

## Revision of the Metadilepididae (Cestoda: Cyclophyllidea) from Caprimulgiformes (Aves)

Boyko B. GEORGIEV<sup>1</sup> & Claude VAUCHER<sup>2</sup>

<sup>1</sup> Central Laboratory of General Ecology, Bulgarian Academy of Sciences,

2 Gagarin Street, 1113 Sofia, Bulgaria. E-mail: bbg@ecolab.bas.bg

<sup>2</sup> Natural History Museum, PO Box 6434, 1211 Geneva 6, Switzerland.

E-mail: claude.vaucher@mhn.ville-ge.ch

**Revision of the Metadilepididae (Cestoda: Cyclophyllidea) from Caprimulgiformes (Aves).** - The type series of *Metadilepis globacantha* from *Caprimulgus europaeus* in Sweden and *M. caprimulgorum* from *Chordeiles minor* in Brazil are redescribed. The occurrence of the latter cestode species in *Hydropsalis climacocerca* (as mentioned by Fuhrmann, 1908b, 1932) is questioned. Two new species of *Metadilepis* from Paraguay are described: *Metadilepis kornyushini* sp. n. from *Nyctibius griseus* and *M. spasskiorum* sp. n. from *Setopagis parvula*. *Metadilepis caprimulgina* from *Caprimulgus europaeus* in Central Russia is considered a species inquirenda. The diagnosis of *Metadilepis* is amended in order to conform it to the characteristics of *M. kornyushini* and *M. spasskiorum*. An identification key to the species of *Metadilepis* is proposed. *Proparuterina aruensis* from *Podargus papuensis*, Aru Island (Indonesia), the type species of *Proparuterina*, is redescribed. The genus *Proparuterina* is recognised as monotypic. *Proparuterina lali* from *Passer domesticus* in India is considered a species incertae sedis. *Mariauxilepis* gen. n. with type species *M. paraguayensis* sp. n. from *Nyctidromus albicollis* (type host) and *Setopagis parvula* from Paraguay is erected. *Urutaulepis* gen. n. is proposed as a monotypic genus for *Dilepis pifanoi* from *Nyctibius griseus* in Venezuela. The type species is redescribed on the basis of a paratype specimen and transferred from the Dilepididae to the Metadilepididae as *Urutaulepis pifanoi* comb. n.

**Key-words:** Cestoda - Metadilepididae - Caprimulgiformes - *Metadilepis* - *Proparuterina* - *Mariauxilepis* gen. n. - *Urutaulepis* gen. n.

### INTRODUCTION

The family Metadilepididae Spasskii, 1959 was erected for three genera of the Dilepididae Railliet & Henry, 1909 exhibiting several similarities with paruterinid cestodes (Spasskii, 1959). It has been considered a full family within the superfamilies Paruterinoidea (see Spasskaya & Spasskii, 1971) or Biuterinoidea (see Kornyushin,

1989). Recent studies on the phylogenetic relationships within the order Cyclophyllidea (Hoberg *et al.*, 1999) confirmed Metadilepididae and Paruterinidae Fuhrmann, 1907 (as defined by Korniyushin & Georgiev, 1994, and Georgiev & Korniyushin, 1994) as sister taxa. The most recent survey on the systematics of the metadilepidids recognised 8 genera in this family; they occur in the Caprimulgiformes, Coraciiformes and Passeriformes, mostly in tropical representatives of these avian orders (Korniyushin & Georgiev, 1994).

Until now, two metadilepidid genera have been known from caprimulgiform hosts, *Metadilepis* Spasskii, 1949 (three species) and *Proparuterina* Fuhrmann, 1911 (one species) (see Spasskii, 1959; Spasskii & Spasskaya, 1977; Korniyushin, 1989; Korniyushin & Georgiev, 1994). During the last 20 years, new material of metadilepidids has been collected from nightjars and nighthawks (Caprimulgidae) and potoos (Nyctibiidae) in Paraguay by expeditions of the Natural History Museum, Geneva. Preliminary studies showed that these specimens represented undescribed taxa. This stimulated a revision of the metadilepidids from caprimulgiform hosts. The results of this taxonomic study are given in the present article.

#### MATERIALS AND METHODS

Cestodes from the collection of the Natural History Museum, Geneva (MHNG, INVE) were studied for this revision. Some specimens of a new species have been retained in the collection of the senior author. Details of the cestodes studied are given in the text for each species.

The Paraguayan specimens were collected by expeditions of MHNG. The intestines examined were opened longitudinally, placed in water for a few minutes and fixed in hot 4% neutral formalin. Subsequently, cestodes were removed under a stereomicroscope, washed in water and stored in 70% ethanol. Strobila were stained in Mayer's hydrochloric carmine or iron acetocarmine, dehydrated in an ethanol series, cleared in eugenol and mounted in Canada balsam. Some scoleces were mounted in Berlese's medium to facilitate observations of the rostellar hooks.

The metrical and meristic data are presented as the range, the mean in parentheses and the number of measurements or counts (*n*). The measurements are given in  $\mu\text{m}$  unless otherwise stated.

Several ratios are used for more adequate characterisation and differentiation of the species of *Metadilepis*. These are:

$R_{\text{vag/cs}}$ , ratio of the length of copulatory vagina (measured as curve) to the length of cirrus sac in the same proglottis (calculated for mature and post-mature proglottides);

$R_{\text{ov/pr}}$ , ratio of the width of the ovary to the width of the proglottis (calculated for fully developed mature proglottides only);

$R_{\text{cs/pr}}$ , ratio of the length of the cirrus sac to the width of the proglottis (calculated for mature and post-mature proglottides).

The terms used for the developmental stages of proglottides are as previously described (Georgiev & Vaucher, 2001). The nomenclature of birds follows Wolters (1982).

#### SYSTEMATIC SURVEY

##### *Metadilepis* Spasskii, 1947

*Dilepis* (*Metadilepis*) Spasskii, 1947a: 48-58.

*Metaskrjabinolepis* Spasskii, 1947b: 723-724.

*Metadilepis* Spasskii, 1947: Spasskii, 1949: 50-54; Yamaguti, 1959: 248; Schmidt, 1986: 376; Korniyushin, 1989: 173; Korniyushin & Georgiev, 1994: 586.

##### DIAGNOSIS

Rostellum sucker-like, armed with two rows of rostellar hooks. Hooks in each row of almost equal length; blade curved, handle and guard with large epiphyseal thickenings. Proglottides craspedote, usually wider than long, sometimes gravid proglottides as wide as long. Genital pores unilateral or irregularly alternating in long series. Genital atrium simple, infundibular, surrounded by moderately developed masses of glandular cells. Genital ducts ventral to osmoregulatory canals. Testes in two groups, lateral or postero-lateral to female glands. Cirrus sac thick-walled, overlapping or crossing poral osmoregulatory canals, containing masses of intensely staining cells situated along its walls. External vas deferens highly coiled, covered with prostate cells and forming together with them transversely elongate body situated at antiporal end of cirrus sac. Internal vas deferens coiled, in gravid proglottides may expand, resembling internal seminal vesicle. Vitellarium median, compact or slightly lobed, oval or with irregular shape, near posterior proglottis margin. Ovary wide, transversely elongate, mostly with irregular shape, not clearly divided into two wings, slightly to deeply lobed. Vagina thick-walled, opens posteriorly or postero-laterally to orifice of cirrus sac. Uterus saccular, thick-walled, entirely in median field. Eggs round, with thin outer shell; embryophore and oncosphere round. In Caprimulgiformes (Caprimulgidae and Nyctibiidae), Holarctic, South America.

Type species: *Metadilepis globacantha* (Fuhrmann, 1913) Spasskii, 1949.

##### REMARKS

The previous diagnosis of this genus (Korniyushin & Georgiev, 1994) has been based on the characters of the two species from which material has been available, i.e., *M. globacantha* and *M. caprimulgorum*. The present study has revealed two further species from Neotropical caprimulgiform birds, which have morphological features allowing their placement in *Metadilepis*. However, *M. korniyushini* sp. n. is characterised by genital pores alternating in long series (compared to the unilateral position in the remaining species). It has also been found that gravid proglottides of *M. spasskiorum* sp. n. and *M. globacantha* can be almost as long as wide. In addition, we have observed that the cirrus sac contains intensely staining cellular masses extending along its walls in the four species considered. These amendments are introduced in the above-presented new version of the generic diagnosis.

In the following key to the species (see also Table I), characters connected with rostellar hooks are not used because of some discrepancies in the description of *M. caprimulgorum* (see the remarks on this species). *M. caprimulgina* (Neslobinsky, 1911) is not included in the key due to the scarce data on its morphology.

TABLE 1. Metrical and meristic data of the species of the genus *Metadilepis* (all based on the present study except where otherwise stated).

	<i>M. globacantha</i>	<i>M. caprimulgorum</i>	<i>M. kornyushini</i>	<i>M. spasskiorum</i>
Body:				
length (mm)	-	20 <sup>(2)</sup>	90	~ 60
maximum width (mm)	1.51/2.73 <sup>(1)</sup>	1.03	1.99-2.05	1.12-1.53
Scolex: diameter	-	160 <sup>(2)</sup>	482-505	279-310
Suckers: diameter	-	70 <sup>(2)</sup>	152-183	102-120
Rostellum: diameter	-	-	148-157	123-153
Rostellar hooks:				
number	40	36 <sup>(2)</sup>	38(?) - 40-44	40(?) - 42-46
length				
anterior hooks	38-39	50 <sup>(2)</sup>	48-51	41-45
posterior hooks	32-34	30 <sup>(2)</sup>	41-43	34-37
Testes: number	20-25	18-26(?)	18-25	17-25
Cirrus sac:				
mature proglottides				
length	162-212	84-117	156-224	152-172
width	63-75	32-43	58-87	50-56
pre-gravid and gravid proglottides				
length	317-382	122-151	198-254	158-192
width	195-228	49-60	94-114	50-70
Copulatory vagina:				
length	134-170	98-120	168-185	217-301
width	29-37	19-23	18-27	19-33
R vag/cs	0.77-0.90	0.85-1.16	0.95-1.13	1.38-1.74
R cs/pr	0.22-0.27	0.13-0.18	0.17-0.22	0.13-0.18
Vitellarium: width	118-155	77-99	224-291	66-124
Ovary: width	259-291	193-222	470-642	234-285
R ov/pr	0.30-0.35	0.32-0.38	0.38-0.45	0.23-0.29
Seminal receptacle:				
length	29-51	32-55	-	52-59
width	25-31	25-32	18-27	25-50
Eggs:				
outer shell: diameter	36-39	-	34-41	58-66
Embryophore: diameter	34-37	-	27-35	36-44
Oncosphere: diameter	28-31	-	26-32	28-32
Embryonic hooks				
central pair: length	19-20	-	18-19	18-19
massive: length	16-17	-	16-17	17-18
thin: length	14-15	-	16-17	13-15

(1) In Berlese's medium.

(2) After Fuhrmann (1908a).

KEY TO THE SPECIES OF THE GENUS *METADILEPIS*

- 1 Genital pores unilateral . . . . . 2
- Genital pores alternating . . . . . *M. kornyushini*
- 2 Copulatory part of vagina 1.4-1.8 times longer than cirrus sac in same proglottis . . . . . *M. spasskiorum*

- Copulatory part of vagina shorter or slightly (up to 1.2 times) longer than cirrus sac in same proglottis . . . . . 3
- 3 Cirrus sac longer than 150 µm in mature and post-mature proglottides, and than 300 µm in pre-gravid and gravid proglottides . . . . . *M. globacantha*
- Cirrus sac shorter than 130 µm in mature and post-mature proglottides, and than 200 µm in pre-gravid and gravid proglottides . . . . . *M. caprimulgorum*

*Metadilepis globacantha* (Fuhrmann, 1913)

Figs 1-8

*Dilepis globacantha* Fuhrmann, 1913: 14-16, Figs 4-6; Fuhrmann, 1932: 99, 292-293; López-Neyra, 1944: 233-234, Fig. 15(4-7); Spasskii, 1946: 257, Fig. 5; Matevosyan, 1963: 54-57, Figs 24-25.

*Dilepis (Metadilepis) globacantha* Fuhrmann, 1913: Spasskii, 1947a: 52-53.

*Metaskrjabinolepis globacantha* (Fuhrmann, 1913) Spasskii, 1947b: 723-724.

*Metadilepis globacantha* (Fuhrmann, 1913) Spasskii, 1949: 50-54; Yamaguti, 1959: 248, Fig. 263; Shumilo & Spasskii, 1976: 36; Schmidt, 1986: 376; (?) Kugi, 1988: 106, Figs 167-170; Kornyushin, 1989: 170-173, Fig. 54; Kornyushin & Georgiev, 1994: 586-587, Figs 28.1-28.6.

*Hosts: Caprimulgus europaeus* L. (type host), *C. ruficollis* Temminck and (? - see remarks) *C. indicus jota* Temminck & Schlegel (Caprimulgidae).

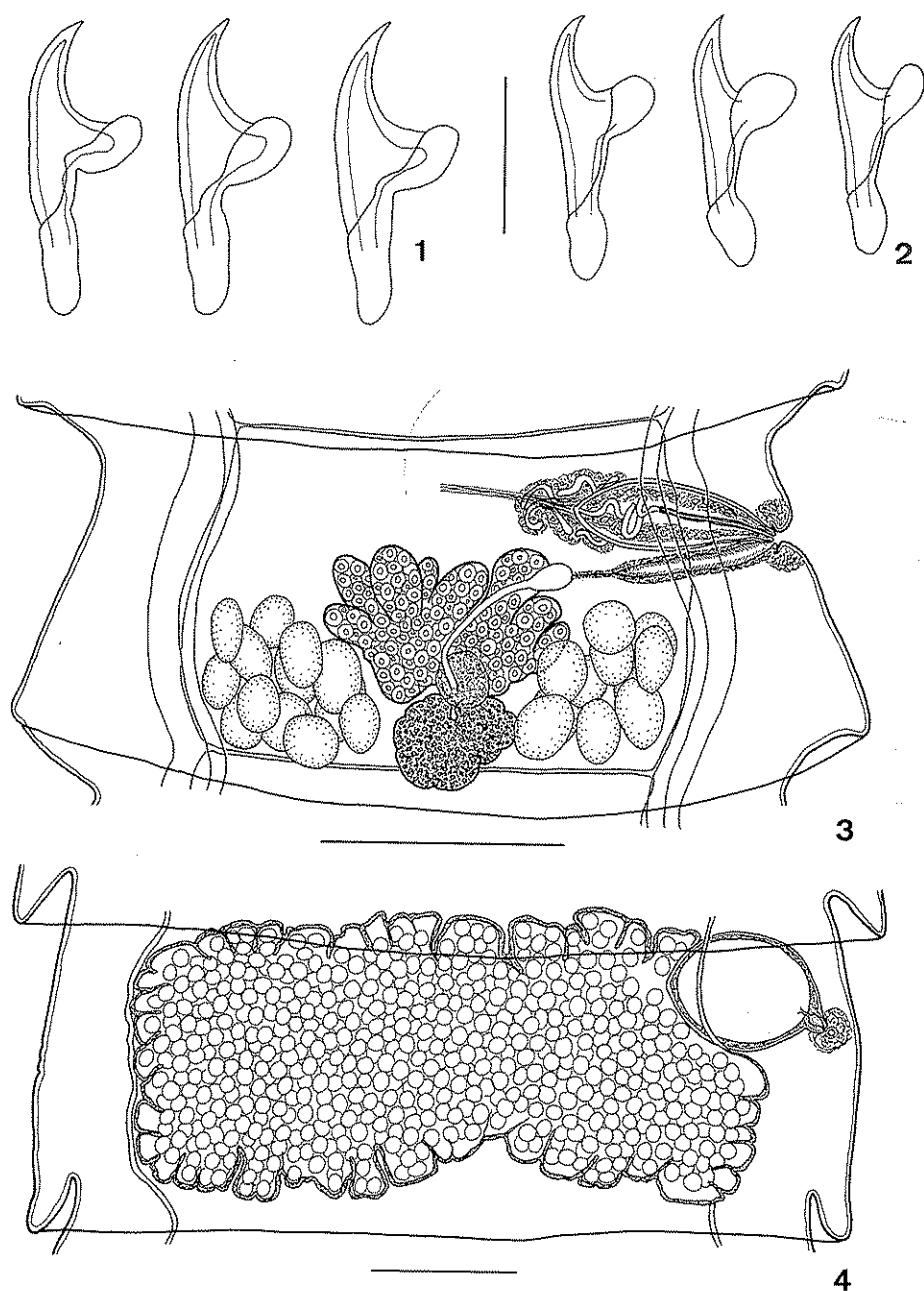
*Material studied:* MHNG (Collection Neuchâtel) Nos. 81/54-56, 3 slides (labelled by Fuhrmann), syntypes, Bohuslän, Busholmen, Sweden, fragments from one or two specimens. No. 81/54, two stained fragments in good condition, one consisting of 16 mature proglottides and the other of 9 pre-gravid and gravid proglottides, carmine, whole mount in Canada balsam; 81/55, a squashed scolex in Berlese's medium; 81/56, squashed gravid proglottides in Berlese's medium.

## REDESCRIPTION

Rostellar hooks 40, in two regular rows. Anterior and posterior hooks of different size, with similar shape, with epiphyseal thickening comprising both handle and guard. Anterior hooks (Fig. 1) 38-39 (n = 3) long. Posterior hooks (Fig. 2) 32-34 (n = 3) long.

Maximum width of strobila at gravid proglottides, 1.51 mm in stained whole mount (2.73 mm in a squash in Berlese's medium). Proglottides craspedote, wider than long (Figs 3, 4) excluding most developed gravid proglottides, which are as long as wide. Ventral osmoregulatory canals 23-46 (n = 5) wide in mature proglottides and 52-83 (n = 5) in gravid proglottides, with narrow transverse anastomoses along posterior margin of each proglottis. Dorsal osmoregulatory canals 10-17 (n = 5) wide in mature proglottides and 8-12 (n = 5) in gravid proglottides. Genital ducts ventral to longitudinal osmoregulatory canals. Genital pores unilateral, situated in anterior half of lateral proglottis margin in both mature and gravid proglottides. Genital atrium consists of pore surrounded by circular musculature, infundibular canal widening at its bottom to form small cavity; atrium encircled by intensely stained glandular cell aggregations (Figs 5, 6). No genital papilla.

Testes 20-25 (24, n = 10), situated in two distinct compact groups lateral to vitellarium and postero-lateral to ovary (Fig. 3); antiporal group of testes larger than poral, e.g., 8+17, 9+16, 11+14, 12+13; testicular field not overlapping longitudinal osmoregulatory canals. External vas deferens forms several coils near antiporal end of cirrus sac; densely covered by prostate cells, forming together with them compact



FIGS 1-4

*Metadilepis globacantha* (Fuhrmann, 1913), syntypes: 1, anterior rostellar hooks; 2, posterior rostellar hooks; 3, mature proglottis, dorsal view; 4, gravid proglottis, dorsal view. Scale bars: 1-2 = 20  $\mu$ m; 3-4 = 250  $\mu$ m.

body; overlapping antiporal end of cirrus sac both ventrally and dorsally. Cirrus sac in mature proglottides (Figs 5, 6) mostly elongate-oval, sometimes rather claviform, thick-walled, 162-212 x 63-75 (191 x 68, n = 10); relatively large:  $R_{cs/pr}$  0.22-0.27 (0.24, n = 6); crossing poral osmoregulatory canals about its middle; sometimes forming constriction near poral end (Fig. 6). Intensely stained cells extending within cirrus-sac along its walls (Figs 5, 6). Internal vas deferens may form several coils in antiporal half of cirrus sac (Figs 3) in early mature proglottides; in late mature proglottides, internal vas deferens as straight or slightly winding tube with walls forming longitudinal folds (Fig. 6). Distinct retractor muscle extending from antiporal end of cirrus sac to middle of proglottis (Figs 3, 5) in mature proglottides. In gravid proglottides, cirrus sac rounded, with tapering poral end (Figs 4, 7), 317-382 x 195-228 (334 x 215, n = 8); internal vas deferens forming large oval to spherical bladder similar to internal seminal vesicle; layers of intensely-stained cells pressed between walls of cirrus sac and walls of internal vas deferens. Evaginated cirrus cylindrical (Fig. 6), with diameter 13-15 (14, n = 4), armed with small needle-shaped spines with length between 2 and 3 mm; at maximum evagination, cirrus 94 long.

Vitellarium situated in middle of proglottis, near posterior proglottis margin; oval or with irregular shape near to oval, slightly lobed, 118-155 (135, n = 10) wide. Ovary transversely elongate, not divided into two wings, deeply lobed; 259-291 (275, n = 6) wide, relatively large, occupying about one third of width of proglottis, i.e.,  $R_{ov/pr}$  0.30-0.35 (0.32, n = 6). Mehlis' gland distinct, globular, with diameter 58-66 (62, n = 6). Seminal receptacle small, drop-like to oval, situated anteriorly to poral part of ovary (Fig. 3); measuring 24-35 x 23-29 (30 x 25, n = 4) when empty and 29-51 x 25-31 (40 x 29, n = 3) when filled; connected with Mehlis' gland by wide seminal duct. Vagina opens postero-ventrally (n = 8) or posteriorly (n = 6) to male pore and passes posteriorly to cirrus sac; in one case, vagina opening rather postero-dorsally. Copulatory and conductive parts distinct (Figs 5, 6). Copulatory part straight or slightly curved, 134-170 (158, n = 10) long, slightly shorter than cirrus sac, i.e.,  $R_{vag/cs}$  0.77-0.90 (0.84, n = 8); provided with thick sleeve of intensely stained cells; width of vagina together with cellular sleeve 29-37 (33, n = 10). Vaginal canal thick-walled, with diameter of lumen 12-19 (16, n = 10), lined with long microtriches. No vaginal sphincter. Conductive part as straight narrow tube.

Uterus not distinct in mature proglottides available. In pre-gravid and gravid proglottides, uterus occupying whole median field, sometimes overlapping longitudinal osmoregulatory canals (Fig. 4); its wall thick, forming distinct anterior, posterior and lateral diverticula. Eggs rounded, with diameter 36-39 (38, n = 10); outer shell thin. Embryophores rounded, with diameter 34-37 (36, n = 10). Oncospheres round, with diameter 28-31 (29, n = 10). Embryonic hooks (Fig. 8) of central pair thin, 19-20 long; lateral pairs consist of one massive hook with length 16-17 and one thin hook with length 14-15.

## REMARKS

In the catalogue of the Collection Neuchâtel (Fuhrmann - Baer), the present material is mentioned as type and also as originating from the Museum of Stuttgart ("Stuttgart, 83"). Since this is the only material of this species deposited in this

TABLE II. Metrical and meristic characters of *Metadilepis globacantha* from *Caprimulgus* spp. as reported by various authors.

Host	<i>C. europaeus</i>		<i>C. ruficollis</i>		<i>C. europaeus</i>		<i>C. europaeus</i>		<i>C. indicus jotaka</i>	
	Sweden	Present study	Spain	Belarus	Ukraine	Japan	Belarus	Ukraine	Japan	Japan
Locality	Fuhrmann (1913)		López-Neyra (1944)	Spasskii (1949)	Kornyushin (1989)	Kugi (1988)	Spasskii (1949)	Kornyushin (1989)	Kugi (1988)	Kugi (1988)
Body:										
length (mm)	50-60	-	40-45	30	53 <sup>(2)</sup>	56-60	30	53 <sup>(2)</sup>	56-60	56-60
width (mm)	1.7	1.51/2.75 <sup>(1)</sup>	0.9-1	2	1.9	1.0-1.3	2	1.9	1.0-1.3	1.0-1.3
Scolex: diameter	300	-	250-260	270-310	-	332	270-310	-	332	332
Suckers: diameter	120	-	100-130	110-140	-	126	110-140	-	126	126
Rostellum: diameter	120	-	105-112	135-140	-	126	135-140	-	126	126
Rostellar hooks:										
number	about 40	40	-	44	-	34-36	44	-	34-36	34-36
length										
anterior hooks	39.6	38-39	39.6	35	-	32	35	-	32	32
posterior hooks	30	32-34	30	30	-	28	30	-	28	28
Testes: number	about 20	20-25	20-23	20-22	18-25	20	20-22	18-25	20	20
Cirrus sac:										
mature proglottides										
length	180	162-212	75-90	-	140-150	-	-	140-150	-	-
width	-	63-75	-	-	50	-	-	50	-	-
gravid proglottides										
length	-	317-382	250	210-320	220-300	49	210-320	220-300	49	49
width	-	195-228	110	120-140	90-110	35	120-140	90-110	35	35
Cirrus: diameter	14	13-15	100	140	45-54	70-77	140	45-54	70-77	70-77
Vitellarium: width	100	118-155	250	-	330-460	140-161	-	330-460	140-161	140-161
Ovary: diameter	250	259-291	-	-	-	-	-	-	-	-
Seminal receptacle:										
length	-	29-51	-	-	-	-	-	-	-	-
width	-	25-31	-	-	-	-	-	-	-	-
Eggs: diameter	36-40	36-39	38-42	-	25-35	77-80	-	25-35	77-80	77-80
Oncosphere: diameter	28	28-31	28	-	15-17	39	-	15-17	39	39
Embryonic hooks: length	-	14-20	13-15	-	-	14-18	-	-	14-18	14-18

(1) In Berlese's medium.

(2) Without scolex.

collection and its present redescription corresponds very well to the original data (Fuhrmann, 1913), we believe that this is the type material from Sweden. The designation of these slides as lots received from the Stuttgart Museum is probably a *lapsus* made in the course of the initial cataloguing of this collection.

*M. globacantha* is predominantly known as a parasite of *Caprimulgus europaeus*. From this host species, it has been recorded from Sweden (Fuhrmann, 1913), Mogilevskaya Oblast' and Gomel'skaya Oblast', Belarus (Spasskii, 1946, 1947a, 1949), Moldova (Shumilo & Spasskii, 1976) and Vinitskaya Oblast', Ukraine (Kornyushin, 1989). There is also a record from *C. ruficollis* in Granada, Spain (López-Neyra, 1944). The previous descriptions based on specimens from Belarus (Spasskii, 1949), Ukraine (Kornyushin, 1989) and Spain (López-Neyra, 1944) exhibit good morphological correspondence with the type material, including the metrical characters (Table II). The specimens described by López-Neyra (1944) exhibited smaller dimensions of the cirrus sac in mature proglottides (perhaps very young proglottides were measured) but the measurements of the organ in gravid proglottides were in the range reported by other authors (Table II).

Kugi (1988) identified as *M. globacantha* cestodes from *C. indicus jotaka* from Oita Prefecture, Japan. Concerning many characters (number of testes, general measurements of strobila, shape of female glands, etc.), there is a correspondence between Kugi's (1988) data and the present redescription of *M. globacantha*. However, his specimens have been reported as possessing irregularly alternating genital pores, rostellar hooks 32 (anterior) and 28 (posterior) long and an ovoid cirrus sac measuring 49 x 35. The eggs of the specimens from Japan are about twice larger than eggs of those from Europe (Table II). These essential differences question the identification of the Japanese material, which probably belongs to another species.

### *Metadilepis caprimulgorum* (Fuhrmann, 1908)

*Dilepis caprimulgorum* Fuhrmann, 1908a: 49-50, Fig. 35; Fuhrmann, 1908b: 52, 164, 166;

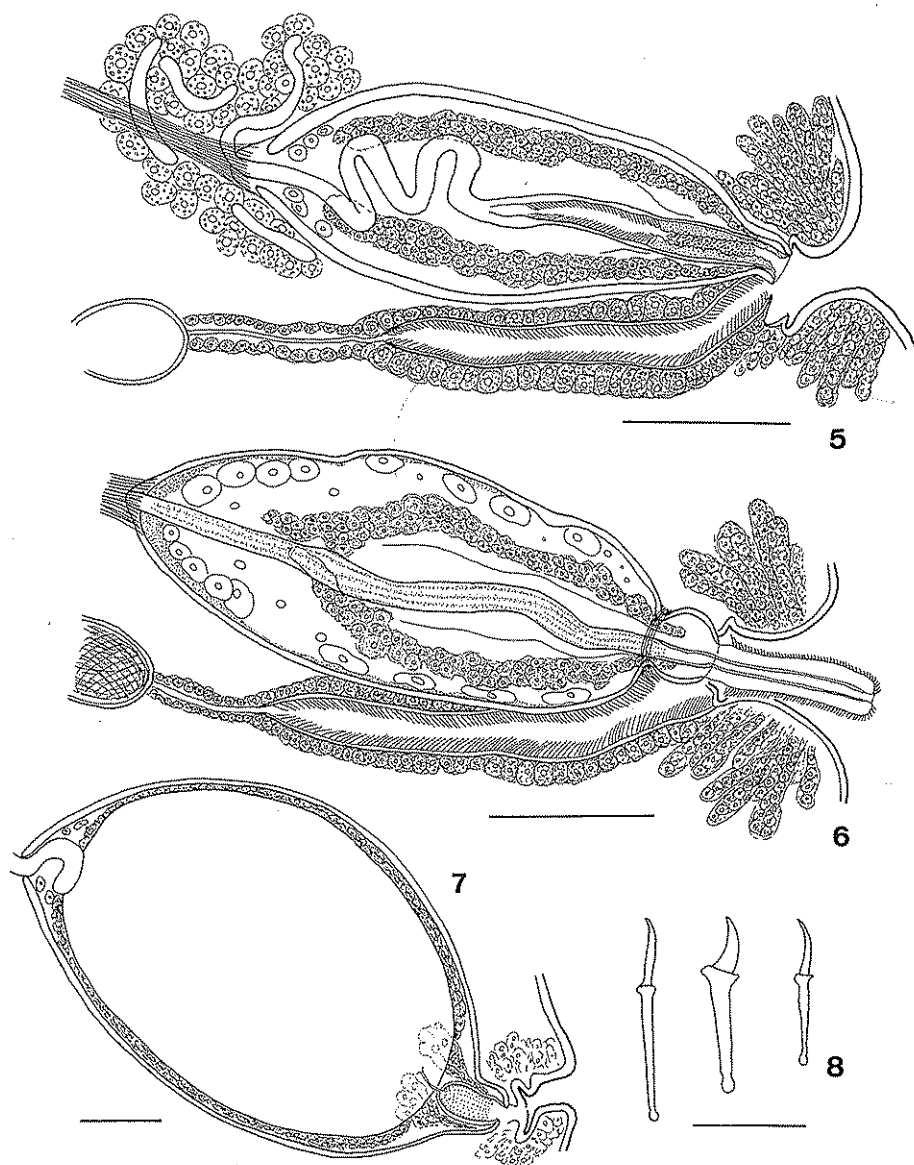
Fuhrmann, 1932: 99, 292, 294; Matevosyan, 1963: 50, Fig. 18.

*Metadilepis caprimulgorum* (Fuhrmann, 1908) Spasskii, 1949: 54; Yamaguti, 1959: 248; Schmidt, 1986: 376.

*Hosts*: *Chordeiles minor* (J.R. Forster, 1771) = *Chordeiles virginianus* (Gmelin, 1789), and (? - see remarks) *Hydropsalis climacocerca* (Tschudi, 1844) (Caprimulgidae).

*Material studied*: From *C. minor*, MHNG (Collection Neuchâtel, 4 slides, Nos. 81/14, 16, 19 and 20), syntypes, Brazil, labelled by Fuhrmann "*Dilepis caprimulgorum*, *Nyctiprogne virginianus*, 440 Wien". No. 81/14 contains unrecognisable squashed fragments in Berlese's medium. No. 81/16, seven stained fragments of strobila consisting of mature or gravid proglottides (probably belonging to a single specimen), hematoxylin, whole mount in Canada balsam, in poor condition. No. 81/19, squashed fragments of proglottides with underdeveloped eggs in Berlese's medium; No. 81/20, longitudinal sections through gravid proglottides.

From *H. climacocerca*, MHNG (Collection Neuchâtel, 3 slides, Nos. 81/15, 17 and 18), Brazil, labelled by Fuhrmann "*Dilepis caprimulgorum*, *Hydropsalis climacereus*, 442 Wien"; mentioned by Fuhrmann (1908b, 1932). No. 81/15 contains squashed fragments of strobila consisting of post-mature and pre-gravid proglottides in Berlese's medium. No. 81/17, squashed fragment (scolex?) in Berlese's medium, no rostellar hooks. No. 81/18, eight stained fragments of strobila, mostly contracted, hematoxylin, whole mount in Canada balsam, in poor condition.



FIGS 5-8

*Metadilepis globacantha* (Fuhmann, 1913), syntypes: 5-6, genital ducts in mature proglottides; 7, cirrus sac in gravid proglottis; 8, embryonic hooks. Scale bars: 5-7 = 50  $\mu$ m; 8 = 10  $\mu$ m.

REDESCRIPTION OF THE TYPE MATERIAL FROM *CHORDEILES MINOR*  
(based on MHNG 81/16, 20)

Figs 9, 10

Total length of fragments available about 34 mm. Maximum width at pre-gravid proglottides, 1.03 mm. Proglottides craspedote (Fig. 9), wider than long at all developmental stages. Longitudinal musculature strongly developed. Dorsal osmoregulatory canals not distinct. Ventral osmoregulatory canals seen in few proglottides, 19-30 (25,  $n = 5$ ) wide, with transverse anastomoses. Genital pores unilateral, situated at border of anterior quarter or third of lateral proglottis margin of mature proglottides and at border of anterior quarter of lateral proglottis margin of pre-gravid proglottides. Slightly expressed genital papilla may present (Fig. 9). Genital atrium infundibular, 11-19 (16,  $n = 10$ ) deep, thin-walled, surrounded by glandular tissue.

Testes 18-26 (21,  $n = 6$ ) in number, in two groups situated laterally to female glands, in two or three layers (Fig. 9); testes in antiporal group more numerous than those in poral group (e.g., 7+12, 8+13, 10+16). Some testes may overlap lateral lobes of ovary; diameter of fully developed testes 42-52 (46,  $n = 10$ ). External vas deferens highly coiled, surrounded by prostate cells and forming together with them dense, transversely elongate body situated at antiporal end of cirrus sac near anterior proglottis margin; diameter of external vas deferens 3-6 (4,  $n = 10$ ). Distinct retractor muscle extending from antiporal end of cirrus sac to anterior proglottis margin. Cirrus sac elongate-oval, with tapering poral end, often transformed into pipette-like protrusion; slightly tapering or rounded antiporal end. Cirrus sac thick-walled, containing aggregations of cells extending along walls (Fig. 10); cirrus sac in mature and post-mature proglottides 84-117 x 32-43 (107 x 37,  $n = 10$ ), relatively small, i.e.,  $R_{cs/pr}$  0.13-0.18 (0.16,  $n = 6$ ); in pre-gravid proglottides 122-151 x 49-60 (134 x 55,  $n = 7$ ). Internal vas deferens forms several coils in antiporal end of cirrus sac; in many pre-gravid proglottides, portion of internal vas deferens may expand to form structure resembling internal seminal vesicle (Fig. 10). Evaginated cirrus not observed. Withdrawn cirrus as thin-walled canal; armament not seen in it.

Vitellarium transversely elongate, oval, reniform or with irregular shape, compact or slightly lobed, 77-99 (91,  $n = 7$ ) wide, situated at middle of posterior proglottis margin (Fig. 9). Ovary transversely elongate, with irregular shape, not forming two wings, slightly lobed, when fully developed 193-222 (205,  $n = 5$ ) wide, occupying one third or more of proglottis width (Fig. 9), i.e.,  $R_{ov/pr}$  0.32-0.38 (0.36,  $n = 5$ ). Mehlis' gland distinct in few proglottides, globular, with diameter 29-36 ( $n = 3$ ). Seminal receptacle not distinct in all proglottides; spherical to ovoid, when filled 32-55 x 25-32 (43 x 29), situated anteriorly to poral branches of ovary; connected with Mehlis' gland by wide, curved seminal duct. Vagina with distinct copulatory and conductive parts. Copulatory part 98-120 (109,  $n = 10$ ), almost as long as cirrus sac, i.e.,  $R_{vag/cs}$  0.85-1.16 (1.02,  $n = 10$ ); opening laterally to orifice of cirrus sac and passing mostly posteriorly to cirrus sac. Vaginal canal thin-walled, surrounded by cellular sleeve. Diameter of vagina 19-23 (21,  $n = 6$ ), diameter of lumen 11-17 (13,  $n = 6$ ). Vagina provided with distinct sphincter situated near its orifice. Conductive part thin, straight or slightly curved.

Initial stages of uterine development not distinct. Uterus in pre-gravid proglottides occupying almost all proglottis, thick-walled, with rather short anterior, posterior and lateral diverticula (distinct in sectioned material only). Eggs underdeveloped.

OBSERVATIONS ON SPECIMENS FROM *HYDROPSALIS CLIMACOCERCA* IDENTIFIED BY FUHRMANN (1908b, 1932) AS *M. CAPRIMULGORUM* (based on MHNG 81/18)

Total length of fragments about 9 mm. Maximum width at gravid proglottides, 1.06 mm. Proglottides craspedote, wider than long at all developmental stages. Longitudinal musculature very strongly developed. Genital pores unilateral. Strong genital papilla, comparable in size with velum, may present. Internal morphology not discernible, cirrus sac only can be characterised. Cirrus sac elongate-oval, thick-walled, with tapering poral end and rounded antiporal end (Fig. 11); cirrus sac 110-142 x 38-55 (130 x 45, n = 7) in mature proglottides and 147-190 x 62-81 (171 x 71, n = 7) in gravid proglottides. Internal vas deferens may expand to form structure resembling internal seminal vesicle (Fig. 11) in gravid proglottides; forming several coils in antiporal part of cirrus sac. Vagina opening laterally to orifice of cirrus sac; vaginal sphincter present. Outer shell of eggs not distinct; embryophore round, with diameter 30-38 (34, n = 10); diameter of oncosphere 28-33 (31, n = 10). Embryonic hooks of central pair thin, 16-17 long; lateral pairs consisting of one massive hook, 13-14 long, and one thin hook, 13-14 long.

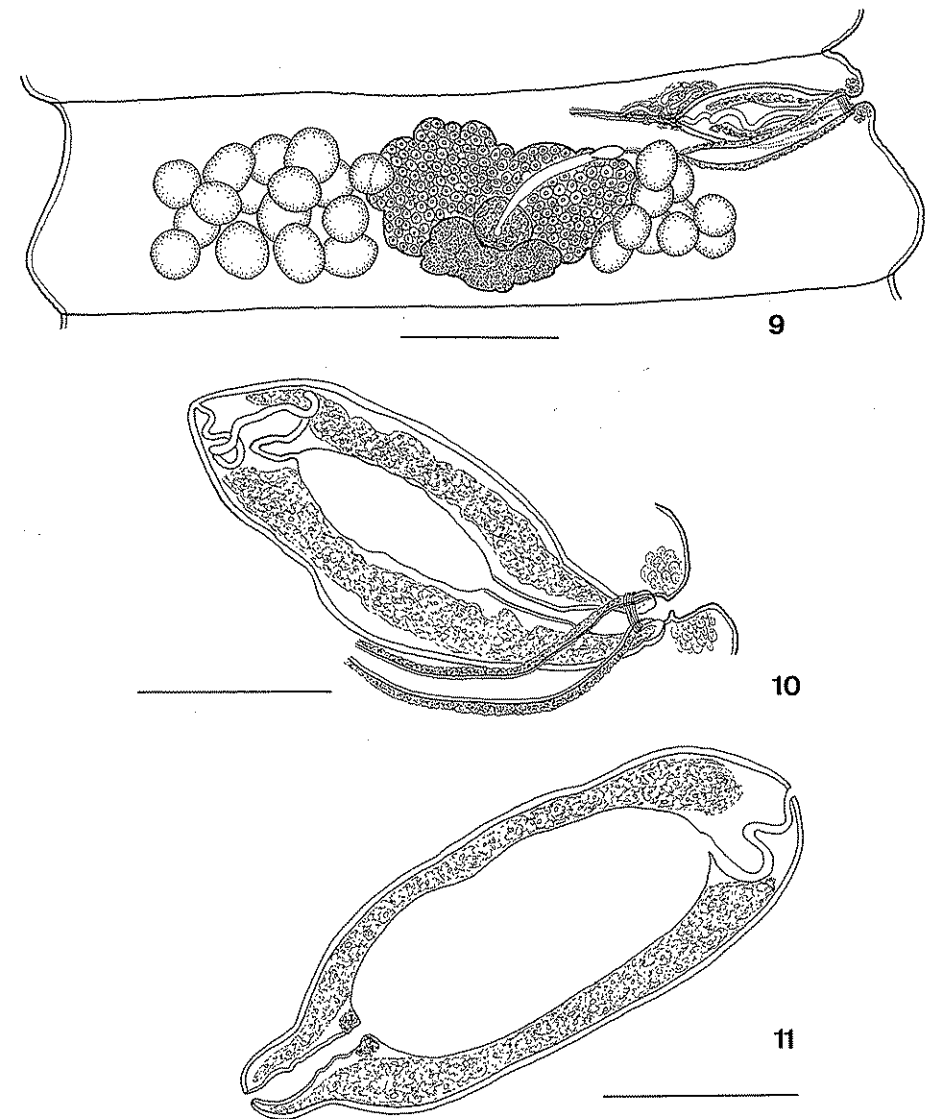
#### REMARKS

*M. caprimulgorum* was described on the basis of specimens from *Chordeiles minor* from Brazil (see Fuhrmann, 1908a). Fuhrmann (1908b, 1932) identified as the same species specimens from *Hydropsalis climacocerca* from Brazil. There are no further records of this species.

The present redescription of the type material is in good agreement with the brief original description (Fuhrmann, 1908a) and adds to it numerous details concerning internal morphology of this cestode species. However, several important characters (the position of the genital ducts relative to the osmoregulatory canals, the uterine development, and the ripe eggs) remain undescribed, mostly due to the poor condition of the material. Unfortunately, we have not been able to examine scoleces and rostellar hooks of this species. Fuhrmann (1908a) described the rostellum armament as consisting of 36 hooks with length of 50  $\mu$ m (anterior) and 30  $\mu$ m (posterior). However, the lengths of the anterior and posterior hooks presented in his illustration are related to one another as 4:3 rather than as 5:3. If we accept that the measurements of the anterior hooks are properly presented in the original description, then the lengths of the anterior and posterior hooks are 50  $\mu$ m and 37-38  $\mu$ m (cf. *M. kornyushini* and *M. spasskiorum*), respectively. On the other hand, if the posterior hooks are accepted as a basis, then the lengths are 40  $\mu$ m and 30  $\mu$ m (cf. *M. globacantha*). According to Fuhrmann (1908a), the diameters of the scolex and the suckers are 160  $\mu$ m and 70  $\mu$ m, respectively. No species with such small dimensions of the scolex and the suckers were found in the new Paraguayan material. Obviously, a new Neotropical material from the type host is needed in order to fill the gaps in the description of *M. caprimulgorum*.

The re-examination revealed that the material from *H. climacocerca* is in poor condition and does not permit adequate studies on the internal morphology. Nevertheless, the comparison with the above description of the type material shows several essential differences. The specimens from *C. minor* have a slightly expressed

Fig. 11



FIGS 9-11

*Metadilepis caprimulgorum* (Fuhrmann, 1908): 9-10, syntypes from *Chordeiles minor*; 9, mature proglottis; 10, cirrus sac in a pre-gravid proglottis; 11, material from *Hydropsalis climacocerca*, Brazil, cirrus sac in a pre-gravid proglottis. Scale bars: 9 = 100  $\mu$ m; 10-11 = 50  $\mu$ m.

genital papilla while those from *H. climacocerca* have a large genital papilla, which is comparable in size with the velum of the proglottis. The dimensions of the cirrus sac in the type material are smaller than those in cestodes from *H. climacocerca* (in gravid proglottides, 122-151 x 49-60 compared to 147-190 x 62-81). Unfortunately, no other

anatomical details are available for comparisons. Therefore, we consider *M. caprimulgorum* as a specific parasite of *C. minor* and question its occurrence in *H. climacocerca*.

Yamaguti (1959) and Schmidt (1986) mentioned this species as recorded also from North America. As we do not know of other original records of *M. caprimulgorum* except those given by Fuhrmann (1908a, 1908b, 1932), we suppose that this is an error arising from the text included by Fuhrmann (1908a) concerning the geographical range of the host species.

***Metadilepis* (?) *caprimulgina*** (Neslobinsky, 1911), species inquirenda

*Dilepis caprimulgina* Neslobinsky, 1911: 437-438, Figs 1-4; Fuhrmann, 1932: 99, 292-293; Matevosyan, 1963: 49, Fig. 17.

*Metadilepis* ? *caprimulgina* (Neslobinsky, 1911) Spasskii, 1965: 79.

*Host*: *Caprimulgus europaeus* (Caprimulgidae).

*Material studied*: none.

REMARKS

This species is known from its original description only, based on specimens from *C. europaeus* from Central Russia. According to the original description (Neslobinsky, 1911), it is characterised by a body 50 mm long and 1.1 mm wide, diameter of scolex 240, diameter suckers 106, rostellum armed with 34 hooks with length 33. The testes are 7, arranged in two groups. The cirrus sac is 160 long, internal and external seminal vesicles are present. The seminal receptacle is 160 long, the diameter of eggs is 40 and diameter of oncospheres is 20. The original illustrations show rather triangular rostellar hooks (and not elongate, as they are in the remaining species of *Metadilepis*). In addition, the vitellarium is shown as strongly disposed in the poral direction. These two characters, as well as the presence of an external seminal vesicle, question the affiliation of this species to *Metadilepis*. Unfortunately, the location of the type material is unknown. Therefore, we recognise it as a species inquirenda.

***Metadilepis kornyushini* sp. n.**

Figs 12-21

*Host*: *Nyctibius griseus* (Gmelin, 1789) (Nyctibiidae).

*Material studied*: Three specimens, stained with hydrochloric carmine, whole mount in Canada balsam. *Holotype*: MHNG 33843 INVE, Santa Maria, province Itapua, Paraguay, 26 October 1982 (4 slides). *Paratypes*: MHNG 33844, Itaipu, province Alto Parana, Paraguay, 12 February 1989, 2 specimens (slightly contracted), 2 slides: a slide with stained scolex and fragments of two specimens and a slide with a scolex squashed in Berlese's medium.

ETYMOLOGY

The species is named after Professor V.V. Kornyushin (Institute of Zoology, Kiev, Ukraine) in recognition of his contribution to the systematics of the Metadilepididae.

DESCRIPTION

Gravid specimen band-like, with total length 90 mm, consisting of 415 proglottides ( $n = 1$ ); maximum width 1.99-2.05 mm at pre-gravid proglottides.

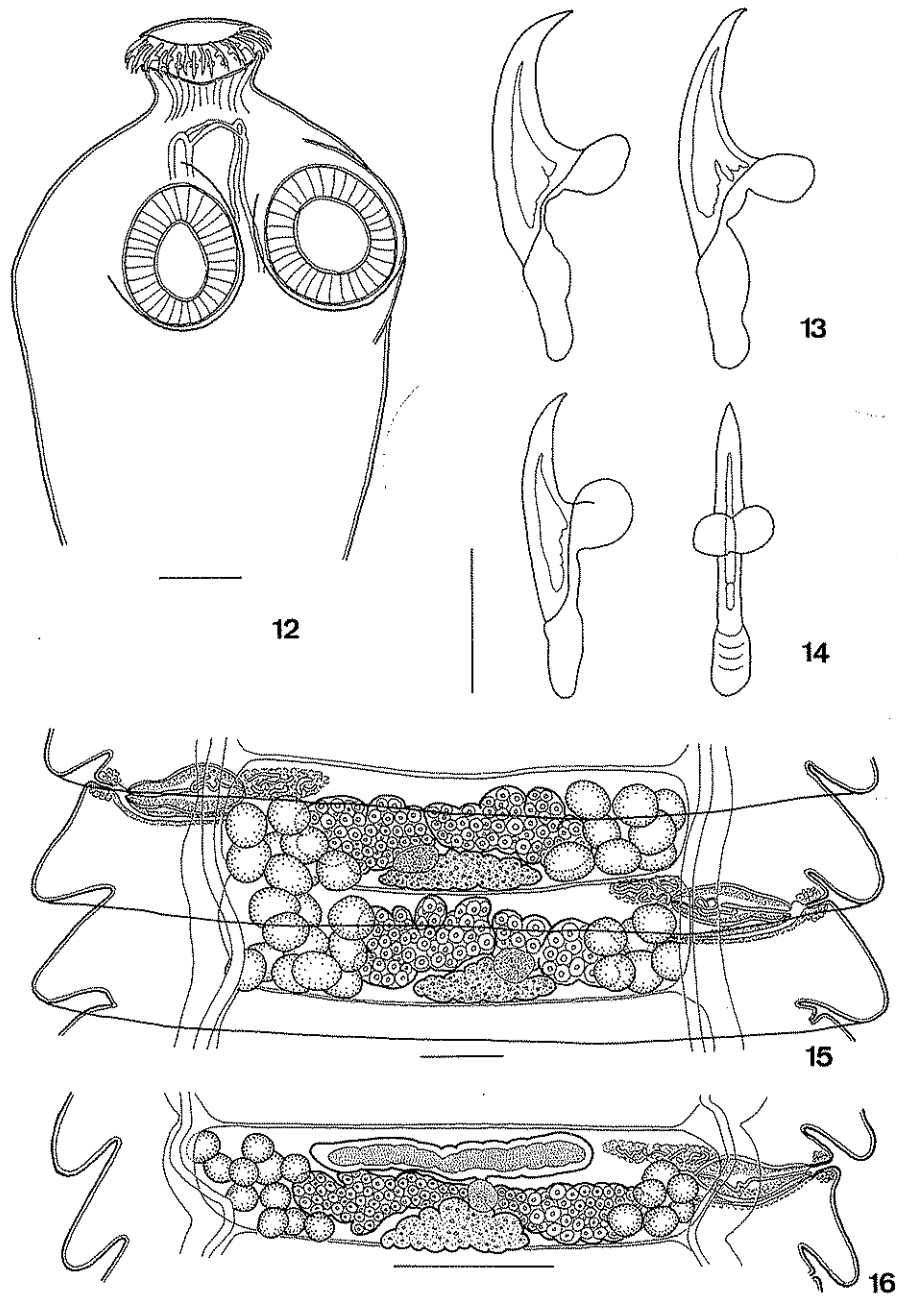
Scolex not clearly outlined from neck (Fig. 12), with maximum diameter at level of middle of suckers, 482-505 ( $n = 2$ ). Rostellar pad with diameter 148-157 ( $n =$

2); numerous muscular fibres, perpendicular to pad surface, present within it. Retractor muscles extending from rostellar pad periphery in posterior direction. Glandular elements not observed. No rostellar pouch. Rostellar hooks 38 (?), 40 or 44 ( $n = 3$ ) in number, situated in two regular rows. Epiphyseal thickening of each hook comprising both handle and guard. Guard bifid. Anterior and posterior hooks of different shape and size. Anterior hooks 48-51 (50,  $n = 4$ ) long, with blade slightly shorter than handle (Fig. 13). Posterior hooks 41-43 (42,  $n = 4$ ) long, with blade considerably shorter than handle (Fig. 14). Suckers round to oval, with apertures directed dorsally and ventrally; their musculature well developed; diameter of suckers 152-183 (170,  $n = 8$ ). Segmentation starts at 550-654 from posterior end of suckers. Neck with diameter 206-310 ( $n = 2$ ) in its narrowest part.

Proglottides craspedote, wider than long at all stages of their development (Figs 15-18). Osmoregulatory canals reaching in anterior direction to level just posterior to rostellar pad (Fig. 12). In strobila, ventral osmoregulatory canals 36-125 (78,  $n = 10$ ) wide, with transverse anastomoses along posterior margin of each proglottis. Dorsal osmoregulatory canals 9-28 (20,  $n = 10$ ). Genital pores irregularly alternating, mostly in long series, e.g., ... 19, 16, 26, 11, 29, 11, 28..., or ... 13, 21, 32, 12, 8, or ... 48, 4, 36, 23; situated at border of anterior fifth (in mature proglottides) or anterior quarter (in gravid proglottides) of lateral proglottis margin. Slightly expressed genital papilla may present (Fig. 16). Genital atrium thick-walled, tubular, with infundibular orifice and slightly expanded base, surrounded by intensely stained cellular masses; 36-66 (51,  $n = 10$ ). Genital ducts ventral to osmoregulatory canals.

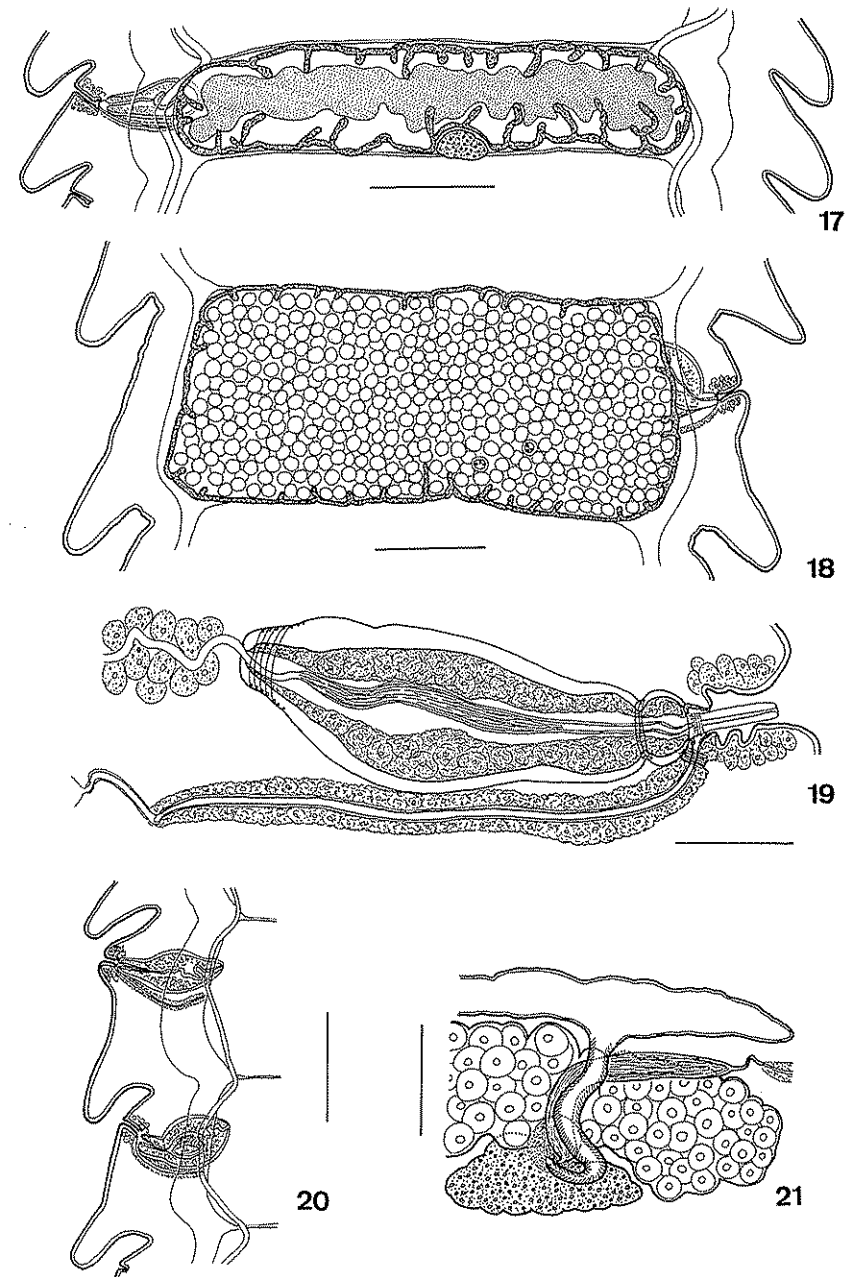
Testes 18-25 (20,  $n = 10$ ) in number, in two groups lateral to female glands, round to slightly oval (Figs 15-16); may overlap lateral lobes of ovary and ventral osmoregulatory canals. Testes in antiporal group usually more numerous than those in poral group (e.g., 5 + 13, 6 + 12, 7 + 18, 8 + 13). Maximum diameter of testes 63-75 (69,  $n = 10$ ). External vas deferens highly coiled; forming together with surrounding prostate cells dense, transversely elongate body situated in anterior poral corner of median field and overlapping antiporal part of cirrus sac both ventrally and dorsally; diameter of external vas deferens 7-12 (9,  $n = 10$ ). Cirrus sac in mature and post-mature proglottides oval, with tapering poral end and rounded antiporal end, often with constriction near its poral end (Figs 19); 156-224 x 58-87 (186 x 75,  $n = 10$ ),  $R_{cs/pr}$  0.17-0.22 (0.19,  $n = 10$ ); cirrus sac overlapping or just crossing poral osmoregulatory canals. Intensely stained cells extending within cirrus sac along its walls (Fig. 19), delimiting cavity in which internal vas deferens is situated. Internal vas deferens may form few coils in cirrus sac (Fig. 15). In pre-gravid and gravid proglottides, cirrus sac 198-254 x 94-114 (219 x 107,  $n = 8$ ); in few proglottides internal vas deferens is transformed in structure resembling internal seminal vesicle (Fig. 20) with dimensions 85-89 x 63-76 ( $n = 2$ ). Withdrawn cirrus as thick-walled canal. Cirrus evaginated in few proglottides; cylindrical, with maximum length 54 ( $n = 1$ ) and diameter at base 9-11 (10,  $n = 4$ ); its base armed with sparse, small (less than 1  $\mu$ m) triangular spines (Fig. 19).

Vitellarium central or slightly porally disposed, situated at posterior proglottis margin, compact or slightly lobed, transversely elongate (Figs 15-16), when fully developed with measurements 224-291 x 76-94 (250 x 83,  $n = 6$ ). Ovary slightly lobed, its shape varying from transversely elongate with irregular shape to rather two-winged



FIGS 12-16

*Metadilepis kornyushini* sp. n.: 12, scolex; 13, anterior rostellar hooks; 14, posterior rostellar hooks; 15, mature proglottides, dorsal view; 16, mature proglottis showing an early stage of uterine development, dorsal view. Scale bars: 12, 15 = 100  $\mu$ m; 13-14 = 20  $\mu$ m; 16 = 250  $\mu$ m.



FIGS 17-21

*Metadilepis kornyushini* sp. n.: 17, pre-gravid proglottis; 18, gravid proglottis; 19, genital ducts in post-mature proglottis; 20, detail of genital ducts in two adjacent gravid proglottides showing different functional conditions of the internal vas deferens; 21, detail of the female genital system, dorsal view. Scale bars: 17-18, 20 = 250  $\mu$ m; 19 = 50  $\mu$ m; 21 = 100  $\mu$ m.

(Figs 15-16); sometimes lateral branches thicker and creating impression for two-winged organ; wide, occupying between one third and almost half of proglottis width, i.e.,  $R_{ov/pr}$  0.38-0.45 (0.41,  $n = 8$ ); when fully developed 470-642 (547,  $n = 7$ ) wide. Mehlis' gland globular, with diameter 52-67 (59,  $n = 8$ ); often not distinct. Seminal receptacle tubular, with tapering poral end, often curved, with diameter 18-27 (23,  $n = 10$ ). Vagina opening and passing posteriorly to cirrus sac (Fig. 19). Copulatory part (measured as curve) 168-185 (173,  $n = 8$ ) long, slightly shorter or slightly longer than cirrus sac, i.e.,  $R_{vag/cs}$  0.95-1.13 (1.07,  $n = 8$ ); with infundibular orifice and sphincter near it (not always distinct). Vaginal canal surrounded by thick cellular sleeve. Diameter of vagina (together with cellular sleeve) 18-27 (22,  $n = 10$ ). Vaginal canal thick-walled, with diameter of lumen 4-6 (5,  $n = 10$ ). Conductive part straight or slightly curved, thin.

Uterus initially seen in mature proglottides as empty, transversely elongate tube situated anteriorly to ovary (Fig. 21), sometimes overlapping it dorsally. With further development, filled with developing eggs (Fig. 16). In post-mature proglottides, uterine walls thick, with deep diverticula (Fig. 17). In gravid proglottides, uterus occupying entire median field; diverticula persisting, not deep (Fig. 18). Eggs round to slightly oval, with diameter 34-41 (38,  $n = 10$ ), with thin outer shell. Embryophore thick, with diameter 27-35 (32,  $n = 10$ ). Oncosphere round to oval, with diameter 26-32 (30,  $n = 10$ ). Embryonic hooks of central pair 18-19 ( $n = 10$ ) long, of lateral pairs 16-17 ( $n = 10$ ) long.

#### REMARKS

Only one metadilepidid species is known for the moment from potoos (Nyctibiidae), *Urutaulepis pifanoi* (Díaz-Ungria & Jordano, 1958) from *Nyctibius griseus* in Venezuela (see below for a redescription). It is characterised by longer rostellar hooks (anterior 71.5-73.5  $\mu\text{m}$ , posterior 59-61  $\mu\text{m}$ , compared to 48-51 and 41-43 in the new species). The rostellar hooks of *U. pifanoi* have very small epiphyseal thickenings (Figs 51-52) while those of *M. kornyushini* have handle and guard comprised by a common epiphyseal structure (Figs 13-14). There are also substantial differences in the strobilar anatomy between the two species (see Table I for metrical differences). The number of testes of *U. pifanoi* is twice as larger as in the new species. Its mature proglottis contains some postvitellarian testes while, in *M. kornyushini*, the vitellarium is situated near the posterior proglottis margin and there are no postvitellarian testes. The genital atria of the two species have very different structures (Figs 19, 56-58).

Compared with all the species of *Metadilepis*, *M. kornyushini* has a longer strobila and is the only one characterised by alternating genital pores and by a seminal receptacle which is highly elongate and curved (not oval and situated anteriorly to poral parts of ovary). It can also be easily distinguished from *M. globacantha* and *M. spasskiorum* by the longer rostellar hooks, the large relative size of the ovary and the large absolute dimensions of the ovary and vitellarium (Table I).

#### *Metadilepis spasskiorum* sp. n.

Figs 22-30

*Host*: *Setopais parvula* (Gould, 1837) (Caprimulgidae).

*Material studied*: 10 specimens, stained with hydrochloric carmine, whole mounts in Canada balsam. *Syntypes*: MHNG 33839 INVE, 4 specimens (fragmented, 2 slides of stained

whole mounts and 2 slides of squashed scoleces in Berlese's medium), at the km 293 on the Transchaco Road, province Presidente Hayes, Paraguay, 2 November 1988. *Other material*: MHNG 33842 INVE, 2 specimens (fragmented, 1 slide of stained whole mounts), the locality and the date as for the syntypes; MHNG 33841 INVE, 1 mature specimen (fragmented, 1 slide of stained whole mounts), at km 17 of the road from Teniente Montania to Puesto Santo Domingo, province Alto Paraguay, Paraguay, 5 November 1988 (1 specimen); MHNG 38340 INVE, a specimen without scolex, stained whole mount, Santa Maria, province Itapua, Paraguay, 24 October 1982; collection of B. Georgiev, 2 specimens (fragmented, 1 slide of stained whole mounts), Santa Maria, province Itapua, Paraguay, 24 October 1982.

#### ETYMOLOGY

The species is named after Professor A.A. Spasskii and the late Dr L.P. Spasskaya (Institute of Zoology, Kishinev, Republic of Moldova) in recognition of their contribution to the systematics of the Metadilepididae.

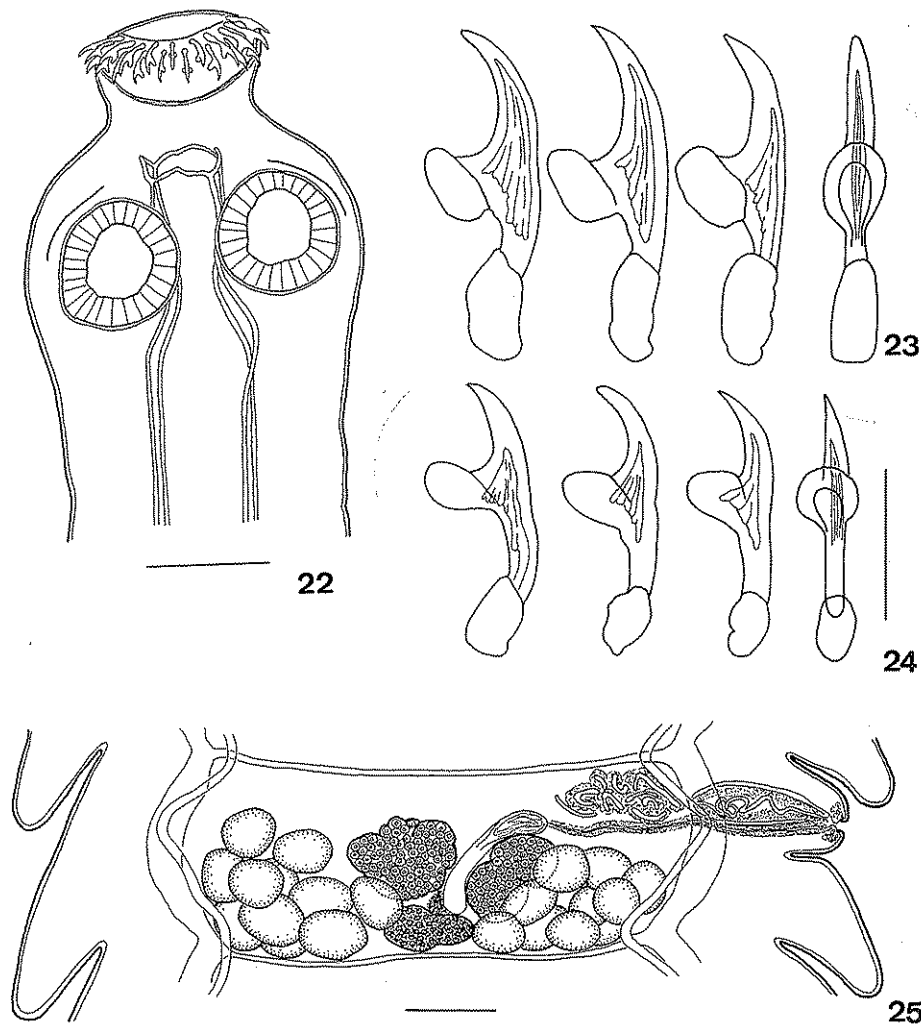
#### DESCRIPTION

Total length of gravid specimens estimated at about 60 mm (based on lengths of fragments available). Maximum width of strobila at pre-gravid proglottides, 1.12-1.53 mm (1.22 mm,  $n = 4$ ).

Scolex not clearly outlined from neck, with maximum diameter at middle of suckers, 279-310 (292,  $n = 4$ ); anterior part of scolex protruded (Fig. 22). Rostellar pad with diameter 123-153 (135,  $n = 4$ ), containing numerous muscular fibres perpendicular to pad surface. No rostellar pouch. Rostellar hooks 40 (? ,  $n = 2$ ), 42 ( $n = 1$ ), 44 ( $n = 1$ ) or 46 ( $n = 1$ ), in two regular rows. Anterior and posterior hooks of different size and shape; with separate epiphyseal structures of handle and guard. Anterior hooks (Fig. 23) 41-45 (43,  $n = 9$ ) long. Posterior hooks (Fig. 24) 34-37 (35,  $n = 8$ ) long. Suckers round to oval, with apertures directed dorsally and ventrally, with well-developed musculature; diameter of suckers 102-120 (111,  $n = 13$ ). Segmentation starts at 250-380 from posterior end of suckers.

Proglottides craspedote, wider than long (Figs 25-26); most developed gravid proglottides only almost as long as wide (Fig. 27). Ventral osmoregulatory canals 22-32 (28,  $n = 10$ ) wide in mature proglottides and 35-47 (41,  $n = 10$ ) in gravid proglottides, with narrow transverse anastomoses along posterior margin of each proglottis. Dorsal osmoregulatory canals 7-11 (10,  $n = 10$ ) wide in mature proglottides and 7-13 (12,  $n = 10$ ) in gravid proglottides. Genital ducts ventral to longitudinal osmoregulatory canals. Genital pores unilateral, situated in anterior third of lateral proglottis margin in both mature and gravid proglottides. Genital atrium infundibular, slightly widening at its bottom; thick-walled, 16-34 (24,  $n = 8$ ) deep; atrium encircled by intensely stained glandular cell aggregations. Well-expressed genital papilla present.

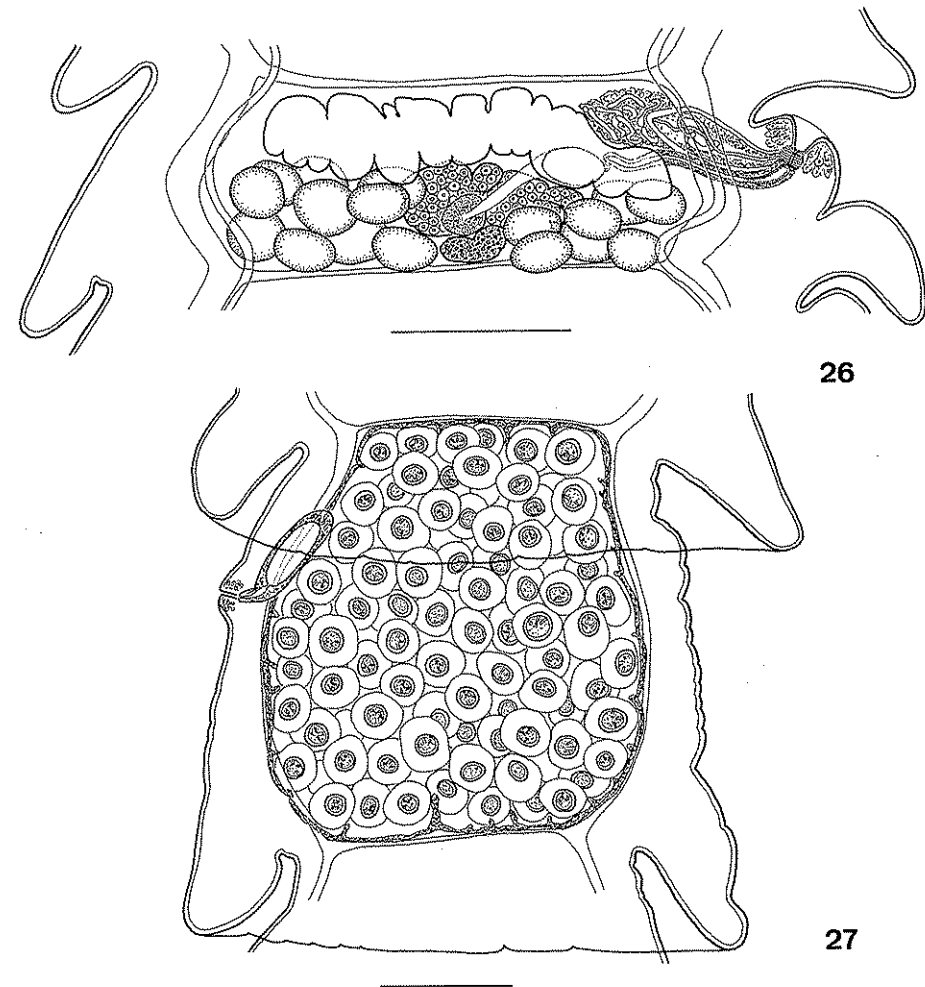
Testes 17-25 (20,  $n = 14$ ), in two distinct compact groups situated laterally to vitellarium and postero-laterally to ovary (Figs 25-26); rarely, single testes situated dorsally to vitellarium and then two lateral groups merged. Testes often overlapping longitudinal osmoregulatory canals but not crossing them. Testes in antiporal group more numerous than those in poral group (e.g., 8+9, 9+13, 9+10, 11+14); sometimes two groups contain equal number of testes (e.g., 9+9, 10+10). Fully developed testes with diameter 66-88 (77,  $n = 10$ ). External vas deferens highly coiled near antiporal end of cirrus sac; covered by prostate cells, forming together with them compact, trans-



FIGS 22-25

*Metadilepis spasskiorum* sp. n.: 22, scolex; 23, anterior rostellar hooks; 24, posterior rostellar hooks; 25, mature proglottis, dorsal view. Scale bars: 22, 25 = 100  $\mu$ m; 23-24 = 20  $\mu$ m.

versely elongate body situated in median field near anterior proglottis margin; diameter of external vas deferens 8-11 (9, n = 10). Cirrus sac in mature proglottides (Fig. 28) elongate-oval, with tapering poral end, thick-walled, 152-172 x 50-56 (163 x 53, n = 10),  $R_{cs/pr}$  0.13-0.18 (0.15, n = 10), overlapping or slightly crossing poral osmoregulatory canals. Distinct retractor muscle extending from antiporal end of cirrus sac to middle of anterior proglottis margin. Intensely stained cells extending within cirrus-sac along its walls (Figs 28-29). Internal vas deferens forms several coils in antiporal half of cirrus sac. In pre-gravid and gravid proglottides, cirrus sac wider, with tapering



FIGS 26-27

*Metadilepis spasskiorum* sp. n.: 26, mature proglottis showing an early stage of uterine development, dorsal view; 27, gravid proglottis, ventral view. Scale bars: 26-27 = 200  $\mu$ m.

poral end, 158-192 x 50-70 (174 x 61, n = 10). Poral (uncoiled) part of internal vas deferens may form large elongate-oval bladder similar to internal seminal vesicle, often with irregular shape (Fig. 29), sometimes almost spherical. Layers of intensely stained cells pressed between walls of cirrus sac and walls of internal vas deferens. Several coils of internal vas deferens present in most antiporal portion of cirrus sac. Evaginated cirrus not observed; armament consisting of punctiform spines (shorter than 1  $\mu$ m) seen in canal of withdrawn cirrus in pre-gravid and gravid proglottides.

Vitellarium situated in middle of proglottis, near posterior proglottis margin; reniform, elongate-oval or with irregular shape near to oval, compact or slightly lobed, 66-124 (93,  $n = 15$ ) wide. Ovary with irregular shape, transversely elongate, often not divided into two wings (Fig. 26); sometimes lateral branches more developed and creating impression for two-winged organ (Fig. 25); anterior and lateral margins of ovary slightly lobed; 234-285 (259,  $n = 10$ ) wide;  $R_{ov/pr}$  0.23-0.29 (0.25,  $n = 10$ ), i.e., occupying about one quarter of proglottis width. Mehlis' gland globular, with diameter 39-54 (47,  $n = 6$ ). Seminal receptacle oval, situated anteriorly to poral part of ovary (Figs 25-26), 52-99 x 25-50 (78 x 36,  $n = 10$ ) when filled, connected with Mehlis' gland by wide seminal duct. Vagina opening postero-dorsally to cirrus-sac orifice and passing posteriorly to cirrus sac. Copulatory and conductive parts distinct (Fig. 28). Copulatory part straight or slightly curved, 217-301 (258,  $n = 10$ ) long, longer than cirrus sac,  $R_{vag/cs}$  1.38-1.74 (1.60,  $n = 10$ ); provided with thick sleeve of intensely stained cells; width of vagina together with cellular sleeve 19-33 (26,  $n = 10$ ). Vaginal sphincter (not always distinct) present near orifice of copulatory part (Fig. 28). Vaginal canal thick-walled, with diameter of lumen 5-13 (9,  $n = 10$ ), its poral part lined with long microtriches (Fig. 28). Conductive part short and narrow, straight or slightly convoluted.

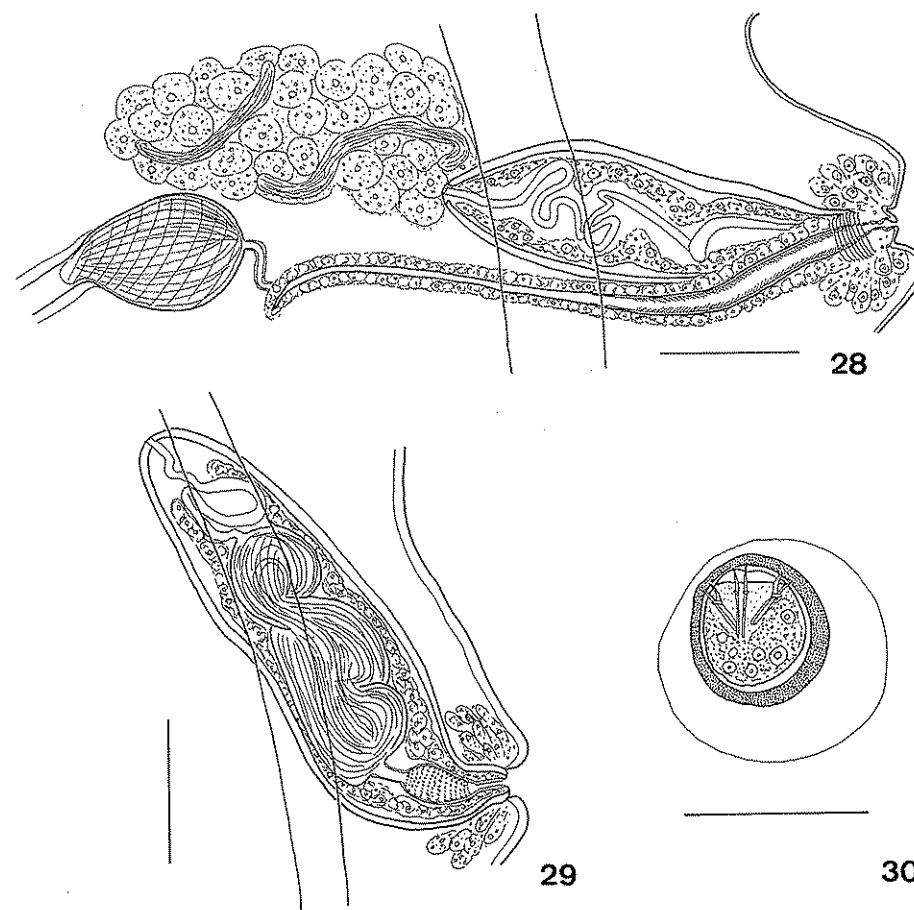
Uterus initially seen in mature proglottides as transversely elongate lobate body situated anteriorly to ovary and often overlapping it dorsally (Fig. 26). In post-mature proglottides, walls of uterus becoming thicker, with anterior, posterior and lateral diverticula. In pre-gravid and gravid proglottides, uterus occupying entire median field, often overlapping longitudinal osmoregulatory canals; diverticula of uterine walls not deep (Fig. 27). Eggs rounded, with diameter 58-66 (62,  $n = 10$ ), with thin outer shell. Embryophore rounded, consisting of thick external layer with granular appearance and with diameter 36-44 (40,  $n = 10$ ) and thin refractive inner layer with diameter 31-36 (34,  $n = 10$ ) (Fig. 30). Oncospheres rounded, with diameter 28-32 (30,  $n = 10$ ). Embryonic hooks of central pair thin, 18-19 long; lateral pairs consist of one massive hook with length 17-18 and one thin hook with length 13-15.

#### REMARKS

Our material resembles *M. globacantha* and *M. caprimulgorum*. It is clearly separated from both species by the very long copulatory part of the vagina, which is considerably longer than the cirrus sac ( $R_{vag/cs}$  1.38-1.74). In addition, the relative width of the ovary is smaller. This organ occupies about one quarter of the proglottis width (compared to about one-third in the other two species).

From the Palearctic species *M. globacantha*, our specimens can also be distinguished by the longer rostellar hooks (41-45 and 34-37 compared to 38-39 and 32-34), having also a different shape (Figs 1-2, 23-24), and the relatively smaller cirrus sac ( $R_{cs/pr}$  0.13-0.18 compared to 0.22-0.27 in *M. globacantha*).

Compared with the Neotropical species *M. caprimulgorum*, the above-described cestodes from Paraguay can be distinguished by the larger absolute dimensions of the cirrus sac (152-172 x 50-56 versus 84-117 x 32-43 in mature and post-mature proglottides, and 158-192 x 50-70 versus 122-151 x 49-60 in pre-gravid and gravid proglottides). They also have a considerably wider ovary (234-285 compared to 193-222).



Figs 28-30

*Metadilepis spasskiorum* sp. n.: 28, genital ducts in a mature proglottis, dorsal view; 29, cirrus sac in a gravid proglottis; 30, egg. Scale bars: 28-30 = 50  $\mu$ m.

Therefore, we consider that our material from *Setopagis parvula* from Paraguay belongs to a new species.

#### *Proparuterina* Fuhrmann, 1911

*Proparuterina* Fuhrmann, 1911: 265-266; Fuhrmann, 1932: 113; Yamaguti, 1959: 255; Matevosyan, 1963: 209; Schmidt, 1986: 411; Korniyushin & Georgiev, 1994: 590-592.

#### DIAGNOSIS

Scolex with sucker-like rostellum. Rostellar hooks in two rows, elongate, handle longer than blade; handle with large epiphyseal thickening; guard bifid, also with epiphyseal thickening. Proglottides craspedote; mature proglottides wider than long, post-mature proglottides almost as wide as long, pre-gravid and gravid pro-

glottides unknown. Genital pores irregularly alternating in short series. Genital ducts pass between osmoregulatory canals. Testes numerous, posterior to female glands. External vas deferens coiled, covered by prostate cells, forming together with them compact body. Cirrus sac elongate-oval, with thick muscular walls, can reach or overlap poral osmoregulatory canals. Vitellarium median, irregular, slightly lobed, at some distance from posterior proglottis margin. Ovary usually reniform, slightly lobed, symmetrical. Seminal receptacle elongate-oval, situated dorsally to poral part of ovary. Vagina opening postero-laterally to orifice of cirrus sac; copulatory and conductive parts distinct, both surrounded by thick cellular sleeve. Developing uterus in post-mature proglottides horseshoe-shaped, with free ends directed posteriorly. Gravid uterus, eggs and oncospheres unknown. In Podargidae (Caprimulgiformes), Aru Island (Indonesia).

Type species: *Proparuterina aruensis* Fuhrmann, 1911.

#### REMARKS

The present diagnosis follows that proposed by Korniyushin & Georgiev (1994); few amendments are introduced, mainly in order to facilitate the easier differentiation between *Proparuterina* and the genera *Metadilepis* (in the concept as presented above) and *Mariauxilepis* gen. n.

*Proparuterina lali* Baugh & Saxena, 1976 was described from *Passer domesticus* (L., 1758) in India (Baugh & Saxena, 1976). The shape of the gravid uterus of this cestode corresponds to that of the developing uterus of the type species of *Proparuterina*. However, *P. lali* differs from *P. aruensis* by many morphological peculiarities, which do not permit us to consider the two species congeneric. In contrast to the type species, the vitellarium of *P. lali* is situated at the posterior proglottis margin (not at some distance from it). The ovary of the Indian species is clearly two-winged (not reniform). Its testicular field passes anteriorly to the vitellarium and some testes may reach almost to the anterior margin of the ovary as shown in figure 21 of Baugh & Saxena (1976) (not entirely postvitellarian and postovarian). The rostellar hooks of *P. lali* are small (with length 8-12 µm) and triangular while those of *P. aruensis* are relatively large (up to 58 µm) and longitudinally elongate. The morphology of the scolex and mature proglottides of *P. lali* and the shape of its gravid uterus resemble to a great extent these characters in some species of the paruterinid genus *Biuterina* Fuhrmann, 1902. Similar species are, e.g., *B. quelea* (Mettrick, 1963) and *B. ugandae* Baylis, 1919 (see redescrptions by Georgiev *et al.*, 2002). However, there are no data in the original description (Baugh & Saxena, 1976) about the presence of a paruterine organ in *P. lali* and, for this reason, we cannot transfer it to the family Paruterinidae. It cannot be excluded that this species is a representative of an undescribed genus of the family Metadilepididae. Therefore, we recognise *P. lali* as a species incertae sedis and *Proparuterina* as a monotypic genus.

*Proparuterina aruensis* Fuhrmann, 1911

Figs 31-38

*Proparuterina aruensis* Fuhrmann, 1911: 265-266, Fig. 24; Fuhrmann, 1932: 113-114, 292, 294, Fig. 88; Yamaguti, 1959: 255, Fig. 341; Matevosyan: 1963, 209-210, Fig. 154; Schmidt: 1986, 411, Fig. 436; Korniyushin & Georgiev, 1994: 590-592, Figs 28.23-28.25.

Host: *Podargus papuensis* Quoy & Gaimard, 1830 (Podargidae).

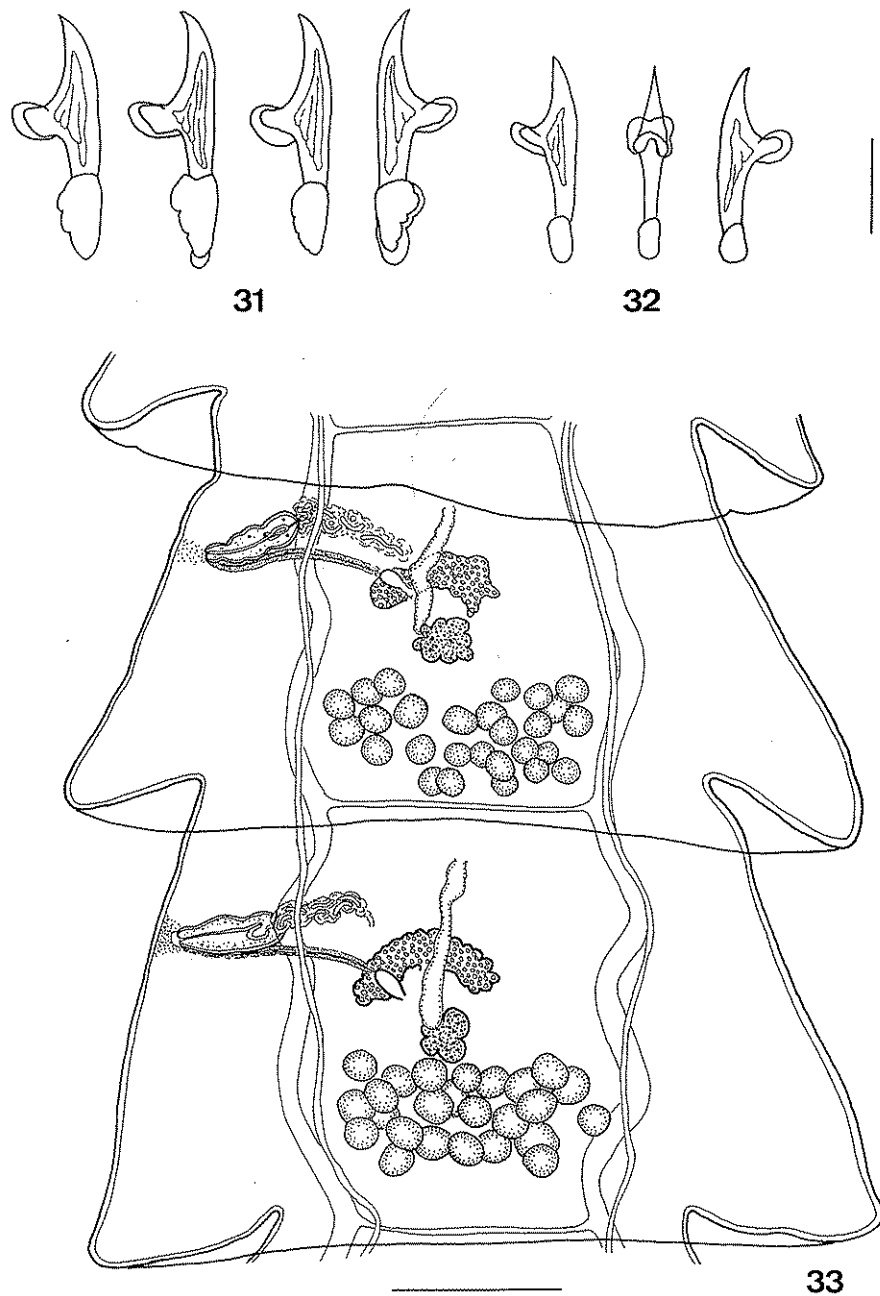
Material studied: MHNG (Collection Neuchâtel) Nos 18/49 and 18/50, 2 slides, syntypes, labelled by Fuhrmann "T. aruensis, *Proparuterina*, *Podargus*, Ruix 90"; No. 18/49, fragments of 2 specimens, carmine (?), Canada balsam; No. 18/50, a scolex squashed in Berlese's medium, containing 14 large (anterior?) and 13 small (posterior?) rostellar hooks; a further slide, no 18/51, containing 2 fragments of a capillariid nematode, is labelled and catalogued as belonging to the type series.

#### REDESCRIPTION

Length of fragments starting with juvenile and terminating with not fully developed mature proglottides 34-36 mm. Maximum width at contracted mature proglottides (1.25 mm) or at relaxed post-mature proglottides (1.15 mm). Scolex lacking in the material studied. Rostellar hooks elongate with separate epiphyseal structures of handle and guard; guard bifid. Anterior rostellar hooks (Fig. 31) 54-58 (56, n = 7) long. Posterior rostellar hooks (Fig. 32) 41-44 (42, n = 6).

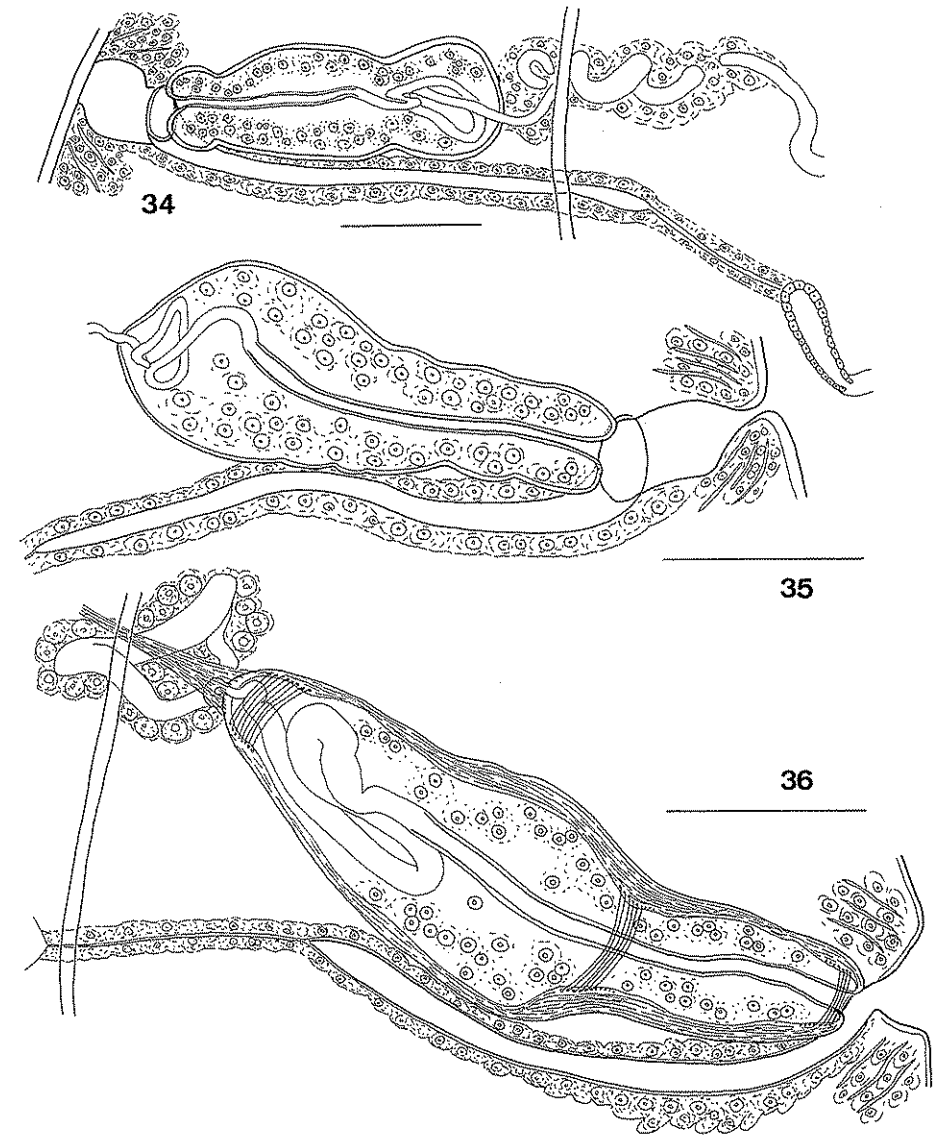
Proglottides craspedote, mature proglottides wider than long (Fig 33), post-mature proglottides might be almost as wide as long (Fig. 37). Ventral osmoregulatory canals 16-43 (33, n = 10) wide, with transverse anastomoses along posterior margin of each proglottis. Dorsal osmoregulatory canals 4-14 (8, n = 10). Genital pores irregularly alternating in short series, e.g., ... 3, 3, 1, 2, 1, 2, 2, 2, 4, 2, 1, 1, 2, 1...; situated at border of anterior third of lateral proglottis margin. Genital pore appears in fully developed mature proglottides (Figs 33-35). Developed atrium thick-walled, mostly infundibular, often with tubular basal part, 9-20 (16, n = 5) deep, with diameter 23-34 at orifice and 7-11 at base; surrounded by radial muscular fibres; intensely stained cells present around atrium in mature proglottides and lacking in post-mature proglottides. Genital papilla mostly lacking (Fig 33), in some post-mature proglottides can be slightly expressed (Fig. 37). Genital ducts passing between longitudinal osmoregulatory canals.

Testes 26-30 (28, n = 5), occupying posterior part of median field (Fig. 33), entirely posterior to vitellarium and ovary (in well-relaxed proglottides); sometimes single testes overlap longitudinal osmoregulatory canals; maximum diameter of testes (in post-mature proglottides) 58-76 (68, n = 10). External vas deferens highly coiled, forming with surrounding prostate cells transversely elongate body situated in anterior poral corner of median field and in adjacent portion of poral lateral field; diameter of external vas deferens 5-11 (9, n = 6). Cirrus sac in mature proglottides oval, 111-124 x 38-45 (117 x 40, n = 5), with maximum width in middle or at antiporal third; often with one or two constrictions; walls rather thin (Figs 34-35). Cirrus sac in post-mature proglottides elongate-oval, 165-179 x 48-57 (171 x 52, n = 5), not reaching longitudinal osmoregulatory canals; walls thick, muscular (Fig. 36). Withdrawn cirrus and ejaculatory duct cannot be distinguished from one another, forming together straight or slightly curved thick-walled canal with diameter 4-7, occupying about two thirds of cirrus-sac length (Figs 35-36). Internal vas deferens forming 1-3 coils in antiporal part of cirrus sac; no formation of structure resembling internal seminal vesicle observed. Prostate cells within cirrus sac moderately developed. Evaginated cirrus (n = 1) cylindrical, conically tapering at tip, with diameter of basal part 5-6; armament not observed.



FIGS 31-33

*Proparuterina aruensis* Fuhrmann, 1911, syntypes: 31, anterior rostellar hooks; 32, posterior rostellar hooks; 33, mature proglottides, dorsal view. Scale bars: 31-32 = 20  $\mu\text{m}$ ; 33 = 200  $\mu\text{m}$ .



FIGS 34-36

*Proparuterina aruensis* Fuhrmann, 1911, syntypes, development of the genital atrium and genital ducts: 34-35, genital atrium and genital ducts in young mature proglottides; 36, genital ducts in post-mature proglottis. Scale bars: 34-36 = 50  $\mu\text{m}$ .

Vitellarium median, with irregular shape, slightly lobed (Fig. 33), 58-71 ( $n = 4$ ) wide. Ovary median, more or less reniform, symmetrical, slightly lobed (Figs 33, 38), 142-167 ( $n = 4$ ) wide. Mehlis' gland not distinct. Seminal receptacle in early mature proglottides empty, situated dorsally to poral part of ovary, with thick walls consisting

of cells arranged in single layer (Figs 34, 38); in post-mature proglottides, seminal receptacle elongate-oval, 120-140 x 43-72 (131 x 60, n = 5), ventral to uterus. Vagina opening postero-laterally (mostly postero-ventrally, sometimes postero-dorsally) and passing just posteriorly along posterior wall of cirrus sac; both copulatory and conductive part covered with thick cellular sleeve. Copulatory part (Figs 34-36) occupying about 3/4 of length of vagina; diameter of lumen 5-11 (9, n = 10), diameter of vagina together with cellular sleeve 18-29 (22, n = 10).

Uterus appearing in mature proglottides as longitudinal process starting from vitellarium, crossing ovary dorsally and reaching almost to anterior proglottis margin (Figs 33, 38). Further stages cannot be followed because relevant proglottides are lacking in material studied. In late post-mature proglottides, general shape is horse-shoe-like, with free ends directed posteriorly; walls forming numerous diverticula, including very deep (Fig. 37).

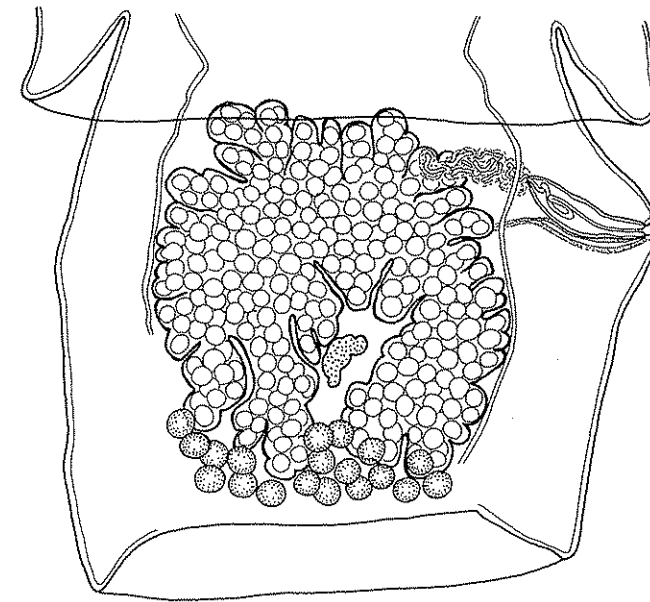
#### REMARKS

*Proparuterina aruensis* is known from its original record only (Fuhrmann, 1911). The present observations provide further details about the internal anatomy of this species, especially relative to the structure of the cirrus sac and vagina, female gonads and early stages of uterine development. However, because of the state of the type material, it is not possible to provide new data on the morphology of the scolex and some external characters. According to the original description (Fuhrmann, 1911), the entire specimens are 40-50 mm long and 1.3 mm wide, the scolex is with a diameter of 300-360 and the diameter of the suckers is 120. The total number of hooks has been described as 44-48.

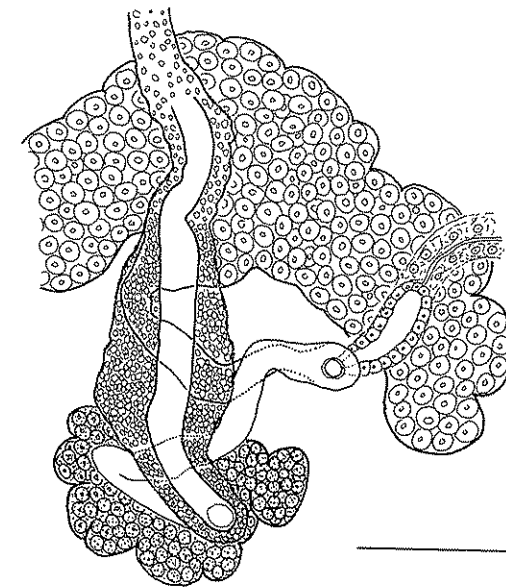
#### *Mariauxilepis* gen. n.

#### DIAGNOSIS

Scolex with sucker-like rostellum. Rostellar hooks in two regular rows. Handles and guards of anterior hooks embedded by common epiphyseal structure. Posterior hooks often with indistinct epiphyseal structure of handle. Hooks of ventral/dorsal position in crown and those with lateral position with different shape and size. Proglottides craspedote, mature slightly wider than long, gravid twice as wide as long. Genital pores irregularly alternating in short series, situated about middle of lateral proglottis margin. Genital atrium simple, infundibular, surrounded by moderately developed masses of glandular cells. Genital ducts passing between osmoregulatory canals. Transverse anastomosis of ventral osmoregulatory canals very wide. Testes posterior to ovary, mostly lateral to vitellarium, few testes only postero-dorsal to vitellarium; sometimes two lateral groups of testes entirely interrupted by vitellarium. External vas deferens densely coiled, together with surrounding glandular tissue forming small dense body. Cirrus sac oblique, oval to pyriform, with rounded and thick-walled antiporal part, not reaching or slightly overlapping poral osmoregulatory canal. Internal vas deferens forming few coils in antiporal half of cirrus sac; no structure similar to internal seminal vesicle. Vitellarium central, mostly with irregular shape, transversely elongate, highly lobed. Ovary reniform, with deeply lobed anterior



37



38

FIGS 37-38

*Proparuterina aruensis* Fuhrmann, 1911, syntypes: 37, post-mature proglottis, dorsal view; 38, detail of the female genital system in a mature proglottis, dorsal view. Scale bars: 37 = 200  $\mu$ m; 38 = 50  $\mu$ m.

margin, occupying almost entire width of median field. Mehlis' gland strongly developed, large, rounded or slightly irregular. Seminal receptacle oval to fusiform. Vagina opening posteriorly, sometimes slightly postero-laterally to male pore and passing posteriorly to cirrus sac; vaginal canal thin-walled, surrounded by thick cellular sleeve; no distinct conductive part. Developing uterus lobate, transversely elongate, dorsal to ovary and seminal receptacle, with numerous diverticula; developed uterus occupying whole median field, reaching osmoregulatory canals, with deep anterior, posterior and lateral diverticula. Developing eggs oval, with oval embryophores and oncospheres. In most developed gravid proglottides only, eggs becoming elongate-oval, with thin outer envelope and thick embryophore; embryonic hooks almost parallel to each other, forming bunch with polar position in oncosphere. Parasites of Caprimulgiformes, South America.

Type species: *Mariauxilepis paraguayensis* sp. n.

#### ETYMOLOGY

The new genus is named after Dr J. Mariaux (Natural History Museum, Geneva) in recognition of his contribution to the systematics of the family Metadilepididae. Its name is of feminine gender.

#### REMARKS

Eight genera were included in the family Metadilepididae, according to the revision of Kornushin & Georgiev (1994). Following their key, *Mariauxilepis* belongs to a group with 3 other genera characterised by irregular alternation of genital pores: *Proparuterina* (see above), *Schmidneila* Spasskii & Spasskaya, 1973 (parasites of polioptiline passeriforms in Central America) and *Hamatofuhrmannia* Spasskii, 1969 (parasites of the Formicariidae from South America). The latter two genera are characterised by a single crown of rostellar hooks, and in *Hamatofuhrmannia* the genital ducts pass dorsally to poral osmoregulatory canals.

*Mariauxilepis* can be considered unique among the Metadilepididae relative to two characters: the peculiar structure of the ripe eggs and the polar, almost parallel position of the embryonic hooks in them, and the wide transverse anastomoses of the ventral osmoregulatory canals. Another interesting peculiarity is the different shape and size of the rostellar hooks with ventral/dorsal position and those with lateral position on the rostellum. Among metadilepidids, a similar peculiarity has been observed only in the genus *Skrjabinoporus* Spasskii & Borgarenko, 1960 (see Spasskii & Borgarenko, 1960; Mariaux & Vaucher, 1989; Kornushin & Georgiev, 1994), which includes parasites of the Old World coraciiform birds.

The most similar genus to the present material is *Proparuterina* (see above for the generic diagnosis and for a redescription of the type species), also including parasites of caprimulgiform birds. Compared to this genus, *Mariauxilepis* has a wide ovary, occupying the whole width of the median field (versus a small ovary, not reaching longitudinal osmoregulatory canals) and testes mostly lateral to the vitellarium (versus testes entirely postvitellarian). The type species of *Proparuterina* has separate epiphyseal thickenings of the handle and the guard of the rostellar hooks while, in *M. paraguayensis*, the handle and the guard of anterior hooks are embedded

by a common epiphyseal structure. The early uterus of *Mariauxilepis* is transversely elongate, situated entirely dorsally to the ovary while the early uterus in *Proparuterina* is a longitudinally elongate process passing the anterior margin of the ovary. The shape of developing uterus of *Proparuterina* resembles an inverted U while the developing uterus of *Mariauxilepis* has never this shape. In addition, the type species of *Mariauxilepis* has well-developed and prominent Mehlis' gland; in contrast, this organ in *Proparuterina aruensis* is not distinct as a glandular structure.

The new genus has to be compared also with *Metadilepis* in its present concept, since the latter genus now includes not only species with unilateral genital pores but also a species (*M. kornyushini*) with genital pores alternating in long series. The two genera can be distinguished by the position of the osmoregulatory canals ventral to the genital ducts in *Metadilepis* and the genital ducts passing between the osmoregulatory canals in *Mariauxilepis*. Further differences are connected with the peculiarities of the ripe eggs, the possibility of the internal vas deferens forming a structure similar to internal seminal vesicle, the degree of lobation of the female gonads, etc.

#### *Mariauxilepis paraguayensis* sp. n.

Figs 39-49

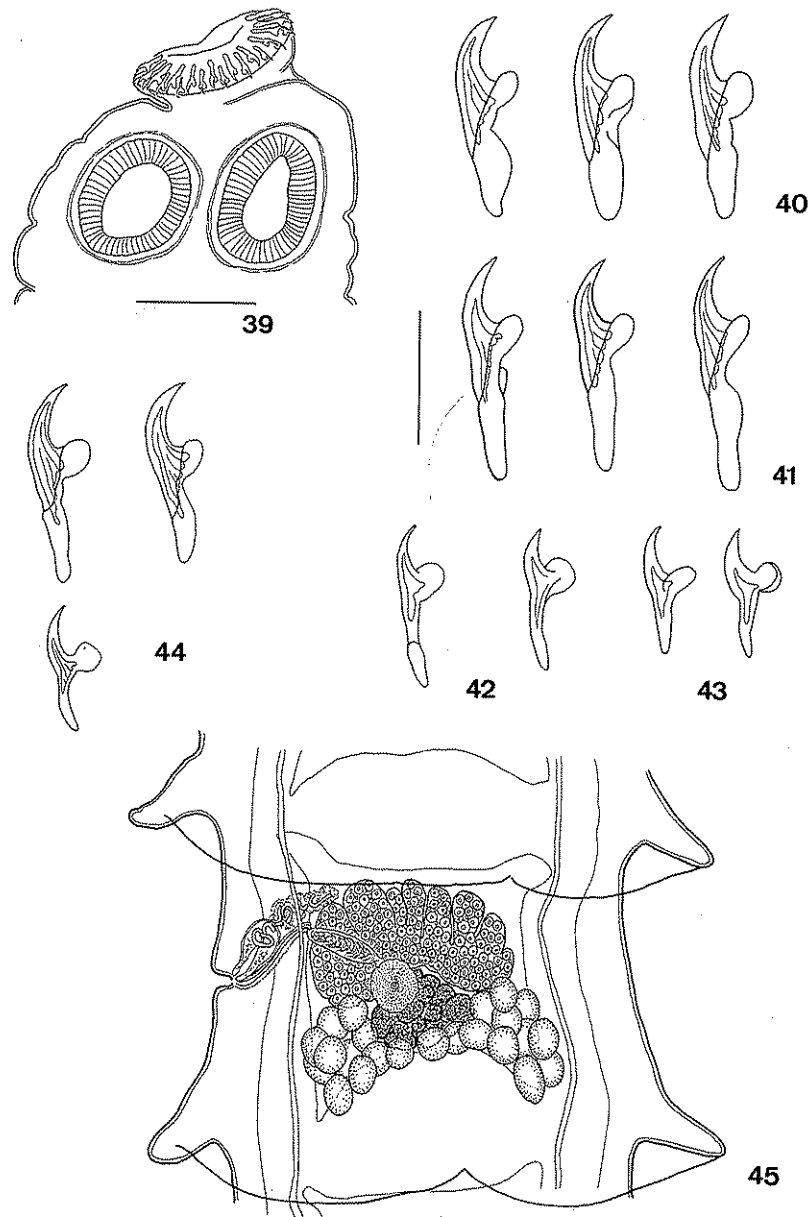
Hosts: *Nyctidromus albicollis* (Gmelin, 1789) (type host) and *Setopagis parvula* (Caprimulgidae).

Material studied: 2 entire specimens, stained with hydrochloric carmine, whole mount in Canada balsam. Holotype: MHNG 33845 INVE, from *N. albicollis*, arroyo Tagatija-Mi, province Concepcion, Paraguay, 16 October 1983 (1 slide). Paratype: MHNG 33846 INVE, from *S. parvula*, Pilar, province Neembucu, 19 October 1982 (1 slide).

#### DESCRIPTION

Holotype: Total length 37 mm. Gravid strobila consisting of 175 proglottides: primordia of gonads appearing in about 60th proglottis, functioning testes in about 110th, functioning female glands in about 115th, uterus predominating over female glands in 160th; gravid proglottides 8 in number. Maximum width at pre-gravid proglottides, 1.18 mm.

Scolex with maximum diameter 290, at level posterior to suckers; not clearly outlined from neck (Fig. 39). Rostellar pad discoid, with diameter 125; its anterior surface concave; muscular fibres, perpendicular to pad surface, present within pad. Retractor muscles and glandular elements not distinct. Rostellar hooks in two regular rows, their total number exceeding 40 (33 hooks present, perhaps 3 anterior and 8 posterior hooks lost). Anterior and posterior hooks of different shape and size (Figs 40-43). Hooks of ventral/dorsal and those of lateral position in crown with different shape and size. Anterior hooks with handles and guards comprised of common epiphyseal structure; anterior hooks of dorsal/ventral position in crown 30-31 ( $n = 3$ ) long, with thicker and shorter handle (Fig. 40); anterior hooks of lateral position in crown 33-35 ( $n = 3$ ) long, with slender and longer handle (Fig. 41). Posterior hooks often with indistinct epiphyseal structure of handle; posterior hooks of dorsal/ventral position 24 ( $n = 1$ ) long, with longer handle (Fig. 42); these of lateral position shorter, 18-19 ( $n = 2$ ) long (Fig. 43); intermediate hooks with intermediate length, e.g., 22 ( $n = 1$ ). Suckers oval, 102-111 (107,  $n = 3$ ), with apertures directed dorsally and ventrally; musculature moderately developed. Neck long, 183 wide in its narrowest part; proglottides appear at 880 from posterior margins of suckers.



Figs 39-45

*Mariauxilepis paraguayensis* gen. n., sp. n., holotype (from *Nyctidromus albicollis*) and paratype (from *Setopagis parvula*): 39, scolex of the holotype; 40-43, rostellar hooks of the holotype: 40, anterior rostellar hooks with ventral or dorsal position in the crown; 41, anterior rostellar hooks with lateral position in the crown; 42, posterior rostellar hook with dorsal (or ventral) position (left) and rather intermediate position (right) in the crown; 43, posterior rostellar hooks with lateral position in the crown; 44, rostellar hooks of the paratype; 45, mature proglottis, dorsal view, holotype. Scale bars: 39, 45 = 100  $\mu$ m; 40-44 = 20  $\mu$ m.

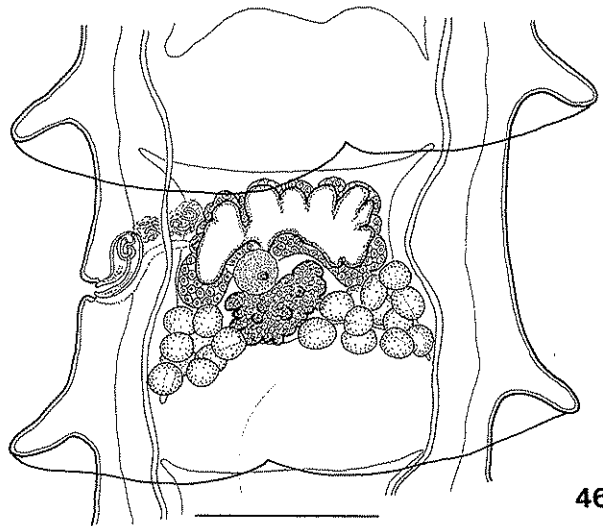
Proglottides craspedote; velum well developed (Figs 45-47). Mature proglottides slightly wider than long (Fig. 45-46); gravid proglottides twice as wide as long (Fig. 47). Genital pores irregularly alternating in short series, e.g., 2, 2, 2, 1, 2, 1, 4, 2, 1, 1, 2, 1, 1, 1, 2, 3, 1, 3, 2, 1, 4, 1, 1...; situated in middle of lateral proglottis margin in mature proglottides and slightly anteriorly in gravid proglottides. Genital papilla not observed. Genital atrium 21-32 (24,  $n = 10$ ) deep, with infundibular orifice and almost cylindrical basal part with diameter 14-20 (18,  $n = 10$ ); its walls thick; no glandular elements observed around it (Fig. 48). Genital ducts passing between osmoregulatory canals.

Ventral osmoregulatory canals 27-89 (62,  $n = 10$ ) wide, with very wide transverse anastomoses, reaching width 116-291 (186,  $n = 10$ ) and occupying 1/3-1/4 of proglottis length. Dorsal osmoregulatory canals 5-9 (7,  $n = 10$ ) wide.

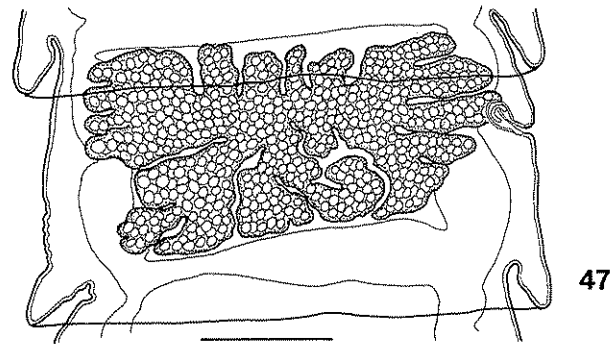
Testes 21-28 (24,  $n = 10$ ) in number, situated in posterior half of median field, slightly overlapping posterior margins of vitellarium and ovary (Fig. 45-46); most testes lateral to vitellarium, few testes only postero-dorsal to vitellarium; testes slightly overlapping ventral osmoregulatory canals and transverse anastomosis. In some proglottides, testes entirely interrupted by vitellarium and forming two lateral groups (Fig. 46). Maximum diameter of testes 46-66 (56,  $n = 10$ ). External vas deferens densely coiled, together with surrounding glandular tissue forms small dense body in anterior poral part of proglottis; diameter of external vas deferens 5-9 (7,  $n = 10$ ). Cirrus sac oblique, oval to pyriform, not reaching or slightly overlapping poral ventral osmoregulatory canal, rarely reaching to dorsal canal; walls of cirrus sac relatively thick (especially of antiporal part), with poorly developed musculature; antiporal end widely rounded, poral end slightly tapering; 66-88 x 39-48 (81 x 45,  $n = 10$ ). Internal vas deferens forms few coils in antiporal half of cirrus sac (Figs 45-46, 48); do not form structure similar to internal seminal vesicle. Evaginated cirrus not observed; canal of withdrawn cirrus widening in poral direction; no armament observed in canal of withdrawn cirrus.

Vitellarium central, mostly with irregular shape, transversely elongate, highly lobed, 79-120 x 111-151 (93 x 133,  $n = 10$ ). Ovary almost reniform, with deeply lobed anterior margin, wide, occupying almost all median field. Mehlis' gland large, rounded or slightly irregular, situated between ovary and vitellarium, disposed slightly porally, with diameter 63-77 (72,  $n = 10$ ). Seminal receptacle oval to fusiform, 89-123 x 30-41 (96 x 37,  $n = 7$ ), dorsal to ovary. Vagina (Fig. 48) opens posteriorly, sometimes slightly postero-laterally to male pore and passes posteriorly to cirrus sac; vaginal canal thin-walled, surrounded by thick cellular sleeve; no distinct conductive part.

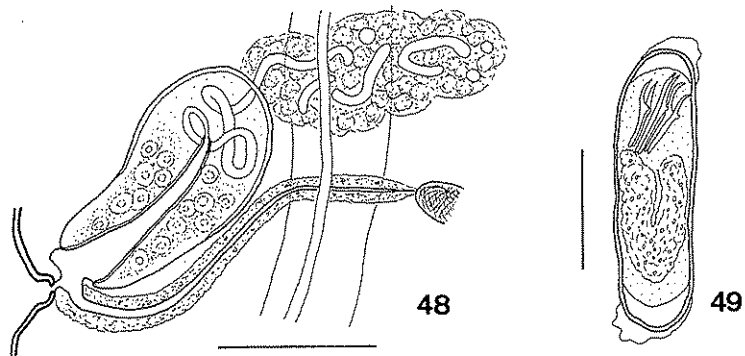
In mature proglottides, uterus lobate, transversely elongate, dorsal to ovary and seminal receptacle (Fig. 46). Further uterine development comprising enlargement in anterior, posterior and lateral directions and formation of numerous diverticula. In pre-gravid and gravid proglottides, uterus occupying almost whole median field and just overlapping ventral osmoregulatory canals; deep anterior, posterior and lateral diverticula present (Fig. 47). Developing eggs oval, with oval embryophores and oncospheres. In most developed three gravid proglottides only, eggs becoming elongate-oval (Fig. 49), 45-51 x 13-16 (48 x 15,  $n = 7$ ), with thin outer envelope; embryophore rather thick, oval, with length 40-45 x 13-16 (43 x 15,  $n = 7$ ); oncospheres oval, 37-41 x 12-



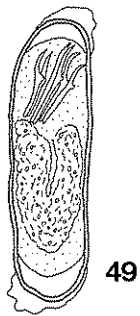
46



47



48



49

FIGS 46-49

*Mariauxilepis paraguayensis* gen. n., sp. n., specimen from *Nyctidromus albicollis* (holotype): 46, mature proglottis showing an early stage of the uterine development, dorsal view; 47, pre-gravid proglottis; 48, genital ducts, dorsal view; 49, egg. Scale bars: 46-47 = 250  $\mu$ m; 48 = 50  $\mu$ m; 49 = 20  $\mu$ m.

15 (39 x 13, n = 7). Embryonic hooks almost parallel to each other, forming bunch having polar position in oncosphere (Fig. 49); central pair 17-18 (n = 5) long, lateral pairs 14-16 (n = 5) long.

*Paratype*: Specimen slightly contracted; scolex deformed. Main metrical and meristic data: total length 28 mm, maximum width 1.13 mm (at pre-gravid proglottides), number of proglottides 175. Diameter of scolex 237; diameter of rostellum 122; diameter of suckers 102-118 (n = 2). Number of rostellar hooks 44; anterior hooks 30-31 (n = 3) long; posterior hooks 18-22 (n = 3) long (Fig. 44). Number of testes 19-26 (23, n = 10). Cirrus sac 76-86 x 32-39 (83 x 36, n = 10). Vitellarium 56-87 x 86-143 (64 x 120, n = 7). Eggs 39-46 (43, n = 6) long, embryophore 34-43 x 11-14 (39 x 13, n = 6), oncosphere 36-42 x 10-13 (38 x 12, n = 6). Embryonic hooks of central pairs 17-18 (n = 3) long, embryonic hooks of lateral pairs 13-14 (n = 3) long.

#### *Urutaulepis* gen. n.

##### DIAGNOSIS

Rostellum sucker-like, with two rows of hooks. Hooks in each row with almost equal length and shape; blade curved, handle and guard with small epiphyseal structures. Anterior hooks longer, with straight handle; posterior hooks with curved handle. Genital pores unilateral, about middle of lateral proglottis margin in mature proglottides and in anterior third in pre-gravid proglottides. Slightly expressed genital papilla may present. Genital atrium consists of long tubular canal surrounded by powerful circular musculature and internal enlargement surrounded by layer of radial muscular fibres and glandular layer. Osmoregulatory canals in strobila not seen. Testes numerous (about 40), situated mostly laterally to ovary and vitellarium, few testes posterior to them; antiporal testes more numerous than poral. External vas deferens with several large coils anterior to female genital ducts; no distinct prostate cells. Cirrus sac thick-walled, oval to pyriform, poral end may form pipette-like papilla. Internal vas deferens forming numerous coils, mainly in antiporal half but often also in poral half of cirrus sac; no structure similar to internal seminal vesicle. Vitellarium and ovary disposed slightly porally. Vitellarium transversely elongate, oval or with irregular shape, compact or slightly lobed. Ovary two-winged, deeply lobed. Mehlis' gland not distinct. Seminal receptacle highly elongate, fusiform, extending from level of cirrus sac to level of poral wing of ovary. Vagina opens posteriorly and slightly postero-laterally to male pore and passes posteriorly to cirrus sac; usually curved; vaginal canal thick-walled, surrounded by thick cellular sleeve; no distinct conductive part. Uterus in mature proglottides as transversely elongate sac, anteriorly to ovary, genital ducts and antiporal testes; further development connected with enlargement in posterior direction and overlapping ovary. In pre-gravid proglottides, uterus with distinct anterior, posterior and lateral diverticula, occupying almost whole proglottis excluding most lateral portions only. Underdeveloped eggs oval, with thin outer envelope and thicker embryophore; developing oncospheres oval. In Caprimulgiformes (Nyctibiidae), South America.

Type species: *Urutaulepis pifanoi* (Díaz-Ungría & Jordano, 1958) comb. n.

## ETYMOLOGY

The name of the new genus derives from the trivial name of the host species in South America, "*urutau*". It is of feminine gender.

## REMARKS

The type species of the new genus was initially described as a member of the family Dilepididae (Díaz-Ungría & Jordano, 1958). Spasskii (1965) supposed that this species might be a member of the Metadilepididae but did not transfer it to this family because of the lack of adequate data in the original description.

As seen from the present redescription, the structure of the rostellar apparatus of *U. pifanoi* is clearly different from that of the Dilepididae (see Bona, 1994; Stoitsova *et al.*, 1997) and very close to those of genera of the families Paruterinidae and Metadilepididae. Though the material does not allow us to specify the position of the developing uterus relative to the female gonads (dorsal or ventral), *Urutaulepis pifanoi* is evidently a member of the Metadilepididae by the structure of the rostellar apparatus and by the absence of a paruterine organ. Unfortunately, the only specimen available does not provide a reliable basis for the description of the position of the genital ducts relative to the osmoregulatory canals. Its unilateral genital pores correspond well to the diagnosis of *Metadilepis*. However, it differs from *Metadilepis* spp. in several essential characters, which do not allow its placement in the latter genus. These are the presence of postvitellarian testes, the slight development of the epiphyseal structures of the rostellar hooks and the peculiar structure of the genital atrium consisting of a long tubular canal surrounded by powerful circular musculature and an internal cavity encircled by radial muscles and a thick glandular layer. Additional differentiating characters distinguishing *Urutaulepis* gen. n. from *Metadilepis* are the lack of conductive part of the vagina of the former and its presence in the latter as well as the different shape of the seminal receptacle.

The new genus differs from the remaining two metadilepidid genera from Caprimulgiformes, *Proparuterina* and *Mariauxilepis*, by the unilateral position of its genital pores and the slight development of the epiphyseal structures of its rostellar hooks.

Following the key by Korniyushin & Georgiev (1994), *Urutaulepis* gen. n. needs to be distinguished from several genera with unilateral genital pores. *Skrjabinoporus* Spasskii & Borgarenko, 1960 includes parasites of Meropidae (Coraciiformes) in the Old World. It is characterised by highly elongate suckers with weak musculature, testes forming compact group in the posterior half of the proglottis dorsally to the vitellarium, and a small globular seminal receptacle (Spasskii & Borgarenko, 1960; Mariaux & Vaucher, 1989; Korniyushin & Georgiev, 1994). *Cracticotaenia* Spasskii, 1966, a parasite of the Cracticidae (Passeriformes) in Australia, has almost triangular rostellar hooks, a large vaginal sphincter and testes forming one group posterior and dorsal to the female gonads (Korniyushin & Georgiev, 1994). *Yapolepis* Mariaux, 1991 and *Pseudadelphoscolex* Mariaux, Bona & Vaucher, 1992 from African passeriform birds are readily distinguished from the new genus because the lack of rostellum armament in the former and the peculiar T-shaped rostellar hooks in the latter (Mariaux, 1991; Mariaux *et al.*, 1992; Korniyushin & Georgiev, 1994).

Therefore, though we cannot describe some details connected with the disposition of the osmoregulatory canals, we believe that the remaining characters justify the erection of the new genus.

*Urutaulepis pifanoi* (Díaz-Ungría & Jordano, 1958) comb. n. Figs 50-58

*Dilepis pifanoi* Díaz-Ungría & Jordano, 1958: 3-7, Fig. 1-9; Yamaguti, 1959: 233; Matevosyan, 1963: 73-74, Fig. 44; Schmidt, 1986: 381.

*Host*: *Nyctibius griseus* (Gmelin, 1789) (Nyctibiidae).

*Material studied*: MHNG (Collection Neuchâtel) 112/77, paratype, Isla Margarita, Venezuela, single specimen, hematoxylin, whole mount in Canada balsam (1 slide).

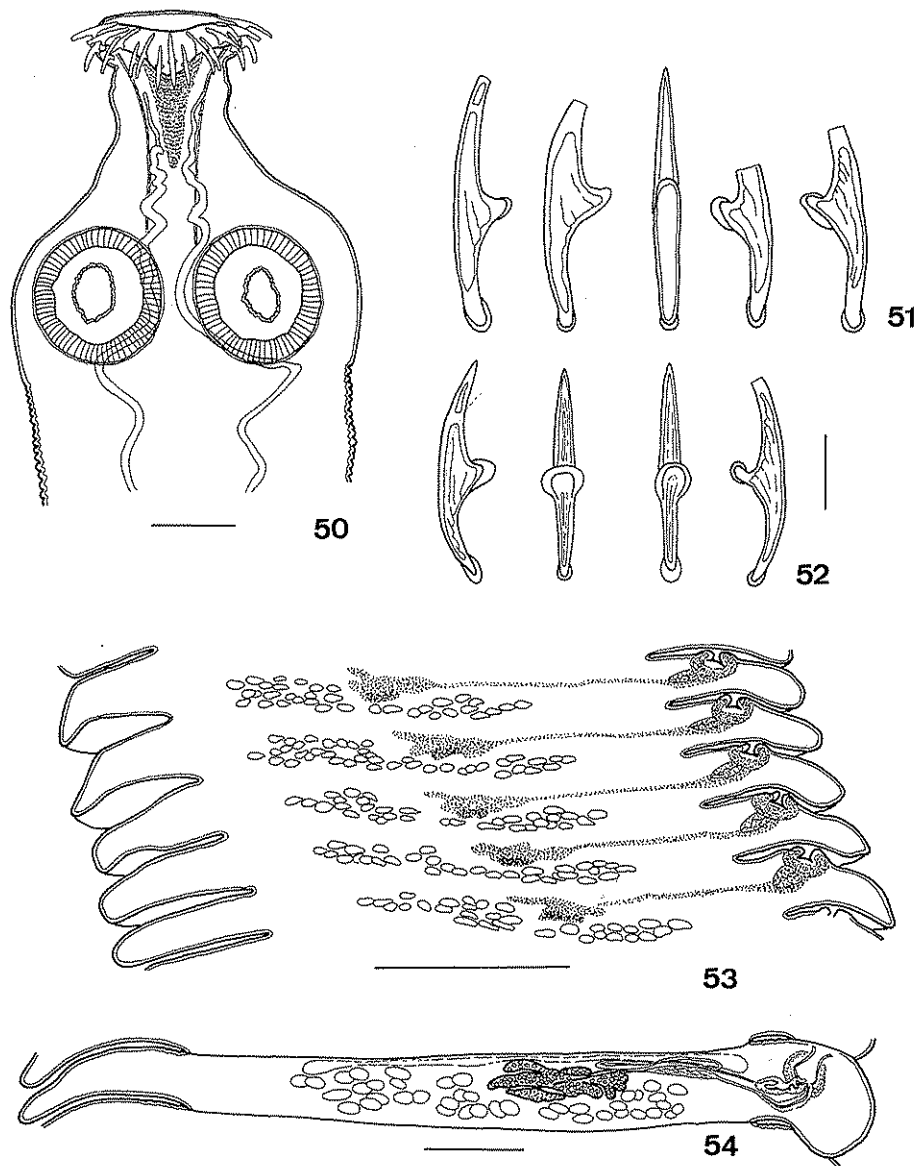
## REDESCRIPTION

Specimen contracted; long portions of strobila twisted. Total length more than 35 mm. Strobila consists of 320 proglottides; maximum width at post-mature proglottides, 2.19 mm.

Scolex with maximum diameter at level of middle of suckers, 433; anterior part of scolex conically protruded (Fig. 50). Rostellar apparatus consists of muscular pad and associated with it retractor muscles, glandular elements and circular musculature; no rostellar pouch. Rostellar pad with diameter 192; its anterior surface concave; numerous muscular fibres, perpendicular to pad surface, present within pad. Retractor muscles extending from rostellar pad periphery and continuing as longitudinal muscular bundles of strobila. Glandular elements form dense granular formation, situated medially just posterior to muscular pad, gradually tapering in posterior direction; loose circular muscular fibres surround glandular aggregation. Rostellar hooks 32 in number, situated in two regular rows (few hooks in lateral position, most of hooks with broken tips). Handles and guards provided with small epiphyseal structures, often not clearly distinct (Figs 51-52). Anterior and posterior hooks of different shape and size. Anterior hooks 71.5-73.5 (n = 2) long, with straight handle (Fig. 51). Posterior hooks 59-61 (60.2, n = 3) long; handle curved (Fig. 52). Suckers round, with apertures directed dorsally and ventrally; their musculature moderately developed; diameter of suckers 165-170 (169, n = 4). Formation of proglottides starts just posterior to suckers. No distinct neck.

Osmoregulatory canals distinct in scolex only, reaching level just posterior to rostellar pad. Proglottides wider than long at all developmental stages, craspedote. Genital pores unilateral, situated about middle of lateral proglottis margin in mature proglottides and in anterior third of lateral proglottis margin in pre-gravid proglottides. Slightly expressed genital papilla may present. Genital atrium (Figs 56-58) consists of deep tubular canal leading to internal enlargement; walls of tubular canal surrounded by thick layer of circular musculature; internal cavity surrounded by layer of radial muscular fibres and layer of glandular cells.

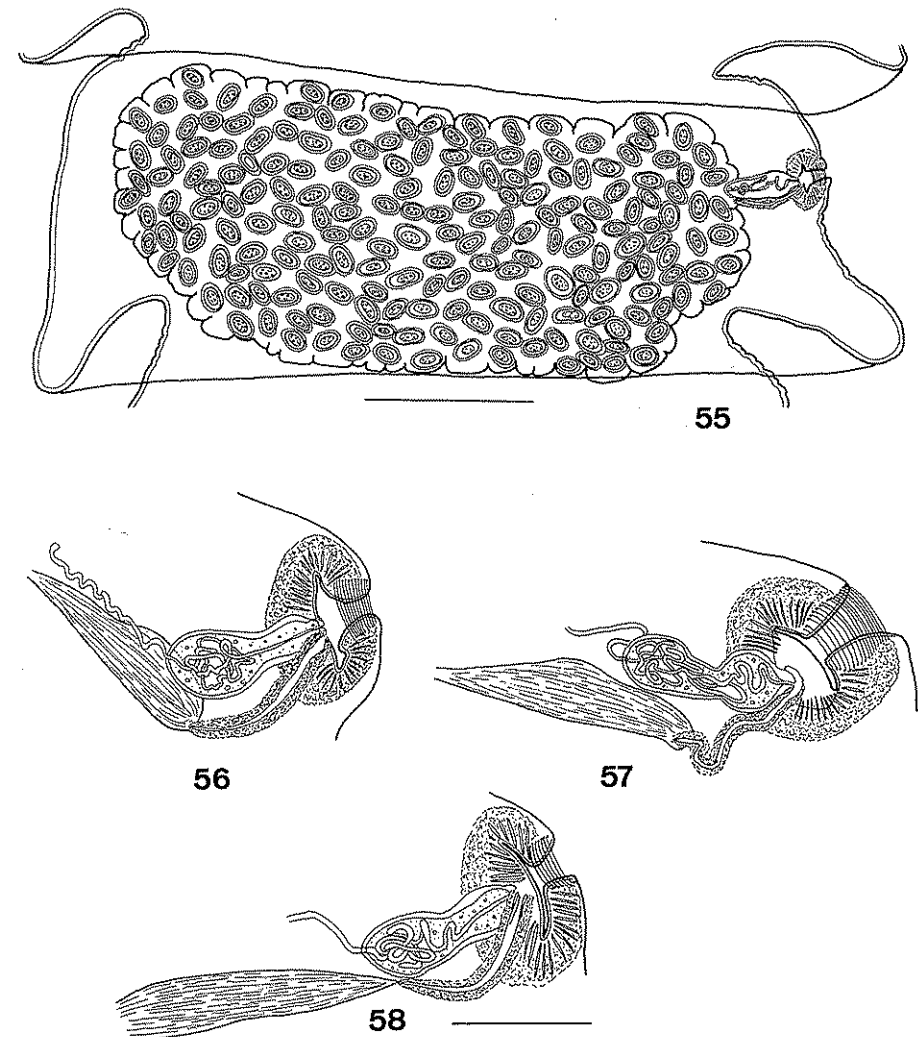
Testes 34-43 (38, n = 10), situated mostly laterally to ovary and vitellarium; few testes posterior to female gonads; antiporal testes more numerous than poral testes (Figs 53-54). External vas deferens forms several large coils anterior to female genital ducts; no distinct prostate cells around it. Cirrus sac oval to pyriform, with constriction about its middle; antiporal end widely rounded; poral end may form pipette-like papilla



Figs 50-54

*Urutaulepis pifanoi* (Díaz-Ungría & Jordano, 1958) gen. n., comb. n., paratype: 50, scolex; 51, anterior rostellar hooks; 52, posterior rostellar hooks; 53, pre-mature proglottides; 54, mature proglottis. Scale bars: 50 = 100  $\mu$ m; 51-52 = 20  $\mu$ m; 53 = 500  $\mu$ m; 54 = 250  $\mu$ m.

entering into genital atrium; cirrus sac thick-walled, 113-143 x 43-52 (124 x 46, n = 10). Internal vas deferens forms numerous coils, mainly in antiporal half of cirrus sac (Figs 56, 58) but sometimes also in poral half of organ (Fig. 57); does not form



Figs 55-58

*Urutaulepis pifanoi* (Díaz-Ungría & Jordano, 1958) gen. n., comb. n., paratype: 55, pre-gravid proglottis; 56-58, variability of the genital atrium and terminal genital ducts. Scale bars: 55 = 250  $\mu$ m; 56-58 = 100  $\mu$ m.

structure similar to internal seminal vesicle. Evaginated cirrus cylindrical, unarmed, with diameter 14-17 (n = 2).

Vitellarium and ovary disposed slightly porally (at 43-47% of pre-mature proglottis width, n = 7); due to strobila twisting, some proglottides create impression of strong poral or antiporal disposition of female gonads. Vitellarium transversely elongate, oval or with irregular shape, compact or slightly lobed. Ovary two-winged (frequently, perhaps due to strobilar contraction, two wings not distinct); deeply lobed. Mehlis' gland not observed. Seminal receptacle highly elongate, fusiform, extending

from level of cirrus-sac antiporal end to level of poral wing of ovary; in most typical cases, maximum width of seminal receptacle about its middle; in some cases, maximum width of seminal receptacle near its connection with vagina (Fig. 56). Vagina opens posteriorly and slightly postero-laterally to male pore and passes posteriorly to cirrus sac; copulatory part usually curved, comparable in length with cirrus sac; vaginal canal thick-walled, surrounded by thick cellular sleeve; no distinct conductive part, seminal receptacle begins just after copulatory part.

Uterus seen in some mature proglottides as sac-like transversely elongate formation along anterior proglottis margin, situated anteriorly to ovary, genital ducts and antiporal group of testes. Further development connected with enlargement of uterus in posterior direction, initially its lateral ends and then its middle part, thus overlapping ovary, testes and degenerating ovary. In pre-gravid proglottides, uterus occupying almost whole proglottis, excluding most lateral proglottis portions only; its wall forming distinct anterior, posterior and lateral diverticula (Fig. 55). Underdeveloped eggs (embryonic hooks not entirely formed) oval, with thin outer envelope and thicker embryophore; developing oncospheres oval.

#### CONCLUDING COMMENTS

The present study on the metadilepidid cestodes from caprimulgiform birds revealed that their diversity is considerably greater than previously known. Kornyushin & Georgiev (1994) summarised data on 8 genera and 11 species of metadilepidids; among them, 2 genera and 4 species were from the Caprimulgiformes. Our study adds further 2 genera and 4 species. Thus, the present results corroborate the belief of previous authors (Spasskii & Spasskaya, 1973; Mariaux, 1991) that the diversity of the metadilepidids is considerably greater than known in that time.

Kornyushin & Georgiev (1994) believed that the potential number of genera is considerably greater than known at the time of their publication and their discovery was a matter for the future. Their statement was based on the fact that metadilepidids were mostly known from tropical birds, which were insufficiently studied. Each extensive faunistic survey on the cestode parasites from tropical birds carried out during the last two decades has confirmed that belief. A survey of the avian cestodes of the Ivory Coast (West Africa) revealed the presence of 3 metadilepidid genera (Mariaux & Vaucher, 1989; Mariaux, 1991, 1994; Mariaux *et al.*, 1992). The present study was provoked by the extensive survey of the avian parasites in Paraguay carried out by the Natural History Museum, Geneva. It also showed a considerably higher diversity of metadilepidids than previously known.

#### ACKNOWLEDGEMENTS

We thank the Ministry of Agriculture and Livestock of Paraguay for providing facilities during the field work and the members of the expeditions for collecting specimens (C. Dlouhy, F. Baud, V. Mahnert, J.-L. Perret and C. Weber). P. Nikolov (Sofia) made useful suggestions on an early draft of the present paper. This investigation was supported by the National Research Council of the Republic of Bulgaria, Grant no. B-819.

#### REFERENCES

- BAUGH, S. C. & SAXENA, S. K. 1976. On cestodes of *Passer domesticus*. I. *Choanotaenia*, *Raillietina* and *Proparuterina*. *Angewandte Parasitologie* 17: 146-160.
- BONA, F. V. 1994. Family Dilepididae Railliet & Henry, 1909 (pp. 443-554). In: KHALIL, L. F., JONES, A. & BRAY, R. A. (eds). Keys to the cestode parasites of vertebrates. *CAB International, Wallingford, U.K.*, 751 pp.
- DÍAZ-UNGRÍA, D. & JORDANO, D. 1958. Cestodos de Venezuela. — III) *Dilepis pifanoi* nov. sp. (Cestoda Dilepididae), parasita del *Nyctibius griseus* (Aves: Caprimulgi). *Revista Ibérica de Parasitología* 18: 3-12.
- FUHRMANN, O. 1908a. Nouveaux Ténias d'Oiseaux. *Revue suisse de Zoologie* 16: 27-73.
- FUHRMANN, O. 1908b. Die Cestoden der Vögel. *Zoologische Jahrbücher*, Supplementband 10(1): 1-232.
- FUHRMANN, O. 1911. Vogelcestoden der Aru-Inseln. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 34: 251-266.
- FUHRMANN, O. 1913. Nordische Vogelcestoden aus dem Museum von Göteborg. *Göteborgs Kungliga Vetenskaps- och Vitterhetssamhälles Handlingar. Fjärde Följden* 15: 1-41.
- FUHRMANN, O. 1932. Les Ténias des Oiseaux. *Mémoires de l'Université de Neuchâtel* 8: 1-381.
- GEORGIEV, B. B. & KORNYUSHIN, V. V. 1994. Family Paruterinidae Fuhrmann, 1907 (sensu lato) (pp. 559-584). In: KHALIL, L. F., JONES, A. & BRAY, R. A. (eds). Keys to the cestode parasites of vertebrates. *CAB International, Wallingford, U.K.*, 751 pp.
- GEORGIEV, B. B. & VAUCHER, C. 2001. Revision of the genus *Parvirostrum* Fuhrmann, 1908 (Cestoda: Cyclophyllidae: Paruterinidae). *Systematic Parasitology* 50: 13-29.
- GEORGIEV, B. B., VASILEVA, G. P., BRAY, R. A. & GIBSON, D. I. 2002. The genus *Biuterina* Fuhrmann, 1902 (Cestoda, Paruterinidae) in the Old World: redescription of four species from Afrotropical Passeriformes. *Systematic Parasitology* 52: 111-128.
- HOBERG, E. P., JONES, A. & BRAY, R. A. 1999. Phylogenetic analysis among the families of the Cyclophyllidae (Cestoda) based on comparative morphology, with new hypotheses for co-evolution in vertebrates. *Systematic Parasitology* 42: 51-73.
- KORNYUSHIN, V. V. 1989. [Fauna of Ukraine. Volume 33. Monogenea and Cestoda. Issue 3. Davaineoidea. Biuterinoidea. Paruterinoidea]. *Naukova Dumka, Kiev*, 252 pp. (In Russian).
- KORNYUSHIN, V. V. & GEORGIEV, B. B. 1994. Family Metadilepididae Spasskii, 1959 (pp. 585-593). In: KHALIL, L. F., JONES, A. & BRAY, R. A. (eds). Keys to the cestode parasites of vertebrates. *CAB International, Wallingford, U.K.*, 751 pp.
- KUGI, G. 1988. Studies on the helminth fauna of vertebrates in Oita Prefecture. Part. 2. Avian helminths. *Published by the author, Beppu City*, 186 pp.
- LÓPEZ-NEYRA, C. R. 1944. Compendio de Helminología Ibérica. Parte II. Capítulo III. Familia Dilepididae Fuhrmann 1907. *Revista Ibérica de Parasitología* 4: 209-314.
- MARIAUX, J. 1991. Cestodes of birds from the Ivory Coast. *Yapolepis yapolepis* n. g., n. sp., a new metadilepidid (Cyclophyllidae: Paruterinoidea) parasite of the icterine greenbul (Aves: Pycnonotidae). *Systematic Parasitology* 18: 187-191.
- MARIAUX, J. 1994. Avian cestodes of the Ivory Coast. *Journal of the Helminthological Society of Washington* 61: 50-56.
- MARIAUX, J. & VAUCHER, C. 1989. Cestodes d'oiseaux de Côte-d'Ivoire. II. Parasites de Coraciiformes et Piciformes. *Systematic Parasitology* 14: 117-133.
- MARIAUX, J., BONA, F. V. & VAUCHER, C. 1992. A new genus of Metadilepididae (Cestoda: Cyclophyllidae) parasitic in *Terpsiphone rufiventer* (Aves: Muscicapidae) from the Ivory Coast. *The Journal of Parasitology* 78: 309-313.
- MATEVOSYAN, E. M. 1963. [Dilepidoidea - tapeworms of domestic and wild animals]. In: SKRYABIN, K. I. (ed.). *Osnovy Tsestodologii*, 3. *Izdatel'stvo Akademii Nauk SSSR, Moscow*, 688 pp. (In Russian).
- NESLOBINSKI, N. 1911. Zur Kenntnis der Vogeltänien Mittelrusslands. *Centralblatt für Bakteriologie, Parasitenkunde und Infektionskrankheiten. Abteilung Originale* 57: 436-442.

- SCHMIDT, G. D. 1986. CRC handbook of tapeworm identification. *CRC Press, Boca Raton, Florida*, 675 pp.
- SHUMILO, R. P., SPASSKII, A. A. 1976. [Cestodes of wild terrestrial birds of Moldavian SSR] (pp. 31-49). In: SPASSKII, A. A. (ed.). *Parazity teplokrovnykh zhivotnykh Moldavii. Izdatel'stvo Shtiintsa, Kishinev*, 164 pp. (In Russian).
- SPASSKAYA, L. P. & SPASSKII, A. A. 1971. [Cestodes of birds in Tuva]. *Izdatel'stvo Shtiintsa, Kishinev*, 252 pp. (In Russian).
- SPASSKII, A. A. 1946. [Contribution to the knowledge of the fauna of avian cestodes in the USSR] (pp. 252-261). In: POD'YAPOLSKAYA, V. P. (ed.). *Gel'mintologicheskiy Sbornik. Izdatel'stvo Akademii Nauk SSSR, Moscow and Leningrad*, 240 pp. (In Russian).
- SPASSKII, A. A. 1947a. [Materials to the knowledge on cestodes in Gor'kovskaya Oblast']. *Trudy Gosudarstvenogo Pedagogicheskogo Instituta Imeni M. Gor'kogo* 12: 48-58. (In Russian; not seen, cited after Matevosyan, 1963).
- SPASSKII, A. A. 1947b. [On the position of the genus *Echinorhynchotaenia* Fuhrmann, 1909 in the cestode system]. *Doklady Akademii Nauk SSSR* 58: 723-724. (In Russian).
- SPASSKII, A. A. 1949. *Metadilepis*, a new cestode genus parasitising birds. *Doklady Akademii Nauk SSSR* 69: 1513-1515. (In Russian).
- SPASSKII, A. A. 1959. [On the phylogenetic relations of the subfamily Metadilepidinae nov. subfam. (Cestoda: Cyclophyllidea)]. *Helminthologia* 1: 155-158. (In Russian).
- SPASSKII, A. A. 1965. [Revision of the genus *Dilepis* (Cestoda: Cyclophyllidea)]. *Parazity Zhivotnykh i Rasteniy* 1: 65-83. (In Russian).
- SPASSKII, A. A. & BORGARENKO, L. F. 1960. [*Skrjabinoporus* gen. nov. (Cestoda: Cyclophyllidea)]. *Izvestiya Akademii Nauk Tadzhikskoy SSR. Otdelenie Sel'skokhozyaistvennikh i Biologicheskikh Nauk*, No. 2: 113-118. (In Russian).
- SPASSKII, A. A. & SPASSKAYA, L. P. 1973. [Genus *Schmidneila* gen. n. (Cestoda: Metadilepididae)]. *Izvestiya Akademii Nauk Moldavskoy SSR. Seriya Biologicheskikh i Khimicheskikh Nauk*, No. 1: 58-60. (In Russian).
- SPASSKII, A. A. & SPASSKAYA, L. P. 1977. [Brief summary of the phylogenetic analysis of two tribes of dilepidid tapeworms: Dilepidini and Laterotaeniini] (pp. 3-30). In: SPASSKII, A. A., SHUMILO, R. P. & KHARSUN, A. I. (eds). *Ekto- i endoparazity zhivotnykh Moldavii. Izdatel'stvo Shtiintsa, Kishinev*, 180 pp. (In Russian).
- STOITSOVA, S. R., GEORGIEV, B. B., DACHEVA, R. B., VINAROVA, M. I. 1997. Scolex glands associated with the rostellum in three species of the Dilepididae (Cestoda: Cyclophyllidea). *Acta Zoologica, Stockholm* 78: 187-193.
- WOLTERS, H. A. 1982. Die Vogelarten der Erde. Eine systematische Liste mit Verbreitungsangaben sowie deutschen und englischen Namen. *Paul Parey Verlag, Hamburg*, 745 pp.
- YAMAGUTI, S. 1959. Systema helminthum. Volume II. The cestodes of vertebrates. *Interscience Publishers, New York & London*, 860 pp.