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Subulura mackoi n. sp. (Nematoda: Subuluridae) and the zoogeography of subulurids parasitizing birds

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Summary

A new nematode species, *Subulura mackoi* n. sp., is described based on specimens from the colon and caecum of the Eurasian Scops Owl *Otus scops* (L.) (Aves: Strigiformes) from the Czech Republic, collected in 2011. Males are characterized by 10 pairs of caudal papillae, a single papilla on the upper lip of the cloaca, and small unequal spiculae; female distinguishing features are body length, distance of the vulva from the anterior extremity, tail length, and egg dimension.

Analysis of the zoogeographical distribution and host specialization (in the bird orders) of 68 valid species from the genus *Subulura* Molin, 1860 shows significantly high species diversity in the tropical zones. Only one species, *S. brumpti*, is a cosmopolitan parasite of *Gallus gallus* f. *domestica* and other domesticated gallinaceous birds. Zoogeographical-host interactions may be utilized to support the identification of morphospecies of the genus *Subulura*.

Keywords: *Subulura*; new species; *Otus scops*; Aves; distribution

Introduction

So far, twelve species of owls have been confirmed in the avifauna of the Czech Republic; the rarest and most interesting of them is the Eurasian Scops Owl *Otus scops* (L.). The Czech and Slovak Republics are their northernmost nesting area in Central Europe. The Eurasian Scops Owl returns there from its wintering grounds in the sub-Saharan region between the end of April and the beginning of May (Hudec & Šťastný, 2005). Nematodes determined as *Subulura* spp. in *O. scops* were found only by Ferrer *et al*. (2004) in Spain. The morphometric study of specimens in our collection and comparison with all bird species of *Subulura* Molin, 1860 revealed that it represents a new species, which is described herein. The geographical distributions of all valid species parasitizing birds were analyzed.

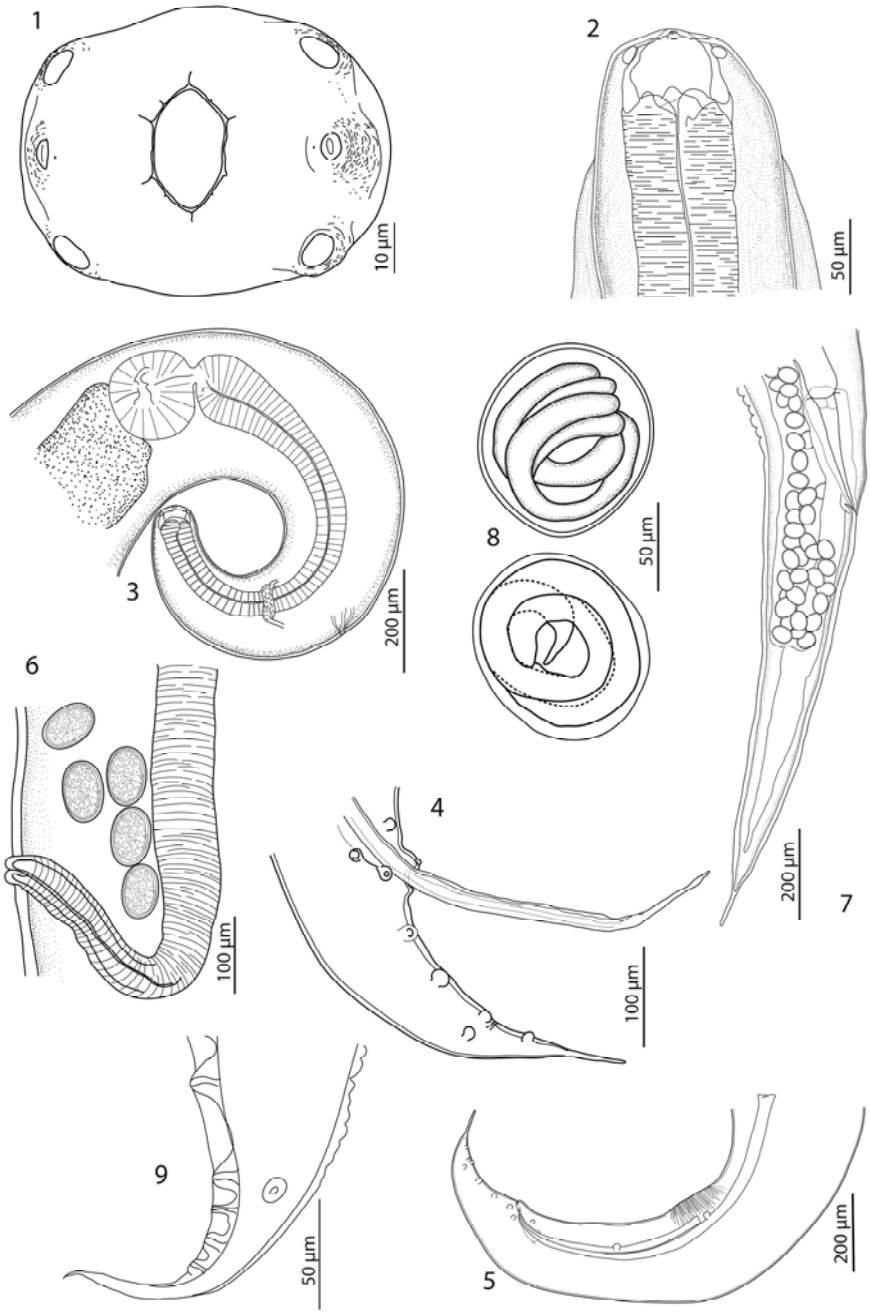
Material and methods

One already dead specimen of Eurasian Scops Owl (roadkill – 28.4.2011, Přerov, Czech Republic) was helminthologically examined. In total, eight *Subulura* nematodes (5 males and 3 females) were obtained from the colon and caecum. The nematodes were washed in physiological saline, then fixed and stored in 4% formaldehyde solution. For light microscopy three males and two females were cleared with glycerine. Specimens were examined under an Olympus BX51 light microscope equipped with Nomarski (DIC) optics differential interference contrast, a digital image analysis system (Motion Stream, Olympus), and a drawing tube attachment. Measurements are in micrometers (μm), unless otherwise stated. Two males and one female were used for scanning electron microscopy (SEM). They were prepared by standard methods described by Mašová (2012) and examined using a Quanta TM 250 FEG scanning electron microscope at an accelerating voltage of 10kV. The names of strigiform birds follow Del Hoyo *et al*. (1999). The names of biogeogrephical realms follow Olson *et al*. (2004).

Results

Subuluridae Yorke et Maplestone, 1926
Subulura mackoi n.sp.
(Figs. 1 – 19)

Description: Whitish nematodes tapering to both extremities, anterior part with obtuse cephalic end. Cephalic plate with smooth cuticle, mouth opening terminal, hexagonal and dorsoventrally protracted (Figs. 1, 10), surrounded by six reduced labial lobes, each with two tiny cuticular lappets without papillae (Fig. 11). Four large cephalic papillae present on lateral margin of cephalic plate arranged in two groups; prominent amphid opening located between papillae. Buccal capsule sclerotized and thickly walled, round in



Figs. 1 – 8. *Subulura mackoi* n.sp.; line drawings. Fig. 1. Female cephalic end (apical view); Fig. 2. Female anterior end (dorsal view); Fig. 3. Male anterior part (lateral view); Fig. 4. Paracloacal and postcloacal papillae on male posterior end (lateral view); Fig. 5. Male posterior end with precloacal sucker (lateral view); Fig. 6. Vulval region (lateral view); Fig. 7. Female posterior end (lateral view); Fig. 8. Eggs; Fig. 9. *Subulura glaucidii* (López-Neyra, 1945); distribution of lower group of postcloacal caudal papillae (according to López-Neyra 1945).

cross section, anterior rim smooth (Figs. 2, 11). Anterior end of pharynx prolonged into three sclerotized teeth (Fig. 2); oesophagus dilated posteriorly with short neck followed by bulb containing dental apparatus (Fig. 3). Two lateral cervical alae, 50 – 63 in maximum width, beginning at level of anterior end of short pharynx (Fig. 12), ending slightly anterior to oesophageal bulb. Deirids not observed. Body cuticle with numerous and varied transverse striations, including slender tail point (Fig. 18).

Male (3 specimens; holotype and measurements of 2 paratypes in parentheses): Body 10.77 (10.71 – 11.69) mm long, 360 (329 – 342) greatest width near middle of body. Buccal capsule 23 (21 – 26) long, 47 (43 – 54) wide, teeth in oesophageal funnel 9 (10) long. Total oesophagus 923 (1083 – 1198) long, oesophageal bulb 179 (144 – 172) wide. Nerve ring 290 (289 – 311) and excretory pore 570 (468 – 530) from anterior end, respectively. Tail (cloaca to tail tip) 264 (259 – 260) long, prolonged into slender point

48 (58 – 60) long. Praecloacal muscular sucker elliptical without cuticular ring 224 (197 – 201) long, its bottom margin 370 (356 – 375) from cloaca (Figs. 5, 14). Total of ten pairs of caudal papillae present, three being precloacal, two paracloacal, and five postcloacal. One median single papilla located on the upper lip of cloaca (Fig. 13). Papillae in pairs arranged as follows: first pair lateral and approximately in half of length of preanal sucker; second pair approximately half way between bottom margin of preanal sucker and cloaca; third pair between previous pair of papillae and cloaca; fourth and fifth pair juxtaposed paracloacally; sixth to eighth pair equally distributed in one line ventrally, ninth pair of papillae located laterally at the level of the eighth pair of postcloacal papillae; tenth pair again lies ventrally (Figs. 4, 14, 15). Spiculae unequal, right spicule 621 (539 – 582) long, left spicule 815 (807-855) long, both spicules bialate (Fig. 16). Alae end approximately 84 (82) µm from the acerate top of spicule (Fig. 17). Gubernaculum 106 (99 – 123) long, Y-shaped.

Female (2 specimens; allotype and measurements of 1 paratype in parentheses): Body 16.90 (11.90) mm long, 460 (376) maximum width in middle of body, body width at level of anus 176 (171). Buccal capsule 31 (28) long, 51(45) wide, teeth in oesophageal funnel 16 (15) long. Total oesophagus 1787 (1234) long. Posterior oesophageal bulb 178 (202) wide. Nerve ring 283 (246) and excretory pore 443 (399) from anterior end, respectively. Vulva preequatorial, 6.43 (5.50) mm from anterior end of body, form of transverse slit with slightly elevated margins (Fig. 6). Tail 870 (832) long, prolonged into slender point 76 (72) long (Figs. 7, 19). Eggs (n = 15 for both specimens) ovoid with smooth shell, 46 – 52 (mean 49.6) long, 39 – 48 (mean 42.3) wide, with well-developed larvae (Fig. 8).

Taxonomic summary

Type specimens: Holotype – male; Allotype – female; two male and one female paratypes (cat. N-995) deposited in the Helminthological collection of the Institute of Parasitology, the Biology Centre, ASCR, v.v.i., Branišovská 31, 370 05 České Budějovice, Czech Republic.

Type host: *Otus scops* (Linnaeus, 1758), Strigidae (Otini) – Eurasian Scops Owl.

Site of infection: colon and caecum.

Type locality: Přerov, 6570 (number of map field according to the European mapping network), Czech Republic, Europe.

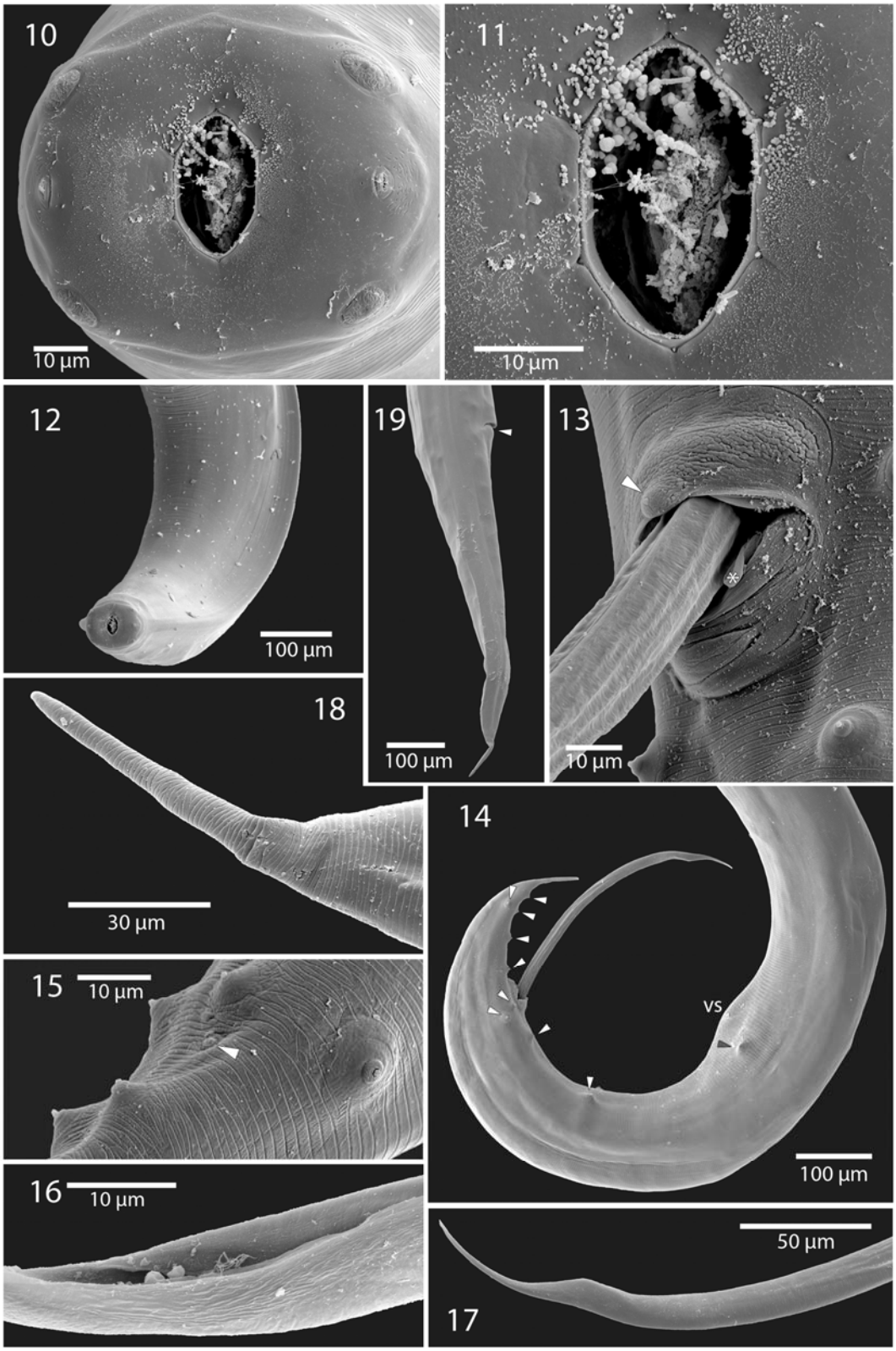
Intensity of infection: Eight nematode specimens (5 males and 3 females) in a single host.

Etymology: Specific epithet in honour of our colleague Josef K. Macko, Institute of Parasitology, the Slovak Academy of Sciences, Košice, Slovak Republic, a world-renowned specialist in morphology, systematics, the species diversity of helminth parasites of birds, and general helminthology.

Remarks

The new species is placed in *Subulura* Molin, 1960 (Nematoda: Subuluridae) because its morphology fully corresponds with the generic diagnoses by Yamaguti (1961), Skryabin *et al*. (1964) and Vincente *et al*. (1995). Sixty-seven valid species of the genus *Subulura* parasitizing birds are widely recognized (see zoogeographical analysis). Out of these species, 10 species are specialized parasites of birds of the order Strigiformes. They are divided into two morphological groups. The first group with six species contains males with equal spicules and 10 or 11 pairs of caudal papillae: *Subulura alfenensis* Pinto, 1968 – host *Athene cunicularia* (Molina), Brasil; *S. chinensis* Schwartz, 1926 – *Otus stictonotus* (Sharpe), China; *S. noctuae* (Seurat, 1914) – *Athene noctua glaux* (Savigny), Africa, Algeria; *S. bolivari* (López-Neyra, 1922) – *Athene noctua* (Scopoli), Europe, Spain all have ten pairs of caudal papillae; and *S. albai* Argawal, 1965 – *Tyto alba* (Scopoli), India, Lucknow and *S. similis* (Gendre, 1909) – from three bird orders (Coraciiformes, Cuculiformes and Strigiformes), Africa all have 11 pairs of caudal papillae. We consider the last mentioned species as *species inquirenda* by virtue of its incomplete description and the existence of host differences. Cram (1927) in her determination key [and also López-Neyra (1945)] placed the species *S. similis* in the group of subulurids with equal spicules and described a group of the lower caudal papillae as follows: "the most posterior pairs of caudal papillae are dissimilar, the second being shorter and more slender, the third ventral pair is at least as large as the first pair and is in close juxtaposition with the second pair." *Subulura mackoi* n. sp. differs from *S. similis* in the number and distribution of caudal papillae and unequal spiculae. According to Gendre (1909), in *S. similis* from the host *Ptilopsis leucotis* (Temminck), the body length of males is 12.6 – 15.0 mm, and that of females is 20.12 – 22.45 mm. The ratio of vulva distance from anterior body end for samples of all three different hosts is 1:2.3. The vulva of females from *P. leucotis* is a shorter distance (6.09 – 6.80 mm) from the anterior body end than the vulva in *S. mackoi* n. sp., i. e. in ratio of vulva distance from anterior body end to total body length 30.2 – 30.3 %, only. Another two species of subulurids, described from other host orders which were later found in Strigiformes, are known besides the above mentioned parasites from this morphological group. The first is *S. forcipata* (Rudolphi, 1819) – an obligatory parasite of *Cuculiformes* in South America (Vicente *et al*., 1995) reported by Kinsella *et al*. (2001) in *Athene cunicularia* in USA (Florida). Males of this species have 10 pairs of caudal papillae and an equal spiculae length of 677 (Barreto, 1919); the second is *S. galloperdicis* Baylis et Daubney, 1922 – a common parasite of Galliformes reported once by Sood (2006) in *Tyto alba* in India. Males have 11 pairs of caudal papillae and an equal spiculae length of 760 – 800 (Baylis, 1936). Both taxa are clearly different from *S. mackoi* n. sp. in virtue of these and other species value characters.

The newly described *S. mackoi* n. sp. belongs to the second group of four specialized parasites of Strigiformes, in which males are characterized by unequal spiculae and 10



Figs. 10 – 18. *Subulura mackoi* n.sp.; SEM micrographs. Fig. 10. Female cephalic end (apical view); Fig. 11. Detail of female hexagonal mouth opening with six small labial lobes; Fig. 12. Female anterior end with lateral alae; Fig. 13. Male cloacal region with protruding spicule and distal part of gubernaculum (asterix) and single papilla at upper cloacal lip (arrowhead); Fig. 14. Male posterior end (lateral view) with precloacal sucker (vs), protruding spicule, arrowheads indicate ten pairs of caudal papillae; Fig. 15. Lower group of postcloacal caudal papillae with phasmid (arrowhead); Fig. 16. Detail of spicule with smooth channel; Fig. 17. Needle-like extremity of spicule; Fig. 18. Female tail point showing annulation; Fig. 19. Female posterior end with anus (arrowhead).

or 11 pairs of caudal papillae. These are *S. acutissima* Molin, 1860 (*typus generis*); *S. lutzi* Barreto, 1919; *S. longispicula* Wang, 1980; and *S. glaucidii* (López-Neyra, 1945). Only one species, *S. reclinata* (Rudolphi, 1819), a specialized parasite of South American Piciformes (Barreto 1919; Vicente *et al*. 1995), was reported by Kinsella *et al*. (2001) in *Asio otus* (L.) from the USA (Florida).

The main distinguishing features of all species from this group are as follows: males (Table 1) – number and topography of caudal papillae, shape of spiculae, length of spiculae, ratio of spiculae length (in %), tail length, ratio of tail length and body length (in %); females (Table 2) – body length, shape of vulva, distance of vulva to anterior end of body, ratio of vulva distance to body length (in %), tail length, ratio of tail length and body length (in %), and egg dimensions.

Subulura glaucidii and *S. mackoi* n. sp. are similar in the shape of the distal ends of spiculae. The most important distinguishing characters are the presence of the odd papilla on the upper lip of cloaca in *S. mackoi* n. sp., which is absent in *S. glaucidii*, the number and distribution of the lower group of postcloacal caudal papillae (Figs. 4, 9), and the other above mentioned features. Ferrer *et al*. (2004) found and assigned nematodes in *O. scops* in Spain as *Subulura* spp., without more detailed morphometric data. These nematodes are probably different from the well-known *S. bolivari* from *Athene noctua* reported in Spain by López-Neyra (1922) and Illescas *et al*. (1993) and may be conspecific with *S. mackoi* n.sp.

Two subulurid species with 10 pairs of caudal papillae and unequal or subequal spiculae have been found in non strigiform birds wintering in sub-Saharan Africa and breeding in the temperate zone of the Palaearctic realm. The first is *S. subulata* (Rudolphi, 1819) parasitizing *Caprimulgus europaeus* L. (according to Chabaud, 1957, spiculae length 960 and 1 540, eggs 85 × 55, female tail length 78). *Subulura mackoi* n. sp. has smaller spiculae and eggs; the female tail length is slightly longer. The second, *S. sisoworonki* Iwanizky, 1940 from *Coracias garrulus* L., is well-differentiated by the length of its subequal spiculae (809 and 747), and by its shorter tail (312) in the male (Iwanitzky, 1940). We emphasize that this species has a median odd papilla on the upper lip of the cloaca, similarly to *S. mackoi* sp. n. However, this character is absent or not described in any other avian subulurids. Undoubtedly, zoogeographical aspects and host specificity are important characters for distinguishing these subulurids taxa.

Zoogeographical analysis

The systematics of the Subuluridae family has been reviewed by Barreto (1919), López-Neyra (1945), Skryabin and Shikhobalova (1949), Skryabin *et al*. (1954), Inglis (1958, 1960), and Quentin (1969, 1971), and summarized by Chabaud (2009). The nominotypic genus *Subulura* Molin, 1860 includes numerous species parasitizing birds and mammals; only one (*S. lacertilia*) parasitizes Brazilian reptile (Vicente *et al*., 2000). For the zoogeographical analysis of subulurids in birds we prefer to regard *Subulura* in the broader sense of the generic diagnosis by Yamaguti (1961) and Skryabin *et al* (1964). In accordance with Bar-

Table 1. Selected differential features (dimensions in mm) of male specimens from the genus *Subulura* with unequal spiculae, parasitizing Strigiformes (*S. reclinata* found in *Asio otus* L. by Kinsella *et al*. 2001)

Species / Features	***S. acutissima***	***S. longispicula***	***S. mackoi* n.sp.**	***S. glaucidii***	***S. lutzi***	***S. reclinata***
Body length	9.66 – 10.50	12.80 – 13.60	10.71 – 11.69	6.10 – 8.30	14.0	11.0
Number of caudal papillae	10	10	10 + 1	11	11	11
Length of spicula (1)	1.06 – 1.26	2.40 – 3.00	0.539 – 0.621	0.425 – 0.490	0.794	1.105
Length of spicula (2)	1.60 – 1.81	2.88 – 3.36	0.807 – 0.855	0.720 – 0.860	1.270	1.516
Ratio of spiculae length (in %)	66 – 70	83 – 89	67 – 76	56 – 59	62	73
Tail length	0.26 – 0.31	0.158 – 0.160	0.259 – 0.264	0.150 – 0.220	0.169	0.210
Ratio tail body length (in %)	2.69 – 2.95	1.18 – 1.23	2.22 – 2.45	2.46 – 2.65	1.21	1.90
Hosts	*Glaucidium brasilianum* (Gmelin)	*Ninox scutulata* (Raffles)	*Otus scops* (Linnaeus)	*Glaucidium passerinum* (Linnaeus)	*Strix* sp.	*Crotophaga ani* Linnaeus
Distribution	Brasil	China	Czech Republic (Europe)	Spain (Europe)	Brasil	Brasil
Reference	Freitas et al. (1970)	Wang (1980)	Our data	López-Neyra (1945)	Barreto (1919)	Barreto (1919)

Table 2. Selected differential features (dimension in mm) of female species of the genus *Subulura*, parasitizing Strigiformes (Reference are in Table 1)

Species / Features	*S. acutissima*	*S. longispicula*	*S. mackoi* n.sp.	*S. glaucidii*	*S. lutzi*	*S. reclinata*
Body length	7.69 – 12.15	17.60 – 18.80	11.90 – 16.90	10.0 – 12.3	11.0 – 22.5	14.30 – 20.50
Distance vulva-anterior end	3.23 – 5.86	Slightly behind middle of body	5.50 – 6.43	5.50	First third of body length	Slightly behind middle of body
Ratio vulva/ body length (in %)	42 – 48	–	38 – 46	47	33 – 35	–
Eggs	0.048x0.040	0.070 – 0.080x 0.052 – 0.056	0.046 – 0.052x 0.039 – 0.048	0.055 – 0.060x 0.040 – 0.050	0.083x0.050	0.076x0.050
Tail length	0.830 – 1.110	0.880 – 1.080	0.832 – 0.870	0.400 – 0.450	0.443	1.285
Ratio tail/ body length (in %)	9.14 – 10.79	5.00 – 5.74	5.14 – 6.99	3.60 – 4.00	1.96 – 4.01	6.63 – 8.98

reto (1919), Baylis (1936), Yamaguti (1961), Skryabin *et al*. (1964), Vincente *et al*. (1995) and others, we accept the genus *Allodapa* Diesing, 1861 as a synonym of the genus *Subulura* (see Skryabin *et al*., 1964). Campana-Rouget (1956) ranked the genus *Travassodolapa* López-Neyra, 1945 as a synonym of *Subulura*. The presence of unequal spicules was found in type species *S. acutissima* Molin, 1860 by Freitas *et al*. (1970), which supported this synonymy. In addition, Sonin and Baruš (1996) assigned *Alaplectana* Azim, 1931 and Sood (2006) assigned *Inglisubulura* Devamma, 1975 as synonyms of *Subulura*. Primates and occasionally rodents are obligatory hosts of *Primasubulura* Inglis, 1958. Three species parasitizing birds which Sood (2006) retained in this genus (*P. alata* Devamma, 1975; *P. pavonis* Devamma, 1975; and *P. singhi* Balamani et Devamma, 1985) evidently belong to *Subulura*. We agree with Chabaud (2009) that *Paraheterakis* Nama et Jain, 1974 seems to be a synonym of *Subulura*. Also *Gallioxynema* Shamim et Deshmukh, 1980 parasitizing *Gallus gallus* f. *domestica* from India, and mentioned by Gibbons (2010), is probably congeneric and a synonym of *Subulura*.

In the present zoogeographical analysis, we evaluated all valid nominal taxa in species level of the genus *Subulura* parasitizing birds with remarks on its synonymy and specialization in avian orders.

Palaearctic Realm

Galliformes – *S. amherstii* (Azim, 1931); *S. brumpti* (López-Neyra, 1922); *S. curvata* (Linstow, 1883) [syn. *Allodapa seurati* Barreto, 1917]; *S. differens* (Sonsino, 1890); *S. gracilis* (Linstow, 1899); *S. gallopavonis* López-Neyra, 1945; *S. skrjabini* (Semenov, 1926) [syn. *S. coturnicis* Yamaguti, 1941, *S. coturnicis* López-Neyra, 1945*, S. baylisi* López-Neyra, 1946]; *S. tetraogalli* Spaul, 1929 [*syn. S. kabulanus* Akhtar, 1937]. Strigiformes – *S. bolivari; S. glaucidii; S. mackoi* n. sp.; *S. noctuae.* Caprimulgiformes – *S. leprincei* (Gendre, 1909); *S. subulata.* Coraciiformes – *S. sisoworonki*. Gruiformes – *S. halli* Barreto, 1917; *S. rima* (Linstow, 1906). Charadriiformes – *S. skrjabinensis* Borgarenko, 1960. Passeriformes – *S. brumpti*.

Note: Ortlepp (1938), Inglis (1964) and Ogden (1966) considered *S. suctoria*, *S. differens* and *S. brumpti* as conspecific. Barreto (1919), Cuckler and Alicata (1944), Skryabin and Shikhobalova (1949) and Hartwich (1975) pointed to significant differences in their zoogeography and hosts (*S. suctoria* – Caprimulgiformes, Brazil; *S. differens* and *S. brumpti* – Galliformes, Old World). *Subulura brumpti* was described from domestic fowl from Spain (*Gallus gallus* f. *domestica*) by López-Neyra (1922). *Subulura suctoria* has not been found in birds of the Old World. Sonin and Baruš (1996) declared that domestic fowl was typical host for *S. brumpti*; however, the parasite was referred from other domestic birds (*Meleagris, Numida, Guttera*) and very rarely free-living gallinaceous birds. As a result of domestication and the breeding of fowl, the geographic distribution of *S. brumpti* is cosmopolitan. *Subulura brumpti* was found in Passeriformes (*Sturnus vulgaris* L.) in the temperate zone in Poland only and reported under the name *S. suctoria* (Gundlach, 1965; Okulewicz, 1997). Meredov *et al*. (1970) reported *S. suctoria* in *Athene noctua* from Turkmenistan. For the above mentioned reasons we are convinced that this species was misidentified and is probably a different species with equal spicules (*S. noctuae* or *S. bolivari*) parasitizing Strigiformes in the Palaearctic Region. The species *S. coturnicus* (Standel, 1874) from *Coturnix coturnix* (L.) in Ukraine is considered by Sonin and Baruš (1996) as "*species inquirenda*". *Subulura differens* was described by Sonsino (1890) from domestic fowl (*Gallus gallus* f. *domestica*) in Italy, and is widespread, according to Sonin and Baruš (1996), in domestic fowl and free-living gallinaceous birds (*Alectoris*, *Perdix*, *Coturnix*, *Francolinus*, *Numida*) in the southern (subtropical) belt of

the Palaearctic realm, and in the whole the Afrotropical and Neotropic realms.

Afrotropical Realm
Galliformes – *S. acuticauda* (Linstow, 1901); *S. brumpti*; *S. dentigera* Ortlepp, 1937; *S. differens; S. poculum* (Linstow, 1909). Strigiformes – *S. similis* (?). Caprimulgiformes – *S. subulata* ; *S. leprincei.* Cuculiformes – *S. similis* (?). Coraciiformes – *S. recurvata* (Linstow, 1901); *S. similis.* Gruiformes – *S. otidis* Ortlepp, 1938; Coliiformes – *S. armata* Vuylsteke, 1957. Pelecaniformes – *S. plotina* Baylis, 1919.
Note: Railliet and Henry (1914) suggested that reports of *S. similis* by Gendre (1909) from the hosts *Coracias abyssinicus* Hermann*, Eurystomus afer* Gray, *Centropus monachus* Rüppell*, C. superciliosus* Hemprich et Ehrenberg, and *Ptilopsis leucotis* might be confused. Barreto (1919) considered that Gendre (1909) was dealing with several species from this wide variety of hosts and suggested that the samples from *E. afer* might be *S. recurvata* described by Linstow (1901) from the same host in Africa (Lake Nyassa). Skryabin (1916) identified *S. suctoria* (Molin, 1860) from *C. superciliosus.* Barreto (1919) considered that these nematodes were conspecific with *S. similis* identified by Gendre (1909) from the same host and region (tropical Africa). We prefer to preserve the name *S. similis* for a taxon from Coraciiformes hosts from Africa. However, redescription of the taxon from the typical host (*C. abyssinicus*) is needed. Junker and Boomker (2007) found *subulurids* (*S. suctoria* and *S. dentigera*) in Guinea fowl *Numida meleagris* (L.) and *Guttera edouardi* Hartlaub and provided an overview of their occurrence in African gallinaceous birds which shows that *S. dentigera* is a specialized parasite in this region. In our opinion, the determination of *S. suctoria* is wrong (see note above – Palaearctic region); it is probably *S. brumpti*. For comparison, redescriptions of *S. suctoria* from *Caprimulgus* sp. (Brasil) by Barreto (1919), *C. cubensis* (Lawrence) (Cuba) by Baruš and Lorenzo Hernández (1970), and *S. brumpti* from *G. gallus* f. *dom*. (Cuba) by Baruš (1969) could be used. The occurrence of *S. suctoria* in various Madagascan wild birds reported by Inglis (1964) cannot be accepted from the zoogeographical and host perspective.

Indo-Malay Realm
Galliformes – *S. brumpti; S. galloperdicis* Baylis et Daubney, 1922; *S. minetti* Bhalerao, 1941; *S. francolinusi* Jehan, 1970; *S. fotedari* Gupta, 1982; *S. haitinhensis* Phan, 1969; *S. indica* Rathore et Nama, 1986; *S. inglisi* (Devamma, 1975); *S. multipapillata* (Chandler, 1926); *S. pavonis* (Devamma, 1975); *S. perdicularia* Dey Sarkar, 1999; *S. skrjabini* [syn. *S. alata* (Devamma, 1975), *Inglisubulura singhi* Devamma, 1975, *S. singhi* Balamani et Devamma, 1985]; *S. taiwanensis* Yamaguti, 1935. Strigiformes – *S. albai; S. chinensis; S. galloperdicis; S. longispicula.* Caprimulgiformes – *S. tulsidasi* Dey Sarkar, 1995; *S. galloperdicis.* Coraciiformes – *S. albai;S. leachii* Kirschner, 1938. Cuculiformes – *S. rimula* (Linstow, 1903); *S. sinensis* Kumar et Gupta, 1976. Falconiformes – *S. kanpurensis* Gupta, 1980. Passeriformes – *S. alii* Ilyas, 1982; *S. helicospiculata* Schmidt et Kuntz, 1971; *S. turnicis* Maplestone, 1931; *S. turdoidae* Soota et Dey Sarkar, 1981.
Note: Among the species from this area *S. olympioi* Barreto, 1919 reported from India (Lucknow) by Gupta and Kazim (1978) in *Turdoides striatus* (Dumont) (Passeriformes) cannot be included. This species is a specialized parasite of Tinamiformes (Nascimento *et al*., 1992; Pinto *et al*., 2006) and its distribution is limited to the Neotropical realm (Barreto, 1919; Vicente *et al*., 1995). The species *S. alata*, *S. singhi* and *I. singhi* are conspecific to *S. skrjabini,* a specialized parasite of galliform birds in the Old World (genera *Alectoris*, *Perdix*, *Coturnix*, *Phasianu*s, rarely ocuring in *Gallus gallus* f. *domestica*); *S. skrjabini* males are characterized by equal spicules and 11 pairs of caudal papillae. Also *S. suctoria* reported by Sood (2006) from Caprimulgiformes, Cuculiformes, Galliformes and Coraciiformes was misdetermined in this region. It is probably a "species complex" of a total of 11 taxa previously described mainly from South Asia; they should be subject to revision. Ilyas (1982) gived the names of two new species, *Subulura francolini* with subequal spicules (840 and 750) and *S. schikhobalovi* with equal spicules (570 – 1060), with only data about the body length of males and females (figures absent) in the key. Therefore, we consider them as a *species inquirenda*. Sood (2006) did not mention either name in the checklist of nematode parasites of birds from South Asia. He included *Duplicaecum ibisi* Majumdar et Chakravarty, 1963 (host *Bubulcus ibis* L.*,* Ciconiiformes) into *Subulura*. However, morphologically, it clearly belongs to the order Ascaridida, of the Anisakidae family (because an oesophageal ventriculus, ventricular and intestinal appendices, and a mouth with three lips are present). The findings of *S. galloperdicis* [typical host *Galloperdix spadicea* (Gmelin), Galliformes] in *Tyto alba* registered by Sood (2006) and in *Caprimulgus* sp. by Soota (1981) in India might be considered as host switching. Revision of the species of this genus, which parasitize birds in the Indo-Malayan Region, is badly needed. For example, in one host, *Turdoides striatus* (Passeriformes) is parasitized by *S. alii*, *S. olympioi* (evidently misdetermined, as it is a specialized parasite of Brasilian Tinamiformes – Vicente *et al*., 1995; Pinto *et al*., 2006), *S. turdoides* and *S. turnicis*, which is very unusual.

Australasian Realm
Galliformes – *S. brumpti*. Cuculiformes – *S. clelandi* Johnston et Mawson, 1941. Caprimulgiformes – *S. clelandi.*
Note: Ogden (1966) considered *S. clelandi* described by Johnston and Mawson (1941) from *Podargus strigoides* Latham, and *Scythrops novaehollandiae* Latham as synonyms of *Allopada* (=*Subulura*) *suctoria*. The reasons for exclusion of the presence of *S. suctoria* in birds from these orders in the Australasian Region are given above (Palae-

arctic and Afrotropical Realms). *S. clelandi* is evidently a valid taxon in this zoogeographical realm, near to *S. differens*. However, it differs by having a longer body length, shorter spicules, and smaller eggs (Johnston & Mawson, 1941).

Oceanic Realm
Galliformes – *S. brumpti*.
Note: The life cycle of *S. brumpti* was studied for the first time by Alicata (1939) and Cuckler and Alicata (1944) in this zoogeographical realm on Hawaii.

Nearctic Realm
Galliformes – *S. brumpti; S. strongylina* (Rudolphi, 1819).
Strigiformes – *S. forcipata* (Rudolphi, 1819); S. *reclinata.*
Passeriformes – *S. papillosa* (Molin, 1860).
Note: The complex history of the names and synonymy of taxa *S. forcipata* and *S. strongylina* was analyzed by Skryabin *et al*. (1954). The opinions of Skryabin and Schikhobalova (1949) and Baruš (1970c) that these species recorded in galliform birds of the Old World were misdetermined and that they are the taxon *S. differens* were respected by Sonin and Baruš (1996). Barreto (1919) emphasized the importance of the specialization of these species to their definitive hosts: *S. forcipata* to Cuculiformes and *S. strongylina* to Tinamiformes in the Neotropical Region (Nasaimento *et al*., 1992). Samples of nematodes from *Caprimulgus* sp. denoted by Schneider (1866) as *Heterakis forciparia* (=*S. forciparia*) were considered as true *S. suctoria* by Barreto (1919). We consider records of the species *S. forcipata* and *S. reclinata* by Kinsella *et al*. (2001) in *Athene cunicularia* and *Asio otus* (USA, Florida) to indicate a co-accommodation phenomenon or the host-switching of parasites in places of geographical contact between hosts. The findings of *S. strongylina* from *Colinus virginianus* (L.) (Galliformes) in Ohio (USA) by Biester and Schwarte (1968) require revision.

Neotropical Region
Galliformes – *S. brumpti*; *S. differens*. Strigiformes – *S. acutissima*; *S. lutzi*; *S. alfenensis* [syn. *S. freitaslauroi* Pinto, 1970]. Caprimulgiformes – *S. suctoria*. Cuculiformes – *S. carlosi* Barreto, 1919; *S. forcipata; S. reclinata* (Rudolphi, 1819); *S. rudolphii* Santos, 1970; *S. samanamudi* Ibáñez, 1969; *S. travassosi* Barreto, 1919. Trogoniformes – *S. bentocruzi* Barreto, 1919; *S. trogoni* Barreto, 1919. Tinamiformes – *S. olympioi* Barreto, 1919; *S. strongylina.* Cariamiformes – *S. allodapa* (Creplin, 1853). Charadriiformes – *S. huaynacapaci* Freitas, Vincente et Ibáñez, 1968. Passeriformes – *S. papilllosa*. Anseriformes – *Subulura* sp.; *S. brumpti*.
Note: An excellent overview of subulurid nematode fauna parazitizing birds from this region was presented by Barreto (1919) and Vincente *et al*. (1995), with other species ascertained by Ibañez (1969) and Freitas *et al*. (1968). Freitas *et al*. (1970) presented a very important study on the stability of the genus *Subulura*, with a complete redescription of type species *S. acutissima* from a type host and a type locality (Brasil). This species is specialized to hosts from Strigiformes (Vicente *et al*., 1995) and has markedly unequal spiculae. The occurrence of subulurids in hosts of Anseriformes is very rare. Only Ribeiro-Machado *et al*. (2006) recorded *Subulura* sp. from *Cairina moschata* (L.), and Baruš and Blažek (1970) experimentaly infected *Anas platyrhynchos* f. *domestica* with *S. brumpti* in Cuba.

Discussion

Barreto (1919), who evaluated 26 taxa parasitizing birds, already noted the importance of host specialization and zoogeographical distribution in identifying morphospecies of the genus *Subulura*. In our analysis, we considered 68 valid species parasitizing birds currently classified in this genus. Only *S. brumpti* has a cosmopolitan distribution; it is a parasite specialized to domestic fowl (*Gallus gallus* f. *domestica*), rarely occurring in other domesticated or wild gallinaceous birds (Sonin & Baruš, 1996). The cosmopolitan distribution is the result of human activity (poultry farming). For the same reason, *S. differens* is spread over the three zoogeographic regions (Palaearctic, Afrotropical and Neotropical). The natural occurrence of *S. skrjabini* is in two regions (Palaearctic and Indomalayan); it is a characteristic parasite of wild gallinaceous birds of the genera *Coturnix*, *Perdix*, *Alectoris*, *Phasianus*, *Tetrao*, and *Francolinus*. It has been detected very rarely in domestic fowl (Sonin & Baruš, 1996). *Subulura subulata* and *S. leprincei* occur in the Palaearctic and Afrotropical realms; in the Neotropical and Nearctic realms, the species *S. forcipata, S. reclinata*, and *S. strongylina* occur. All other evaluated species and their hosts have zoogeographical distribution in the Old World (45 species), the New World (14 species) and the Australasian Region (2 species). They are distributed mainly in the tropical zone of the Afrotropical, Indo-Malayan and Neotropical Regions; smaller number of species extends to the subtropical zone of the Palaeartic and Nearctic Regions, but rarely to the temperate zone. In our opinion, the main factor determining this geographic distribution of subulurids parasitizing birds is the phenomenon of thermophily, which is manifested by the influence and importance of temperature during development of the larval stage in intermediate hosts. This hypothesis is supported by results of studies on the *S. brumpti* development cycle by Alicata (1939), Cuckler and Alicata (1944) in Hawaii, and Abdou and Selim (1957) in Egypt. Baruš (1970a) demonstrated experimentally that in *S. brumpti* (erroneously named *S. suctoria*) in Cuba the development of larvae in intermediate hosts was fully realized only at a temperature of 20º C or higher. The development stops at lower temperatures. Although intermediate hosts (various species of Dermaptera, Blattaria, Orthoptera, and Coleoptera) and gallinaceous domestic birds as definitive hosts are present in the temperate zone of the appropriate zoogeographical area, the lower temperature inhibits or completely excludes the life cycle and thus the infection of hosts (Baruš, 1970b).

Therefore, the temperature is the main zoogeographical factor that determines the presence and distribution of *S. brumpti* and probably most of the other species of the genus *Subulura* parasitizing birds.

Infection with subulurids in birds nesting in temperate zones of geographical regions (the northern zone in the Palaearctic Region in our case) was observed only in hosts wintering in tropical regions. *S. subulata* parasitizing *C. europaeus* had its northernmost distribution in the Palaearctic Realm (Czech Republic – Sitko & Okulewicz, 2010; Austria – Rudolphi, 1819); in the southern zone of Palaearctic Region it was reported from Algeria, Spain, Corsica, and Tunisia (López-Neyra, 1945; Chabaud, 1957). *Subulura leprincei* from *C. europaeus* was reported in the northern zone in Belorussia (Merkusheva & Bobkova, 1981), and in the southern zone in Georgia (Kurashvili 1957), Armenia (Akhumyan, 1966), Turkmenistan (Meredov, 1976) and Spain (Cordero del Campillo *et al*., 1977). A single record of *S. brumpti* from *Sturnus vulgaris* was reported from Poland (Gundlach, 1965; Okulewicz, 1997). *S. sisoworonki* was reported from *C. garrulus* in Azerbaijan (Sadychov, 1970), Turkmenistan (Meredov *et al*., 1970) and Ukraine (Ivanickyi, 1940). *S. skrjabini* from *Alectoris chukar* (Gray), *Francolinus francolinus* (L.) and *Perdix perdix* (L.) was found in Armenia (Akhumyan, 1966); *S. skrjabinensis* from *Burhinus oedicnemus* (L.) was found in Kazakhstan (Gvozdev & Kasymzhanova, 1965) and Tajikistan (Borgarenko, 1960, 1990). Data on the presence of *S. allodapa* from *Alectoris chukar* in Armenia (Akhumyan, 1966) and Azerbaijan (Vaidova, 1964; Kasimov, 1947, 1956; Kasimov & Feyzullaev, 1965) are wrong, because this species is a specialized parasite of *Cariama cristata* (L.) (Cariamiformes) in the Neotropical Region in Brasil (Vincente *et al*., 1995). This is probably a species characteristic to gallinaceus birds in the Palearctic Realm (males possess from 10 to 11papillae and equal or subequal spicules, which corresponds with *S. brumpti* or *S. differens*).

This phenomenon, the origin of bird parasites and their transmission from wintering (epiareal) to nesting (euareal) territory, was analyzed by Dogel (1962). The abovementioned species of Europaean subulurids of the Palaearctic Realm evidently belong to the group of "southern species" which infect hosts in the wintering grounds. Birds are not infected by these parasites in the nesting grounds, and parasitic fauna of these hosts disappears. Many intestinal helminths live approximately one to three months, so findings of southern species in the nesting areas are rare and limited to a relatively short time after arrival. Another reason for the rare occurrence of subulurids in the Czech Republic is the fact that they parasitize hosts with a small population density and often at the northern boundary of their distribution (*C. garrulus, O. scops, B. oedicnemus*). Parasitological research in the Czech Republic has not been carried out on some migratory bird species which are infected by subulurids in other zoogeographic regions – for example, *Cuculus canorus* L. and *Coturnix coturnix* L.

The zoogeography and host specialization of the genus *Subulura*, which includes numerous species, manifest interesting and taxonomically significant relationships that can be used to identify morphospecies.

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