmatus*, *Nothoaspis*, *Antricola*, *Parantricola*, *Carios* and *Chiropterargas* (the two later formerly in Argasinae because the morphological features of the adult stages). According to these conclusions, the characters in the larvae would provide a concept about the phylogenetic categorization of the Argasidae, while some other features in adults would drive to a totally different organization. Two of the morphological features acknowledged to characterize the phylogenetic relationships among argasids, namely the larval chaetotaxy and the presence of a lateral body suture in adults, would provide an incompatible arrangement of *Ornithodoros*. This example does not indorses a criticism about a particular notion, but is intended only to illustrate the difficulties in finding a constant and coherent set of characters of application to the whole family in providing a comprehensive classification.

The genus *Carios sensu* Klompen and Oliver (1993a) could then be diagnosed in the adults by the presence of cheeks (a kind of cuticular flaps covering the lateral faces of the gnathosome) and the micromamillated cuticle of the legs, but both characters are reversed in *Reticulinasus* and *Chiropterargas* which are considered by these authors as subgenera in *Carios*. The reduction of setal complement of the capsule of Haller's organ is unknown in several terminal taxa. Most species share the presence of a postcoxal seta and the presence of the genual seta pr1 I in the larvae. It is specifically stated by these authors that several of the recognized groupings within *Carios* appear to be monophyletic, since none of the defining characters are shared by all the species included in *Carios*. As mentioned by Klompen and Oliver (1993a), "the recog-

nition of these groupings as subgenera would create a proliferation of poorly supported higher taxa". This new conception of *Carios* would include all the known species parasitizing bats, including those previously grouped in the genus *Alectorobius* which have been also recorded on bats.

LIFE HISTORY, ADAPTATIONS TO PARTICULAR HOSTS AND RESTRICTED GENETIC FLOW

Nearly all the argasids have more than two feeding instars. Exceptions are the two-host *Ornithodoros lahorensis* and the one host *Otobius megnini* and *O. lagophilus*. Recently, it has been demonstrated that nymphal *Antricola* species also feed upon bats (Estrada-Peña *et al.*, 2008). Argasids feed on hosts which regularly remain near the argasid shelter for only a few weeks annually or which irregularly return to the shelter area for short periods (Hoogstraal, 1985). Differences between argasid and ixodid life styles include several nymphal bloodmeals and instars (only one in ixodid ticks), matting off the host, excess water and ion excretion via coxal glands (via salivary fluids in ixodids) and several adult bloodmeals and small egg batches (single adult bloodmeal and single larger egg batch in ixodids) (Hoosgtraal, 1985). That kind of feeding pattern would be also responsible for a low dispersal capacity. Ticks disperse only by hosts transport. In ixodid ticks, which feed for days or even weeks, hosts can potentially disperse tick populations to long distances.

Two reviews by Hoogstraal (1985) and Klompen *et al.* (1996) concluded that host preferences do not provide any clue about phylogenetic arrangements of the argasids. These studies were made over the previous and differing arrangements of genera according to the taxonomic view of the authors. Although it is difficult to disentangle further details in such a large and variable group of species, it seems that host preferences are driven by the tick preferences towards a defined niche of abiotic conditions. As stated by Hoogstraal (1985) all *Carios*, *Chiropterargas*, *Antricola*, *Parantricola*, *Reticulinasus*, *Subparmatus*, and *Nothoaspis*, together with some species

in *Alectorobius* and *Secretargas*, parasitize bats, without a narrow specificity towards a given host genus. All the species in *Argas* feed upon birds in nesting colonies or resting groups and all *Persicargas* species feed on birds in arboreal nests (with the exception of the group of species parasitizing vultures in the Old World). The single species in *Microargas* is unique in spending its entire life cycle, including the egg stage, on the skin below the carapace of the Galapagos giant tortoise. *Ornithodoros*, with its unique feeding pattern (the larva molts to the first nymphal stage without feeding) and *Pavlovskyella* feed upon a wide number of ground resting mammals. Hosts of *Alectorobius* are bats, birds, reptiles, and mammals. All studied larvae of *Alectorobius* are slow feeders (Hoogstraal, 1985). *Alveonasus* constitutes a diverse branch parasitizing medium and large-sized mammals, also with slow feeding larvae. The genus *Otobius* is unusual in being one-host tick. *Otobius* adults have non functional mouthparts, do not feed, and mate on the ground.

Host associations and particular adaptations to different habitats have been extensively reviewed by Hoogstraal (1985) and they will be not repeated herein. Summarizing, all the *Argas* shelter in crevices of rock ledges or in stony ground near the bird hosts, but two Neotropical species, namely *A. monachus* and *A. dulus*, and the Nearctic *A. brevipes*. Two *Argas* species, *A. macrostigmagus* and *A. cucumerinus*, parasitize marine birds and are biologically and structurally distinctive. It is extremely interesting to note that *A. macrostigmatus* is the only *Argas* species known to share habitat and host with an *Ornithodoros* (*O. maritimus*). The extreme morphological modifications observed in *A. macrostigmatus*, like the unusually large spiracular plates, are not found in the *Ornithodoros* partner (Hoogstraal, 1985). At least in this case, the use of the same group of hosts and the same habitat did not lead to a kind of convergent evolution. Another interesting example of lack of adaptation to hosts, but to a given environment, is provided by species in *Secretargas sensu* Hoogstraal, 1957. *A. (S.) transgariepinus* parasitizes solitary bats breeding in dry places from South Africa to Spain and Afghanistan. *A. hoogstraali* and *A. echinops* are restricted to the

hot, semiarid savanna zone in Madagascar. The former infests lizards and the latter infests hedgehogs. In this case, the three species are adapted to a kind of eco-climatic conditions, and not a given type of hosts. In this sense, Venzal and Estrada-Peña (2006) demonstrated that *O. puertoricensis*, a species commonly found on Sigmodontine rodents in the Neotropics, could readily attack and feed on Palearctic reptiles. The contrary was observed for *O. rostratus*, also a Neotropical argasid. As mentioned by Klompen et al (1996) the specificity of Argasinae is compatible with an ecological specificity of the group. Hosts for Argasinae may be phylogenetically separated, but are nearly always ecologically close, i.e. they use the same ecological niche, where the ticks are present.

To our knowledge, there are few empirical studies on the genetic similarity within and among populations of a given argasid species. There are some data about the gene flow of *O. coriaceus* in North America, being the larvae the only stage that remains attached to the host for an extended period (García, 1963). This tick is most commonly found in association with deer and cattle bedding sites (Furman and Loomis, 1984). Teglas *et al.* (2005) studied patterns of variability in a 420 base pairs segment of the 16S mithochondrial rDNA sequence among 210 individuals of this species for 14 sites in California, Oregon, and Nevada. The majority of the 63 unique haplotypes identified in the ticks tested were unique to their particular collection sites. Only four collection sites shared haplotypes. The minimum spanning tree and the high F_{st} values calculated by Teglas *et al.* (2005) showed that limited gene flow occurred among widely distributed tick populations, and that combined effects of isolation and random drift could have led to the creation of unique haplotypes and development of genetic variants unique to a specific tick population. Similar results on gene flow were found for *O. sonrai* from Senegal and Mauritania (Vial *et al.*, 2006).

The alternative hypothesis is that 16S rDNA is not suitable to track populations of the same species (see, i.e., Balloux, 2010). These findings must to be taken with caution because they were derived from only two species and using only one mitochondrial

gen. However, they settle the hypothesis of an unexpectedly rich biodiversity of argasids in the nature. The lack of adequate field samplings drove to an inadequate knowledge of the possible wide morphological variability of the species in the family. The absence of genetic data for a reasonable number of taxa (see below) probably drove to the misconception that such a high morphological variability was a result of intra-specific variation. In any case, we think that the restricted genetic flow reported for these two species of *Ornithodoros* is coherent with the ecological picture of the family, and may be the result of a variability higher than expected. While these gaps remain unfilled, we will be unable to have a more complete picture of the phylogenetic arrangement within argasids. According to these preliminary studies, we should expect different local populations within the geographical range of a species, with a clinal component of genetic differences among these populations. The evolutionary forces acting over such a genetic pool of differentiating populations would lead to homozygosis, as an adaptation to the local prevailing niche (climate and/or hosts) and because the limited gene flow among these populations.

Environmental determinants of evolution: ecological fitting

We hypothetize that many factors derived from the tracking of ecological resources contributed to a high morphological diversity in argasids. Our hypothesis is that several argasid species, in need of the same environmental resource, and evolving from separate ancestral branches of the family, converged into a similar ecological niche. Further adaptation to such a common niche, together with geographical isolation and restricted gene flow promoted an allopatric speciation process. We are far to have all the empirical proofs necessary to validate such an hypothesis, and therefore phylogeographic studies combining biogeographic patterns, ecology and genetics are strongly needed.

The term ecological fitting was coined by Janzen (1985). It is generally investigated in insect-plant systems, because researches can reconstruct phy-

logenetic patterns of association between the two clades, then examine the processes underlying those patterns by (1) identifying the resource being tracked by the insect, (2) determining the distribution of that resource among host plants, and (3) delineating the host preference hierarchy of the insects (Brooks and McLennan 2002). Currently, we do not have this degree of detailed information for any host-argasid system. However, we can think in terms of ecological traits rather than host taxonomy, and conclude that argasids might be able to switch hosts if the trait they are tracking (i.e. a given environmental condition) is shared by several groups of hosts. Brooks *et al.* (2006) discussed that any given parasite might be a resource specialist, but also might share that specialist trait with one or more relatives. This specialization on a particular resource can be plesiomorphic within a group (Brooks and MacLennan, 2002). We use the term ecological fitting not on a particular resource that a group of hosts could provide with to the argasids (in terms of blood composition or particular life habits of the host) but related to the abiotic features in the environment, in the same line as Vial (2009). If all the argasid-parasite associations are the result of ecological fitting, then all host taxa are interchangeable from the point of suitability for the parasites, and associations will be determined solely by the habitats the host utilizes (Brooks *et al.*, 2006). The alternative hypothesis is the preference towards a given host type and then host-associated genetic differentiation, as demonstrated from studies on ixodids (McCoy *et al.*, 2001).

Ecological fitting in argasids has received little attention, because of the broad range of niches available to argasids. Support for the hypothesis of an ecological adaptation regardless of the hosts available comes from the observations that some argasids may parasitize phylogenetically well-separated hosts which share the same habitat. Further support is obtained from laboratory studies, when argasid specimens are offered with hosts different from the usual range found in nature. Some studies reported that many argasids may readily attack and feed on non-usual hosts, but few studies are devoted to describe the effects on
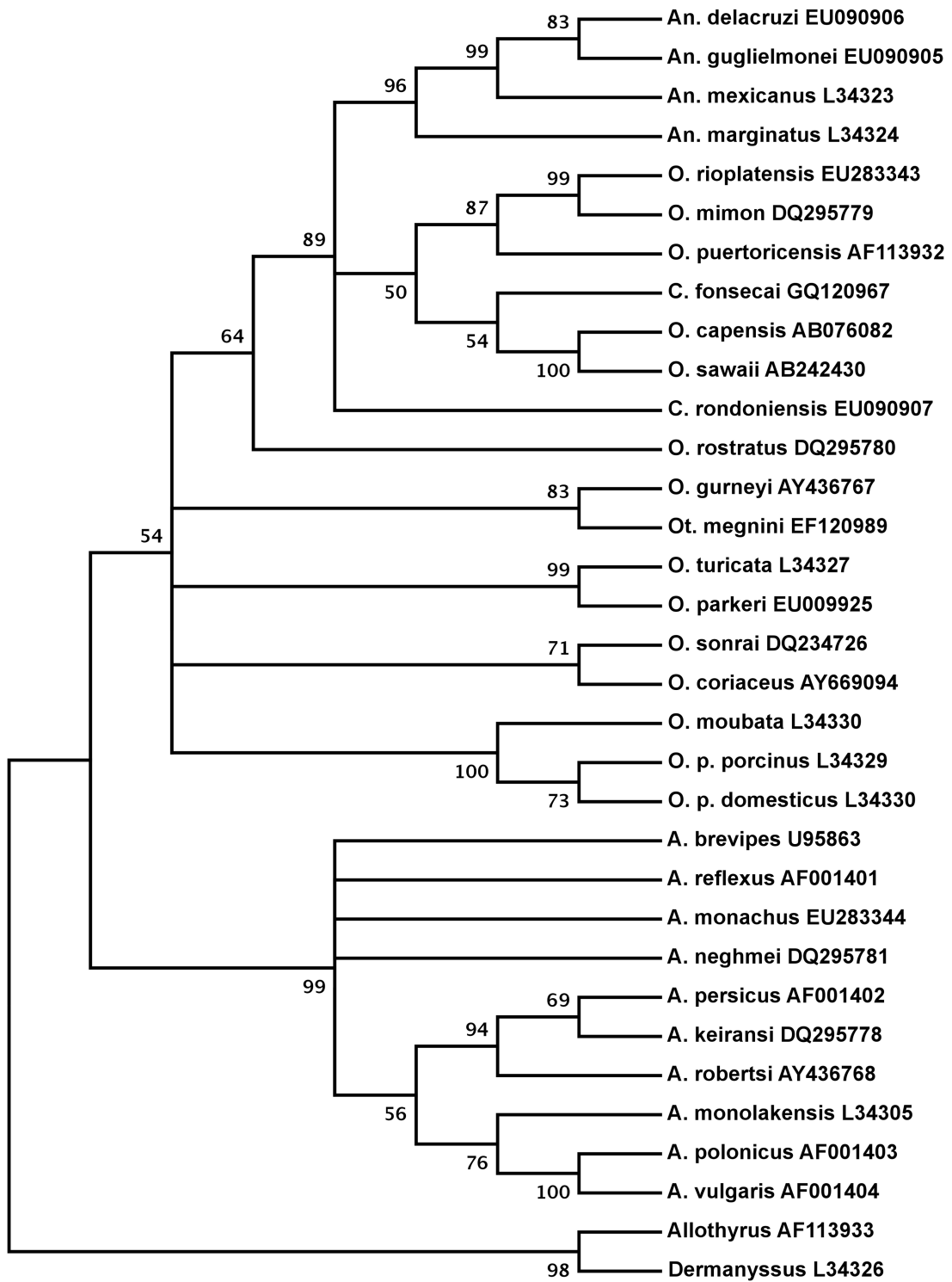
FIGURE 1: See next page

tick physiology.

This hypothesis is of applicability to the bat parasitizing argasids. Hoogstraal and Aeschlimann (1982) categorized bat-feeding ticks in *Carios* as with strict-total host preference. Species in *Carios* (*sensu* Hoogstraal, 1985) been recorded on different genera of bats. Therefore, this could be interpreted either as an adaptation to bats by a subset of the primitive Argasidae pool, or as a convergent evolution towards bats as hosts derived from the life style of argasids, resting in protected environments as caves. In such a way, the parasitism on bats could have evolved several times in different parts of the argasids range. Klompen *et al.* (1996) citing "Klompen and Oliver, in preparation" proposed a dispersal event of their *Carios* assemblage, to colonize bats in the Old World "because the basal lineages are New World endemics". It is difficult to ascertain how a group of ticks associated to bats, living in hot and humid caves, and currently distributed in the Neotropics (the representatives of *Alveonasus Nothoaspis*, *Subparmatus*, *Reticulinasus*, *Antricola* and *Parantricola* lineages) could migrate to the Old World to evolve into the *Carios-Chiropterargas* lineage, since those hosts are not known to migrate over large distances. The *Carios* lineage is associated to dry environments and morphologically closer to the *Argas-Persicargas* representatives because the features of postcoxal setae in larvae, the hypostome and some other characters of body integument in adults. If we consider the spread of a branch of the primitive Neotropical bat-associated argasids, into the Oriental, Palearctic and Tropical regions, we should consider first a deep change in habits. However, the evolution of the primitive Old World Argasinae stock into differing species associated to bats requires less "evolutive steps" considering both morphological and biological processes. While it seems obvious that the bat-associated lineage of Neotropical argasids is close to *Alectorobius*, the hypothesis of a phylogenetic link of such a lineage with *Carios-Chiropterargas* is not clear.

The relatively similar morphological and behavioural patterns observed simultaneously in several members of the family does not necessarily mean that all these taxa share a common phylogenetic ancestor, because other prominent details point to separate basal pools, with habitat selection as driver of convergent evolution. The divergence during speciation is continuous by nature. In example, bat-parasitizing Argasidae have a similar look and behavioural habits, but without sharing critical characters. Examples supporting this hypothesis are numerous: the reticulate Haller's organ capsule in the *Alectorobius* species which parasitize bats is morphologically near to species placed in other groups, but larvae in *Alectorobius* have a 2/2 dentition in hypostome and 2 successive molts to the second nymph stage, an important and advanced biological feature absent in other groups of species. In this sense, *O. viguerasi*, which feeds also on bats in the Caribbean is very different morphologically to other *Ornithodoros*, with sclerotized ventral plates in adults and the presence in the larvae of cornua and auricula-like projections. On the other hand, the genus *Antricola* lacks the presence of claws in legs, a character constant in every other argasid species. This seems to be a modern feature, which should have arisen as a feature independent to every other evolutive branch. Because many other species of Argasidae share the same habitat, we should discard ecological pressure as the driving factor to the lack of the claws, revealing a totally different ancestor for the species of *Antricola*. Further

FIGURE 1: The evolutionary history of the members of the family Argasidae for which adequate samples of DNA are available. Sequences were aligned using Clustal W (Thompson *et al.*, 1994) with default parameters. The evolutionary history was inferred using the Neighbor-Joining method (Saitou and Nei, 1987). The optimal tree with the sum of branch length = 2.36569528 is shown. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) is shown next to the branches. The tree is drawn to scale, with branch lengths in the same units as those of the evolutionary distances used to infer the phylogenetic tree. The evolutionary distances were computed using the Kimura 2-parameter method (Kimura, 1980) and are in the units of the number of base substitutions per site. Bootstrap values of 70% were used to collapse branches. All positions containing alignment gaps and missing data were eliminated only in pairwise sequence comparisons (pairwise deletion option) using MEGA 4.0 (Tamura *et al.*, 2007). There were a total of 480 positions in the final dataset.

on this, Haller's organ details are extremely different in *Carios*, *Chiropterargas*, *Reticulinasus*, and *Antricola*. Those morphological features are well fixed in the argasids and contribute to support the hypothesis of a primary ecological assemblage of unrelated species, followed by a secondary process of speciation. It would be of interest to know what characters are promoted because a way of life and what are retained from the primitive ancestor, because they are unaffected by the ecological niche and its pressure.

WHAT MOLECULAR BIOLOGY TELLS ABOUT THE PHYLOGENY OF ARGASIDAE?

Figure 1 displays a phylogenetic tree of 30 argasid species (*O. porcinus* is represented by 2 subspecies), using the available published sequences of 16S rDNA. All the technical details for the preparation of the tree are included in the legend for the figure 1. The phylogenetic arrangement obtained in the tree introduced herein, using only 16S rDNa has not basic differences with other previously published trees using either nuclear or mitochondrial, coding or not-coding genes (i.e. Black and Piesman, 1994; Crampton *et al.*, 1996; Norris *et al.*, 1996; Fukunaga *et al.*, 2000; Beati and Keirans, 2001; Murrell *et al.*, 2000, 2001). The clusters of species as discussed herein are based only on those supported by bootstrap values higher than 70%. This tree does not add nothing new to previous studies in terms of phylogenies (Nava *et al.*, 2009), most probably because the mutation rate of this gene is not adequate for separation at the level necessary to track the evolution of Argasidae. Some criticism to the use of only mitochondrial DNA alone for tracking evolution has been raised (i.e. Balloux, 2010). Some other genes, like COI, may be better trackers of the separation among species (Cruikshank, 2002). The presented tree is the largest to date in terms of number of species. Some of the conclusions already raised by Nava *et al.* (2009) can also be observed in such a tree. First at all, *Ornithodoros* is not monophyletic (as well as *Carios*) and *Antricola* species form a definite cluster, clearly separated from other representatives of the group (96% of support). Ushijima *et al.* (2003) studied the 16S gene sequence of *O. capensis* and they reported to support the erection of *Car-ios sensu* Klompen and Oliver (1993a). However, when some other taxa are included, this species fits relatively far away from the only representatives (*Antricola*) considered as belonging to *Carios*. The problem here is that important representatives of the genus *Carios sensu* Klompen and Oliver (1993a) are not included into that tree, and therefore we ignore if these species would fit into the same grouping together with *Antricola*. Other species described in recent years as belonging to *Carios* (*fonsecai* and *rondoniensis*) fall well within the assemblage of *Ornithodoros* species but we must to insist that important representatives (i.e. species in the subgenus *Alveonasus*) are not included in such a tree. The level of resolution is also relatively poor for the subgenera *Ornamentum* (*O. coriaceus*) and *Pavlovskyella* (*O. rostratus*, *O. parkeri*, *O. gurneyi*, *O. turicata* and *O. sonrai*) but the latter fall definitely far away as to be considered at the same level of subgeneric arrangement. Furthermore, the genus *Otobius* and its striking morphological and biological features, would not fit in a separate branch of the tree, but related to several species of *Ornithodoros* s.l. The genus *Argas*, considering only the subgenera *Argas* and *Persicargas*, seems to be monophyletic, supporting the findings by Klompen and Oliver (1993a). It is also noteworthy that the few *Persicargas* species included in that molecular study (*persicus*, *keiransi* and *robertsi*) are clustered into a group with 94% of support, well within other *Argas* s.l. species. Another interesting feature is the lack of relationships between the *O. moubata* group and *Otobius*, even if they share some morphological features.

FUTURE DIRECTIONS IN THE RESEARCH ON ARGASIDAE

This review was intended only to demonstrate our lack of adequate features for the determination of natural groups for many species, the current problems existing in the taxonomic arrangement of the family Argasidae, and the interpretations of its evolution. The cladistic analysis of the family carried out by Klompen and Oliver (1993a) is an important contribution towards understanding the phylogeny of the family; additionally, this study generated a fruitful discussion about the taxonomic ar-

TABLE 1: The type species of the different genera proposed in the different systematic arrangement of the family Argasidae. DNA Material from these species is of special interest in the evaluation of a phylogenetic tree of the family based on molecular biology. Included is the genus for which it is considered the type species, as well as other genera where the species have been included in some classifications by other authors. Genera and species are named according to Hoogstraal (1985).

Species	Genus	Other genera	Distribution
Antricola coprophilus (Macintosh, 1935)	*Antricola*	*Carios*	Neotropical-Palearctic
A. marginatus (Banks, 1910)	*Parantricola*	*Parantricola, Carios*	Neotropical
Argas brumpti Neumann, 1907	*Ogadenus*	*Ogadenus*	Afrotropical-Palearctic
A. reflexus (Fabricius, 1794)	*Argas*		Palearctic
A. transversus Banks, 1902	*Microargas*	*Microargas, Ornithodoros*	Neotropical
A. vespertilionis (Latreille, 1796)	*Carios*	*Carios*	Afrotropical-Oriental-Palearctic
Nothoaspis reddelli Keirans & Clifford, 1975	*Nothoaspis*	*Carios*	Neotropical
Ornithodoros lahorensis Neumann, 1908	*Alveonasus*	*Alveonasus, Argas*	Oriental-Palearctic
O. savignyi (Audouin, 1826)	*Ornithodoros*		Afrotropical-Oriental-Palearctic
O. talaje (Guérin-Meneville, 1849)	*Alectorobius*	*Alectorobius, Carios*	Neotropical

rangement of these species. Although we do not totally adhere to that proposal we do recognize its value for a further insight into Argasidae.

There are some urgent needs in future research regarding the Argasidae, concerning both the recognition of stable and coherent morphological features, taking into account the intra- and inter-species variability, linked to the phylogenetic relationships derived from molecular analysis and the ecological requirements. The inclusion in a future phylogenetic tree of the rare *Nothoaspis* and representatives of the Old World *Carios*, *Chiropterargas* and *Secretargas* would greatly improve the resolution of the phylogenies within Argasidae. It would be also of great interest to obtain DNA from the type species of each one of the former genera (*sensu* eastern and western schools of taxonomists) to have a broader view of the landscape within Argasidae. These samples should optimally include representatives of the several proposed genera according to the different classification schemes. Table 1 displays a simple proposal of the type species of each of the "classic" genera, from which DNA and further sequencing would be much welcome. Further on this, there are very few species from the Old World for which DNA sequences are available, therefore providing a biased view of the phylogenetic relationships within the group. The above mentioned tree, based on 16S rDNA, could be greatly transformed when more species from Old World taxa are

included and more genes sequenced. The collection of new material would provide also sequences for other more conserved genes with greater resolutive power, like 18S and 28S. From the future phylogenetic tree, more conclusions about the evolution, sharing and/or conservation of morphological features within the family could be drawn, providing a deeper view of the morphological features necessary for the adequate determination of the species.

Many species are known only by the larval stage or by adult one. Further on this, it is necessary to associate the larval and adult stages of some species known only by one stage or another. Because the difficulty in finding engorged females or to establish a laboratory colony, adult and larval stages of species already described as separate taxa, have not been associated for some species described as different ones. The adoption of adequate morphological features able to determine both larvae and adults should be used for a reappraisal of the family, addressed to establish the actual distribution of the many species that remain poorly known.

The Ixodidae received much of the scientific interest in the recent past, and many papers continue to accumulate about the many facets of their morphology, ecology, physiology and behaviour. However, we need to devote additional efforts to understand many aspects of the diverse family Argasidae, because rules obtained from the study of Ixodidae

cannot apply to such a heterogeneous group. We hope this review will contribute to stimulate future studies, and to consider the need to develop new approaches to the study of the largely forgotten soft ticks. Table 1. The type species of the different genera proposed in the different systematic arrangement of the family Argasidae. DNA Material from these species is of special interest in the evaluation of a phylogenetic tree of the family based on molecular biology. Included is the genus for which it is considered the type species, as well as other genera where the species have been included in some classifications by other authors. Genera and species are named according to Hoogstraal (1985).

REFERENCES

Agassiz L. 1846 — Nomenclatoris zoological index universalis, continens nomina systematica classium, ordinum, familiarum et generum animalium omnium, tam viventium quam fossilium, secundum ordinem alphabeticum unicum disposita adjectis homonymiis plantarum, nec non variis adnotationibus et emendationibus. Soloduri, 393 pp. Cited by Hoogstraal H. 1970. — Bibliography of ticks and tickborne diseases. Vol. 1, Special Publication NAMRU3, 499 pp.

Balloux F. 2010. — Mitochondrial phylogeography. The worm in the fruit of the mitochondrial DNA tree — Heredity, 104: 419-420.

Banks N. 1912 — New American mites — Proc. Entomol. Soc. of Washington, 14: 96-99.

Beati L, Keirans J.E. 2001 — Analysis of the systematic relationships among ticks of the genera *Rhipicephalus* and *Boophilus* (Acari: Ixodidae) based on mitochondrial 12S ribosomal DNA gene sequences and morphological characters — J. Parasitol., 87: 32-48.

Black WC, Piesman J. 1994 — Phylogeny of hard- and soft-tick taxa (Acari: Ixodida) based on mitochondrial 16S rDNA sequences — P. Natl. Acad. Sci. USA, 91: 10034-10038.

Brooks DR, McLennan D.A. 2002 — The nature of diversity: an evolutionary voyage of discovery — University of Chicago Press, Chicago, Illinois, USA.

Brooks DR, León-Règagnon VL, McLennan D, Zelmer D. 2006 — Ecological fitting as a determinant of the community structure of Plathyhelminth parasites of Anurans — Ecology, 87: S76-S85.

Camicas JL, Morel P.-C. 1977 — Position systématique et classification des tiques (Acarida: Ixodida) — Acarologia, 18: 410-420.

Camicas JL, Hervy JP, Adam F, Morel P.-C. 1998 — Les tiques du monde. Nomenclature, stades décrits, hotes, répartition (Acarida, Ixodida) — Orstom, Paris.

Černý V. 1967 — Two new species of argasid ticks (Ixodoidea, Argasidae) from Cuba — Folia Parasitol., 14: 141-148.

Chabaud AG. 1954. — L'*Ornithodoros erraticus* (Lucas 1849): multiplicité des races — Bull. Soc. Pathol. Exot., 24: 89-130.

Clifford CM, Kohls GM, Sonenshine D.E. 1964 — The systematics of the subfamily Ornithodorinae (Acarina: Argasidae). I. The genera and subgenera. Ann. Entomol. Soc. Am., 57: 429-437.

Cooley RA, Kohls G.M. 1942 — *Antricola*, new genus, *Amblyomma gertschi* new species, and notes on *Ixodes spinipalpis* (Acarina: Ixodidae) — Pub. Health Rep., 57: 1733-1736.

Crampton A, McKay I, Barker S.C. 1996 — Phylogeny of ticks (Ixodida) inferred from nuclear ribosomal DNA — Int. J. Parasitol., 26: 511-517.

Cruikshank, R.H. 2002. — Molecular markers for the phylogenetics of mites and ticks — Exp. Appl. Acarol., 7: 3-14.

Edwards M.A. 1975 — The chaetotaxy of the pedipalps and legs of some ticks (Acari: Argasidae) — Trans. Zool. Soc. London, 33: 1-76.

Envall M. 2008 — On the differences between mono-, holo- and paraphyletic groups: a consistent distinction of process and pattern — Biol. J. Linn. Soc., 94: 217-220.

Filippova N.A. 1961 — Larvae and nymphs of the subfamily Ornithodorinae (Ixodoidea, Argasidae) in fauna of the Soviet Union — Parazitol. Sbornik, 20: 148-182 (In Russian, English translation 1-18-63 NIH).

Filippova N.A. 1966 — Argasid ticks (Argasidae) — Zoologicheskogo Institut Akademii Nauk SSSR, Moscow-Leningrad (in Russian).

Fukunaga M, Yabuki M, Hamase A, Oliver JH, Nakao M. 2000 — Molecular phylogenetic analysis of Ixodid ticks based on the ribosomal DNA spacer, internal transcribed spacer 2, sequences — J. Parasitol., 86: 38-43.

Furman D, Loomis E. 1984 — The ticks of California (Acari: Ixodida) — University of California Press, Berkeley, CA, USA.

García R. 1963 — Studies on the ecology of *Ornithodoros coriaceus* Koch (Acarina: Argasidae) — University of California, Berkeley, USA.

Hoogstraal H. 1955 — Bat ticks of the genus *Argas* (Ixodoidea, Argasidae). I. The subgenus *Chiropterargas* — Fieldiana Zool., 37: 579-600.

Hoogstraal H. 1957 — Bat ticks of the genus *Argas* (Ixodoidea, Argasidae). 2. *Secretargas* new subgenus

and *A. transgariepinus* White, 1846, its adult and immature stages; with a definition of the subgenus *Argas* — Ann. Entomol. Soc. Am., 50: 544-549.

Hoogstraal H. 1985 — Argasid and nuttalliellid ticks as parasites and vectors. Adv. Parasitol., 24: 135-238.

Hoogstraal H, Aeschlimann A. 1982 — Tick-host specificity — Bull. Soc. Entomol. Suisse, 55: 5-12.

Hoogstraal H, Kohls GM. 1966 — *Argas* (*Microargas*) *transversus* Banks (new subgenus) (Ixodoidea, Argasidae), a diminutive parasite of the Galapagos giant tortoise: Redescription of the holotype male and description of the larva — Ann. Entomol. Soc. Am., 59: 247-252.

Hoogstraal H, Uilenberg G, Blanc CP. 1967 — The *Argas* subgenus *Secretargas* (Ixodoidea, Argasidae) in Madagascar: descriptions of *A. (S.) echinops*, new species, and of the adults and nymphs of *A. (S.) hoogstraali* — Ann. Entomol. Soc. Am., 60: 149-162.

Janzen D. H. 1985 — On ecological fitting — Oikos, 45: 308-310.

Kaiser MN, Hoogstraal H, Kohls G.M. 1964 — The subgenus *Persicargas*, new subgenus (Ixodoidea, Argasidae, *Argas*). 1. *A. (P.) arboreus*, new species, an Egyptian *persicus*-like parasite of wild birds, with a redefinition of the subgenus *Argas* — Ann. Entomol. Soc. Am., 57; 60-69.

Keirans J.E. 2009 — Order Ixodida. In Krantz G.W., Walter D.E. (Eds.) A manual of acarology 3rd ed — Texas Tech Univ. Press, pp. 111-123.

Keirans JE, Clifford C.M. 1975 — *Nothoaspis reddelli*, new genus and new species (Ixodoidea: Argasidae), from a bat cave in Mexico — Ann. Entomol. Soc. Am., 68: 81-85.

Keirans JE, Hoogstraal H, Clifford C.M. 1977 — *Ornithodoros* (*Proknekalia*) *vansomereni* new subgenus and new species (Acarina: Ixodoidea: Argasidae), a swallow next parasite in Kenya — Ann. Entomol. Soc. Am., 70: 221-228.

Kimura M. 1980 — A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences — J. Mol. Evol., 16: 111-120.

Klompen J.S.H. 1992 — Comparative morphology of argasid larvae (Acari: Ixodida: Argasidae) with notes on phylogenetic relationships — Ann. Ent. Soc. Am., 85: 541-560.

Klompen JSH, Oliver J.H. 1993a — Systematic relationships in the soft ticks (Acari: Ixodida: Argasidae) — Syst. Entomol., 18: 313-331.

Klompen JSH, Oliver J.H. 1993b — Haller's organ in the tick family Argasidae (Acari: Parasitiformes: Ixodida) — J. Parasitol., 79: 591-603.

Klompen JSH, Black WC, Keirans JE, Oliver J.H. 1996 — Evolution of ticks — Ann. Rev. Entomol., 41: 141-161.

Kluge AG, Strauss R.E. 1985 — Ontogeny and systematics — Ann. Rev. Ecol. & Systematics, 16: 247-268.

Koch C.L. 1844 — Systematische Uebersicht über die Ordnung der Zecken. Arch. Naturgesch., 10 J, 1: 217-239.

Latreille P.A. 1796 — Précis des caractères génériques des insectes disposes dans un order naturel — Brive, 202 pp.

Morel P.-C. 1965 — Les tiques d'Afrique et du bassin Méditerranéen (Ixodoidea). Distribution, Biologie, rôle pathogène — Inst. d'Elev. Med. vet. Pays Trop., Maisons-Alfort. 1342 pp.

Murray A. 1878 — Economic Entomology. Aptera — Chapman and Hall, London, 1, 433 pp.

Murrell A, Campbell NJH, Barker S.C. 2000 — Phylogenetic analyses of the rhipicephaline ticks indicate that the genus *Rhipicephalus* is paraphyletic — Mol. Phylogenet. Evol., 16: 1-7.

Murrell A, Campbell NJH, Barker S.C. 2001 — A total-evidence phylogeny of ticks provides insights into the evolution of life cycles and biogeography — Mol. Phylogenet. Evol. 21: 244-258.

Nava S, Guglielmone AA, Mangold A.J. 2009 — Overview of systematics and evolution of ticks — Frontiers in Bioscience, 14: 2857-2877.

Norris DE, Klompen JSH, Black W.C. 1999 — Comparison of the mitochondrial 12S and 16S ribosomal DNA genes in resolving phylogenetic relationships among hard ticks (Acari: Ixodidae) — Ann. Entomol. Soc. Am., 92: 117-129.

Oliver J.H. 1989 — Biology and systematics of ticks (Acari: Ixodida) — Ann. Rev. Ecol. & Syst., 20: 397-430.

Pocock R.I. 1909 — Ticks. In A system of medicine, Allbut & Rolleston (eds.) — Macmillan, London, vol. 2, part 2, pp. 187-203.

Pospelova-Shtrom M.V. 1946 — On the Argasidae system (with description of two new subfamilies, three new tribes and one new genus). Meditsnkaia Parazitologia, Paratizarn. Bolezni, 15: 47-58 (In Russian, English translation NIH).

Pospelova-Shtrom M.V. 1950 — Subgenera, species and the lower taxonomic subdivisions of ticks of the subfamily Ornithodorinae in the fauna of the USSR — Med. Parasitologia, Parazitarn. Bolezni, 19: 55-70. (In Russian).

Pospelova-Shtrom M.V. 1969 — On the system of classification of ticks of the family Argasidae Can., 1890 — Acarologia, 11: 1-22.

Saitou N, Nei M. 1987 — The neighbor-joining method: A new method for reconstructing phylogenetic trees — Mol. Biol. & Evol., 4: 406-425.

Schulze P. 1941 — Das Geruchsorgan der Zecken — Okol. Tiere, 37: 491-564.

Sonenshine DE, Clifford CM, Kohls G.M. 1966 — The systematics of the family Ornithodorinae (Acarina: Argasidae). III. Identification of the larvae of the Eastern hemisphere — Ann. Entomol. Soc. Am., 59: 92-122.

Tamura K, Dudley J, Nei M, Kumar S. 2007 — MEGA4: Molecular Evolutionary Genetics Analysis (MEGA) software version 4.0 — Mol. Biol. and Evol., 24:1596-1599.

Teglas MB, May B, Crosbie PR, Stephens MR, Boyce W.M. 2005 — Genetic structure of the tick *Ornithodoros coriaceus* (Acari: Argasidae) in California, Nevada, and Oregon — J. Med. Entomol., 42: 247-253.

Thompson, JD, Higgins, DG, Gibson, T.J. 1994 — CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position specific gap penalties and weight matrix choice — Nucleic Acids Res., 22: 4673-4680.

Ushijima Y, Oliver JH, Keirans JE, Tsurumi M, Kawabata H, Watanabe H, Fukunaga M. 2003 — Mitochondrial sequence variation in *Carios capensis* (Neumann) a parasite of seabirds collected on Torishima island in Japan — J. Parasitol., 89: 196-198.

Van der Hammen L. 1983 — New note son the Holothyrida (Anactinotrichid mites). Zoologisches Verhandelingen, Leiden, 207: 1-48.

Venzal JM, Estrada-Peña A. 2006 — Larval feeding performance of two Neotropical *Ornithodoros* ticks (Acari: Argasidae) on reptiles — Exp. Appl. Acarol., 39: 315-320.

Venzal JM, Estrada-Peña A, Mangold AJ, González-Acuña D, Guglielmone A.A. 2008 — *Ornithodoros* (*Alectrobius*) *talaje* species group (Acari: ixodidae: Argasidae): description of *Ornithodoros* (*Alectorobius*) *rioplatensis* n. sp. from southern South America — J. Med. Entomol., 45: 832-840.

Vial L. 2009. Biological and ecological characteristics of soft ticks (Ixodida: Argasidae) and their impact for predicting tock and associated disease transmission — Parasite 16: 191-202.

Vial L, Durand P, Arnathau C, Halos L, Diatta G, Trape JF, Renaud F. 2006 — Molecular divergences of the *Ornithodoros sonrai* soft ticks species, a vector of human relapsing fever in West Africa — Microbes & Infection, 8: 2605-2611.

SUPPLEMENTARY MATERIAL

The arrangement of genera and subgenera as proposed by the different schools of classification of the family Argasidae.

1. The systematic arrangements of the family Argasidae according to eastern school

Subfamily Argasinae (Trouessart, 1892, pro parte) Pospelova-Shtrom, 1946.

- Tribe Argasini Pospelova-Shtrom, 1946

    - genus *Argas* Latreille, 1796 with the subgenera

        * *Argas* s. s.
        * *Persicargas* Kaiser, Hoogstraal and Kohls, 1964
        * *Carios* Latreille, 1796
        * *Chiropterargas* Hoogstraal, 1955
        * *Secretargas* Hoogstraal, 1957

Subfamily Ornithodorinae Pospelova-Shtrom, 1946

- Tribe Otobiini Pospelova-Shtrom, 1946

    - genus *Otobius* Banks, 1912

    - genus *Alveonasus* Schulze, 1941 with the subgenera

        * *Alveonasus* s. s.
        * *Ogadenus* Pospelova-Shtrom, 1946
        * *Proknekalia* Keirans, Hoogstraal and Clifford, 1977 (*Proknekalia* replaced *Aviaogadenus*, as iniatially recognized by the eastern school. Both Filippova (1961) and Pospelova-Shtrom (1969) agreed on that replacement).

- Tribe Ornithodorini Pospelova-Shtrom, 1946

    - genus *Ornithodoros* Koch, 1844 with the subgenera

        * *Ornithodoros* s. s.
        * *Pavlovsvkyella* Pospelova-Shtrom, 1950
        * *Theriodoros* Pospelova-Shtrom, 1950
        * *Ornamentum* Clifford, Kohls and Sonenshine, 1964
        * *Alectorobius* Pocock, 1909
        * *Reticulinasus* Schulze, 1941
        * *Subparmatus* Clifford, Kohls and Sonenshine, 1964
        * *Antricola* Cooley and Kohls, 1942.

2. The systematic arrangements of the family Argasidae according to western school

Subfamily Argasinae

- genus *Argas* with the subgenera *Argas s.s.*, *Persicargas*, *Microargas* Hoogstraal and Kohls 1966, *Carios*, *Chiropterargas* and *Secretargas*.

Subfamily Ornithodorinae

- genus *Otobius*

- genus *Ornithodoros* with the subgenera *Proknekalia*, *Alveonasus*, *Pavlovskyella*, *Ornamentum*, *Reticulinasus* Schulze 1941 and *Subparmatus.*

- genus *Antricola* with the subgenera Antricola and Parantricola Črný, 1967

- genus *Nothoaspis* Keirans and Clifford, 1975

3. Taxonomic arrangement proposed by Camicas and Morel, 1977

Subfamily Argasinae

- genus *Argas* with the subgenera *Argas* s. s., *Microargas*, *Persicargas*, and   *Secretargas*

- genus *Carios* with the subgenera *Carios s.s.* and *Chiropterargas*

- genus *Ogadenus* with the subgenera *Ogadenus s.s.*, *Secretargas* and 0.5cm*Aviaogadenus* Pospelova-Shtrom, 1969 (the genus *Proknekalia* was not described at the time of this proposal, and Camicas and Morel did not realized the lack of adequate description of *Aviaogadenus*)

Subfamily Ornithodorinae

- genus *Alectorobius* with the subgenera *Alectorobius s.s.*, *Ornamentum*, *Reticulinasus*, *Subparmatus* and *Theriodoros.*

- genus *Alveonasus*

- genus *Antricola*

- genus *Parantricola*

- genus *Nothospasis*

- genus *Ornithodoros*

- genus *Otobius*

4. Taxonomic arrangement proposed by Camicas *et al.,* 1998

Subfamily Argasinae

- genus *Argas* with the subgenera *Argas s. s.* and *Persicargas*

- genus Carios with the subgenera *Carios s. s.* and *Chiropterargas*

- genus *Ogadenus* with the subgenera *Ogadenus* s. s., *Proknekalia* and *Secretargas*

Subfamily Ornithodorinae

- genus *Alectorobius* with the subgenera *Alectorobius s. s.*, *Reticulibius* Morel (sensu Camicas *et al.*, 1998), *Reticulinasus*, *Subparmatus* and *Theriodoros* (plus 3 unnamed and undefined subgenera)

- genus *Alveonasus*

- genus *Antricola*

- genus *Parantricola*

- genus *Microargas*

- genus *Nothoaspis*

5. Cladistic arrangement of Argasidae (Klompen and Oliver, 1993a)

Subfamily Argasinae

- genus *Argas* (including the previously recognized genera or subgenera *Argas*, *Persicargas*, *Secretargas*, *Ogadenus*, *Proknekalia* and *Alveonasus*).

Subfamily Ornithodorinae

- genus *Otobius*

- genus *Ornithodoros* (including *Ornithodoros*, *Pavlosvkyella*, *Theriodoros*, *Ornamentum* and *Microargas*)

- genus *Carios* (including *Carios*, *Chiropterargas*, *Alectorobius*, *Subparmatus*, *Reticulinasus*, *Antricola*, *Parantricola* and *Nothoaspis*)

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