A NEW CAMAENID LAND SNAIL FROM THE WET TROPICS BIOGEOGRAPHIC REGION, NORTHEASTERN QUEENSLAND (EUPULMONATA:CAMAENIDAE)

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A new camaenid land snail, *Monteithosites helicostracum* gen. et sp. nov., is described from the rainforested summits of Bakers Blue Mountain and Hanns Tableland, NE Queensland. These localities are western outliers of the Wet Tropics rainforest massif. The species displays periostracal sculpture and genital anatomy which suggest that its relationships are with camaenids much further to the south. Biogeographic implications of this discovery are discussed. ☐ *Mollusca, Camaenidae, Wet Tropics, biogeography.*

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A number of large-sized camaenid land snails are known from the Wet Tropics region of northeastern Queensland (NEQ). Smith (1992) placed these in *Hadra* Albers, 1860, *Sphaerospira* Morch, 1867, *Spurlingia* Iredale, 1933 and *Jacksonena* Iredale, 1937. *Monteithosites helicostracum* gen. et sp. nov. from the summits of Bakers Blue Mountain (Mtn) and the Hanns Tableland, southwest of Mount Molloy, NEQ is a biogeographically significant addition to this fauna.

Bakers Blue Mtn and the Hanns Tableland (Fig.1) are elevated western outliers of the main Wet Tropics rainforest massif. They are separated from the more expansive Carbine and Windsor Tablelands in the north by the valley of the Mitchell River but are interconnected by a series of low ridges and hills which continue through to the Herberton Range in the south. The lower slopes generally support eucalypt woodland. However the peaks in these outliers exceed 1000m and their summits, where rainfall is adequate, support rainforest. The dominant rainforest type is araucarian notophyll vine forest with austral conifers (*Agathis robusta, Araucaria cunninghamii*) (Tracey, 1982). Floristic relationships of this rainforest appear to be with Mt Lewis in the north (Godwin, 1986). Rainforest on Hanns Tableland is confined to the northern end and to scattered valleys and fireproof niches. The peaks of Bakers Blue Mtn are cooler and wetter than those of the Hanns Tableland and consequently support larger areas of rainforest. Nix (1991) identified these outliers as distinct biogeographic units within the Wet Tropics region.

M.helicostracum gen. et sp. nov. provides important new information on these isolated refugia and their historical relationship to other parts of the Wet Tropics.

SYSTEMATICS

Class GASTROPODA
Order EUPULMONATA
Suborder STYLOMMATOPHORA
Superfamily CAMAENOIDEA
Family CAMAENIDAE

Previous taxonomic studies of the large Camaenidae of the Wet Tropics, NEQ have been largely shell-based. Pilsbry (1894) grouped all these species under *Thersites* Pfeiffer, 1855 in a revision that was partially based on genital anatomy. Iredale (1933, 1937) abandoned Pilsbry's conservative system and introduced a large number of new species and genera, solely on the basis of shell features. Some of these taxa have somewhat doubtful status (Burch, 1976) and have yet to be critically revised. Pace (1901) and Solem (1979) presented anatomical data on the very large *Hadra bipartita* (Ferussac, 1822). Smith (1992) produced an updated but critically untested listing of taxa. Stanisic et al. (1994) produced a preliminary report on the land snails of the Wet Tropics which presented distribution data for a large number of described and undescribed camaenids; the new species described herein was identified as Camaenidae WT 11.

The description of this new land snail has entailed a precursory anatomical examination of several other camaenid species in order to place it in systematic context. These revisionary studies will be more fully pursued elsewhere but do

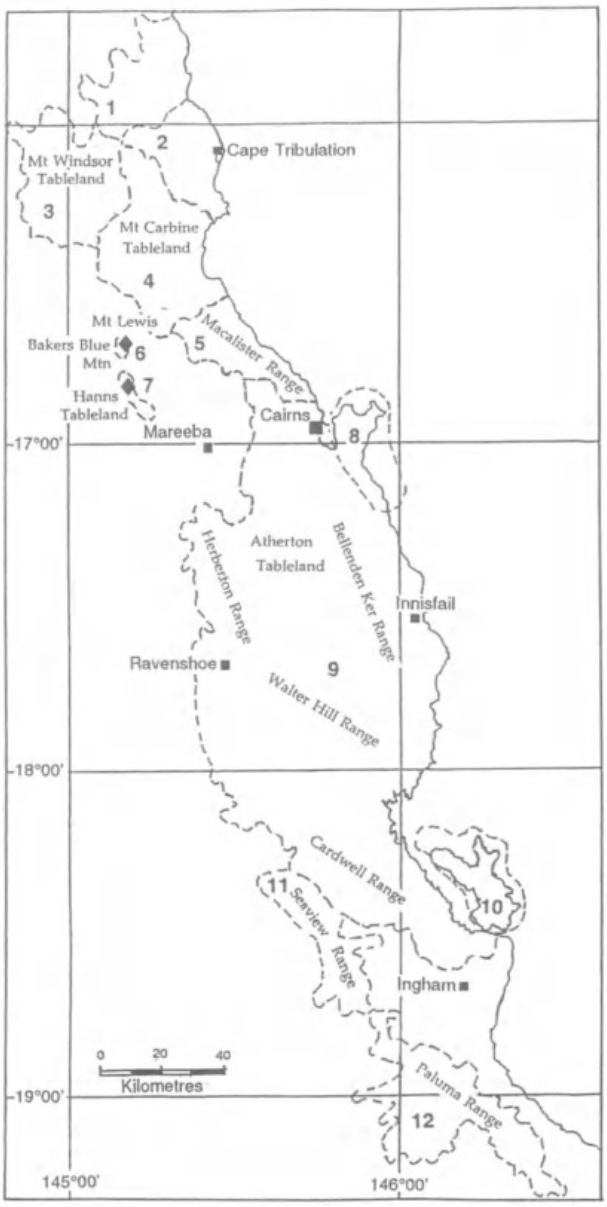

FIG. 1. Distribution of *Monteithosites helicostracum* sp.nov. - ♦ and the biogeographic units of the Wet Tropics (after Nix, 1991). [1, Finnigan; 2, Thornton; 3, Windsor; 4, Carbine; 5. Macalister; 6, Bakers Blue; 7, Hanns; 8, Malbon Thompson; 9, Atherton; 10, Hinchinbrook; 11, Seaview; 12, Paluma].

identify *M. helicostracum* as an unusual member of the Camaenidae of the Wet Tropics.

Monteithosites gen. nov.

ETYMOLOGY. For Dr Geoff Monteith and in reference to the similarity to *Bentosites* from mideastern Queensland (MEQ).

TYPE SPECIES. *Monteithosites helicostracum* sp. nov.

DIAGNOSIS. Shell large (to 33.88mm in diameter), yellow with few to many, dark reddish-brown spiral bands; lip dark brown and reflected. Shell sculpture of very fine, crowded, radial thread-like periostracal wrinkles and prominent, widely spaced spiral periostracal cords. Penis short, stout, with a thick sheath and highly muscularised walls; verge absent. Epiphallus with a weakly expanded ascending arm; entering penis apically through a simple pore. Vas deferens and epiphallus bound to penial sheath. Animal with reddish mantle and tail and dark brown tentacles.

COMPARATIVE REMARKS. The unusual periostracal sculpture readily separates *Monteithosites* from other large camaenids of the Wet Tropics. *Hadra* (sensu Smith, 1992) has bicoloured shells with reduced banding and either almost smooth periostracal sculpture or, in the case of *H. bellendenkerensis* (Brazier, 1875) and *H. beddomae* (Brazier, 1878), fine radial threads with prominent radially disposed, zig-zag periostracal thickenings; *Spurlingia* and *Jacksonena* have comparatively drab shells with strongly rugose sculptures and prominent periostracal scales; *Sphaerospira* Morch, 1867 (sensu Smith, 1992) contains a large number of species with banded shells occurring from SEQ to NEQ and previously included in 5 genera (Iredale, 1937). Unpublished studies by the author suggest that this genus, as defined by Smith (1992), is polyphyletic. A primary division is expressed in animal colour. The greater proportion of species have animals with orange to reddish-orange mantle tissue and tails, and orange to brown tentacles e.g. *S. yulei* (Forbes, 1851) from MEQ. A smaller number have all-over grey to black animals e.g. *S. fraseri* (Griffith & Pidgeon, 1833) from SEQ. The animal of *Monteitosites* bears a strong, external resemblance to the former group particularly those species from MEQ which were previously included in *Bentosites* Iredale, 1933 and *Varohadra* Iredale, 1933 (see Iredale, 1937).

Periostracal sculpture in *Sphaerospira* s.l. varies from a simple microscopic pattern of very fine, crowded, radial periostracal, thread-like wrinkles (*S. yulei*), to one in which these fine wrinkles are supplemented by coarse, wavy or zigzag, radial periostracal ribs (*S. fraseri*) not too dissimilar from those in some *Hadra* spp. The

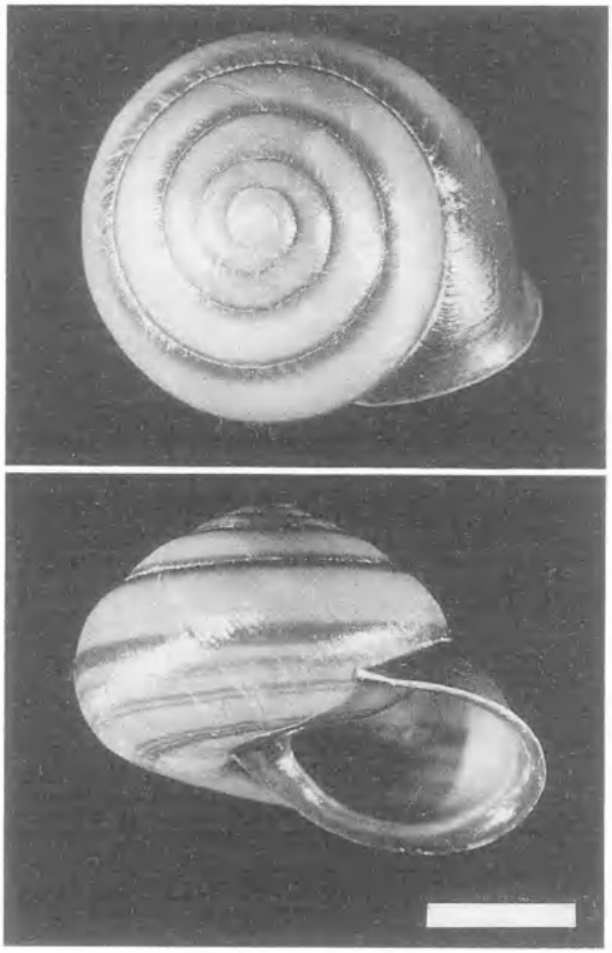

FIG. 2. *Monteithosites helicostracum* sp. nov. Shell of holotype, QMMO57242. Scale line = 10mm.

latter pattern is seen in both black-mantled species (SEQ to NEQ) and red-mantled species from the southern parts of the Wet Tropics (NEQ) only. *Monteithosites* displays yet a third level of variation. However the underlying microsculpture of radial thread-like wrinkles in *Monteithosites* is identical to that in the red-mantled forms from MEQ and NEQ suggesting that the periostracal cords may be merely a functional equivalent of the zigzag to wavy types seen in other hadroid camaenids and of limited value in establishing relationships.

Genital anatomy relates *Monteithosites* to red-mantled *Sphaerospira* s.l. from MEQ and NEQ rather than *Sphaerospira* s.l. from SEQ or *Hadra* from the Wet Tropics. The comparatively weakly muscular epiphallus of *Monteithosites* contrasts with the strongly muscular, elongate condition of *Sphaerospira* s.l.(Solem, 1992) from SEQ and *Hadra* (Solem, 1979). *Hadra* is also characterised by well-developed epiphallic caeca. *S. yulei* from MEQ has the epiphallus reduced to such an extent that the ascending arm is narrow and barely differentiated from the vas deferens (Solem, 1992); a penial verge and tiny epiphallic flagellum are present. This species also has the simple epiphallic entry and sheath- bound vas deferens of *Monteithosites*. Similar genital anatomy is found in other red-mantled *Sphaerospira* from MEQ and the southern parts of the Wet Tropics. In contrast *S. fraseri* (and other black-mantled species) have a strongly developed epiphallus, no accessory epiphallic structures and usually lack penial verges (Bishop, 1978; Solem, 1992; Stanisic, unpubl.). The penis of *Monteithosites* appears to be highly specialised and finds no correlatives among hitherto illustrated species.

Monteithosites helicostracum sp. nov.
(Figs 2-5)

ETYMOLOGY. Latin *helico*, spiral, referring to the spiral periostracal cords.

MATERIAL EXAMINED. HOLOTYPE QMMO57242, Bakers Blue Mtn, c.17km W Mt Molloy, NEQ (16°42'S, 145°10'E), rainforest, under logs, Collected G.Monteith, D.Cook, 11-12 September, 1981. Height of shell 25.54mm, diameter 33.88mm, H/D ratio 0.754, whorls 6 1/8. PARATYPES QMMO48172, 1 adult, 1 juvenile, same data as holotype; QMMO57240, 1 adult, 1 juvenile, Bakers Blue Mtn, upper slopes, NEQ (16°43'21"S, 145°10'15"E), microphyll vine forest/basalt talus, under logs, J.Stanisic, G.Ingram, 1 Jul 1995; QMMO56834, 7 adults, Hanns Tableland, N end, NEQ (16°49'S, 145°11'E), rainforest, 950-1000m, G.Monteith, G.Thompson, 11-14 Dec 1995. OTHER MATERIAL QMMO48181, 3 juveniles, Bakers Blue Mtn, c.17km W Mt Molloy, NEQ (16°42'S, 145°10'E), rainforest, 800-1000m, ANZSES Expedition, 30 Dec 1989-9 Jan 1990.

DESCRIPTION. Shell (Fig. 2A,B) large, diameter 29.26-33.88mm (mean 31.66mm), with 5 3/4-6 1/8 (mean 5 7/8-) whorls. Apex and spire moderately elevated, height 20.56-25.54mm (mean 22.71mm). H/D ratio 0.699-0.762 (mean 0.727). Protoconch c.1 1/2 whorls. Apical sculpture of crowded, slightly curved, weak radial growth ridges. Spire and body whorl (Fig. 3) with very fine, crowded, radial thread-like periostracal wrinkles and conspicuous, more widely spaced, spiral, coarse, periostracal cords. Umbilicus barely open, covered by the reflection of the collumellar lip. Sutures weakly impressed. Whorls evenly rounded. Last whorl descending rapidly in front.

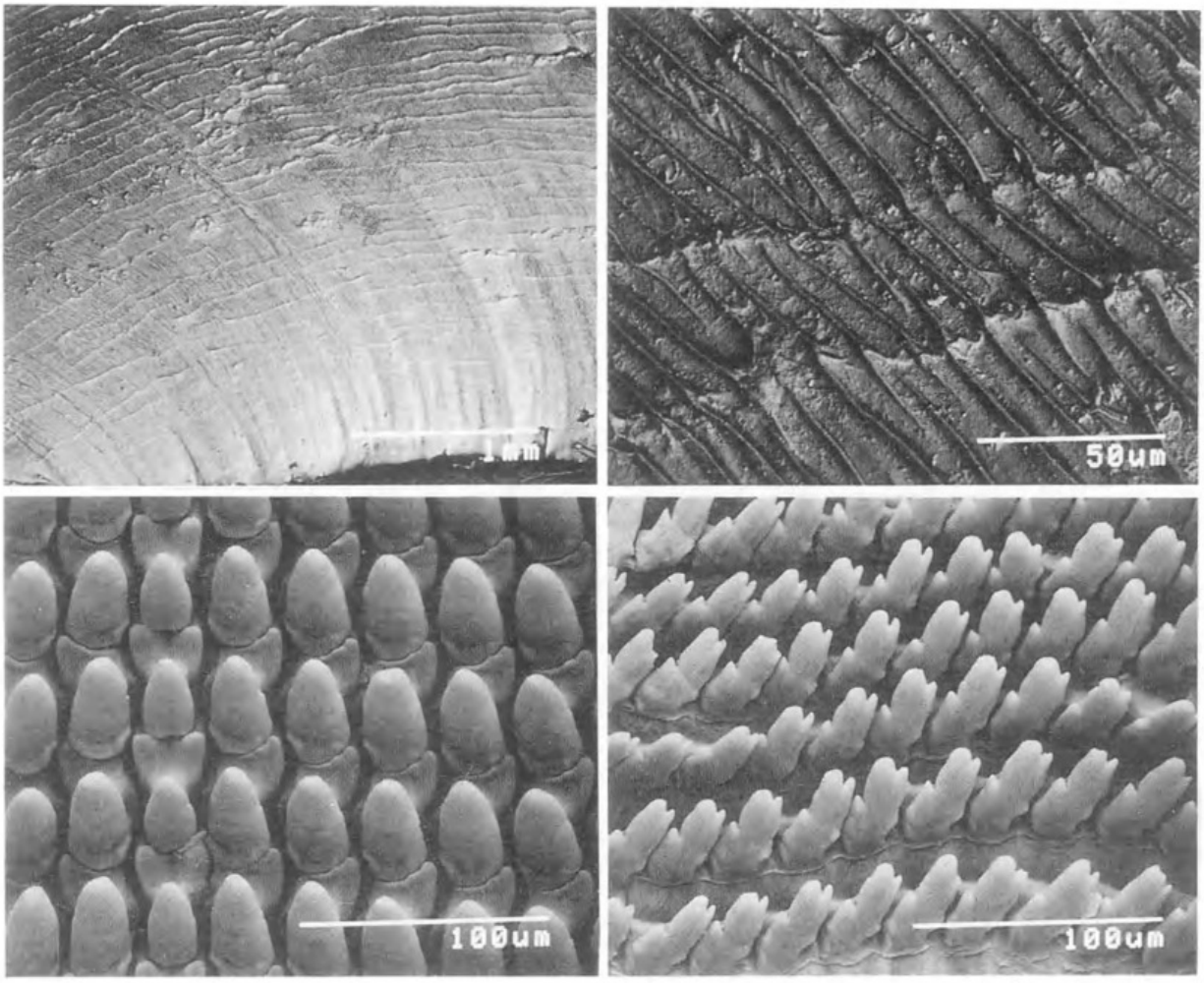

FIG. 3. *Monteithosites helicostracum* sp. nov., QMMO48172. A,B, details of adult shell sculpture; C,D, details of radula. Scale lines as marked.

Aperture lunately ovate; lip strongly reflected. Shell colour yellow-horn with dark reddish-brown spiral bands; subsutural and peripheral bands moderately wide sometimes split into a series of narrower bands; basally a series of narrow bands sometimes coalesced into a single broader band; several narrow intermediate brown bands may also be present. Umbilical chink and lip dark brown. Parietal callus shiny, dark chocolate-brown. Area behind lip with a dark brown suffusion which may extend rearwood for 1/8 whorl. Based on 9 measured adults (QMMO48172, QMMO56834, QMMO57240, QMMO57242).

Genitalia (Fig. 4A) with ovotestis (G, Fig. 4B) comprised of several clumps of finger-like lobes of alveoli lying in the apical whorls of the digestive gland (Z). Hermaphroditic duct (GD) strongly convoluted; talon (GT) short, finger-like. Spermatheca (S) with head lying at the base of the albumen gland (GG); stalk (SS) long, bound to the prostate-uterine surface. Uterus (UT) white, without unusual features; prostate (DG) a series of light brown acini appressed to the uterine surface. Free oviduct (UV) short. Vagina (V) short, about 1/2 length of penis, internally with numerous longitudinal thickenings; spermathecal entrance a simple pore. Epiphallus (E) with short thick descending arm and narrow, weakly expanded ascending arm, about 2/5 length of penis, internally with a large longitudinal pilaster; entering penis apically through a simple pore (EP). Ascending arm of epiphallus and vas deferens bound to penial sheath by connective tissue. Vas deferens (VD) a thin tube, barely differentiated from the epiphallus. Penis (P, Fig. 4C) relatively short, stout, strongly muscularised with a thick sheath (PS). Penial wall (PW) extremely thick and penial lumen reduced to a very narrow tube. Internally, penis with a conspicuous,

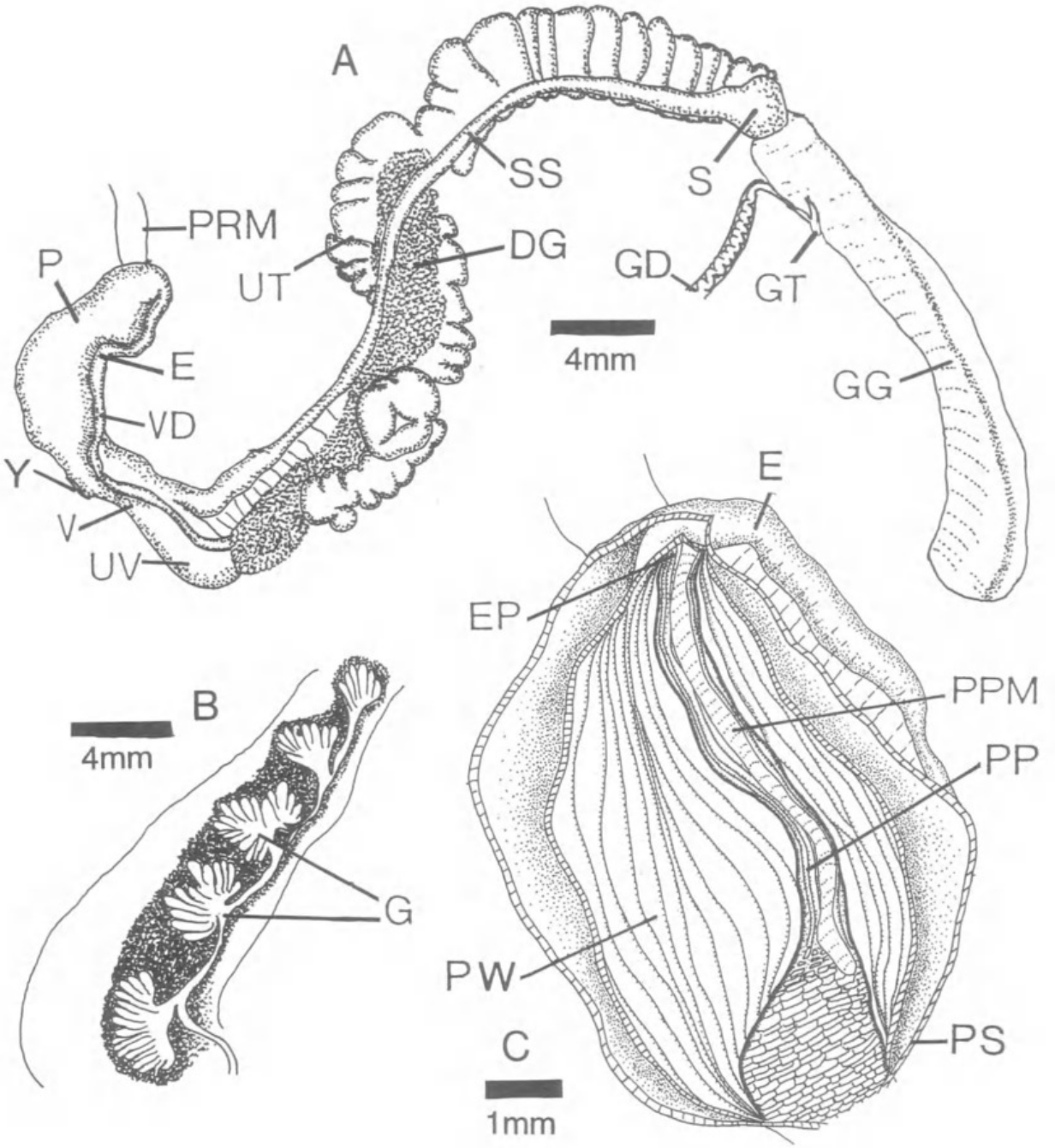

FIG. 4. *Monteithosites helicostracum* sp. nov., QMMO56834. A, genitalia; B, ovotestis; C, details of penis interior. Scale lines as marked.

central longitudinal pilaster (PPM) and several, narrower minor longitudinal pilasters (PP); lower penial chamber with short, rectangular pustules; verge absent. Atrium (Y) very short and without unusual features. Animal (Fig. 5) grey to dark brown with reddish tail and mantle and dark brown tentacles. Head wart present. Radula (Fig. 3B, C) with broadly unicuspid central and lateral teeth, central tooth slightly smaller; anterior flare weak, basal plate prominent. Marginal teeth tricuspid with ectocone low down and endocone high up on mesoconal cutting edge; basal plate and anterior flare reduced. Jaw typically camaenid. Based on two dissected specimens (QMMO57242, QMMO56834).

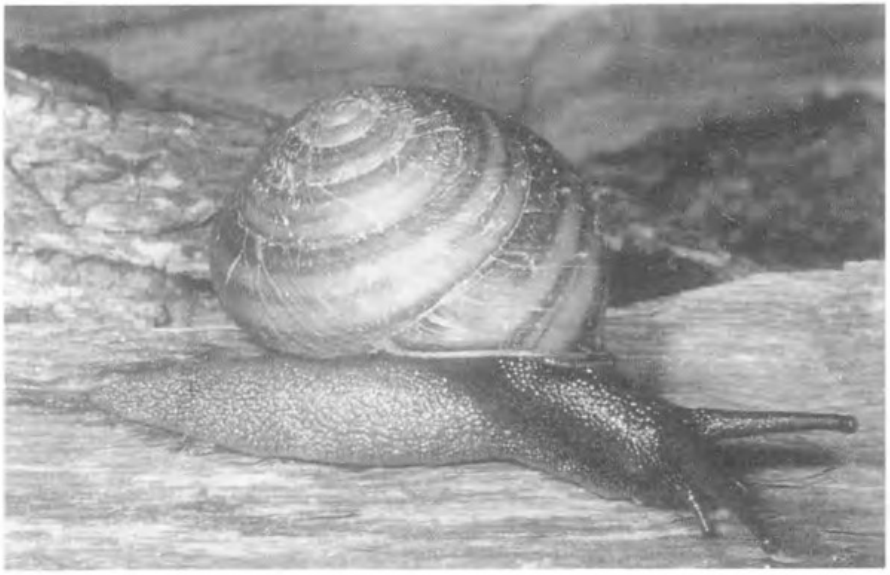

FIG. 5. *Monteithosites helicostracum* sp. nov., Hanns Tableland, QMMO56683.

COMPARISONS. The shell of *M. helicostracum* comes closest in appearance to that of some *Sphaerospira* (sensu Smith, 1992) from NEQ and MEQ. It resembles *S. saxicola* (Iredale, 1937) from the Bowen area, MEQ which possesses fine thread-like periostracal wrinkles, but lacks any major periostracal elements. Some species in the *S. sardalabiata* (Cox, 1871) complex (sensu Smith, 1992) from the southern parts (Paluma, Seaview and Cardwell Ranges) of the Wet Tropics bear an overall similarity to the new species in size and shape. However, *M.helicostracum* is distinguished from these species by its spiral periostracal cords. *S. sardalabiata* s.l. has coarse, wavy to zigzag, radial periostracal thickenings (Stanisic, unpubl.).

Sphaerospira spp. from NEQ and MEQ also show some anatomical similarity to *M. helicostracum* in reduction of the epiphallus, penial structures, form of the radula (Pilsbry, 1894; Solem, 1992; Stanisic, unpubl.) and animal colour. However the rather unusual penis of *M. helicostracum* distinguishes it from all of these species (Stanisic, unpubl.).

HABITAT AND DISTRIBUTION. Under logs in araucarian notophyll vine forest with austral conifer emergents on Bakers Blue Mtn and Hanns Tableland, NEQ.

REMARKS. The adult periostracal sculpture of coarse spiral cords and the penial specialisation of *M. helicostracum* is a combination of characters not seen in other hadroid camaenids. The periostracal spiral cords may be functionally analagous to the more widely occurring zigzag to wavy variety but the unusual penis is more difficult to correlate. *Sphaerospira rockhamptonensis* (Cox, 1873) from The Caves area, Rockhampton, MEQ has a penis with thick muscular walls and reduced lumen (Stanisic, unpubl.). However this species has a dark-grey to black animal with a greatly enlarged epiphallus and is not closely related. It has a simple periostracal sculpture of very fine wrinkles. An analagous reduction in penial lumen width (in this case caused by a dramatic narrowing of the entire penis) was noted by Solem in *Turgenitubulus pagodula* Solem, 1985, an unrelated camaenid from NW Australia. In this instance more fundamental characters indicated the species' relationship to a widespread genus with otherwise strongly consistent genital anatomy. Similarly the general patterns of shell, animal, and anatomical characters displayed by *M. helicostracum* suggest a relationship with those species with banded shells and orange to red coloured animals from NEQ and MEQ. The simple internal structure of the penial chamber and absence of a verge may be the result of spatial constraints associated with the overall reduction in size of the penial lumen. However, this proposition needs to be more thoroughly tested through a comprehensive revision of all the hadroid camaenids.

DISCUSSION

The relationships of *M. helicostracum* to other hadroid camaenids from eastern Queensland still need to be fully confirmed but appear to rest with a widespread radiation consisting of rainforest-bound species now separated by large tracts of drier countryside. These species are part of *Sphaerospira* s.l. and are characterised by having banded shells and animals with orange to red mantles. In the southern part of the Wet Tropics these species inhabit the drier rainforest between Innisfail and Townsville; in MEQ they occur in drier araucarian vine forests and vine thickets

between Mackay and Bowen; and in SEQ possibly more distantly related species (also with reddish mantles) live in a variety of dry rainforests. These rainforests are peripheral to core wet, upland refugia and presumably land snails in these environments would have been more strongly affected by climatic shifts. The Wet Tropics and MEQ radiations of *Sphaerospira* s.l. are separated by an extensive relatively dry corridor between Bowen and Townsville, NEQ where coastal ranges are absent and orographic rainfall is low (Dick, 1974). In S Queensland a dry corridor in the St Lawrence-Gladstone area separates SEQ and MEQ radiations. Similarly, Bakers Blue Mtn and Hanns Tableland are separated from the main massif of the Wet Tropics by dry valleys and ridges (Nix, 1991). Thus biogeographic interpretation of the history of *M. helicostracum* and its allies would appear to involve climate-induced fragmentation of rainforest communities. This view is supported by Bishop (1981) who suggested that the history of *Sphaerospira* s.l. was intimately linked to the deterioration of the climate and involved subdivision of once more extensive ranges.

It is generally accepted that the Camaenidae are a northerly derived element of the Australian land snail fauna (McMichael & Iredale, 1959; Bishop, 1981; Solem, 1992). In the east, dispersal would have been from the New Guinea region across the Torres Strait following collision of the Australian continental plate with the Asiatic and Pacific Ocean plates (Doutch, 1972). *Sphaerospira* s.l. today extends from the Wet Tropics to northern NSW indicating a long history of dispersal. The moisture dependence and relative low vagility of land snails are important limitations to their dispersal and distribution in eastern Australia (Bishop, 1981; Stanisic, 1994). The present day confinement of these hadroid camaenids to rainforest indicate that tracts of dry sclerophyll forest are effective dispersal barriers. The contraction of rainforest which led to the creation of barriers to their dispersal began in the Miocene with the onset of major aridity episodes (Kemp, 1981). These barriers would have reached their acme in the Plio-Pleistocene when more rapid climatic change isolated mesic communities in montane refugia (Galloway & Kemp, 1981). The effects on *Sphaerospira* s.l. should have been dramatic and it is not surprising that current distribution patterns are complex and that differentiation of the group appears to have occurred on opposite sides of major arid corridors in the St Lawrence-Gladstone and Bowen-Townsville areas (Bishop, 1981).

M. helicostracum shows a level of differentiation which suggests that its isolation from its allies has been long-term, possibly in the same time frame as the separation of the red-mantled NEQ and MEQ species groups. Recent fluctuations in rainforest distribution (c. 120,000 yBP) within the Wet Tropics (Kershaw, 1981) do not appear to have had an effect on the distribution of *M. helicostracum*. Nix (1991) proposed a possible connection between the Bakers Blue biogeographic unit and other units to the north and east during cool-wet and warm-wet phases of the last 10,000 years, yet *M. helicostracum* remains isolated in the two outliers. Either the proposed connection did not exist or was too brief to allow dispersal of this species.

It is probably significant that *Monteithosites* and its allies are absent from the core of the Wet Tropics. The present day preference of *Sphaerospira* s.l. with reddish to orange coloured animals for drier rainforest types often dominated by hoop-pine (*Araucaria cunninghamii*) (unpubl. data) suggests a disposition for a very particular environmental regime. This is most notable in MEQ and SEQ where araucarian microphyll vine forest is more widespread. *A. cunninghamii* (and its associated dry rainforest type) is relict in NEQ (Tracey, 1982) although it has shown considerable fluctuation in occurrence since the Plio-Pleistocene (Kershaw, 1981).

The absence of *Sphaerospira* s.l. with orange to red-mantled animals from the Atherton biogeographic unit (now dominated by *Hadra* and its allies) and from other moist upland refugia (higher peaks of the Wet Tropics, NEQ and Eungella, MEQ) might indicate that this group only ever occupied marginally wet rainforest types peripheral to the larger massifs. Equally it may indicate displacement from wetter types by the dark animal hadroids which now dominate the truly moist refugia from SEQ to MEQ. Lack of knowledge about the inter-relationships of these species currently makes it difficult to be sure of the accuracy of either alternative. However, some speculation is possible.

The bioclimatic analyses of Kershaw & Nix (1988) support the view that there was no recent connection between Bakers Blue Mtn and Hanns Tableland. In contrast, presence of *M. helicostracum* on both these outliers indicates a past connection which most likely predates the time scale of their analyses. Connections between the outliers and with the Atherton unit in the south

were less likely during recent times but could have been present in the Plio-Pleistocene when araucarian vine forests may have been in comparative ascendency (Kershaw et al., 1991). However, absence of related camaenids from the Herberton Range (a subunit of the Atherton unit) which has summits in excess of 1000m and extensive areas of rainforest, might suggest that the group never colonised this region. These summits should have provided moist refugia during the driest periods of the Plio-Pleistocene. Yet presence of the probable nearest relatives of *M. helicostracum* in the Cardwell, Seaview and Paluma Ranges points to a NW-SE dispersal track on the drier western edge of the Wet Tropics. In these circumstances it is a strong possibility that the suitable dispersal corridors which may have existed on the western edge of the Atherton have been lost since the Miocene. The preference of *M. helicostracum* and its purported allies for a very specific environmental regime which is now restricted in the north would seem to provide support for this proposition. It is possible that the differentiation and speciation within the group needs to be viewed as occurring along very subtle environmental gradients defined by rainforest structural types. A revision of the hadroid camaenids of the Wet Tropics is needed to more fully understand past dispersal routes but indications are that these land snails have the potential to more accurately define current hypotheses.

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