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A protandric assimineid gastropod: *Rugapedia androgyna* n. gen. and n. sp. (Mollusca : Caenogastropoda : Rissooidea) from Queensland, Australia

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Abstract

A new genus and species of Assimineidae, *Rugapedia androgyna*, is described from mangrove swamps in Queensland, Australia. It differs from other assimineid genera in several anatomical and radular characters, including an anterior pedal mucous gland composed of elongate cells arranged in a transverse row (unique for the subfamily Assimineinae), and the sole of the foot has distinct transverse rugae, a trait which is unique for the family. This species is also shown to be the first case of protandry in the family.

Additional keywords: Assimineidae, Gastropoda, hermaphrodite, protandry, mangrove, anatomy, taxonomy.

Introduction

Assimineids occur worldwide in all temperate and tropical areas, with marine, estuarine, freshwater and terrestrial taxa. Members of the family are common in estuarine habitats in many parts of Australia, but the Australian fauna has never previously been revised. Fukuda and Ponder (2003) reviewed the family and genus-group names attributed to the Assimineidae. Many of these taxa are poorly known, in some cases only from shells. Nevertheless, their review makes it possible to allocate genera and recognise new taxa with reasonable certainty.

This paper represents one of a series describing the temperate and subtropical Australian taxa. During this work a new species that could not be placed in any of the existing genera was investigated and found to be protandric.

Materials and methods

Specimens used in this study are mostly housed in the Australian Museum (AMS) with paratypes lodged in the Queensland Museum (QM) and the Laboratory of Conservation of Aquatic Biodiversity, Faculty of Agriculture, Okayama University (OKCAB). Dissected specimens were fixed in ~10% formalin and stored in 7% seawater formalin.

Specimens were measured using a digitising pad as described by Ponder *et al*. (1989). The shells of a subset of these specimens were then removed and the animals sexed. The remaining unsexed specimens were retained as vouchers.

Dissections were carried out using a Leica stereoscopic microscope using a drawing apparatus. Radulae, opercula and shells were examined using a Leo 435 VP scanning electron microscope and were mounted using standard techniques.

The graph of sex and shell size was generated using SYSTAT ver. 7 (SPSS Inc., Chicago, IL, USA).

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Systematics

Rugapedia n. gen.

Type species: *Rugapedia androgyna* n. sp.

Diagnosis

Shell solid, opaque, conical; protoconch consisting of protoconch I and II with indistinct thread below suture; teleoconch whorls slightly convex, sutures weakly impressed, with distinct subsutural spiral cord, otherwise smooth except for fine collabral growth lines; colour uniform dark brown; aperture pyriform with thin outer lip and thick, wide columellar lip; no varix, outer lip prosocline (~30°); lower base with spiral ridge surrounding umbilical area; umbilicus closed or with narrow chink. Operculum simple, pyriform, paucispiral, horny, translucent. Head–foot with no cephalic tentacles, with distinct omniphoric groove; anterior pedal mucous gland composed of several elongate, white cells arranged in transverse row just behind slit; sole slender when foot extended; propodium flat, smooth; metapodium usually shows many distinct regularly spaced wrinkles visible when extended or contracted. Radula taenioglossate; central teeth with no basal cusps; lateral teeth rectangular; inner marginal teeth long, slender; outer marginal teeth extremely wide, triangular, fan-shaped, with many tiny cusps but no secondary cusps. Prostate gland simple, slender; penis simple, large, with weak keel on outer edge of middle portion and distal end with short, narrow papilla with opening at tip. Coiled (renal) oviduct with one loop; seminal receptacle large, oval, colourless except for iridescent contents; arises from oviduct slightly anterior to end of coiled oviduct and lies between anterior end of bursa copulatrix and posterior end of albumen gland; bursa copulatrix large, elongately triangular, posterior to albumen gland; bursal duct long, straight; arises from oviduct at point where oviduct enters albumen gland; opens to anterior portion of bursa at ventral edge; pallial oviduct long, runs nearly straight to opening of pallial cavity; albumen gland white, opaque; capsule gland with three glandular zones; sperm duct completely surrounded by glandular pallial oviduct within central region of oviduct; vestibule narrow, muscular, with genital opening at anterior end. Right pleural and supraoesophageal ganglia separated from each other by long pleural-supraoesophageal connective; left pleural ganglion completely fused with suboesophageal ganglion.

Remarks

Anatomically, *Rugapedia* resembles *Aviassiminea* (Fukuda & Ponder, 2003) in most of the features of the pallial cavity, alimentary canal (other than the radula) and nervous system. However, the reproductive system differs in several details. There are no other published detailed anatomical studies of other genera of Assimineinae (see Fukuda and Ponder 2003 for a summary of known information).

Rugapedia has no basal cusps on the central teeth of the radula and lacks cephalic tentacles. This combination of characters is known in nine valid genera of the Assimineidae listed under Group 2 *sensu* Fukuda and Ponder (2003). Basal cusps are absent in a few additional genera for which the head-characters are unknown. A few of these resemble Group 2 taxa rather than Omphalotropidinae (Group 3). The genera without basal cusps and those in Group 2 can be divided up according to characters of the shell and operculum as follows:

Key to genera of Assimininae lacking basal cusps on the central teeth of the radula

1. Operculum with calcareous layer on outer side . . . . . *Metassiminea* Thiele, 1927
   Operculum horny, simple 2
2. Shell with spiral ridge on base . . . . . *Cyclotropis* Tapparone-Canefri, 1883; *Taiwanassiminea* Kuroda & Habe, 1950
   Shell with no spiral ridge on base 3
3. Umbilicus absent . . . . . *Optediceros* Leith, 1853; *Paludinella* Pfeiffer, 1841; *Leucostele* Thiele, 1927; *Pseudassiminea* Thiele, 1927
   Umbilicus present 4
4. Translucent, fragile colourless shell. . . . . *Acmella* Blandford, 1869; *Cavernacmella* Habe, 1942
   Opaque, brown, strong shell . . . . . *Ekadanta* Rao, 1928; *Solenomphala* Heude, 1882

Among these genera, *Cyclotropis* and *Taiwanassiminea* are the most similar to the new genus in being based on species having both a distinct basal ridge and a spiral cord or groove just below the suture. *Cyclotropis* differs from *Rugapedia* in radular characters, the central teeth being much shorter and wider (van Benthem Jutting 1963; Brandt 1974; Fukuda and Ponder in press) and in having a much larger, distinctly umbilicate shell. *Taiwanassiminea* also has short central teeth with a narrow thickening on the lateral edges and the shell has a spiral cord or groove on the periphery, but this is located just above the suture (Habe 1942; Pace 1973; Fukuda and Mitoki 1996*a*) not below it in the type species. However, other taxa included in *Taiwanassiminea* (Fukuda and Ponder in press) have the spiral cord below the suture and lack a peripheral cord or groove. There are several other important differences between *Taiwanassiminea* and *Rugapedia* including the former genus having a simple sole and the capsule gland consisting of a single glandular mass, not three distinct zones (Fukuda and Ponder in press).

The radula of *Rugapedia* is unique and the combination of tooth shape seen in this genus has not been reported in other assimineids. The fan-shaped wide outer marginal teeth with a simple row of cusps are also known in *Solenomphala* and several genera listed as Group 3 (= subfamily Omphalotropidinae) by Fukuda and Ponder (2003). However, members of this group have cephalic tentacles (e.g. *Allepithema* Tomlin, 1930; *Ditropisena* Iredale, 1933; *Paludinellassiminea* Habe, 1994). The radula of *Ditropisena* (H. Fukuda, personal observation) is most similar to that of *Rugapedia* but differs in the expansion of the ventral region of the central teeth in the new genus. Moreover, *Ditropisena* has a depressed trochiform shell with strong spiral and axial ribs and a wide umbilicus, as well as a circular operculum with a central nucleus and long cephalic tentacles (Fukuda and Ponder 2003).

The head–foot of *Rugapedia* is unique in having numerous transverse rugae on the sole of the foot that persist even in fixed material. This character is unknown in any other assimineid and may even be unique within the Rissooidea. It also has multiple glandular sacs opening to the anterior edge of the foot, another character not seen in any other Assimineinae but known in a few Omphalotropidinae (H. Fukuda, personal observation).

Because anatomical studies are few, we cannot compare the anatomical characters of *Rugapedia* with most of the assimineine genera listed by Fukuda and Ponder (2003). One Australian species of *Taiwanassiminea* (Fukuda and Ponder in press) differs from *Rugapedia* in having the vestibule arising from the mid-ventral portion of the capsule gland but we do not know if this is typical of that genus. General arrangements of the reproductive and nervous systems of *Rugapedia* are generally similar to those of *Assiminea* Fleming, 1828, a genus of Fukuda and Ponder's (2003) Group 1 (= subfamily Assimineinae; cephalic tentacles absent, central teeth of the radula with basal cusps), but the type species of *Assiminea* has a strongly coiled anterior vas deferens around the prostate gland, a

longitudinal row of distinct papillae on the penis, and a black seminal receptacle (Fukuda and Ponder unpublished observations).

Although the species described below is a protandrous hermaphrodite, two others that appear to be congeneric are dioecious, one from Queensland and one from Okinawa. These will be described elsewhere.

Etymology

Ruga (Latin): wrinkle; *pedis* (Latin): foot.

Rugapedia androgyna n. sp.

(Figs 1–4)

Material examined

Holotype. Tooan Tooan Creek, Hervey Bay, QLD, 25°17′S, 152°50.683′E, upper shore among dead leaves on sand in mangroves, W. F. Ponder & H. Fukuda, 3 Mar. 2003 (AMS C.429858).

Paratypes. **Queensland**: same locality as holotype (AMS C.429527, 8 wet specimens: 4 complete shells and 4 bodies); South Trees Inlet, SE of Gladstone, 23°57.833′S, 151°20.250′E, mangrove swamp, 8 Sep. 2003, H. Fukuda & J. Studdert (AMS C.429092, 69 wet: 49 shells, 20 bodies, 8 dry, 1 on s.e.m. stub; QM MO64286, 3 wet; OKCAB M5424, 5 wet; AMS C.429859, 1 dry specimen, figured); Toolara, Tin Can Bay, 25°55.400′S, 153°0.483′E, upper shore, mangrove swamp, 4 Mar. 2003, W. F. Ponder & H. Fukuda (AMS C.429528, 7 wet specimens: 2 shells and 5 bodies; AMS C.429529, 1 dry specimen, figured); NE of Gympie, Tin Can Bay, 25°57′S, 153°0′E, small mangrove creek, under bark on dead roots, 22 Oct. 1976, I. Loch (AMS C.414899, 4 shells, 1 body).

Other material examined. **Queensland**: Gladstone, 23°51′S, 151°16′E, 1904 (AMS C.018798, 12 shells); 0.5 km S of Urangan Boat Anchorage, Hervey Bay, 25°19′S, 152°54′E, under leaves and wood in pools in mangroves, 24 Oct. 1976, I. Loch & B. Duckworth (AMS C.416547, 2); Pine River, N of Brisbane, 27°52.5′S, 153°0′E, under bark of rotting log, 1975, J. McNalty (AMS C.414866, 12).

Description

Shell (Fig. 1) small, ovate-conic to conic (Fig. 1*A–C*), thick, opaque. Protoconch (Fig. 1*D*, *E*) of ~2.1–2.2 weakly convex whorls, with smooth surface except for spiral cord below suture (Fig. 1*G*). Teleoconch uniform dark chestnut brown, of up to about four weakly convex whorls, sculptured with weak collabral growth lines; suture shallow, weakly impressed; distinct subsutural spiral keel (becomes groove if eroded, as observed in species of *Angustassiminea* Habe, 1943 by Fukuda and Mitoki (1996*b*)) below suture. Aperture wide, pyriform; peristome complete, sharp, with no apertural varix; outer lip prosocline, not expanded; parietal lip narrow, rather long, slightly curved, thin, transparent; columellar lip thick, wide, distinctly curved, anterior end forming strong projection crossing anterior part of outer lip, forming shallow canal. Umbilicus narrow chink or closed; umbilical area surrounded by strong spiral ridge (Fig. 1*F*). Dimensions (Table 1).

Operculum (Fig. 2*A*, *B*) pyriform, paucispiral, with last whorl very large; horny, thin, flat, yellowish, transparent, simple on inner surface; muscle scar elongate, occupying ~2/3 of length of columellar side of inner surface.

Head–foot (Fig. 3*A–E*). Majority of head–foot covered with dense (less well developed in some specimens) black pigment in many specimens (Fig. 3*A*, *B*), except for colourless, translucent eye lobe, anterior end of snout (in some specimens), sole, omniphoric groove and opercular lobe. Triangular eye lobes (el, Fig. 3*B*) each with conspicuous, black eye at middle and crescent-shaped black pigmentation spot at tip. Cephalic tentacles absent. Snout long, bilobed. Foot large, wide, anterior and posterior ends simple and rounded. Opening to anterior mucous gland (Fig. 3*E*) wide, transverse slit just

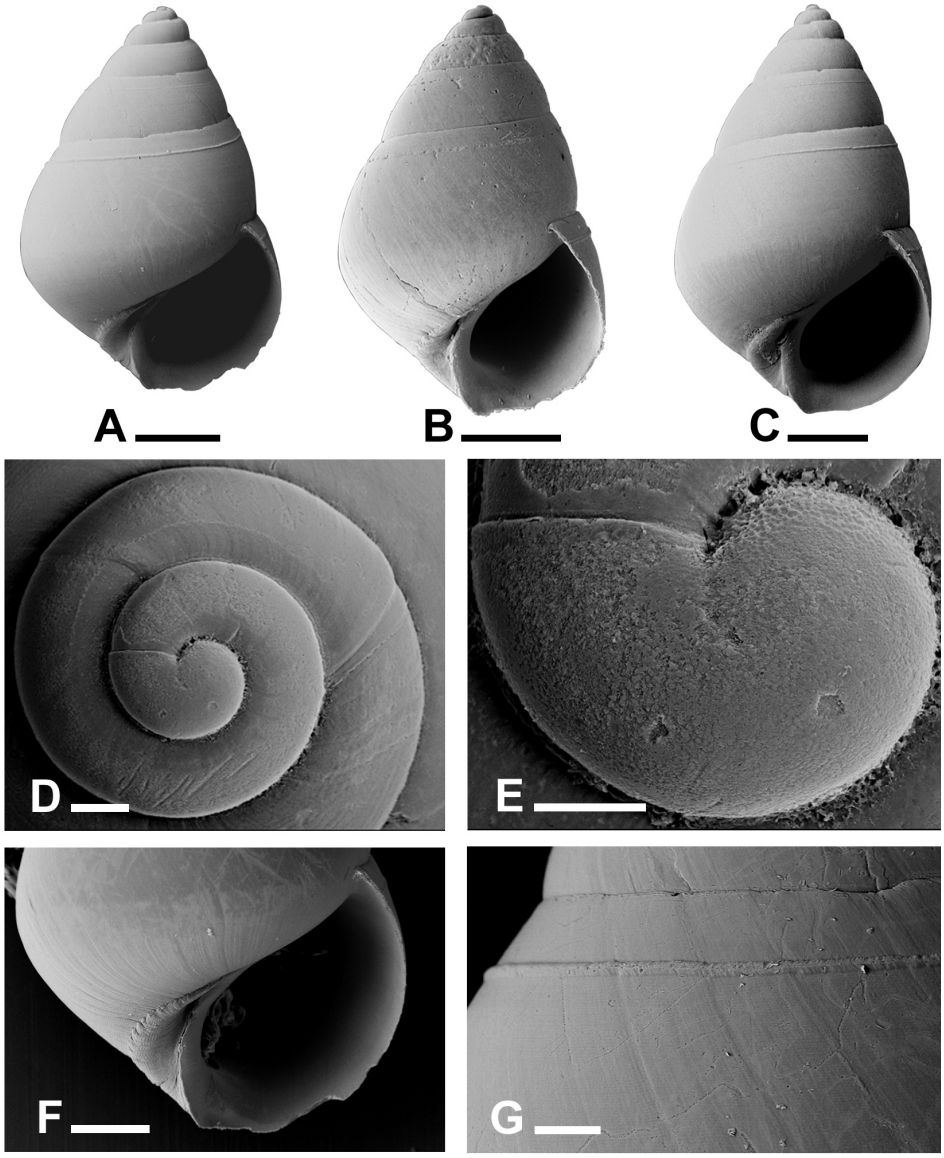

Fig. 1. *Rugapedia androgyna* n. sp. *A–C*, shell: *A*, holotype, Tooan Tooan Ck, Hervey Bay, Qld (AMS C.429858); *B*, paratype, Toolara, Tin Can Bay, Qld (AMS C.429529); *C*, South Trees inlet, SE of Gladstone, Qld (AMS C.429092); *D–G*, details of shell of holotype: *D*, *E*, protoconch; *F*, detail of base; *G*, suture area on last whorl, showing subsutural thread. Scale bars: *A–C*, 500 μm, *D*, 50 μm, *E*, 30 μm, *F*, 300 μm, *G*, 100 μm.

posterior to anterior end of foot; posterior lip of slit usually bent backward when animal alive. Anterior pedal mucous gland (apg, Fig. 3*D*, *E*) composed of several elongate, white cells (Fig. 3*E*, *F*), each with two or three tiny ducts visible through translucent sole epithelium; mucous cells arranged in transverse row just behind slit. No posterior pedal mucous gland or metapodial tentacle present. Wide omniphoric grooves (og, Fig. 3*A*) run ventrally on both sides of head; right groove wider than left. Right groove carries faecal

Table 1. Shell dimensions of *Rugapedia androgyna* n. sp.
Number of specimens given in brackets after the registration number. Ranges: minimum–maximum (mean) ± standard deviation (mm).

	Shell length	Shell width	Aperture length	Aperture width	Length of last whorl	Total whorls
Holotype	2.37	1.64	1.08	0.88	1.77	5.6
Figured specimens						
(C.429529)	2.37	1.58	1.15	0.93	1.73	5.9
(C.429092)	2.78	1.70	1.24	1.02	1.91	6.1
Paratypes C.429528 (8)	1.29–1.56 (1.86) ± 0.47	0.99–1.65 (1.31) ± 0.27	0.66–1.06 (0.85) ± 0.14	0.52–0.96 (0.76) ± 0.14	0.98–1.88 (1.37) ± 0.32	4.4–5.8 (5.0) ± 0.51
Paratypes C.414899 (9)	2.06–3.01 (2.64) ± 0.36	1.37–1.99 (1.76) ± 0.22	0.86–1.45 (1.20) ± 0.19	0.79–1.13 (1.01) ± 0.12	1.50–2.21 (1.95) ± 0.25	5.1–6.0 (5.6) ± 0.31
C.414866 (13)	1.64–3.09 (2.53) ± 0.38	1.21–2.00 (1.74) ± 0.22	0.77–1.33 (1.11) ± 0.17	0.75–1.15 (1.00) ± 0.11	1.30–2.28 (1.91) ± 0.27	4.3–5.4 (5.1) ± 0.29
C.416547 (2)	2.89, 2.91	1.88, 1.93	1.29, 1.30	1.05, 1.11	2.02, 2.11	5.4, 6.0
C.18798 (7)	1.97–2.81 (2.44) ± 0.33	1.36–1.74 (1.55) ± 0.16	0.90–1.21 (1.09) ± 0.12	0.79–1.06 (0.92) ± 0.10	1.39–1.89 (1.70) ± 0.19	5.5–6.1 (5.9) ± 0.23
C.429527 (10)	1.49–2.40 (1.93) ± 0.36	1.04–1.64 (1.34) ± 0.24	0.71–1.10 (0.89) ± 0.15	0.63–0.89 (0.77) ± 0.10	1.14–1.78 (1.49) ± 0.25	4.7–5.8 (5.3) ± 0.36

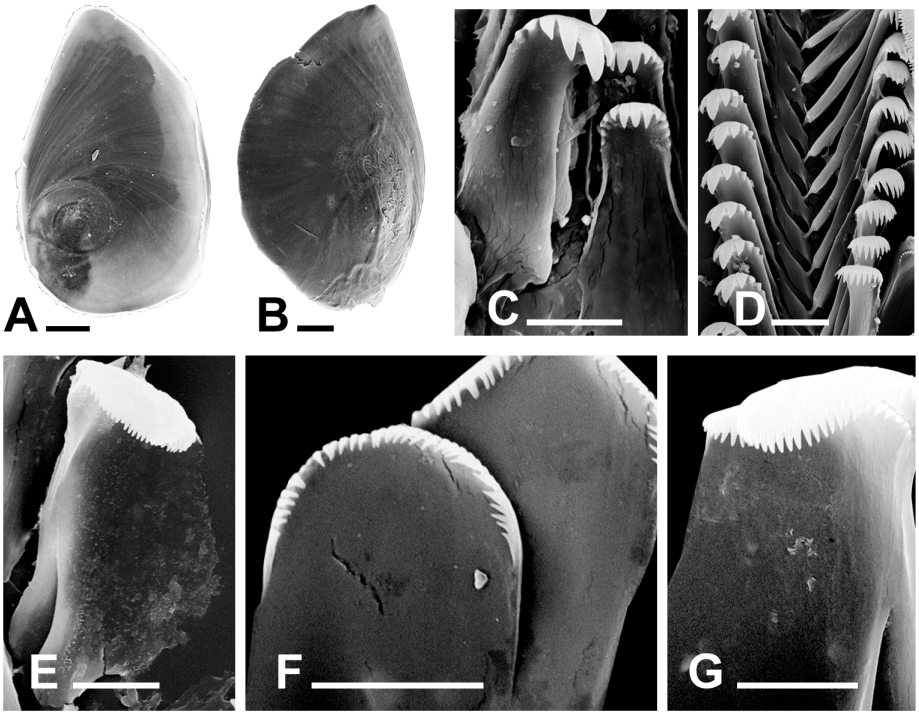

Fig. 2. *Rugapedia androgyna* n. sp. *A*, *B*, opercula: *A*, outer side; *B*, inner side, from paratypes, Tooan Tooan Creek, Hervey Bay, Qld (AMS C.429527). *C–G*, radula: *C–E*, *G*, Tin Can Bay, Qld (AMS C.414899); *F*, paratype, Toolara, Tin Can Bay (AMS C.429528); *C*, central and lateral teeth; *D*, lateral and inner marginal teeth; *E–G*, outer marginal teeth. Scale bars: *A*, *B*, 100 μm, *C–G*, 10 μm.

pellets from inside pallial cavity to exterior. Sole (Fig. 3*C*, *D*) slender when foot extended; propodium flat, smooth; metapodium usually shows ~20 distinct regularly spaced wrinkles visible when extended or contracted. Mode of locomotion 'step-like'.

Pallial cavity. Pallial cavity large, spacious, occupies about two thirds of last whorl. Pallial roof with black pigmentation, particularly in dorsal half and anterior mantle roof. Kidney opening conspicuous, in posterior-most corner of cavity; kidney entirely behind pallial cavity, compact, consisting of mass of colourless, transparent cells. Gill rudimentary, a row of four blunt, finger-like filaments consisting of only gf1 (inner side of filament; see Fukuda and Ponder 2003); on posterior portion of efferent vein on left side of cavity. Osphradium similar to *Aviassiminea* (Fukuda and Ponder 2003: fig. 4*A*), small, elongate-oval, containing conspicuous osphradial ganglion. Hypobranchial gland absent.

Digestive system. Mouth opens between pair of muscular lips into buccal cavity. Buccal mass large, wide, occupying most of snout. Radula (Fig. *2C–G*) taenioglossate; central teeth (Fig. 2*C*) spatula-shaped, much longer than wide; with 11–14 long, triangular cusps on cutting edge; three middle cusps longer than lateral ones, median cusp not markedly larger than pair of adjacent cusps; no basal cusps; lateral edges slightly thickened in upper two thirds, unthickened ventrally, nearly straight and parallel for about one third of length, then gently splayed; ventral region about twice as wide as cutting edge; base convex, simple, with no basal tongue. Lateral teeth (Fig. 2*C*, *D*) slightly longer than central teeth, rectangular, with no cusp on face of tooth; cutting edge with pointed median cusp

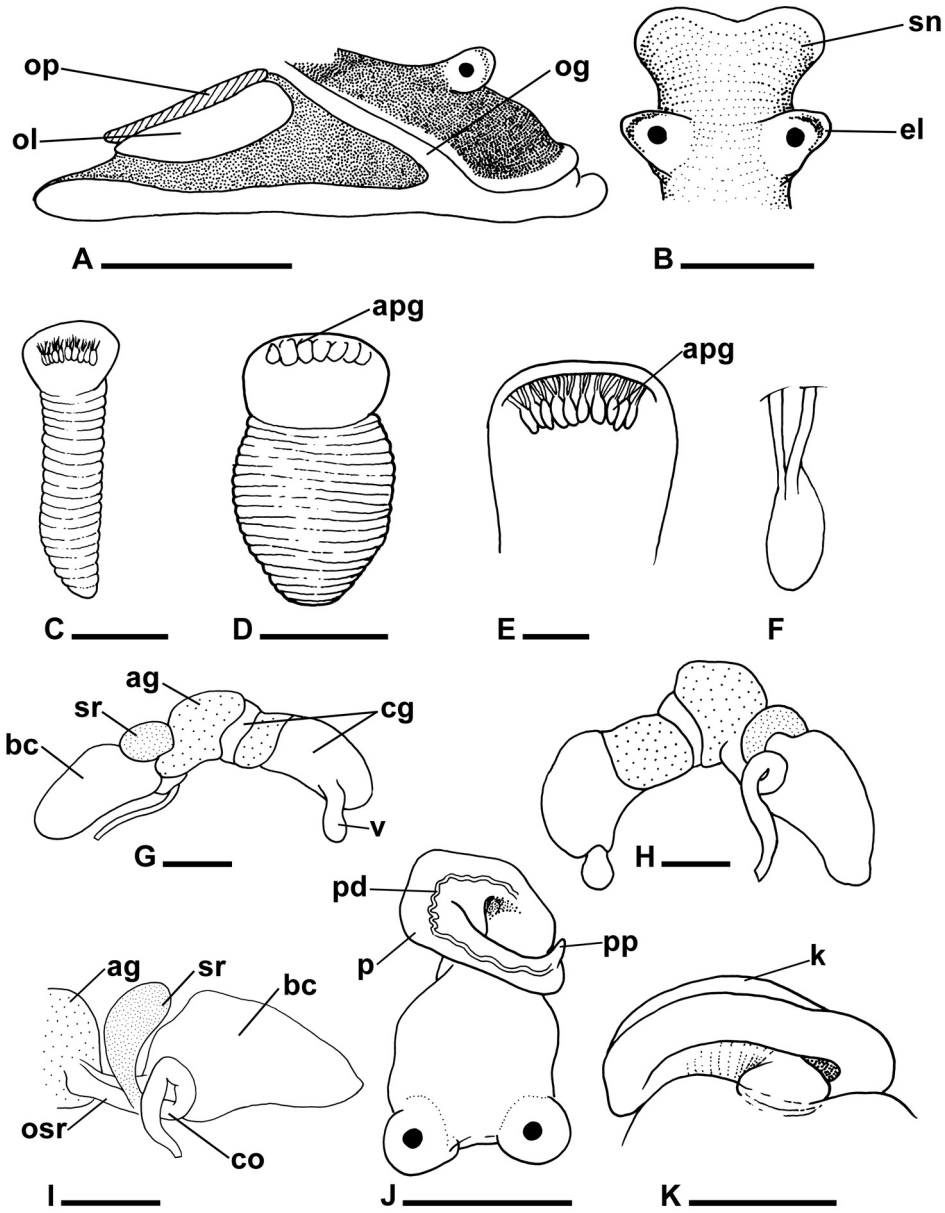

Fig. 3. *Rugapedia androgyna* n. sp., Tooan Tooan Creek, Hervey Bay, Qld (AMS C.429527). *A*, head–foot from right side; *B*, dorsal view of head; *C*, *D*, sole of foot, *C*, extended, *D*, contracted; *E*, schematic dorsal view of anterior end of foot showing detail of anterior pedal mucous gland; *F*, detail of one of pedal mucous gland elements; *G–I*, female reproductive system, *G*, view from right side, *H*, view from left side, *I*, detail of sperm sacs and coiled oviduct from left side; *J*, dorsal view of head and penis; *K*, lateral view of penis. Scale bars: *A–D*, *J*, 500 µm; *E*, *K*, 250 µm; *G*, *H*, 150 µm; *I*, 200 µm. Key to abbreviations: ag, albumen gland; apg, anterior pedal mucous gland; bc, bursa copulatrix; cg, capsule gland; co, coiled oviduct; el, eye lobe; k, keel (on penis); og, omniphoric groove; ol, opercular lobe; op, operculum; osr, oviduct anterior to seminal receptacle; p, penis; pd, penial duct; pp, penial papilla; sn, snout; sr, seminal receptacle; v, vestibule.

(about twice as long as adjacent cusps) and 3–4 pairs of smaller cusps on outer edge, one on inner edge; moderately long, oblique accessory plates at outer side of lateral teeth (Fig. 2*D*). Inner marginal teeth (Fig. 2*D*) long (about twice as long as central teeth), slender, gently curved, with parallel sides, cutting edge with 8–10 long, sharp cusps; base simple, rounded. Outer marginal teeth (Fig. 2*E–G*) extremely wide, triangular, fan-shaped, expanded in distal region; with more than 20 simple, tiny, sharp cusps on broad cutting edge; no secondary cusps; inner lateral edge thickened; base simple. Oesophagus opens widely to buccal cavity. Pair of glandular, black buccal pouches at posterior-most corner of dorso-lateral sides of buccal mass. Salivary glands short, simple, club-like, with black pigmentation, located at dorso-lateral sides of buccal mass, not passing through nerve ring. Oesophagus simple; enters stomach on left side at junction of anterior and posterior chambers. Stomach with single opening to digestive gland posterior to oesophageal opening. Digestive gland pale lemon-yellow; composed of two parts; anterior portion mass of small cells covering part of anterior and posterior stomach, posterior part two rows of large, finger-like lobes in upper whorls of visceral coil; lobes of outer row longer than those of inner rows. Style sac large, with crystalline style, bean-shaped. Origin of intestine at right anterior end of anterior chamber of stomach. Intestine tightly looped over anterior tip of style sac before continuing to rectum; rectum forms conspicuous S-shaped coil in middle of pallial roof. Oval faecal pellets queued in single file in intestine and rectum. Anus simple, situated slightly posterior to anterior mantle edge.

Male reproductive system. Testis large, bright orange, consisting of 6–10 bundles of wide lobes. Coiled seminal, tubular vesicle arises from vas efferens in antero-ventral region of digestive gland; wide, highly convoluted. Posterior vas deferens runs from seminal vesicle as straight tube crossing over oesophagus and running to middle part of prostate gland just within pallial cavity. Prostate gland slender, whole gland equal to about half length of pallial cavity. Anterior vas deferens arises from middle part of prostate gland close to entry point of posterior vas deferens, passes straight across pallial roof and enters muscular wall of neck, nearly straight before reaching proximal end of penis. Penis (Fig. 3*J*, *K*) large, muscular, on right side of head; forming anticlockwise coil when at rest; simple, tapering; with weak keel (k, Fig. 3*K*) on outer edge of middle portion; penial duct weakly undulating within penis; located in middle; distal end with short, narrow papilla (pp, Fig. 3*J*) with opening at tip. Transitional male with penial scar (absent in mature females).

Female reproductive system (Fig. 3*G–I*). Ovary simple sac with many white cells, covering ventro-lateral area of digestive gland. Posterior oviduct convoluted slightly, runs along oesophagus, on right lateral edge. Coiled (renal) oviduct (co) with one loop. Seminal receptacle (sr) large, oval, long, lacks distinct duct, colourless except for iridescent contents; arises from oviduct slightly anterior to end of coiled oviduct and lies between anterior end of bursa copulatrix and posterior end of albumen gland, distal half visible on right side of oviduct. Oviduct anterior to seminal receptacle (osr) of moderate length, straight, with small pocket just posterior to point where it enters left ventro-posterior end of albumen gland. Bursa copulatrix (bc) large, elongately triangular, posterior to albumen gland. Bursal duct long, straight; arises from oviduct at point where oviduct enters albumen gland; opens to anterior portion of bursa at ventral edge. Pallial oviduct long, runs nearly straight to opening of pallial cavity; clearly divided (in dissection) into albumen gland posteriorly and capsule gland anteriorly. Albumen gland (ag) white, opaque. Capsule gland (cg) with three glandular zones; anterior and (short) posterior ones translucent; middle one opaque, similar in appearance to albumen gland. Sperm duct muscular, completely surrounded by glandular pallial oviduct and fused with lumen of oviduct (= median egg

channel) within central region of oviduct. Narrow muscular vestibule (v) extends beyond anterior end of capsule gland, genital opening at anterior end.

Nervous system. Not examined in detail. Each cerebral ganglion large, rather slender. Cerebral commissure as long as cerebral ganglion. Right pleural and supraoesophageal ganglia separated from each other by long pleural-supraoesophageal connective. Left pleural ganglion completely fused with suboesophageal ganglion. Each pedal ganglion moderate in size, separated by a short, distinct commissure.

Distribution and habitat

Known from Gladstone to Brisbane in southern Queensland (Fig. 4). Amongst leaves in wet areas in back part of mangroves.

Remarks

Given the scant sampling for small gastropods in mangrove habitats in Queensland, this species may well have a larger range than indicated by the available material. It is found living together with '*Assiminea*' *buccinoides* (Quoy and Gaimard, 1834), '*A.*' *tasmanica* Tenison-Woods, 1876, and '*A.*' n. sp. (Fukuda and Ponder in press), and can be distinguished from these species by its uniformly dark brown shell and the presence of a basal ridge. Another superficially similar species of assimineid included in *Taiwanassiminea* (see above) is found in the upper parts of large estuaries from at least Rockhampton to the Shoalhaven River. This has a prominent basal ridge but differs in having a larger, banded shell as well as in radular and anatomical characters (Fukuda and Ponder unpublished observations).

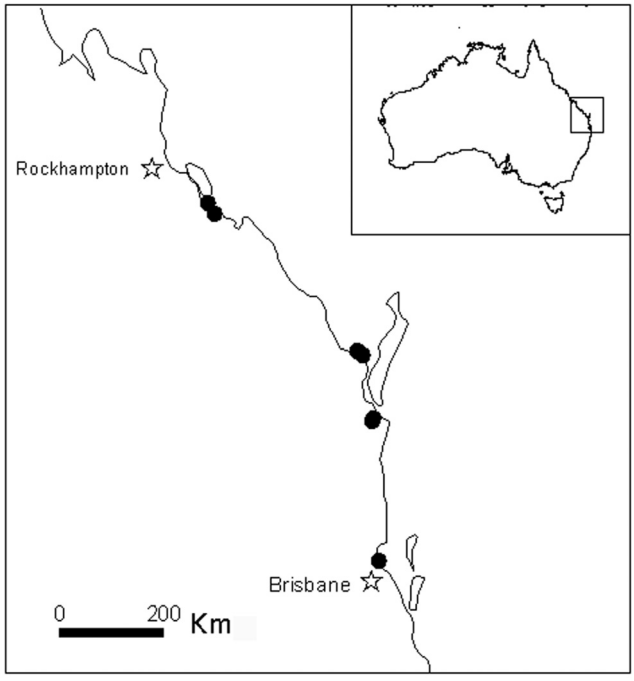

Fig. 4. Distribution of *Rugapedia androgyna* n. sp.

As mentioned above, at least two similar species are known, one from Queensland and the other from Okinawa. Preliminary investigation of these samples indicates that these species are both dioecious. Thus, if they are congeneric, protandry is not a generic character.

Etymology

Androgynus (Latin): hermaphrodite.

Sex change

The available samples contained only a few juveniles. These were all investigated and the results are summarised in Tables 2 and 3 and in Fig. 5.

Mature males are small and have a large penis. One transitional specimen was observed with a detached penis lying in the mantle cavity, and a scar was visible on the head where the penial base was attached. The scar is absent in mature females. This observation suggests the possibility that the penis is detached and shed rather than being absorbed during the transition from male to female.

Discussion

Small gastropods in mangrove habitats have been very poorly collected let alone studied in Queensland, an observation reinforced by the discovery of this unusual assimineid in what amounts to little more than casual collecting.

The great majority of caenogastropods are dioecious, with only a very few known to be protandric hermaphrodites (Webber 1977; Hoagland 1978; Wright 1988; Fretter and Graham 1994). By far the best known are the calyptraeids (e.g. Fretter and Graham 1994;

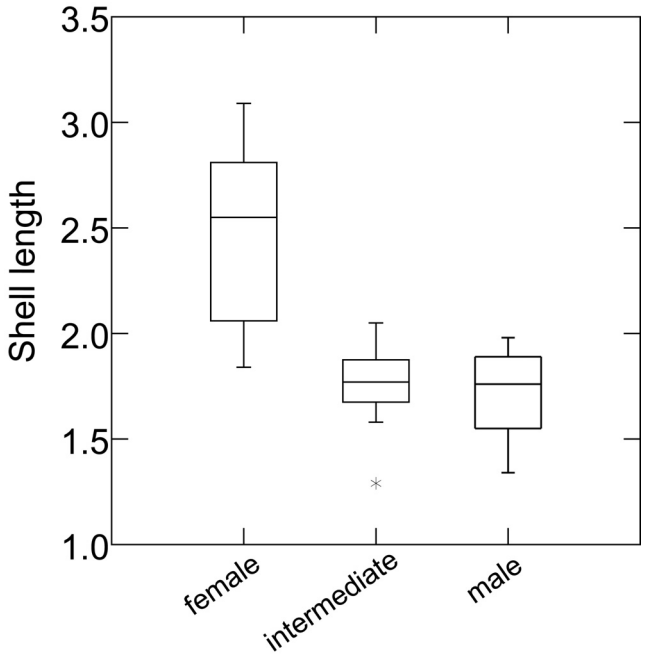

Fig. 5. Box plot of shell lengths and sex of *Rugapedia androgyna* n. sp. The horizontal line represents the median value; the limits of the box mark the first and third quartiles (i.e. the central 50% of values fall within the box. The whiskers represent the range of values that fall within 1.5 H spreads of the hinges (see SYSTAT *v.* 7 Graphics manual). The asterix represents an outlying value.

Table 2. Sex of individual specimens

Specimen lot	Shell length (mm)	Gonad (and seminal vesicle)	Penis	Prostate	Bursa	Pallial oviduct	Sex
C.429092	1.6, 1.8, 1.9, 1.9, 1.9, 2.0	Large testis and seminal vesicle	Large	Large	Absent	Absent	Male
	1.8, 1.8, 1.8, 2.1	Small ovary	Absent	Absent	Small	Small	Intermediate
	2.0	Large ovary	Absent	Absent	Small	Small	Intermediate
	1.8, 1.9, 2.0, 2.3, 2.3, 2.6, 2.8, 2.8, 2.9	Large ovary	Absent	Absent	Fully developed	Fully developed	Female
C.429520	1.3, 1.4	Large testis and seminal vesicle	Large	Large	Absent	Absent	Male
	1.9, 1.9	Large ovary	Absent	Absent	Fully developed	Fully developed	Female
	1.3	Small ovary	Shed	Absent	Small	Small	Intermediate
C.414899	2.7, 2.8, 2.9, 3.0	Large ovary	Absent	Absent	Fully developed	Fully developed	Female
C.429527	1.6	Large testis and seminal vesicle	Large	Large	Absent	Absent	Male
	1.6	Large testis and seminal vesicle	Large	Absent	Small	Small	Intermediate
	2.1, 2.1	Large ovary	Absent	Absent	Fully developed	Fully developed	Female
C.414866	2.5, 2.6, 2.6, 3.1	Large ovary	Absent	Absent	Fully developed	Fully developed	Female

Table 3. Size ranges of shell lengths of sexed specimens

Sex (no. specimens)	Size: minimum–maximum (mm) (mean)
Males (9)	1.34–1.98 (1.70)
Intermediate (7)	1.29–2.05 (1.74)
Females (21)	1.84–3.09 (2.45)

Collin 1995; Warner *et al*. 1996; Chaparro *et al*. 2001). Eulimids show a variety of strategies, including protandry (Hoagland 1978; Ponder and Gooding 1978; Warén 1983). Other examples include the cerithioidean *Vermicularia* (Bieler and Hadfield 1990), the littorinid *Mainwaringia* (Reid 1986), the pelagic ptenoglossan *Janthina* (Laursen 1953; Graham 1954) and the coral-inhabiting neogastropod *Coralliophila violacea* (Soong and Chen 1991). Houbrick (1981, 1989) suggested the possibility of protandry in *Campanile* but this has not been demonstrated with certainty.

All other studied assimineids are dioecious with the exception of possible parthenogenesis reported in one African taxon *Pseudogibbula* Dautzenberg, 1891 (Brown 1980, 1994). The discovery of protandry in an assimineid is therefore surprising, especially as there has only been one other case reported within the very large and diverse superfamily Rissooidea: in a North American vitrinellid, which also appears to detach its penis before becoming female (Bieler and Mikkelsen 1988).

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