Acta entomologica serbica, Supplement, 2006, 39-50 UDC 595.771 (6.15)

ZOOPHILY AND ANIMAL FILARIAE IN *SIMULIUM DAMNOSUM* S. L.: ON THE INDICATIVE PROPERTY OF TARSAL CLAWS IN FEMALES

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ABSTRACT – Females of some populations of the West African *Simulium sanctipauli* subcomplex (Diptera: Simuliidae: *S. damnosum* complex) were found to have enlarged basal teeth of their tarsal claws, indicating zoo-/ornithophilic behavior. Indeed, old reports emphasized the abundant presence of unknown filarial larvae in *S. soubrense* from Liberia, and some of these larvae resembled wild bird filariae. A morphological comparison of the tarsal claws of virtually all members of the *S. sanctipauli* subcomplex from across West Africa confirmed that the 'claw index' of Liberian *S. soubrense* is significantly pronounced, whereas *S. sanctipauli* s.str. had claws typically seen in the *S. damnosum* complex. These data are also compared with other, mostly anthropophilic members of the *S. damnosum* complex. However, both *S. soubrense* and *S. sanctipauli* are proven vectors of *Onchocerca volvulus*, the causative agent of human 'river blindness'. Hence, the claw shape of Liberian *S. soubrense* should be regarded as a convergent adaptation leading to less specialized host preferences.

KEY WORDS: Simuliidae, onchocerciasis, West Africa, *Simulium damnosum* complex, *S. sanctipauli*, *S. soubrense*, tarsal claw index, zoophily

INTRODUCTION

The blinding form of human onchocerciasis ('river blindness') seriously affected wide parts of the West African savanna until 1974. This date marks the launch of the Onchocerciasis Control Program (OCP), which, in a combined vector-control and drug strategy, succeeded in eliminating onchocerciasis as a disease of public health importance until the program closed in 2002 (HOUGARD ET AL., 1997; MOLYNEUX & DAVIES, 1997; BORSBOOM ET AL., 2003). This world's largest vector-control scheme ever was directed against several members of the *Simulium damnosum* species complex, one of them being *S. sanctipauli* sensu lato which constitutes the only exclusively West African subcomplex of the *S. damnosum* complex (BOAKYE, 1993). Hence, its range is relatively small compared with other members of the complex, which can be found across sub-Saharan

Africa, e.g. *S. damnosum* sensu stricto or *S. squamosum*. On the other hand, *S. sanctipauli* s. l. was the first species of the complex that became resistant to insecticides (POST & KURTAK, 1987; OSEI-ATWENEBOANA ET AL., 2001).

Originally, VAJIME & DUNBAR (1975) erected the two cytospecies *S. sanctipauli* and *S. soubrense* as members of the subcomplex. POST (1986) revised the cytotaxonomy of both species, which resulted in significant uncertainties regarding all previous records using the original identification tools of Vajime & Dunbar (KASHAN & GARMS, 1987). This confusing situation also arose from the etymology of both taxa. The type locality of *Simulium sanctipauli* is the Bandama River (Ivory Coast) though the name had originally been derived from the St. Paul River in Liberia (VAJIME & DUNBAR, 1975), where there actually occurs *S. soubrense* only (POST, 1986; KASHAN & GARMS, 1987). Vice versa, the name *soubrense* had been derived from the village of Soubré on the Sassandra River (Ivory Coast), which is actually inhabited by *S. sanctipauli*, while its type locality is in Northern Ivory Coast (the Leraba River), hence apart from the strongholds of *S. soubrense* in Guinea and Liberia. Subsequently, further taxa were described, namely *S. leonense* (BOAKYE ET AL., 1993), *S. konkourense* (BOAKYE ET AL., 1993), *S. soubrense* 'Beffa' form (MEREDITH ET AL., 1983), and *S. sanctipauli* 'Djodji' form (SURTEES ET AL., 1988). The latter is thought eradicated due to the OCP activities (BOAKYE ET AL., 1998, 1999). However, further distinctions on the informal level of cytoforms were proposed for *S. sanctipauli*, namely the 'Comoé', 'Pra' and 'Sassandra' forms (BOAKYE ET AL., 1999), for *S. soubrense*, namely the 'Farmington' and 'St. Paul' forms sensu GÜZELHAN & GARMS (1991), and the 'Chutes Milo' form sensu BOAKYE ET AL. (1993); and for *S. konkourense*, namely the 'Konkouré' form sensu QUILLÉVÉRÉ ET AL. (1982) and the 'Menankaya' form sensu BOAKYE ET AL. (1993).

The hydro-geological situation of West Africa is characterized by a longitudinal series of large river basins such as those of the Konkouré, Moa, St. Paul, Cestos, Cavally, Sassandra, Bandama, Comoé, Pra, and Volta Rivers draining the interior of the sub-continent towards the Atlantic Ocean and the Gulf of Guinea, respectively. In addition, the region is characterized by a latitudinal transition of climatic and phytogeographic zones. Both the latitudinal and longitudinal patterns may have contributed to a stepped cline of speciation and adaptation of different taxa of the subcomplex whose members are all considered 'forest' species together with *S. yahense* and *S. squamosum*, as opposed to the 'savanna' species of the *damnosum* subcomplex. It was mainly the latter that was of greatest concern during the vector control operations of the Onchocerciasis Control Program (MOLYNEUX & DAVIES, 1997).

In West Africa, the majority of populations and taxa of the *S. damnosum* complex are incriminated vectors of *Onchocerca volvulus* (BOAKYE ET AL., 1998) and hence are regarded as anthropophilic, but some observations exist that point towards certain degrees of zoophily. GARMS & VOELKER (1969) and VOELKER & GARMS (1972) described high infection rates with several unknown filariae in Liberian *S. sanctipauli* s.l. (later treated as *S. soubrense*, GARMS, 1987). Through feeding experiments and filaria surveys of wild animals, they concluded that these were avian parasites and that this *S. soubrense* population was highly ornithophilic.

Other hints for ornithophily were reported from Uganda by MCCRAE (1967), who observed feeding of *S. damnosum* s.l. on the crown crane: and by KRÜGER ET AL. (1998), who collected *S. pandanophilum* exclusively in chicken-baited traps. In the latter study, *S. soubrense* from Liberia was also mentioned because its females were found to have enlarged tarsal claw basal teeth compared with the typical claw of *S. damnosum* s. l. In general, *S. damnosum* s. l. is known to exhibit small, conical teeth on claws that are intermediate between the toothless claws of certain (mam-

Table 1. Collection and identification details of specimens of the *S. sanctipauli* subcomplex used for tarsal claw morphometrics. ([1] Group numbers according to those used in Table 2 and Fig 2. [2] Tropenmed. Parasit., 29: 483-491).

No.[1]	Species	Collection site	Collection date	Number examined	Identification source
1	*S. konkourense* s.l.	Guinea, Kakrima R., Sagoghi	03.04.1987 ep	3	Boakye et al., 1993
1		Guinea, Konkouré R., Konkouré	16.11.1986 wc?	6	Boakye et al., 1993
6	*S. konkourense*	Sierra Leone, Rokel R., Bumbuna	29.11.1981 ep	3	Post, 1986
6	'Menankaya'	Sierra Leone, Sewa R., Njaiama-Sewafe	16.09.1989 wc	5	Boakye et al., 1993
3	*S. leonense/konkourense*	Guinea, Kolenté R., Badekanti	21.09.1987 wc	6	
3		Guinea, Kolenté R., Kolenté	14.11.1986 wc	5	Boakye et al., 1993
2	*S. leonense*	Sierra Leone, Wanje R., Bandajuma	21.06.1983 ep	7	Post, 1986
2		Sierra Leone, Gt. Scarcies R., Kanka	02.12.1981 ep	2	Post, 1986
2		Sierra Leone, Gbangbaia R., Palima	11./12.09.1989 wc	5	Post, 1986
9	*S. soubrense* 'Milo'/	Guinea, Milo R., Lékoro	01.07.1963 ?	1	
9	*konkourense*	Guinea, Milo R., Balan	September 1986 wc	4	
9		Guinea, Balé R., Menankaya	August 1985 wc	5	Boakye et al., 1993
4	Menankaya ?	Liberia, Lofa R., Kessli	18.02.1974 wc	2	Kashan & Garms, 1987
4	(IL-B.C)		06.07.1970 wc	1	
4			05.08.1983 wc	5	
4		Liberia, Lofa R., Darbu	08.03.1985 wc	6	
10	*S. soubrense* s.l. ?	Ivory Coast, Sassandra R. 14	04.05.1978 ep	3	
10		Ivory Coast, Bafing R. 7	31.05.1978 ep	3	Boakye et al., 1993

Table 1. Continued.

10		Ivory Coast, Djirila (Baoulé R.)	23.06.1977 wc	7	
8	*S. soubrense* s.l.	Liberia, Cestos R., Darlu	06.05.1971 ep	1	Post, 1986
8		Liberia, Cestos R., Bah Town	18.05.1984 wc	6	
7		Liberia, Cavally R.	18.12.1970 ep	1	Garms, 1978[2]
7			13.12.1970 pupae	4	
7		Liberia, St. PauR. l, Gengema	28.09.1983 wc	3	
7			27.02.1985 wc	7	
7		Liberia, St. Paul R., Haindi	02.07.1986 ep	1	Güzelhan & Garms, 1991
7			11.04.1989 ep	1	
7		Liberia, St. PauR. l, Beyan's Town	14.09.1970 wc	5	
7		Liberia, Farmington R., Firestone	08.07.1986 ep	1	Güzelhan & Garms, 1991
7		Liberia, St. John R.	03.12.1987 ep	3	Güzelhan & Garms, 1991
7		Liberia, from chicken	11.07.1984 wc	1	
17	*S. soubrense* 'Beffa'	Benin, Okpara R. Pl.12	27.06.1979 ep	1	Meredith et al., 1983
17		Benin, Beffa R.	26.06.1979 ep	10	Meredith et al., 1983
5	*S. sanctipauli* s.l.	Liberia/Guinea, Makona R.	20.11.1986 ep	1	Güzelhan & Garms, 1991
5			10.-13.12.1986 ep	2	
5		Liberia/Guinea, Makona R., Yalamba	September 1986 wc	5	
5		Sierra Leone/Guinea, Makona R., Sambalu	22.09.1989 wc	5	

Table 1. Continued.

5	*S. sanctipauli/ leonense/*	Sierra Leone, Mano R.	19.09.1989 wc	5	Güzelhan & Garms, 1991
5	'Menankaya'	Sierra Leone, Moa R., Kpolu	11.09.1989 wc	5	
11	*S. sanctipauli* 'Sassandra'	Ivory Coast, Sassandra R. 3, Soubré	28.06.1978 ep	7	Boakye et al., 1999
12	*S. sanctipauli*	Ivory Coast, Sassandra R. 5, Semien	31.05.1978 ep	9	
12		Ivory Coast, Sassandra R. 1	27.06.1978 ep	4	
12		Ivory Coast, Pt. Seguela (Banoroni/YaranR. i)	03.07.1979 wc	2	
13	*S. sanctipauli* s.s.	Ivory Coast, Bandama R., Ch. Gauthier	03.06.1976 ?	11	Boakye et al., 1999
14	*S. sanctipauli* 'Comoé'	Ivory Coast, Comoé R., Amoukoukro	24.07.1976 wc ?	10	Boakye et al., 1999
15	*S. sanctipauli* 'Pra'	Ghana, Ayebiahwe	29.10.2001 wc	3	
15		Ghana, Buabinso	28.10.2001 wc	2	
15		Ghana, Pra R.	28.10.2001 ep	5	Boakye et al., 1999
15		Ghana, Fosu (Pra R.)	28.10.2001 wc	5	
16	*S. sanctipauli* 'Djodji'	Togo, Kamassé R., MÔ	12.11.1987 ?	2	
16		Togo, Gban-Houa R., Djodji	09.08.1982 wc	3	Surtees et al., 1988
16			22.06.1982 wc	1	
16		Togo, Kpaza R.	20.06.1979 ep	1	Surtees et al., 1988

Table 2. Mann-Whitney statistics of differences between claw indices. Significant differences are marked in gray. Groups: 1, *S. konkourense* s. l.; 2, *S. leonense*; 3, *S. leonense/konkourense* (Kolenté); 4, 'Menankaya'? (Lofa); 5, *S. sanctipauli* s. l. (Moa/Mano/Makona); 6, *S. konkourense* 'Menankaya' (Sierra Leone); 7, *S. soubrense* s. l (Liberia); 8, *S. soubrense* s. l. (Cestos); 9, *S. soubrense* 'Milo'/*konkourense*; 10, *S. soubrense* s. l.? (Ivory Coast); 11, *S. sanctipauli* 'Sassandra'; 12, *S. sanctipauli* (Sassandra); 13, *S. sanctipauli* s. s.; 14, *S. sanctipauli* 'Comoe'; 15, *S. sanctipauli* 'Pra'; 16, *S. sanctipauli* 'Djodji'; 17, *S. soubrense* 'Beffa'.

Groups	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	—	0.38	0.025	0.044	0.008	0.01	0.0002	0.009	0.18	0.14	0.46	0.37	0.23	0.57	0.57	0.63	0.21
2		—	0.095	0.12	0.027	0.015	0.0001	0.037	0.64	0.36	0.82	0.13	0.68	0.5	0.08	0.12	0.44
3			—	0.72	0.73	0.21	0.008	0.19	0.22	0.36	0.026	0.0065	0.04	0.01	0.0005	0.0021	0.22
4				—	0.4	0.12	0.002	0.15	0.32	0.48	0.048	0.0094	0.12	0.015	0.0005	0.0015	0.5
5					—	0.29	0.0056	0.39	0.15	0.24	0.02	0.001	0.02	0.0035	<0.0001	0.0007	0.13
6						—	0.37	0.86	0.07	0.06	0.01	0.003	0.007	0.004	0.0005	0.001	0.0475
7							—	0.29	0.003	0.003	0.0002	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.0004
8								—	0.1	0.13	0.009	0.0034	0.009	0.006	0.0007	0.004	0.037
9									—	0.6	0.7	0.09	0.9	0.3	0.028	0.06	0.75
10										—	0.16	0.05	0.5	0.09	0.007	0.0097	>0.99
11											—	0.3	0.45	0.5	0.057	0.1	0.26
12												—	0.09	0.35	0.75	0.97	0.052
13													—	0.16	0.006	0.011	0.43
14														—	0.21	0.26	0.16
15															—	0.9	0.015
16																—	0.02
17																	—

malophilic) *Simulium* species such as *S.* (*Metomphalus*) *hargreavesi* (FREEMAN & DE MEILLON, 1953) and the prominently toothed claws found in many (ornithophilic) *Simulium* species. However, a few members of the *S. damnosum* complex are also known for their toothed claws. Such species are *S. pandanophilum* (KRÜGER ET AL., 1998), *S. juxtadamnosum* (GOUTEUX, 1977), and *S. mengense* (MUSTAPHA ET AL., 2004).

In order to validate this finding in the context of the entire *S. sanctipauli* subcomplex, female specimens from virtually all taxonomic entities within the subcomplex collected from all over its distribution range during the past 35 years were scored for their tarsal claw morphology.

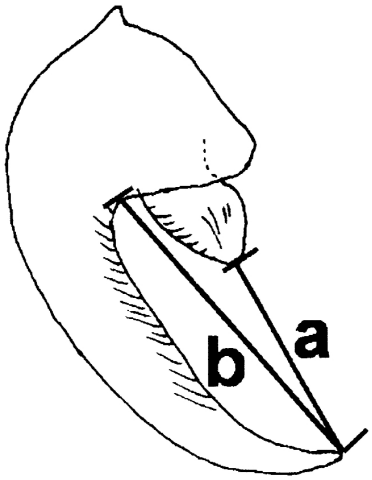

Fig 1. Claw index.

MATERIAL AND METHODS

Details about the specimens used in this study are listed in Table 1. A total of 212 specimens of the *S. sanctipauli* subcomplex were examined from throughout West Africa, together with 40 West African and Ugandan specimens of related species for comparison (details for these are available upon request). Dry or ethanol-preserved females *Simulium damnosum* s. l. from the various collections were assessed by extracting at least one tarsal claw. In all cases, the fore tarsus was used, but in most cases together with the mid or hind tarsi. The extracted tarsi were mounted on a slide, submersed in a drop of absolute ethanol, transferred to Euparal mounting medium, and finally covered with cover slips for microscopic examination. The character of interest was size of the claw's basal tooth relative to that of the entire claw. In order to measure this morphological trait, a ratio ('claw index') was introduced (Fig. 1) that consists of the distance between the apical tip of the tooth and that of the claw (= a) divided by the distance between the tarsal notch and the apical tip of the claw (= b). Measurements were taken subsequent to digital micro-photographic documentation of single claws using a Zeiss Axioskop-2 compound microscope with an attached Nikon CoolPix 950 digital camera.

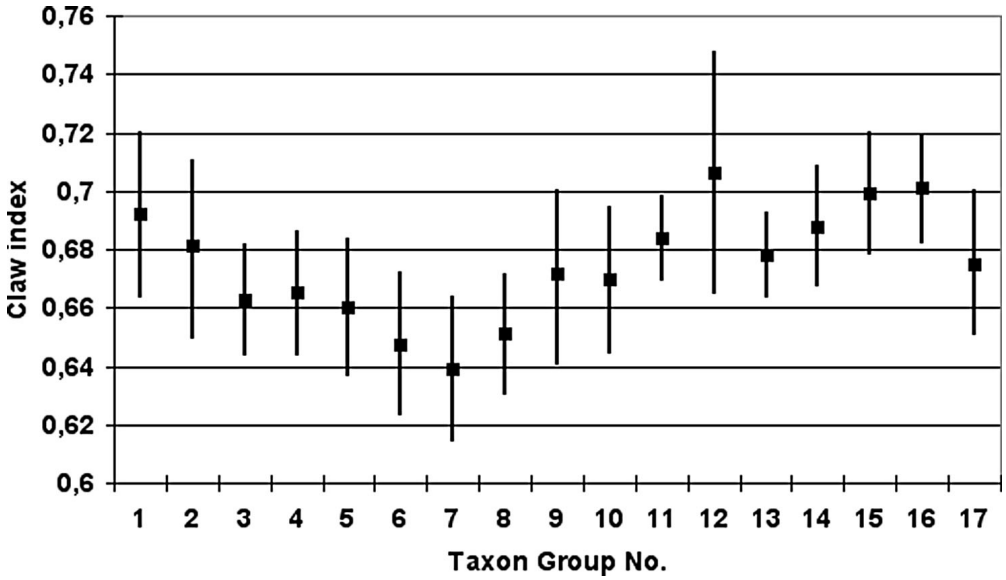

Fig 2. Claw indices of female *S. sanctipauli* subcomplex. Group nos. as in Tables 1 and 2.

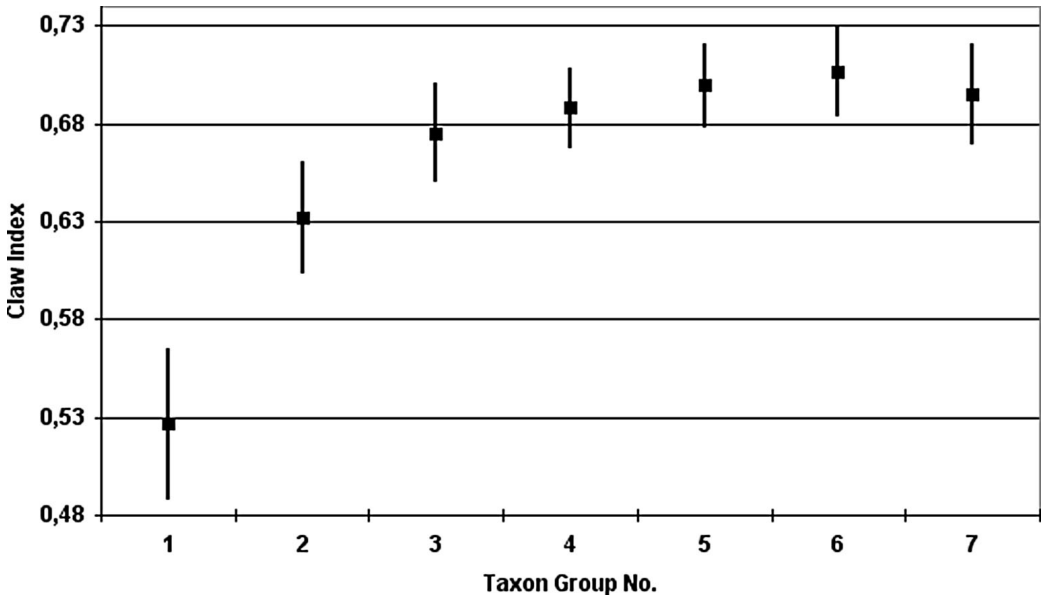

Fig 3. Claw indices of female *S. damnosum* s.l.: Groups: 1, *S. pandanophilum* (*N*=9); 2, *S. soubrense* s.l. (Liberia); 3, *S. soubrense* 'Beffa'; 4, *S. sanctipauli* 'Comoe'; 5, *S. sanctipauli* 'Pra'; 6, *S. yahense* (*N*=6); 7, *S. damnosum/sirbanum* (*N*=12).

Measurements of specimens from the same collections and other con-specific samples were totaled and the geometric mean (with standard deviations) calculated for taxonomic groups as indicated in Table 1. The taxonomic identity was in most cases assumed to correspond to previously published cytotaxonomic records from the same collection sites (references listed in Table 1). In order to test for significant differences, the Mann-Whitney test was performed on the mean claw index values for each entity.

RESULTS AND DISCUSSION

Figure 2 illustrates the claw indices for different taxa of the *S. sanctipauli* subcomplex. The order of presentation from left to right more or less corresponds to the geographical distribution from West (Guinea, Sierra Leone) to East (Benin) of the respective taxa, in agreement with Table 1. Altogether, the absolute claw indices ranged from 0.59 (Liberian *S. soubrense* s. l.) to 0.79 (*S. sanctipauli* 'Sassandra'), with half of the indices found at 0,65-0,69 (median 0.67).

Significant differences were observed between Liberian *S. soubrense* s. l. (incl. Cestos) and all remaining taxa (except 'Menankaya'/Sierra Leone), between most western (groups 3-8) and eastern (groups 11-16) populations, and within the eastern taxa (*S. konkourense*/*leonense* against the remaining taxa of groups 3-8) (Table 2). Thus, the variation within *S. soubrense* s. l. is as great as between *S. soubrense* s. l. and *S. sanctipauli* s. l., whereas it is rather slight within *S. sanctipauli* s. l.

In order to generalize the above findings in a broader context of the entire *S. damnosum* complex, Fig. 3 shows a comparison of the claw indices of selected taxa of the *S. sanctipauli* subcomplex, *S. pandanophilum* from Uganda, and *S. yahense* and *S. damnosum*/*sirbanum* from West Africa. The Liberian *S. soubrense* now almost appear as intermediates between the prominently toothed *S. pandanophilum* and the remaining taxa with 'typical' basal teeth.

Geographical plotting of the results (not shown) does not indicate a cline along the West African sub-continent within the *S. sanctipauli* subcomplex as a whole. Rather, it confirms the exclusive tarsal claw morphology of Liberian *S. soubrense* as suggested previously (KRÜGER ET AL., 1998), although it now turned out that *S. konkourense* from Sierra Leone ('Menankaya' form sensu BOAKYE ET AL., 1993) had a similarly low claw index, followed next by populations of assumed *S. soubrense* from northwestern Ivory Coast. Regarding the taxonomic status of the Liberian populations, no conclusive data exist. KASHAN & GARMS (1987) and GÜZELHAN & GARMS (1991) - subsequent to POST'S (1986) revision of the subcomplex - provided evidence for a close relationship of their two recognized forms ('Farmington' and 'St Paul') to both *S. soubrense* 'Chutes Milo' (i.e., the 'typical' *S. soubrense*) and *S. konkourense* 'Menankaya' (BOAKYE ET AL., 1993). As there was no morphological difference detectable between Liberian populations from the St. Paul River as opposed to the Farmington/St. John Rivers, the cytological separation could not be reconstructed. Instead, the claw indices of *S. konkourense* 'Menankaya' (Rokel River, Sierra Leone) almost matched those of the Liberian specimens, whereas the indices of 'typical' *S. soubrense* remain unclear. The specimens from the rivers Milo and Lofa may represent such 'typical' *S. soubrense*, but according to BOAKYE ET AL. (1993) they widely occur sympatrically with easterly populations of *S. konkourense* 'Menankaya', which makes a clear designation impossible. The specimens from Djirila and the upper Sassandra (site 14) may also correspond to 'typical' *S. soubrense*, but those from both the Milo/Lofa and the Djirila/Sassandra sites differ from the Liberian populations in that the former occur in true savanna areas, while the Liberian sites are clearly sylvatic. Further taxonomic clarification was impossible due to the unavailability of specimens from the type locality on

the Leraba River. This situation is further aggravated by the fact that the Leraba apparently never was a regular breeding site of *S. soubrense* s.s. and there exist virtually no records subsequent to the type series collection in 1971.

The morphological peculiarity of Liberian-Ivorian *S. soubrense* and *S. konkourense* 'Menankaya' in the form of the enlarged basal teeth supplements earlier reports from Liberia indicating highly zoophilic behavior of these flies. As tarsal claw morphology is closely linked with the ability of simuliids to penetrate either mammal fur (toothless) or avian feathers, our findings suggest ornithophilic behavior.

In view of the available phylogenetic evidence (DUNBAR & VAJIME, 1981; KRUEGER & HENNINGS, 2006), it is assumed that this morphological trait of *S. soubrense* s. l. is an incipient and hence convergent adaptation to ornithophily within the Liberio-Guinean forest, but has no phylogenetic link to apparently 'old' bird-feeding species such as *S. pandanophilum* or those of other subgenera of *Simulium*.

ACKNOWLEDGEMENTS

I would like to thank Rolf Garms (Hamburg) and Rory Post (London) for providing all the specimens used in this study.

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