*Systematic Parasitology* **56:** 219–233, 2003.



# Taxonomic revision of *Joyeuxilepis* Spassky, 1947 (Cestoda: Amabiliidae): redescriptions of *J. acanthorhyncha* (Wedl, 1855) and *J. fuhrmanni* (Solomon, 1932), a key and a new generic diagnosis

Gergana P. Vasileva[1,2], David I. Gibson[1] & Rodney A. Bray[1]
[1]*Parasitic Worms Division, Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK*
[2]*Permanent address: Central Laboratory of General Ecology, Bulgarian Academy of Sciences, 2 Gagarin Street, 1113 Sofia, Bulgaria*

Accepted for publication 10th June, 2003

**Abstract**

Two species of *Joyeuxilepis* Spassky, 1947 with 14 rostellar hooks are redescribed: *J. acanthorhyncha* (Wedl, 1855) on the basis of specimens from *Tachybaptus ruficollis* in Bulgaria and *J. fuhrmanni* (Solomon, 1932) on the basis of the holotype from 'coot' (= ? Podicipedidae) in Kenya. The critical analysis of the previous records of *J. acanthorhyncha* reveals that the host-range of this species includes *T. ruficollis*, *Podiceps nigricollis* and *P. grisegena*. The reliable diagnostic characters of *Joyeuxilepis* are re-evaluated. *J. biuncinata* (Joyeux & Baer, 1943), *J. acanthorhyncha*, *J. decacantha* (Fuhrmann, 1913), *J. pilatus* Borgarenko & Gulyaev, 1991, *J. fuhrmanni*, *J. uralensis* Gulyaev, 1989, *J. decacanthoides* Borgarenko & Gulyaev, 1991, *J. octacantha* (Rees, 1973), *J. azerbaijanica* (Matevosyan & Sailov, 1963) and *J. fimbriata* (Borgarenko, Spasskaya & Spassky, 1972) are recognised as valid species of *Joyeuxilepis*. A new generic diagnosis for this genus and an identification key to its constituent species are presented.

## Introduction

In our previous paper (Vasileva et al., 2003c), three similar species of *Joyeuxilepis* Spassky, 1947 with 10 rostellar hooks were re-described on the basis of specimens from Palaearctic grebes (Aves: Podicipedidae). The aim of this paper is to present redescriptions of two further species, which have 14 rostellar hooks, i.e. the widely-distributed and frequently recorded *J. acanthorhyncha* (Wedl, 1855) and a similar species, *J. fuhrmanni* (Solomon, 1932), which is known from its original material only. The current investigation on the morphology of the species of *Joyeuxilepis* (Vasileva et al., 2003c; present study) provided grounds for a re-evaluation of the reliable diagnostic characters of *Joyeuxilepis*, applicable at both the generic and species levels.

## Materials and methods

Specimens of *J. acanthorhyncha* were collected from the small intestine of one *Tachybaptus ruficollis* (Pallas), which was captured at the village of Krapec (the northern part of Bulgarian Black Sea coast) on 4th of April 1986 by members of the Parasite Biodiversity Group, Central Laboratory of General Ecology, Bulgarian Academy of Sciences. Cestodes were isolated from the intestines, relaxed in tap-water, fixed in 10% formalin solution and preserved in 70% ethanol. They were then stained in iron acetocarmine (Georgiev et al., 1986), dehydrated in an ascending alcoholic series, cleared in eugenol and mounted in Canada balsam. Some whole specimens were mounted in Berlese's medium in order to facilitate observations of the rostellar hooks and cirrus armament. Voucher material is deposited in The Natural History Museum, London and the remaining specimens are in the collection of Drs B.B. Georgiev and G.P. Vasileva.

The holotype of *J. fuhrmanni* from 'coot' in Kabete, Kenya from The British Museum (Natural History) Collection (BMNH) at The Natural History Museum, London, was re-examined.

As comparative material, voucher specimens of *J. acanthorhyncha* from *Tachybaptus ruficollis poggei* (Reichenow) in Taiwan from the Collection of the Harold W. Manter Laboratory of Parasitology, University of Nebraska, Lincoln were also re-examined.

The following specialised terms are used in the descriptions of the species: the term 'rhynchus' is applied in accordance to the terminology proposed by Vasileva et al. (2003a), and the term 'acanthorhynchoid type' of rostellar hook is used following the terminology proposed by Gulyaev (1990) and Vasileva et al. (2003c). The terms describing the developmental stages of the proglottides are used in accordance to the terminology proposed by Georgiev & Vaucher (2001).

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.

### *Joyeuxilepis acanthorhyncha* (Wedl, 1855) Borgarenko & Gulyaev, 1990

Syns *Taenia acanthorhyncha* Wedl, 1855; *Amoebotaenia acanthorhyncha* (Wedl, 1855) Cohn, 1900; *Tatria acanthorhyncha* (Wedl, 1855) Kowalewski, 1904

*Specimens studied*

From *Tachybaptus ruficollis*, Krapec, Bulgaria, 04.04.1986, one slide with one mature specimen, stained whole-mount; 4 whole specimens mounted in Berlese's medium (Voucher specimen BMNH Reg. No. 2002.12.10.6).

From *Tachybaptus ruficollis poggei* (Reichenow), Taiwan, 30.03.1960 (Collection of the Harold W. Manter Laboratory of Parasitology, University of Nebraska, Lincoln, No 7454BB4-6), 6 mature specimens, 11 detached scoleces and fragments of strobila, stained whole-mounts (3 slides), recorded as '*Tatria acanthorhyncha*' by Jensen et al. (1983).

*Collection of Prof. G. Rees, Cardiganshire, Wales:*

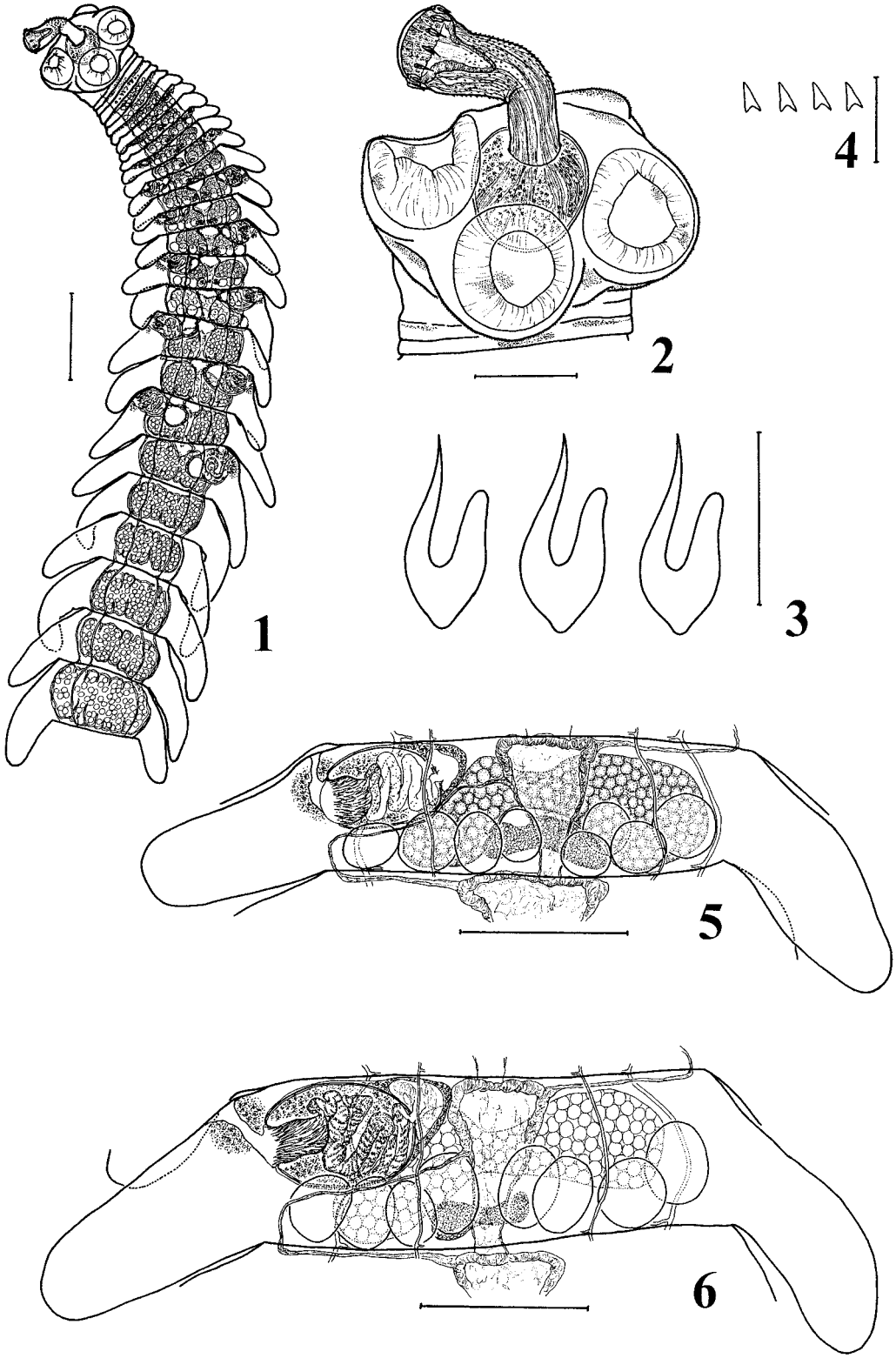
From *Tachybaptus ruficollis*, BMNH 1976.4.21.1-4, recorded as '*Tatria acanthorhyncha'* by Rees (1973), 4 immature specimens, stained whole-mounts (4 slides).

From *Enallagma cyathigerum* Charp, one slide with one stained whole-mounted cysticercoid, BMNH 1976.4.20.75.

*Redescription* (Figures 1–10)

(Based on specimens from Bulgaria). Strobila (Figure 1) ribbon-shaped, with well-developed long lateral processes; maximum width at level of pregravid proglottides. Scolex (Figure 2) oval or almost square; entire surface covered with fine spines. Suckers oval, muscular, covered with fine punctiform spines of equal length. Rostellum short, mushroom-like, thick-walled, with apical muscular enlargement at level of crown; intensely staining glandular cells present in rostellar cavity. Rostellar sheath thick-walled, usually reaches level of posterior margins of suckers, contains intensely staining glandular masses and very strong retractor muscular bundles. Rhynchus long; its cylindrical region covered with numerous small accessory hooks (Figures 2, 4); apical end of rhynchus with enlarged tegumental pad. Rostellum armed with single crown of 13-14 acanthorchynchoid hooks (Figure 3). Neck very short. Proglottides (Figures 5–8) wider than long; mature and pregravid proglottides with long digitiform lateral processes. Male genital pores regularly alternating, open close to anterior proglottis margin. Male genital atrium (Figures 5–7) deep, surrounded by intensely staining cells. Genital ducts pass between osmoregulatory canals. Dorsal osmoregulatory canals pass closer to mid-line of proglottides than do ventral canals; both dorsal and ventral canals with transverse anastomoses along posterior proglottis margin.

Strobila with slightly expressed protogynous development. Female genital primordia appear in second or third proglottides. Ovary (Figures 5, 6) with 2 distinct transversely elongate lobes, with antiporal lobe usually slightly larger than poral, median, ventral to testes, fully developed in 15th-17th proglottides. Vitellarium (Figures 5, 6) compact, transversely elongate or reniform, median, posterior and dorsal to ovary, ventral to testes. Seminal receptacle (Figures 5–7) thick-walled, almost triangular or oval, appears as enlarged region of common seminal canal which runs longitudinally and medially, close to anterior proglottis margin. Seminal receptacles of mature proglottides connected to each other via 2 seminal canals (Figures 5–7); main seminal canal longitudinal, wide, passes along mid-line of proglottides, dorsally to ovary and uterus; additional seminal canal sigmoid, narrow, follows course from seminal receptacle in poral and posterior direction, then passes posteriorly and ventrally to cirrus-sac between dorsal and ventral poral osmoregulatory canals; at level of testes, canal turns posteriorly in poral lateral field, crosses posterior




*Figures 1-6. Joyeuxilepis acanthorhyncha* (Wedl, 1855) from *Tachybaptus ruficollis* in Bulgaria. 1. General view of strobila. 2. Scolex. 3. Rostellar hooks. 4. Accessory hooks of rhynchus. 5. Mature 'female' proglottis. 7. Mature hermaphroditic proglottis. *Scale-bars*: 1, 250 $\mu$m; 2,5,6, 100 $\mu$m; 3, 20 $\mu$m; 4, 10 $\mu$m.

proglottis margin and joins with seminal receptacle of subsequent proglottis.

Testes (Figures 5–7) oval, compact, with primordia appearing in 3rd proglottis, fully developed in 16th-17th proglottides, dorsal and posterior to female glands, usually in 2 groups, 3-4 porally and 3-4 antiporally to median seminal canal; lateral testes usually cross ventral osmoregulatory canals. External seminal vesicle (Figures 7, 9) oval, thin-walled, surrounded by sleeve of large intensely staining glandular cells. Cirrus-sac and external seminal vesicle with thin common outer sheath. Cirrus-sac (Figures 5–7) elliptical, thick-walled, with wide poral region, almost oval when cirrus is evaginated (Figure 9), usually crosses poral osmoregulatory canals. Withdrawn cirrus very long, convoluted, covered by fine spines, surrounded by intensely staining glandular cells. Evaginated cirrus (Figure 9) with 2 well-differentiated regions. Proximal region stout, conical, armed by rosethorn-shaped spines of variable length; longest spines hook-like with wide bases and curved tips (Figure 10); distal region of evaginated cirrus long, cylindrical, armed by small triangular spines. Fully-evaginated cirrus not available in specimens studied; cirrus extirpated after traumatic copulation.

Young uterus (Figure 7) first appears in 17th-18th proglottides, just after disappearance of ovary, median, thin-walled, consisting of 2 distinct, oval lobes. Pregravid uterus (Figure 8) sac-like, thick-walled, with anterior and posterior sacculations. Gravid uterus and fully-developed eggs not found in material available.

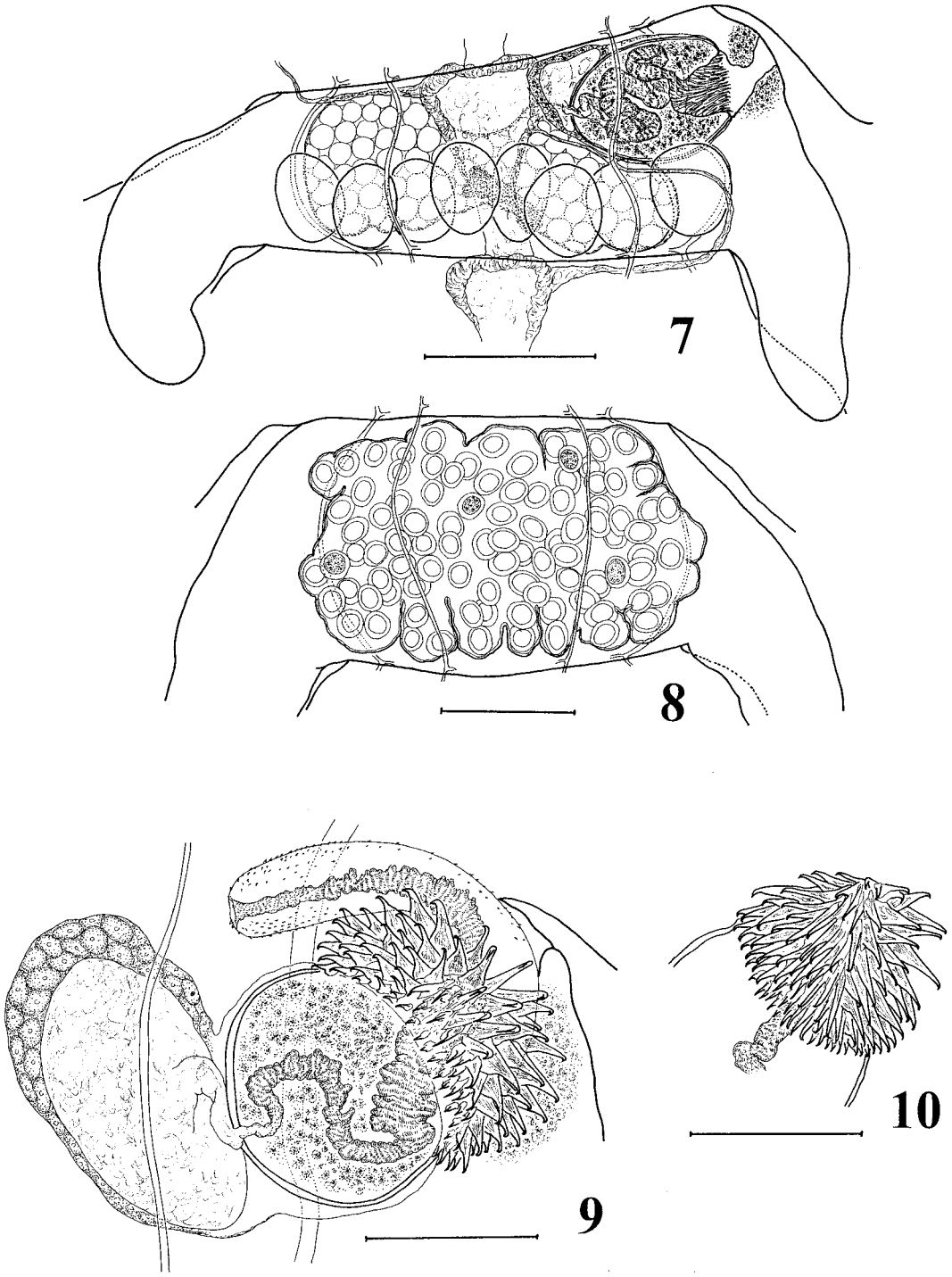
*Measurements.* See Table 1. Additional measurements: length of accessory hooks of rhynchus 4-5 (5, n=10); rostellar hooks: length of blade 15-16 (16, n=6), length of base 17-18 (17, n=6), distance between blade-tip and guard-tip 8-9 (9, n=6); neck length 64 (n=1), minimum width 206 (n=1); diameter of osmoregulatory canals: ventral 3-8 (5, n=6), dorsal 3-5 (3, n=6).

*Remarks*

*J. acanthorhyncha* was described from *Podiceps nigricollis* (Brehm) in Hungary (Wedl, 1855). The original description is very brief and presents little in the way of data on the length and width of the strobila and the shape, length and number of the rostellar hooks. This species was transferred to *Tatria* Kowalewski, 1904 by Kowalewski (1904) on the basis of common features in the morphology of the scolex and the strobila between *J. acanthorhyncha* and *Tatria biremis* Kowalewski, 1904. *J. acanthorhyncha* is one of the most frequently recorded amabiliid species. During last century it was recorded in grebes from various localities in Europe (Mrazek, 1905; Macko, 1959; Dollfus, 1961; Korpaczewska & Sulgostowska, 1974; Illescas-Gomez & Lopez-Roman, 1980; Galkin, 1986; Greben & Kornyushin, 2001) and Asia (Yamaguti, 1940; Johri, 1959; Singh, 1959; Borgarenko et al., 1972).

A comparison of the previous records of *J. acanthorhyncha*, which included morphological data on the specimens studied, with the present results highlighted a few discrepancies concerning misinterpretations of the morphology of this species. Most previous records include measurements of the rostellum, which was usually described as highly elongate, slender and covered by numerous accessory spines (Yamaguti, 1940; Korpaczewska & Sulgostowska, 1974; Macko, 1959; Johri, 1959; Singh, 1959; Borgarenko et al., 1972). In fact, the present study has revealed that all these data relate to the features of the rhynchus; the real rostellum in *J. acanthorhyncha* is a short, mushroom-like organ with thick, muscular walls (see Figure 2). Some of the previous redescriptions of *J. acanthorhyncha* include information on the presence of a small internal seminal vesicle in the cirrus-sac, which is readily visible, especially in young proglottides (Johri, 1959; Korpaczewska & Sulgostowska, 1974; Illescas-Gomez & Lopez-Roman, 1980; Ryzhikov & Tolkacheva, 1981; Galkin, 1986; Greben & Kornyushin, 2001). However, our observations confirmed that this species does not have an internal seminal vesicle; the withdrawn cirrus is very long, thick-walled and coiled. In addition, the cirrus-sac and the external seminal vesicle are surrounded by a common outer sheath. In young proglottides these two organs are enclosed by a common thick sleeve of intensely staining cells and the external seminal vesicle resembles part of the cirrus-sac, i.e. as an 'internal seminal vesicle' (see Figure 5).

Some additional misinterpretations relate to the cirrus armament. Yamaguti (1940) considered that the long, hook-like spines which cover the proximal portion of the cirrus arise from the base of the genital atrium. Our observations are in agreement with the opinion of Ryzhikov & Tolkacheva (1981), who considered that in fact these spines are a readily visible part of the cirrus armament. The large rosethorn-shaped spines can be also seen in incompletely developed cirrus-sacs in young 'female' proglottides (see Figure 5). Singh (1959) observed extirpated cirri




*Figures 7-10. Joyeuxilepis acanthorhyncha* (Wedl, 1855) from *Tachybaptus ruficollis* in Bulgaria. 7. Proglottis with young uterus. 8. Pregravid proglottis. 9. Male terminal ducts. 10. Armament of proximal part of evaginated cirrus. *Scale-bars*: 7,8, 100 $\mu$m; 9,10, 50 $\mu$m.

*Table 1.* Metrical and meristic data for *Joyeuxilepis acanthorhyncha* (Wedl, 1855).

| Hosts | | *Tachybaptus ruficollis* | *Podiceps grisegena*, *P. nigricollis*, *T. ruficollis* | *T. ruficollis* | | |
|---|---|---|---|---|---|---|
| Locality | | Japan | Poland | Bulgaria | | |
| Source | | Yamaguti (1940) | Korpaczewska & Sulgostowska (1974) | Present study | | |
| | | Range | Range | Range | Mean | n |
| Strobila | length (mm) | 3.5 | 5-7 | 2.5-3.8 | 3.1 | 5 |
| | width (mm) | 0.7 | 0.9 | 0.6-1.4 | 1.0 | 5 |
| Proglottides | number | 20-23 | 40 | 29 | – | 1 |
| Scolex | length | – | 172 | 315-437 | – | 2 |
| | width | 270-300 | 198 | 321-386 | – | 2 |
| Suckers | diameter | 80-100 | 72-99 | 116-129 | 123 | 6 |
| Rostellum | length | – | – | 95 | – | 1 |
| | max. width | 50-75 | – | 72 | – | 1 |
| Rostellar sheath | length | – | – | 86 | – | 1 |
| | width | 110-140 | – | 103 | – | 1 |
| Rostellar hooks | number | 13-14 | 14 | 13-14 | 14 | 6 |
| | total length | 21-22 | 20-21 | 21-23 | 22 | 6 |
| Rhynchus | length | – | 181 | 174-193 | – | 2 |
| | min. width | – | 23 | 32-45 | – | 2 |
| Ovary | width | 180 | 116 | 186-193 | 188 | 3 |
| Vitellarium | length | 63 | 40 | 57-70 | 63 | 5 |
| | width | 30 | – | 21-26 | 23 | 5 |
| Testes | number | 6-7 | 6-7 | 6-8 | 7 | 8 |
| | diameter | 36-50 | 26-30 | 39-49 | 45 | 10 |
| Ext. sem. vesicle | length | 75 | 99 | 70-80 | 76 | 4 |
| | width | 48 | 82 | 46-77 | 57 | 4 |
| Cirrus-sac | length | 84 | 149 | 90-116 | 103 | 4 |
| | width | 60 | 99 | 70-80 | 74 | 4 |
| Evaginated cirrus | length | – | – | 39-54 | 48 | 4 |
| | width | – | 33-39 | 57-72 | 65 | 4 |

in the seminal receptacles of some of his specimens, and he misinterpreted them as a 'centrally situated accessory apparatus' heavily armed by long spines.

Johri (1959) described a narrow, tubular 'vagina' just posterior to the cirrus-sac, which it 'has been possible to detect only in sagittal sections'. The present study completely confirmed the previous observations of Mrazek (1905) concerning the presence of two accessory seminal canals in *J. acanthorhyncha*, i.e. a main, longitudinal, wide, median canal and an additional narrow, sigmoid canal. Perhaps, Johri (1959) observed the part of the sigmoid accessory seminal canal which passes posteriorly to the cirrus-sac and misinterpreted it as a distinct 'vagina'.

Despite the above-mentioned discrepancies, our study corresponds well with the previous redescriptions of Yamaguti (1940) and Korpaczewska & Sulgostowska (1974), including the metrical data (see Table 1). The following records of *J. acanthorhyncha* can also be confirmed: from *Podiceps* sp. in Denmark (Krabbe, 1869); from *Tachybaptus ruficollis* in the Slovak Republic (Macko, 1959), India (Johri, 1959; Singh, 1959), France (Dollfus, 1961), Hungary (Sey, 1968, 1969), Tadzhikistan (Borgarenko, 1972; Borgarenko et al., 1972), Spain (Illescas-Gomez & Lopez-Roman, 1980), Estonia and Turkmenia (Ryzhikov & Tolkacheva, 1981) and the Baltic Sea (Russia) (Galkin, 1986), and from both *T. ruficollis* and *P. nigricollis* in the Ukraine (Greben & Kornyushin, 2001).

Rees (1973) recorded *J. acanthorhyncha* from *T. ruficollis* and described the cysticercoids from larvae of dragonfly *Enallagma cyathigerum* in Cardigan-

shire, Wales. This record was confirmed after a re-examination of the voucher specimens in the British Museum (Natural History) Collection. The record of Jensen et al. (1983) from *T. ruficollis poggei* in Taiwan was also confirmed on the basis of a re-examination of vouchers from the Harold W. Manter Laboratory of Parasitology, University of Nebraska, Lincoln.

*Tatria azerbaijanica* Matevosyan & Sailov, 1963 was described from *Podiceps cristatus* (L.) and *Tachybaptus ruficollis* in Azerbaidzhan. This species is characterised with a small strobila consisting of 10-15 proglottides, 14 acanthorhynchoid rostellar hooks with a length of 24 $\mu$m, accessory hooks on the rhynchus which are arranged in eight longitudinal rows, unarmed suckers and an oval seminal receptacle situated medially close to the anterior proglottis margin (Matevosyan & Sailov, 1963). These features differ from the morphology of *J. acanthorhyncha*. Therefore, in contrast with the opinion of Ryzhikov & Tolkacheva (1981), we consider that *T. azerbaijanica* cannot be recognised as a synonym of *J. acanthorhyncha*. Since it also possesses acanthorhynchoid rostellar hooks, a transversely elongate vitellarium and sacculations of the uterus, we agree with the combination *Joyeuxilepis azerbaijanica*, proposed by Borgarenko & Gulyaev (1990), but consider that this species requires further study.

The following records of *J. acanthorhyncha* lack information on the morphology of the specimens studied: Lühe (1910), Dubinina (1950), Shakhtakhtinskaya (1959), Korpaczewska (1963), Yun Lian (1973), Frank (1977) and Zhuk et al. (1982). Cysticercoids of *J. acanthorhyncha* have been recorded from naturally infected larvae of various Odonata (see von Linstow, 1892; Mrazek, 1927; Rees, 1973) and experimentally infected Copepoda (see Jarecka, 1960). Solomon (1932) wrongly cited the name of *J. acanthorhyncha* as '*Tatria acanthocephala*'.

The host range of *J. acanthorhyncha* (based on confirmed records only) includes *Tachybaptus ruficollis*, *Podiceps nigricollis* and *P. grisegena* (Boddaert). Movsesyan (1963) recorded *J. acanthorhyncha* from *Aythya nyroca* (Guld.) in Moldavia. Some of the data from this description are in agreement with the present results. However, the presence of six pairs of osmoregulatory canals, the long cylindrical cirrus and the presence of filaments on the embryophores of the eggs do not permit us to confirm this record. The geographical range of *J. acanthorhyncha* includes Europe and Asia.

***Joyeuxilepis fuhrmanni* (Solomon, 1932) Borgarenko & Gulyaev, 1990**

Syn. *Tatria fuhrmanni* Solomon, 1932

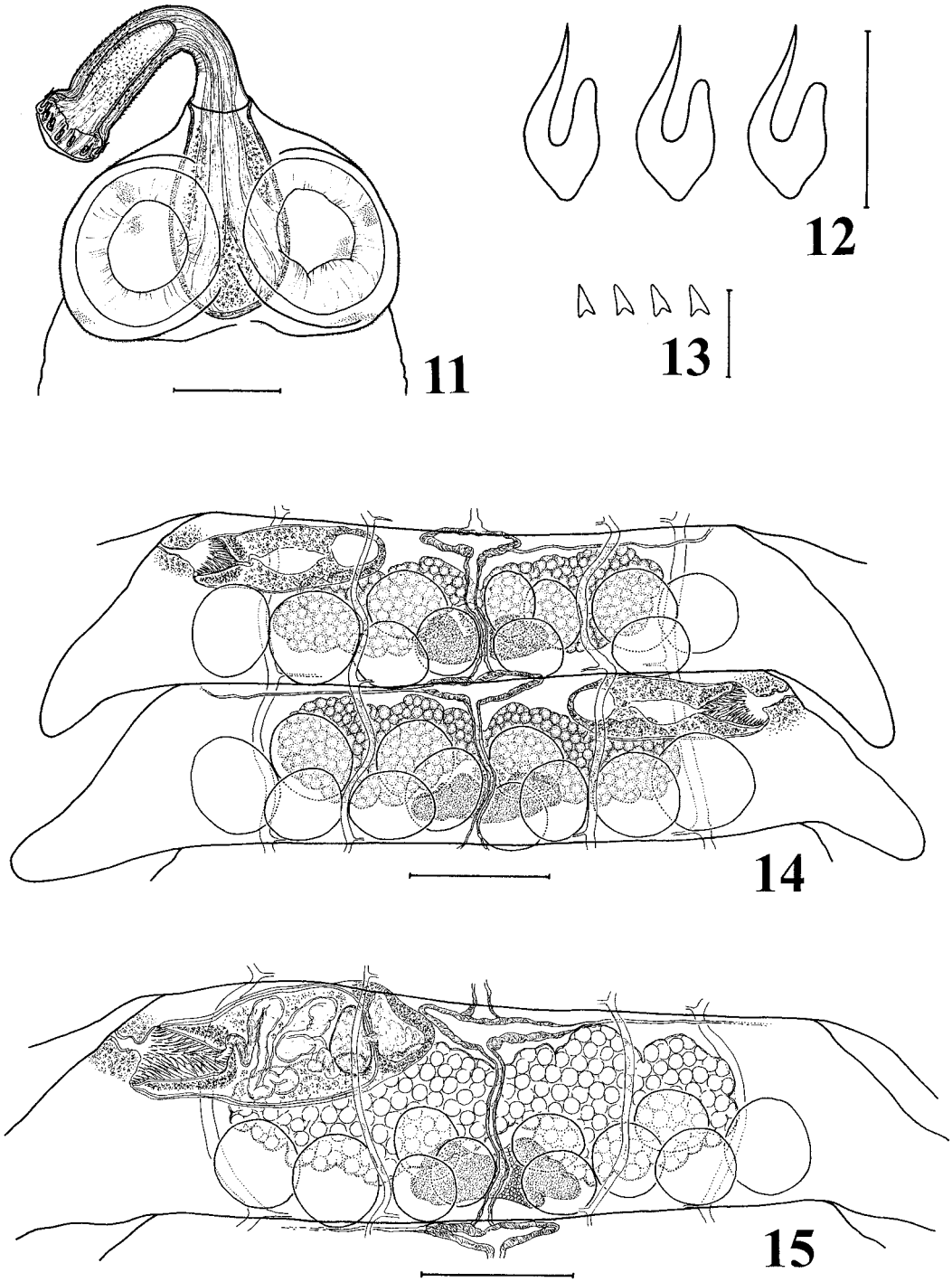
*Specimens studied*

BMNH 1980.6.3.86, holotype, from 'coot' (= ? *Podiceps* sp.), Kabete, Kenya, a slide with a single stained mature specimen.

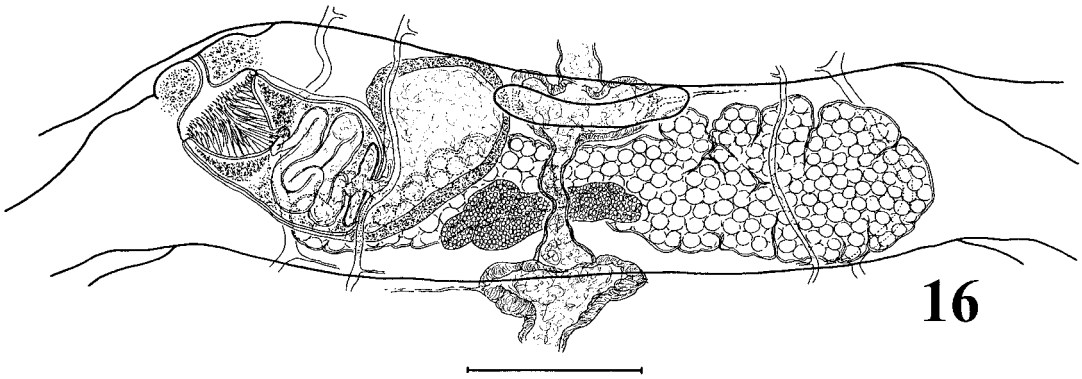
*Redescription* (Figures 11–17)

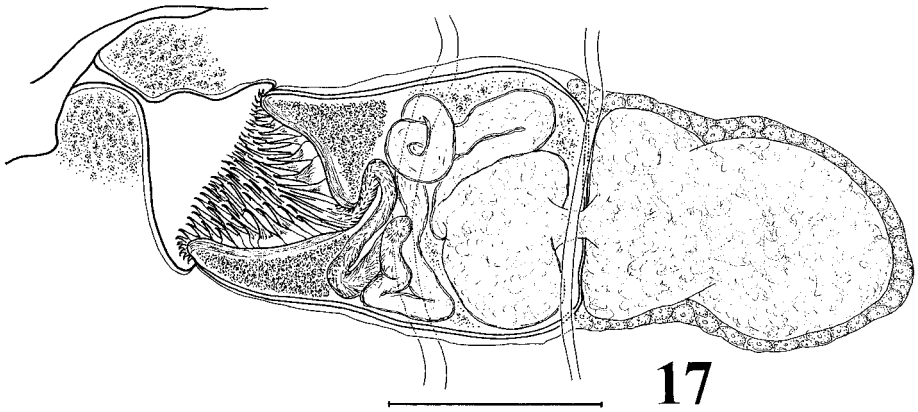
Strobila long, ribbon-shaped, with long lateral processes, digitiform in terminal proglottides; maximum width at level of proglottides with developing uterus. Scolex (Figure 11) more or less rounded, with well-expressed anterior protrusion; entire surface covered with punctiform spines which are readily lost. Suckers oval, muscular, covered with fine punctiform spines. Rostellum short, mushroom-like, thick-walled, with apical muscular enlargement at level of crown; intensely staining glandular cells present in rostellar cavity. Rostellar sheath thick-walled, almost reaches level of posterior margins of suckers, contains intensely staining glandular cells and strong retractor muscular bundles. Rhynchus elongate, covered with numerous small accessory hooks (Figures 13); apical end of rhynchus with enlarged tegumental pad. Rostellum armed with single crown of 14 acanthorhynchoid hooks (Figure 12). Neck well developed. Proglottides (Figures 14–16) much wider than long. Male genital pores regularly alternating, open close to anterior proglottis margin. Male genital atrium (Figures 16, 17) thick-walled, wide, surrounded by intensely staining cells; usually atrium of mature proglottides forms short, wide genital papilla (Figures 16, 17). Genital ducts pass between osmoregulatory canals. Dorsal osmoregulatory canals pass closer to mid-line of proglottides than do ventral canals; dorsal and ventral osmoregulatory canals with transverse anastomoses along posterior proglottis margin.

Strobila with slightly expressed protogynous development. Female genital primordia appear in 9th-10th proglottides. Ovary (Figure 14) with 2 transversely elongate wings with slightly lobed margins, median, ventral to testes, fully developed in 27th-30th proglottides. Vitellarium (Figures 14–16) transversely elongate or almost reniform, with slightly lobed margins, median, posterior and dorsal to ovary, ventral to testes, disappears in last proglottides with developing uterus. Seminal receptacle (Figures 14–16) appears in mature proglottides with developed ovary, thick-




*Figures 11-15. Joyeuxilepis fuhrmanni* (Solomon, 1932), holotype from 'coot' (=? *Podiceps* sp.) in Kenya. 11. Scolex. 12. Rostellar hooks. 13. Accessory hooks of rhynchus. 14. Mature hermaphroditic proglottides. 15. Proglottis with young uterus. *Scale-bars*: 11,14,15, 100 $\mu$m; 12, 20 $\mu$m; 13, 10 $\mu$m.




*Figures 16-17. Joyeuxilepis fuhrmanni* (Solomon, 1932), holotype from 'coot' (=? *Podiceps* sp. ) in Kenya. 16. Proglottis with developing uterus. 17. Male terminal ducts. *Scale-bars*: 16, 150 $\mu$m; 17, 100 $\mu$m.

walled, elliptical, median, close to anterior proglottis margin; those of neighbouring proglottides connected to each other via longitudinal, thick-walled, median seminal canal which runs dorsally to ovary and uterus; additional narrow seminal canal follows course from seminal receptacle in antiporal direction and finishes blindly close to anterior edge of antiporal lateral proglottis margin (Figures 14, 15).

Testes (Figures 14, 15) oval, compact, with primordia appearing in 10th-12th proglottides, fully developed in 29th-30th proglottides, dorsal and posterior to female organs, usually in 2 groups, 5-6 porally and 5-6 antiporally to median seminal canal. External seminal vesicle (Figures 15–17) elliptical, voluminous, thin-walled, surrounded by sleeve of large intensely staining glandular cells. Cirrus-sac and external seminal vesicle with common outer sheath. Cirrus-sac (Figures 15–17) elongate, thick-walled, with wide, cylindrical poral region and almost rounded antiporal region usually with greater diameter than poral region, crosses poral osmoregulatory canals passing between dorsal and ventral canals. Internal seminal vesicle elliptical, thick-walled (Figures 15–17). Withdrawn cirrus (Figures 16, 17) with 2 well-differentiated regions. Poral region stout, conical, armed by hook-like spines of variable length; antiporal region of withdrawn cirrus cylindrical, covered by small spines. Ejaculatory duct long, convoluted. Evaginated cirrus not available in holotype. Copulatory orifices (Figure 16) elliptical, median, readily visible on dorsal surface of strobila, close to anterior proglottis margin.

Early stage uterus (Figure 15) first appears in 30th-32nd proglottides, just after disappearance of ovary, median, thin-walled, consisting of 2 distinct, usually lobed wings. Developing uterus (Figure 16) sac-like, thick-walled, with anterior and posterior sacculations. Pregravid uterus, fully-developed uterus and fully-developed eggs not available. Last 28 proglottides of holotype sterile.

*Table 2.* Metrical and meristic data for *Joyeuxilepis fuhrmanni* (Solomon, 1932) from 'coot' (= ? *Podiceps* sp.) from Kenya.

| Source | | Solomon (1932) | Present study | | |
|---|---|---|---|---|---|
| | | Range | Range | Mean | n |
| Strobila | length (mm) | 12 | 12 | – | 1 |
| | width (mm) | 0.5-1.4 | 1.5 | – | 1 |
| Proglottides | number | 98 | 99 | – | 1 |
| Scolex | length | – | 418 | – | 1 |
| | width | 320 | 307 | – | 1 |
| Suckers | diameter | 140-160 | 135-150 | 141 | 4 |
| Rostellum | length | – | 156 | – | 1 |
| | max. width | – | 69 | – | 1 |
| Rostellar sheath | length | 120 | 180 | – | 1 |
| | width | – | 114 | – | 1 |
| Rostellar hooks | number | 14 | 14 | – | 1 |
| | total length | 20 | 20-21 | 20 | 4 |
| Rhynchus | length | 260* | 255 | – | 1 |
| | min. width | – | 36 | – | 1 |
| Ovary | width | – | 237-311 | 269 | 10 |
| Vitellarium | width | – | 120-156 | 142 | 10 |
| Testes | number | 11-13 | 11-13 | 12 | 15 |
| | diameter | – | 81-99 | 89 | 15 |
| Ext. sem. vesicle | length | – | 144-165 | 158 | 10 |
| | width | – | 81-102 | 94 | 10 |
| Int. sem. vesicle | diameter | – | 66-85 | 73 | 6 |
| Cirrus-sac | length | – | 150-180 | 170 | 10 |
| | width | – | 120-129 | 126 | 10 |
| Cirrus | max. diameter | – | 76-85 | 82 | 10 |

*The length of 'rostellum' according to Solomon (1932).

*Measurements.* See Table 2. Additional measurements: length of accessory hooks of rhynchus 4-5 (4, n=10); rostellar hooks: length of blade 14 (n=4), length of base 14-15 (15, n=4), distance between blade-tip and guard-tip 7-8 (8, n=4); neck length 84 (n=1), minimum width 265 (n=1); diameter of osmoregulatory canals: ventral 9-13 (11, n=10), dorsal 6-8 (7, n=10); maximum length of cirrus spines 25-28 (26, n=10).

*Remarks*

*J. fuhrmanni* was originally described from a 'coot' in Kenya (Solomon, 1932). The original record is the one and only finding of this species. As supposed by Solomon (1932), the host of *J. fuhrmanni* probably represents a grebe (*Podiceps* sp.). Three species of the Podicipedidae occur in Africa south of the Sahara, i.e. *Podiceps cristatus*, *P. nigricollis* and *Tachybaptus ruficollis* (see Vlug & Fjeldså, 1990; Storer, 2000). It is very likely that the host of *J. fuhrmanni* is *T. ruficollis*, since it has a uniform coloration and is similar to coots in size. Moreover, another cestode was found in the same 'coot' specimen (Solomon, 1932); this was *Confluaria multistriata* (Rudolphi, 1810), a species which is considered primarily a parasite of *T. ruficollis* (see Vasileva et al., 1999).

The present re-examination of the holotype confirms some of the data in the original description, and the metrical data also correspond well (see Table 2). However, there are a few exceptions which relate mainly to the morphology of the genital system. In contrast with the observations of Solomon (1932), the present study revealed that *J. fuhrmanni* has a regular alternation of the genital pores and the testes are situated in two, almost equal, groups on the poral and antiporal sides of the mature proglottides. Solomon (1932) observed a 'vaginal canal' which runs outwards from the seminal receptacle and follows a course towards the cirrus. According to the figure 11

of Solomon (1932), this author has interpreted the external seminal vesicle as a 'pyriform' seminal receptacle and a 'vaginal canal' was drawn as following a course toward the male genital atrium. However, our observations have shown that *J. fuhrmanni* does not have this type of vaginal canal; the seminal receptacles are not pyriform and they are connected to each other via longitudinal median canal. In addition, we could not see the fully-developed uterus and mature eggs in the holotype, which have been described by Solomon (1932). The current study presents new information on the structure of the scolex, the osmoregulatory system and the presence of sacculations of the pregravid uterus.

## Discussion

### *Generic level*

The brief original diagnosis of *Joyeuxilepis* (see Spassky, 1947) included only data on the morphology of the cysticercoids of the type-species, *J. biuncinata*. *Joyeuxilepis* was characterised as possessing a rhynchus covered by small hook-like spines, a single crown of rostellar hooks situated at the base of the rhynchus and suckers whose margins are armed by a few rows of small spines. The original family allocation of *Joyeuxilepis* was within Hymenolepididae Ariola, 1899. The nominal genus was transferred to the Amabiliidae Braun, 1900 by Spassky & Spasskaya (1976). These authors conditionally proposed dividing all known *Tatria* spp. into two subgenera on the basis of the different shape of their rostellar hooks. Four species, possessing rostellar hooks in which the handle is longer than the guard were to be left in the subgenus *Tatria* with the type-species, *T. biremis*. The second subgenus included the remaining five species with aploparaksoid rostellar hooks (with a handle shorter than the guard) under the name *Joyeuxilepis*. Ryzhikov & Tolkacheva (1981) did not confirm the separation of these two groups and proposed an amended generic diagnosis for *Tatria* (*sensu lato*), which included the characters of all nine species, despite differences in the shape of their rostellar hooks. After the taxonomic reorganisation of *Tatria* proposed by Gulyaev & Tolkacheva (1987), Borgarenko & Gulyaev (1990, 1991) and Gulyaev (1990, 1992), all known species of *Tatria* (*sensu lato*) with an acanthorhynchoid shape of the hooks were included in *Joyeuxilepis*.

In addition to the five species re-examined in the current revision (Vasileva et al., 2003c; present study), Borgarenko & Gulyaev (1990, 1991) considered the following species as members of *Joyeuxilepis*: *J. fimbriata* (Borgarenko, Spasskaya & Spassky, 1972), *J. octacantha* (Rees, 1973), *J. azerbaijanica*, *J. uralensis* Gulyaev, 1989 and *J. decacanthoides* Borgarenko & Gulyaev, 1991. Some of the original descriptions of these species did not provide enough information on the structure of the osmoregulatory system, the seminal receptacles and the male terminal ducts. *Tatria octacantha* was described on the basis of cysticercoids from dragonfly nymphs (Odonata) and two immature specimens from *Tachybaptus ruficollis* in Cardiganshire, Wales (Rees, 1973). The re-examination of the single adult type-specimen (BMNH 1972.8.17.3) did not provide adequate information on the morphology of this species. We also re-examined voucher material from *T. ruficollis* in Norfolk, England, recorded as '*Tatria decacantha'* by Baylis (1939) (BMNH 1938.8.8.27-45). Five specimens of these vouchers possess eight rostellar hooks and scoleces which fit to the morphology of *J. octacantha*. However, the strobila were in poor condition and a detailed redescription of *J. octacantha* could not be made. *J. fimbriata* and *J. azerbaijanica* are known from their original sources only and their descriptions are not very detailed. We consider that the preparation of complete re-descriptions of these three poorly known species requires further investigations, based on a newly collected material. Nevertheless, *J. fimbriata*, *J. octacantha*, *J. azerbaijanica*, *J. uralensis* and *J. decacanthoides* are characterised by acanthorhynchoid rostellar hooks, the presence of a simple external seminal vesicle and a sac-like uterus without sleeve of intensely stained cells. Therefore, despite the incompleteness of some of the descriptions, we are in agreement with the opinion of Borgarenko & Gulyaev (1990) and confirm the position of these five species within *Joyeuxilepis*.

*Tatria iunii* Korpaczewska & Sulgostowska, 1974 was described from *Tachybaptus ruficollis* in Poland. This species is similar to *J. acanthorhyncha* in the number of testes, the shape of the ovary and the shape and armament of the cirrus (see Korpaczewska & Sulgostowska, 1974). However, the rostellar hooks of *T. iunii* are 8–10 in number and 9–12 $\mu$m long, and, judging from Figure 5f of Korpaczewska & Sulgostowska (1974), their shape is not acanthorhynchoid. In addition, the description lacks data on the osmoregulatory system, the seminal vesicle and the

uterus. Therefore, we consider that the generic allocation of *T. iunii* needs further study.

Gulyaev & Tolkacheva (1987) did not propose a revised generic diagnosis for *Joyeuxilepis*. In the latest revision of the Amabiliidae, Jones (1994) provisionally considered *Joyeuxilepis* a synonym of *Tatria*, pending the establishment of taxonomically significant characters of the *Tatria* spp. with acanthorhynchoid hooks. The current revision of *Joyeuxilepis* (Vasileva et al., 2003c; present study) has revealed that the five re-examined species possess several morphological features which distinguish them from the species of *Tatria* (*sensu stricto*) (see Vasileva et al., 2003a,b) and support the validity of *Joyeuxilepis*. *J. biuncinata*, *J. decacantha*, *J. pilatus*, *J. acanthorhyncha* and *J. fuhrmanni* are characterised by the same arrangement of the dorsal osmoregulatory canals in relation to the mid-line of the strobila; for comparison, the species of *Tatria* (*sensu stricto*) have both dorsal and ventral osmoregulatory canals passing equidistant from the mid-line. The re-examined *Joyeuxilepis* spp. have a transversely elongate or reniform shape of the vitellarium, versus the oval vitellarium of *Tatria* spp. One of the most important characters of *Joyeuxilepis* spp. is the presence of a common sheath around the cirrus-sac and the external seminal vesicle; this structure is not observed in *Tatria* (*sensu stricto*). Another shared feature of the *Joyeuxilepis* spp. is the simple external seminal vesicle, which is not subdivided into two or three parts, as in *Tatria* spp. The species of *Joyeuxilepis* also differ from *Tatria* by possessing a sacculate pregravid uterus, which is not surrounded by a sleeve of intensely staining cells. With respect to the nature of the development of the strobila, as mentioned in our previous paper (Vasileva et al., 2003c), our results have shown that protandrous development cannot be considered a reliable diagnostic character for *Joyeuxilepis.* Almost all of the species re-examined (except for *J. decacantha*) have a slightly expressed protogynous development.

On the basis of our observations on the species of *Joyeuxilepis,* the following revised generic diagnosis is proposed:

### ***Joyeuxilepis* Spassky, 1947**

*Diagnosis*: Strobila small, wedge-shaped or ribbon-shaped. Proglottides craspedote with well-developed, often digitiform lateral processes. Scolex oval or almost square, conical anteriorly, usually with armed surface. Suckers muscular, usually armed. Rostellum muscular, glandular, elongate, with apical muscular enlargement. Rostellar sheath sac-like, containing strong retractor muscle bundles. Rhynchus long, with apically enlarged tegumental pad, covered with small accessory hooks. Rostellar hooks 8, 10-12 or 13-14 in various species, with acanthorhynchoid 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 canals pass closer to mid-line of proglottides than do ventral canals. Ovary bilobed, rarely asymmetrical, compact, median. Vitellarium transversely elongate or reniform, compact, median, postovarian. Seminal receptacle usually well differentiated, elliptical or almost triangular, sac-like, near anterior proglottis margin, rarely close to posterior margin. Seminal receptacles of neighbouring mature proglottides connected to each other by accessory sigmoid or median longitudinal canal; sometimes both types of canals present. Testes few (5-13), in two lateral groups or single transverse row, in posterior half of median field. Internal seminal vesicle usually absent. External seminal vesicle elongate, simple. Cirrus-sac thick-walled, elongate, pyriform or spherical; cirrus-sac and external seminal vesicle with common outer sheath. Cirrus cylindrical or with hemispherical basal enlargement, armed. Copulation traumatic, followed by extirpation of cirrus. Uterus sac-like, initially bilobed, thick-walled; pregravid uterus with sacculations. Eggs with thin outer shell; embryophores elliptical, thick-walled; oncospheres oval. In intestine of Podicipediformes: Europe, Asia and Africa. Type-species *J. biuncinata* (Joyeux & Baer, 1943).

*Other species: J. acanthorhyncha* (Wedl, 1855), *J. decacantha* (Fuhrmann, 1913), *J. pilatus* Borgarenko & Gulyaev, 1991, *J. fuhrmanni* (Solomon, 1932), *J. uralensis* Gulyaev, 1989, *J. decacanthoides* Borgarenko & Gulyaev, 1991, *J. octacantha* (Rees, 1973), *J. azerbaijanica* (Matevosyan & Sailov, 1963) and *J. fimbriata* (Borgarenko, Spasskaya & Spassky, 1972).

*Species level*

On the basis of our observations on five species of *Joyeuxilepis* and the original descriptions of *J. azerbaijanica*, *J. fimbriata*, *J. octacantha* and *J. dec-*

*Table 3.* Main distinguishing features of *Joyeuxilepis* spp.

| Species | Rostellar hooks | | Seminal receptacle | | Accessory seminal canals | | Testes number | Cirrus shape |
|---|---|---|---|---|---|---|---|---|
| | number | length ($\mu$m) | shape | position | number | shape | | |
| *J. biuncinata*[1] | 10 | 17-18 | almost triangular, sac-like | anterior | 2 | median and sigmoid | 5-6 | cylindrical, conically tapering distally |
| *J. decacantha*[1] | 10 | 19-21 | oval or elliptical | anterior | 1 | sigmoid | 6-8 | with basal enlargement |
| *J. pilatus*[1] | 10-12 | 21-23 | oval or elliptical | posterior | 1 | single, blind | 6 | with basal enlargement |
| *J. acanthorhyncha*[2] | 13-14 | 21-23 | almost triangular, sac-like | anterior | 2 | median and sigmoid | 6-8 | with basal enlargement |
| *J. fuhrmanni*[2] | 14 | 20-21 | elliptical | anterior | 1 | median | 11-13 | with basal enlargement |
| *J. octacantha*[3] | 8 | 20 | ? | anterior | ? | ? | 7 | cylindrical, enlarged distally |
| *J. decacanthoides*[4] | 10 | 15-16 | oval or elliptical | anterior | 1 | sigmoid | 5-6 | cylindrical, conically tapering distally |
| *J. azerbaijanica*[5] | 14 | 24 | oval | anterior | ? | ? | 5-6 | with basal enlargement |
| *J. fimbriata*[6] | 10 | 16 | oval | anterior | ? | ? | 10 | cylindrical (?) |

*Sources*: [1]Vasileva et al. (2003c), [2]Present study, [3]Rees (1973), [4]Borgarenko & Gulyaev (1991), [5]Matevosyan & Sailov (1963), [6]Borgarenko et al. (1972).

*acanthoides*, a re-evaluation of the reliable diagnostic criteria at the species level can be made.

(i) As in the case of the species of *Tatria* (*sensu stricto*) (see Vasileva et al., 2003b), the basic characters for distinguishing species of *Joyeuxilepis* are the number and the length of the rostellar hooks. The shape of the rostellar hooks of *Joyeuxilepis* spp. is acanthorhynchoid and it is very similar for all species. The number of the hooks varies from 8 to 14 and their total length measures from 15 to 24 $\mu$m (see Table 3).

(ii) The shape of the seminal receptacles and the type of connection between them are also important distinguishing characters. Contrary to the situation in *Tatria* (see Vasileva et al., 2003b), most of the species of *Joyeuxilepis* have well-differentiated, oval or elliptical seminal receptacles situated close to the anterior proglottis margin (except for *J. pilatus*). *J. acanthorhyncha* and *J. biuncinata* have almost triangular, thick-walled, sac-like seminal receptacles. The type of the connection between the seminal receptacles of the neighbouring mature proglottides in *Joyeuxilepis* is also a useful character (Table 3). The seminal receptacles may connect to each other via a median, longitudinal accessory canal or via a sigmoid canal. *J. biuncinata* and *J. acanthorhyncha* are characterised by the presence of both median and sigmoid canals.

(iii) Another important character for distinguishing *Joyeuxilepis* spp. is the structure of the cirrus. There are two main groups of species with respect to this feature (Table 3). The first group includes the species with an almost cylindrical cirrus, i.e. *J. biuncinata*, *J. decacanthoides* and *J. octacantha.* However, in the former two species, the evaginated cirrus has an enlarged mid-region and a conically tapering distal portion, whilst *J. octacantha* has a cirrus with a distal enlargement (see Rees, 1973). The second group of species includes *J. decacantha*, *J. acanthorhyncha*, *J. fuhrmanni*, *J. pilatus* and *J. azerbaijanica*, which have a cirrus with a powerfully armed hemispherical basal enlargement and a thin, cylindrical distal region. These four species differ from each other by the shape and the length of the cirrus spines.

Using these differentiating characters, an identification key to nine species of *Joyeuxilepis* is presented below. *J. uralensis* is not included in the key, since it was described on the basis of the cysticercoids only and there are no available data on the morphology of the adult form.

*Key to the species of* Joyeuxilepis

1a. Rostellar hooks 8 ..... *J. octacantha*
1b. Rostellar hooks > 8 ..... 2
2a. Rostellar hooks 10-12 ..... 3
2b. Rostellar hooks 13-14 ..... 7
3a. Rostellar hooks 10-12; seminal receptacles close to the posterior proglottis margin; cirrus with hemispherical basal enlargement, covered by long, needle-shaped spines ..... *J. pilatus*
3b. Rostellar hooks 10; seminal receptacles close to the anterior proglottis margin; cirrus cylindrical or with basal enlargement, armed by triangular or rosethorn-shaped spines ..... 4
4a. Rostellar hooks 19–21 $\mu$m long; cirrus with powerfully armed basal enlargement .. *J. decacantha*
4b. Rostellar hooks 15–18 $\mu$m long; cirrus almost cylindrical, with conical apex ..... 5
5a. Rostellar hooks 17–18 $\mu$m long; entire surface of scolex and suckers covered by small spines ..... *J. biuncinata*
5b. Rostellar hooks 15–16 $\mu$m long; scolex and suckers unarmed ..... 6
6a. Proglottides with short, wide lateral processes; testes 5-6 ..... *J. decacanthoides*
6b. Proglottides with long, digitiform lateral processes; testes 10 ..... *J. fimbriata*
7a. Strobila long, consisting of > 90 proglottides; rostellar hooks 20–21 $\mu$m long; testes 11-13 ..... *J. fuhrmanni*
7b. Strobila small, consisting of 10-40 proglottides; rostellar hooks 21–24 $\mu$m long; testes 5-8 ..... 8
8a. Accessory hooks of rhynchus in 8 longitudinal rows; suckers unarmed; seminal receptacle oval or elliptical ..... *J. azerbaijanica*
8b. Accessory hooks of rhynchus in numerous longitudinal rows; suckers armed; seminal receptacle almost triangular, thick-walled ..... *J. acanthorhyncha*

## Acknowledgements

This investigation was completed during the first author's tenure of a NATO/Royal Society postdoctoral fellowship at The Natural History Museum, London. We are grateful to Drs S.L. Gardner and S. Sterner, Harold W. Manter Laboratory of Parasitology, University of Nebraska State Museum, Lincoln, for the loan of specimens and to Prof. V.D. Gulyaev and Dr B.B. Georgiev for the helpful suggestions during the preparation of the manuscript. Thanks are also due to Mr I. Stoyanov (Central Laboratory of General Ecology, Bulgarian Academy of Sciences), who kindly translated two articles from German. Funding and support for this research was provided in part by The National Science Fund of the Republic of Bulgaria (grant B-1104/2001).

## References

Baylis, H.A. (1939) Further records of parasitic worms from British vertebrates. *Annals and Magazine of Natural History*, Ser. 11, **4**, 473–498.

Borgarenko, L.F. (1972) [Helminths of grebes (Podicipediformes) in Tadzhikistan.] *In*: Narzikulov, M.N. & Abdusalyamov, I.A. (Eds) *Voprosy Zoologii Tadzhikistana*. Dushanbe: Donish, pp. 39–47. (In Russian).

Borgarenko, L.F. & Gulyaev, V.D. (1990) On morphology of the type species of the genus *Joyeuxilepis* (Cestoda, Schistotaeniinae). *Parazitologiya*, **24**, 350–353. (In Russian).

Borgarenko, L.F. & Gulyaev, V.D. (1991) Two new amabiliid cestodes from grebes in Tadzhikistan. *Sibirskiy Biologicheskiy Zhurnal*, **1**, 44–48. (In Russian).

Borgarenko, L.F., Spasskaya, L.P. & Spassky, A.A. (1972) [Cestodes of the genus *Tatria* from the water fowl birds in Tadzhikistan. ] *Izvestiya Akademii Nauk Tadzhikskoy SSR. Otdel Biologicheskih Nauk*, **4**, 53–57. (In Russian).

Dollfus, R.P. (1961) Contribution a la faune parasitaire régionale. Chap. 1. Liste des parasites par hôtes. Oiseaux. *Annales de Parasitologie Humaine et Comparée*, **36**, 191–231.

Dubinina, M.N. (1950) [Tapeworms of birds overwintering in southern Tadzhikistan.] *Parazitologicheskiy Sbornik*, **12**, 351–381. (In Russian).

Frank, C. (1977) Contribution to the helminthology of different wild birds from East Austria. *Zeitschrift für Angewandte Zoologie*, **64**, 409–439.

Galkin, A.K. (1986) On the cestode fauna of grebes (*Podiceps*) of the Kurish Spit. *Trudy Zoologicheskogo Instituta AN SSSR*, **155**, 119–127. (In Russian).

Georgiev, B.B., Biserkov, V. & Genov, T. (1986) In toto staining method for cestodes with iron acetocarmine. *Helminthologia*, **23**, 279–281.

Georgiev, B.B. & Vaucher, C. (2001) Revision of the genus *Parvirostrum* Fuhrmann, 1908 (Cestoda: Cyclophyllidea: Paruterinidae). *Systematic Parasitology*, **50**, 13–29.

Greben, O.B. & Kornyushin, V.V. (2001) New species of amabiliid (Cestoda, Cyclophyllidea) for Ukraine fauna. *Vestnik Zoologii*, **35**, 23–30. (In Russian).

Gulyaev, V.D. (1990) [On the morphology and taxonomy of *Tatria* (s. l.) (Cestoda, Schistotaeniinae) from the grebes of Western Siberia and Trans-Urals.] *In*: Cherepanov, A.I. (Ed.) *Novye i Maloizvestnye Vidy Fauny Sibiri. Redkie Gel'minty, Kleshchi i Nasekomye*. Novosibirsk: Izdatel'stvo 'Nauka' – Sibirskoe Otdelenie, pp. 4–19. (In Russian).

Gulyaev, V.D. (1992) Morphological criteria of *Tatria* Kowalewski, 1904 (Cestoda: Schistotaeniinae). *Sibirskiy Biologicheskiy Zhurnal*, **4**, 68–75. (In Russian).

Gulyaev, V.D. & Tolkacheva, L.M. (1987) New genus of the tapeworms of the grebes *Ryjikovilepis* gen. n. and redescription of *R. dubininae* (Ryjikov et Tolkatscheva, 1981) comb. n. *In*: Cherepanov, A.I. (Ed.) *Novye i Maloizvestnye Vidy Fauny Sibiri.*

*Nasekomye, Kleshchi i Gel'minty*. Novosibirsk: Izdatel'stvo 'Nauka' – Sibirskoe Otdelenie, pp. 80–88. (In Russian).

Illescas-Gomez, P. & Lopez-Roman, R. (1980) *Tatria acanthorhyncha* (Wedl, 1855) Mrazek, 1905, parasito intestinal de *Podiceps ruficollis* Pallas. *Revista Iberica de Parasitologia*, **40**, 11–19.

Jarecka, L. (1960) Life cycles of tapeworms from lakes Goldapivo and Mamry Polnoczne. *Acta Parasitologia Polonica*, **8**, 47–66.

Jensen, L.A., Schmidt, G.D. & Kuntz, R.E. (1983) A survey of cestodes from Borneo, Palawan and Taiwan, with special reference to three new species. *Proceedings of Helminthological Society of Washington*, **50**, 117–134.

Johri, G.N. (1959) Descriptions of two amabiliid cestodes from the little grebe, *Podiceps ruficollis*, with remarks on the family Amabiliidae Braun, 1900. *Parasitology*, **49**, 454–461.

Jones, A. (1994) Family Amabiliidae Braun, 1900. *In*: Khalil, L.F., Jones, A. & Bray, R.A. (Eds) *Keys to the cestode parasites of vertebrates*. Wallingford, UK: CAB International, pp. 399–405.

Korpaczewska, W. (1963) Tapeworms of aquatic birds in some Mazurian lakes. *Acta Parasitologica Polonica*, **11**, 315–336.

Korpaczewska, W. & Sulgostowska, T. (1974) Revision of the genus *Tatria* Kowalewski, 1904 (Cestoda: Amabiliidae), including description of *Tatria iunii* sp. n. *Acta Parasitologica Polonica*, **22**, 67–91.

Kowalewski, M. (1904) Studya helmintologiczne. VIII. O nowym tasemcu: *Tatria biremis* gen. nov., sp. nov. *Rozprawy Wydzialu Matematyczno-Przyrodniczego Polskiej Akademii Umiejetnosci, Dzial B, Krakow*. Seria III, **4**, 284–303.

Krabbe, H. (1869) Bidrag til Kundskab om Fuglenes Bændelorme. *Kongelige Danske Videnskabernes Selskabs Skrifter, Kjöbenhavn*, **8**, 251–368.

Lühe, M. (1910) Parasitische Plattwurmer. II. Cestodes. *Die Süsswasserfauna Deutschlands*, **18**, 1–151.

Macko, J.K. (1959) K helmintofaune potápkovitých vtákov na východnom Slovensku. *Československá Parasitologie*, **6**, 127–158. (In Czech).

Matevosyan, M. & Sailov, D.I. (1963) [A new cestode species *Tatria azerbaijanica* nov. sp. from grebes in the Kazyl-Agachs National Reserve.] *Trudy Vsesoyuznogo Instituta Gel'mintologii Imeni Akademika K.I. Skryabina*, **10**, 8–11. (In Russian).

Movsesyan, S.O. (1963) [A finding of the cestode *Tatria acanthorhyncha* (Wedl, 1855) in the ferruginous duck *Aythya nyroca*.] *In*: Ershov, V.S. (Ed.) *Gel'minty cheloveka, zhivotnykh i rastenii i bor'ba s nimi, k 85-letiyu Akad. K.I. Skryabina*. Moscow: Izolatel'stro Akademiya Nauk, pp. 157–159. (In Russian).

Mrazek, A. (1905) Über *Taenia acanthorhyncha* Wedl. *Sitzungsberichte der Koniglichen Böhmischen Gesellschaft der Wissenschaften. Mathematisch-naturwissenschatliche Classe,* Art. VII, 24 pp.

Mrazek, A. (1927) Organisace a ontogenie larvy druhu *Tatria acanthorhyncha* (Wedl). *Věstník Královské České Společnosti Nauk.* Art. VII, pp. 1–12.

Rees, G. (1973) Cysticercoids of three species of *Tatria* (Cyclophyllidea: Amabiliidae) including *T. octacantha* sp. nov. from the haemocoele of the damsel-fly nymphs *Pyrrhosoma nymphula* Sulz and *Enallagma cyathigerum* Charp. *Parasitology*, **66**, 423–446.

Ryzhikov, K.M. & Tolkacheva, L.M. (1981) [Acoleata – tapeworms of birds.] *In*: Freze V.I. (Ed.) *Osnovy Tsestodologii*. Moscow: Nauka, **10**, 215 pp. (In Russian).

Sey, O. (1968) Cestodes from birds living along the Tisza. *Tiscia* (*Szeged*), **4**, 69–78.

Sey, O. (1969) Galandfergek vadszatihalaszati azempontbol jelentös madarainkbol. *Allattani Kozlemenyek*, **56**, 121–129.

Shakhtakhtinskaya, Z.M. (1959) [Helminths of domestic and wild aquatic birds in Azerbaidzhan SSR.] *In*: Ershov, V.S. (Ed.) *Raboty po gel'mintologii, k 80-letiyu akad. K.I.Skryabina*. Moscow: Nauka, pp. 197–202. (In Russian).

Singh, K.P. (1959) Some avian cestodes from India, IV. Species belonging to families Amabiliidae, Diploposthidae and Progynotaeniidae. *Indian Journal of Helminthology*, **11**, 63–74.

Solomon, S.G. (1932) On a collection of parasitic worms from East Africa. *Journal of Helminthology*, **10**, 209–230.

Spassky, A.A. (1947) [The position of the genus *Echinorhynchotaenia* Fuhrmann, 1909 in the Cestoda.] *Doklady Akademii Nauk SSSR*, **58**, 513–515. (In Russian).

Spassky, A.A. & Spasskaya, L.P. (1976) [On the systematics of amabiliids and davaineids (Cestoda: Amabiliidae, Davaineidae).] *In*: Spassky, A.A., Shumilo, R.P. & Kharsun, A.I. (Eds) *Parazity teplokrovnyh zhivotnyh Moldavii*. Kishinev: Shtiintza, pp. 3–31. (In Russian).

Storer, R.W. (2000) The metazoan parasite fauna of grebes (Aves: Podicipediformes) and its relationship to the birds' biology. *Miscellaneous Publications. Museum of Zoology, University of Michigan*, No. 188, 90 pp.

Vasileva G.P., Georgiev B.B. & Genov T. (1999) Palaearctic species of the genus *Confluaria* Ablasov (Cestoda, Hymenolepididae): redescriptions of *C. multistriata* (Rudolphi, 1810) and *C. japonica* (Yamaguti, 1935), and a description of *Confluaria* sp. *Systematic Parasitology*, **44**, 87–103.

Vasileva, G.P., Gibson, D.I. & Bray, R.A. (2003a) Taxonomic revision of *Tatria* Kowalewski, 1904 (Cestoda: Amabiliidae): redescriptions of *T. biremis* Kowalewski, 1904 and *T. minor* Kowalewski, 1904, and the description of *T. gulyaevi* n. sp. from Palaearctic grebes. *Systematic Parasitology*, **54**, 177–198.

Vasileva, G.P., Gibson, D.I. & Bray, R.A. (2003b) 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*). *Systematic Parasitology*, **55**, 97–113.

Vasileva, G.P., Gibson, D.I. & Bray, R.A. (2003c) Taxonomic revision of *Joyeuxilepis* Spassky, 1947 (Cestoda: Amabiliidae): redescriptions of *J. biuncinata* (Joyeux & Baer, 1943), *J. decacantha* (Fuhrmann, 1913) and *J. pilatus* Borgarenko & Gulyaev, 1991. *Systematic Parasitology*, in press.

Vlug, J.J. & Fjeldså, J. (1990) Working bibliography of grebes of the world with summaries of current taxonomy and of distributional status. *Zoological Museum, University of Copenhagen*, 210 pp.

von Linstow, O. (1892) Beobachtungen an Helminthenlarven. *Archiv für Mikroskopische Anatomie*, **39**, 325–340.

Wedl, C. (1855) Charakteristik mehrerer grösstentheils neuer Tänien. *Sitzungsberichte der Akademie der Wissenschaften, Wien. Mathematisch-Naturwissenschatliche Classe*, **18**, 5–27.

Yamaguti, S. (1940) Studies on the helminth fauna of Japan. Part 30. Cestodes of birds. II. *Proceedings from Japanese Journal of Medical Science. VI. Bacteriology and Parasitology,* **1**, 175–211.

Yun Lian (1973) A survey of the helminths of birds from Bai-Yang-Dien Lake, Hopeh Province, China. III. Cestodes. *Acta Zoologica Sinica*, **19**, 257–266.

Zhuk, V.I., Tashliev, A.O. & Meredov, M. (1982) [Cestodes of birds from the Tedzhen valley.] *Izvestiya AN Turkmenskoy SSR, Seriya Biologicheskikh Nauk*, **6**, 47–53. (In Russian).