



Taxonomic revision of *Tatria* Kowalewski, 1904 (Cestoda: Amabiliidae): redescriptions of *T. appendiculata* Fuhrmann, 1908 and *T. duodecacantha* Olsen, 1939, a key and an amended diagnosis of *Tatria* (*sensu stricto*)

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Abstract

Tatria appendiculata Fuhrmann, 1908 is redescribed on the basis of syntypes from *Tachybaptus dominicus* in Brazil and voucher specimens from the same host species in Cuba previously recorded by Rysavy & Macko (1971). Paratypes of *T. duodecacantha* Olsen, 1939 from *Podilymbus podiceps* in the USA are also redescribed and, in contrast with the opinion of Ryzhikov & Tolkacheva (1981), the species is recognised as valid. The major reliable diagnostic characters of *Tatria* and the distinguishing criteria applicable at the species level are re-evaluated. An amended generic diagnosis of *Tatria* (*sensu stricto*) and an identification key to its constituent species are presented.

Introduction

In our previous publication (Vasileva et al., 2003), three species of *Tatria* Kowalewski, 1904 were described and discussed on the basis of specimens from Palaearctic grebes (Aves: Podicipedidae). The aim of this paper is to present redescriptions of the remaining two species, *T. appendiculata* Fuhrmann, 1908 and *T. duodecacantha* Olsen, 1939, parasites of grebes from South and North America. The current observations on the morphology of the species of *Tatria* (*sensu stricto*) (Vasileva et al., 2003; present study) have enabled a re-evaluation of the useable diagnostic criteria relevant at both generic and species levels.

Materials and methods

This study is based on a re-examination of the type-specimens of two species of *Tatria* from the parasitological collections of the Museum für Naturkunde, Berlin (MNKB) and the Harold W. Manter Laboratory of Parasitology, University of Nebraska, Lincoln (HWML). As comparative material, specimens of *Ta-*

tria appendiculata from the collection of the Parasitological Institute of the Slovak Academy of Sciences, Košice (PIK) were also examined. Details of the hosts, localities and collection numbers are given below for each species.

Syntypes of *T. appendiculata* from *Tachybaptus dominicus* (L.) (= *Podiceps dominicus*) at Ipanema, Brazil (MNKB) were received as dried out material. The specimens were re-hydrated in a weak tribasic sodium phosphate solution for about an hour and preserved in 80% ethanol. Subsequently, 12 specimens and a few fragments of strobila were stained in iron acetocarmine (Georgiev et al., 1986), dehydrated in an ascending alcoholic series, cleared in creosote and mounted in Canada balsam. Four whole specimens were mounted in Berlese's medium in order to facilitate the observations of the rostellar hooks and cirrus armament. The remaining specimens (about 15) were preserved in 80% ethanol.

The terms 'rhynchus' and 'rostelloid type' of rostellar hooks are used in accordance with the terminology proposed by Vasileva et al. (2003). The following measurements of the rostellar hooks were taken: the total length of the hook; the length of the blade (mea-

sured from its base to the tip); the length of the base (distance between guard-tip and handle-tip); and the distance between blade-tip and guard-tip. The metrical data are given as the range, with the mean in parentheses, and the number of measurements taken (n). The measurements are given in micrometres unless otherwise stated.

***Tatria appendiculata* Fuhrmann, 1908**

Specimens studied

From *Tachybaptus dominicus*, syntypes, Ipanema, Brazil (MNKB 2511); 12 mature specimens and about 5 fragments of strobila, stained whole-mounts (5 slides); 4 whole specimens mounted in Berlese's medium; voucher specimens, Cuba, Reserve Jazero, 1968, identified by J.K. Macko (PIK 1911f, i, h, n), 10 mature specimens (6 of them with damaged strobila) and 4 fragments of strobila, stained in Semichon's carmine and mounted in Canada balsam (4 slides), reported by Rysavy & Macko (1971).

Redescription of syntypes (Figures 1–6)

Strobila (Figure 1) small, wedge-shaped, with maximum width at level of last proglottides; lateral processes well developed, very long in last and detached proglottides. Scolex (Figures 2,5) triangular, with conical anterior protrusion; scolex entirely covered by small spines; surface of scolex surrounding posterior margins of suckers covered with slightly larger, densely distributed, triangular spines with maximum length 1–3 (Figure 5). Suckers large, elliptical, muscular, covered with fine punctiform spines. Rhynchus (partly everted) conical; accessory hooks and spines not visible. Rostellum armed with single crown of 10 small, rostelloid hooks (Figure 3). Neck short, covered with small spines. Proglottides (Figure 1) craspedote, wider than long at all stages of development. Male genital pores regularly alternating, open close to anterior proglottis margin. Evaginated cirrus (Figure 6) cylindrical, slightly tapering distally, armed by small triangular spines, slightly longer and more sparsely distributed in median region of cirrus; distal end almost unarmed.

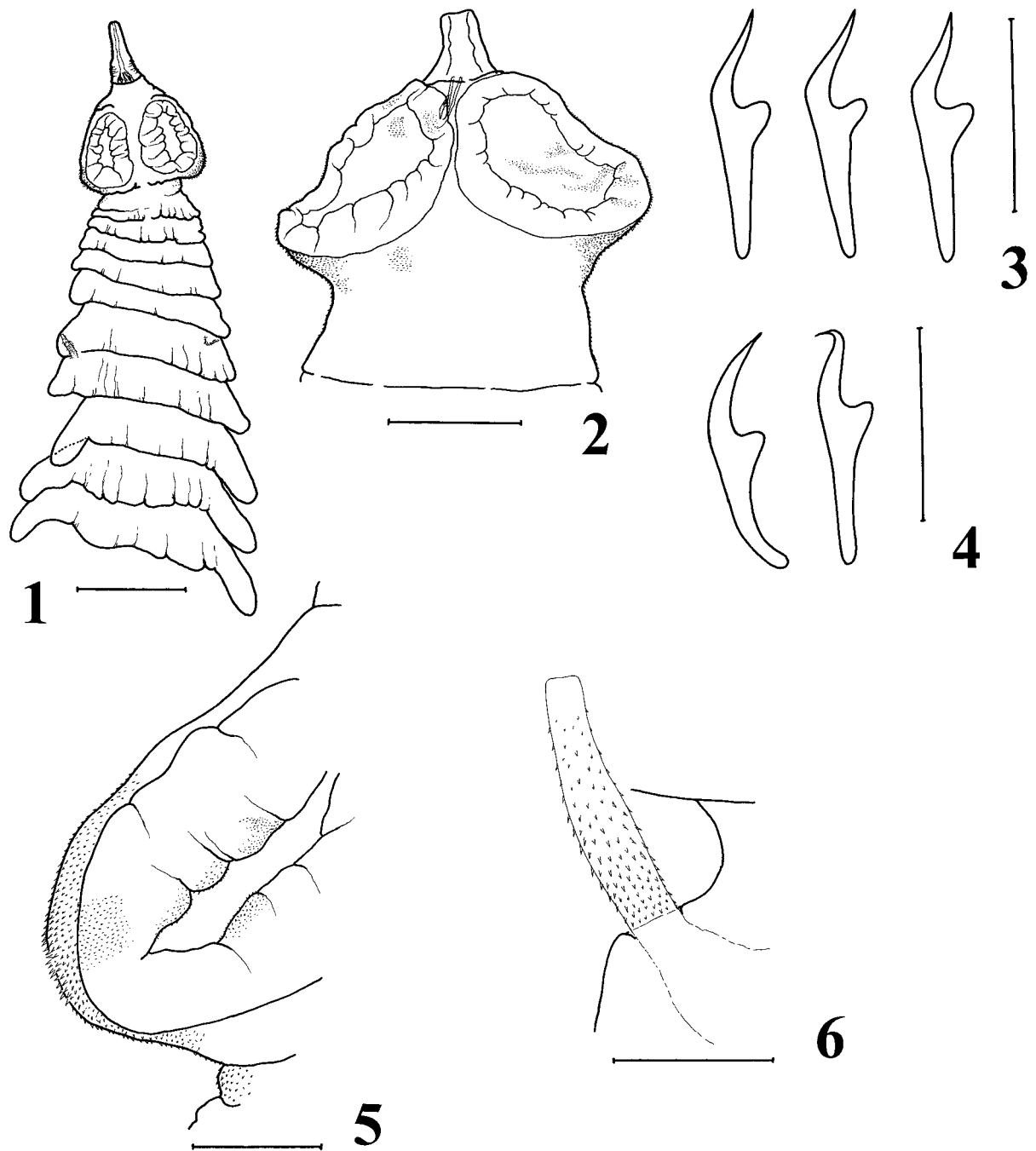
Measurements. See Table 1. Additional measurements: length of rhynchus (partly everted) 35–65 (51, n=4); minimum width of rhynchus 8–13 (10, n=4); rostellar hooks: length of blade 9–11 (10, n=8), length of base 16–18 (17, n=8), distance between blade-tip

and guard-tip 9–11 (10, n=8); neck length 39–55 (45, n=6), minimum width 62–91 (78, n=6).

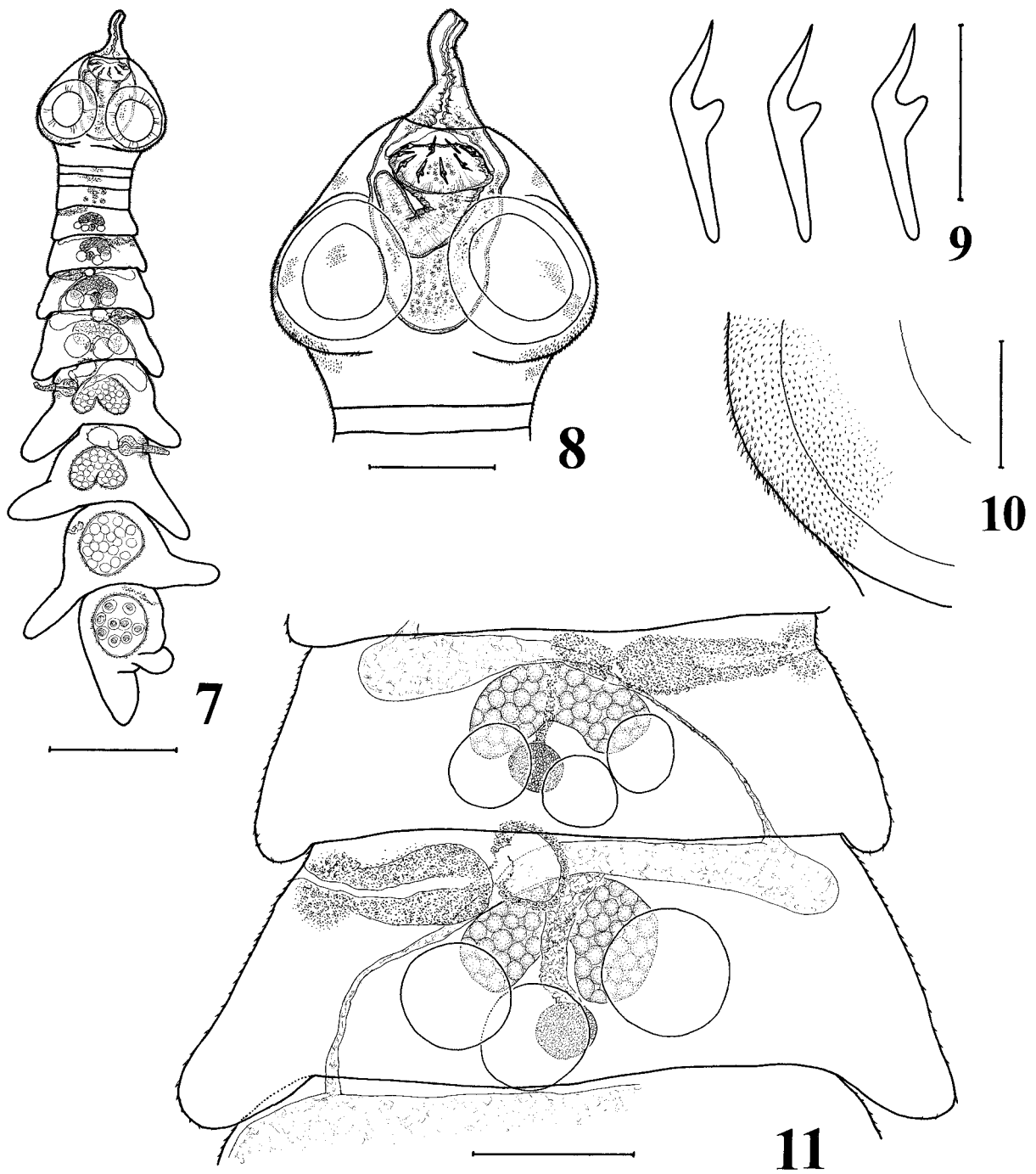
Redescription of voucher specimens from T. dominicus in Cuba (Figures 7–15)

Strobila (Figure 7) small, wedge-shaped, with well-developed lateral processes; maximum width at level of pregravid proglottides. Scolex (Figure 8) almost triangular, with rounded posterior portion and conical anterior protrusion; entire surface of scolex covered with small spines; surface of scolex surrounding posterior margins of suckers covered with slightly larger triangular spines (Figure 10). Suckers large, oval, muscular; entire surface covered with small punctiform spines. Rostellum elongate, thick-walled, very muscular, with apical enlargement at level of crown provided with strong musculature; intensely staining glandular cells present in rostellar cavity. Rostellar sheath thin-walled, does not usually reach posterior margins of suckers, contains intensely staining glandular masses. Rhynchus (partly everted) elongate (Figure 8); entire surface covered with small triangular accessory spines; when rhynchus retracted, small bulb-like protrusible swelling situated anteriorly to level of crown (Figure 8). Rostellum armed with single crown of 10 small rostelloid hooks (Figure 9). Neck short, entirely covered with small triangular spines. Proglottides (Figures 11,12,14) craspedote, wider than long at all stages of development. Small triangular, readily visible spine-like microtriches cover almost entire surface of immature and mature proglottides (Figures 11,12); surface of lateral processes of pregravid and gravid proglottides without spine-like microtriches. Male genital pores regularly alternating, open in anterior third of lateral proglottis margin. Male genital atrium (Figure 13) cylindrical, surrounded by intensely staining cells. Dorsal and ventral osmoregulatory canals not visible.

Strobila with slightly expressed protogynous development and rapid maturation. Female genital primordia appear in 1st-2nd proglottides. Ovary (Figure 11) compact, almost horseshoe-shaped or with 2 indistinct lobes connected by very wide isthmus, ventral to testes, median, fully-developed in 6th-7th proglottides. Vitellarium (Figure 11) compact, oval, posterior to ovarian isthmus, usually slightly antiporal, between middle and antiporal testes. Seminal receptacle (Figures 11,12) not well differentiated, sac-like, thin-walled, transversely-elongate, situated close to anterior proglottis margin. In well-developed her-



Figures 1–6. *Tatria appendiculata* Fuhrmann, 1908, syntype specimens. 1. General view of strobila. 2. Scolex. 3. Rostellar hooks in strict lateral position. 4. Rostellar hooks with deformations in shape. 5. Detail of scolex with armament on its posterior surface. 6. Evaginated cirrus. Scale-bars: 1, 100 μm ; 2, 50 μm ; 3–6, 20 μm .



Figures 7–11. *Tatria appendiculata* Fuhrmann, 1908, voucher specimens from Cuba. 7. General view of strobila. 8. Scolex. 9. Rostellar hooks. 10. Detail of scolex with armament on its posterior surface. 11. Mature 'female' proglottides. Scale-bars: 7, 250 μm ; 8, 100 μm ; 9, 10, 20 μm ; 11, 50 μm .

Table 1. Metrical and meristic data for *Tatria appendiculata* Fuhrmann, 1908 from *Tachybaptus dominicus*.

Locality		Brazil				Cuba			
Source		Fuhrmann (1908)	Present study		Rysavy & Macko (1971)		Present study		
		Range	Range	Mean	n	Range	Range	Mean	n
Strobila:	length (mm)	0.8–1.1	0.509–0.828	0.608	8	1.268–2.120	0.938–1.426	1.169	3
	width (mm)	0.340–0.450	0.235–0.305	0.274	8	0.392–0.530	0.289–0.385	0.353	3
	N	16–20	10–15	12	8	14–19	10–13	12	5
Scolex:	length	–	103–164	129	6	–	249–386	300	6
	width	–	115–174	141	6	308*	240–282	254	6
Suckers:	length	–	71–95	86	12	88–114	114–135	119	20
	width	–	47–62	54	12	–	96–126	108	20
Rostellum:	length	–	–	–	–	–	104–113	109	3
	max. width	–	–	–	–	61–75	72–81	76	4
Rostellar sheath:	length	–	–	–	–	–	146–165	156	5
	width	–	–	–	–	–	95–113	102	5
Rostellar hooks	total length	27	26–27	27	8	22–24	23–25	24	32
Lateral processes	max. length	–	95–199	157	25	176–220	93–135	122	10
Ovary	max. width	–	–	–	–	39–58	72–85	78	7
Vitellarium	diameter	–	–	–	–	15	21–28	24	10
Testes:	number	–	–	–	–	3	3	–	7
	diameter	–	–	–	–	20–27	45–53	48	16
ESVpp:	length	–	–	–	–	–	49–76	57	10
	width	–	–	–	–	20–27	36–47	41	10
Cirrus-sac:	length	80	–	–	–	39–54	34–43	38	10
	width	–	–	–	–	20–28	28–40	35	10
Evaginated cirrus:	length	100	32–41	35	5	79	21–70	46	10
	width	–	8–9	8	5	13	11–17	14	10
Embryophore:	diameter	40	–	–	–	35–40	36–38	37	10
Oncosphere:	diameter	–	–	–	–	–	19–21	20	10

*Maximum width of scolex in whole-mounted specimen; maximum width of scolex in fresh specimens 193–237 μm (Rysavy & Macko, 1971).

Abbreviations: N, number of proglottides; ESVpp, prostatic part of external seminal vesicle.

maphroditic proglottides (Figure 12) seminal receptacle is full of sperm, voluminous sac-like organ, situated in antiporal half of proglottis, close to anterior proglottis margin. Seminal receptacles of neighbouring mature proglottides connected to each other via thin sigmoid accessory canal (Figures 11,12). Accessory canal follows course from seminal receptacle in poral and posterior direction, then passes posteriorly and ventrally to cirrus-sac, turns posteriorly at level of testes, crosses posterior proglottis margin and joins with seminal receptacle of subsequent proglottis.

Testes (Figures 11,12) oval, compact, with primordia usually appearing in 3rd proglottis, fully-developed in 7th–8th proglottides, posterior to ovary in median field of proglottis, usually arranged in shallow triangle, rarely in one indistinct row. External seminal vesicle (Figures 12,13) with 2 parts; pre-

bursal part short, thin-walled, adjacent to antiporal end of cirrus-sac; prostatic part elliptical or oval, surrounded by thin sleeve of glandular cells; usually, parts join immediately after they become full of sperm and form common seminal reservoir. Cirrus-sac (Figure 13) thin-walled, pyriform, with very short cylindrical poral region and rounded antiporal region, close to anterior proglottis margin. Ejaculatory duct slightly curved, surrounded by intensely staining glandular cells. Cirrus-sac and external seminal vesicle without common outer sheath. Evaginated cirrus (Figure 13) cylindrical, usually slightly tapering distally; almost entire surface armed by dense, triangular spines, slightly longer in median region; distal end of fully-evaginated cirrus almost unarmed. Cirrus extirpated after traumatic copulation.

Uterus and ovary never seen together in same proglottis. Uterus (Figures 12,14) first appears in 7th–8th proglottides, just after disappearance of ovary. Young and developing uterus (Figure 12) horseshoe-shaped; gravid uterus (Figure 14) oval, sac-like, thick-walled, occupies entire median field of proglottis, surrounded by thin sleeve of intensely staining cells, usually contains small number of ripe eggs. Eggs (Figure 15) with thin transparent outer shell. Embryophores elliptical, thick-walled; oncospheres oval or elliptical, thin-walled.

Measurements. See Table 1. Additional measurements: length of rhynchus (partly everted) 91–150 (115, n=4); minimum width of rhynchus 15–27 (19, n=4); rostellar hooks: length of blade 9–10 (9, n=32), length of base 15–16 (15, n=32), distance between blade-tip and guard-tip 8–9 (8, n=32); neck length 18–28 (22, n=6), minimum width 147–192 (165, n=6); eggs: diameter of outer shell 60–66 (64, n=10); length of embryonic hooks 8–9 (8, n=10).

Remarks

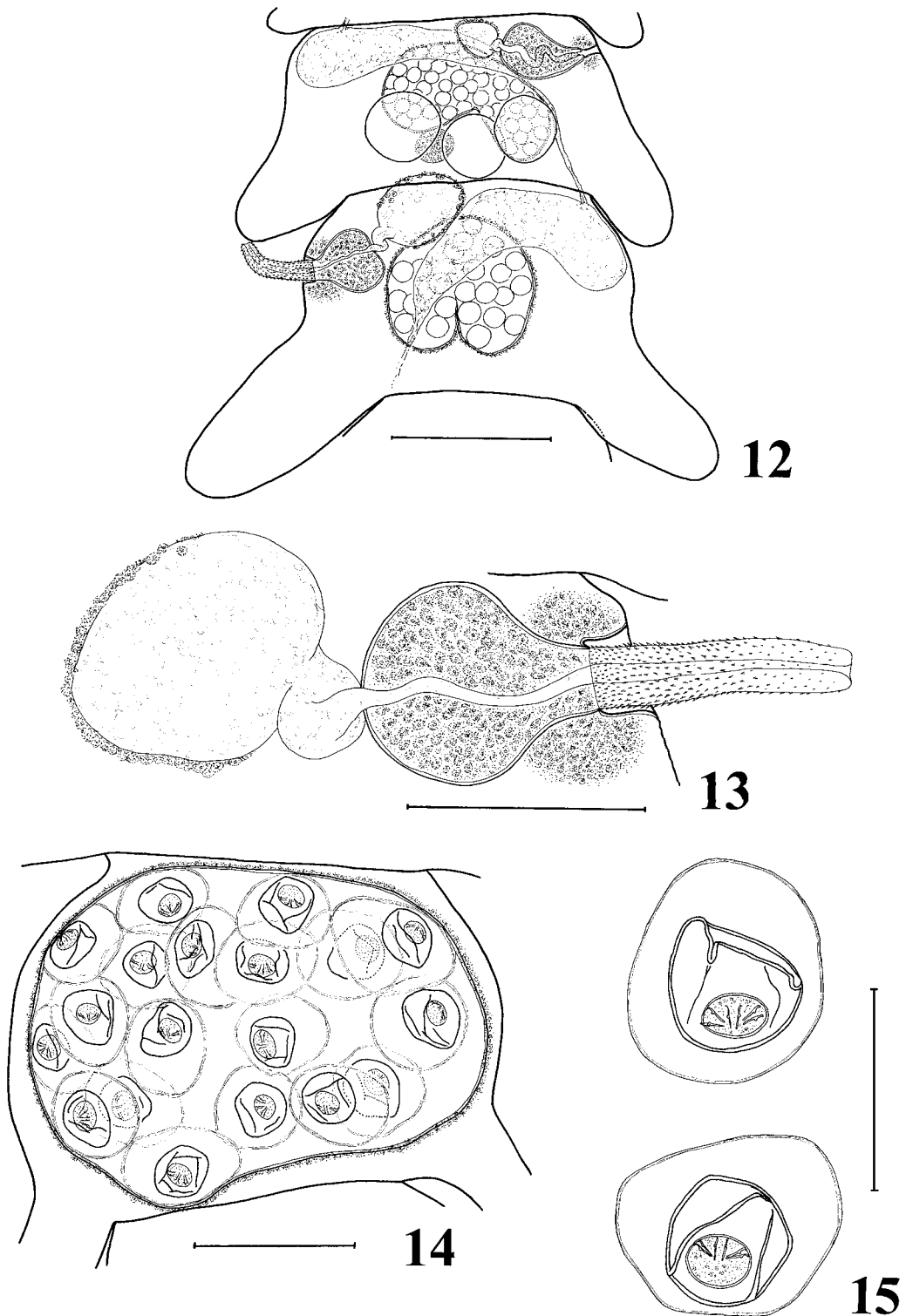
Unfortunately, despite rehydration, the syntype specimens of *T. appendiculata* were in poor condition and the morphology of the rostellum, rostellar sheath, osmoregulatory system and genital organs and their state of development could not be seen. Nevertheless, for the most part, the present observations on the syntypes and the metrical data (see Table 1) agree well with the brief original description of the species (Fuhrmann, 1908). We observed specimens with fewer proglottides in the strobila as compared with Fuhrmann's (1908) description, but this can be explained as a result of the drying of the material. Moreover, we found numerous detached and damaged proglottides in the vial. There is, however, one very important difference in the shape of the rostellar hooks. Judging by figure 57 of Fuhrmann (1908), the hook of *T. appendiculata* has a blade curved in the direction of the guard. This was previously observed and mentioned by Olsen (1939). Our observations of the syntypes indicate that the rostellar hooks, which are mounted laterally on the slide, have a straight blade or it is slightly curved away from the guard (see Figure 3). The rostellar hooks of *T. appendiculata* have a rostelloid shape. In some of the specimens, the hooks are not aligned laterally on the slides, such that their shape becomes deformed (see Figure 4) and their blades can be seen in different positions; an example is the hook illustrated in Fuhrmann's figure 57 (Fuhrmann, 1908).

The present comparative study demonstrates that the voucher specimens of Rysavy & Macko (1971) from *Tachybaptus dominicus* in Cuba are very similar to the syntypes of *T. appendiculata*. They possess a similar strobila, the same type of spines on the surfaces of the scolex and suckers, and a similar shape of the rostellar hooks and cirrus. The metrical data also correspond well (see Table 1). There are a few differences in the measurements of the scolex and suckers, which are larger in the specimens from Cuba, but this can be explained by possible changes in the length and width of the scoleces of the syntype specimens during drying or by the method of fixation of the specimens from Cuba. Moreover, Rysavy & Macko (1971) mentioned that the maximum width of the scolex in fresh material is considerably less than in whole-mounted specimens (see Table 1). The drying of the syntypes is a possible reason for the lack of the peculiar armament of spine-like microtriches on the tegument of the proglottides of the syntypes. This armament is readily visible in all of the voucher specimens from Cuba. The rostellar hooks of the syntypes are slightly longer than those of the Cuban specimens (26–27 μm versus 23–25 μm). Since their shape is very similar, we think this difference is within the limits of the intraspecific variation. The lateral processes of the last proglottides of the syntypes are slightly longer than those of the vouchers (see Figures 1,7; Table 1). The longest voucher specimen we re-examined had 13 proglottides only. Rysavy & Macko (1971) described specimens with 14–19 proglottides and their figure 21 illustrates a gravid specimen with considerably longer lateral processes, compared with those of the vouchers studied by us. The present observations on the specimens of *T. appendiculata* from Cuba correspond almost completely with the description of Rysavy & Macko (1971). There is only one exception, the shape of the ovary is compact but not multi-lobed, as previously described.

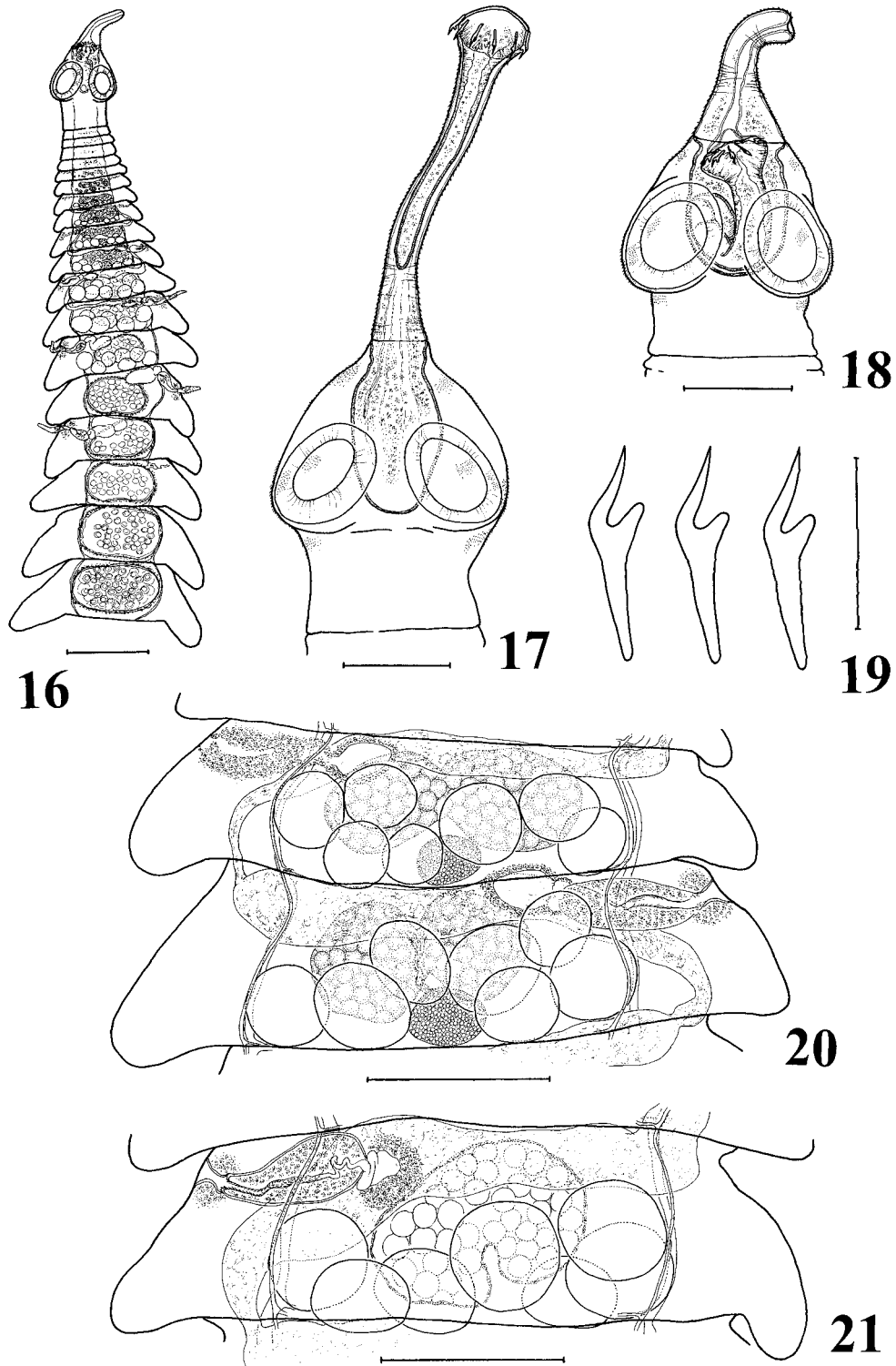
Tatria duodecakantha Olsen, 1939

Specimens studied

From *Podilymbus podiceps* (L.), paratypes, Iowa, USA (NWML 21651); 4 mature and 3 gravid specimens, stained and mounted in Canada balsam (6 slides).



Figures 12–15. *Tatria appendiculata* Fuhrmann, 1908, voucher specimens from Cuba. 12. Proglottides with developing uterus. 13. Male terminal ducts. 14. Gravid proglottis. 15. Eggs. Scale-bars: 12,14, 100 μm ; 13,15, 50 μm .



Figures 16–21. *Tatria duodecacanthe* Olsen, 1939, paratype specimens. 16. General view of strobila. 17. Scolex with fully everted rhynchus. 18. Scolex with partly everted rhynchus. 19. Rostellar hooks. 20. Mature 'female' proglottides. 21. Mature 'hermaphroditic' proglottis. Scale-bars: 16, 250 μm ; 17,18, 20,21, 100 μm ; 19, 20 μm .

Redescription (Figures 16–25)

Strobila (Figure 16) wedge-shaped, with wide well-developed lateral processes; maximum width at level of last proglottides. Scolex (Figures 17,18) almost triangular, with well-developed anterior conical protrusion; small spines cover surface of scolex anterior to suckers and at level of posterior third of suckers. Suckers elliptical, muscular; entire surface covered with punctiform spines. Rostellum highly elongate, thick-walled, muscular, with apical enlargement at level of crown provided with strong musculature; intensely staining glandular cells present in rostellar cavity. Rostellar sheath thin-walled, does not usually reach posterior margins of suckers, contains intensely staining glandular masses. Rhynchus highly elongate (Figure 17); entire surface covered with small triangular accessory spines; apical end of rhynchus with enlarged tegumental pad; when rhynchus retracted, small bulb-like protrusible swelling situated anteriorly to level of crown (Figure 18). Rostellum armed with single crown of 12 small rostelloid hooks (Figure 19). Neck short, covered anteriorly with fine, punctiform spines. Proglottides (Figures 20–22, 24) craspedote, wider than long at all stages of development. Male genital pores regularly alternating, open in anterior third of lateral proglottis margin. Male genital atrium (Figure 23) cylindrical, thick-walled, surrounded by intensely staining cells; when cirrus evaginated, atrium sometimes forms very short genital papilla (Figure 23). Genital ducts pass between dorsal and ventral poral osmoregulatory canals. Dorsal and ventral osmoregulatory canals with transverse anastomoses along posterior margin of proglottis.

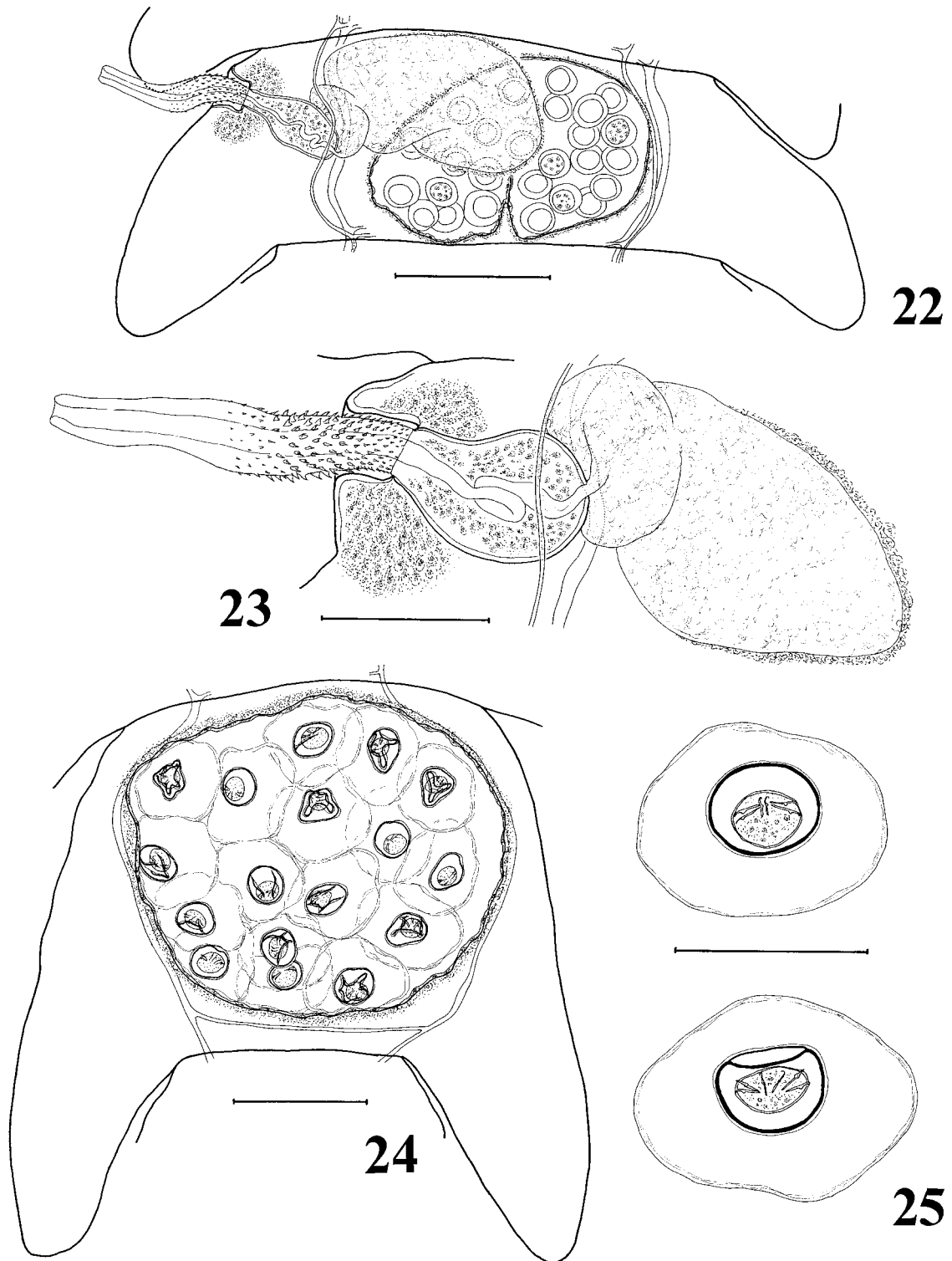
Strobila with slightly expressed protogynous development. Female genital primordia appear in 3rd–4th proglottides. Ovary (Figure 20) with 2 transversely elongate or oval lobes connected by wide isthmus, ventral to testes, median, fully-developed in 10th–11th proglottides. Vitellarium (Figure 20) compact, oval, median, posterior to ovarian isthmus, dorsal to ovary and ventral to testes. Seminal receptacle not well differentiated, sac-like, thin-walled, transversely elongate, situated close to anterior proglottis margin, dorsally to ovary and uterus; in well-developed hermaphroditic proglottides (Figure 21), seminal receptacle full of sperm, sac-like and voluminous. Seminal receptacles of neighbouring mature proglottides connected to each other via wide sigmoid canal (Figures 20,21), which follows course from seminal receptacle in poral and posterior direction, then passes

ventrally to cirrus-sac, between dorsal and ventral poral osmoregulatory canals; at level of testes, canal turns posteriorly in poral lateral field, crosses posterior proglottis margin and joins with seminal receptacle of subsequent proglottis; in well-developed hermaphroditic proglottides (Figure 21), seminal receptacles and sigmoid canal form common voluminous seminal duct.

Testes (Figures 20,21) oval, compact, with primordia appearing in 5th–6th proglottides, fully-developed in 12th–14th proglottides, situated dorsally to female organs in posterior half of median field of proglottis, arranged in 2 groups, 3–4 porally and 3–4 antiporally to vitellarium; lateral testes usually overlap osmoregulatory canals. External seminal vesicle (Figures 22,23) with 2 well-differentiated parts; prebursal part small, oval or elliptical, thin-walled, adjacent to antiporal end of cirrus-sac; prostatic part elliptical, elongate, surrounded by thick sleeve of large glandular cells; with further maturation, 2 parts of seminal vesicle remain distinct (Figures 22,23). Cirrus-sac (Figure 23) thin-walled, elongate-pyriform, with short cylindrical poral region and rounded antiporal region, close to anterior proglottis margin, usually crosses poral osmoregulatory canals, passing between them. Ejaculatory duct convoluted, surrounded by intensely staining gland-cells. Cirrus-sac and external seminal vesicle without common outer sheath. Evaginated cirrus (Figure 23) cylindrical, usually slightly enlarged in median region and tapering distally; basal portion armed with dense, small, triangular spines; median region of proximal half of cirrus covered with more sparsely distributed larger rosethorn-shaped spines arranged in spiral rows; almost entire distal half of fully-evaginated cirrus unarmed; cirrus extirpated after traumatic copulation.

Uterus and ovary never seen together in same proglottis. Uterus (Figures 21,22) first appears in 11th–12th proglottides, just after disappearance of ovary. Young and developing uterus (Figures 21,22) horseshoe-shaped, with thick walls which consist of large, flattened, intensely staining cells; gravid uterus (Figure 24) oval, sac-like, thick-walled, occupies entire median field of proglottis, surrounded by thin sleeve of intensely staining cells. Eggs (Figure 25) with thin transparent outer shell. Embryophores elliptical, with thick walls, consist of thick refractive internal layer and very thin external covering. Oncospheres oval or elliptical, thin-walled.

Measurements. See Table 2. Additional measurements: length of rhynchus (partly everted) 110–158 (142, n=5); length of rhynchus (fully everted) 268–



Figures 22–25. *Tatria duodecakantha* Olsen, 1939, paratype specimens. 22. Proglottis with developing uterus. 23. Male terminal ducts. 24. Gravid proglottis. 25. Eggs. Scale-bars: 22,24, 100 μm ; 23,25, 50 μm .

316 (n=2); minimum width of rhynchus 24–32 (28, n=7); rostellar hooks: length of blade 9–11 (10, n=15), length of base 16–19 (17, n=15), distance between blade-tip and guard-tip 6–8 (8, n=15); neck length 50–85 (73, n=7), minimum width 126–189 (146, n=7); diameter of osmoregulatory canals: ventral 5–8 (7, n=10), dorsal 2–5 (3, n=10); eggs: diameter of outer shell 66–73 (69, n=10); embryophore 27–34 × 22–30 (31 × 25, n=10); diameter of oncosphere 16–19 (18, n=10); length of embryonic hooks 8–9 (8, n=10).

Remarks

This species was originally described by Olsen (1939) from *Podilymbus podiceps* in Iowa. One year later, Schultz (1940) recorded it from the same host species in Oklahoma and provided new data on the morphology of the female genital ducts. The present observations on *T. duodecakantha* are in good correspondence with both previous descriptions, including the metrical data (see Table 2). There are a few differences concerning the presence of an armament on the scolex surface, the presence of small spines covering the entire surface of the suckers and the lack of an internal seminal vesicle. The present results give new information on the structure of the external seminal vesicle, which consists of two well-differentiated parts, and on the morphology of the eggs. Olsen (1939) reported the presence of a vagina in *T. duodecakantha*, observed by him in transverse serial sections. We did not have the opportunity to re-examine the slides with sections of the type-specimens. However, our observations on the whole-mounted paratypes showed that this species lacks a real, well-differentiated vagina, as is the case for all species of the Amabiliidae (Ryzhikov & Tolkacheva, 1981; Jones, 1994). The seminal receptacles of the neighbouring mature proglottides in the strobila connect to each other via a wide, sigmoid canal, which follows a course from the seminal receptacle in a poral and posterior direction, passing ventrally to the cirrus-sac. It is likely that the region of the sigmoid seminal canal in the poral lateral field was visible in the serial sections and interpreted by Olsen (1939) as a vagina. Schultz (1940) observed a penetrated cirrus in the posterior margin of the adjacent lateral enlargement of the preceding proglottis. He considered this as an indication for the presence of “a posterolateral vaginal pore contralateral to the male pore of the same proglottis” (Schultz, 1940). However, this author did

not observe this pore or a vaginal canal connecting it with the seminal receptacle, and neither did we.

Ryzhikov & Tolkacheva (1981) considered this species to be a synonym of *T. appendiculata*. In contrast with their opinion, the present study has confirmed that these two species differ significantly from each other in the length, development and armament of the strobila, the shape and armament of the scolex, the number of testes, the shape and width of the ovary, the shape of the seminal receptacles and the length and armament of the cirrus. In addition, *T. duodecakantha* has 12 rostellar hooks and *T. appendiculata* only 10. On this basis, we recognise *T. duodecakantha* as a valid species.

Neylans (1952) reported *T. duodecakantha* from *Podilymbus podiceps* in Georgia, USA. Since this record lacks any morphological data on the specimens studied, it cannot be confirmed.

Previously, *T. duodecakantha* has only been reported from *P. podiceps* in the Nearctic and it can be considered as a specific parasite of this grebe species.

Discussion

Generic level

The original generic diagnosis of *Tatria* (see Kowalewski, 1904) is very brief and was based mainly on the description of *T. biremis* Kowalewski, 1904. This author decided that two previously described species should be included in the new genus, i.e. *Taenia acanthorhyncha* Wedl, 1855 and *T. scolopendra* Diesing, 1856, although Kowalewski (1904) considered the latter as a ‘*species inquirenda*’. The following important features of *Tatria* were included in the original diagnosis: proglottides with long lateral processes; rostellum armed at its apex with crown of few larger hooks and with its surface covered by numerous small hooks, arranged in circles; single genital organs, relatively few testes, two seminal vesicles; compact ovary, seminal receptacles situated in mid-line of strobila and connected to each other by sigmoid vaginal canal, and thick-walled uterus. Later, numerous other species of *Tatria* have been described (Fuhrmann, 1908, 1913; Olsen, 1939; Tretjakova, 1948; Mathevossian & Sailov, 1963; Borgarenko et al., 1972; Rees, 1973; Korpaczewska & Sulgostowska, 1974; Ryzhikov & Tolkacheva, 1981), including species with characters differing from the original diagnosis (Okorokov, 1956; Mathevossian & Okorokov, 1959).

Table 2. Metrical and meristic data for *Tatria duodecantha* Olsen, 1939 from *Podilymbus podiceps* in the USA.

Locality Source		Iowa Olsen (1939) Range	Oklahoma Schultz (1940)* Range	Iowa Present study Range	Mean	n
Strobila:	length (mm)	2.3	2.0	1.9–2.7	2.2	6
	width (mm)	0.57	0.46	0.56–0.64	0.60	6
	N	20	14	19–22	21	6
Scolex:	length	162	309–442	284–509	354	7
	width	171–250	230–255	189–237	207	7
Suckers:	length	106–180	109–123	95–112	104	10
	width	76–83	68–77	62–85	74	10
Rostellum:	length	266–380	154–168	227–262	–	2
	max. width	57–76	73	63–76	69	5
Rostellar sheath:	length	–	164	110–199	160	6
	width	–	105	71–92	82	6
Rostellar hooks:	number	10–13	12	12	–	6
	total length	25–27	27–29	24–27	25	15
Ovary	max. width	133	147	129–150	140	5
Vitellarium	diameter	24	34	28–33	30	7
Testes:	number	6–9	7	7	–	10
	diameter	38–46	34–39	54–79	67	15
ESVpb	diameter	–	–	24–44	35	6
ESVpp:	length	50–68	59–77	87–156	111	7
	width	30–38	44–55	44–79	64	7
Cirrus-sac:	length	80–87	95–98	60–82	73	10
	width	30–38	39–41	30–39	34	10
Evaginated cirrus:	length	–	68	47–114	84	7
	width	–	18	17–21	18	7

*Measurements of the specimens were re-calculated on the basis of figures 1–4 and 6 of Schultz (1940).
Abbreviations: N, number of proglottides; ESVpb, prebursal part of external seminal vesicle; ESVpp, prostatic part of external seminal vesicle.

As a result, *Tatria* became a composite genus. In the most recent taxonomic revision of the Amabiliidae, Ryzhikov & Tolkacheva (1981) considered some of the previously described *Tatria* spp. as belonging to *Schistotaenia* Cohn, 1900.

Spassky (1947) erected *Joyeuxilepis* for *Echinorhynchoaenia biuncinata* Joyeux & Baer, 1943, described on the basis of a cysticeroid from ephemeroptera in Morocco (Joyeux & Baer, 1943). Originally, this genus was included in the Hymenolepididae, and later Spassky & Spasskaya (1976) transferred it to the Amabiliidae. Following the previous observation of Rees (1973), Spassky & Spasskaya (1976) divided all known *Tatria* spp. into two groups on the basis of the different shape of their rostellar hooks. Ryzhikov & Tolkacheva (1981) did not agree with the transfer of *J. biuncinata* to the Amabiliidae and did not confirm the separating of the two groups within *Tatria*.

They proposed an amended generic diagnosis for *Tatria* (*sensu lato*), which included the characters of all known species, despite the differences in the shape of their rostellar hooks.

Recently, a taxonomic reorganisation of *Tatria* was proposed by Gulyaev & Tolkacheva (1987), Borgarenko & Gulyaev (1990) and Gulyaev (1990, 1992). The species of *Tatria* (*sensu lato*) with an aploparaksoid shape of the rostellar hooks and a protandrous development of the strobila were transferred to *Joyeuxilepis* Spassky, 1947, with the type-species *J. biuncinata* (Gulyaev & Tolkacheva, 1987; Borgarenko & Gulyaev, 1990). The remaining five species, possessing rostelloid rostellar hooks and a protogynous development of the strobila were left in *Tatria* (*sensu stricto*) with the type-species *T. biremis*. A new diagnosis of *Tatria* (*sensu stricto*) was proposed on the basis of the re-examination of the Palaearctic *Tatria*

spp. (Gulyaev, 1992). Borgarenko & Gulyaev (1990) abstained from proposing a new generic diagnosis for *Joyeuxilepis* because they found that the taxonomically significant characters of the remaining species of *Tatria (sensu lato)* need to be established. On the basis of this conclusion, Jones (1994) provisionally considered *Joyeuxilepis* as a synonym of *Tatria*, pending further investigation.

The current revision on *T. biremis*, *T. minor* Kowalewski, 1904, *T. appendiculata* and *T. duodecancantha*, the species included in *Tatria (sensu stricto)* by Gulyaev (1992), and *T. gulyaevi* Vasileva, Gibson & Bray, 2003 (Vasileva et al., 2003; present study) has demonstrated that they are characterised by numerous common morphological features which distinguish them from other species of *Tatria (sensu lato)*. Most of these characters were included in the original diagnosis of *Tatria* by Kowalewski (1904). Moreover, our recent observations on the remaining species of *Tatria (sensu lato)* with aploparaksoid hooks show that *Joyeuxilepis* can be recognised as a valid genus on the basis of numerous additional morphological features. The results of this study will be a subject of another publication.

One of the main reliable characters at the generic level is the shape of the rostellar hooks. The hooks of all five species of *Tatria (sensu stricto)* have long, straight or slightly curved blades, straight handles of almost the same length as the blades or slightly longer, and well-developed guards which are considerably shorter than the blades. This shape conforms to the rostelloid shape of hook according to the classification of Spasskaya (1966). Another important generic character is the position of the osmoregulatory canals. In all of the examined *Tatria* spp., except for *T. appendiculata* in which the osmoregulatory system was not visible, both the dorsal and ventral osmoregulatory canals are at the same distance from the mid-line of the proglottides.

The species of *Tatria (sensu stricto)* are characterised by a protogynous development of the strobila, a compact bi-lobed ovary and an oval vitellarium. All of the species, except for *T. minor*, have sac-like and rather indistinct seminal receptacles situated close to the anterior margin of the proglottides. The male genital system in *Tatria* spp. tends to be similar; all species have a small number of testes which are fully mature in proglottides with a developing uterus, and all have a similarly shaped cirrus-sac (see Figure 17). One of the most important characters of the genus is the lack of a common sheath around the cirrus-sac and the ex-

ternal seminal vesicle. Another shared feature of the species examined is the presence of a well-developed, bi- or tripartite external seminal vesicle. In addition, the present study confirmed the presence of a thick-walled sac-like uterus in all species of *Tatria (sensu stricto)*. The pregravid uterus of *Tatria (sensu stricto)* spp. lacks sacculations and is surrounded by a sleeve of intensely staining cells.

T. skrjabini Tretjakova, 1948 was described from *Tachybaptus ruficollis* (Pallas) in the Trans-Urals (Chelyabinsk Region, Russia). Rees (1973) and Korpaczewska & Sulgostowska (1974) included it in the group of *Tatria* spp. possessing rostellar hooks with a handle longer than the guard. According to the very brief description of this species, it has very long rostellar hooks (171 μm) with blades which are curved ventrally and the tip of the handle has a small epiphyseal thickening (see figure 2 of Tretjakova, 1948). This shape of the hooks differs considerably from that of the hooks of true *Tatria* spp. and it is closer to the skrjabinoid shape (after Spasskaya, 1966), rather than to rostelloid. On this basis, Ryzhikov & Tolkacheva (1981) considered that this species probably belongs to *Lateriporus* Fuhrmann, 1907 (Dilepididae). In addition, incomplete data on the morphology of the gonads and genital ducts of this species do not provide sufficient grounds to include it in *Tatria (sensu stricto)*. We regard *T. skrjabini* as a species *incertae sedis* and consider that its taxonomic status needs further investigation.

The two most recent diagnoses of *Tatria* were proposed by Gulyaev (1992) and Jones (1994). The former emphasises a few key characters and lacks data on the rostellum, the rostellar sheath, the testes, the female genital organs, the terminal genital ducts and the structure of the eggs. The second diagnosis was based on the characters of *Tatria (sensu lato)* and thus contains the features of the species with aploparaksoid rostellar hooks, i.e. those included in *Joyeuxilepis* by Borgarenko & Gulyaev (1990). We consider that the clarification of the validity of *Joyeuxilepis* and the determination of reliable differentiating characters between these two related genera necessitate the elaboration of a detailed generic diagnosis for *Tatria (sensu stricto)*. On the basis of our observations on the species of *Tatria* the following amended diagnosis is proposed:

Tatria Kowalewski, 1904

Diagnosis: Strobila small, wedge-shaped, with protogynous development. Proglottides craspedote with well-developed, often digitiform lateral processes. Scolex triangular and conically protruded anteriorly, usually with armed surface. Suckers muscular, armed. Rostellum musculo-glandular, elongate, with apical muscular enlargement. Rostellar sheath sac-like, muscular. Rhynchus long, with apically enlarged tegumental pad, covered with small accessory hooks or spines. Rostellar hooks 10 or 12, with rostelloid shape. Genital pores regularly alternating. Genital ducts pass between ventral and dorsal osmoregulatory canals. Genital organs single. Osmoregulatory canals two pairs, with transverse anastomoses; dorsal and ventral canals at same distance from mid-line of proglottides. Ovary bi-lobed, rarely horseshoe-shaped, compact, median. Vitellarium oval, compact, postovarian, usually median. Seminal receptacle usually not well differentiated, sac-like or oval, close to anterior proglottis margin. Seminal receptacles of neighbouring mature proglottides connected to each other by accessory sigmoid or median longitudinal canal. Testes few (3–14), in two lateral groups or in two indistinct rows in posterior half of median field. Internal seminal vesicle usually absent. External seminal vesicle elongate, bi- or tripartite. Cirrus-sac small, pyriform; cirrus-sac and external seminal vesicle without common outer sheath. Cirrus cylindrical, armed. Copulation traumatic, followed by extirpation of cirrus. Uterus sac-like, initially bi-lobed or horseshoe-shaped, thick-walled, without sacculations, surrounded by sleeve of intensely staining cells. Eggs with thin outer shell; embryophores elliptical, thick-walled; oncospheres oval. In Podicipediformes; Europe, Asia, North and South America. Type-species *T. biremis* Kowalewski, 1904. Other species: *T. minor* Kowalewski, 1904 (syn. *T. mircia* Gulyaev, 1990), *T. gulyaevi* Vasileva, Gibson & Bray, 2003, *T. appendiculata* Fuhrmann, 1908 and *T. duodecakantha* Olsen, 1939.

Species level

Our observations on the species of *Tatria* (*sensu stricto*) provide morphological data which enable a re-evaluation of reliable diagnostic criteria useful at the species level.

(i) The basic characters for distinguishing species in this group are the number and the length of the rostellar hooks. All species have 10 rostellar hooks, except

for *T. duodecakantha*, which has 12. There is a difference in the length of the hooks, i.e. *T. biremis*, *T. minor* and *T. gulyaevi* have considerably longer hooks (av. 42–54 μm , see Vasileva et al., 2003) compared with those of *T. appendiculata* and *T. duodecakantha* (av. 23–27 μm , present study).

(ii) The shape of the seminal receptacles and the type of connection between them are also important distinguishing characters. The only species with well-differentiated oval seminal receptacles is *T. minor*. Those of the neighbouring mature proglottides of *T. biremis*, *T. minor*, *T. appendiculata* and *T. duodecakantha* connect to each other via a sigmoid accessory canal, but in *T. gulyaevi* they connect by a median longitudinal canal.

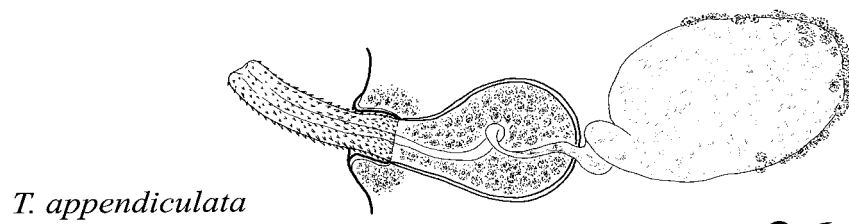
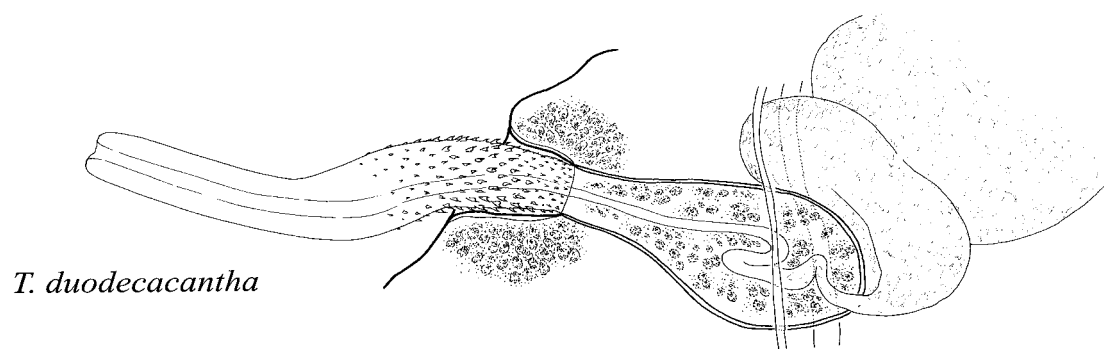
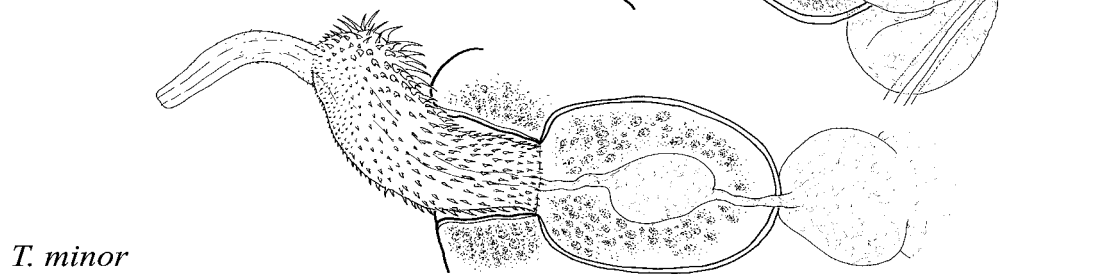
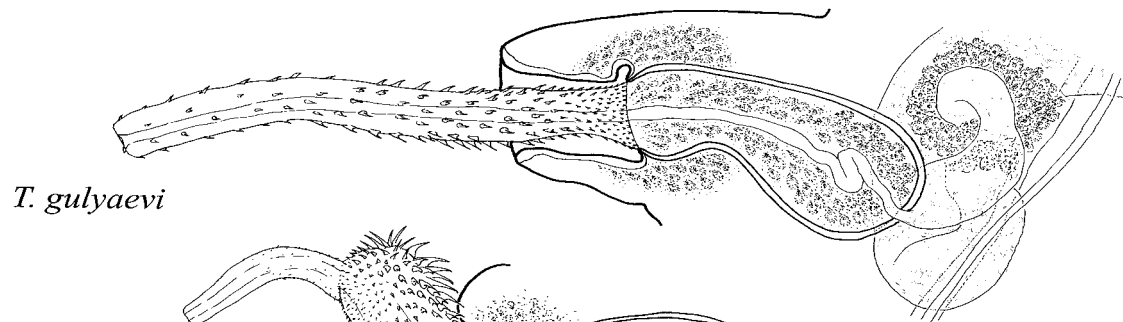
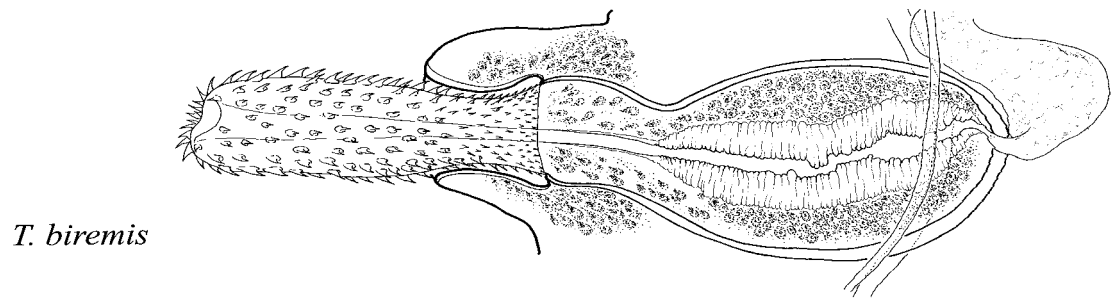
(iii) The number and the position of the testes can also be used as characters of taxonomic importance. *T. appendiculata* has three testes only, arranged in a shallow triangle. *T. biremis*, *T. duodecakantha* and *T. minor* have an average of six to nine testes, which are situated in two groups laterally to the vitellarium, whilst *T. gulyaevi* has 10–14 testes situated in two indistinct transverse rows. In relation to the features of the seminal vesicles, *T. minor* is the only species which has a well-differentiated internal seminal vesicle (see Figure 26). *T. gulyaevi* is characterised by the presence of a tripartite external seminal vesicle, whereas it is bipartite in the remaining species.

(iv) Another important character for distinguishing *Tatria* spp. is the structure of the evaginated cirrus (Figure 26). The species examined differ from each other in the shape, size and armament of the cirrus: powerful and distally enlarged in *T. biremis*; long, cylindrical and tapering distally but with a different type of armament in *T. gulyaevi*, *T. appendiculata* and *T. duodecakantha*; and with an asymmetrical enlargement in the middle region and a thin, cylindrical distal end in *T. minor*.

Using these differentiating characters, an identification key to the five species of *Tatria* (*sensu stricto*) is presented below.

Key to the species of the genus Tatria (sensu stricto)

- 1a. Rostellar hooks 12 *T. duodecakantha*
- 1b. Rostellar hooks 10 2
- 2a. Rostellar hooks 23–27 μm long; almost entire strobila covered with spine-like microtriches visible by light microscopy *T. appendiculata*



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Figure 26. Male terminal ducts of species of *Tatria* (*sensu stricto*). Scale-bar: 50 μ m.

- 2b. Rostellar hooks > 30 μm long; strobila without visible spine-like microtriches 3
- 3a. Testes 10–14 in number, in two indistinct transverse rows in posterior half of proglottis; seminal receptacles connected to each other via median longitudinal accessory canal *T. gulyaevi*
- 3b. Testes 6–9 in number, in two lateral groups in posterior half of proglottis; seminal receptacles connected to each other via sigmoid accessory canal 4
- 4a. Seminal receptacles not well differentiated, sac-like, thin-walled; cirrus symmetrically enlarged distally *T. biremis*
- 4b. Seminal receptacles well differentiated, oval, thick-walled; cirrus asymmetrically enlarged distally, ending with thin, almost unarmed, portion *T. minor*

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