

Kampimodromus aberrans (Acari: Phytoseiidae) from the USA: morphological and molecular assessment of its density

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Abstract

Morphological measurements and a mitochondrial molecular marker (COI) were used to identify specimens reported as *Kampimodromus aberrans* on hazelnut in the USA. Several species and populations of this genus were studied to assist with identification. Both data types showed that specimens from the USA differed from *K. aberrans* from other regions. USA specimens seem to belong to the same species as *Kampimodromus* specimens from France on hazelnut. These mites were morphologically similar to *Kampimodromus coryli* and *K. corylosus*, which according to the original descriptions, are distinguished by the presence or absence of a tooth on the movable digit of the chelicera, with *K. coryli* having one tooth and *K. corylosus* none. As chelicerae of *Kampimodromus* from hazelnut in the USA and France are toothless, they are assigned to the species *K. corylosus*. Studies showed that morphological characters traditionally used to identify *Kampimodromus* species, such as setal length, are of less value than other characters that are difficult to observe, such as the numbers of solenostomes and the presence of teeth on the movable digit of the chelicerae. Some synonyms are discussed.

Keywords: Phytoseiidae, *Kampimodromus*, taxonomy, cytochrome oxidase 1, mites, morphology

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Introduction

Phytoseiid mites are important predators of phytophagous mites on many crops worldwide (McMurtry & Croft, 1997). The Phytoseiidae includes 89 genera and more than 1980 species (Chant & McMurtry, 2003; Moraes *et al.*, 2004; Chant & McMurtry, 2004a,b, 2005a,b). The genus *Kampimodromus* Nesbitt (1951) belongs to the Amblyseinae

subfamily and contains 15 species, nearly all from the West Palearctic (Moraes *et al.*, 2004; Kolodochka, 2005). *Kampimodromus aberrans* (Oudemans), the most studied species in the genus, is an efficient natural enemy of mites in vineyards of southern Europe (Barret & Kreiter, 1992; Duso, 1992; Camporese & Duso, 1996; Kreiter *et al.*, 2000) and occurs mostly on plants with domatia and 'hairy leaves' (Duso *et al.*, 1993; Tixier *et al.*, 2000; Kreiter *et al.*, 2002). It is also reported from the USA on hazelnut (*Corylus avellana* L.) (Krantz, 1973; Moraes *et al.*, 2004); there its phoretic dispersal was observed on female aphids of *Myzocallis coryli* (Goeze) (Krantz, 1973).

Although *Kampimodromus* on hazelnut in the USA are recognized as *K. aberrans*, there is evidence that this may

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Table 1. Characteristics of the mite species and populations studied within the genus *Kampimodromus*. For molecular tests, the accession numbers reported in the Genbank data base are given.

Species	Number of solenostomes	Country	Locality	Host plant	Number of females measured	Morphology examined	Molecular tests
<i>K. aberrans</i>	4	France	Montpellier	<i>Celtis australis</i>	35	X	EF372605
<i>K. aberrans</i>	4	France	Montpellier	<i>Quercus pubescens</i>	30	X	EF372606
<i>K. aberrans</i>	4	France	Montpellier	<i>Corylus avellana</i>	10	X	
<i>Kampimodromus</i> sp.	5	France	Montpellier	<i>Corylus avellana</i>	23	X	
<i>Kampimodromus</i> sp.	5	France	Burgundy	<i>Corylus avellana</i>	26	X	EF372604
<i>Kampimodromus</i> sp.	5	USA	Corvallis (Oregon)	<i>Corylus avellana</i>	22	X	EF372610
<i>K. ericinus</i>	5	France	Montpellier	<i>Cystus monspelliensis</i>			EF372607
<i>K. ericinus</i> ⁽¹⁾	5	Italy	Catanzaro	<i>Rubus</i> sp.	1	X	
<i>K. alettae</i> ⁽¹⁾	5	South Africa	Transvaal	<i>Tapinanthus natalitius</i>	1	X	
<i>K. echii</i> ⁽¹⁾	5	Canary Islands	Sepultura del Gigante	<i>Echium decaisnei</i>	1	X	
<i>K. langei</i> ⁽³⁾	5	Italy	Padova	<i>Ostrya carpinifolia</i>	1	X	EF372609
<i>K. coryli</i> ⁽²⁾	5	Ukraine	Teremky	<i>Corylus avellana</i>	1	X	
<i>K. coryli</i> ⁽²⁾	5	Russia	Moscow	<i>Corylus avellana</i>	1	X	
<i>K. karadaghensis</i> ⁽²⁾	5	Crimea	Karadag	<i>Crataegus</i> sp.	1	X	
<i>K. hmiminai</i>	6	Morocco	Meknes	<i>Ficus carica</i>			EF372608

⁽¹⁾Measurements of a holotype; ⁽²⁾Measurements from the published descriptions (holotype); ⁽³⁾Measurements from non-holotype specimens.

not be so. Phoretic dispersal reported for *K. aberrans* in the USA has not been seen among *K. aberrans* in Europe (Krantz, 1973). Morphological differences between larval stages of European and USA populations have been noted (Croft, unpublished data). Adult female *K. aberrans* from the USA have five solenostomes (glandular pores) on the dorsal shield, whereas *K. aberrans* have only four (Ragusa & Tsolakis, 1994). According to the last world revision of the genus (Ragusa & Tsolakis, 1994), this latter morphological difference would not key the USA specimens to *K. aberrans*. However, solenostomes are difficult to observe and their use for species diagnostics is controversial (Athias-Henriot, 1969, 1971, 1975; Chant & McMurtry, 1994, 2003). The aim of this study was to determine species identification of USA *K. aberrans* and assess morphological characters used to separate *Kampimodromus* species.

Material and methods

Species and populations studied (table 1)

K. aberrans were collected in Montpellier (south of France) from European hackberry (*Celtis australis* L.), downy oak (*Quercus pubescens* Willdenow) and hazelnut (*Corylus avellana*) (table 1). Morphological and molecular studies were carried out on the two former populations, whereas only morphological analysis was conducted on hazelnut specimens. On hazelnut mites, *Kampimodromus* with four solenostomes (identified as *K. aberrans*) and with five solenostomes (*Kampimodromus* sp.) were observed, and it was impossible to separate them for DNA typing. Specimens of *Kampimodromus* sp. with five solenostomes from hazelnut in Burgundy were measured and DNA typed.

Kampimodromus sp. mites from the USA, taken from the same hazelnut tree in Corvallis, Oregon, where *K. aberrans* had been reported by Krantz (1973), were measured and DNA typed. To identify mites with five solenostomes from hazelnut in France and the USA, seven species of *Kampimodromus* having five solenostomes were examined. Morphological measurements (see below) were carried out on

holotypes of *K. ericinus* Ragusa (University of Palermo, Italy), *K. alettae* Ueckermann & Loots (Agriculture Research Council, Plant Protection Research Institute, Pretoria, South Africa) and *K. echii* Ferragut & Pena-Estevéz (Universita Politecnica de Valencia, Spain). Similar measurements of *K. langei* Wainstein & Arutunian were based on non-holotype specimens collected in Italy by Carlo Duso on *Ostrya carpinifolia* Scopoli, and those of *K. coryli* Meshkov, *K. corylosus* Kolodochka and *K. karadaghensis* Kolodochka were from the original published descriptions (Meshkov, 1999; Kolodochka, 2003, 2005).

It was impossible to get live or alcohol-preserved specimens of the seven described species having five solenostomes to sequence DNA (described below). Only DNAs of *K. langei* and *K. ericinus* were sequenced. Specimens of *K. langei* were collected on *O. carpinifolia* in Padova (Italy) and those of *K. ericinus* in Villeneuve (France) from rockrose, *Cystus monspelliensis* L. Two other species were also sequenced: *Kampimodromus hmiminai* McMurtry & Bounfour from Moroccan fig trees with six solenostomes, and *Typhlodromus pyri* Scheuten (Phytoseiidae: Typhlodrominae) from southern France on *Rubus* sp. (berries). Mites belonging to sequenced populations were mounted on slides and deposited in the Agro-M/INRA Acarology collection in Montpellier, France.

Morphological analysis

Terminology for chaetotaxy and adenotaxy follow those of Rowell *et al.* (1978) and Athias-Henriot (1975), respectively. Between 8 and 34 female specimens of each population or species of *Kampimodromus* were mounted on slides in Hoyer's medium.

Dorsal seta length is a useful trait in species identification of *Kampimodromus*. Thus, 18 idiosomal dorsal setae of females were measured: j1, j3, j4, j5, j6, J2, J5, z2, z4, z5, Z1, Z4, Z5, s4, S2, S5, r3, R1. Lengths of macroseta on basitarsus IV and the numbers of solenostomes on dorsal shield and teeth on the movable digit of chelicera were also recorded.

Molecular analysis

DNA extraction

DNA was extracted from eggs, when possible, or starved females to avoid contamination from ingested prey. CTAB extraction was used. Several individuals (3–10 eggs, 5 females) were crushed and homogenized in 75 µl extraction buffer (2% CTAB, 1.4M NaCl, 0.2% 26-mercaptoethanol, 100 mM EDTA, 100 mM Tris-HCl, and pH 8.0). Tubes were incubated for one hour at 65°C. Later, 75 µl of chloroform: isoamyl alcohol mixture (24:1) was added and tubes were centrifuged at 6°C for 5 min at 1000 g. Forty µl of isopropanol was added to the decanted aqueous phase and chilled at –20°C for 20 min for DNA precipitation. After centrifugation (15 min, 6°C, 1000 g), the pellet was suspended in 100 µl of 96% alcohol at 4°C. After a final centrifugation of 10 min (6°C, 1000 g), the dried pellet was suspended in 20 µl of de-ionized water.

Marker used

Many molecular markers have been used in entomology (Loxdale & Lushai, 1998) while few have been used for mites (Navajas & Fenton, 2000; Cruickshank, 2002). Mitochondrial DNA (mt-DNA) has been widely used for studies with insects (Simon *et al.*, 1994; Roehrdanz & Degrugillier, 1998) and for some mites (Navajas *et al.*, 1996; Navajas & Fenton, 2000; Toda *et al.*, 2000, 2001; Otto & Wilson, 2001; Cruickshank, 2002; Evans & Lopez, 2002). The sequence variability of the mt-marker allows separation of genetic entities at species or subspecies levels (Harrison, 1989; Loxdale & Lushai, 1998) and has been used to study synonymy of mites (Navajas *et al.*, 1994, 1999; Anderson & Trueman, 2000; Toda *et al.*, 2000; Cruickshank, 2002).

DNA amplification and electrophoresis

The primers used to amplify a fragment of COI were the same as those used by Navajas *et al.* (1996) for Tetranychidae: 5'-3', TGATTTTTTGGTCACCCAGAAG and 5'-3' TACAGCTCCTATAGATAAAAC. PCR was performed in a total volume of 25 µl containing 2 µl of mite DNA, 1 µl of dNTP (2.5 mM for each nucleotide), 2.5 µl of Taq buffer, 1 µl of each primer (100 µM), 0.5 µl of Taq polymerase (Quiagen, 5 U µl⁻¹) and 18.9 µl of water. Thermal cycling conditions were as follow: 95°C for 1 min followed by 40 cycles of 92°C for 1 min, 45°C for 1 min and 72°C for 1 min. An additional 5 min at 72°C was allowed for final strand elongation. Electrophoresis was carried out in a 1.5% agarose gel in 0.5 X TBE buffer for 30 min at 100 volts.

DNA sequencing

PCR products were sequenced using the dynamic ET terminator cycle sequencing kit. Purification of DNA was carried out with Exosap-IT (Amersham). The sequencer used was the Megabase 1000 apparatus. All DNA fragments were sequenced along both strands.

Data analysis

Morphological data

Multiple variance (and Newman and Keuls means comparison test) and multifactorial analyses (Statistica[®],

2001) were performed to assess morphological differences between the different populations and species studied.

Molecular data

Sequences were checked and read manually using bioedit[®] (Hall, 1999). They were aligned using ClustalW[®] (1997) (Higgins *et al.*, 1994) and tested with Mega3.1[®] (Kumar *et al.*, 2004). A distance matrix was constructed with the Jukes & Kantor model because the rate transition/reversion is near 1 (0.9). A Neighbour Joining tree was constructed with a 1000 bootstrap.

Results

Morphological data

Significant differences were observed between *K. aberrans* and *Kampimodromus* sp. for all the characters ($P < 0.05$) (table 2). However, these differences were very small, and a great homogeneity within the populations was observed (low standard errors). No notable morphological differences were observed between the French and USA populations having five solenostomes and between *K. aberrans* and the US population, except for setae j3, J2 being slightly longer for *K. aberrans* and seta S5 being slightly smaller for *K. aberrans*. The multifactorial analysis confirms these results (fig. 1). The first factorial component (axis 1), explained by s4, j5, S2, Z1 and Z4, did not separate *K. aberrans* populations from each other and from the USA population. On this axis, the USA population has a similar position as populations with five solenostomes from hazelnut in Burgundy and Montpellier. The second factorial component (axis 2), mainly explained by seta S5, identified two groups. One was for all *K. aberrans*; the second was for French and USA populations with five solenostomes.

According to our analyses, seta measurements did not separate *K. aberrans* from *Kampimodromus* sp. with five solenostomes from France and USA. Only seta S5 showed this separation, having a value $< 14 \mu\text{m}$ for *K. aberrans* and $> 14 \mu\text{m}$ for *Kampimodromus* sp. No morphological character (seta lengths, solenostomes or occurrence of a tooth on the mobile digit) differentiated populations of *Kampimodromus* sp.

Kampimodromus ericinus and *K. karadaghensis* differed from other species, but were similar to each other in morphological measurements (table 2); only setae j1 and j3 differed in length. They also differed from other specimens in the multifactorial analysis (fig. 1). *K. echii* was also different from all other species (table 2, fig. 1). Seta measurements would, thus, give an accurate diagnostic for identification of these species. However, *K. alettae*, *K. coryli*, *K. langei* and *K. corylosus*, *K. aberrans* and *Kampimodromus* sp. had similar seta measurements (table 2, fig. 1).

Molecular data

Actual lengths of DNA fragments amplified from each species and isolate could not be determined, as the 5' and 3' ends of the sequences could not be read. Nonetheless, we could align 355 nucleotides of the sequences for analysis. A Blast search of the Genbank database showed that the sequences blasted with other COI sequences, and the best query coverage was obtained with *Varroa* sp. (Acari: Mesostigmata). The best score was 77% with *K. aberrans*.

Table 2. Values of the seta measurements and of other morphological characters of the populations and species of *Kampimodromus* (SD = standard deviation). Letters correspond to the results of the mean comparison test (Newman & Keuls).

	n	j1		j3		j4		j5		j6		J2		J5		z2		z4		z5	
		mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
<i>Kampimodromus</i> sp. 1	20	18.06b	0.54	27.44b	0.53	14.63b	0.27	14.13b	0.26	16.69ab	0.32	23.31c	0.74	5.31b	0.33	25.25b	0.58	34.06b	0.61	15.50ab	0.43
<i>kampimodromus</i> sp. 2	23	20.16a	0.51	27.55b	0.46	14.33b	0.24	13.65b	0.23	16.06b	0.28	21.01d	0.65	7.31a	0.29	25.24b	0.51	32.79b	0.54	14.95ab	0.38
<i>Kampimosdromu</i> sp. USA	22	20.06a	0.52	30.85a	0.50	15.85a	0.26	15.06a	0.25	16.90ab	0.31	26.25b	0.70	6.88a	0.31	28.47a	0.55	37.27a	0.58	15.89ab	0.42
<i>K. aberrans</i>	34	16.38b	0.42	31.87a	0.40	15.62a	0.21	15.82a	0.20	17.85a	0.24	29.55a	0.57	6.49a	0.25	27.61a	0.45	36.33a	0.47	16.41a	0.33
<i>K. aberrans</i>	8	16.25b	0.86	31.88a	0.83	15.16ab	0.43	15.63a	0.41	18.44a	0.50	31.09a	1.17	4.29c	0.56	28.75a	0.92	36.09a	0.97	15.91ab	0.68
<i>K. aberrans</i>	27	17.35b	0.47	31.88a	0.44	14.46b	0.23	14.46ab	0.22	17.33a	0.27	31.14a	0.62	6.33a	0.28	28.16a	0.49	37.60a	0.52	14.35b	0.36
<i>K. ericinus</i>		12.70		17.3		21		21		28		38		8		33		38		19	
<i>K. langei</i>		15		29		17		17		17		24		7		27		32		14	
<i>K. alettae</i>		18.3		30		18.3		17		21		27		5		31		40		16	
<i>K. coryli</i>		21		30		16		14		16		23		8		27		36		16	
<i>K. corylosus</i>		22		29		14		14		16		23		7		25		34		15	
<i>K. echii</i>		18		33		24		24		22		31		8		28		43		20	
<i>K. karadaghensis</i>		20.5		32.5		21		22		27.5		36.5		6.5		30.5		42		17.8	

	n	Z1		Z4		Z5		s4		S2		S5		r3		R1		STIV		Number of solenostomes	Number of tooth on mobil digit
		mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD				
<i>Kampimodromus</i> sp. 1	20	20.75b	0.52	40.13c	0.72	50.75b	1.12	43.63c	0.69	44.50b	0.82	16.46b	0.40	37.37b	0.55	24.25c	0.49	21.56bc	0.41	5	0
<i>kampimodromus</i> sp. 2	23	20.00b	0.45	36.63d	0.64	47.12c	0.98	39.09d	0.60	42.02c	0.72	17.45b	0.34	36.63b	0.47	24.42c	0.43	19.81d	0.36	5	0
<i>Kampimosdromu</i> sp. USA	22	23.69a	0.49	43.47b	0.69	56.48a	1.07	47.50b	0.65	50.11a	0.78	20.42a	0.37	40.40a	0.51	28.30a	0.47	22.31b	0.41	5	0
<i>K. aberrans</i>	34	21.02b	0.40	40.68c	0.56	43.12d	0.86	45.55bc	0.53	44.46bc	0.63	11.41d	0.29	34.85c	0.41	22.97cd	0.38	20.75cd	0.33	4	0
<i>K. aberrans</i>	8	20.94b	0.82	47.97a	1.14	53.44b	1.77	51.09a	1.08	48.91a	1.30	12.75c	0.77	37.32b	0.91	26.43b	0.83	23.59a	0.65	4	0
<i>K. aberrans</i>	27	20.56b	0.44	41.59bc	0.61	45.86c	0.95	46.69b	0.58	46.22b	0.70	9.98e	0.32	33.84c	0.45	21.70d	0.42	21.14bcd	0.35	4	0
<i>K. ericinus</i>	33		43		51		51		51		18		39		30		25		5	0	
<i>K. langei</i>	20		43		51		34		37		20		37		31		24		5	1	
<i>K. alettae</i>	20		43		51		34		37		20		37		31		24		5	?	
<i>K. coryli</i>	22		43		53		44		48		18		41		28				5	1	
<i>K. corylosus</i>	21		39		48		41		43		18		35		25		22		5	0	
<i>K. echii</i>	33		35		36		55		44		12		39		21		34		5	1	
<i>K. karadaghensis</i>	34.8		44		49.5		53.5		56.5		20		37.5		29		26		5	0	

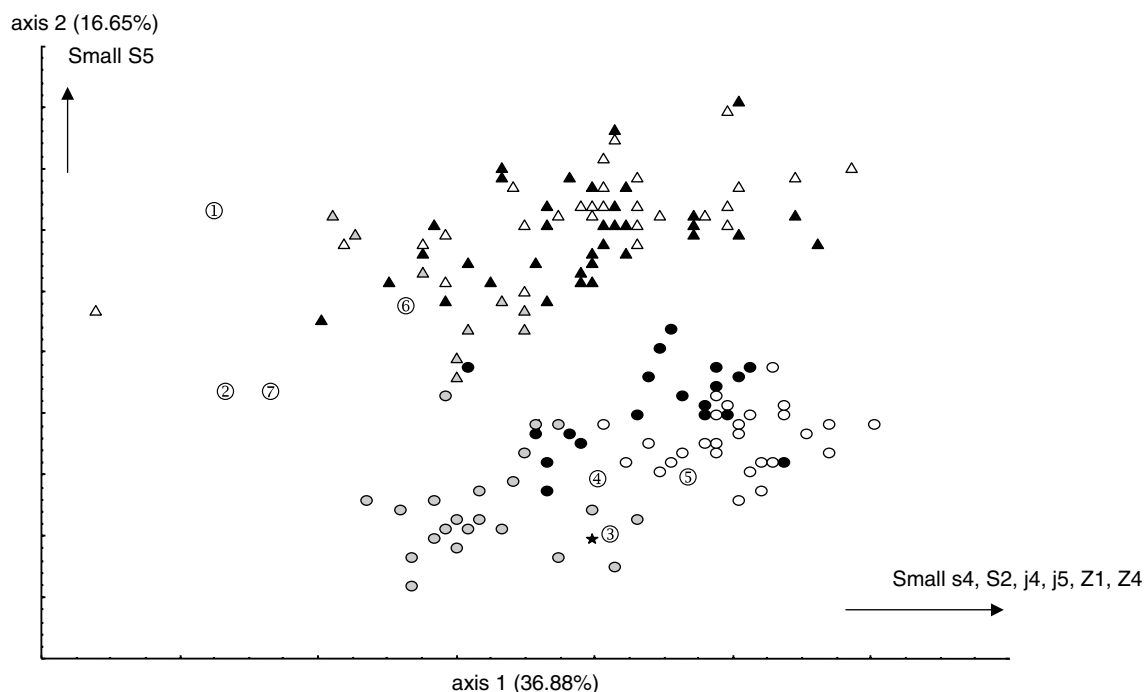


Fig. 1. Multifactorial analysis based on seta lengths of all the populations tested and of paratypes of several species of the genus *Kampimodromus*. ①, *K. echii*; ②, *K. ericinus*; ③, *K. coryli*; ④, *K. langei*; ⑤, *K. corylosus*; ⑥, *K. alatae*; ⑦, *K. karadaghensis*; ○, *Kampimodromus* sp. USA, 5 solenostomes; ●, *Kampimodromus* sp. C. *avellanae* 5 solenostomes Montpellier; △, *Kampimodromus* sp. C. *avellanae* 4 solenostomes Montpellier; ☆, *K. aberrans* Q. *pubescens*; ▲, *K. aberrans* C. *australis*; ○, *Kampimodromus* sp. C. *avellanae* 5 solenostomes Burgundy.

DNA analysis showed a high percentage of adenine and thymine (fig. 2) and these rates were constant for all species and populations. Pairwise (uncorrected) distances between sequences are shown in table 3. The greatest distance was between the out-group, *T. pyri* and *Kampimodromus* spp. (table 3). The greatest distances among *Kampimodromus* spp. were between *K. langei* and *K. aberrans*, and *K. ericinus* and *K. langei*. The smallest genetic distance was between two populations of *K. aberrans* (1.7%) and between specimens with five solenostomes from France and USA on hazelnut (1.4%) (table 3). The Neighbour Joining tree is in fig. 3. The groupings between *Kampimodromus* sp. from France and USA, and between the two populations of *K. aberrans* were confirmed by a high bootstrap value. *Kampimodromus langei* and *K. ericinus* (five solenostomes) were grouped with *Kampimodromus* sp., whereas *K. himiminai* was most related to *K. aberrans*. Bootstrap values for these latter groupings were low.

The *Kampimodromus* CO-I sequences were submitted to Genbank data base under their accession numbers (table 1). The accession number of *T. pyri* was EF372611.

Discussion

Similarities between USA and French *Kampimodromus* populations

The USA *Kampimodromus* sp. was morphologically like the French *Kampimodromus* sp., both with five solenostomes. Their genetic distance (based on CO-I sequence) was 1.4%, which is less than the intraspecific distance detected between

two populations of *K. aberrans* (1.7%) and far higher than between different *Kampimodromus* species (11.9–18.4%). These small and large distances also match levels of intraspecific and interspecific divergence observed in other mites (Anderson & Trueman, 2000; Salomone *et al.*, 2002; Walter & Campbell, 2003). Hence, we conclude that the small genetic distance between the USA and French *Kampimodromus* sp. represent intraspecific diversity and both belong to the same species, which we hereafter refer to as *Kampimodromus* sp.

Identity of the USA population: usefulness of morphological characters and DNA sequencing

The genetic distances detected among species of *Kampimodromus* (13.2–18.4%) are high compared to among Tetranychids (Navajas *et al.*, 1999; Hinomoto *et al.*, 2001) but similar to those for species of Dermassynae (genus *Stratiolaelaps*) (Walter & Campbell, 2003) and Oribatidae mites (Salomone *et al.*, 2002). Based on COI sequence differences (from 14.9–17.4%), *Kampimodromus* sp. specimens did not belong to *K. aberrans*, despite their small differences in seta length. Our results confirm the lack of importance of these characters for differentiation and the value of solenostome numbers to separate *K. aberrans* from *Kampimodromus* sp. Furthermore, results indicate that morphologically similar species, *Kampimodromus* sp. and *K. aberrans*, co-habit hazelnut trees in France.

Seven species, *K. langei*, *K. alettae*, *K. coryli*, *K. corylosus*, *K. echii*, *K. karadaghensis* and *K. ericinus*, have five

<i>Kampimodromus</i> sp. Burgundy	TTTGGGATTATTTCTCATAGAATTTTATTTCAAAGAATAAAATACAAACTTTTGGAGCT
<i>K. aberrans</i> <i>C. australis</i>	TTTGGTATTATTTCTCATAGAATTTTATTTCAATAGAATGAAATCTCAAACCTTTTGGGGCT
<i>K. aberrans</i> <i>Q. pubescens</i>	TTTGGTATTATTTCTCATAGAATTTTATTTCAATAGAATGAAATCTCAAACCTTTTGGGGCT
<i>K. ericinus</i>	TTTGGTATTATTTCTCATAGATTTTATTTCAAAGGATAAAATACAGACTTTTGGGGCA
<i>K. hmiminai</i>	TTTGGTATTATTTCTCATACTATTTTATCCAGAGAATAAAATACAAACTTTTGGTTCCT
<i>K. langei</i>	TTTGGTATTATTTCTCATAGCATTATTTCAAAGGATAAAATGCAAACTTTTGGGGCT
<i>Kampimodromus</i> sp. USA	TTTGGGATTATTTCTCATAGAATTTTATTTCAAAGAATAAAATACAAACTTTTGGAGCT
<i>Kampimodromus</i> sp. Burgundy	TTAGGTATAATTTATGCTATAATAACAATTTGGAATTTTAGGTTTTATTGTATGGGCTCAT
<i>K. aberrans</i> <i>C. australis</i>	TTGGGTATAATTTATGCCATAATAACTATTGGGGTGTGGGTTTTATTGTATGGGCTCAT
<i>K. aberrans</i> <i>Q. pubescens</i>	TTGGGTATAATTTATGCCATAATAACTATTGGGGTGTGGGTTTTATTGTATGGGCTCAT
<i>K. ericinus</i>	TTAGGGATAATTTATGCAATAATAACAATTTGGTGTTTTAGGGTTTTATTGTATGAGCCAT
<i>K. hmiminai</i>	TTAGGTATAATTTATGCGATATTGACTATTGGAATTTTAGGTTTTATTGTTTTGGGCTCAT
<i>K. langei</i>	TTGGGCATAATTTATGCTATATTGACAATTTGGGGTGTAGGGTTTTATTGTGTAGGCTCAT
<i>Kampimodromus</i> sp. USA	TTAGGTATAATTTATGCTATAATAACAATTTGGAATTTTAGGTTTTATTGTATGGGCTCAT
<i>Kampimodromus</i> sp. Burgundy	CACATATTTACAGTAGGAATAGATATTGATTTCCCGTGTCTATTTTACTGCAGCAACTATA
<i>K. aberrans</i> <i>C. australis</i>	CATATATTTACAGTAGGCATAGATATTGATTTCTCGTGCTTATTTTACAGCGGCTACAATG
<i>K. aberrans</i> <i>Q. pubescens</i>	CATATATTTACAGTAGGCATAGATATTGATTTCTCGTGCTTATTTTACAGCGGCTACAATG
<i>K. ericinus</i>	CATATATTTACAGTGGGTATAGATATTGACTCTCGTGCTTATTTTACTGCAGCTACTATA
<i>K. hmiminai</i>	CATATATTTACTGTGGGTATAGATATTGATTTCTCGAGCCTATTTTACAGCGGCTACTATA
<i>K. langei</i>	CATATATTTACAGTGGTATAGATATTGACTCAGTGCTTATTTTACAGCAGCTACAATA
<i>Kampimodromus</i> sp. USA	CATATATTTACAGTAGGAATAGATATTGATTTCCCGTGTCTATTTTACTGCAGCAACTATA
<i>Kampimodromus</i> sp. Burgundy	ATTATTTGCCATTCTACAGGAATTTAAAATTTTTTCATGGTTGTCAACTCTTTATGGTTCT
<i>K. aberrans</i> <i>C. australis</i>	ATTATTTGCTATTCTACTGGGATTTAAAATTTTTTCTTTGGTTGTCTACAATTTACGGATCT
<i>K. aberrans</i> <i>Q. pubescens</i>	ATTATTTGCTATTCTACTGGGATTTAAAATTTTTTCTTTGGTTGTCTACAATTTACGGGCTCT
<i>K. ericinus</i>	ATTATTTGCTATTCTACAGGAATTTAAAATTTTTTCTTTGGTTATCAACTTTATGGATCA
<i>K. hmiminai</i>	ATTATTTGCGATTCTACAGGAATTTAAAATTTTTTCTTTGATTTGTCAACTATTATGGTTCT
<i>K. langei</i>	ATTATTTGCAGTTCTACAGGAATTTAAAATTTTTTCTTTGACTTTCAACTTTATATGGTTCT
<i>Kampimodromus</i> sp. USA	ATTATTTGCCATTCTACAGGAATTTAAAATTTTTTTCATGGTTGTCAACTCTTTATGGTTCT
<i>Kampimodromus</i> sp. Burgundy	TGAGTTAAGTGAAATGTGGTGCTATATGGAATATAGGTTTTATTTTTTATTTACAGTA
<i>K. aberrans</i> <i>C. australis</i>	TGAATTTAAATGAAGAGTTGTTATTATATGAAATATAGGGTTTTATTTTTTATTTACAGTA
<i>K. aberrans</i> <i>Q. pubescens</i>	TGAATTTAAATGAAGAGTTGTTATTATATGAAATATAGGGTTTTATTTTTTATTTACAGTA
<i>K. ericinus</i>	TGAGTTAAGTGAAATGTGGTTCTATATGAAATATAGGGTTTTATTTTTTGTTTACAGTA
<i>K. hmiminai</i>	TGAATTTAAATGAAATGTAATTTGCTCATATGAAATTTAGGGTTTTATTTTTTATTTACAGTG
<i>K. langei</i>	TGAATTTAAATGAAATGTGGTAAATATATGAAATTTAGGTTTTATTTTTTATTTTACAGTA
<i>Kampimodromus</i> sp. USA	TGAGTTAAGTGAAATGTGGTATCTATATGGAATATAGGTTTTATTTTTTATTTACAGTA
<i>Kampimodromus</i> sp. Burgundy	GGGGGAATTACTGGTGTTTTTATAGCTAATTTCAATTGATATTATTTTACATG
<i>K. aberrans</i> <i>C. australis</i>	GGGGGGGTGACCGGTGTAATTTTAGCAAATTTCTCAGTAGATATTATTTCTTCATG
<i>K. aberrans</i> <i>Q. pubescens</i>	GGAGGGGTGACTGGTGAATTTTAGCAAATTTCTCAGTAGATATTATTTCTTCATG
<i>K. ericinus</i>	GGGGGGTAAACAGGTGTAATTTTAGCTAATTTCTTATTGATATCATTTCTTCATG
<i>K. hmiminai</i>	GGAGGAGTGACTGGAGTAGTTTTAGCAAATTTCTCAATTTGATATTATTTTACATG
<i>K. langei</i>	GGAGGAGTAAACAGGTGTTATTTGGCCAATTTCTTATTGATATTATTTTACACG
<i>Kampimodromus</i> sp. USA	GGGGGGATTACTGGTGTTTTTATAGCTAATTTCAATTGATATTATTTTACATG

Fig. 2. Alignment of the sequences of the Col gene for the following *Kampimodromus* species: *K. langei*, *K. ericinus*, *K. aberrans* (*Celtis australis* and *Quercus pubescens*), *Kampimodromus* sp. (Hazelnut: USA and France, Burgundy) and *K. hmiminai*.

solenostomes like *Kampimodromus* sp. However, *Kampimodromus alettae* differs by having two pairs of preanal setae instead of three like all of the former. According to this difference, *Kampimodromus* sp. should not belong to this species. However, nothing is known about the reliability of the number of preanal setae for species identification, and molecular tests with this species would be required to conclude on this point.

Molecular differences between *K. ericinus* and *Kampimodromus* sp. suggest that specimens of *Kampimodromus* sp. do not belong to *K. ericinus*. Lengths of seta j3, j6, j4, j5 and J2 can separate them. Small morphologic differences (lengths of j1 and j3) were noted between *K. ericinus* and *K. karadaghensis*; these two species do not bear tooth on the movable digit and have similar seta lengths. Kolodochka (2005), in the original description of *K. karadaghensis*, emphasized that *K. ericinus* had different serration of setae J5 and S5. According to these small differences, synonymy between *K. ericinus* and *K. karadaghensis* could be suspected.

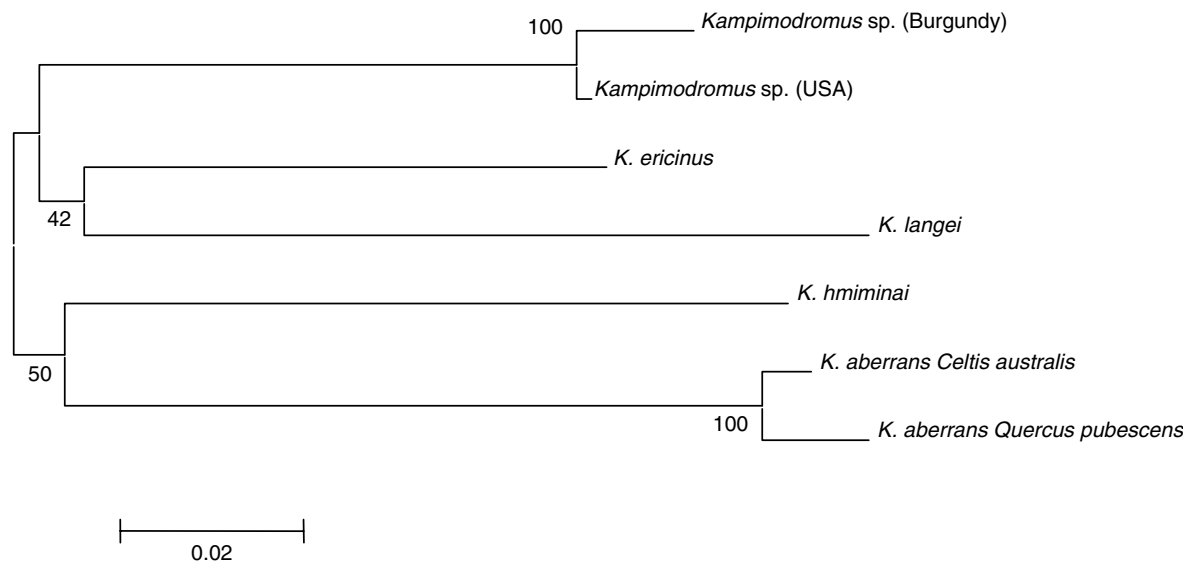
Genetic distances between *K. langei* and *Kampimodromus* sp. are great, suggesting they are separate species. The only morphologic difference between them is the presence of a tooth on the movable digit for *K. langei*.

Kampimodromus sp. differs from *K. echii* for some seta lengths (S5, Z5, STIV and to a lesser extent j4, j5 and J2) and a tooth occurrence of the mobile digit. In the absence of molecular data to ascertain reliability of these characters, we conclude, based on morphological characteristics and data concerning importance of tooth presence, that *Kampimodromus* sp. does not belong to *K. echii*.

The two other species having five solenostomes are *K. coryli* and *K. corylosus*. The setae lengths of these species are similar to those of specimens of *Kampimodromus* sp. The only difference between *K. coryli* and *K. corylosus* is the presence of a tooth on the mobile digit. According to the importance of digit dentition trait, we assume that *K. coryli* and *K. corylosus* are valid species. Furthermore, as no morphologic differences separate *K. coryli* and *K. corylosus* from *Kampimodromus* sp., specimens of *Kampimodromus* sp.

Table 3. Distances of Jukes and Cantor for the gene studied (part of mt-COI) for the populations and species within the genus *Kampimodromus* and *Typhlodromus pyri*.

	<i>Kampimodromus langei</i>	<i>Kampimodromus hmiminai</i>	<i>Kampimodromus</i> sp. Burgundy	<i>Kampimodromus</i> sp. USA	<i>Kampimodromus ericinus</i>	<i>Kampimodromus aberrans</i> on <i>Celtis australis</i>	<i>Kampimodromus aberrans</i> on <i>Quercus pubescens</i>	<i>Typhlodromus pyri</i>
<i>Kampimodromus langei</i>	–							
<i>Kampimodromus hmiminai</i>	17.0	–						
<i>Kampimodromus</i> sp. Burgundy	16.3	14.9	–	0				
<i>Kampimodromus</i> sp. USA	15.3	14.6	1.4	–				
<i>Kampimodromus ericinus</i>	14.2	16.6	13.2	11.9	–			
<i>Kampimodromus aberrans</i> on <i>Celtis australis</i>	18.4	16.3	16.3	14.9	14.2	–		
<i>Kampimodromus aberrans</i> on <i>Quercus pubescens</i>	18.4	16.3	17.4	15.9	15.3	1.7	–	
<i>Typhlodromus pyri</i>	23.6	22.6	25.0	24.0	21.6	25.0	25.0	–

Fig. 3. Neighbour Joining tree based on genetic distances between the different *Kampimodromus* species. The numbers at nodes correspond to bootstrap values.

without a tooth are assumed to be *K. corylosus*. As such, *Kampimodromus* sp. from France and USA will be called *K. corylosus* hereafter.

Justification for species status for *Kampimodromus* species

This study emphasizes the value of morphological characters, especially the solenostome gd8, setal length and occurrence of a tooth on the movable digit of the chelicerae,

for identification within *Kampimodromus*. The presence of gd8 seems to be of primary importance. It allows distinction of specimens having only slight differences in setae lengths and sharing the same chelicera dentition, such as *K. corylosus* and *K. langei* from *K. aberrans*. We emphasize the reliability of tooth occurrence on the movable cheliceral digit for differentiation when the number of solenostome is similar. Indeed, molecular analysis showed that *K. langei* and *K. corylosus* only differed by this character. It is also assumed

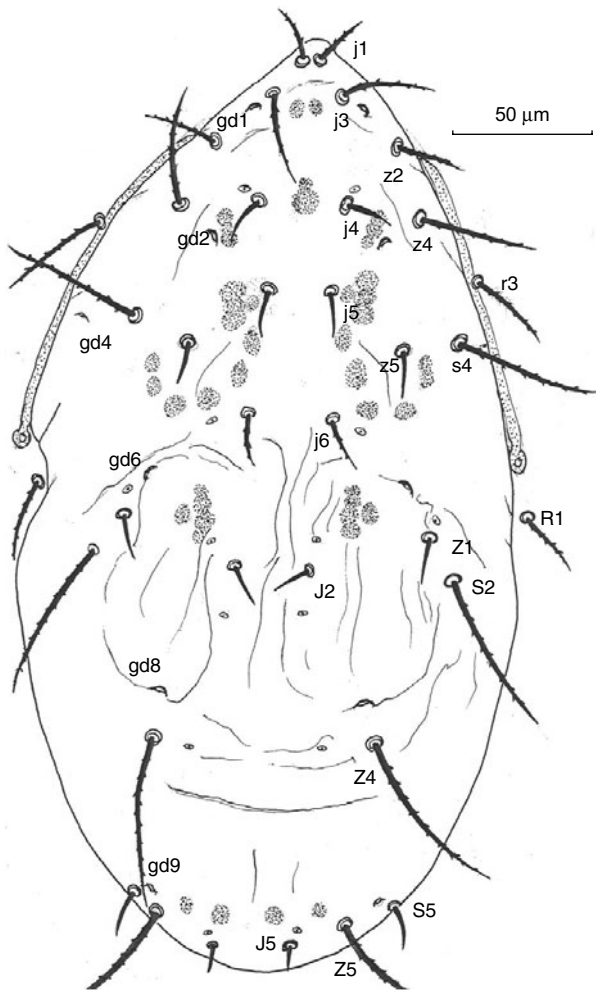


Fig. 4. Dorsal shield of *Kampimodromus* sp. with seta and solenostome nomenclatura.

that *K. ericinus* and *K. echii*, which have similar seta lengths but different cheliceral dentation, are also valid species. However, cheliceral dentation is not easy to assess, especially when chelicerae are closed. At last, for species having the same numbers of solenostomes and teeth on the mobile digit, seta lengths may allow differentiation, as shown for *K. ericinus* and *K. corylosus*. However, this paper confirms that this criterion must not be considered as a major trait, because of high variations between and within species (Tixier *et al.*, 2003). *Kampimodromus echii*, *K. langei* and *K. coryli* all have the same number of solenostomes and one tooth on the movable digit. *Kampimodromus echii* differs from the two in seta measurements, especially Z5, s4 and S5. Considering these differences, we suggest that *K. echii* is a valid species, with molecular tests needed to confirm this hypothesis. No notable morphological differences were seen between *K. coryli* and *K. langei* (five solenostomes, one tooth on the mobile digit and identical setal lengths) nor between *K. ericinus* and *K. karadaghensis* (five solenostomes, absence of tooth on the mobile digit and identical setal lengths). Synonymy is, thus, suspected between these species that are only differentiated by serration of some setae. Molecular

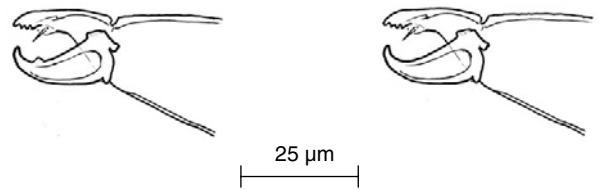


Fig. 5. Chelicera of the females of *Kampimodromus* sp. with one tooth or without tooth on the movable digit.

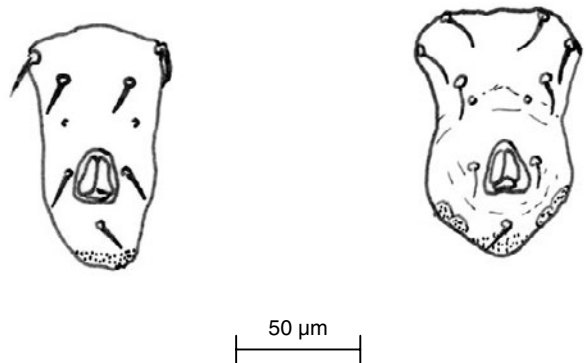


Fig. 6. Ventrianal shield of the females of *Kampimodromus* sp. with two (ZV2, JV2) or three (JV1, ZV2, JV2) on.

investigations would be needed to test these possible synonymies.

Key to identifying all species of Kampimodromus

Considering our results and those for *Kampimodromus* species bearing three, four and six solenostomes (Ragusa & Tsolakis, 1994; Cargnus *et al.*, 2002; Tixier *et al.*, 2003, 2006), we propose a diagnostic key for *Kampimodromus* spp. This key emphasizes the importance of the characters listed above, as well as the need for further molecular studies to evaluate the reliability of setae on the ventrianal shield and the synonymy between *K. aberrans* and *K. molle*, *K. ragusai* and *K. keae*, *K. langei* and *K. coryli*, and *K. ericinus* and *K. karadaghensis*.

Key to species of the genus Kampimodromus

1. Dorsal shield with six solenostomes (gd1, gd2, gd4, gd6, gd8, gd9) (fig. 4) This ***Kampimodromus hmiminai* McMurtry & Bounfour** (synonym of *Kampimodromus adrianae* Ferragut & Pena Estevez, after Tixier *et al.* (2006))
- 1'. Dorsal shield with less than six solenostomes (absence of gd4)
- 2 (1'). Dorsal shield with three solenostomes (gd2, gd6, gd9) (fig. 4) ***Kampimodromus judaicus* (Swirski and Amitai)**
- 2'. Dorsal shield with four or five solenostomes
- 3 (2'). Dorsal shield with four solenostomes (gd1, gd2, gd6, gd9) (fig. 4)

- 3'. Dorsal shield with five solenostomes (gd1, gd2, gd6, gd8, gd9) 5
- 4 (3'). Movable digit of chelicera with one tooth (fig. 5)
No distinguishable character to differentiate *Kampimodromus ragusai* Swirski and Amitai and *K. keae* (Ueckermann & Loots) 5
- 4'. Movable digit of chelicera without tooth (fig. 5)
No distinguishable character to differentiate *Kampimodromus molle* (Ueckermann and Loots) from *K. aberrans* (Oudemans) 5
- 5 (3'). Ventrianal shield with two pre-anal setae (ZV2, JV2) (fig. 6)
Kampimodromus alettae (Papadoulis & Emmanouel) 5
- 5'. Ventrianal shield with three pre-anal setae (JV1, ZV2, JV2) (fig. 6) 6
- 6 (5'). Movable digit of chelicera with one tooth (fig. 5) 7
- 6'. Movable digit of chelicera without tooth 8
- 7 (6). Setae Z5 short (40 µm), seta S5 shorter than 15 µm, s4 long (50 µm), Z1 around 30 µm
Kampimodromus echi Ferragut & Pena-Estevez 7
- 7'. Setae Z5 longer than 40 µm (50 µm), S5 longer than 15 µm, s4 shorter than 45 µm, Z1 around 20 µm.
No distinguishable character to differentiate *Kampimodromus langei* Wainstein & Arutunian and *K. coryli* Meshkov 7
- 8 (5'). Setae j3 and j1 around 20 µm, j6 around 30 µm, J2 around 40 µm
No distinguishable character to differentiate *Kampimodromus ericinus* Ragusa and *K. karadaghensis* Kolodochka 8
- 8'. Setae j3 around 30 µm, j1 around 15 µm, J2 around 20 µm
Kampimodromus corylosus Kolodochka 8

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