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Family Dioecocestidae Southwell, 1930

A. JONES

*International Institute of Parasitology, 395A Hatfield Road. St Albans,
Herts AL4 0XU, UK.*

Introduction

The family Dioecocestidae was first proposed by Southwell (1930b) with *Dioecocestus* Fuhrmann, 1900 as the type and only genus, distinguished by possession of entirely separate male and female strobilae. The composition of the family has varied as other dioecious cyclophyllideans from birds were added or removed. The absence of a vagina with its own aperture led to its being grouped close to or combined with other families which share this character. A number of species are imperfectly known, which has added to the confusion. Fuhrmann (1936b) suppressed it, placing *Dioecocestus* in the Acoleidae Fuhrmann, 1899* but in a distinct subfamily, the Dioecocestinae Southwell, 1930, with a separate subfamily Acoleinae for *Shipleya* Fuhrmann, 1907, *Gyrocoelia* Fuhrmann, 1899 and others. Most subsequent authorities, however, have accepted family status. Burt (1939a) restored the Dioecocestinae to family rank, including in it *Dioecocestus*, his new genus *Infula* and both *Shipleya* and *Gyrocoelia* on the grounds that the dioecious state was more significant than the absence of a vaginal pore. Burt's scheme was adopted by Wardle & McLeod (1952) and by Yamaguti (1959) who restored the Dioecocestinae for *Dioecocestus* and established the new subfamily Gyrocoeliinae for *Gyrocoelia*, *Shipleya*, *Infula* and his new genus *Pseudoshipleya*. Subsequent additions are *Neodioecocestus* Siddiqi, 1960 and *Echinoshipleya* Tolkacheva, 1979. On the basis of embryonic development and egg structure, Coil (1963, 1966, 1968, 1970a,b) retained Yamaguti's family and subfamilies, with *Dioecocestus* the sole genus in the Dioecocestinae and *Gyrocoelia* and *Shipleya* in the Gyrocoeliinae. He believed the latter two genera to be more closely related to each other than either *Infula* or *Dioecocestus* were to them and that *Infula* and *Shipleya* were sufficiently different in egg structure to be placed in separate families or at least subfamilies. Coil (1970a)

* Fuhrmann (1899a) erected the subfamily Acoleinae, elevating it to family rank (1907b) as the Acoleinidae, amended by Ransom (1909) to Acoleidae. According to ICZN Art. 36(a) the date for the family should be 1899.

recommended a separate subfamily for *Dioecocestus* on the grounds that the male and female organs were completely separated into different strobilae, but was unable to reach any conclusions on relationships from a study of the relatively unspecialized egg of *D. acotylus*.

More recently, Ryzhikov & Tolkacheva (1981) recognized the Dioecocestidae as a monotypic family and amended the status of the Gyrocoeliinae to family rank for the remaining genera, the main distinction being the retention of male copulatory organs in the female strobila in the Gyrocoeliidae. Schmidt (1986) adopted only the Dioecocestidae, without subfamilies, for all the dioecious genera of cyclophyllideans.

Traditionally, the characters used to distinguish taxa at the suprageneric level have been the completely or functionally dioecious nature of the strobila, the retention of male copulatory organs in the female strobila (of all genera except *Dioecocestus*), duplication of the male organs (in *Dioecocestus* only) and the absence of a typical vagina with an independent external aperture. Genera have been separated by the shape of the uterus, and the presence or absence of a rostellum and of rostellar armature.

There has been a great deal of debate on the dioecious nature of these cestodes, particularly in regard to *Gyrocoelia* and *Shipleya*. Reproductive processes in dioecious cestodes are not clearly understood. There are reports of both monoecious and dioecious species in the genus *Gyrocoelia* (see Burt, 1939a, Cable & Myers, 1956) but, while both conditions may exist, descriptions of some species are inadequate or contradictory and Burt (1939a) concluded that the evidence for the presence of testes in female strobilae was unsatisfactory. More recently described species have been established as dioecious (e.g. Mettrick, 1962; Rego, 1968; Cable & Myers, 1956). *G. albaredei* Lopez-Neyra, 1952, described as hermaphroditic, was based on a single specimen (Lopez-Neyra, 1952), attempts to trace which have been unsuccessful. The species was regarded as invalid by Baer (1959) and Ryzhikov & Tolkacheva (1981). While *Gyrocoelia* has been generally accepted as functionally dioecious, Rausch & Rausch (1990) have shown that specimens of the related genus *Shipleya* can be hermaphroditic. *S. inermis* is normally functionally dioecious but some members of either sex were found with rudimentary organs of the other and two predominantly male strobilae had fully functional female organs capable of egg production. It appears, however, that testes and female organs are generally not found in the same strobila. In female *S. inermis* with testes, the testes were underdeveloped, lacking a connection to the genital duct, and the worms were functionally female (Rausch & Rausch, 1990).

The absence of a typical vagina, although not restricted to the dioecious cyclophyllideans, has been one of their main characters. *Dioecocestus* females have a vagina with an occluded distal region which does not open externally but a separate vagina with an exterior aperture has generally been regarded as absent in the other genera. Various authors have, however, described other ducts which fulfil the same function. Burt (1939a) described a narrow duct connecting the cirrus-sac in female *Infula burhini* to the seminal receptacle and believed that insemination by a male strobila took place via the cirrus-sac. Coil (1955) reported a similar duct in *I. macroballus* (synonymized with *I. burhini* by Ryzhikov &

Tolkacheva, 1981) and (1963) in *Gyrocoelia pagollae*. It has also been found in *Shipleya inermis* by Rausch & Rausch (1990). They suggested that *S. inermis* had evolved from a hermaphroditic ancestor and that, during evolution to the dioecious state, the cirrus-sac was retained in the female where it functioned as a vagina, a separate vagina was lost and a genital duct was formed by fusion of the vas deferens with the proximal region of the original vagina. It seems clear that at least in *Shipleya* and *Infula*, and possibly in *Gyrocoelia*, there is a modified duct which functions as a vagina but a typical separate vagina with an external aperture is lacking in all genera.

The key presented here is intended to facilitate identification and does not attempt to reflect phylogenetic relationships which will become clearer when more information is available on life-cycles and embryonic development. The family Dioecocestidae is considered to include cyclophyllideans which are anatomically or functionally dioecious, in which the male copulatory apparatus (but not the testes) is retained in the female strobila of all but one genus and may be modified for insemination, and in which a typical vagina with an external aperture is lacking. The Dioecocestinae has been retained for *Dioecocestus*, in which the sexes are entirely separate, and the Gyrocoeliinae for the remaining genera which are normally functionally dioecious and in which the female strobila retains a cirrus-sac like that of the male in appearance.

Neodioecocestus Siddiqi, 1960, described from a single male specimen lacking a rostellum or hooks by Siddiqi (1960) has not been accepted as valid. *Dioecocestus* as presently constituted includes species with or without a rostellum, rostellar armature or suckers and *Neodioecocestus* falls within the current concept of the genus, in which these differences have been treated as significant at the species level only. Several species are poorly known and attempts to obtain specimens of these and the type of *Neodioecocestus cablei* have not been successful. Outside *Dioecocestus*, the presence of a rostellum and rostellar armature has been awarded greater significance. The presence of a rostellum and the presence and nature of its armature are the characters distinguishing *Shipleya* and *Echinoshipleya* Tolkacheva, 1979, which are both accepted here, following Ryzhikov & Tolkacheva (1981) and Schmidt (1986). However, with regard to *Dioecocestus*, it is considered preferable to continue the traditional conservative approach rather than to proliferate genera based on species which are still, as yet, inadequately known. *Hamulocestus* Spasskii, 1992 is considered synonymous with *Dioecocestus*.

Following Ryzhikov & Tolkacheva (1981), *Pseudoshipleya* Yamaguti, 1959 is synonymized with *Infula*. The type-species, *Shipleya farrani*, described by Inamdar (1942), can be excluded from *Shipleya* by the presence of an unarmed rostellum and a ring-shaped uterus. The original description differs from *Infula* in that a small number of testes were said to be present 'only in a few mature segments'. The type specimens are not available for examination but it seems possible that ovarian lobes have been misinterpreted as testes.

Most illustrations are original; others are redrawn from the sources acknowledged in the figure legends.

Family Dioecocestidae Southwell, 1930

(Syn. Gyrocoeliidae Yamaguti, 1959)

Diagnosis: Large cestodes with numerous proglottids. Entirely or partly dioecious. Male and female strobilae entirely separate or female strobila retains male copulatory apparatus. Rostellum present or absent; if present, armed or unarmed. Suckers present or absent. Longitudinal musculature in two layers, transverse musculature in three. Male organs single or double. If single, genital pores alternate regularly in male strobila. Testes numerous, in one median group or two lateral groups. Internal seminal vesicle well-developed or not, external seminal vesicle absent. Cirrus-sac muscular. Cirrus robust, armed with spines. Female organs single. Genital pores absent in *Dioecocestus* female strobila, alternate regularly or irregularly in other genera. Ovary lobed, bialate to fan-shaped. Vitellarium postovarian. Seminal receptacle poral to vitellarium or between ovary and vitellarium. Typical vagina with external opening absent, may be replaced functionally in female strobila by the modified male duct. Young uterus transverse, ring-shaped or horseshoe-shaped. Uterine pore present or absent. Eggs oval. Parasites of birds (Charadriiformes and Podicipediformes). Type-genus *Dioecocestus* Fuhrmann, 1900.

Key to subfamilies

1a. Male and female strobilae entirely separate. Male genitalia duplicated. Vestigial vagina present, lacking external opening. Uterus a transverse tube
 Subfamily Dioecocestinae Southwell, 1930.

Diagnosis: Strobila large. Rostellum present or absent; if present, armed or unarmed. Suckers present or absent. Genital ducts pass between osmoregulatory canals. Male genitalia duplicated, male pores bilateral. Cirrus-sac small, muscular; cirrus spinous. Testes numerous, in two lateral groups. Female organs single. Ovary multilobed, usually bialate. Vitellarium lobed, postovarian. Seminal receptacle slightly poral to vitellarium, connects with vagina. Vagina alternates irregularly. Early uterus a transverse tube, becoming lobate. In grebes.

1b. Female strobila retains male copulatory apparatus. Male genitalia single. Typical vagina absent, may be functionally replaced by modified duct. Early uterus ring- or horseshoe-shaped
 Subfamily Gyrocoeliinae Yamaguti, 1959.

Diagnosis: Functionally dioecious. Rostellum present or absent; if present, armed or unarmed. Suckers present. Reproductive organs single. Genital ducts pass between osmoregulatory canals. Male copulatory apparatus present in female strobila. Cirrus-sac large, muscular. Cirrus robust, armed with numerous spines. Testes numerous, in single central group. Genital pores alternate regularly in male strobila, regularly or irregularly in female strobila. Ovary submedian, multilobed, bialate to fan-shaped. Vitellarium lobed, postovarian. Seminal receptacle between ovary and vitellarium. Uterus lobate when mature. Uterine pore present or absent. In charadriiform birds.

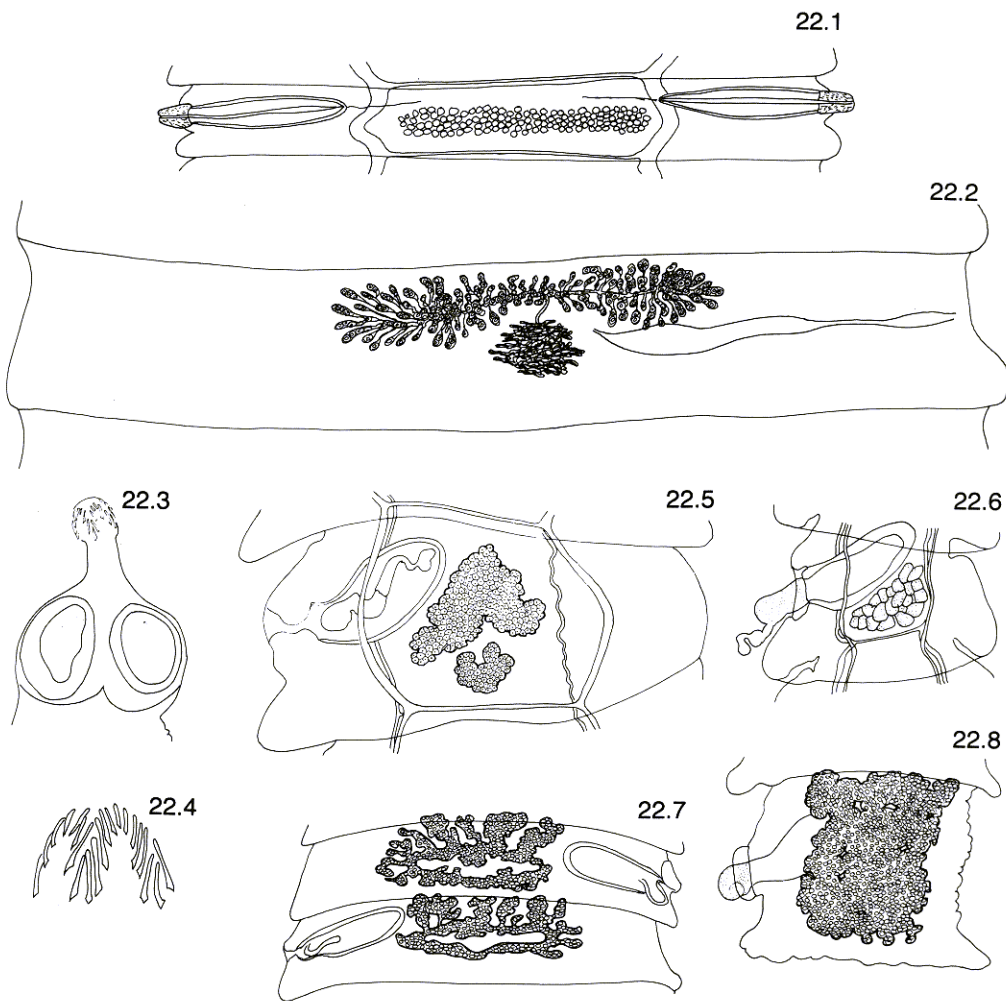
Subfamily Dioecoestinae Southwell, 1930

This subfamily contains only one genus.

Genus *Dioecocestus* Fuhrmann, 1900 (Figs 22.1, 22.2)

(Syns *Hamulocestus* Spasskii, 1992; *Neodioecocestus* Siddiqi, 1960)

Diagnosis: With the characters of the subfamily. In Ciconiiformes and Podicipediformes. Cosmopolitan. Type-species *D. paronai* Fuhrmann, 1900.



Figs 22.1, 22.2 *Dioecocestus acotylus* Fuhrmann, 1904. 22.1. Male proglottid. 22.2. Female proglottid. After Rysavy & Macko (1973).

Figs 22.3-22.8 *Gyrocoelia perversa* Fuhrmann, 1899. 22.3. Scolex. 22.4. Rostellar hooks. 22.5. Female proglottid. 22.6. Male proglottid. 22.7. Early gravid proglottid. 22.8. Gravid proglottid.

Subfamily Gyrocoeliinae Yamaguti, 1959

Key to genera

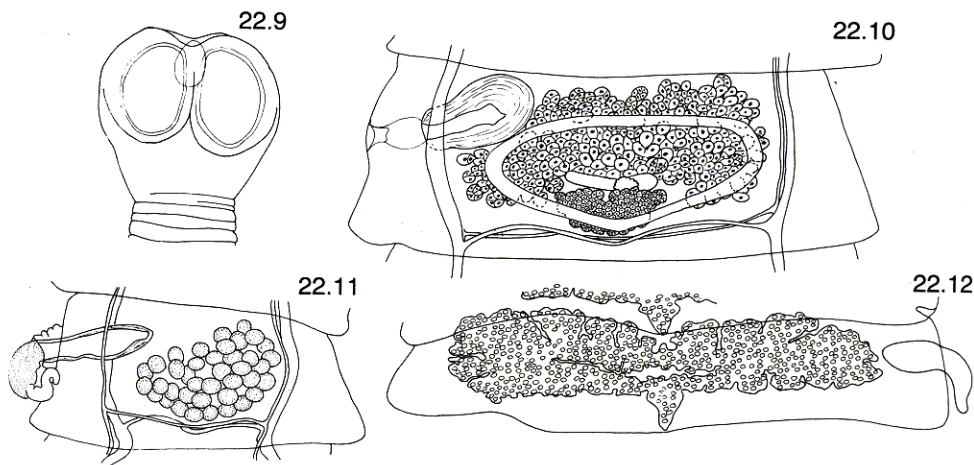
- 1a. Rostellum present. Uterus ring-shaped, uterine pores present 2.
 1b. Rostellum present or absent. Uterus horseshoe-shaped, uterine pores absent 3.

2a. Rostellum armed with a single zig-zag row of hooks
 *Gyrocoelia* Fuhrmann, 1899. (Figs 22.3–22.8)
 (Syn. *Brochocephalus* Linstow, 1906.)

Diagnosis: Strobila functionally dioecious. Rostellum capitate. One set of reproductive organs per proglottid. Genital pores alternate regularly in males, regularly or irregularly in females. Cirrus-sac large, muscular, retained in female strobila; cirrus robust, conspicuously armed. Genital ducts pass between osmoregulatory canals. Testes numerous, in median group. External seminal vesicle absent, internal seminal vesicle well-developed or not. Ovary median, bilate to multilobed, fan-shaped. Seminal receptacle between ovary and vitellarium. Typical vagina absent, may be replaced functionally by cirrus-sac and modified male duct. Young uterus ring-shaped, becoming lobed. Uterine pores present. Eggs oval. In Charadriiformes and occasionally Pelecaniformes. Cosmopolitan. Type-species *G. perversa* Fuhrmann, 1899.

2b. Rostellum present but unarmed
 *Infula* Burt, 1939. (Figs 22.9–22.12)
 (Syn. *Pseudoshipleya* Yamaguti, 1959.)

Diagnosis: Strobila functionally dioecious. One set of reproductive organs per proglottid. Genital pores alternate regularly in males, regularly or irregularly in



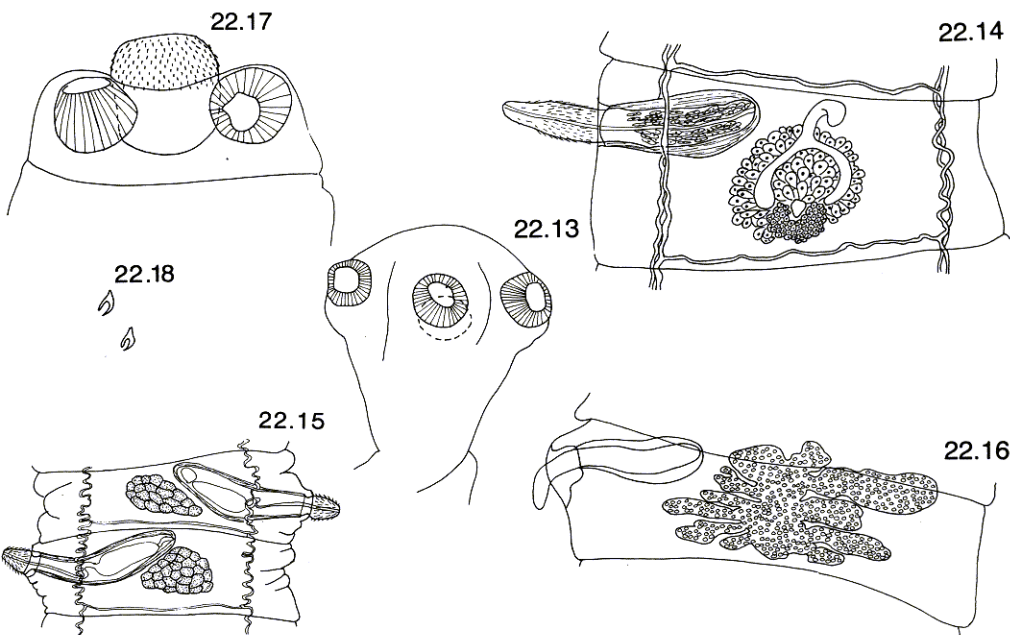
Figs 22.9–2.12 *Infula burhini* Burt, 1939. 22.9. Scolex. 22.10. Female proglottid. 22.11. Male proglottid. 22.12. Gravid proglottid.

females. Cirrus-sac large, muscular, retained in female strobila. Cirrus robust, armed. Genital ducts pass between osmoregulatory canals. External seminal vesicle absent, internal seminal vesicle present. Testes numerous, in median group. Ovary median, bialate, multilobed. Seminal receptacle between ovary and vitellarium. Typical vagina absent but replaced functionally by cirrus-sac and modified male duct. Uterus ring-shaped, becoming lobate. Uterine pore present at posterior margin of proglottid. Eggs oval; middle envelope thick, with polar plugs. In Charadriiformes. Cosmopolitan. Type-species *I. burbini* Burt, 1939.

3a. Rostellum absent *Shipleya* Fuhrmann, 1908. (Figs 22.13–22.16)

Diagnosis: Normally functionally dioecious but may be incompletely gonochoristic or hermaphroditic. Reproductive organs single. Genital pores alternate regularly. Genital ducts pass between osmoregulatory canals. Cirrus-sac large, muscular. Cirrus armed. Testes numerous, in median group. Ovary median, multilobed, fan-shaped. Cirrus-sac retained in female strobila, functions as vagina. Typical vagina absent. Seminal receptacle between ovary and vitellarium, linked to cirrus-sac by narrow duct. Early uterus horseshoe-shaped with anterior arm. Uterine pores absent. In Charadriiformes. North and South America. Type-species *S. inermis* Fuhrmann, 1908.

3b. Rostellum present, armed with rows of numerous small aploparaksoid hooks *Echinoshipleya* Tolkacheva, 1979. (Figs 22.17, 22.18)



Figs 22.13–22.16 *Shipleya inermis* Fuhrmann, 1908. 22.13. Scolex. 22.14. Female proglottid. 22.15. Male proglottids. 22.16. Gravid proglottid.

Figs 22.17, 22.18 *Echinoshipleya semipalmati* Tolkacheva, 1979. 22.17. Scolex. 22.18. Rostellar hooks. After Tolkacheva (1979).

Diagnosis: Strobila functionally dioecious. Reproductive organs single. Genital pores alternate regularly in both sexes. Cirrus-sac large, muscular, retained in female strobila. Genital ducts pass between osmoregulatory canals. Testes in single median group. Ovary median, multilobed, fan-shaped. Typical vagina absent. Early uterus horseshoe-shaped with anterior arm. Uterine pores absent. Eggs oval. In Charadriiformes. USSR. Type-species *E. semipalmati* Tolkacheva, 1979.