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Native species *Maxvachonia chabaudi* Mawson, 1972 (Nematoda: Cosmocercoidea) found in the invasive marine toad *Rhinella marina* (Linnaeus) (Anura: Bufonidae) in Australia

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Abstract: The genus *Maxvachonia* Chabaud et Brygoo, 1960 (Ascaridomorpha: Cosmocercidae) is a poorly known group of parasitic nematodes. Species of *Maxvachonia* are native to Madagascar-Australo-Papuan Region, where they are known to parasitise frogs, snakes and skinks. Unfortunately, most of *Maxvachonia* species have been inadequately described. In the present study, we report the native species *Maxvachonia chabaudi* Mawson, 1972 from the intestine of the invasive marine toad *Rhinella marina* (Linnaeus) in Australia for the first time. We speculate that the marine toads infected with *M. chabaudi* are likely related to their eating skinks or the similarity in diet/habitat/ecology between the toad and the skinks. The detailed morphology of *M. chabaudi* was studied using light microscopy and, for the first time, scanning electron microscopy, based on the newly collected specimens. Some characters important for the specific diagnosis of *M. chabaudi* are reported for the first time, including each lip with distinct inner flanges, the location of vulva varying from anterior to posterior of the oesophageal bulb and the presence of single medio-ventral precloacal papilla. An identification key to the species of *Maxvachonia* is provided.

Key words: parasite, nematode, Ascaridomorpha, Amphibia, Australian region, morphology, taxonomy

The genus *Maxvachonia* Chabaud et Brygoo, 1960 (Ascaridomorpha: Cosmocercoidea: Cosmocercidae) is a small group of parasitic nematodes, currently including seven nominal species, *M. adamsoni* Moravec et Sey, 1990, *M. brygooi* Mawson, 1972, *M. chabaudi* Mawson, 1972, *M. dimorpha* Chabaud et Brygoo, 1960 (type species), *M. ewersi* Mawson, 1972, *M. flindersi* (Johnston et Mawson, 1941), and *M. ingens* Bursey, Goldberg et Kraus, 2011 (Chabaud and Brygoo 1960, Mawson 1972, Moravec and Sey 1990, Bursey et al. 2011), which parasitise amphibians and reptiles in Madagascar, Australia and Papua New Guinea. Unfortunately, most of these species have been inadequately described and illustrations are often highly diagrammatic.

Maxvachonia chabaudi was originally described from some skinks including *Ctenotus australis* (Gray), *C. labillardieri* (Duméril et Bibron), *C. leae* (Boulenger), *Eulamprus kosciuskoi* (Kinghorn), *Hemiergis peronii* (Gray), *Lerista bougainvillii* (Gray), *Morethia lineoocellata* (Duméril et Bibron) and *Underwoodisaurus milii* (Bory de Saint-Vincent) and a snake *Pseudonaja* cf. *affinis* Günther in Australia (Mawson 1972). During a helminthological survey in Australian amphibians, some nematodes identified as *M. chabaudi* were collected from the marine toad *Rhinella marina* (Linnaeus) (Anura: Bufonidae). The detailed morphology of *M. chabaudi* was studied using light microscopy and, for the first time, scanning electron microscopy, based on the newly collected specimens.

MATERIALS AND METHODS

Nematodes recovered from the intestine of the marine toad *Rhinella marina* in various locations from Queensland, Australia, were fixed and stored in 70% ethanol until study. The marine toad was identified according to Barker et al. (1995) and Cogger (2014). For light microscopical studies, nematodes were cleared in lactophenol. For scanning electron microscopy (SEM), specimens were re-fixed in 4% formaldehyde solution, post-fixed in 1% OsO_4, dehydrated via an ethanol series and acetone, and then critical point-dried. Samples were coated with gold and examined using a Hitachi S-4800 scanning electron microscope at an accel-

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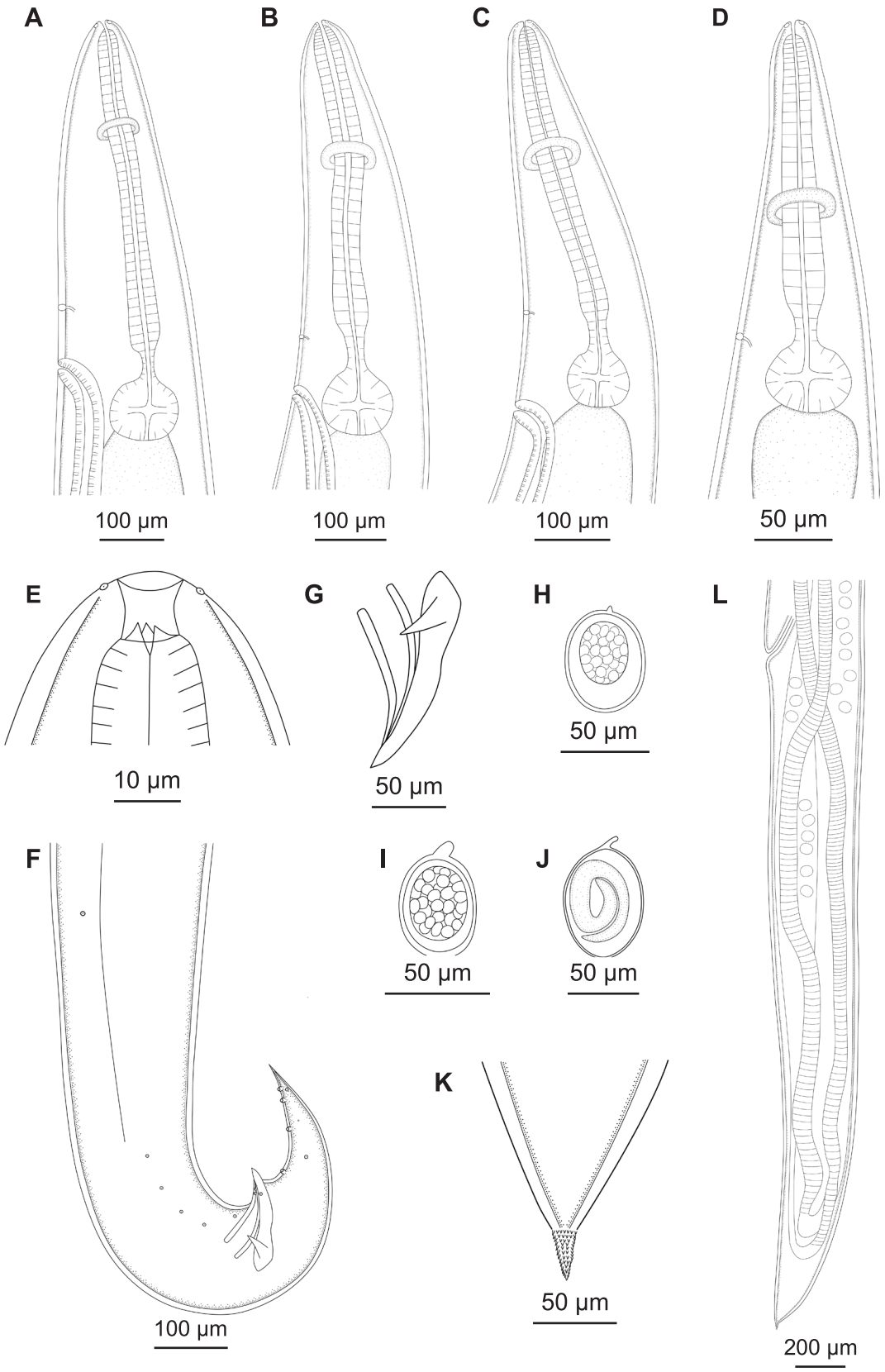

Fig. 1. *Maxvachonia chabaudi* Mawson, 1972 from the marine toad *Rhinella marina* (Linnaeus) (Anura: Bufonidae) in Australia. **A–C** – anterior part of female (showing variable position of vulva in different individuals), lateral view; **D** – anterior part of male, lateral view; **E** – magnified image of cephalic end, lateral view; **F** – posterior end of male, lateral view; **G** – gubernaculum and spicules, lateral view; **H–J** – different developmental stages of eggs; **K** – tail tip of female; **L** – posterior end of female, lateral view.

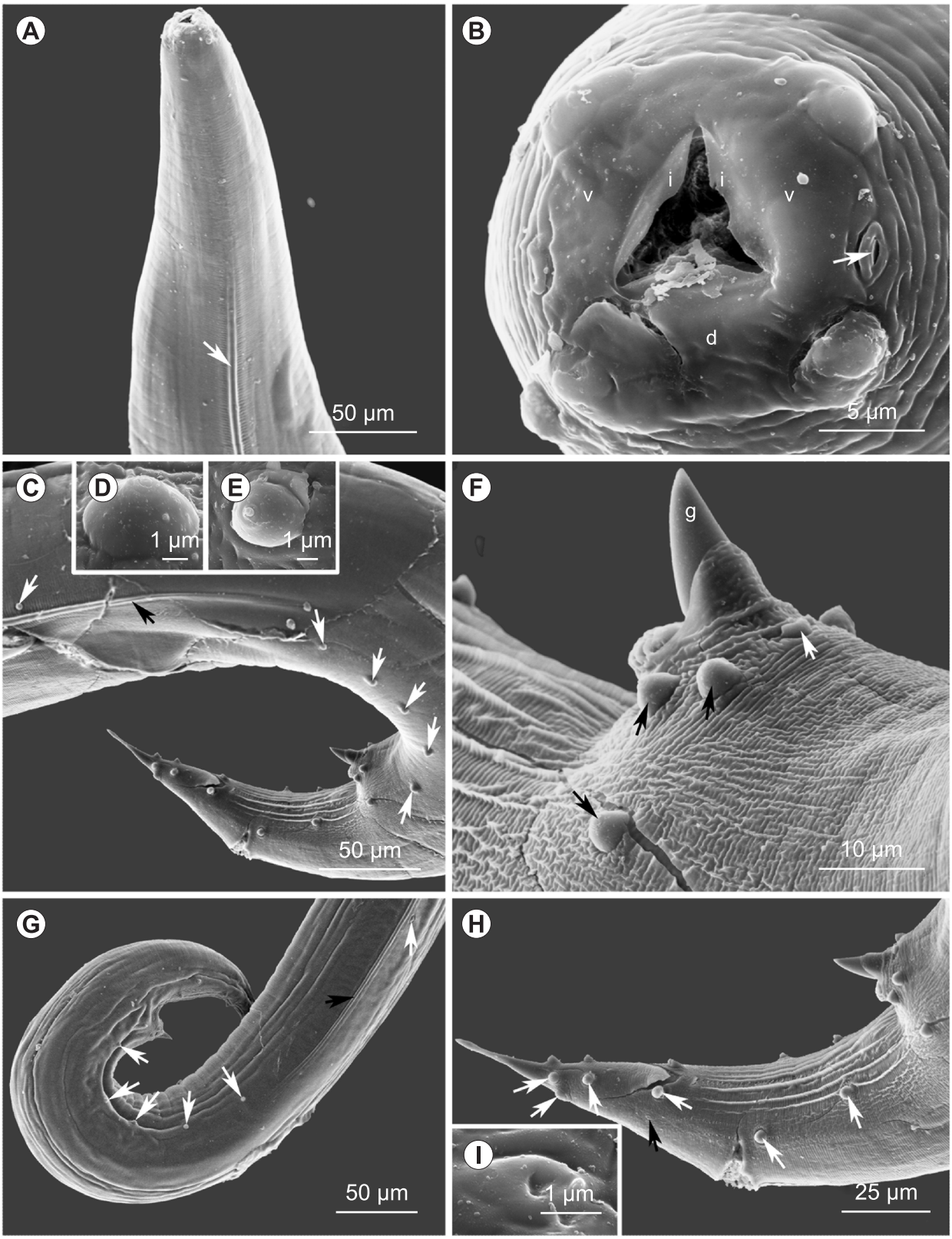

Fig. 2. Scanning electron micrographs of *Maxvachonia chabaudi* Mawson, 1972 from the marine toad *Rhinella marina* (Linnaeus) (Anura: Bufonidae) in Australia, male. **A** – anterior part of body (lateral ala arrowed), lateral view; **B** – cephalic end (amphid arrowed), apical view; **C**, **G** – posterior end of different individuals (white arrows showing precloacal papillae, black arrow showing lateral ala), lateral view; **D** – magnified image of precloacal papilla; **E** – magnified image of postcloacal papilla; **F** – magnified image of cloacal region (white arrow showing precloacal medio-ventral papilla, black arrows showing paracloacal papillae); **H** – tail (white arrows showing postcloacal papillae, black arrow showing phasmid), lateral view; **I** – magnified image of phasmid. *Abbreviations*: d – dorsal lip; g – tip of gubernaculum; i – inner flange of lips; v – ventrolateral lip.

erating voltage of 20 kV. Measurements are given in micrometers (μm) unless otherwise stated. The holotype of *Maxvachonia chabaudi* (No. AHC 41502) and paratypes of *M. flindersi* (No. AHC 5153) deposited in the South Australian Museum (AHC) were examined and compared. Voucher specimens were deposited in the College of Life Sciences, Hebei Normal University, Hebei Province, China (CLS-HBNU).

RESULTS

Family Cosmocercidae Railliet, 1916

Genus *Maxvachonia* Chabaud et Brygoo, 1960

***Maxvachonia chabaudi* Mawson, 1972** Figs. 1–3

Small, whitish nematodes. Body cylindrical, maximum width at about region of mid-body. Cuticle with fine transverse striations. Somatic papillae absent. Cephalic end rounded. Oral aperture simple, somewhat triangular, surrounded by 3 small lips, each with inner flanges (Figs. 2B, 3D). Dorsal lip with 1 pair of large double cephalic papillae, subventral lips with single large double cephalic papilla and amphid (Figs. 2B, 3D). Buccal capsule short, with three small teeth-like projections at base (Fig. 1E). Oesophagus divided into anterior indistinct pharynx, cylindrical corpus, narrow isthmus and terminal posterior bulb with valves (Fig. 1A–D). Lateral alae only present in male (Fig. 2A). Nerve ring located at about 1/3–1/2 of oesophageal length. Excretory pore discoid, situated at anterior to oesophageal bulb (Figs. 1A–D, 3A,B). Deirids not observed. Tail of both sexes conical, with pointed tip (Figs. 1F,K,L, 2C,H, 3F,G).

Male (based on two mature specimens): Body 2.07–2.24 mm long; maximum width 140–220. Entire oesophagus 261–338 long (including posterior oesophageal bulb), representing 13–15% of body length; pharynx + corpus + isthmus 213–280 long, size of oesophageal bulb 48–58 × 53–72. Nerve ring 113–138 and excretory pore 208–256 respectively, from anterior extremity. Lateral alae narrow, extending from level of excretory pore to anterior of second precloacal papillae (Figs. 1F, 2A,C,G). Posterior end of body distinctly ventrally curved (Figs. 1F, 2C,G). Spicules slender, equal in length, distal end pointed, 88–122 long, representing 4.3–5.4% of body length (Fig. 1F,G). Gubernaculum robust, well-sclerotised, with remarkable lateral processes near the proximal end, slightly longer than spicules, 109–146 long (Figs. 1F,G, 2F). Caudal papillae 15 pairs in total, arranged as follows: 6 pairs precloacal (first pair lateral, far from others), 3 pairs paracloacal (2 pairs ventral, close to cloaca; 1 pair ventrolateral, far from cloaca) and 6 pairs postcloacal (4 pairs ventrolateral and 2 pairs dorsolateral (Figs. 1F, 2C–H). Single precloacal medio-ventral papilla present (Fig. 2F). Tail 150–200 long, representing 7.2–8.9% body length (Figs. 1F, 2C,H). One pair of small phasmids located at about posterior 1/3 of tail (near third pair of postcloacal papillae) (Fig. 2H,I).

Female (based on 33 mature specimens): Body 7.20–14.6 mm long; maximum width 180–400. Entire oesophagus 435–676 long (including posterior oesophageal bulb), representing 3.6–8.4% of body length; pharynx + corpus + isthmus 362–580 long, size of bulb 72–111 × 72–111. Nerve ring 163–300 and excretory pore 314–483 respectively, from anterior extremity. Lateral alae absent. Vulva transverse slit, vulval lips not protruded, 411–652 from anterior extremity, at 3.8–7.3% of body length (Figs. 1A–C, 3A,C). Egg oval, thin-walled, with a small nipple at one side, 50–80 × 38–58 (n = 66) (Figs. 1H–J, 3E). Tail 1.50–3.65 mm long, representing 20.3–30.3% body length; tip of tail finger-like, covered with numerous nodular protuberances (Figs. 1L,K, 3F,G). Phasmids not observed.

Host: Marine toad *Rhinella marina* (Linnaeus) (Anura: Bufonidae).

Localities: Cape Weymouth (-12.61611111, 143.43194444), Mareeba (-17.01861111, 143.47000000), northern Queensland; rural areas surrounding Townsville (-19.38472222, 146.96250000 and -19.38472222, 146.96250000), northern Queensland; Boyne Island (-23.93000000, 151.34777778), central Queensland, Australia.

Rate of infection: prevalence 5.1% (33 out of 643 of *R. marina* specimens were infected), with an intensity of 1–9 (mean 2.7) nematodes.

Site of infection: intestine.

Voucher specimens deposited: two males (HBNU–N-2021A005NL), 33 females (HBNU–N-2021A006NL).

Key to the species of *Maxvachonia*

Maxvachonia brygooi was treated as *incertae sedis* and is not included in the key;

1a Spicules longer than gubernaculum ……..... 2
1b Spicules shorter than gubernaculum …..... 3
2a Two pairs of precloacal papillae ..... *M. ewersi*
2b Five pairs of precloacal papillae ..... *M. ingens*
3a Tail tip of female rounded ..... *M. dimorpha*
3b Tail tip of female conical (tail normally with finger-like tip) 4
4a Two or three pairs of precloacal papillae; eggs with long filaments ..... *M. flindersi*
4b Five to six pairs of precloacal papillae; eggs without filaments 5
5a Precloacal longitudinal grooves present in male; tail tip of female without nodular protuberances ... *M. adamsoni*
5b Precloacal longitudinal grooves absent in male; tail tip of female with numerous nodular protuberances .... *M. chabaudi*

DISCUSSION

The location of the vulva at anterior or slightly posterior of they oesophageal bulb, the eggs with a small nipple at one side, the unusually long female tail, the slender and short spicules, and the robust gubernaculum usually with remarkable lateral processes, allow assigning the specimens to the genus *Maxvachonia*.

Mawson (1972) described *Maxvachonia chabaudi* from some skinks and a snake in Australia. We examined the holotype of *M. chabaudi* (No. AHC 41502) deposited in the South Australian Museum. The morphology and measurements of our present material are almost identical to the type specimen and the original description of *M. chabaudi*

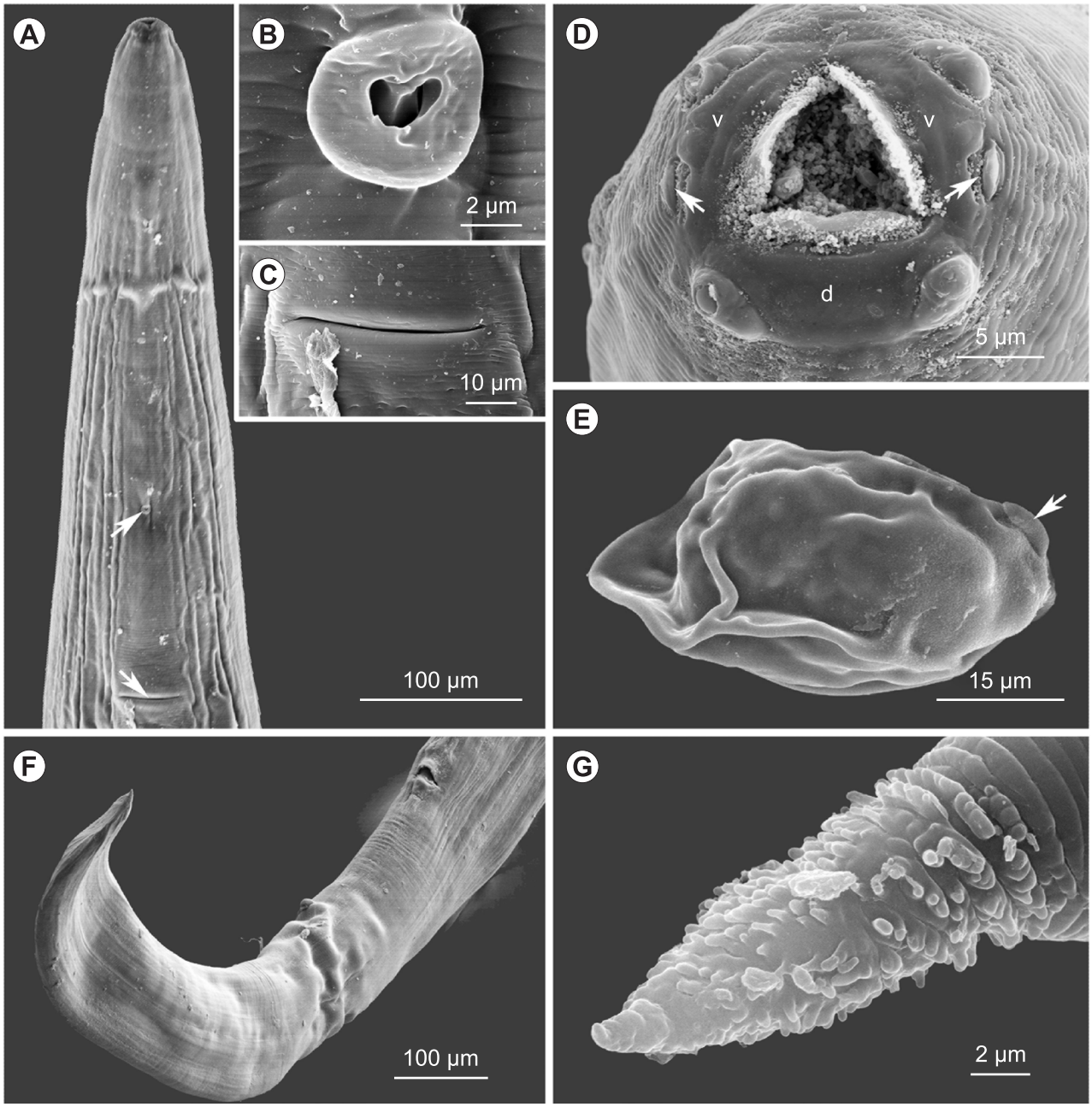

Fig. 3. Scanning electron micrographs of *Maxvachonia chabaudi* Mawson, 1972 from the marine toad *Rhinella marina* (Linnaeus) (Anura: Bufonidae) in Australia, female. **A** – anterior part of body (excretory pore and vulva arrowed), ventral view; **B** – magnified image of excretory pore; **C** – magnified image of vulva; **D** – cephalic end (amphids arrowed), apical view; **E** – egg (small nipple arrowed); **F** – tail, lateral view; **G** – magnified image of tail tip. *Abbreviations*: d – dorsal lip; v – ventrolateral lip.

regarding several features, including the body length of female, the presence of lateral alae in male, the position of the excretory pore, the relative length of the oesophagus and spicules to body length, the position of vulva, the morphology and length of the gubernaculum and tail (see Table 1 for details).

Although Mawson (1972) claimed the presence of 13 pairs of caudal papillae in the original description of *M. chabaudi*, the illustration of this species by the author clearly shows 15 pairs of caudal papillae. The number and arrangement of caudal papillae of our specimens agreed well with Mawson's (1972) material, except the first pair of precloacal papillae being farther from the second pair of precloacal in our specimens. Therefore, we considered that our newly collected specimens from *R. marina* are conspecific with *M. chabaudi*.

Mawson (1972) stated that the female specimens of *M. chabaudi* also have lateral alae, but we did not observe our female specimens with lateral alae using SEM. In addition, our male specimens are slightly smaller than Mawson's (1972) specimens. We also observed the location of the vulva and excretory pore varying among different individuals in our specimens.

Recently, some species of the Cosmocercoidea have been reported to exhibit remarkable morphological variation among different individuals collected from different hosts and localities or the same host in some important

Table 1. Morphometric comparisons of *Maxvachonia chabaudi* Mawson, 1972 (Nematoda: Cosmocercidae) (measurements in millimetres).

Characteristics	Present study		Mawson (1972)	
	Male	Female	Male	Female
Length of body (BL)	2.07–2.24	7.20–14.6	2.30–2.70	6.00–15.5
Length of entire oesophagus (OL)	0.26–0.34	0.44–0.68	0.37–0.52	0.57–0.98
OL/BL (%)	12.6–15.1	3.63–8.39	13.7–20.0	5.59–10.8
Distance excretory pore from anterior end	0.21–0.26	0.31–0.48	0.20–0.33	0.27–0.63
Distance nerve ring from anterior end	0.11–0.14	0.16–0.30	0.15–0.33	0.15–0.32
Spicules length (SL)	0.09–0.12	–	0.12–0.13	–
SL/BL (%)	4.26–5.43	–	4.80–5.22	–
Gubernaculum length	0.11–0.15	–	0.13–0.16	–
Number and arrangement of caudal papillae (pairs)	6, 3, 6	–	6, 3, 6	–
Vulva from anterior end (VA)	–	0.41–0.65	–	0.38–0.80
VA/BL (%)	–	3.82–7.32	–	4.03–7.36
Length of tail (TL)	0.15–0.20	1.50–3.65	N/A	1.50–4.20
TL/BL (%)	7.24–8.91	20.3–30.3	N/A	19.6–30.3
Hosts	marine toad		skinks	
Country	Australia		Australia	

morphological characters (i.e., the position of the excretory pore, the structure and position of the vulva, the shape of the gubernaculum and the number and arrangement of caudal papillae – González et al. 2019, Ni et al. 2022). Consequently, we speculated that the presence of morphological difference in the above-mentioned respects between our specimens and Mawson's (1972) material or among different individuals of the present specimens should be considered as intraspecific variation, possibly owing to the different hosts, localities and development. Some characters important for the specific diagnosis of *M. chabaudi* are reported for the first time: each lip with distinct inner flanges and the presence of a single medio-ventral precloacal papilla in male. *Rhinella marina* represents a new host record for *M. chabaudi*.

Within the genus *Maxvachonia*, *M. adamsoni*, *M. ewersi* and *M. ingens* were reported from Papua New Guinea (Mawson 1972, Moravec and Sey 1990, Bursey et al. 2011). *Maxvachonia chabaudi* could be easily distinguished from *M. ingens* by having the spicules slightly shorter than the gubernaculum (*vs* spicules slightly longer than the gubernaculum in *M. ingens*) and different morphology of the tail tip in females (tail with finger-like tip, covered with numerous nodular protuberances in *M. chabaudi vs* tail tip rounded without any ornamentation in the latter).

Maxvachonia ewersi has only two pairs of precloacal papillae in the male and the tail tip of female is also rounded, which is different from *M. chabaudi* with six pairs of precloacal papillae and tail of female with finger-like tip. *Maxvachonia chabaudi* also differs from *M. adamsoni* by the slightly shorter tail in male (0.15–0.20 mm, representing 7.2–8.9% of body length in *M. chabaudi vs* 0.26 mm, representing 10.5% of body length in the latter), the absence of precloacal longitudinal grooves in male and the tail tip of female covered with numerous nodular protuberances (*vs* the tail tip of female without nodular protuberances in *M. adamsoni*).

Maxvachonia brygooi and *M. flindersi* were both described in Australia (Johnston and Mawson 1941, Mawson 1972). *Maxvachonia brygooi* with only ''female specimen'' reported from agamid lizards by Mawson (1972), should be treated as *incertae sedis*. Johnston and Mawson (1941) described *Aplectana flindersi* from the whistling tree frog *Litoria ewingi* (Duméril et Bibron) (Anura: Hylidae) in Australia. Later, Inglis (1968) placed this species into the genus *Austracerca* Inglis, 1968 and redescribed it based on specimens collected from three species of frogs in western Australia. Mawson (1972) transferred this species into the genus *Maxvachonia* and also reported new hosts, including the marine toad *R. marina*. However, *M. flindersi* can be easily distinguished from *M. chabaudi* by having only 2–3 pairs of precloacal papillae in the male (*vs* six pairs of precloacal papillae present in *M. chabaudi*) and the tail tip of female without nodular protuberances (*vs* tail tip of female covered with numerous nodular protuberances in the latter).

The type species *M. dimorpha* was originally reported from the panther chameleon *Furcifer pardalis* (Cuvier) (Reptilia: Squamata) in Madagascar (Chabaud and Brygoo 1960). *Maxvachonia chabaudi* differs from *M. dimorpha* by having more precloacal papillae (six pairs in *M. chabaudi vs* five pairs in *M. dimorpha*), distinctly smaller body size and different morphology of the eggs and tail tip in female (body 7.20–14.6 mm long, tail with finger-like tip covered with numerous nodular protuberances *vs* body 16.0–18.0 mm long, tail tip rounded in the latter) (Chabaud and Brygoo 1960). A revision of *Maxvachonia* with integrated morphological characters and genetic data needs to be undertaken to evaluate the validity of the currently recognised known species or to reveal new cryptic species and clarify the systematic status of this group.

The marine toad *R. marina* is a large exotic amphibian species in Australia, which is natively distributed in Central and South America (Zug and Zug 1979, Lever 2001). Our specimens of *M. chabaudi* were collected from the marine toad, which is different from all the known hosts (skinks and snake). As the known geographical distribution of *Maxvachonia* species is in the Australo-Papuan Region, with the exception of *M. dimorpha* which is distributed in Madagascar (Chabaud and Brygoo 1960, Mawson 1972, Moravec and Sey 1990, Bursey et al. 2011), we speculate that *Maxvachonia* may have originated in the Australo-Papuan Region. Consequently, the marine toad was infected with *M. chabaudi* following its introduction to Australia.

The life cycle of *Maxvachonia* is unknown, but related species have a direct life cycle, with infective third-stage larvae either being ingested (by tadpoles) or penetrating the skin (Anderson 1992). Thus, it is possible that the marine toad became infected with *M. chabaudi* due to a similarity in diet/habitat/ecology between the toad and skinks, which has allowed the parasites to transfer between the host species. The large list of hosts for the various *Maxvachonia* spp. also suggests that they have wide host specificity, and thus transfer to a new host would be possible. Additionally, the toad has acquired a number of parasites since its introduction to Australia (see Barton 1997) and many of these have also only previously been reported in reptiles.

The impacts of these parasites on the biology and/or ecology of the marine toad or on native Australian amphibians and reptiles is unknown, primarily due to the lack of baseline data of infections prior to the arrival of the marine toad (Barton 1997). However, the possibility of the marine toad to act as an amplifier of infection for native hosts (spillback, as defined in Lymbery et al. 2014) is high, given the sheer numbers of marine toads present in the environment and their expanding distribution (Barton 1997). The present study further confirms that invasive animals can be infected by native endoparasites and could potentially affect host-parasite dynamics.

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Authors' contributions. XFN, HXC and LL contributed to the morphological study and species identification of the nematode specimens. DPB collected the nematode specimens and compared the type material of *M. chabaudi* and *M. flindersi*. XFN, DPB and LL wrote and revised the manuscript. All authors read and approved the final manuscript.

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