DASYUROTAENIA ROBUSTA BEDDARD, 1912, AND *D. DASYURI* SP. NOV., FROM CARNIVOROUS AUSTRALIAN MARSUPIALS

by IAN BEVERIDGE*

Summary

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Dasyurotaenia robusta Beddard, 1912, is redescribed from specimens collected from the type host, the Tasmanian devil, *Sarcophilus harrisii* (Boitard). The rostellar hooks are described for the first time. *Dasyurotaenia dasyuri* sp. nov., from the tiger cat, *Dasyurus maculatus* (Kerr), in Queensland and Tasmania differs from *D. robusta* in the size and shape of the rostellar hooks, the presence of transverse osmoregulatory canals and the number of uterine branches. Specimens from *Dasyurus maculatus*, described in earlier works as *D. robusta* cannot now be assigned to either species with certainty. Lesions associated with *D. dasyuri* sp. nov. are described and the taxonomic position of the genus discussed.

KEY WORDS: Cestoda, Taeniidae, marsupials, *Dasyurotaenia*.

Introduction

Dasyurotaenia robusta was first described by Beddard (1912) from specimens found in a Tasmanian devil, *Sarcophilus harrisii* (Boitard) (= *Dasyurus ursinus*) which died in London at the Gardens of the Zoological Society. Beddard (1912) described a number of unusual morphological features including suckers armed with hooks, and placed the species, with some reservations, in the Taenioidea. Baer (1925) re-examined Beddard's types and indicated that a number of misinterpretations of the morphology of the cestode had been made, including the "armed suckers" which proved to be an armed rostellum. Baer (1925) concluded that the species belonged to an independent genus within the Taenioidea, while Wardle & McLeod (1952), with considerable reservation, placed the genus within the family Taeniidae.

Subsequently, Sandars (1957) redescribed the species based on cestodes collected from two *Dasyurus maculatus* (Kerr) from Tasmania, confirming most of Baer's (1925) observations and concluding that the genus did belong within the Taeniidae. This taxonomic position was accepted by Yamaguti (1959), but it has been questioned by Rausch (1981) on phylogenetic grounds.

Recent collections of cestodes from dasyurids indicate that two independent species of *Dasyurotaenia* have been formerly confused under a single specific name, largely because the rostellar hooks of the species have never described (Beddard 1912, 1915; Baer 1925; Sandars 1957). In addition, a re-examination of the morphology of the two species supports Rausch's contention (1981) that this genus may not belong to the Taeniidae. In this paper, *Dasyurotaenia robusta* is redescribed from *Sarcophilus harrisii*, the type host, and a new species is described from *Dasyurus maculatus*.

Materials and Methods

Cestodes were relaxed in water, fixed in 10% neutral buffered formol saline, and stored in 70% ethanol. Whole mounts were stained with Celestine blue, dehydrated in graded ethanols, cleared in clove oil and mounted in balsam. Scoleces were mounted in Berlese's fluid, and digital pressure was applied to the cover slip to enable examination of the rostellar hooks. Serial sections cut at a thickness of 5 μm, were stained with haematoxylin and eosin. Gravid proglottides of *D. dasyuri* which had been fixed in formalin were diced into small cubes, post-fixed in osmium tetroxide and embedded in araldite. Thin sections were stained with lead citrate and uranyl acetate and viewed with a Joel 100 CX electron microscope. Additional specimens of *Dasyurotaenia* were obtained from preserved carcasses of *Dasyurus maculatus* held in the National Museums of Victoria, Melbourne.

Measurements are given in the text, in mm, as the range followed, in parentheses, by the mean and the number of measurements made.

Abbreviations of institutions cited in text: AHC—Australian Helminth Collection, housed in the South Australian Museum, Adelaide. BMNH—British Museum (Natural History), London. MHNG—Muséum d'Histoire Naturelle, Geneva. SAM—South Australian Museum, Adelaide. WAM—Western Australian Museum, Perth. WL—Commonwealth Scientific and Industrial Research Organisation, Division of Wildlife and Rangelands Research, Canberra.

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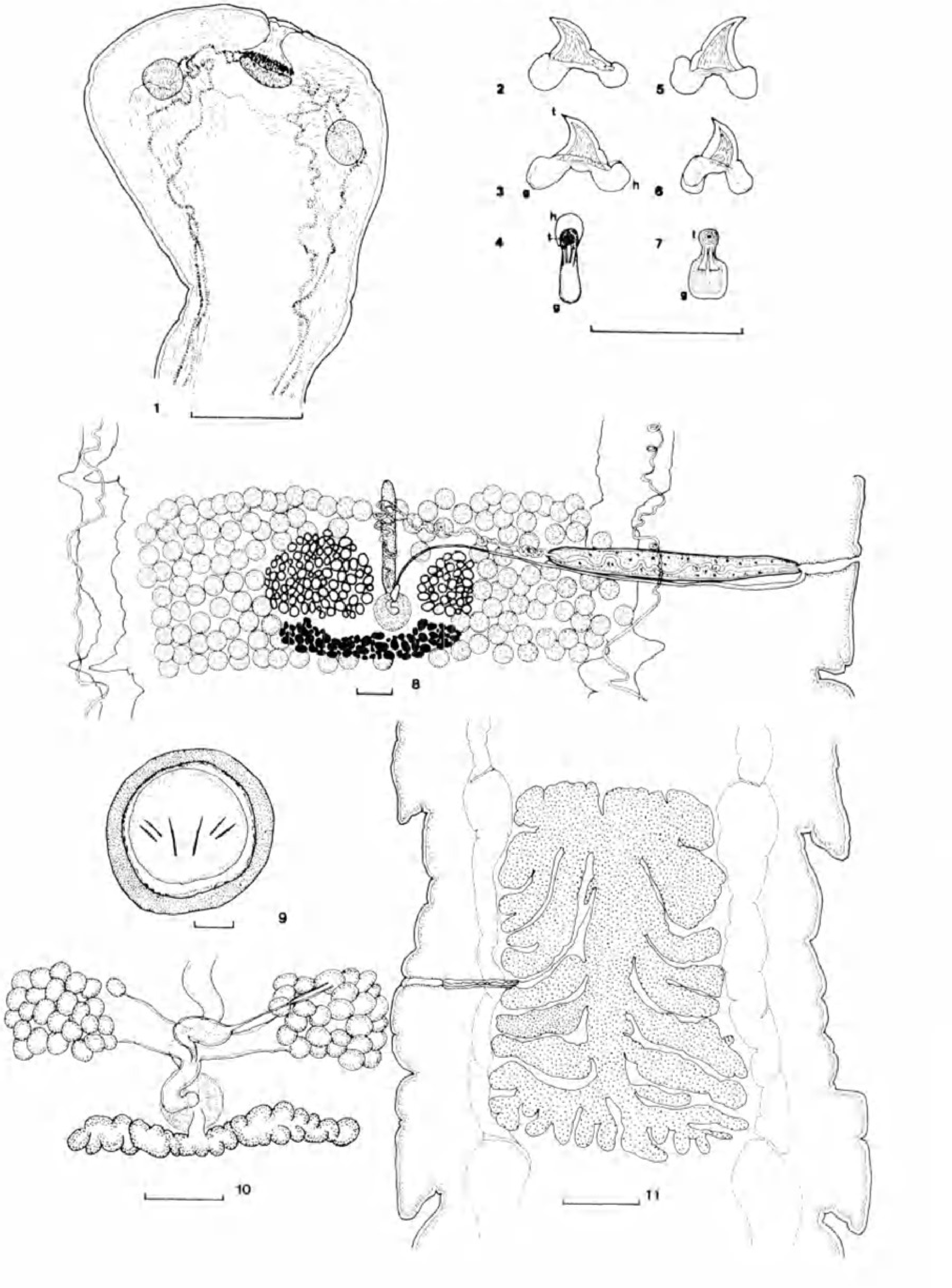
Dasyurotaenia robusta Beddard, 1912
FIGS 1-11, 26-28

Description: Cestodes of moderate size, up to 140 in length, 4 wide with up to 290 proglottides in gravid strobila. Scolex large (Fig. 1), 2.36 (n=1) in diameter, deeply embedded in intestinal mucosa of host. Suckers 0.30-0.38 (0.33, n=3) in diameter; rostellum 0.44 × 0.15 (n=1) retracted within scolex, extremely muscular, sucker shaped, with 42 (n=1) rostellar hooks arranged in 2 rows. Large or anterior rostellar hooks (Figs 2-4, 26) 0.046-0.058 (0.054, n=10) long, base 0.056-0.062 (0.059, n=10) long; blade large, core striated, sometimes vacuolated; handle extremely short, relatively wide; guard long, wide, single lobe (Figs 4, 27). Small or posterior rostellar hooks (Figs 5-7) 0.042-0.052 (0.047, n=10) long, base 0.044-0.060 (0.054, n=10) long; blade large, core striated; handle extremely short, knob-like; guard large, flattened, almost bilobed distally (Figs 7, 28). Neck present.

Musculature of mature proglottides poorly developed. Outer longitudinal muscles single or in very small bundles; inner longitudinal muscles in larger bundles containing 20 or more fibres. Transverse muscles in several bands; including bands internal to inner longitudinal muscles and separating inner and outer longitudinal muscles; more poorly defined bands between bundles of inner longitudinal muscles. Dorso-ventral muscles sparse, crossing cortex and medulla at irregular intervals. Longitudinal osmoregulatory canals paired; ventral canal 0.10-0.19 (0.13, n=5) wide in mature proglottides, not joined by transverse canals, with valve-like flaps protruding into lumen at junction of proglottides; in one strobila, ventral canals of gravid proglottides with several smaller projections of canal wall in addition to major valves. Dorsal canal extremely narrow, sinuous, 0.05 (n=1) in diameter in mature proglottides, dorsal or external to ventral canal. Mature proglottides 0.35-0.60 (0.48, n=5) × 2.45-3.05 (2.77, n=5), length:width ratio 4.8-7.1 (6.0, n=5) (Fig. 8). Gravid proglottides 1.45-2.20 (1.75, n=5) × 2.60-3.50 (3.18, n=5), length:width ratio 1.2-2.3 (1.9, n=5). Genital pores almost exclusively unilateral, occasional genital pore on alternate side. Genital atrium narrow, situated in middle of lateral proglottis margin in mature proglottides dividing margin in ratio of 1:0.67-1:1.00 (1:0.88, n=5); in middle or posterior half of margin of gravid proglottides, dividing margin in ratio of 1:1.00-1:1.66 (1:1.35, n=5). Genital ducts pass between longitudinal osmoregulatory canals. Cirrus sac elongate, thin-walled, invariably extending beyond osmoregulatory canals into medulla, 0.60-0.85 (0.74, n=10) × 0.06-0.09 (0.07, n=10) in mature proglottides. Cirrus slender, approximately 0.01 in diameter, coiled, armature of extremely fine bristles visible on mid-region of cirri in section. Internal and external seminal vesicles absent. Vas deferens greatly coiled, narrow duct, loops medially, then at midline turns posteriorly, terminating between lobes of ovary. Vasa efferentia not seen. Testes numerous, situated in 1-2 layers in dorsal plane. Testes occupy most of medulla between osmoregulatory canals, occasionally extend over osmoregulatory canals on poral side of proglottis with small numbers of testes being outside canals (Fig. 8); testes confluent anterior to ovaries and frequently confluent posterior to vitellarium in 1 or 2 rows; row of testes posterior to vitellarium sometimes interrupted; always some testes posterior to vitellarium; small numbers of testes overlie ovaries. Testes number 170-223 (200, n=10) per proglottis; diameter 0.05-0.10 (0.08, n=10). Vagina 0.010-0.020 (0.015, n=5) in diameter, straight, lined internally by hairs or bristles, surrounded by single layer of glandular cells. Proximal of 0.16 of vagina of wider internal diameter, unarmed. Seminal receptacle small, 0.06-0.08 (0.07, n=5) × 0.02-0.04 (0.03, n=5), situated in mid-line between lobes of ovary (Fig. 10). Ovary bilobed, poral lobe smaller, 0.14-0.32 (0.21, n=10) × 0.21-0.40 (0.29, n=10), aporal lobe 0.16-0.30 (0.23, n=10) × 0.27-0.48 (0.38, n=10), joined by narrow isthmus. Vitellarium posterior to ovary, elongate laterally 0.07-0.14 (0.11, n=10) × 0.47-0.90 (0.70, n=10). Mehlis' gland spherical, 0.08-0.10 (0.09, n=5), in diameter, between vitellarium and seminal receptacle. Uterus arises as tubular structure in midline. Uterus in gravid proglottides with 6-9 (7, n=10) poral and 7-10 (9, n=10) aporal lateral uterine branches; uterine branches frequently subdivided laterally (Fig. 11). Eggs approximately spheroidal 0.033-0.048 (0.042, n=10) × 0.035-0.040 (0.038, n=10)(Fig. 9); embryophore thick, homogenous, non-striated, oncosphere 0.028-0.033 (0.030, n=10) × 0.023-0.030 (0.027, n=10); oncospheral hooks 0.008-0.010 (0.009, n=10).

Development of genital organs in single specimen 140 long: testes first visible in proglottis 95; first mature proglottis approx. 160; uterine filling commences in proglottis 190; male and female genitalia involuted by proglottis 230; fully branched uterus

Figs 1-11. *Dasyurotaenia robusta* Beddard. 1. Scolex with rostellum retracted; 2-7, rostellar hooks; 2, 3, large or anterior rostellar hooks, lateral view; 4, large rostellar hook, radial view; 5, 6, small or posterior rostellar hooks, lateral view; 7, small rostellar hook, radial view; 8, mature proglottis; 9, egg; 10, female genitalia; 11, gravid proglottis. Scale lines: fig. 1, 1.0 mm; figs 2-8, 11, 10, 0.1 mm; fig. 9, 0.1 mm. g—guard; h—handle; t—tip.



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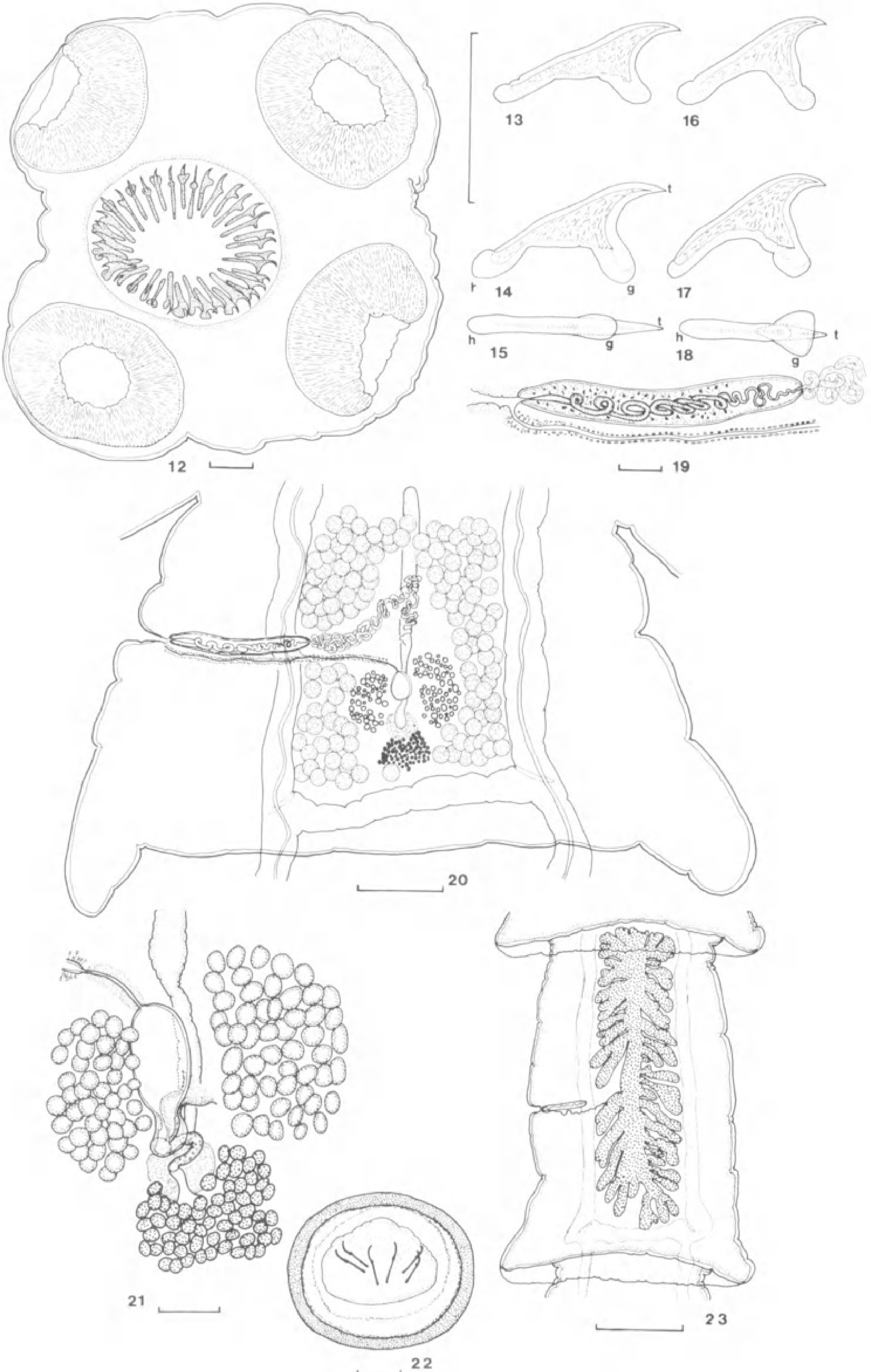
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present by proglottis 250; first gravid proglottis 278; total number proglottides 290.

Host: Sarcophilus harrisii (Boitard, 1841) (Marsupialia: Dasyuridae).

Site in host: Small intestine.

Types: Collected: London Zoological Society Gardens; slides of serial sections MHNG 24/53–61.

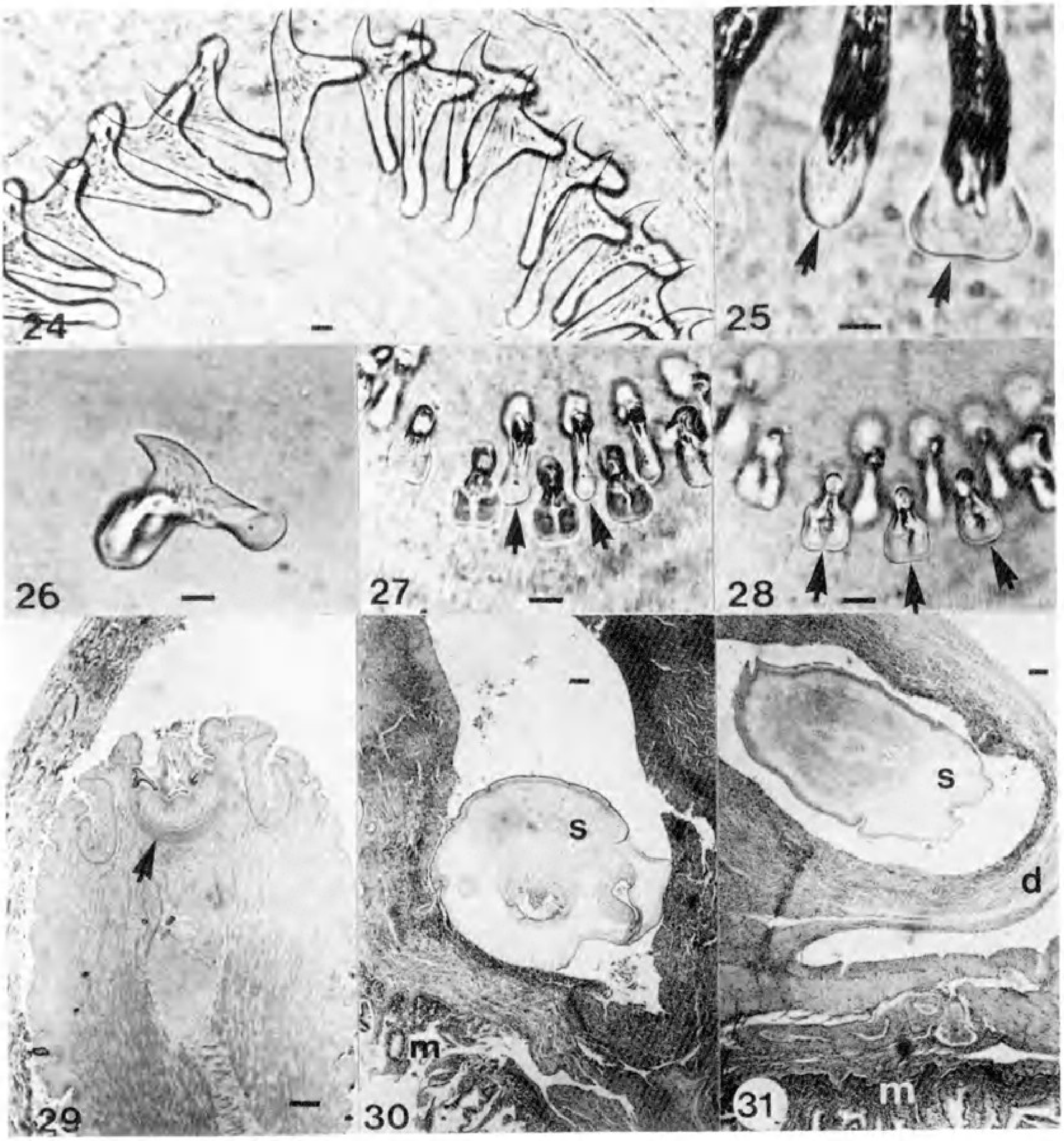
Material examined: types; 3 specimens, Adelaide Zoological Gardens, 7.xi.1980, collected by M. G. O'Callaghan, AHC 8291 and S1384; 1 specimen (without scolex), Chicago Zoological Gardens, collected by V. Rouhan, BMNH.1967.9.28.23.

Dasyurotaenia dasyuri sp.nov.

FIGS 12–23, 24, 25, 29–31

Description (from types): Large cestodes, 237–506 (400, n=5) in length, 2.5–3.9 (2.8, n=5) wide, with 280–330 (310) proglottides in gravid strobilae. Scolex large, 2.40 (n=1) in diameter, deeply embedded in mucosa of host. Suckers 0.32–0.38 (0.35, n=9) in diameter, rostellum 0.38–0.50 (0.43, n=4) in diameter with 36–38 (n=4) rostellar hooks arranged in two rows (Fig. 12). Large or anterior rostellar hooks 0.105–0.110 (0.107, n=20) long, base 0.077–0.093 (0.085, n=20) long (Figs 13, 14, 24): blade large, core frequently vacuolated; handle extremely small; guard elongate, not enlarged towards extremity (Figs 15, 25). Small or posterior rostellar hooks 0.080–0.093 (0.087, n=20) long, base 0.060–0.083 (0.075, n=20) long (Figs 17, 24); blade large, core frequently vacuolated; handle virtually absent, guard large, broad, frequently bilobed distally (Figs 18, 25). Neck present. Musculature not strongly developed. Outer longitudinal muscles single or in small bundles of 2–5 fibres, inner longitudinal muscles in larger bundles, up to 0.025 in diameter, containing 20 or more fibres. Transverse muscles in several bands; two most prominent bands immediately internal to inner longitudinal muscles and separating inner and outer longitudinal muscles; poorly defined bands between bundles of inner longitudinal muscles. Dorso-ventral muscles sparse, single, crossing cortex and medulla at irregular intervals. Longitudinal osmoregulatory canals paired; ventral canals 0.11–0.17 (0.15, n=5) in diameter in mature proglottides, joined at posterior margin of each proglottis by broad transverse canal. Ventral canals with valve like flaps protruding into lumen at junction of proglottides. Dorsal canal extremely narrow, sinuous, 0.01 (n=5) in diameter in mature proglottides. Mature proglottides 1.4–2.5 (1.7, n=10) × 2.5–3.0 (2.9, n=10), length:width ratio 1.02–2.64 (1.84, n=10) (Fig. 20). Gravid proglottides 1.8–3.9 (2.7, n=10) × 1.9–3.3 (2.8, n=10), length:width ratio 0.71–1.53 (1.07, n=10). Genital pores mainly unilateral, occasionally alternate irregularly. Genital atrium shallow, situated in anterior half of lateral proglottis margin in mature proglottides, dividing margin in ratio 1:1.3–1:2.4 (1:1.8, n=10); in middle of margin in gravid proglottides, dividing margin in ratio 1:0.9–1:1.5 (1:1.1, n=10). Genital ducts pass between longitudinal osmoregulatory canals. Cirrus sac elongate, thin-walled (Fig. 19) invariably extending beyond osmoregulatory canals into medulla, 0.50–0.71 (0.57, n=10) × 0.08–0.12 (0.10, n=10) in mature proglottides. Cirrus slender, 0.01–0.02 (0.015, n=5) in diameter, coiled, armature of fine hairs visible on distal region of some cirri under high magnification. Internal and external seminal vesicles absent. Vas deferens greatly coiled, narrow duct, loops medially and anteriorly, then at mid-line turns posteriorly, terminating near seminal receptacle. Vasa efferentia not seen. Testes numerous, situated in 1–2 layers in dorsal planes. Testes occupy most of medulla between osmoregulatory canals, except area of female genitalia; testes confluent anterior to vas deferens; testes usually confluent posterior to vitellarium, or with 1–3 testes posterior to and overlying vitellarium; occasionally no testes posterior to vitellarium. Testes number 150–160 (n=2) per proglottis; diameter 0.06–0.08 (0.07, n=10). Vagina approximately 0.12 in diameter, straight, lined internally by fine hairs, surrounded externally by single layer of glandular cells. Proximal 0.15 of vagina narrow, surrounded by thicker muscle layer than remainder of vagina, lacking glandular cell investment. Seminal receptacle ovoid (Fig. 21), 0.11–0.16 (0.14, n=10) × 0.07–0.10 (0.9, n=10) when filled, situated in mid-line between lobes of ovary. Ovary bilobed, poral lobe small, 0.26–0.39 (0.31, n=10) × 0.12–0.25 (0.20, n=10), aporal lobe 0.32–0.44 (0.37, n=10) × 0.15–0.30 (0.21, n=10), joined by narrow isthmus. Vitellarium posterior to ovary, reniform 0.12–0.24 (0.20, n=10) × 0.18–0.31 (0.23, n=10). Mehlis' gland spherical, 0.07–0.11 (0.09, n=10) in diameter, between vitellarium and seminal receptacle. Uterus arises as tubular structure in midline. Uterus in gravid proglottides (Fig. 23) with 6–17 (12, n=10) poral and 10–20 (15, n=10) aporal lateral uterine branches; uterine branches frequently subdivided laterally. Egg approximately spheroidal

Figs 12–23. *Dasyurotaenia dasyuri*, sp.nov. 12, Scolex, apical view; 13–18, rostellar hooks, 13, 14, large or anterior rostellar hooks, lateral view; 15, large rostellar hook, apical view, 16, 17, small or posterior rostellar hooks, lateral view; 18, small rostellar hook, apical view; 19, cirrus sac and distal vagina; 20, mature proglottis; 21, female genitalia; 22, eggs; 23, gravid proglottis. Scale lines: Figs 12, 13–19, 21, 0.1 mm; fig.20, 0.35 mm; fig. 22, 0.01 mm, fig. 23, 1.0 mm. g—guard; h—handle; t—tip.



Figs 24–25. Rostellar hooks of *Dasyurotaenia dasyuri,* sp.nov.; 24, apical view of rostellum, hooks in lateral view; 25, apical view of hooks showing differences in shape of guards of large and small hooks (arrowed). Scale lines 0.01 mm.

Figs 26–28. Rostellar hooks of *Dasyurotaenia robusta* Beddard; 26, large rostellar hooks, lateral view; 27, 28, apical view of hooks showing difference in shape of guard of large and small hooks (arrowed). Scale line 0.01 mm.

Figs 29–31. Histological features of scolex of *Dasyurotaenia dasyuri* sp.nov. and associated pathology; 29, sagittal section through scolex showing partly withdrawn rostellum; 30 scolex(s) lodged in muscularis externa immediately below mucosa (m); 31, scolex(s) lodged in muscularis close to serosal margin showing dome shaped projections of tissues (d) beyond normal serosal surface intestine and mucosa (m). Scale lines 1 mm.

(Fig. 22), 0.035–0.040 (0.038, n = 10) × 0.030–0.034 (0.032, n = 10); embryophore thick, homogenous, non-striated, oncosphere 0.022–0.025 (0.024, n = 10) × 0.016–0.018 (0.017, n = 10); oncospheral hooks 0.008–0.010 (0.008, n = 10). Development of genital organs in 5 specimens: anlage first visible in proglottides 60–120 (85); testes first visible in proglottides 180–190 (187); first mature proglottis approximately 205–220 (215); uterine filling commences in proglottides 225–265 (245); first gravid proglottis 270–320 (305); total proglottides 280–330 (310).

Variation: Specimens from Tas.; identical to types, except in the following minor features: rostellar hook number more variable than in types, 32–40 (37, n = 3); large rostellar hooks 0.110–0.120 (0.116, n = 10), and small rostellar hooks 0.093–0.098 (0.095, n = 10) both slightly larger (approximately 0.010) than hooks of type specimens; testes number 169–226 (186, n = 10) per proglottis, higher than in types; vitellarium 0.10–0.15 (0.13, n = 10) × 0.21–0.38 (0.30, n = 10) relatively wider and shorter than in types.

Host: Dasyurus maculatus (Kerr, 1792) (Marsupialia: Dasyuridae).

Site in host: Small intestine.

Types: Holotype, 8 paratypes, Mt Windsor Tableland, Qld, 16°12′S, 145°05′E, 17.vii.1982, coll. D. M. Spratt. Holotype, 2 slides SAM V3459, 3 paratypes, SAM V3460–V3462; 4 paratypes, AHC S2169–S2172, HC 12322; 1 paratype, BMNH 1983.6.13.1–2; 1 scolex, strobilar fragments, paratypes, in collection of R. L. Rausch.

Fine structure of the egg envelopes (Fig. 32): The following envelopes were recognised surrounding the oncosphere. The outer envelope of the egg is bounded by a thin vitelline membrane, enclosing an irregular cytoplasmic layer. The outer

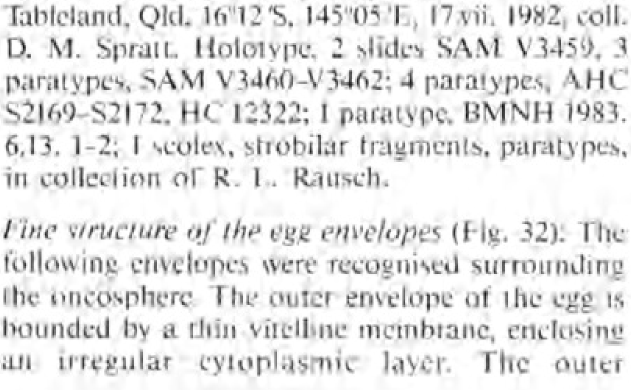


Fig. 32. Transmission electron micrograph of egg envelopes, *Dasyurotaenia dasyuri*. Scale line, 50 μm. e—embryophore; g—granular layer; ie—inner embryophoric membrane; oe—outer embryophoric membrane; vl—vacuolated layer; vm—vitelline membrane.

embryophoric membrane lies immediately external to the thickened embryophore. The embryophore is of uniform thickness and is composed of relatively homogeneous electron dense material which is not organised into regular embryophoric blocks and is without lacunae or internal circular bodies. Some areas within the embryophore are less electron dense and suggest cavities between blocks but are not arranged in a regular fashion. A zone of electron dense granules, the granular layer, lies between the embryophore and a broad sub-embryophoric vacuolated area which may represent aggregations of lipid bodies. The vacuolated zone and granular layer is bounded internally by the inner embryophoric membrane. Internal to this lies the oncosphere bounded by the oncospheral membrane.

Material examined: Qld: types; Tas.: 3 specimens, Smithton, coll. B. L. Munday, 1.vii.1979; 3 specimens, Smithton, coll. D. M. Spratt, 26.iii.1968, WL C282, C43; 2 specimens, Lilydale, coll. B. L. Munday, 2.vii.1976, AHC, HC10732; fragments of specimens, Wynard, coll. unknown, 22.xi.1922, whole preserved carcass NMV C6304, cestodes AHC 9785.

Associated Lesions (Figs 29–31): Scoleces of *D. dasyuri* lie deeply embedded in the external muscle layers of the wall of the small intestine of the host, either superficially, that is immediately below the submucosa, or, close to the serosal margin of the musculature such that the position of the cestode scolex is indicated by a raised dome-shaped projection on the serosal surface. The neck and anterior region of the strobila lie in a narrow tunnel which opens into the intestinal lumen. Two specimens of *D. dasyuri* were embedded singly, two were embedded together, and a further three worms were embedded at a single site. The superficial layers lining the cavities induced by cestode invasion consist primarily of necrotic cells and of cell debris together with viable cells compressed by the distention of surrounding tissues. There are in addition, surrounding the scoleces, a few small localised areas of necrosis of the myocytes and infiltrations by inflammatory cells. The principal host reaction is a chronic inflammatory one with an infiltration of macrophages and lymphocytes and a few plasma cells into tissues surrounding the cestode. Polymorphonuclear leukocytes are uncommon, but Langhans-type giant cells are occasionally present at the edges of lesions. Fibroblasts are prominent in a few areas on the outer edges of infiltrated areas.

Discussion

In none of the previous descriptions of *Dasyurotaenia* by Beddard (1912, 1915), Baer (1925) or Sandars (1957) have the rostellar hooks been adequately described. Beddard (1912) provided drawings of the histology of a purported sucker of *D. robusta* showing sections of sclerotized hooks but did not describe the size or shape of the hooks. Baer (1925) had no scoleces to examine, but concluded from Beddard's description that the cestode in question possessed a rostellum armed with taeniid-like hooks. Sandar's specimens (1957), here attributed to another species, were without rostellar hooks, but were re-described under the name *D. robusta*. She estimated that some 96 hooks were normally present.

The material described above indicates that in the past two (or more) independent species have been confused under the single name *D. robusta*. The two species described in this paper differ markedly in the size and shape of the rostellar hooks, but have few differences of note in strobilar morphology, and this has undoubtedly led to the confusion.

D. robusta is known only from the type series collected from Tasmanian devils in the London Zoological Gardens, from the three specimens described here, collected from the same host species in the Adelaide Zoological Gardens and from a single specimen without scolex from the Chicago Zoo. Beddard (1915) reported the species in four of nine devils dying in the Gardens; however, examination of 294 devils in Tasmania has not revealed its existence (Gregory *et al.* 1974).

The present redescription, although based upon a very limited series of specimens is considered justified as the species may now be rare, and since the material available allows a fairly full description to be made for the first time, including the distinguishing features of the rostellar hooks.

D. robusta is distinguished from *D. dasyuri* by the form and size of the rostellar hooks (Figs 2–7, 13–18). The large rostellar hooks of *D. robusta* are only 0.046–0.058 long compared with 0.105–0.120 in *D. dasyuri*. In addition, the size of the hook blade is relatively smaller in *D. robusta* so that the length of the hook base is larger, on average, than the total length of the hook; in *D. dasyuri* the length of the base is less than the total hook length. In both species, the guard of the small hook is particularly broad, and this is more marked in *D. robusta* than in *D. dasyuri*.

The principal strobilar character distinguishing *D. robusta* from *D. dasyuri* is the transverse osmoregulatory canal joining the ventral canals on both sides of the strobila in each proglottis. The difference is not immediately obvious in mature proglottides, but the canals are readily visible in most gravid and near gravid proglottides and the presence or absence of transverse osmoregulatory canals can be readily ascertained. Beddard (1912) noted the lack of transverse canals in the type specimens of *D. robusta*, and Baer (1925) confirmed that the canals were not visible in Beddard's sections, but suggested that their absence might be more apparent than real owing to the severely contracted nature of the type specimens. The new material confirms Beddard's (1912) observations that transverse canals do not exist.

Beddard (1912) discussed at some length the "membranes" stretching across the lumen of the osmoregulatory canals, noting that the lumen was occluded by "membranes" once in each proglottis. Baer (1925) explained Beddard's observations in terms of oblique histological sections passing through consecutive coils of the osmoregulatory canal, suggesting that the "membranes" were essentially artefacts due to the state of contraction of the specimens. The new specimens indicate that Beddard's observations were correct. At the posterior end of the proglottis in *D. robusta* and *D. dasyuri*, the lumen of the osmoregulatory canal is largely occluded by a valve-like extension of the canal wall. The structure is in most respects identical to valves which occur in comparable positions in the osmoregulatory canals of species of *Taenia*, described in detail by Kohler (1894). In specimens of *D. robusta*, the ventral canals are of extremely variable diameter, and in some incompletely relaxed proglottides, there are occasional folds in the canal wall similar to the incomplete "membranes" described by Beddard (1912). Baer (1925) was probably correct in ascribing these changes to the state of relaxation of the specimens.

The two species also differ in the number of lateral uterine branches, with 6–10 (9) in *D. robusta* and 6–20 (14) in *D. dasyuri*. Although these differences appear to be consistent in the material examined, they should be treated with some caution since Verster (1967) in a rescription of *Taenia solium* Linnaeus, 1758 and *T. saginata* Goze, 1782, two species which have frequently been identified from gravid proglottides by difference in the number of uterine branches, found that overlap in uterine branch number occurred if a sufficient number of proglottides was examined. Some overlap obviously occurs in uterine branch numbers of *Dasyurotaenia* spp. and more extensive series of specimens are required to test the validity of uterine branch number as a taxonomic character in this genus.

A number of minor morphological differences noted between *D. robusta* and *D. dasyuri* require more detailed examination in larger numbers of specimens before their reliability can be established. (i) The vitellarium was much shorter and wider in *D. robusta* (Figs 10, 20); however, this may have been due to the incomplete state of relaxation of the specimens of *D. robusta*. In addition, there was variation in the dimensions of the vitellarium between specimens of *D. dasyuri* from Tas. and Qld the latter specimens (the types) having much narrower vitellaria. (ii) In specimens of *D. robusta*, testes were occasionally found overlying the osmoregulatory canals or even entirely lateral to them, in contrast to *D. dasyuri* in which the testes invariably lie between the canals. (iii) The seminal receptacle in *D. robusta* was smaller than *D. dasyuri*, and the cirrus sac slightly longer and more prominent. All features mentioned require examination in an extensive series of specimens before any confidence can be placed upon their ability to distinguish the two species.

The data presented above suggest that *D. robusta* is confined to *Sarcophilus harrisii* and that *D. dasyuri* occurs only in *Dasyurus maculatus*. Sandar's (1957) specimens described under the name *D. robusta* but collected from *Dasyurus maculatus* in Tas. cannot definitely be assigned to either species, since they had no rostellar hooks. She stated that no transverse osmoregulatory canals could be seen, but prefaced her remarks by saying that details of the osmoregulatory canals could not be determined. It would therefore be unwise to assume that her specimens were *D. robusta* based on her failure to find transverse osmoregulatory canals. Her figure (Fig. 27) of a gravid proglottis reveals 12–14 lateral uterine branches, suggesting that the specimens she described may have been in fact *D. dasyuri* and not *D. robusta*. However, *Dasyrurotaenia* is probably represented by several species in dasyurid marsupials. In addition to the new species described here, a single juvenile cestode with 96 rostellar hooks, probably representing yet another species, was co-parasitic with the type specimens of *D. dasyuri* and has been deposited in AHC (S2173). Sandar's (1957) specimens could be attributed to this species or could have been a mixture of two species, *D. dasyuri* and the undescribed species. Another probably new species with 18–22 hooks, 0.100–0.108 and 0.092–0.104 long from *Dasyurus albopunctatus* Schlegel, 1880, in New Guinea is represented by two specimens only in the collection of the BMNH (1973.7.9.5–6). More specimens are required before the species can be described adequately. Finally, juvenile cestodes with 54 hooks 0.152–0.156 and 0.122–0.126 long were present in a specimen of *Satanellus hallucatus* Gould, 1842 from W.A. The specimens probably represent a new species of *Dasyurotaenia* and have been deposited in WAM (79, 80, 81–1983).

A metacestode of *Dasyurotaenia*, identified as *D. robusta* was reported from the peritoneal cavity of *Potorous tridactylus* (Kerr, 1792) in Tas. by Gregory (pers. comm. in Beveridge, 1978). This particular specimen had been identified by comparison with scolices from *Dasyurus maculatus*, and is now considered to be a metacestode of *D. dasyuri*.

The occurrence of the scolex deeply embedded within the intestinal wall of the host is unusual among cestodes. *Paradilepis scolecina* (Rudolphi, 1819) burrows into the small intestine of cormorant *Phalacrocorax carbo* Linnaeus, the scolex lodging in the muscularis externa close to the serosa (Karstad *et al.* 1982), and a similar localisation has been reported for *Paradilepis delachauxi* (Fuhrmann, 1909) in *Phalacrocorax africanus* (Gmelin) by Baer (1959). In mammals, the anoplocephalid *Ectopocephalium abei* Rausch & Ohbayashi, 1974, occurs with its scolex deeply buried in the wall of the sacculus rotundus of the pikas *Ochotona roylei* (Ogilby) and *O. macrotis* (Gunther) (Rausch & Ohbayashi, 1974). The mechanisms of invasion of *Dasyurotaenia* were not clear from the material studied. *Dasyurotaenia* spp. do not have prominent rostellar glands to secrete proteolytic enzymes such as are present in *E. abei*, but material from *D. maculatus* (WL C43) does suggest that the juvenile cestodes of *D. dasyuri* become deeply embedded in the small intestine wall before the initiation of proglottisation. The histological reaction to the scolex of *D. dasyuri* is similar to that described for *P. scolecina* and *E. abei*.

The genus *Dasyurotaenia* was allocated to the Taeniidae by Baer (1925) and this was confirmed subsequently by Sandars (1957). Rausch (1981) however has emphasised that the family, in the form recognised by Abuladse (1965) and Yamaguti (1959) is obviously polyphyletic. *Cladotaenia* Cohn, 1901 as indicated by Freeman (1973), belongs to the Dilepididae, based on the morphogenesis of the metacestodes, though the morphology of mature and gravid proglottides is similar to the taeniids. *Anoplotaenia* Beddard, 1911, a parasite of the Tasmanian Devil, likewise has a proglottis morphology akin to the Taeniidae while metacestode development indicates affinities with the Linstowiidae (Beveridge 1982). In ascertaining the true relationship of genera within the Taeniidae, it is obvious that a knowledge of metacestode development is a pre-requisite, and these data currently are lacking for *Dasyurotaenia*. As a consequence, morphological data cannot be the basis for a final determination of its taxonomic position, but may provide clues.

Dasyurotaenia is distinguished from other genera of The Taeniidae (*sensu* Yamaguti 1959) by the large scolex embedded deeply in the tissues of the host and by the essentially unilateral genital pores. Sandars (1957) mentioned the general body shape, the structure of the scolex, the form of the cirrus sac and the development of the musculature as features distinguishing the genus. While the form of the cirrus sac is markedly different from *A. dasyuri*, a coparasite of the Tasmanian devil, it does not differ from most *Taenia* spp. and therefore cannot be considered diagnostic. Of the characters mentioned by Sandars (1958), only the arrangement of the musculature seems worthy of consideration as it is apparently unique in the family. Unfortunately, the musculature of many species of the Taeniidae has not been described in detail, and its value as a taxonomic character for *Dasyurotaenia* is therefore open to some doubt at present.

The structure of the egg likewise is inconclusive. The embroyophore is extremely thick, as in taeniids, but is not composed of radially arranged blocks with lacunae (see Fairweather & Threadgold 1981) nor is it characteristic of dilepidid eggs (Pence 1967). In *A. dasyuri*, the structure of the egg was interpreted as being typically taeniid (Beveridge *et al.* 1975) yet the morphogenesis of the metacestode of this species indicates linstowiid affinities. Hence, there is some doubt as to the taxonomic significance of egg structure, and little weight can be placed upon the presence of a thick embryophore and insignificant outer envelope in the egg of *D. dasyuri*.

In *D. robusta*, the rostellum is apparently retractable, and can be retracted fully within the scolex. This characteristic, shown in Fig. 1, has been overlooked by previous writers, but it is not a characteristic of *Taenia* or *Echinococcus* (see Wardle & McLeod 1952), the only two genera considered by Rausch (1981) as belonging to the Taeniidae. A retractable rostellum is a feature of the Dilepididae and Hymenolepididae (Wardle & McLeod 1952) and may indicate an affinity with these groups rather than with the Taeniidae.

In summary, none of the morphological data provided allows the definitive allocation of *Dasyurotaenia* to a family. Superficially it resembles the Taeniidae, but the retractable rostellum of the type species, the musculature, and structure of the egg, cast doubt on such affinities.

Rausch (1981) suggested that *Dasyurotaenia* could not be allocated to the Taeniidae on phylogenetic as well as morphological grounds, alluding to the evolution of the Dasyuridae in isolation from eutherian mammals, and the belief that the true taeniids have evolved exclusively within recent Carnivora. If this is the case, *Dasyurotaenia* may exhibit a strobilar morphology convergent with species of *Taenia*, yet be derived from alternative origins, either the Linstowiidae of dasyurid and peramelid marsupials (Beveridge *et al.* 1975, Beveridge 1982) or Diplepididae from accipitriform birds (Beveridge *et al.* 1975). Elucidation of the life cycle of the parasite will be required before a final answer can be given.

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