



***Raillietiella trachea* n. sp., a pentastomid from the trachea of an oriental white-backed vulture *Gyps bengalensis* taken in Pakistan, with speculation about its life-cycle**

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Abstract

A cephalobaenid pentastomid, *Raillietiella trachea* n. sp., from the trachea of a fledgling oriental white-backed vulture *Gyps bengalensis* taken in Punjab Province, Pakistan, is described. This is the first record of a pentastomid from a fully terrestrial bird. Overall, gross morphology was typical of *Raillietiella* Sambon, 1910 in most respects. However, the hooks of *R. trachea* were of equal size, whereas in other members of the genus anterior hooks are smaller than the posterior hooks. The diagnosis of *R. trachea* was made on the basis of four near-patent females, all of which contained relatively few eggs (c.570), all at the same stage of maturity. Comparison with the only other genus known to infect birds (two species of *Reighardia* Ward, 1899 from the air-sacs of marine birds) revealed striking parallels in this aspect of the functional anatomy of the female reproductive tract. As far as we know, this mode of egg-production is not found in other raillietiellids. Extrapolating primarily from the experimental life-cycle studies of *Reighardia sterna*e (Diesing, 1864) Ward, 1899, we surmise that the life-cycle of *R. trachea* has to be direct and that parasite behaviour is an integral part of parasite transmission. The evidence suggests that transmission is from vulture-to-vulture, *per os*.

Introduction

The phylum Pentastomida comprises two orders that can be readily distinguished primarily by differences in the disposition of the hooks relative to the mouth and on the form of the reproductive tract. About 130 species of pentastomids have been described and, in the 40 or so belonging to the order Cephalobaenida, the ventral mouth is nearly terminal and anterior to the hooks which are disposed in a trapezium. The uterus is saccate and the vagina opens anteriorly on the ventral surface of the abdomen close to the junction of the trunk with the head (Riley, 1986; Bush et al., 2001).

The order Cephalobaenida comprises just three genera, one of which, *Cephalobaena* Heymons, 1935 is monotypic, and this species inhabits the lung of South American tree snakes. The life-cycle is unknown. *Reighardia* Ward, 1899 has two species that

infect marine birds, such as gulls and alcids (guillemots and puffins) (Riley, 1972; Threlfall, 1971; Dyck, 1975; Böckeler, 1984), and hitherto these are the only pentastomids known to utilise an avian definitive host. An unusual mode of gull-to-gull transmission occurs during the direct life-cycle of *Reighardia sterna*e (Diesing, 1864) (see Banaja et al., 1975; Böckeler, 1984). The remaining genus, *Raillietiella* Sambon, 1910, embraces at least 35 species, most of which inhabit the lungs of reptiles (snakes, lizards and amphisbaenians), but three species infect amphibian lungs (Krishnasamy et al., 1995). Insects, amphibians, lizards and possibly snakes are intermediate hosts in these life-cycles (Ali, 1985; Bosch, 1986; Riley, 1994).

Here we describe mature females of a new raillietiellid from the trachea of an aberrant host, a vulture taken in Pakistan, and this is the first pentastomid

known to attain maturity in a fully terrestrial bird. Speculation about the life-cycle is also presented, based largely upon the unusual functional anatomy of the female reproductive tract and its close correspondence to that of *Reighardia* spp. (Banaja et al., 1976).

Materials and methods

Detailed necropsies of 32 oriental white-backed vultures *Gyps bengalensis* Gmelin were carried out and pentastomids were found in the trachea of a single host, a male fledgling that was dying of starvation. A total of four gravid female raillietiellids were recovered from the trachea, three from the mid-section and one from the bifurcation of the bronchi. These were fixed and stored in 70% alcohol for later examination. One paratype female was punctured and this was whole-mounted on a slide in Hoyer's medium, following the removal of the head region, which was flattened separately under a cover-slip for observation of the hooks and mouth. One of the remaining three specimens was observed intact in a water film under an environmental scanning electron microscope (Philips XL 30 ESEM FEG), following progressive hydration (at an accelerating voltage of 25 kV, held at 6 Torr with a stage cooled to 4°C). The specimen was then returned to 70% alcohol and dissected in Hoyer's medium on a slide for a total egg-count and other measurements. The two remaining specimens, a holotype and paratype, were left intact. Attempts to count the annuli were made on all four specimens, but always the annuli on the anterior third were compressed to varying degrees and precise counts were not possible. Therefore, such counts were estimated to the nearest one, or even two, annuli. All measurements are in micrometres, except where indicated. Hooks were measured along two dimensions: AB, the distance from hook tip to notch at the top of the hook shank, where it united with the dorsal surface of the barb, and BC, the distance from this notch to the extreme tip of the flared base of the shank (see Figure 1A of Riley, McAllister & Freed, 1988).

Raillietiella trachea n. sp.

Type-host: Oriental white-backed vulture, *Gyps bengalensis* Gmelin.

Type-locality: Dholewala, Punjab Province, Pakistan (collected by Dr Martin Gilbert, May 2001).

Site: Trachea.

Type-material: Holotype female; US National Parasite Collection (USNPC) accession no. 92561). Paratypes: three females (USNPC accession no. 92562)

Description (Figure 1)

All 4 specimens possess a small, broadly triangular and pyramidal head, flattened on the ventral surface and which merged smoothly with a uniformly thick, squat trunk (in most raillietiellids the trunk gradually tapers over the last third or so towards a bluntly pointed caudal extremity). The trunk terminated as a rounded tail in the 3 paratype specimens, but was slightly more pointed in the distinctly banana-shaped holotype (Figure 1A). In all 4 worms, the tail was devoid of lobes and the anal opening could not be seen. The 3 intact specimens measured 5.1–5.35 (mean 5.25) mm in length by 1.1–1.25 mm wide. Annuli were prominent over most of the trunk, especially over the ventral surface, but were very compressed and indistinct anteriorly. The annulus number was estimated at 21–23, in addition to the terminal segment. ESEM observations of the head revealed a comparatively large oval mouth flanked by 4 apparently equal-sized, but very small, protruding hook barbs. No other distinguishing features were apparent because wrinkling of the cuticle obscured surface details. Hooks, held within a U-shaped fulcrum and measured on the 2 dissected specimens, were exceptionally tiny and therefore difficult to flatten. This may account for the observed small variation in their measurements. Hooks were measured as follows: anterior AB 42–47, BC 68–84; posterior AB 47, BC 73–78. Unusually, the hook shank was bent through almost 90° in its mid-section (Figure 1B,C). The mouth, which could only be measured on one specimen, was supported by a simple Y-shaped cadre of chitin that was 89 long and 110 wide and the delicate barrel-shaped pharynx measured 92 × 110 (Figure 1D,E).

The egg mass in the uterus of the slide-mounted specimens was composed of mostly maturing, oval eggs measuring 167 (158–178) × 109.5 (99–119) which were at the same stage of development. A thin outer egg-shell, enclosed a folded and pleated inner cuticular embryonic membrane which was continuous with an apical depression above the dorsal organ (Figure 1H). Apart from the elliptical annulus (measuring 18 × 8) that constituted the apex of the dorsal

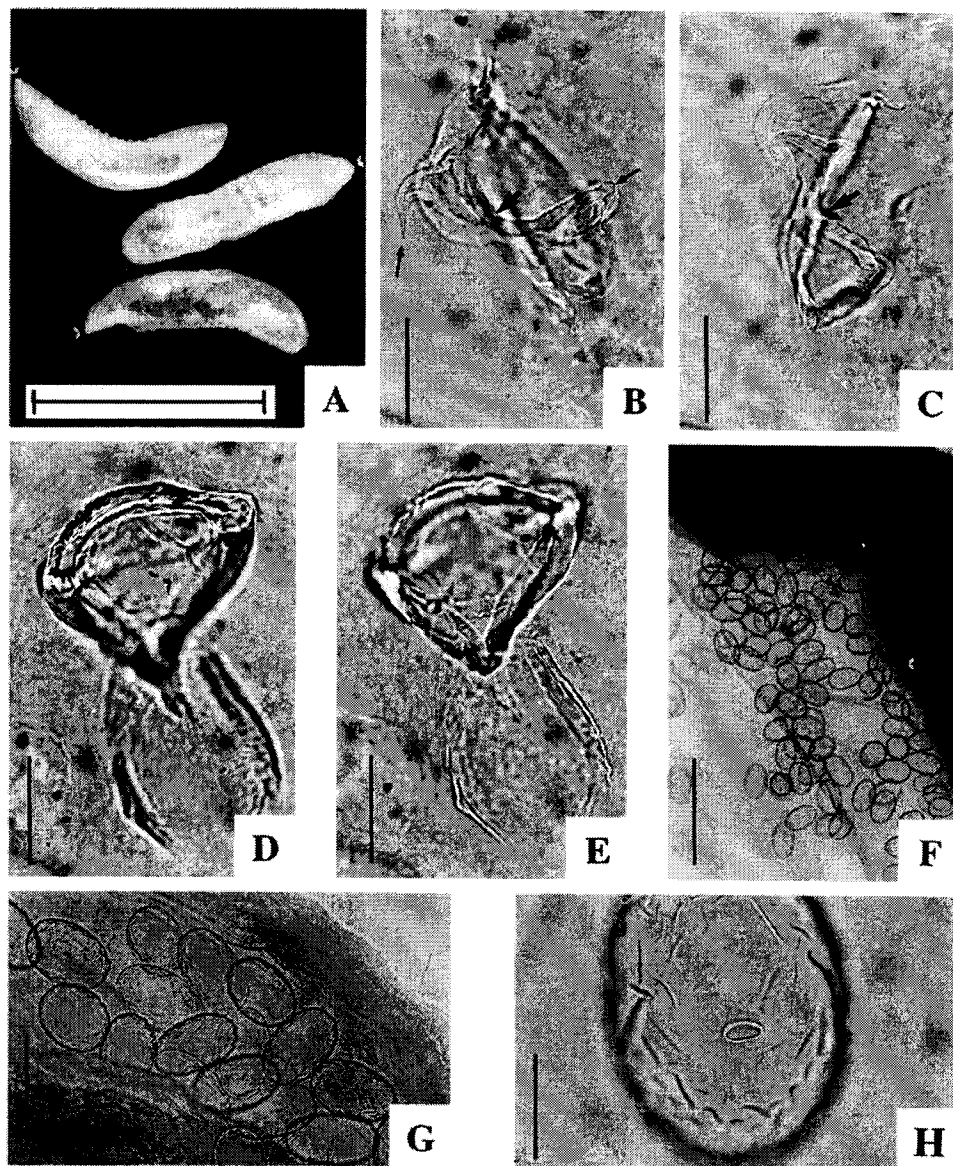


Figure 1. Raillietiella trachea n. sp. A. Whole holotype (top) and paratype specimens showing variation in external morphology. The small arrows indicate the head in each specimen. The top and bottom specimens are viewed from the lateral aspect and their inner curvature is the ventral surface, upon which some annulations can be seen. The middle specimen, which was subsequently observed by SEM and then dissected for egg-counts etc., is viewed from the ventral surface; B. The posterior hook of a paratype female. The point of the hook barb is arrowed (left) as is the notch where the hollow barb closes at the rear (uppermost arrow). AB is the distance between these two points. The distance between the notch and the base of the hook (also arrowed) is measurement BC. The large arrow indicates the bend in the mid-section of the hook; C. The anterior hook of the other dissected paratype female showing the right-angled bend in the mid-section of the hook (arrowed). The final image has been spliced because the barb and the base of the hook were photographed in slightly different focal planes; D,E. The mouth of a paratype female photographed in two different focal planes. The Y-shaped oral cadre is towards the top and the barrel-shaped pharynx is below; F. Part of the trunk of a paratype female showing the black intestine and a mass of eggs. All eggs are of a similar size except for a cluster of four small, unfertilised eggs immediately to the left of the white arrow; G. Detail of some maturing eggs showing a thin outer egg-shell, with the folded cuticle of the larva below; H. The elliptical annulus which surrounds the apex of the dorsal organ, photographed in plan view. Pleats in the embryonic cuticle are evident beneath the egg-shell, which is out of focus. Scale-bars: A, 5 mm; B-E,H, 50 μ m; F, 1 mm; G, 200 μ m.

organ, no other details of the embryo were apparent. The entire egg burden, counted on the dissected slide-mounted female, whose uterus had been partly shredded, totalled between 560–580 eggs and the vast majority of these were of a similar size and stage of development. About 30 comparatively small eggs were probably unfertilised (Figure 1F-H).

Discussion

In ascribing the new cephalobaenid species from a vulture to a genus, the possibility, albeit remote, that the host could have acquired an adult pentastomid infection whilst scavenging an already infected definitive host should be borne in mind. This is especially important given that experimentally transplanted pentastomids have been known to survive in totally unnatural hosts for long periods (reviewed in Riley, 1994). Nevertheless, two of the three cephalobaenid genera can be immediately eliminated from further consideration on purely morphological grounds. *Cephalobaena tetrapoda* Heymons, 1922, from South American tree snakes, is characterised by several primitive features, most notably the unique extended podial lobes and elongate head (Haffner & Rack, 1971; Böckeler & Storch, 1990). Mature female *Reighardia* species from marine birds are elongate (7–8 cm) and slender, devoid of clear annulations, and the cuticle possesses numerous tubercles which impart a distinctive knobbly appearance to the surface not found in any other species (Haffner & Rack, 1971; Dyck, 1975).

In virtually all aspects of its morphology *R. trachea* is typical of *Raillietiella*, the most variable of the genera comprising the Cephalobaenida. There are only two points of departure; the equal size of the hooks and the mode of egg maturation and deposition. The latter may have implications for the life-cycle (see below). The taxonomic and systematic groupings of *Raillietiella* was revised by Ali et al. (1985). Six groups were recognised, a scheme based primarily on differences in host preferences. However, 14 species, all infecting small insectivorous lizards, were further subdivided into two (Groups I and II) because of marked differences in the morphology of the posterior hook, an idea originally proposed by Self (1969). In both of these groups, the anterior hook pair is larger than the posterior pair, often quite markedly so, and this is also true of Group III species (from varanid lizards), Group IV (from amphisbaenians) and Group VI (from snakes)

(Ali et al., 1985). Two sharp-hooked raillietiellids described since 1985 belong to Group VI (McAllister et al., 1993). Thus, *R. trachea* n. sp., with similar-sized hooks, cannot be closely related to any of the above.

Two species comprise Group V species from toads and one, *R. rileyi* Krishnasamy, Jeffery, Inder Singh & Oothuman, 1995, is closest to *R. trachea* in that female is small (4.5–6 mm), with tiny hooks (anterior AB 70, BC 123; posterior AB 80, BC 148). Thus, in this species as well, the anterior hooks are smaller than posterior hooks and, incidentally, *R. rileyi* has 29 annuli (Krishnasamy et al., 1995). In conclusion, *R. trachea* has a unique combination of morphological attributes that separate it from all known raillietiellids. Additionally, the hooks of all members of the genus are bent in the mid-section, but none so markedly as those found in *R. trachea* (Figure 1B,C). *R. trachea* merits the creation of an additional Group (VII) and its taxonomic status may require further revision once the male is described.

R. trachea matures small numbers of eggs (about 570) in a single batch – this observation constitutes an important clue concerning the life-cycle; but, before considering the putative role of pentastomid behaviour in the infection of new hosts, it is useful to review the general life-cycle strategies of helminths infecting carrion-feeding birds. There is some question as to how birds like Old World vultures become infected with helminth parasites, many of which have arthropod first intermediate hosts. The answer may lie in paratenic or transport hosts, in which the parasites do not undergo any development, but remain infective to another host. These paratenic hosts, which may be amphibians, reptiles or mammals, can concentrate large numbers of larval stages and bridge an important trophic gap between the intermediate and definitive hosts (Roberts & Janovy, 1996).

Although data on the helminths of vultures of the genus *Gyps* are limited – these are mostly restricted to descriptions of new species – the commonest parasites recorded are nematodes of the genera *Procyrnea* Chabaud, 1958 (as *Habronema* Diesing, 1861) and *Porrocaecum* Railliet & Henry, 1912 (= *Belanisakis* Maplestine, 1932) and acanthocephalans of the genus *Centrorhynchus* Lühe, 1911 (Samedov, 1972; Gupta & Kumar, 1980; Naidu, 1981; Rathore & Nama, 1985). Interestingly, the only helminth found in the present survey, *Porrocaecum gypsei* (Naidu, 1981), was recorded in virtually every bird. All three genera are known to utilise paratenic hosts in their life-cycles. Hsu & Chow (1938) found infective larvae of *Pro-*

cyrnea mansioni (Seurat, 1914), a common parasite of hawks and falcons, encysted in the stomach wall of toads (*Bufo bufo*). When the toads were fed to hawks, adult worms were found in the proventriculus 18-44 days later. Infective larvae of *Porrocaecum angusticolle* (Molin, 1860), another parasite of hawks, have been found in the intestines and under the skin of shrews and moles (Anderson, 2000), and infective cystacanths of *Centrorhynchus conspectus* Van Cleave & Pratt, 1940, a parasite of North American owls, have been found in the mesenteries of snakes and amphibians (Richardson & Nickol, 1995).

Importantly, it should be noted that raptors actively hunt and catch small vertebrate prey species, whereas vultures are strictly carrion-feeding birds and scavenge for comparatively large items of prey. However, in both groups of birds, it seems that the helminths mentioned above commonly utilise arthropod first intermediate hosts, and larvae are then transmitted up an essentially carnivore-to-carnivore food chain. This poses a major problem because, in the Punjab, *Gyps bengalensis* lives on domestic livestock; mainly cattle, buffalo and donkey, and less commonly dog, goat, horse and camel. Only one species on this list is a carnivore. However, Martin Gilbert has observed that even donkeys may be considered as scavengers and will feed on just about anything they can find, including their own kind!

Despite the potential for concentrating larvae within 'carnivorous' paratenic hosts, from an epidemiological standpoint, it seems inevitable that in all cases adult helminths in carrion-feeding birds must discharge considerable numbers of eggs, over a long time span, in order to achieve transmission. This stands in complete contrast to perceived mode of egg production and release in *R. trachea*.

During the prepatent period of most cephalobaenids, eggs accumulate within a saccate uterus after being shed continuously from the ovary and fertilised by sperm stored within the paired spermathecae. The uterus contains eggs of varying sizes, reflecting different states of maturity (Riley, 1994). Cephalobaenids release only mature eggs containing a fully-developed, clawed larva that are immediately infective, and the patent period extends from months to years. In raillietiellids, however, patency begins when the uterus contains a mixture of eggs, with as few as 25% of the total egg load being fully embryonated (Ali & Riley, 1983; Winch & Riley, 1985). This is possible because the vagina is equipped with a selective filter, which, paradoxically, allows large mature embryonated eggs

to pass through for deposition, whilst small immature eggs are retained (Riley, 1986). Thus, many tens of thousands of eggs may be shed over a lifetime, a pattern that is shared by many parasites. We will argue that does not occur in *R. trachea* (and *Reighardia* spp.) because, here, exceptionally low fecundity may be compensated for by a parasite behavioural component directed at increasing the efficiency of transmission.

Both *R. sterna* and *R. lomviae* Dyck, 1975 carry modest egg-loads of 2,660-2,900 and 3,800, respectively (Dyck, 1975; Banaja et al., 1976). Certainly, in the case of *R. sterna*, the prepatent period terminates when all of the eggs in the uterus are fully infective, and females die following a patent period of just a few days duration. Banaja et al. (1976) demonstrated experimentally that, when female *R. sterna* attain patency, they migrate from the air-sacs of the gull host (via the trachea, mouth and alimentary tract?), while simultaneously shedding eggs over 5-11 days before they die. Banaja et al. (1976) and Böckeler (1984) postulated that this behaviour facilitated transmission because migrating gravid females probably irritated their hosts sufficiently for them to regurgitate their stomach contents. The ingestion of the egg-contaminated vomit by other gulls would then effect transmission. Inevitably, autoreinfection safeguards this somewhat tenuous life-cycle, and this may occur in another species of *Raillietiella* (reviewed in Riley, 1994).

A saccate uterus containing a cohort of eggs at the same stage of development in *R. trachea* suggests very clear parallels with *Reighardia* spp. Furthermore, the four nearly mature females of *R. trachea* infested a fledgling vulture that had only ever been fed by its parents. Raillietiellids are very slow to mature (Ali & Riley, 1983) and it is apparent that the young vulture must have been infected, whilst on the nest, directly by eggs derived from a parental infection. The other possible mode of infection, via encysted nymphs present in regurgitated crop contents, is improbable, if not impossible given the low total egg output of *R. trachea*, and can be discounted. Vultures regurgitate to feed their young, are messy, aggressive and highly competitive feeders at a carcass, and will also regurgitate food when attacked or stressed. Clearly, there is ample opportunity for cross infection with parasite eggs, either between adults or from adult to chicks.

Furthermore, the total egg load of gravid female *R. trachea* of about 570 eggs indicates not only a direct life-cycle, but also a parasite behavioural component directed towards increasing the efficiency of the trans-

mission process. For example, we speculate that patent females invade the mouth or throat from the trachea, thereby triggering adverse host reactions culminating in retching and regurgitation [as is thought to happen in the case of *R. sterna* (see Banaja et al., 1976)].

Pentastomid-induced vomiting in hosts is also tenuously linked to transmission in the advanced pentastomid species *Linguatula serrata* Frölich, 1879 that matures in the nasal sinuses of dogs. Infections are acquired when the 3 mm-long infective nymphs, encapsulated in the viscera of domestic herbivores, are ingested in meat or offal. Dogs fed bait containing 5-50 nymphs show early symptoms of nausea, followed by vomiting 5-40 minutes after feeding (Sinclair, 1954). Here, however, vomiting significantly reduces the time taken for nymphs to migrate from the stomach to the nasal sinuses (Sinclair, 1954).

Yet another example of mouth-to-mouth transmission in a pentastomid life-cycle is provided by a most unusual cephalobaenid, *Rileyella petauri* Spratt, 2003, where the minute, 1.5 mm-long females occur in the nasal sinuses of the nectar- and pollen-feeding marsupial sugar glider *Petaurus breviceps* in Australia (Spratt, 2003). This diminutive species, the only one known to infect a mammalian definitive host, is unusual because all instars, with the exception of the adult female, inhabit the lungs. Riley (1994), first speculated that a direct life-cycle must operate in this instance, where gravid females might deposit the unusually large eggs on the long, protrusive tongue. This organ would then contaminate feeding sites (e.g. flowers, sap weeps on tree trunks) thereby transferring eggs to other hosts feeding subsequently at the same site. Amazingly, gravid *R. petauri* contain only seven fully-embryonated eggs at any one time and, furthermore, one of the two infected sugar gliders examined by Spratt (2003) had acquired its pentastomids at a very young age, well in advance of independence. This suggests a direct, probable oral form of transmission, from adult to offspring.

Sugar gliders, like birds, have a coughing and sneezing reflex and it is remarkable that any pentastomid is able remain attached in a potentially hazardous niche, such as the upper respiratory tract. Other pentastomid genera occupying this site, *Leiperia* spp. in the trachea of crocodiles and *Linguatula* spp. in the nasal sinuses of mammals, are securely anchored, being either partly buried in the submucosa, or interleaved between the turbinate bones, respectively (Riley & Huchzermeyer, 1996; Haugerud & Nilssen, 1986).

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