SYSTEMATICS

First Mesozoic Record of a Parasitiform Mite: a Larval Argasid Tick in Cretaceous Amber (Acari: Ixodida: Argasidae)

HANS KLOMPEN [1] AND DAVID GRIMALDI [2]

ABSTRACT A larval argasid tick (Acari: Ixodida: Argasidae) is described from a single specimen preserved in amber from New Jersey. The amber is dated as Turonian, 90–94 mya, and thereby doubles the age of the oldest fossil in the mite order Parasitiformes. The specimen shows general characteristics of the genus *Carios,* but is unique because of its pattern of dorsal setae, featuring a double row of posterior marginal setae. Earlier hypotheses that *Carios* arose after the isolation of South America are challenged but not rejected by the discovery of this fossil. Salvaging these hypotheses seems most compatible with dispersal on birds, an idea consistent with the presence of a small feather in the same outcrop in which the tick fossil was found.

KEY WORDS Argasidae, *Carios,* fossil

THE ACARI ARE generally recognized as an ancient lineage of chelicerate arthropods, but their fossil record is somewhat mixed. The record for the order Acariformes is impressive, with two collections from the Devonian (around 380 mya) (Hirst 1923, Norton et al. 1988), and a considerable number of additional collections from more recent periods (Bernini 1991, Selden 1993). In contrast, the fossil record of its putative sistergroup, the order Parasitiformes, is much less extensive, so far not extending beyond the Upper Eocene (35–40 mya) (Selden 1993). Not a single fossil is known from the small suborders Holothyrida and Opilioacarida, and the currently diverse suborder Mesostigmata is represented solely by *Dendrolaelaps fossilis* Hirschmann from Miocene amber in Mexico (Hirschmann 1963) and a phytoseiid from Upper Eocene Baltic amber (Selden 1993). The record for the fourth and final suborder of Parasitiformes, Ixodida or ticks, is only marginally better. Most records are of Ixodidae or hard ticks: a male *Amblyomma* [resembling *A. testudinis* (Conil)] from Dominican amber (mid-Miocene, 15–20 mya) (Lane and Poinar 1986), *Ixodes tertiarius* Scudder from Oligocene deposits (≈30 mya) in Wyoming (Scudder 1885), and *I. succineus* Weidner from Baltic amber (35–40 mya) (Weidner 1964). Argasidae or soft ticks are represented by *Ornithodoros antiquus* Poinar described from Miocene Dominican amber (Poinar 1995). The discrepancy between the fossil records of the two orders may very well be an artifact of differing probabilities of preservation (Bernini 1991), but it is also consistent with the hypothesis that the Acari are not monophyletic (e.g., Van der Hammen 1977). Within this general context, the discovery

of a larval argasid tick preserved in amber from central New Jersey is of some importance. These amber deposits have been dated palynologically to the Upper Cretaceous; specifically Turonian (90–94 mya) (Christopher 1979, Grimaldi et al. 2000). This discovery doubles the age of the oldest parasitiform fossils, and narrows the gap between the oldest acariform and parasitiform fossils by ≈50 million years.

Here we describe this species with a few notes on how it fits with current views of setation patterns in argasid ticks and with the evolution of the genus *Carios.*

Materials and Methods

The single available specimen is embedded in amber. The amber fragment was prepared at the American Museum of Natural History. Observations were made using both transmitted and reflected light microscopy with magnifications up to 320×. The thickness of the amber fragment did not allow observations under higher power.

Pencil drawings were prepared using a drawing tube on a Zeiss Axioskop compound microscope (Carl Zeiss, Inc., Thornwood, NY). They were scanned and redrawn from the scanned image using Adobe Illustrator (Adobe Systems, Inc., San Jose, CA). Setal designations for the palps and legs follow Klompen (1992).

Systematic Affinities

Provisionally, the larva is assigned to the extant argasid genus *Carios.* The presence of a pair of postcoxal setae on the venter, the reduced complement of palp femoral and tibiotarsal setae, and the possible presence of unpaired seta *dm* on tarsi II-III exclude membership in the Argasinae. Within the Ornithodorinae, the pres-

[1] Acarology Laboratory, Department of Entomology, Ohio State University, Columbus, OH 43212.
[2] Department of Entomology, American Museum of Natural History, New York, NY 10024.
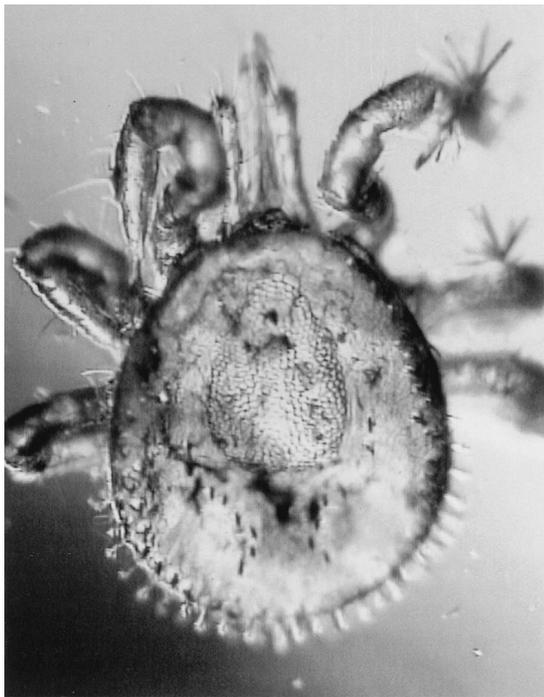
Fig. 1. *C. jerseyi*, dorsal view.

ence of a large median dorsal shield with a more or less narrowed anterior end ("triangular" shape) (Figs. 1 and 2a) and the insertion of setae *l2* on tarsi I at the same level as setae *d2*, are most consistent with membership in the genus *Carios.* Members of the genus
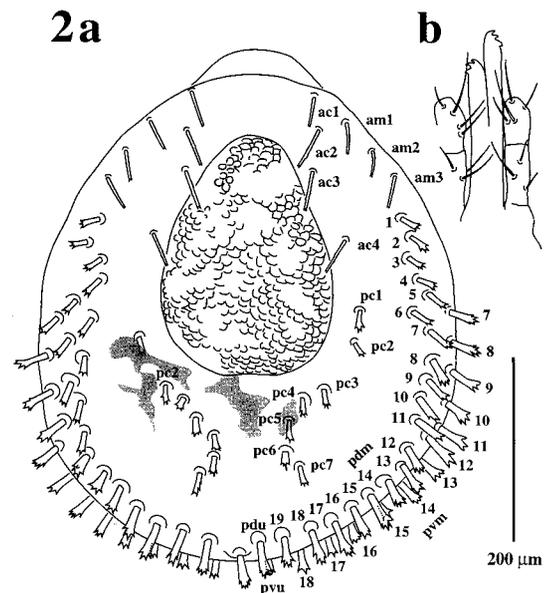

Fig. 2. *C. jerseyi* (a) dorsal view idiosoma; (b) dorsal view hypostome and palps. Designations for body setae reflect tentative associations of *pdm* and *pvm* setae.

Ornithodoros usually lack a dorsal shield, and if present, it is rounded or rectangular, not triangular. They also carry setae *l2* on tarsus I proximal to setae *d2*, rarely retain palp genual setae *al*, and generally lack the postcoxal setae. However, if the observed restriction of hypostomal denticles to ≈40% of the hypostome is real (and not an artifact of suboptimal observation conditions), this would be consistent with membership in *Ornithodoros.* Presence of small spines on the palp trochanter, the diagnostic character for larval *Ornithodoros* (Klompen 1992, Klompen and Oliver 1993), could not be established.

Carios jerseyi n. sp.
(Figs. 1–4)

Gnathosoma. *Hypostome* (Fig. 3). Hypostomal dentition at least 2/2 near the tip. It is possible that the actual dental formula is 3/3, but the marginal areas are not sufficiently visible to distinguish a possible double row near the margins. Overall shape moderately pointed; a corona appears absent. Hypostomal setae not observed.

Palps (Figs. 2b and 3). Palps long and slender, a condition found in all argasid larvae. Trochanters poorly visible, without setae. Femora and genua with, respectively, four (*al, ad, pd, pl*) and five (*al, 2 ad, pd, pl*) setae. Tibiotarsi with one seta on the basal part and about seven in the distal tuft. The expected presence of a ventral seta (*v*) on the basal section of the tibiotarsi could not be established, as the ventral part of that segment was not clearly visible on either palp. The absence of a second *pd* seta on the femur and the presence of at most two setae on the basal section of the tibiotarsus is characteristic for the Ornithodorinae. Larval Argasinae (and Ixodidae) carry two *pd* setae on the femur, and four setae basal on the tibiotarsus. Unlike the legs, the palps are relatively well visible, and the setal formulas for these appendages are close to complete.

Idiosoma (Figs. 1, 2a, and 3). Length, excluding the gnathosoma, ≈520 μm, greatest width ≈445 μm.

Shield. Relatively large median dorsal shield present; posterior end nearly straight, anterior end bluntly pointed. The shield is distinctly patterned in a cobblestone-like fashion (Fig. 1).

Setation. Dorsal setal complement unique among larval Argasidae. Anterior setae long and slender with a few small barbs along the shaft and with bifid tips. Most posterior setae stout and generally shorter, their tips split into 3–5 branches. Such morphological differentiation in dorsal setae is unusual among argasid larvae. A total of 92 setae (14 slender, the rest stout) was observed. In contrast to the condition found in other argasid larvae carrying large setal complements, setal insertions are remarkably symmetrical. The standard setal nomenclature for argasid larvae (Kohls et al. 1965) is insufficient to describe the observed pattern. For the purpose of discussing this pattern, the setae are therefore labeled based on their shape and position (Fig. 2a).
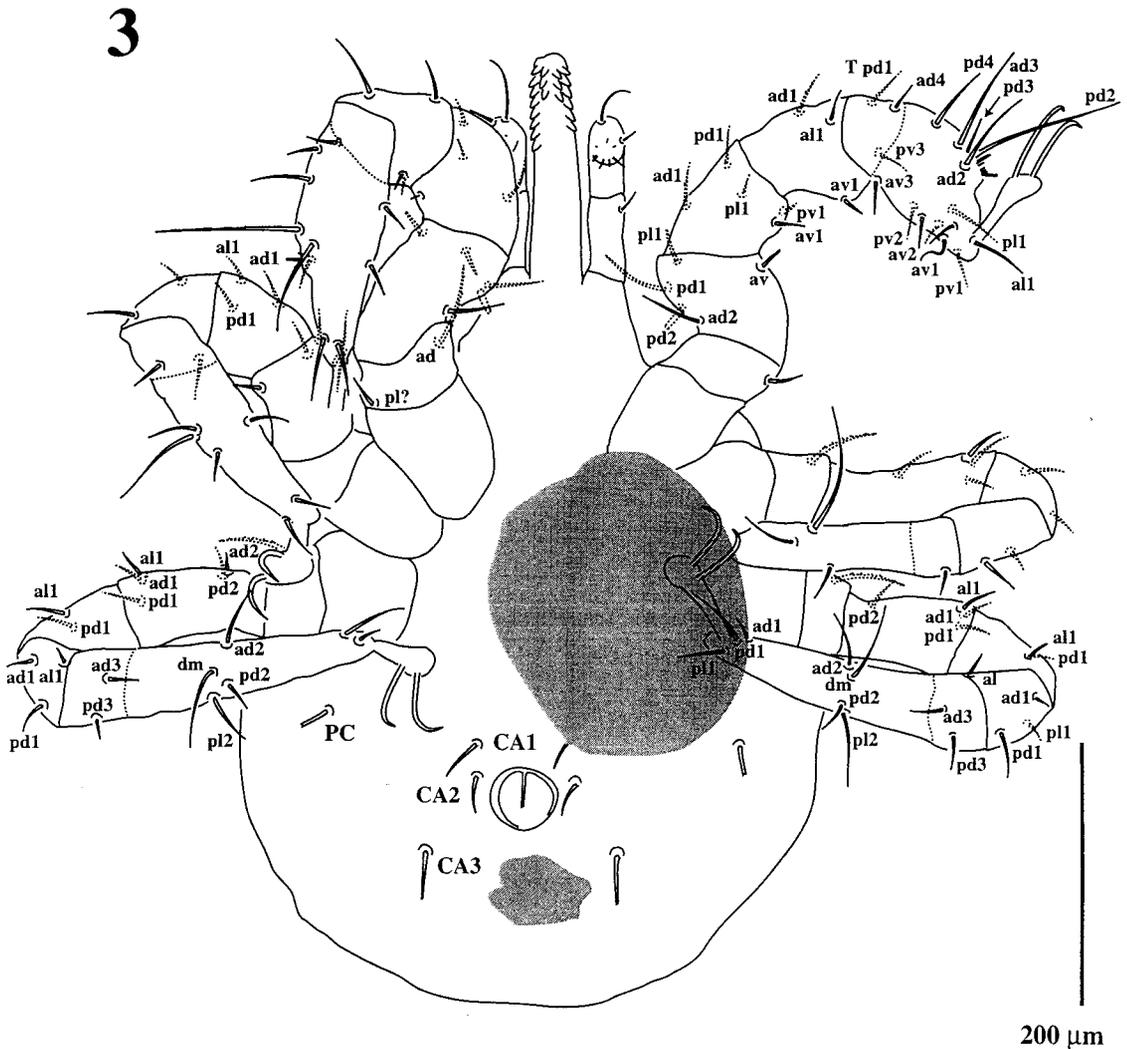
Fig. 3. *C. jerseyi*, ventral view. Designations for the leg setae are provisional, and are added only on segments where the setation complement is assumed to be relatively complete.

The slender, anterior setae are arranged into two series, one central (*ac*), with four pairs, and another marginal (*am*), with three pairs of setae. Similarly, the more posterior stout setae can be divided into central and marginal setae. The marginal setae are arranged in two rows, which for purposes of discussion are designated as posterior dorsal marginal (*pdm*) and posterior ventral marginal (*pvm*). Matches for the first six marginal setae on each side are not obvious. Tentatively they are grouped in the *pdm* series. All other *pdm* setae are easily matched with setae in a *pvm* position. Assumed matches are indicated in Fig. 2a by the use of similar numerals. Only one pair of dorsal marginal setae, designated *pdm19*, has no ventral marginal counterpart. In addition, to the pairs of marginal setae, one set of unpaired setae (*pdu* and *pvu*) is present. Observed symmetry among the less numerous posterior central (*pc*)

setae is almost as good, although there are some distinct positional differences between the *pc2* setae on the right and the left side (Fig. 2a). All remaining central setae (*pc1*, *pc3–pc7*) are matched in number and position.

The observed ventral setal complement is much smaller. The sternal region is poorly visible and none of the expected three pairs of sternal setae was observed. The opisthogaster (Fig. 3) carries three pairs of circumanal (*CA*) and one pair of postcoxal (*PC*) setae (terminology sensu Kohls et al. 1965). A distinct unpaired posterior median (*PM*) seta is absent, but may be represented by the unpaired *pvu* seta discussed above. The unpaired *pdu* seta does not appear to have an obvious homologue in any other argasid larva. The usual pair of anal valve setae was not observed, but these setae are often very small, and their presence cannot be excluded.

Legs (Fig. 3). Of all the different body parts, these were the most difficult to study because of the unfavorable orientation of some leg segments (especially tibiae and genua). In general, setae that do not extend beyond the plane of the segment(s) were difficult to see. Given that it was rarely possible to see all setae on a given segment, setal designations have to be tentative.

Trochanters I-III with a large *ad* seta. An additional smaller seta present posterior on trochanters I (*pl*?). The expected ventral trochanteral setae were not observed. Femora I each with at most five visible setae, assumed to be *ad, pd1, pd2, pl,* and *av.* Relative to other *Carios* larvae, another *ad*, a *pv*, and possibly another *av* seta would have been expected. Setae *pd2* I have an unusual shape, resembling thick, blunt rods, rather than the slender, tapering shape of the other leg setae. Femora II-III carry at least five setae each, including two *ad* and two *pd* setae (left leg III). Setae *pd2* II-III are not rod shaped. Genua I with at least five setae each (*ad1, pd1, pl1, av1, pv1*). No setae were observed in the *al* position, but the presence of two ventral setae is unexpected given that most *Carios* lack setae *pv1.* Tibiae I carry at least four setae each (*al1, ad1, pd1, av1*), all of which are present in extant *Carios* species. Genua and tibiae II–III carry at least three setae each (*al1, ad1, pd1*).

One of the tarsi I (right leg) could be viewed in lateral view, which allowed relatively detailed observations. The resulting pattern appears normal for Ornithodorinae (Klompen 1992), with setal pairs *d2–d4, l1–l2* (*l2* setal pair is not labeled in Fig. 3) present, and setal pairs *l3, l4,* and *v4* absent. Setae *pd3* are inserted at the level of the *d2* setae, with setae *ad3* inserted slightly more basal. The *l2* setae are inserted at the level of the *d2* setae. This condition is found in a few *Argas*, all *Otobius,* and many *Carios,* but setae *l2* setae have shifted to a position distinctly proximal to the *d2* setae in larvae of the remaining argasid taxa (including most *Argas,* and all *Ornithodoros*). The *dm2* setae were not observed, but they are generally very small and positioned between the *d2* setae, thus extremely difficult to see in lateral view of any specimen. The anterior pit of Haller's organ carries at least six sensilla.

The setation pattern of tarsi II–III appears to include an unpaired median dorsal seta (*dm*), based on the following reasoning. The visible surface of tarsi II–III is clearly dorsal, as inferred by the position of two distinct basitarsal setae (only one dorsal pair in nearly all Argasidae). The four median dorsal setae on these tarsi could be interpreted as *al2, ad2, pd2,* and *pl2,* but this suggests that the *al* and *pl* setae are in the same plane, with only the ventral setae (if present) on the other half of the segment. This is not very likely. An easier fit with existing views is to assume that one of the four setae is indeed the unpaired median dorsal seta, with (most probably) *al2* in a position not visible from this angle. In either case, the *l2* setae are positioned at the same level as the *d2* setae, and not distal to the *pd2* setae as found in most extant *Carios.* The

expected ventral setae, pairs *v1* and *v2,* were not observed on any of the tarsi.

Type Material. HOLOTYPE: larva, Sayreville, Middlesex County, NJ, USA, G.R. Case. Depository: amber fossil collection of the Department of Entomology, American Museum of Natural History (AMNH-NJ-8). The specimen was recovered during studies of amber deposits from the Raritan Formation (Turonian) of central New Jersey (Grimaldi et al. 2000).

Discussion

Setal Homologies. The unusual dorsal setal pattern observed in *C. jerseyi* can be derived from more common patterns in the family, but only after considerable modifications. Many larval Argasinae show two or three series of anterior dorsal and three series of posterior dorsal opisthosomal setae, one central, one medio-lateral (both included as centrals by Sonenshine et al. [1962]), and one marginal (the dorsolaterals of Sonenshine et al. [1962]). The pattern observed in *C. jerseyi* could be derived from the argasine pattern, by moving the medio-lateral series in Argasinae to a more marginal position (*pdm* of this study). However, the pattern in *C. jerseyi* differs from that observed in Argasinae by the matching of the *pdm* and *pvm* series setae, a pattern not documented in other larval Argasidae. Larval Ornithodorinae generally have more reduced dorsal setal patterns. At most two posterior dorsal series are recognizable. The pattern in *C. jerseyi* can be related to that in Ornithodorinae by elimination of one of the marginal series and reduction in numbers of the second.

It is tempting to consider preliminary comparisons with idiosomal setal patterns in other Parasitiformes. Such comparisons would be prompted by the distinctly ordered arrangement of the dorsal setae in different series, a characteristic of the modified Hirschmann system (Lindquist and Evans 1965). That system has proven to be very adaptable, not only fitting the majority of Mesostigmata, but also larval Opilioacarida (Klompen 2000) and Ixodidae (Klompen et al. 1996b). However, use of this system for larval Argasidae has so far been precluded, because of the generally variable setal arrangements in many larval argasid larvae.

Despite the distinctly ordered arrangement of the dorsal setae, comparisons of this species with nonargasid Parasitiformes are not straightforward. The central setae most likely are homologous to *j/J* series setae in the Lindquist and Evans system, but the sheer number of marginal setae requires some contortions in setal homology assignments. Two possible hypotheses will serve to illustrate this point. Both assume the absence of *r/R* and *rv/Rv* series, as in other larval Parasitiformes. Both would also fit a model where the slender, anterior setae would be part of ancestral propodosomal segments. In the following discussion we will ignore the setation patterns for the propodosoma, and concentrate on the hysterosoma. The assumption of Klompen et al. (1996b) that the prepodal segments do not contribute to the dorsal propodoso-
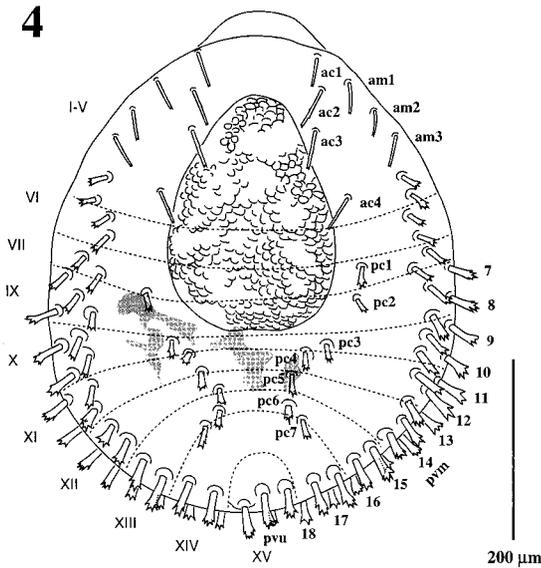
Fig. 4. *C. jerseyi*, dorsal view. Hypothesized segmental borders for the hysterosoma added, segmental borders for the propodosomal region are unclear. Designations for most *pdm* setae are omitted to limit clutter.

mal cuticle is weakly supported, casting serious doubts on their hypotheses of homology for the propodosomal segments. The hysterosoma (segments VI–XV in Fig. 4) is assumed to include remnants of ten ancestral segments, one of which, the pregenital segment (VIII in Fig. 4) is not expressed on the dorsum. This arrangement is the same as proposed for Ixodidae and possibly Mesostigmata (Klompen et al. 1996b). We did modify segmental designations for the hysterosoma relative to more traditional models (e.g., Van der Hammen 1970, Sitnikova 1978, Klompen et al. 1996b) to incorporate new data on embryonic segmentation patterns in Chelicerata (Damen et al. 1998, Telford and Thomas 1998). The latter suggest that legs I–IV represent ancestral segments IV–VII instead of III–VI.

The details are far less clear. The first hypothesis of setal homology assumes duplications in many ancestral positions, assigning most *pdm* setae to the *z*/Z series and all their matching *pvm* setae to the *s*/S series. This retains the *Sv*, *Zv*, and *Jv* designations for ventral setae, as is common for most Mesostigmata. The main problem is that such duplications have never been recorded before, and, second, this hypothesis offers no obvious explanation of why such duplications would not have taken place for the leg-bearing segments (VI–VII in Fig. 4). The second hypothesis requires a radically different interpretation of the ventral setae but it would require no duplications. Under this hypothesis the *pdm* setae are homologous to both the *z*/Z and *s*/S setae (series merged) and the *pvm* setae to the *sv*/Sv and *zv*/Zv setae (series merged). The absence of *pvm* setae on the leg-bearing segments would be expected under this hypothesis, because these segments rarely if ever have setae in the *sv* or *zv*

positions. However, it would leave only the *Jv* series to cover all ventral setae, an unlikely arrangement given the presence of the "postcoxal" setae. In short, while the obvious symmetry of the dorsal setal pattern invites comparisons with other parasitiform suborders, the number of variables seems too large, and the amount of comparative evidence from other argasid species too small, to allow substantiated hypotheses of homology.

Evolution and Distribution. The presence of this specimen raises some interesting questions regarding the distribution, host associations, and age of the genus and, by inference, the family. Previous hypotheses on the origin of the genus, based on a combination of systematic analyses and comparisons of distribution patterns, indicated an origin in the Neotropic region (Klompen et al. 1996a). Presumably this would be after the isolation of South America, around 100 mya. The presence of this species in North America around 90–94 mya is compatible with the timing proposed under this hypothesis, but it would require dispersal across the ocean barrier separating the North and South American land masses at that time. Such a requirement raises its own questions. Most extant species of *Carios* are mammal associated, and the taxa associated with nonvolant mammals are not likely to disperse well across ocean barriers. Bats (order Chiroptera) are common hosts of extant *Carios* species, and bat associated species might disperse across water more easily. However, the earliest bat fossils originate from the early Eocene (Simmons and Geisler 1998), and the group most likely originated in the Paleocene or, at best, in the uppermost Cretaceous (65–70 mya) (N. Simmons, personal communication). This leaves the two main groups of flying archosaurs, birds and pterosaurs, both of which were present in the relevant time period, as most likely hosts for *C. jerseyi*. Although we have only speculation on tick–pterosaur associations, many extant *Carios* are bird associated, and several of these bird associated species have dispersed extensively. For example, *C. capensis* (Neumann) has been recorded from several continents. Consistent with the "bird host" hypothesis, the tick specimen was found in the same outcrop as an amber-encased small feather (Grimaldi and Case 1995).

The next question would be whether this specimen is related to known extant bird associated lineages within *Carios*. At this point, the amount of available data for *C. jerseyi* is insufficient to fully answer that question. Although somewhat similar to both *C. rudis* (Karsch), a South American bird-associated species, and the "*capensis* group" of species, a small lineage of species associated most commonly with ocean-going birds, critical data are missing, disallowing substantiated hypotheses.

Although this specimen provides some welcome hard evidence on the minimum age of Argasidae, Ixodida, and Parasitiformes in general, its presence raises a host of new questions. Additional comparative studies among Argasidae, especially *Carios* species, may help in resolving some of these problems. A morphol-

ogy based analysis of relationships in *Carios*, including this fossil species, is in progress.

Acknowledgment

References Cited

Bernini, F. 1991. Fossil Acarida, pp. 253–262. *In* A. Simonetta and S. C. Morris [eds.], The early evolution of Metazoa and the significance of problematic taxa. Cambridge University Press, Cambridge.

Christopher, R. A. 1979. Normapolles and triporate pollen assemblages from the Raritan and Magothy Formations (Upper Cretaceous) of New Jersey. Palynology 3: 383–399.

Damen, W.G.M., M. Hausdorf, E.-A. Seyfarth, and D. Tautz. 1998. A conserved mode of head segmentation in arthropods revealed by the expression pattern of Hox genes in a spider. Proc. Natl. Acad. Sci. USA 95: 10665–10670.

Grimaldi, D., and G. R. Case. 1995. A feather in amber from the Upper Cretaceous of New Jersey. Am. Mus. Novit. 3126: 1–6.

Grimaldi, D., A. Shedrinsky, and T. Wampler. 2000. A remarkable deposit of fossiliferous amber from the Cretaceous (Turonian) of New Jersey, pp. 1–79. *In* D. Grimaldi [ed.], Studies on fossils in amber, with particular reference to the Cretaceous fauna of New Jersey. Backhuys, Leiden.

Hirschmann, W. 1963. A fossil mite of the genus *Dendrolaelaps* (Acarina, Mesostigmata, Digamasellidae) found in amber from Chiapas, Mexico, pp. 69–70. *In* A. Petrunkovitch [ed.], Studies of fossiliferous amber arthropods of Chiapas, Mexico. University of California Publications in Entomology, Berkeley.

Hirst, S. 1923. On some arachnid remains from the Old Red Sandstone (Rhynie Chert, Aberdeenshire). Ann. Mag. Nat. Hist. (9th series) 12: 455–474.

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

Klompen, J.S.H. 2000. Prelarva and larva of *Opilioacarus (Neocarus) texanus* (Chamberlin & Mulaik) (Acari: Opilioacarida) with notes on the patterns of setae and lyrifissures. J. Nat. Hist. 34: 1977–1992.

Klompen, J.S.H., and J. H. Oliver, Jr. 1993. Systematic relationships in the soft ticks (Acari: Ixodida: Argasidae). Syst. Entomol. 18: 313–331.

Klompen, J.S.H., W. C. Black IV, J. E. Keirans, and J. H. Oliver, Jr. 1996a. Evolution of ticks. Annu. Rev. Entomol. 41: 141–161.

Klompen, J.S.H., J. E. Keirans, N. A. Filippova, and J. H. Oliver, Jr. 1996b. Idiosomal lyrifissures, setae, and small glands as taxonomic characters and potential indicators of ancestral segmentation patterns in larval Ixodidae (Acari: Ixodida). Int. J. Acarol. 22: 113–134.

Kohls, G. M., D. E. Sonenshine, and C. M. Clifford. 1965. The systematics of the subfamily Ornithodorinae (Acarina: Argasidae). II. Identification of the larvae of the Western Hemisphere and descriptions of three new species. Ann. Entomol. Soc. Am. 58: 331–364.

Lane, R. S., and G. O. Poinar, Jr. 1986. First fossil tick (Acari: Ixodidae) in New World amber. Int. J. Acarol. 12: 75–78.

Lindquist, E. E., and G. O. Evans. 1965. Taxonomic concepts in the Ascidae, with a modified setal nomenclature for the idiosoma of the Gamasina (Acarina: Mesostigmata). Mem. Entomol. Soc. Can. 47: 1–64.

Norton, R. A., P. M. Bonamo, J. D. Grierson, and W. M. Shear. 1988. Oribatid mite fossils from a Devonian deposit near Gilboa, New York State. J. Paleontol. 62: 259–269.

Poinar, G. O., Jr. 1995. First fossil soft ticks, *Ornithodoros antiquus* n. sp. (Acari: Argasidae) in Dominican amber with evidence of their mammalian host. Experientia Basel 51: 384–387.

Scudder, S. H. 1885. A contribution to our knowledge of Paleozoic Arachnides. Proc. Am. Acad. Sci. Ser. 2: 12.

Selden, P. A. 1993. Arthropoda (Aglaspidida, Pycnegonida and Chelicerata), pp. 297–320. *In* M. J. Benton [ed.], The fossil record 2. Chapman & Hall, New York.

Simmons, N. B., and J. H. Geisler. 1998. Phylogenetic relationships of *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx* to extant bat lineages, with comments on the evolution of echolocation and foraging strategies in microchiroptera. Bull. Am. Mus. Nat. Hist. 235: 1–182.

Sitnikova, L. G. 1978. The main evolutionary trends of the Acari and the problem of their monophyletism. Entomol. Obozr. 57: 431–457.

Sonenshine, D. E., C. M. Clifford, and G. M. Kohls. 1962. The identification of larvae of the genus *Argas* (Acarina: Argasidae). Acarologia 4: 193–214.

Telford, M. J., and R. H. Thomas. 1998. Expression of homeobox genes shows chelicerate arthropods retain their deutocerebral segment. Proc. Nat. Acad. Sci. USA 95: 10671–10675.

Van der Hammen, L. 1970. La segmentation primitive des Acariens. Acarologia 12: 3–10.

Van der Hammen, L. 1977. A new classification of Chelicerata. Zool. Med. Leid. 51: 307–319.

Weidner, H. 1964. Eine Zecke, *Ixodes succineus* sp. n., im baltischen Bernstein. Veroff. Uberseemus. Bremen 3: 143–151.