

RISSOINA INDISCRETA, A NEW RISSOID SPECIES FROM THE
TROPICAL SOUTHWESTERN ATLANTIC WITH
INDO-WEST PACIFIC AFFINITIES
(MOLLUSCA, GASTROPODA, RISSOIDEA)

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ABSTRACT

A new rissoid, *Rissoina indiscreta*, is described from the northeastern and eastern Brazilian coasts. The new species has been identified for more than 20 years in the literature as *R. elegantissima* d'Orbigny, 1842. Although apparently belonging in the same subgenus *Rissolina*, true *elegantissima* is a distinct species, restricted to the Caribbean Sea. Apart from the number of axial ribs per whorl, no other important variation in conchological characters is found in the different populations of the species. Comparisons indicate that *indiscreta* might be very close phylogenetically to *R. turricula* Pease, 1861, a Recent species with a large distribution range in both the Indian and Pacific Oceans, and also known from the Miocene of west Pacific islands. Three hypotheses accounting for the present-day disjunct distribution of the assumed species-group are discussed, and a vicariant proposition suggesting the existence of a widely-distributed, shallow-water Tethyan ancestor is favored. The other two interpretations, passive larval dispersal by currents across the East Pacific Barrier via the Pacific countercurrent system, or from the Indian Ocean, to South Africa, then to Brazil through the counterclockwise surface circulation of the South Atlantic, would imply the existence of long-lasting planktotrophic (teleplanic) larval stages in the ancestor, a condition unknown in the genus *Rissoina*.

The examination of shallow-water rissoids from the northeastern and eastern coasts of Brazil has shown that several lots that have been identified as *Rissoina elegantissima* d'Orbigny, 1842, in Brazilian collections and literature (Lopes et al., 1966; Rios, 1970; 1975; 1985; Rios and Barcellos, 1979) represent, in fact, a different, unnamed species. The taxon belongs in the subgenus *Rissolina*, which Ponder (1985) considered to contain a small number of species, mostly restricted to the Indo-West Pacific region, that exhibit a very small range of interspecific variation. Comparisons of conchological characters suggest that the new species is closer taxonomically to *R. (Rissolina) turricula* Pease, 1861, from the Indian and Pacific Oceans, rather than to the consubgeneric *R. elegantissima* from the Caribbean Sea. Proceeding from the assumption that *indiscreta* and *turricula* belong to a distinct species-group within the subgenus *Rissolina* and drawing from data on the distribution of Recent and fossil representatives of the subgenus, three hypotheses to explain the broadly disjunct ranges of the two species are discussed: 1) passive dispersal and crossing of the East Pacific Barrier by an ancestor with long-lasting planktotrophic larval stages, with subsequent colonization of the southwestern Atlantic; 2) assuming the former extension of populations of *turricula* to southeastern Africa with passive dispersal through the counterclockwise circulation gyre in the South Atlantic before the onset of the Benguela upwelling system in the late Miocene, and 3) a vicariant event, assuming the splitting (caused by tectonic events) of broadly distributed populations of a shallow-water Tethyan ancestor, followed by allopatric speciation, ultimately giving rise to the present day species-group.

MATERIALS AND METHODS

According to locality data, all the studied material is from calcareous sediment samples obtained in shallow, coralline algal environments in the southwestern Atlantic (Fig. 1). Shells were observed and measured using WILD M-5 dissecting microscope with ocular micrometer, and photographed using an International Scientific Instruments ISI Double Stage DS-130 scanning electron microscope (SEM) at the Electron Microscopy Laboratory, Rosenstiel School of Marine and Atmospheric Science, University of Miami. The smaller unit for measuring the number of whorls is 90° (0.25 whorl). The following abbreviations are used: BMNH, British Museum (Natural History), London; DRM, Donald R. Moore Collection, Miami; MORG, Museu Oceanográfico, Rio Grande; MNRJ, Museu Nacional, Rio de Janeiro; MNHSL, H.S. Lopes Collection, Museu Nacional, Rio de Janeiro; MNHN, Muséum National d'Histoire Naturelle, Paris; UMML, Rosenstiel School of Marine and Atmospheric Science, Miami; USNM, National Museum of Natural History, Smithsonian Institution, Washington.

SYSTEMATIC RESULTS

Family RISSOIDAE Gray, 1847
 Subfamily Rissoiinae Stimpson, 1865
 Genus *Rissoina* d'Orbigny, 1840
 Subgenus *Rissolina* Gould, 1861
Rissoina indiscreta new species
 (Figures 2–7)

Rissoina elegantissima d'Orbigny, 1842; Lopes et al., 1966, p. 6–7, figs. 10–11; Rios, 1970, p. 35, pl. 7; 1975, p. 37, fig. 135; 1985, p. 37, fig. 162; Rios and Barcellos, 1979, p. 109 (*non* d'Orbigny, 1842).

Description. — Shell small, reaching 5.4 mm in length and 2.3 mm in width. Shell opaque to translucent white, with 8.5, convex, shouldered whorls. Protoconch dextral, white, mammillate and involute, about 0.37 mm diameter, 1.5 whorls; suture deeply channeled. Protoconch sculpture of three, narrow, irregular cords, present from first part of embryonic whorl to transition protoconch/teleoconch. Transition protoconch/teleoconch straight, slightly prosocline. Teleoconch whorls 7. Teleoconch sculptured with 12–17 axial ribs per whorl. Axial ribs follow change in orientation of shell surface at shoulder. Axial ribs angulate at periphery of first whorl, at adapical third of second and third whorls and at adapical fourth of remainder of whorls. Axial ribs sometimes lying in same plane with shell axis, aligned in successive whorls, forming straight lines that converge to apex. Axial sculpture weaker at base, but stronger on spiral basal fold, giving it beaded aspect. Spiral sculpture of 16–20 fine, weak, irregularly spaced cords, with microscopic, irregular, wavy threads. Base with a deep spiral groove bordered abapically, at lower base, by a strong spiral fold, both associated with a spiral constriction at the base. Spiral fold continues abaperturally, terminating at varix of outer lip, appearing in apertural view as a blunt projection at anterior extremity of shell. Aperture D-shaped, angulate posteriorly, channeled anteriorly. Parietal region anteriorly with projection that delimits internally the broad, shallow anterior canal. Posterior canal directed posteriorly. Outer lip thick, sinuous in lateral view.

Etymology. — From the Latin adjective *indiscretus*, indistinguishable, united, closely connected, an allusion to its close similarity with the Indo-West Pacific species *turricula*.

Type Locality. — Ponta Verde, Maceió, Alagoas State, Brazil (09°38'S, 35°44'W).

Holotype. — MNRJ 5760, 4.16 mm length, 1.68 mm width, P. S. Cardoso, 'beach drift.'

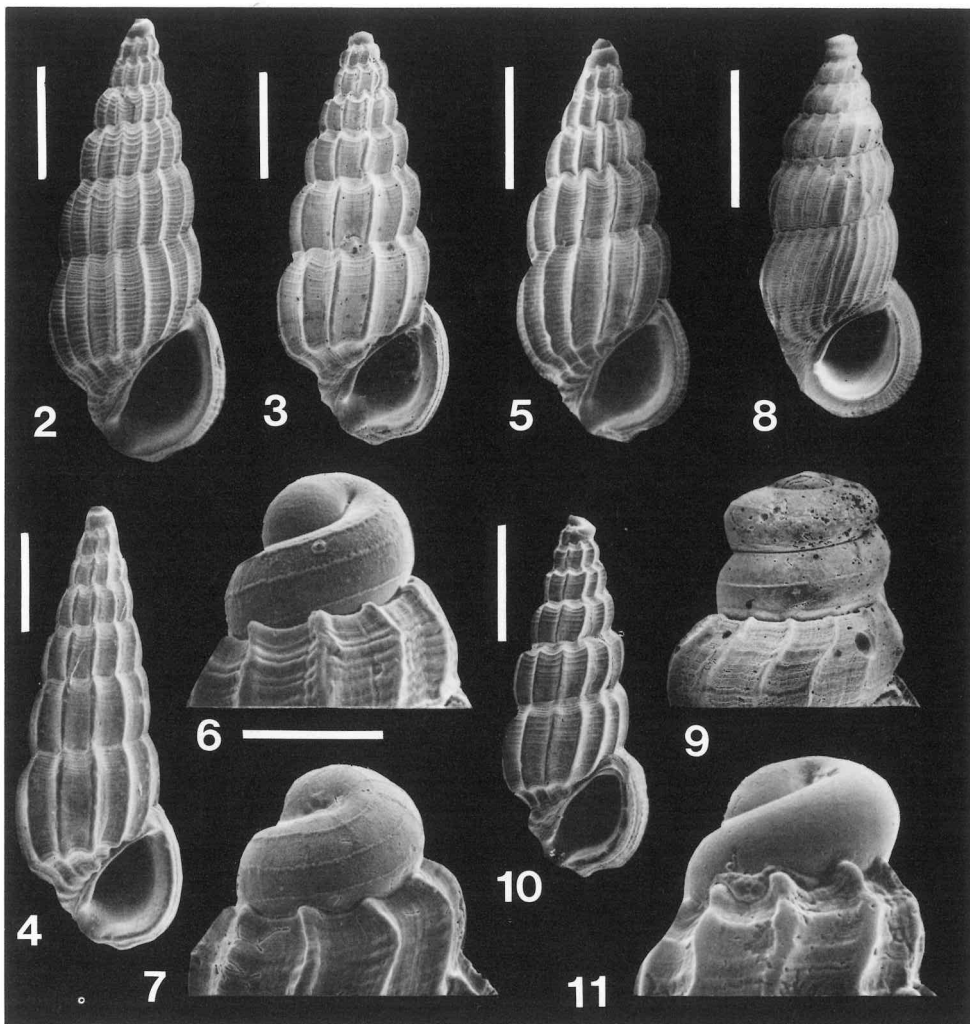
Paratypes. — Paratypes 1–4, MNHSL 6025, type locality, P. S. Cardoso, 'beach drift' (includes material illustrated by Lopes et al., 1966); Paratypes 5–7, MORG 4164, type locality, P. S. Cardoso, 'beach



Figure 1. Distribution of *Rissoina indiscreta* new species; numbers indicate localities: 1. Atol das Rocas; 2. Jaraguá and Ponta Verde, Maceió, Alagoas; 3. Abrolhos Reef Complex, Bahia; 4. Itapoã e Praia do Forte, Bahia. The same numeration for localities 1–3 is present in Table 1.

drift'; Paratypes 8–11, MNHN, type locality, P. S. Cardoso, 'beach drift'; Paratypes 12–15, USNM 859335–38, type locality, P. S. Cardoso, 'beach drift'; Paratypes 16–18, MNRJ 5761, type locality, P. S. Cardoso, 'beach drift'; Paratypes 19–22, BMNH 1988.043, type locality, P. S. Cardoso, 'beach drift'; Paratypes 23–24, MORG 25463, Atol das Rocas (03°52'S, 33°49'W), Brazil, J. H. Leal, G. W. Nunan, C. B. Castro and D. F. Moraes, Jr., 02/1982, 'calcareous sand'; Paratypes 25–28, MORG 25464, Abrolhos Reef Complex (1758'S, 38°42'W), Bahia, MORG Expedition 02/1978; Paratypes 29–30, UMML 8347–48, Jaraguá, Maceió, Alagoas, Brazil (09°38'S, 35°44'W) P. S. Cardoso, 1965.

Other Material Examined. — Type locality: MNHSL 6469, 9 shells, P. S. Cardoso, 'beach drift'; Jaraguá, Maceió, Alagoas: MORG 15933, 3 shells, P. S. Cardoso, 1965; Atol das Rocas: MORG 19121, 13 shells, MORG Atol das Rocas Expedition, 02/1977; Atol das Rocas, Ilha do Farol, MNRJ 4323, 8 shells, J. H. Leal, G. W. Nunan, C. B. Castro and D. F. Moraes Jr., 02/1982, 'calcareous sand'; Praia do Forte, Bahia: MORG 25301, 6 shells, L. Barcellos, 05/1985, 'intertidal'; Itapuá, Salvador, Bahia: MNHSL 6468, 9 shells, A. J. Silva and S. J. Oliveira, 12/1956, 'beach drift' (includes material illustrated by Lopes et al., 1966); MORG 16930, 12 shells, E. Rios, 07/1967, 'praia' [=beach]; Abrolhos Reef Complex, Bahia: MORG 20177, 36 shells, MORG Expedition, 02/1978; MORG 21225, 12 shells, MORG Expedition, 01/1980, 10–15 m depth; MORG 23843, 29 shells, Equipe MORG, 01/1985, 'R. Areia'; *Rissoina elegantissima*: BMNH 1854.10.4.212, lectotype and paralectotypes, Santo Domingo (d'Orbigny collection, lectotype designated by A. A. Luque del Villar, 29.07.1986); DRM, 2 shells, Hook Bank, Belize, D. Marszalek, 10/1971; *R. turricula*: BMNH 196.2845, lectotype; BM(NH) 19.832, 1 paralectotype; BM(NH) 196.2845–46, 3 paralectotypes, all 'Sandwich Islands' [Hawaiian Archipelago] (H. Cummings Collection, lectotype designation by A. Kay); MNHN, 6 shells, Lifu, Loyalty Islands, Bouge Collection; MORG 25473, 2 shells, Maili, Oahu, Hawaiian Archipelago, 1970, leg. D.



Figures 2–7. *Rissoina indiscreta* new species; 2. Holotype, Ponta Verde, Maceió, Alagoas, MNRJ 5760, 4.16 mm length, 1.68 mm width; 3. Paratype 23, Atol das Rocas, MORG 25463, 4.05 mm length, 1.64 mm width; 4. Paratype 24, Atol das Rocas, MORG 25463, 4.91 mm length, 1.82 mm width; 5. Paratype 25, Abrolhos Reef Complex, MORG 25464, 3.50 mm length, 1.50 mm width; 6. Protoconch of holotype; 7. Protoconch of paratype 24. Scale bars for shells = 1 mm, protoconchs = 0.20 mm.

Figures 8–9. *Rissoina elegantissima*; 8. Hook Bank, Belize [55.5657], 2.86 mm length, 1.19 mm width; 9. Protoconch of the same shell. Scale bar for shell = 1 mm; protoconch, same scale as Figure 6.

Figures 10–11. *Rissoina turricula*; 10. Maili, Oahu, Hawaiian Archipelago, MORG 25473, 3.14 mm length, 1.32 mm width; 11. Protoconch of the same shell. Scale bar for shell = 1 mm; protoconch, same scale as Figure 6.

R. Moore; MORG 25474, 7 shells, Kealakekua Bay, Hawaii, Hawaiian Archipelago, '5–10 m from shore,' J. Behinsky 08/1974, leg. D. R. Moore; *R. plicata*: BMNH 198.4131, 5 syntypes, 'Isle of Masbate,' Philippine Islands.

Remarks.—The species is known only from dead specimens obtained from sediment samples; some specimens are very well-preserved, obviously freshly dead

when collected. The disposition of the axial ribs and the absence of prominent spiral sculpture other than the strong spiral fold at the lower base are diagnostic of the subgenus *Rissolina* (Ponder, 1985). According to Ponder, the subgenus is very close taxonomically to *Rissoina* s.s., 'but is maintained largely as a subgenus of convenience for a distinctive species-group centred in the Indo-Pacific.' Ponder (1985) remarked on the small intraspecific variability in the subgenus. In *indiscreta*, the most conspicuously variable character is the number of axial ribs per whorl (Table 1). Mean values for the number of axial ribs/last whorl for Maceió, Alagoas ($\bar{x} = 15.4$, $SD = 1.0$, $N = 10$) and Atol das Rocas ($\bar{x} = 12.5$, $SD = 0.5$, $N = 10$) are consistently different (compare figs. 2, holotype, Maceió and 4, paratype 24, Atol das Rocas; but look at the protoconch in the same two shells, figs. 6 and 7 respectively), without overlap between the two localities. Examination of material from Abrolhos (the southernmost locality where the species was found) has shown, however, a more extensive range of variation ($\bar{x} = 14.1$, $SD = 1.5$, $N = 10$) for the character, including almost all the values for Rocas and Maceió. Also, we found a hardly quantifiable, slight variation in orientation of the axial ribs (compare figs. 3–4, paratypes 23–24, Atol das Rocas; also fig. 5, paratype 25, Abrolhos). Other dimensional and meristic data do not indicate important morphometric variation (Table 1) along the geographic range of *R. indiscreta* (Fig. 1). In the literature, shells of *R. indiscreta* have been incorrectly assigned to the strictly Caribbean *R. elegantissima* (see references in the synonymy above). All the material from the Brazilian coast associated with the name '*elegantissima*' belongs to *indiscreta*. The new species is easily separated from true *elegantissima*, which has a smaller, lighter shell, with more convex whorls, a larger number of axial ribs, sinuous and always strongly oblique to the shell axis (Fig. 8) and a multispiral, cylindrical protoconch (Fig. 9). Shell characters in *indiscreta* are more similar to those in *R. turricula* (Fig. 10), a widely distributed species that occurs from the Red Sea to Mauritius, Cocos-Keeling, Line, Marshall and Hawaiian Islands, and in the Miocene of Fiji and Eniwetok Atoll, western Pacific Ocean (Ladd, 1966; Maes, 1967; Kay, 1979). Although *turricula* has more angulated shoulders, stronger spiral threads in the interspaces between axial ribs, and a larger, blunter, smooth and slightly tilted protoconch (Fig. 11) (spirally sculptured and never tilted in *indiscreta*, Figs. 6–7), characters such as overall size, contour, number of axial ribs and general sculpture pattern, shape of the aperture, and shell angle are extremely similar, rendering almost impossible the separation of given individuals of the two species under the dissecting microscope at low magnifications (compare, for instance, Figs. 3 and 10). Based on this high degree of similarity we proceed assuming that *indiscreta* may be more closely related to *turricula* (and related Indo-West Pacific 'chronospecies,' e.g., *marshallensis* Ladd, 1966, Miocene of Marshall Islands, Eniwetok and Bikini Atolls), than to any other species in the subgenus *Rissolina*.

BIOGEOGRAPHY

Three hypotheses can be taken into account to explain the present largely disjunct distribution of the *indiscreta-turricula* group (Fig. 12): 1) postulating long-distance dispersal and crossing of the East Pacific Barrier by an ancestor with long-lasting planktotrophic larvae; 2) accepting the former existence of populations of *turricula* or a common ancestor in South and southeastern Africa and later dispersal through the surface water circulation system in the South Atlantic, or 3) assuming a vicariance event during which populations of a shallow-water Tethyan ancestor ultimately gave rise to the two species. The first hypothesis

Table 1. Linear shell measurements (mm) and meristic counts for *Rissoina indiscreta* sp. n.; each locality, N = 10. 1) Atol das Rocas, MNRJ 4323, MORG 19121 (protoconch whorls and diameter, N = 5); 2) Macció, Alagoas, MNHSL 6025, MORG 4164, 15933; 3) Abrolhos Reef Complex, Bahia, MORG 20177 (see text and Fig. 11 for further locality data)

Character	Range	\bar{x}	SD
Total length	1) 3.63–5.38	4.19	0.47
	2) 4.12–4.94	4.64	0.28
	3) 3.87–4.87	4.43	0.40
Length of last whorl	1.94–2.75	2.12	0.24
	2.37–2.55	2.49	0.06
	2.00–2.52	2.30	0.19
Shell width	1.47–2.25	1.80	0.21
	1.85–2.18	2.03	0.10
	1.75–2.09	1.91	0.14
Aperture length	1.23–1.85	1.45	0.18
	1.57–1.81	1.72	0.09
	1.35–1.60	1.51	0.10
Aperture width	0.62–0.95	0.71	0.10
	0.74–0.92	0.85	0.06
	0.74–0.89	0.82	0.07
Protoconch diameter	0.37–0.39	0.37	0.01
	0.37–0.38	0.38	0.01
	0.34–0.40	0.37	0.02
Total number whorls	7.00–8.50	7.62	0.39
	7.00–7.75	7.57	0.28
	7.00–8.25	7.57	0.28
Protoconch whorls	1.25–1.50	1.40	0.14
	1.50–1.75	1.64	0.13
	1.50–1.75	1.61	0.12
Axial ribs/last whorl	12–13	12.5	0.5
	14–17	15.4	1.0
	12–16	14.1	1.5
Length/width	2.16–2.47	2.33	0.12
	2.19–2.47	2.29	0.10
	2.12–2.49	2.31	0.12
Aperture length/length	0.30–0.37	0.35	0.02
	0.35–0.38	0.37	0.01
	0.32–0.36	0.34	0.01

assumes the origin of the group somewhere in the area represented today by the Indo-West Pacific (or Eastern Tethys), and subsequent passive dispersal of teleplanic larvae (Scheltema, 1971) through the wide expanses of the East Pacific Barrier via the countercurrent system in the tropical Pacific (Brothers and Thresher, 1985; Glynn and Wellington, 1983; Vermeij, 1987; Scheltema, 1988), followed by colonization of shallow-water environments in Central America before the final closure of the Central American Isthmus (Jones and Hasson, 1985), and later invasion of the tropical southwestern Atlantic. However, no counterparts of *indiscreta-turricula* are known from the Caribbean, tropical west America or from the Tertiary formations in Central America (this latter requirement would be necessary to validate the hypothesis, for ancestral populations should have been present in the region before the uplift of the Panama land bridge, to make it possible for the species to colonize the tropical Atlantic). The already mentioned Caribbean species *elegantissima*, the Miocene *R. (Rissolina) ditomus* Woodring, 1928 from Bowden, Jamaica (Woodring, 1928), and the Mio-Pliocene *R. (Ris-*

solina bicrepida Weisbord, 1962 from the Playa Grande Formation in Venezuela (Weisbord, 1962) are conchologically diverse from the two species. Furthermore, this purely dispersalist hypothesis would require the presence of an ancestor with teleplanic (Scheltema, 1971, long-lasting planktotrophic) larval stages. The teleplanic condition, as defined by Scheltema (1971), although probably present in other rissoid genera, is unknown in *Rissoina* (Ponder, 1985). The second hypothesis would assume the previous existence of populations of *turricula* (or a common ancestor, even though the species was already differentiated in the Miocene (Ladd, 1966)) around the southern extremity of Africa. Passive dispersal of planktotrophic larval stages would enable the colonization of the southwestern Atlantic. Cooling of the southern mid-latitude regions in the late Miocene (with the commencement of the Benguela upwelling system at that time) (Hodell and Kennett, 1985) would cause the extinction of the hypothesized African ancestral populations and the ceasing of passive transport through the South Atlantic. Obstacles to that proposition are the absence of known fossil record of an ancestral species in South or southeastern Africa and, as in hypothesis 1, the inexistence of known *Rissoina* with truly teleplanic larvae. The third hypothesis assumes the presence of a widespread shallow-water Tethyan ancestor. Shallow-water intercommunication between the western and eastern parts of the Tethyan Seaway remained feasible at least until the mid Miocene (Middlemiss and Rawson, 1971; Berggren and Hollister, 1974; Steininger and Rögl, 1984). Planktotrophic development would not be a necessary condition for the maintenance of specific cohesiveness between populations of a shallow-water ancestral species. A vicariance event (Nelson and Platnick, 1981) would follow, characterized by the final closure of the Tethyan Seaway in the mid Miocene (Berggren and Hollister, 1974; Steininger and Rögl, 1984), and late Miocene-Pliocene extinction in the Mediterranean shallow-water environments due to the complex interplay of sea-level fluctuation and glaciation events that began at that time (Raffi et al., 1986). Allopatric speciation would give origin to the known Recent Atlantic and Indo-West Pacific taxa, with no Tethyan-related species remaining in the Mediterranean Sea (Ekman, 1953; Steininger and Rögl, 1984). In fact, no affinities for the species-group are known living in the Mediterranean. The shell illustrated by Nordsieck (1972), as *R. plicata* A. Adams, 1851, from Haifa, Israel, might be included among the morphological limits set by *indiscreta* and *turricula*, and could be indicative of post-Tethyan recolonization event. Anyway, the illustration does not agree with the syntypes of *plicata* (which may not be a true *Rissolina*, lacking the strong basal fold characteristic of the subgenus), making it unsafe to consider Nordsieck's record as evidence of the existence of a Recent Mediterranean counterpart for the two species. Again, no correlated Recent or fossil species are known from the Caribbean or from Tertiary formations in Europe (Lozouet, pers. comm.), conditions that would further support the hypothesis of a Tethyan ancestor.

Although we cannot conclusively reject the other two interpretations due to scarcity of investigations on fossil microgastropods from the discussed regions, the hypothesis of a Tethyan ancestor seems to us to be the most probable. It is congruent with distribution patterns of Recent Tethyan relicts, or Tethyan-related, genera and species of benthic invertebrates (Ekman, 1953; Mayr, 1954; Reid, 1967; Newman, 1976). Furthermore, in opposition to the other two discussed hypotheses, the teleplanic ancestral condition would not be required in order to justify the proposition. Passive larval transport (or rafting in the adult phase) would not be necessary for the ancestral species to achieve its large distribution range, due to the spatial continuity of the Tethyan shallow-water environments. Despite the gaps in the fossil record, the vicariant interpretation seems to be the simplest explanation for the odd, broadly disjunct Recent distribution of the *R.*

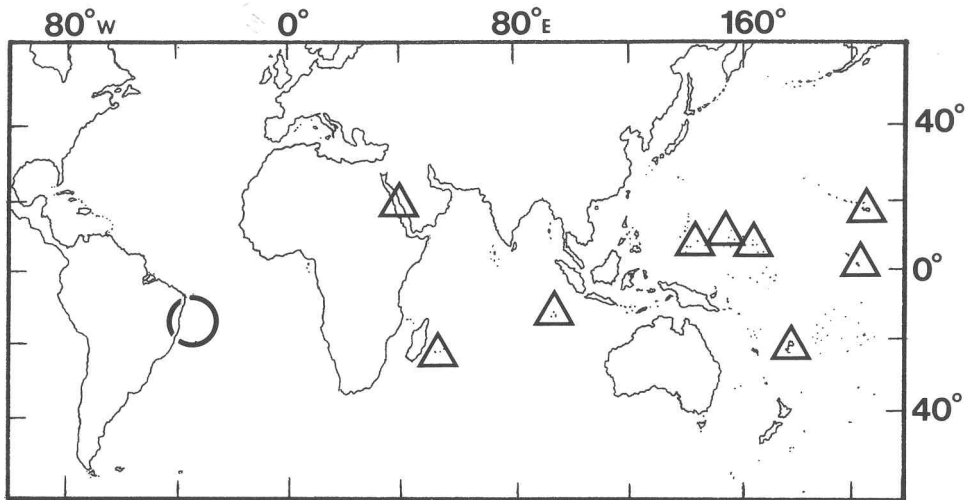


Figure 12. Disjunct distribution of the species-group *R. indiscreta* new species (O)—*R. turricula* (Δ).

indiscreta-turricula species-group. As Ekman (1953) has observed (p. 79), 'the unmistakable relationship between the Atlantic and Indo-West-Pacific fauna is undoubtedly due to long-standing communication between the two, but this is not to say that migration took place preponderantly from east to west. The relationship is due rather to the fact that both these faunas are descended from a more or less homogeneous Tethys fauna.'

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