

Research Note

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Bertiella anapolytica Baylis, 1934 (Cestoda, Anoplocephalidae) in *Rattus* spp.: morphology, distribution and evolutionary history

Voitto Haukisalmi¹ , Alexis Ribas^{2,3}  and Serge Morand⁴ 

¹ Organismal and Evolutionary Biology Research Programme, Faculty of Biological and Environmental Sciences, Helsinki University, Finland;

² Department of Biology, Health and Environment Faculty of Pharmacy and Food Science, University of Barcelona, Spain;

³ Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona, Spain;

⁴ IRL HealthDEEP, CNRS – Kasetsart University – Mahidol University, Bangkok, Thailand

Abstract: The present study describes the morphology and phylogenetic position of two specimens of *Bertiella* Stiles et Hassall, 1902 (Cestoda, Anoplocephalidae) from *Rattus tanezumi* (Temminck) (Muridae) from Đồng Tháp Province in southern Vietnam. The phylogenetic analysis was based on sequences of the large subunit ribosomal RNA gene (28S). The specimens were described and shown to be morphologically similar to *Bertiella anapolytica* Baylis, 1934 from *Rattus* spp. from Indonesia (Sumatra, type locality) and Australia, except for a few quantitative differences. The identification was confirmed by the phylogenetic analysis, which showed a strong affinity and fairly limited genetic divergence between the specimens from Vietnam and Australia. This is the first verified case of *Bertiella* in murid rodents from continental Eurasia. The uterine pore and associated canal present in the posterolateral corners of gravid proglottids of *B. anapolytica* are considered to form a true, functional structure used for egg release prior to apolysis. The phylogenetic analysis suggested that *B. anapolytica* has diverged as a consequence of a shift from marsupials, which probably took place east of the Wallace's line, either in Wallacea or Australasia. The presence of *B. anapolytica* west of the Wallace's line (Vietnam, Sumatra), where marsupials are absent, may be explained by a westward dispersal in commensal rats, possibly *Rattus exulans* (Peale), a species transported throughout the Pacific and South-East Asia by prehistoric people.

Keywords: Cyclophyllidea, phylogeny, 28S, Vietnam, Muridae, rodents

The tapeworms of the genus *Bertiella* Stiles et Hassall, 1902 *sensu* Beveridge (1994) (Cyclophyllidea, Anoplocephalidae) exhibit an exceptionally wide host range, parasitising marsupials (Diprotodontia), dermopterans, rodents and primates, including humans (Beveridge 1976, 1985, 1989, Schmidt 1986). Geographically, the diversity of *Bertiella* centres in Australasia, where the hosts are primarily marsupials. Rodents are hosts for four species of *Bertiella*, which parasitise murids, sciurids and anomalurids (Table 1). However, *Bertiella douceti* Baer, 1954 from *Anomalurus* Waterhouse from Africa does not fully conform to the characteristics of *Bertiella sensu* Beveridge (1994), because in this species the uterus is positioned ventral to the longitudinal osmoregulatory canals (dorsal in *Bertiella*) and the testes are distributed almost throughout the medulla (anterior to the uterus in *Bertiella*).

Therefore, *B. douceti* is considered here a *species incertae sedis*. In addition, Beveridge (1985) identified an undescribed species of *Bertiella* from an Australian murid rodent (*Melomys* Thomas) (Table 1).

Bertiella anapolytica Baylis, 1934 has been listed as a parasite of *Rattus exulans* (Peale) and *R. rattus* (Linnaeus) in Vietnam (Krivolutskii et al. 1991), which represents the only record of *Bertiella* in murid rodents in continental Eurasia. However, no description was provided by Krivolutskii et al. (1991), and their identification therefore remains unverified.

Two specimens of *Bertiella* were recovered in March 2013 from *Rattus tanezumi* (Temminck) from Cao Lãnh and Hồng Ngự in Đồng Tháp Province in southern Vietnam, which allowed us to determine their specific identity and phylogenetic position. The cestodes were processed using standard methods with carmine alum staining, and their whole-mounts were deposited in the Finnish Museum of Natural History (FMNH) (gravid specimen: KN.47004, pregravid specimen: KN.47003). The measurements and counts of various reproductive organs were taken from fully mature proglottids. The measurements are given in micrometres except for the body length and width.

*Address for correspondence: Voitto Haukisalmi, Koukkurannankatu 3 B 37, 33870 Tampere, Finland. Email: haukisal@gmail.com; ORCID-iD: 0000-0001-7660-9670.

Table 1. Records of species of *Bertiella* Stiles et Hassall, 1902 in rodents.

Tapeworm species	Country	Host species (family*)	References
<i>Bertiella anapolytica</i> Baylis, 1934	Indonesia (Sumatra)	<i>Rattus argentiventer</i> (M)	Baylis (1934)
	Australia	<i>R. fuscipes</i> , <i>R. lutreolus</i> (M)	Obendorf (1979), Beveridge (1985)
	New Guinea	<i>Paramelomys lorentzii</i> (M)	Beveridge and Smales (2017)
	Vietnam	<i>R. exulans</i> , <i>R. rattus</i> (M)	Krivolutskii et al. (1991)
	Vietnam	<i>R. tanezumi</i> (M)	Present study
<i>B. baylisi</i> Beveridge, 1985	Australia	<i>Uromys caudimaculatus</i> (M)	Beveridge (1985)
<i>B. musasabi</i> Yamaguti, 1942	Japan	<i>Petaurista leucogenys</i> (S)	Yamaguti (1942)
	Taiwan ³	<i>P. petaurista</i> (S)	Sawada and Kugi (1979)
	India ⁴	<i>P. petaurista</i> (S)	Singh (1962)
	New Guinea	<i>Chiruromys forbesi</i> (M), <i>Pogonomys championi</i> (M)	Beveridge and Smales (2017)
<i>B. douceti</i> Baer, 1953 ¹	Ivory Coast	<i>Anomalurus pelii</i> , <i>A. derbianus</i> (A)	Baer (1953), Hunkeler (1974)
<i>Bertiella</i> sp. ²	Australia	<i>Melomys cervinipes</i> (M)	Beveridge (1985)

* Host families: Muridae (M), Sciuridae (S), Anomaluridae (A).¹ Considered here a *species incertae sedis*. ² An undescribed species. ³ Reported as *Aprostodrya petauristae* Sawada et Kugi, 1979. ⁴ Reported as *Indotaenia indica* Singh, 1962 (for the synonymies, see Beveridge 1989).

Both specimens were sequenced for the large subunit ribosomal RNA gene (28S) with primers XZ-1 (forward, 5'-ACCCGCTGAAATTTAAGCATAT-3') of Waeschenbach et al. (2007), which differs from the original XZ-1 of Van der Auwera et al. (1994) by having one "Y" replaced with "T" (in bold), and 1500R (reverse, 5'-GCTATCCTGAG-GGAAACTTCG-3') of Littlewood et al. (2008), using the procedures described in Haukisalmi et al. (2024). The specimens shared an identical DNA sequence (1716 bp), which was deposited in GenBank (MG099776).

The phylogenetic relationships among *Bertiella* spp. and related species were analysed using the 28S sequences published by Wickström et al. (2005), Hardman et al. (2012) and Doležalová et al. (2015). Phylogenetic relationships were constructed and tested using the Maximum likelihood method and the Bayesian phylogeny inference. *Monoecocystus americanus* (Stiles, 1895) (GenBank AY569772), *Hymenolepis diminuta* (Rudolphi, 1819) (HM138522) and *Dilepis undula* (Schrank, 1788) (AF286915) were used as an outgroup.

Bertiella anapolytica Baylis, 1934

Fig. 1

Description: Length and maximum width of fully gravid specimen 170 mm and 4.7 mm, respectively. Number of proglottids ca. 370. Scolex small, 390–490 (n = 2) in diameter, merging gradually with neck region. Suckers 155–165 (n = 8) in diameter. Neck (unsegmented region) ca. 700 long. Proglottids distinctly craspedote, serrate in posterior strobila, wider than long in all developmental stages. Dimensions of mature proglottids: length 450–670 (x = 586, n = 6), width 2.37–3.20 mm (x = 2.77 mm, n = 6) and length/width ratio 0.19–0.23 (x = 0.21, n = 6).

Ventral longitudinal osmoregulatory canals 25–80 (x = 54, n = 9) wide in mid-region, 100–190 (x = 148, n = 13) wide at junction between longitudinal and transverse canals. Dorsal longitudinal osmoregulatory canals narrow (20–25, x = 23, n = 8), undulating, positioned slightly median to ventral canals or overlapping their median margin. Ventral and dorsal canals from each side of strobila join in scolex. Cirrus sac and vagina crossing longitudinal osmoregulatory canals dorsally. Genitalia single. Genital pores irregularly alternating in short series, opening in posterior half of proglottid margin. Genital atrium narrow and relatively shallow; genital papilla absent.

Testes forming narrow transverse continuous band near anterior margin of proglottids, being in contact with or separated by small gap from longitudinal osmoregulatory canals bilaterally; testicular field separated by distinct gap from early uterus in antero-posterior plane. Number of testes 26–44 (x = 36, n = 6); diameter 90–149 (x = 112, n = 11). Cirrus sac long (410–590, x = 534, n = 6), elongate, always extending distinctly across longitudinal osmoregulatory canals; wall of cirrus sac delicate. Distal sperm duct (ductus cirri) densely lined with fine spines except in distal and proximal ends. Maximum length and width of everted cirrus 380 and 55, respectively. Spines observed on everted cirri throughout their length; length of spines 4–5. Large, elongate internal seminal vesicle present, covering up to 2/3 of cirrus sac length when filled with sperm. Vas deference convoluted throughout its length, slightly expended when filled with sperm; distinct external seminal vesicle absent.

Ovary median or slightly poral, flabelliform, densely lobulate, relatively large, 750–1020 (x = 908, n = 6) wide or approximately 1/3 of proglottid width. Vitellarium relatively small, 210–275 (x = 258, n = 6) in diameter, more or less spherical or slightly wider than long with sparsely lobed, somewhat irregular margins; positioned near posterior margin of proglottid, middle of ovary in transverse plane. Mehlis' gland small (90–140, x = 119, n = 4), poorly visible, positioned at poral margin of ovary. Vagina opens posterior to male pore and runs ventral to proximal cirrus sac and vas deferens. Distal end of vagina narrow, covered by thin layer of intensely stained cells, gradually expanding and curving anteriorly. Proximal part of vagina (seminal canal) long, slightly expanded when filled with sperm, usually with 1–2 loops in region overlapping ovary. Small spherical or ovoid, thick-walled vesicle, previously called "accessory seminal receptacle" or "sperm regulation apparatus", present in proximal end of vagina at poral margin of Mehlis' gland. No lining observed inside vagina.

Uterus appears in mature proglottids as narrow transverse cord positioned slightly posterior to midline of proglottid; ends of early uterus slightly curved towards posterior ends of proglottid margin. Uterus extends dorsally across longitudinal osmoregulatory canals and lies ventral to lateral genital ducts in poral side. Expanding uterus initially simple tube, then forming ca. 20 distinct elongate anterior sacculations;

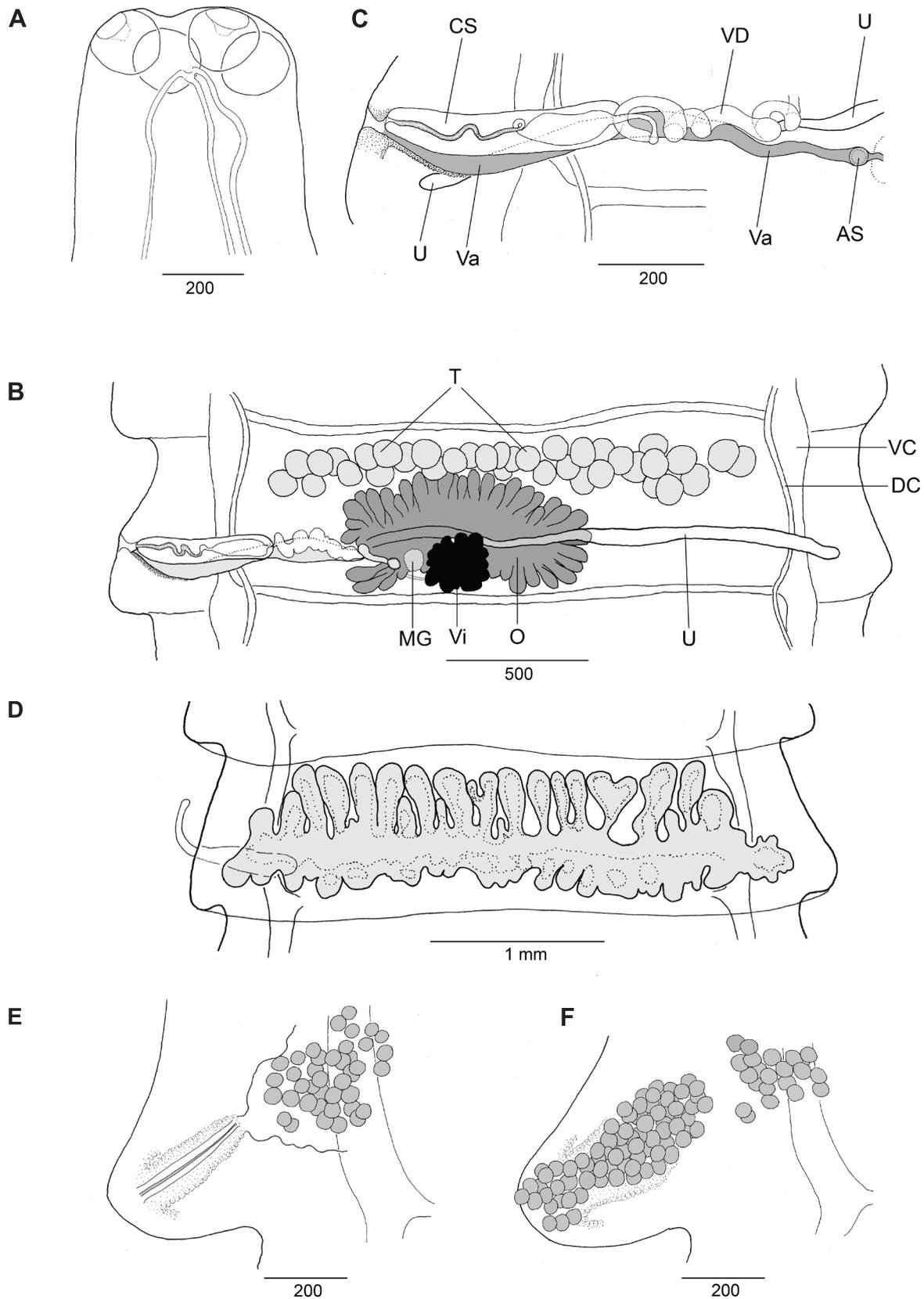


Fig. 1. *Bertiella anapolytica* Baylis, 1934 from *Rattus tanezumi* (Temminck) from Vietnam. **A** – scolex; **B** – mature proglottid; **C** – lateral genital ducts and early uterus; **D** – uterus in a pregravid proglottid; **E, F** – development of the “postero-lateral canal” and “uterine pore” in two consecutive gravid proglottids. AS – “accessory seminal receptacle”; CS – cirrus sac; DC – dorsal longitudinal osmoregulatory canal; MG – Mehlis’ gland; O – ovary; T – testes; U – uterus; Va – vagina; VC – ventral longitudinal osmoregulatory canal; VD – vas deferens; Vi – vitellarium.

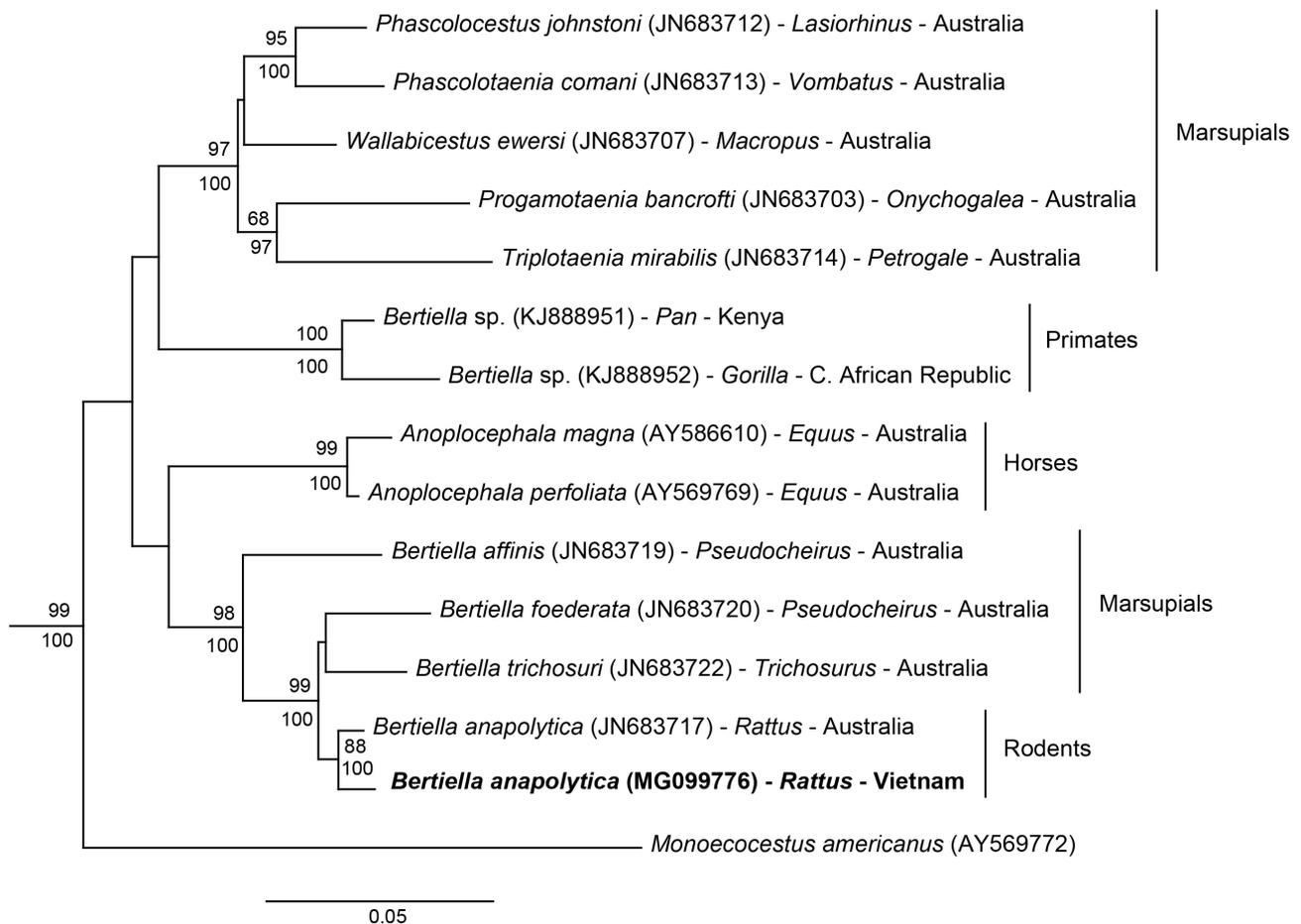


Fig. 2. Phylogenetic relationships of *Bertiella* spp. and related genera based on Maximum likelihood method (ML) with 1,000 replications (bootstrap values above nodes) and Bayesian phylogeny inference with 1 million generations (posterior probabilities below nodes). The topology of the tree is based on the ML analysis. GenBank numbers in parentheses, followed by host genus and country. The two basal outgroup species (*Hymenolepis diminuta* and *Dilepis undula*) with long branches are not shown.

posterior sacculations short, irregular and partly fused. Uterine wall disintegrates in terminal proglottids.

Starting from pregravid proglottids, wide cord of intensely stained cells, positioned in lateral field and directed towards posterolateral corner of proglottid, is formed bilaterally. (Fig. 1E,F) Later, narrow canal lined with poorly stained, evidently non-cellular sleeve is formed within this structure; proximal end of canal becomes connected with uterine wall. No pore or direct connection between canal and external wall of proglottid was observed at this stage. When disintegration of uterine wall commences, distal end of canal opens through rupture in external wall and eggs are gradually released through canal, which is now much expanded. Terminal proglottids almost devoid of eggs. Eggs spherical with delicate wall, 37–43 in diameter. Pyriform apparatus present, ca. 15 in diameter, but no details seen.

Host: *Rattus tanezumi* (Temminck) (Rodentia, Muridae)

Localities: Cao Lãnh and Hồng Ngự in Đồng Tháp Province, southern Vietnam.

Number of specimens collected: Two in two rat specimens examined (collected in March 2013).

Deposition of voucher specimens: FMNH: KN.47003, KN.47004.

Remarks: Beveridge (1985) provided a detailed redescription of *B. anapolytica*, including a type specimen from *Rattus argentiventer* (Robinson et Kloss) from Indonesia (Sumatra) and additional specimens from *Rattus fuscipes* (Waterhouse) and *R. lutreolus* (Gray) from Australia. No significant morphological differences between the Indonesian and Australian specimens were found.

The present specimens from Vietnam are similar to those examined by Beveridge (1985) with respect to their general morphology, but show differences with respect to certain quantitative features. The number of testes in the present specimens (26–44) is smaller than those reported by Baylis (1934) (50–60) and Beveridge (1985) (53–66), and the cirrus sac of the Vietnamese specimens is somewhat longer (410–590) than that of the Indonesian and Australian specimens (250–470). The ovary of the present specimens is absolutely and relatively wider (750–1020 μm or 1/3 of proglottid width) than the ovary of the specimens examined by Beveridge (1985) (380–620 μm or ca. 1/5 of proglottid width). The anterior uterine sacculations appear to be more numerous in the present material, although Beveridge (1985) did not quantify this feature.

Despite these quantitative differences, the overall qualitative similarity suggests that the Vietnamese specimens

are conspecific with those from Indonesia and Australia. A certain degree of quantitative differences is expected to be found within populations and particularly between populations with a wide geographical distribution and evidently a long history in isolation. The strong phylogenetic affinity between the specimens from Vietnam and Australia and their fairly limited genetic divergence (Fig. 2) support their conspecificity.

Baylis (1934) described development and function of a “uterine pore” and an associated canal present in the posterolateral corners of gravid proglottids of *B. anapolytica* and *Bertiella kapul* Baylis, 1934, the latter from a phalangerid marsupial from Papua New Guinea. A similar structure is also present in *Bertiella trichosuri* Khalil, 1970 from another, introduced phalangerid from New Zealand (Khalil 1970). However, the detailed redescriptions of *B. anapolytica* and *B. kapul* by Beveridge (1985), which include type specimens of both species, do not mention such an organ.

The examination of *B. anapolytica* from Vietnam revealed a structure which in its position and development is similar to that of *B. anapolytica*, *B. kapul* and *B. trichosuri* described above, except that Baylis (1934) observed (but did not illustrate) a conical plug in the distal end of the canal, which detaches resulting in release of eggs. The gradual loss of eggs in terminal gravid proglottids was observed also by Baylis (1934) and Khalil (1970). We conclude that the “uterine pore” and the associated “posterolateral canal” form together a true, functional structure which is used for egg release prior to apolysis. Such an organ may be a taxonomically significant feature in *Bertiella*, provided that its occurrence does not vary within species.

Baer (1953) mentioned seeing similar pores in all of the species he assigned to the genus *Prototaenia* Baer, 1927 (now a junior synonym *Bertiella*), which includes cestodes from rodents, dermopterans and marsupials. However, such an organ has not been mentioned in the detailed descriptions of Sluiter (1896), Bourquin (1905) and Beveridge (1976, 1985, 1989) on the species allocated to *Prototaenia*.

Distribution and evolutionary history

Bertiella douceti in anomalurids from Africa evidently does not belong to *Bertiella* sensu Beveridge (1994), and the genus *Bertiella* in non-primate hosts is therefore limited to South, East and South-East Asia (India, Taiwan, Japan, Vietnam), Indonesia (Sumatra, Sulawesi, Java), the Philippines and Australasia (New Guinea, Australia, Timor, New Zealand) (Beveridge 1976, 1985, 1989). *Bertiella anapolytica* is a parasite of *Rattus* spp. in South-East Asia (Vietnam), Indonesia (Sumatra) and Australia; the hosts include at least six species of *Rattus* (Table 1), of which *R. fuscipes* and *R. lutreolus* are Australian endemics. No other cases of *Bertiella* have been detected in connection of a series of extensive investigations on helminths of murid rodents in South-East Asia, including Vietnam, Thailand, Laos and Cambodia (Chaisiri et al. 2012, 2015, Pakdeenarong et al. 2013, Bordes et al. 2015, Ribas et al. 2016, Llopis-Belenguier et al. 2024).

The 28S sequence of the specimens from Vietnam was positioned within the *Bertiella* subclade, which includes

species from Australasian marsupials and rodents, being sister to *B. anapolytica* from Australia with a high statistical support (Fig. 2). As shown earlier (Hardman et al. 2012), the other species in the crown clade are *Bertiella trichosuri* and *B. foederata* Beveridge, 1976 from a phalangerid and pseudocheirid marsupial, respectively. These phylogenetic patterns lead to a suggestion that *B. anapolytica* has diverged as consequence of a shift from marsupials, probably either pseudocheirids (ringtail possums and relatives) or phalangerids (cuscuses, brushtail possums and relatives) to *Rattus*. It most likely happened somewhere east of the Wallace’s line, a region encompassing Wallacea (includes Sulawesi and numerous smaller islands, but excludes the Philippines) and Australasia. The latter regions are inhabited by marsupials, but they are absent west of the Wallace’s line. There are at least three *Bertiella* species in Australian murids (Table 1), and it may be tentatively assumed that the high diversity of these cestodes in Australasia compared with Wallacea indicates longer evolutionary history in the former region.

The genus *Rattus* is generally thought to have originated in continental Eurasia, most likely in South-East Asia and later spread eastward to Australasia, followed by an extensive diversification there (Rowe et al. 2011). However, the presence of *B. anapolytica* west of the Wallace’s Line (Sumatra, Vietnam) should have involved a westward dispersal of cestodes in murid rodents, probably *Rattus*, from Australasia or Wallacea. A possible host candidate for a westward dispersal is the Polynesian rat *R. exulans*, which is a commensal species transported throughout the Pacific and South-East Asia by prehistoric peoples (Matisoo-Smith et al. 1998). The evolutionary history of *Bertiella* spp. should, however, be reanalysed using a more extensive coverage of species, ideally including *B. musasabi* Yamaguti, 1942 from sciurids and species from dermopterans, i.e. *B. elongata* (Bourquin, 1905), *B. plastica* (Sluiter, 1896) and *B. rauschi* Beveridge, 1989.

Based on morphological and molecular evidence (Beveridge 1985, 1989, Doležalová et al. 2015), the *Bertiella* species in primates are apparently distinct from those in other hosts. The type species of *Bertiella* is *B. studeri* (Blanchard, 1891) from humans and other primates, which suggests that the species in dermopterans should be assigned to *Prototaenia* (type species *B. elongata*), but the systematic position of the species in marsupials and rodents remains undefined.

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Author contributions statement. The first author is responsible for the design of the study, morphological, molecular and phylogenetic analyses, and writing of the manuscript. The other authors designed and performed the collection of the host and parasite specimens, and contributed to the analyses and writing of the manuscript.

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