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A new species and a new subspecies of Amphidromus from Atauro Island, East Timor (Gastropoda, Pulmonata, Camaenidae)

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Amphidromus (Syndromus) richardi spec. nov. and A. (S.) richardi manacocoensis subspec. nov. are described from the island of Atauro, East Timor, Lesser Sunda Islands. Zoogeographic and habitat information are given. The new taxa are compared with the Amphidromus forms living on the nearby islands of Wetar, Alor and Timor. A colour plate illustrates individual characteristics for the Amphidromus taxa discussed.

Key words: Gastropoda, Pulmonata, Camaenidae, Amphidromus, taxonomy, conchology, SE Asia, Banda Arc, Indonesia.

INTRODUCTION

The range of Amphidromus Albers, 1850, stretches from Assam, India to the Northern Territory of Australia, but only in the islands of the Banda Arc is the genus found on true oceanic islands. It is on these isolated islands that the genus radiates into some of its most distinctive forms.

Atauro is one of these oceanic islands. There is dry lowland forest along most of the coast and an area of rain forest capping the summit of 1,000 m Mana Coco Mountain at the island’s southern end. The Amphidromus described below are found in the dry coastal forest of the north and west and on the damp summit of Mana Coco. The two forms appear to be completely isolated from one another by a lack of suitable habitat. This isolation appears to have allowed morphological divergence in the shells of the two populations, possibly in response to the availability of water.

Abbreviations of collections: ANSP, Academy of Natural Sciences, Philadelphia, USA; FMNH, Field Museum of Natural History, Chicago, USA; MS, Mike Severns Collection, Kihei, Hawaii, USA; MZB, Museum Zoologicum Bogoriense, Bogor, Indonesia; RLG, Richard L. Goldberg Collection, Columbia, Maryland, USA; RMNH, Nationaal Natuurhistorisch Museum, Leiden, The Netherlands.

SYSTEMATIC PART

Amphidromus (Syndromus) richardi spec. nov. (figs 1-9)

Diagnosis. — See the two subspecies.

Discussion. — There are two complexes of Amphidromus species in the islands east of Lombata and Sumba, the A. (S.) inconstans Fulton, 1898, complex and the A. (S.) contrarius Müller, 1774, complex. A. (S.) richardi spec. nov. is most similar to A. (S.) inconstans in sharing a similar columella and parietal callus structure and a similar colour pattern. Following Laidlaw & Solem (1961: 570) in their analysis of the A. (S.) inconstans and A. (S.) sinistralis Reeve, 1849, complexes, I consider the columella shape and basic colour pattern of A. (S.) richardi to clearly place it in the A. (S.) inconstans complex. Below, A. (S.) richardi is compared with neighbouring species of both complexes.

The A. (S.) inconstans complex (figs 15-21) includes all of the forms of A. (S.) incon-
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platus, A. (S.) richardi, A. (S.) wetaranus F. Haas, 1912, A. (S.) rollei Laidlaw & Solem, 1961, A. (S.) columnellaris Von Moellendorff, 1892, and several as yet undescribed insular species inhabiting the islands of Pantar, Alor, Atauro, Wetar, Romang, Damar, Babar, Sermata and Tanimbar. They differ from the A. (S.) contrarius complex (figs 10-14) by their subovate, often angular aperture, narrower lip, more curved columella and less glossy shell caused by irregular, relatively coarse growth lines and spiral striae.

The A. (S.) contrarius complex includes all of the forms of A. (S.) contrarius, A. (S.) reflexilabris Schepman, 1892 and A. (S.) laeves (Müller, 1774) inhabiting the islands of Rotti, Semau, Timor, Kissar and the three major islands of the Leti Group - Leti, Moa and Lakor. Species of this complex can be separated from the species of the A. (S.) inconstans complex by having a roundly oval aperture; a strong, thickened lip; a straighter columella; a more glossy shell caused by finer, more evenly spaced and weaker growth lines intersected by very fine irregularly-spaced spiral striations.

There are four species of Amphidromus found on the islands neighboring Atauro. A. (S.) inconstans on Alor, A. (S.) wetaranus on Wetar; A. (S.) reflexilabris and A. (S.) contrarius on Timor.

The closest island to Atauro is Timor at about 12 km, but I was unable to find examples of Amphidromus on Timor, closer than 130 km to the west and 30 km inland from the north coast [A. (S.) contrarius nikiensis B. Rensch, 1931]. Amphidromus (S.) reflexilabris was found near Baucau over 80 km to the east of Atauro by the author in 1998.

Geographically A. (S.) wetaranus is the closest Amphidromus population to A. (S.) richardi, separated from Atauro by a narrow channel of 20 km with the small island of Liran lying halfway between Atauro and Wetar. Liran is almost completely covered with a Eucalyptus species, which is unsuitable habitat for Amphidromus. Two full days of search by a group of four, including myself, and talking with villagers living on the island failed to produce any trace or even rumor of the existence of an Amphidromus population on Liran.

Amphidromus richardi spec. nov. is most similar to A. (S.) inconstans. The latter differs from A. (S.) richardi in its less robust shell; weaker, somewhat less irregularly-spaced growth lines; the outer lip of the aperture being less straight, thus the aperture being less squarish; the narrower, thinner columella; the colour markings on the body whorl being reddish brown rather than black; the white apex.

Amphidromus wetaranus differs from A. (S.) richardi by its narrower shell (higher H/D ratio, see table 1); finer growth lines; coarser, more distant spiral striae; the outer lip usually being less straight, thus the aperture being less squarish; the aperture not jutting forward at the insertion at the body whorl, thus the outer lip in side view not S-shaped; a narrower, less massive columella; a different colour pattern: while it principally follows the same design rules as in A. (S.) richardi, the radial scales of short streaks merge com-

Figs 1-21. Amphidromus (Syndromus) spec. 1-6, A. (S.) richardi richardi subspec. nov. 1a-c, holotype, FMNH 308029, 36.7 mm; 2-6, paratypes; 2, FMNH 308030, 37 mm; 3, FMNH 286343, 36.8 mm; 4, ANSP 412196, 33.2 mm; 5, RLG 25710, 38 mm; 6, RLG 25711, 33.4 mm. 7-9, A. (S.) richardi manacocensis subspec. nov. 7a-c, holotype, FMNH 308031, 32 mm; 8-9, paratypes; 8, MS 076, 31 mm; 9, MS 073, 31 mm. 10-14, A. (S.) contrarius complex. 10, A. (S.) contrarius peristome; 11, A. (S.) contrarius, W. Timor, RLG 3227, 37 mm; 12, A. (S.) reflexilabris, W. Timor, RLG 244, 42 mm; 13, A. (S.) contrarius nikiensis, W. Timor, RLG 18981, 32 mm; 14, A. (S.) laeves, Kissar Island, RLG 21025, 34 mm. 15-21, A. (S.) inconstans complex. 15, A. (S.) inconstans peristome; 16, A. (S.) inconstans, Alor Island, MS 948, 37 mm; 17, A. (S.) inconstans, Alor Island, RLG 25609, 32 mm; 18, A. (S.) inconstans gracilis, Alor Island, RLG 2812, 37 mm; 19, A. (S.) oscitans, Alor Island, RLG 139, 32 mm; 20, A. (S.) wetaranus, Wetar Island, RLG 2190, 33 mm; 21, A. (S.) rollei, Moapora Island, east of Romang Island, RLG 1926, 31 mm.
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Table 1. Shell measurements (in mm). Abbreviations: n = number of measured specimens, H min = minimum shell height, H max = maximum shell height, H mn = mean shell height, D min = minimum shell diameter, H max = maximum shell diameter, D mn = mean shell diameter, H/D min = minimum ratio of shell height to diameter, H/D max = maximum ratio of shell height to diameter, H/D mn = mean ratio of shell height to diameter, A min = minimum aperture height, A max = maximum aperture height, A mn = mean aperture height. All shells measured were from the M. Severns collection.

<table>
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<tr>
<th></th>
<th>n</th>
<th>H min</th>
<th>H max</th>
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<th>D max</th>
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<td>30.36</td>
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<td>18.54</td>
<td>18.10</td>
<td>1.69</td>
<td>1.79</td>
<td>1.74</td>
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<td>40.84</td>
<td>36.06</td>
<td>16.27</td>
<td>20.07</td>
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<td>2.17</td>
<td>2.01</td>
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<td>30.05</td>
<td>42.82</td>
<td>35.88</td>
<td>15.96</td>
<td>20.15</td>
<td>17.88</td>
<td>1.89</td>
<td>2.26</td>
<td>2.01</td>
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Completely into elongated, dark, radial stripes in most specimens; in the gap between the stacks of streaks or radial stripes above the main band and also between the main and the basal band many specimens have an orange-brown band which is never found in A. (S.) richardi.

*Amphidromus contrarius* differs from *A. (S.) richardi* by its glossier shell due to finer and more regular growth lines as well as extremely fine and dense spiral striation; the outer lip being well arched and thus the aperture being oval rather than squarish; a sub-triangular tubercle on the parietal calxus and a narrow channel of the inner suture (Laidlaw & Solem 1961: 570) the basal lip hardly bent backward and the outer lip not jutting forward at the insertion, thus the outer lip rather straight when viewed from the side; different colour pattern.

*Amphidromus reflexilabris* differs from *A. (S.) richardi* by its heavier, usually more slender shell; glossier shell surface due to finer and more regular growth lines as well as finer and denser spiral striation; a rounded outer lip and oval aperture; a strongly reflexed lip that is dark (purplish pink to black); different colour pattern.

Etymology. — *Amphidromus (Syndromus) richardi* spec. nov., is named for Richard L. Goldberg who supported my searches in Nusa Tenggara which led to the discovery of several new species of *Amphidromus* and who supplied me with invaluable information from his private library.

*Amphidromus (Syndromus) richardi richardi* subspec. nov. (figs 1-6)

Diagnosis. — Shell with a thin, expanded, slightly reflexed lip, convexly reflexed columnella, black and yellow colour pattern on a white ground, one or two slightly thickened varices, a compression of the body whorl behind the lip and consequently a squarish aperture.

Description. — The shell is sinistral, solid, oblong-conic, opaque, and glossy. The surface is textured with faint, irregularly spaced growth lines and very fine, discontinuous, irregular spiral striae visible under high magnification. On the spire there may be one or two slightly thickened varices defined by a break in the colour pattern indicating a pause in shell growth. The whorls increase in size regularly with an average whorl count of 5.68 for those shells examined (see table 1). The body whorl is laterally compressed immediately behind the aperture causing the outer lip to straighten in frontal view. The aperture
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is oblong-ovate, angular above and angularly rounded below where it joins the columella. (S.) The height of the aperture is about half that of the entire shell. The lip is thin, margined with white, distinctly expanded and slightly reflected. When viewed from the side the lip curves sharply forward in the direction of growth where it joins the body whorl and it is markedly bent back at the base, thus forming the shape of an elongated "S". The columella is white, rounded and reflected, partially obscuring the umbilicus. The umbilical opening is teardrop-shaped. The parietal callus is thin, transparent, yellow and glossy. The apex is reddish brown. The ground colour of the postapical whorls is white with a faintly to intensely yellow cast and dark banding. The broadest and usually darkest band (hereafter referred to as "main band") emanates from the insertion of the aperture at the body whorl and wraps around the latter. A second, usually narrower, dark band emanates from the aperture in the middle of the parietal wall. Above the main band, the whorls are encircled by a series of up to nine narrow, dark bands. These are often periodically interrupted and the resulting segments of the parallel bands form radial series of short streaks. On the upper whorls, two or three of these streaks are often merged together to form dark, rectangular blotches. The more or less modified series of narrow bands above the main band are separated by a band-like gap in the middle of the series. Bands are usually brown on the upper whorls and become increasingly darker on the lower whorls; on the last whorl they are black. The bands end in a short distance behind the reflected lip. The colour pattern shines through on the inside of the aperture. There is some colour variation; additional, narrow bands can occur below the main band and the bands above the main band may be reduced in number and/or they may appear only on the last whorl. Occasionally, all bands, including the main band and the bands below it which are usually solid, are broken up into short streaks and, as a rarity, completely unbanded specimens occur. Dimensions of the holotype (in mm): H = 36.78, D = 18.04, A = 16.58 (for further specimens and explanation of abbreviations see table 1).

Type locality. — Atauro Island, East Timor, Nusa Tenggara (Lesser Sunda Islands) on the northwestern coast at an elevation of 100 m.

Distribution. — A. (S.) richardi richardi subspec. nov. is insular, being restricted to the dry lowland coastal hills of the island of Atauro. A. (S.) r. manacocensis subspec. nov. is restricted to the wet rain forest at the summit of Mana Coco mountain on the island of Atauro.

Habitat. — The species was found on the limbs and branches of small trees growing in small patches among low shrubs and grasses on a practically bare limestone plateau formed from uplifted coral reef. None of the trees were more than 10 m high and only occasionally did they form stands of more than a couple of trees. The bark of the trees was smooth and silver-gray in colour. The trees occupied by snails were often infested with colonies of large red ants whose venomous bite and aggressive behaviour may discourage potential predators from entering the tree. However, empty snail shells beneath the trees showed the kind of damage associated with rat or other small mammalian predation. The area is seasonally very dry causing interruptions in the shell growth as is evident by the presence of one or two varices on all specimens examined.

Type material. — Holotype: FMNH 308029 (M. Severns leg. December 2, 1996). Paratypes (M. Severns leg. December 2, 1996, and May 3, 1997): FMNH 308030/3, figured), 286343/33; MZB/5; RMNH 102842/5; ANSP 412195/1, 412196/1, figured), 412197/1; MS 949/1 to 991/1; RLG 25710/1, figured), 25711/1, figured), 25712/18.

Other material. — Additional specimens in the M. Severns collection.
Amphidromus (Syndromus) richardi manacocoensis subspec. nov. (figs 7-9)

Diagnosis. — Differing from the nominate subspecies by a translucent, thin and fragile, globose-conic shell; a colourless, transparent apex; the lack of a varix; a larger aperture height to shell height ratio; fewer whorls and a smaller height to diameter ratio.

Description. — Shell thin, translucent, globose-conic, glossy. Apex transparent white. The surface of the shell is glossier than in A. richardi s.str., textured with faint, irregularly-spaced growth lines and microscopic spiral striae. There is no varix as a sign of a pause in growth. The body whorl is expanded and only sometimes compressed behind the lip. Aperture subovate with a mean aperture to shell height ratio of 0.59. Lip thin, slightly expanded. Columella thin, white. The umbilicus narrow, narrowly elliptical. Parietal calulus translucent yellow, very thin. Ground colour pale yellow, banding brown. Variation of the colour pattern as in the nominate subspecies. Dimensions of the holotype (in mm): H = 32.11, D = 18.29, A = 18.72 (for further specimens and explanation of abbreviations see table 1).

Type locality and distribution. — Atauro Island, East Timor, on the summit of Mt. Mana Coco at an elevation of 1000 m. Known only from the type locality.

Habitat. — This subspecies was found living on the limbs and trunks of trees and on vines under a dense canopy in an extremely wet environment on the summit of Mt. Mana Coco. They were scarce and difficult to see because they were usually high above the ground and obscured by the vegetation.

Type material. — Holotype: FMNH 308031 (M. Severns leg., December 2, 1996). Paratypes: MS 073, 076 (1 specimen each; data as for holotype).

Etymology. — Amphidromus r. manacocoensis subspec. nov., is named for the type locality, Mt. Mana Coco.

Discussion. — A. (S.) r. manacocoensis is a high elevation subspecies of A. (S.) richardi. It has several morphological differences from the lowland nominate subspecies that may be an adaptation to a constantly wet environment.

The only known population of A. (S.) r. manacocoensis is separated from the nearest A. (S.) richardi population by 900 m in elevation and by several km distance. It inhabits wet forest as compared to A. (S.) richardi, which inhabits a hot, dry coastal escarpment. There were no intermediate forms found in either population.

A. (S.) r. manacocoensis resembles A. (S.) inconstans oscitans (Von Martens, 1899) in having a thin shell with a similar colour pattern. It differs from A. (S.) i. oscitans in not having a dark spot at the shell apex, having a more inflated and slightly flattened body whorl, subovate aperture and more distinctly expanded lip. It is smaller in height but has a smaller shell height to diameter ratio and a larger aperture height to shell height ratio than A. (S.) i. oscitans (table 1).

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REFERENCE