RICHARDS, H. G. 1933. A conchological expedition to Cuba. Proc. Penn. Acad. Sci. 7: 167–172.

SCHWARTZ, A. 1970. A systematic review of *Ameiva auberi* Cocteau (Reptilia, Teiidae) in Cuba and the Bahamas. III. Discussion. Ann. Carn. Mus. 41 (4): 152–168.

SOWERBY, G. B. II. 1839. A conchological manual, London, 5 + 130 pp., 488 figs.

————. 1842. A conchological manual, London, 2nd ed.

THIELE, J. 1925. [in] Kükenthal and Krumbach. Handbuch der Zoologie, 5: (3): 1–160.

————. 1929. Helicinidae [in] Handbuch der systematischen Weichtierkunde, pp. 84–91, figs. 57-67.

THOMPSON, F. G. 1967. A new land snail of the family Proserpinidae from Chiapas, Mexico. Proc. Biol. Soc. Washington 8: 61–64, figs. 1–3.

THOMPSON, F. G. 1968. *Ceochasma*, a remarkable new land snail from Colíma, Mexico (Gastropoda Prosobranchia, Helicinidae) Proc. Biol. Soc. Washington 81: 45–52.

TROSCHEL, F. H. 1857. Proserpinacea [in] Das Gebiss der Schnecken. Berlin 1: 84–85, pl. 6, fig. 2.

WAGNER, A. 1905-1906. Helicinen Studien. Denkschriften der mathem - naturwissen. Klasse, Vol. 77: 357-450, pls. 1–9; Vol. 78: 203–248, pls. 10–14.

————. 1907–1911. Helicinidae. [in] Martini and Chemnitz, Conchylien-Cabinet, (2): 1: sect. 18, pt. 2, 391 pp., 70 pls.

WENZ, W. 1938. Helicinidae [in] Handbuch der Paläozoologie, Gastropoda, pp. 435-448, figs. 1071–1118.

———. 1857. Guide to the systematic distribution of Mollusca in the British Museum. Part I. London, 230 pp.

HENDERSON, J. B. 1916. A list of the land and fresh-water shells of the Isle of Pines. Ann. Carn. Mus., 10 (3 + 4): 315–324.

JACOBSON, M. K. 1956. Malacological notes from western Cuba. Nautilus 70: 1–3.

———. 1970. The land and freshwater gastropods collected in Cuba by M. G. Rutten. Bull. Zool. Mus. Amsterdam 1 (15): 221–233

JACOBSON, M. K. AND K. J. BOSS. 1973. The Jamaican land shells described by C. B. Adams. Occ. Papers Moll., Harvard Univ., 3 (47): 305–519, pls. 54–91.

JAUME, M. L. 1945. Excursión malacológica al Pan de Guajaibón. Revista Soc. Malac. "Carlos de la Torre" 3: 73–83.

KEEN, A. M. 1960. Helicinidae [in] Moore, R. C. (ed.), Treatise on Invertebrate Paleontology, Mollusca. Vol. 1, pp. 285–288, figs. 186-187.

MORLET, L. 1892. Descriptions d'espèces nouvelles provenant de l'Indo-Chine. Jour. de Conch. 40: 315–329.

NEAVE, S. A. 1939. Nomenclator Zoologicus, vol. 2, Zool. Soc. London, 1025 pp.

NEWTON R. B. 1891. Systematic List . . . British Oligocene and Eocene Mollusca . . . British Museum (Natural History), London, 365 pp.

ORBIGNY, A. D'. 1842. Mollusques. [in] Sagra, R. Histoire Physique, Politique et Naturelle de l'Ile de Cuba. Paris, Vol. 2, 264 pp., 28 pls.

PFEIFFER, L. 1848. Monographia Heliceorum Viventium. Volumen primum. Leipzig, 484 pp.

———. 1850. Helix. [in] Martini and Chemnitz, Conchylien-Cabinet, (2): 1: sect. 12, pt. 2, 290 pp.

———. 1853. Monographia Heliceorum Viventium. Supplementum primum. Volumen tertium. Leipzig, 711 pp.

———. 1856. Monographia Auriculaceorum Viventium. Cassell, 209 pp.

———. 1857. Catalogue of Auriculidae, Proserpinidae, and Truncatellidae in the collection of the British Museum. Taylor and Francis, London, 150 pp.

———. 1858. Monographia Pneumonopomorum Viventium. Supplementum primum. Cassell, 249 pp.

———. 1859. Monographia Heliceorum Viventium. Supplementum secundum. Volumen quartum. Leipzig, 920 pp.

———. 1876. Monographia Pneumonopomorum Viventium. Supplementum tertium. Cassell, 479 pp.

POEY, F. 1851–1854. Memorias sobre la Historia Natural de la Isla de Cuba, Havana. Vol. 1, 463 pp., 34 pls.

Boss, K. J. 1972. Minute Jamaican prosobranch gastropods: *Stoastoma* and its congeners. Breviora, No. 393, 13 pp., 2 pls.

Boss, K. J. and M. K. Jacobson. 1973a. Monograph of *Ceratodiscus*. Occ. Papers Moll., Harvard Univ. 3 (45): 253–279, pls. 45–48.

———. 1973b. Monograph of the genus *Alcadia* in Cuba. Bull. Mus. Comp. Zool., Harvard Univ. 145 (7): 311–358, 5 pls., 2 figs., 3 maps.

———. 1974a. Monograph of the genus *Lucidella* in Cuba. Occ. Papers Moll., Harvard Univ. 4 (48): 1–27, pls. 1–4.

———. 1974b. Catalogue of the taxa of *Lucidella*. Occ. Papers Moll., Harvard Univ. 4 (49): 29–38.

———. 1975. Catalogue of the taxa of the subfamily Proserpininae. Occ. Papers Moll., Harvard Univ. 4 (52): 93–102.

Clench, W. J. 1962. New species of land mollusks from the República Dominicana. Breviora, No. 173, 5 pp.

Clench, W. J. and M. K. Jacobson. 1968. Monograph of the Cuban genus *Viana*. Breviora, No. 298, 25 pp., 4 pls., 5 maps.

———. 1970. The genus *Priotrochatella* of the Isle of Pines and Jamaica. Occ. Papers Moll., Harvard Univ. 3 (39): 61–80, pls. 17–20, 1 map.

———. 1971a. Monograph of the Cuban genera *Emoda* and *Glyptemoda*. Bull. Mus. Comp. Zool., Harvard Univ. 141 (3): 99–130, 7 pls.

———. 1971b. A monograph of the genera *Calidviana*, *Ustronia*, *Troschelviana*, and *Semitrochatella* in Cuba. *Ibid.* 141 (7): 403–463, 8 pls., 2 figs.

Darlington, P. J., Jr. 1938. The origin of the fauna of the Greater Antilles, with discussion of dispersal over water and through the air. Quart. Rev. Biol. 13 (3): 274–300, 5 figs.

Farfante, Isabel Pérez. 1942. Moluscos de la región de Camoa y Somorrostro y sus condiciones de vida. Mem. Soc. Cubana Hist. Nat. 16 (1): 45–56.

Gloyne, C. P. 1872. Notes sur le mode de station, les moeurs et les habitudes des Mollusques terrestres de la Jamaïque, avec la description d'une espèce nouvelle. Jour. de Conch. 20: 26–47.

Gray, J. E. 1840. Synopsis of the contents of the British Museum. 42nd Ed. London, 156 pp.

———. 1842. Synopsis of the contents of the British Museum. 44th Ed. London, 308 pp.

———. 1847. A list of the genera of Recent Mollusca, their synonyms and types. Proc. Zool. Soc. London, pt. 15, pp. 129–219.

———. 1856. On the position of the genus *Proserpina* in the system, and a description of its dentition. Proc. Zool. Soc. London, pt. 24, pp. 99–102.

km 14 between Pinar del Río City and Viñales; Mogote Rinconada; Mogote Zacarías; Mogote Coco Sola; Ensenada Hutía; Mogote Dos Hermanos; Pan de Azucar; El Abra; Paredones de la Puerta del Ancón; Guajaní; Laguna de Piedras; Mogote Palmarito (all USNM); Mogote de la Dinamita; Mogote de Justo; El Cuajaní, Sierra de Viñales; Cayos de San Felipe; Santo Tomás (all MCZ). *San Vicente:* La Chorrera; Costanera de San Vicente (both USNM); Cuevas del Río; Cove of Delight; mogotes in middle of west side, Ensenada de San Vicente; Mogote Justo, Baños de San Vicente (all ANSP). ISLE OF PINES: Sierra Caballos; Sierra Columbo; Sierra de Casas; Sierra Bibijagua (all USNM). ORIENTE: Florída Blanca; Subida de la Hembrita; Los Alemanes, La Leonora, Jarahueca (all USNM); El Yunque de Baracoa (MCZ).

BIBLIOGRAPHY

ADAMS, C. B. 1850. Descriptions of supposed new species and varieties of terrestrial shells, which inhabit Jamaica. Contributions to Conchology, No. 5, pp. 76–84.

ADAMS, H. AND A. ADAMS. 1856. The genera of Recent Mollusca. London, Vol. 2, 661 pp.

AGUAYO, C. G. AND M. L. JAUME. 1947-1951. Catálogo Moluscos de Cuba, Nos. 1–725 (mimeographed).

ARANGO, R. 1878-1880. Contribución a la Fauna Malacológica Cubana. Havana. 280 pp. (+ 35, index and errata).

BAKER, H. B. 1922. Notes on the radula of the Helicinidae. Proc. Acad Nat. Sci. Philadelphia 74: 29-67, pls. 3–7.

———. 1923. Proserpinidae. Nautilus 36: 84–85.

———. 1926a. Anatomical notes on American Helicinidae. Proc. Acad. Nat. Sci. Philadelphia 78: 35–56, pls. 4–8.

———. 1926b. The radula of *Proserpina.* Proc. Acad. Nat. Sci. Philadelphia 78: 449–451.

———. 1934a. Jamaican land snails. Nautilus 48: 6–14, 60–67, pl. 2.

———. 1934b. The animal of *Proserpina.* Nautilus 47: 151.

———. 1956. Familial names for land operculates. Nautilus 70: 28–31.

BLAND, T. 1858. On the absorption of parts of the internal structure of their shells by the animals of *Stoastoma, Lucidella, Trochatella, Helicina* and *Proserpina.* Ann. Lyceum Nat. Hist. New York 6: 75–77.

Height	Width	
4.2 mm	5.2 mm	La Chorrera, San Vicente, Pinar del Río
3.5	5.2	Mogote de Justo, Viñales, Pinar del Río
3.4	4.2	Cayos de San Felipe, Viñales, Pinar del Río
3.2	5.2	Sierra de Casas, Isle of Pines

Remarks. *P. globulosa* is most closely related to, and probably a derivative of *P. pisum* of western Jamaica. It is distinguished by its slightly smaller size, less globose body whorl, larger aperture and lower profile. From the other Cuban *Despoenella*, *P. depressa*, with which it is sympatric in Viñales, Pinar del Río, *P. globulosa* can be readily recognized by its smaller size, its higher, subglobular outline, and its columellar lamella which rises from an elevation on the columella rather than directly from the columella itself.

As discussed earlier (see *Zoogeography* in the *Introduction*), *P. globulosa* arose on Cuba having been derived from a Jamaican stock like *P. pisum*. Although Arango wrote (1879: 58) that *globulosa* is found "en casi toda la isla" we have found no records, either published or in museum collections, to support this statement. Presently the species occurs (Map 2) in 4 disjunctive localities: 1) in the west from northwestern Pinar del Río around Luiz Lazo and Viñales; 2) on the Isle of Pines; 3) in the east in south central Oriente around Jarahueca and Florída Blanca; and 4) near the extreme eastern portion of Oriente at Baracoa. It is the only species of *Proserpina* in the Isle of Pines (Henderson, 1916) and unlike *P. depressa*, its range does not extend to Havana Province. Probably at one time *P. globulosa* was widely distributed on the island but now it only lives in several isolated, disjunctive, mainly montane refugia.

Specimens examined. PINAR DEL RÍO: *Viñales:* Mogote Cabrera; Sumidero, Luis Lazo; Hoyo Jaruco; Mogote Marmol; Mogote Cayo de San Felipe; Mogote La Mina;

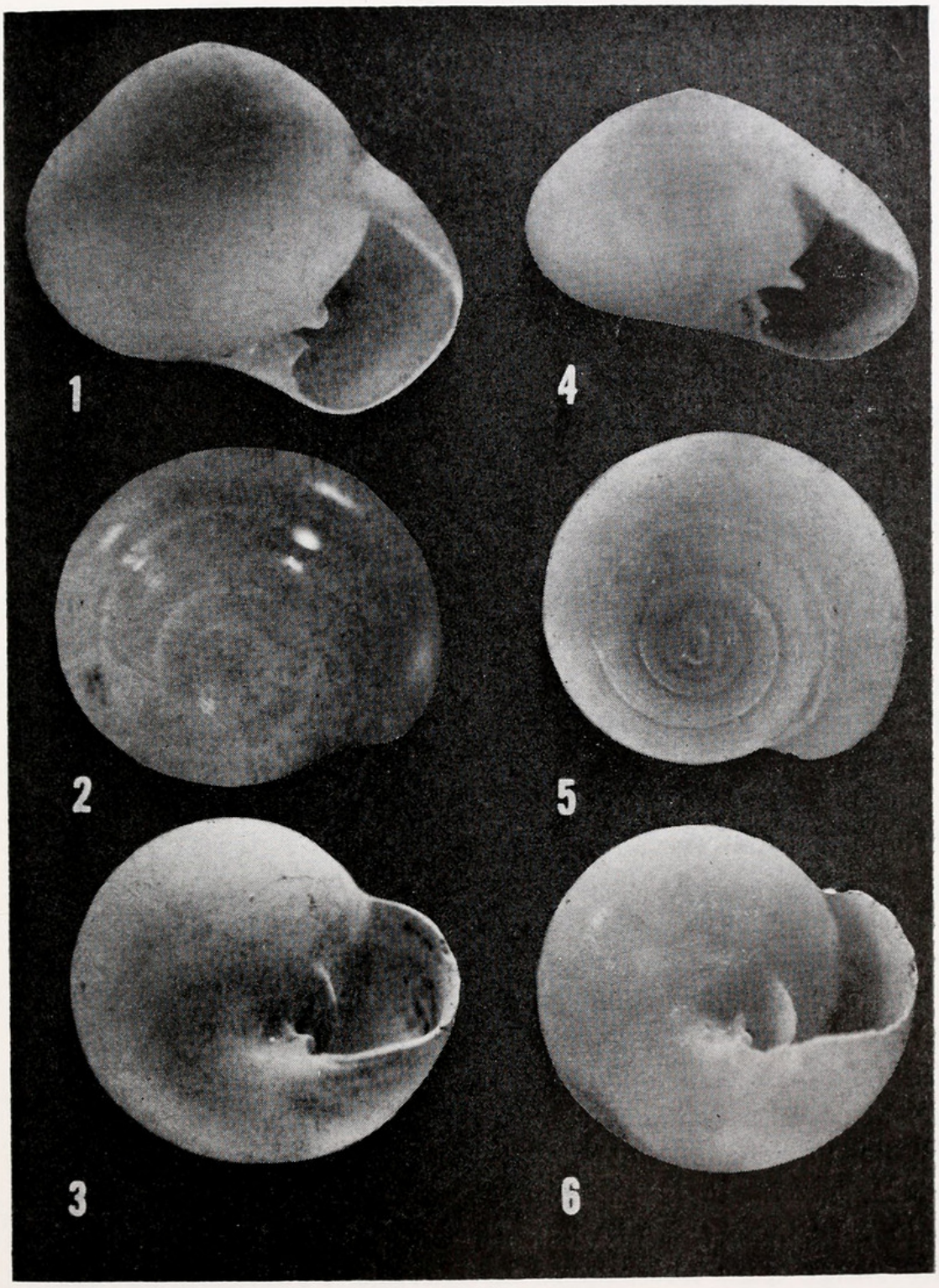


Plate 13

Figs. 1–3. Lectotype of *Proserpina pisum* C. B. Adams, selected by Jacobson and Boss 1973: 404, pl. 71, figs. 10 + 11, Jamaica, 6.1 mm × 5.6 mm, MCZ 177263.

Figs. 4–6. *Proserpina* (*Despoenella*) *globulosa* (Orbigny), Santa Tomas, Viñales, Pinar del Río, Cuba, 5.3 mm × 3.7 mm, MCZ 235260.

Specimens examined. JAMAICA: *Westmoreland:* New Hope (MCZ); *St. James:* 2 to 4 mi SE of Catadupa Station (ANSP); Spring Mount (MCZ); *Trelawney:* 200 ft. W of streambed and entrance to Windsor Cave (Goodfriend).

Proserpina (Despoenella) globulosa (Orbigny)

Plate 13, figs. 4–6; Map 2

Odontostoma globulosa Orbigny 1842. Mollusques [in] Sagra, Histoire Physique, Politique, et Naturelle de l'Ile de Cuba, 1: 239, pl. 18, figs. 8–11 (type-locality, intérieur de l'île; holotype, BMNH).

Odontostoma globulosum Orbigny. Pfeiffer 1848. Monographia Heliceorum Viventium 1: 11.

Proserpina globulosa (Orbigny). Pfeiffer 1850. [in] Martini and Chemnitz, Conch. Cab. (2) 1: pt. 12, sect. 2, p. 12, figs. 19–21.

Description. Shell reaching 5.2 mm in diameter, 4.2 mm in height, imperforate, subglobose, smooth, polished; color pale lemon yellow or white; whorls almost 4–5, quite flat, slowly increasing in width, the last whorl only slightly wider than the penultimate; body whorl well rounded at the periphery; suture very weakly impressed; spire little raised, domelike, apex barely elevated; aperture oblique, narrowly semilunate, with 2 lamellae; parietal lamella stronger; columellar lamella rising from a low elevation in columellar curve; palatal lamellae absent; umbilical area weakly excavated; outer lip entire, somewhat retreating centrally; surface finely punctate and with regularly, closely spaced axial striae becoming obsolete basally (50 ×); punctate; protoconch 1½ whorls, microscopically pebbled, barely elevated; periostracum and operculum lacking.

Description. Shell reaching 6.1 mm in width, 5.6 mm in height, imperforate, globose, smooth, polished; color white or pale lemon yellow; whorls 4–5 +, slightly inflated, slowly increasing, the last whorl little wider than the penultimate; body whorl high, well rounded, shelved in adult individuals, the periphery central; suture well impressed, especially at the body whorl, umbilical area weakly sunken; spire well raised, domelike; aperture slightly oblique, narrowly semilunate, with a columellar lamella closely set to and slightly smaller than a parietal lamella; outer lip thin, simple, somewhat retreating centrally; sculpture of weak, barely perceptible growth lines; the surface weakly punctate and with fine, regularly spaced obsolete internal lineations, obsolete basally (50 ×); protoconch 1½ whorls, microscopically punctate, slightly raised; periostracum and operculum wanting.

Height	Width	
5.6 mm	6.1 mm	lectotype
4.6	5.9	New Hope, Westmoreland
4.2	5.1	paralectotype

Remarks. Proserpina pisum is one of two species of *Despoenella* which live on the island of Jamaica (Map 1). It is easily distinguished from *P. bidentata* by its rounded, globose shape; further, the species are distinctly separated geographically, with *pisum* living in the western regions of the island, from the Parishes of Westmoreland, St. James and Trelawney, and *bidentata* occurring only in the east in the John Crow Mountains. According to Baker (1934a) both species aestivate under rocks during hot and dry periods but emerge to climb rock faces during rain. Gloyne (1872) remarked on the great rarity of the occurrence of *P. pisum.*

P. pisum is most closely related to the Cuban *P. globulosa* with which it shares a similar globular shape and to which it probably gave rise (see *Zoogeography* in the *Introduction*).

'It [*marcanoi*] differs from *depressa* by being smaller in size, proportionally higher, and in having a columellar lamella nearly twice as high as the Cuban species.', *P. marcanoi* is virtually indistinguishable from *P. bidentata* from Jamaica. Unfortunately the series of specimens available for either of these species are limited, and in most every feature the shells of the two species appear to be identical. However, considering the great geographic distance separating these populations and taking into account the extremely small sample size, under close scrutiny we were able to detect some minute differences, which though appearing to be minor in importance may prove to be of a specific diagnostic value once larger samples become available. *P. marcanoi* exhibits a proportionately greater post-embryonic growth than *P. bidentata*. That is to say, that the whorl number of *marcanoi* is greater than that of *bidentata* in specimens of the same size. For example the holotype of *marcanoi* which measures 4.7 mm in diameter has 4 postembryonic whorls while a similarly sized specimen of *bidentata* (ANSP 139451), measuring 4.8 mm in diameter, has only 3½ to 3¾ whorls. The same relationship obtained in other measured comparisons. Lastly, there may be some color differences between the Jamaican and Hispaniolan forms where *bidentata* may be more strongly infused with a greenish tint. We have decided on the basis, especially of biogeographic considerations in combination with the whorl number difference noted above, to maintain *marcanoi* and *bidentata* as separate, but very closely related species, the former probably having been derived from the latter.

Specimens examined. Known only from the type-locality.

Proserpina (Despoenella) pisum C. B. Adams

Plate 13, figs. 1–3; Map 1

Proserpina pisum C. B. Adams 1850. Contribution to Conchology No. 7: 108 (Jamaica; lectotype, MCZ 177263, selected by Jacobson and Boss, 1973: 404, pl. 71, figs. 10–11).

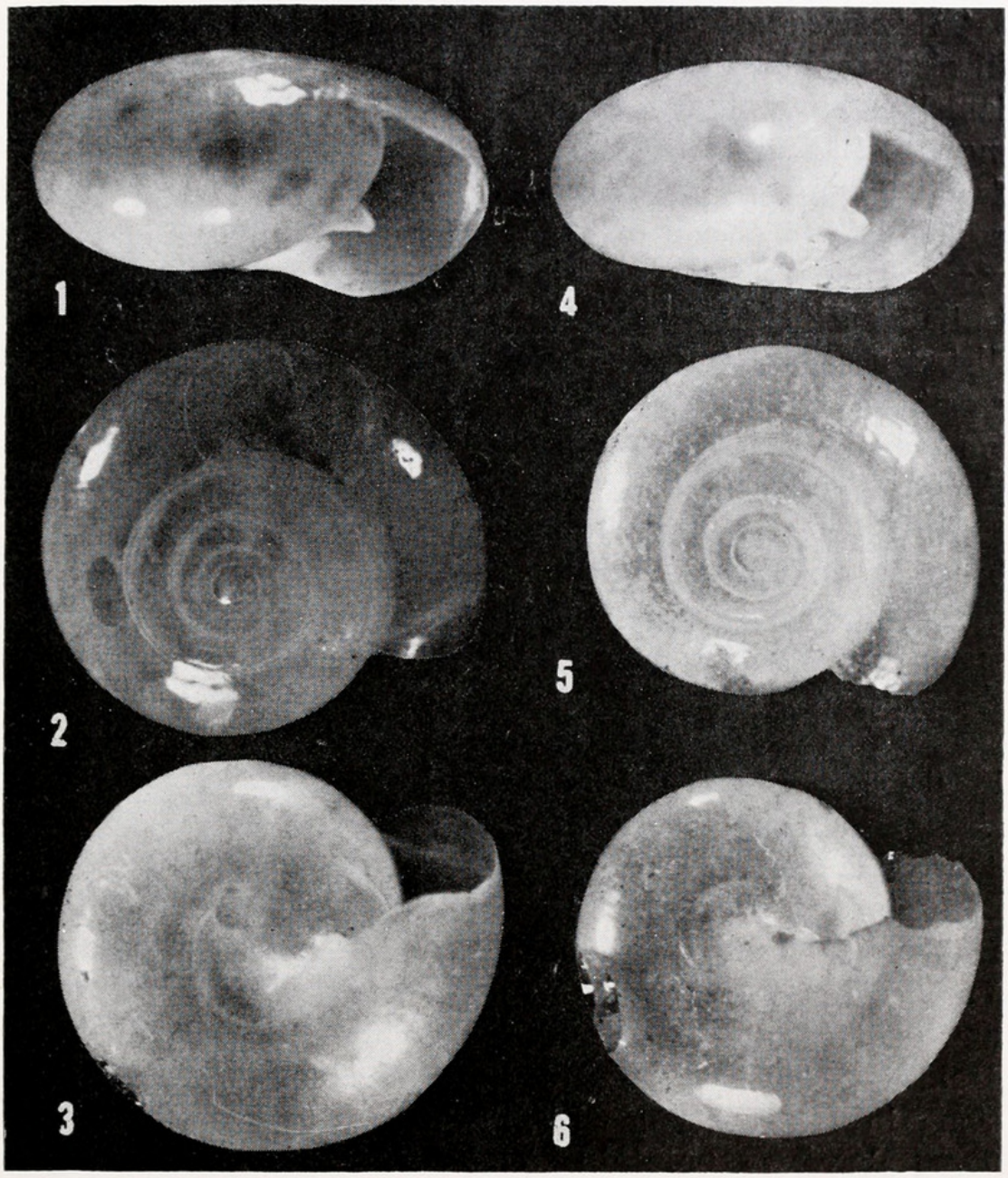


Plate 12

Figs. 1–3. The holotype of *Proserpina marcanoi* Clench, Colonia Ramfis, 20 km W of San Cristobal, Santo Domingo, Hispaniola, 4.7 mm × 2.4 mm, MCZ 188911.

Figs. 4–6. The holotype of *Proserpina bidentata* C. B. Adams, Jamaica, 4.0 mm × 2.2 mm, MCZ 186126.

Nothing is known about the biology of *P. bidentata.* Specific locality records thus far indicate that the species occurs in eastern Jamaica, notably the John Crow Mountains in the Parish of Portland (Map 1).

Specimens examined. JAMAICA: holotype (MCZ); *Portland:* 6.5 mi from Port Antonio, near Nonsuch (ANSP); 3.2 and 4.2 mi S of junction with Route A4, E side of road to Ecclesdown (both Goodfriend); W of Haining (ANSP).

Proserpina (Despoenella) marcanoi Clench
Plate 12, figs. 1–3

Proserpina marcanoi Clench 1962. Breviora, No. 173, p. 2, pl. 1, fig. 3 (Colonia Ramfis, 20 km W of San Cristobal, Santo Domingo [Hispaniola]; holotype, MCZ 188911).

Description. Shell reaching 4.7 mm in diameter, 2.4 mm in height, imperforate, depressed, smooth, polished, thin, fragile, translucent; color light whitish green; whorls 4, barely inflated, rapidly expanding, the last 3 times the width of the penultimate whorl; body whorl well rounded, periphery slightly above the center; suture weakly impressed, somewhat stronger at the body whorl; umbilical area slightly sunken; spire depressed: aperture narrowly semilunate, with a low columellar lamella and a higher parietal one; palatal lamellae lacking; outer lip thin, entire, slightly retreating centrally; sculpture of irregular, very fine growth lines; protoconch 1½ whorls, glassy, transparent, smooth; periostracum and operculum lacking.

Height	Width	
2.4 mm	4.7 mm	holotype
2.2	4.4	paratype
2.1	4.3	paratype

Remarks. Although Clench (1962: 3) remarked on the possible relationship of *marcanoi* with *depressa* of Cuba and differentiated these species thusly:

Proserpina (Despoenella) bidentata C. B. Adams
Plate 12, figs. 4–6; Map 1

Proserpina bidentata C. B. Adams 1850. Contributions to Conchology No. 5: 81 (Jamaica; holotype, MCZ 186126, figured by Jacobson and Boss 1973: 328, pl. 85, figs. 1–2).

Description. Shell reaching 4.0 mm in diameter, 22 mm in height, imperforate, thin, smooth, polished and translucent; color pale yellowish or greenish white; whorls 3-4, weakly inflated, rapidly increasing, the last more than three times the width of the penultimate; body whorl narrowly and unevenly rounded, the periphery distinctly above the center; suture weakly impressed, bordered by an opaque white line; umbilical area weakly sunken; spire depressed; aperture oblique, semilunate with 2 lamellae, one, the smaller one, on the columella, the other, twice the width, set closely above; no palatal lamella; outer lip thin, entire, somewhat retreating centrally; sculpture of weak, irregular growth lines, surface appears weakly punctate and with fine, regular internal lineations, obsolete basally (50 ×); protoconch 1½ whorls, glassy, microscopically punctate, barely raised; periostracum and operculum lacking.

Height	Width	
2.2 mm	4.0 mm	holotype

Remarks. P. bidentata is very closely related to, and probably gave rise to, *P. marcanoi* of Hispaniola, from which it is virtually indistinguishable. Although *bidentata* and *marcanoi* may prove to be conspecific, the widely separated populations represented by extremely small sample sizes are herein treated as separate species (see *Remarks* under *marcanoi*).

The Cuban *P. depressa,* was also probably derived from *P. bidentata.* The latter is considerably smaller in size and differs in being noticeably less depressed with its body whorl somewhat more subglobose than *depressa.*

phery. However, in the 3 lots from the type-locality in the collection of the MCZ, specimens are found in which the band has been only partially developed near the aperture and others in which the band is missing entirely. There is little reason to view this variable feature in a localized population as worthy of taxonomic distinction, particularly since red or reddish coloring in the shell, whatever its adaptive significance, occurs in other proserpine snails. Pfeiffer (1857: 149) reported a variety of *linguifera* Jonas from Jamaica with a red apex, the South American *P. cousini* Jousseaume from Ecuador has a narrow deep red spiral band, and *P. nitida* has reddish variations in its populations (Gloyne, 1872).

Several authors have noted the abundance and provided documentation for local occurrences of *P. depressa* (Richards, 1933; Farfante, 1942; Jaume, 1945; Jacobson, 1970).

Specimens examined. PINAR DEL RIO: Canalete; Rangel; Mogote de la Villa María, Consolación del Norte; El Mamey, Cayajabos; Sierra la Güira; La Furnia, La Güira; Mogotes de Cerro de Cabras; Ensenada de los Burros, Cabezas; Echevarría, San Diego de los Baños; Finca Balastena, Bahía Hondo; Farallón de Juan Alonso, Sierra Quemado, Isabel María; Sierra la Chorrera, San Vicente; Hoyo Jutía (Hutía), 1 km E of San Vicente. *Guane:* Mendoza; Sierra Paso Real; Sierra de Guane. *Viñales:* Hoyo del Niajagual, Cierra del Ancón; Mogote de la Dinamita; El Queque; Mogote Largo; Laguna de Piedras; Km 14 between Pinar del Río City and Viñales; Mogote Capón; Potrero Manuel Sánchez; Mogotico de Torres; mogote between Cayos de San Felipe and Loma de Isabel. HAVANA: Finca la Alianza, Cotorro; Somorrostro, near Jamaica; Loma de Camao; Peña Blanca, Sierra Anafe; Esperón, Sierra Anafe; Managua; Guayabel, Sierra Anafe (all MCZ). ORIENTE: Monte Toro, Guantánamo (MCZ); San Felipe, Monte Toro (USNM). *Miranda:* Nipi Hills, Tibisí; La Cueva, near Júcaro, Tibisí; Birán; Upper Mercedes Valley; top of hill, N of Mercedes Valley; Arroyo del Agua; Cuyo del Rey, near Miranda (all ANSP).

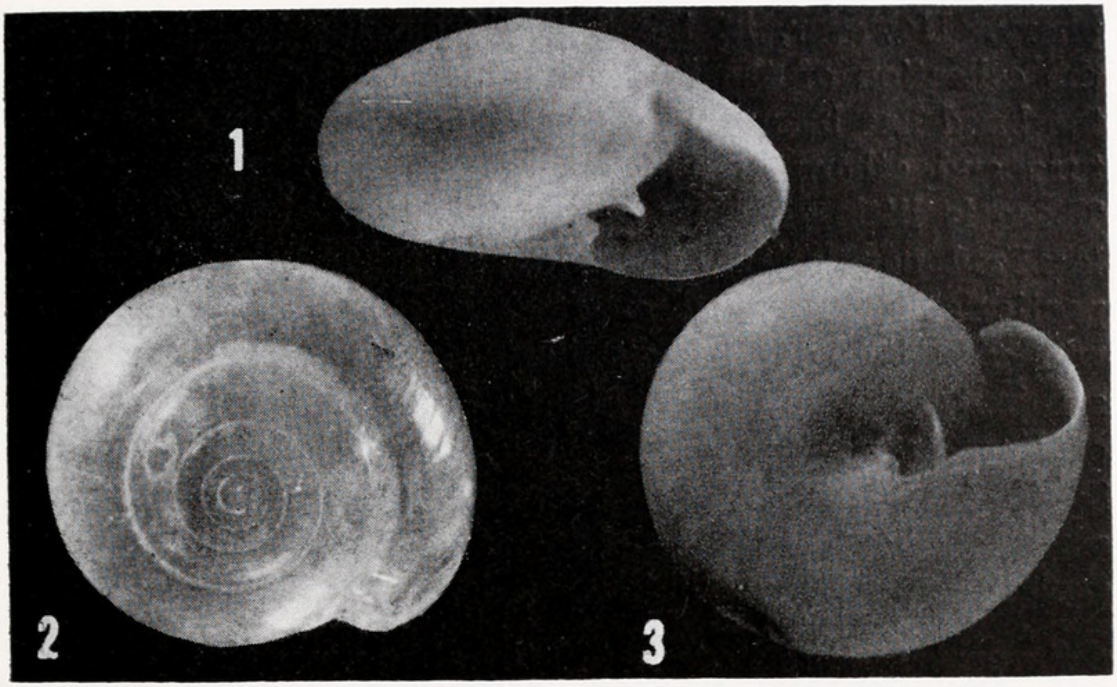


Plate 11

Proserpina (*Despoenella*) *depressa* (Orbigny).

Figs. 1–3. Hoyo Jutia, 1 km E of San Vicente, Viñales, Pinar del Río, Cuba, 6.2 mm × 3.4 mm, MCZ 105397.

face smooth, polished with fine regular pebbling, (at 50 ×), sculptured with irregular barely perceptible growth lines; protoconch 1½ whorls, scarcely elevated, smooth except for microscopic pebbling; periostracum and operculum wanting.

Height	Width	
3.7 mm	8.2 mm	Sierra Anafe, Havana
4.2	7.4	Sierra Paso Real, Guane
3.8	6.2	Sierra Anafe, Havana

Remarks. *P. depressa* is closely related to *P. bidentata* from Jamaica and *P. marcanoi* from Hispaniola (see Remarks under *bidentata* and *marcanoi*). *P. bidentata* is considerably smaller in size and is less depressed in outline, having a somewhat more subglobose body whorl. As discussed elsewhere, *P. depressa* was probably derived from *P. bidentata* and presently occupies disjunct, mainly montane refugia in Cuba (see Map 3 and *Zoogeography* in the *Introduction*).

Of the two species of *Despoenella* found in Cuba, *P. depressa* is larger, more depressed in outline and has its columellar lamella rising directly from the columella and not from a small elevation as in *P. globulosa*. Geographically *P. depressa* is isolated in two disjunct areas (see Map 3). It has a wide distribution in western Cuba reaching from Mendoza near Guane to the central part of Havana Province. In the region of Viñales it is an exceedingly abundant species and is found in large numbers in every suitable location. However, unlike *globulosa*, it does not occur on the Isle of Pines. In eastern Cuba, it has been reported only from the southeastern section of Oriente Province in an area extending from around Miranda to Guantánamo.

The name, *P. depressa rubrocincta*, was given to an isolated population around Luis Lazo, Pinar del Río, in which the shells have a wide orange band around the peri-

Proserpina (Despoenella) depressa (Orbigny)

Plate 11, figs.1–3; Map 3; text fig. 1

Odontostoma depressa Orbigny, 1842. Mollusques [in] Sagra, Histoire Physique, Politique, et Naturelle de l'Ile de Cuba, 1: 238, pl. 18, figs. 4–7 (type-locality, intérieur de l'île; restricted by Aguayo and Jaume, 1947: No. 88, Pan de Guajaibón, Pinar del Río; holotype, BMNH).

Odontostoma depressum Orbigny. Pfeiffer, 1848, Monographia Heliceorum Viventium 1: 11.

Helicina ptychostoma Pfeiffer, 1848. Monographia Heliceorum Viventium 1: 12, footnote (type-locality, Callajabas (*sic*) [= Cayajabos, Pinar del Río]; holotype, destroyed, Clench and Jacobson 1971a: 101).

Proserpina depressa (Orbigny). Pfeiffer 1853. Monographia Heliceorum Viventium 3: 291.

Proserpina depressa rubrocincta (Torre MS) Aguayo and Jaume, 1947, Catálogo Moluscos de Cuba, No. 88 (*nomen nudum*); Aguayo and Jaume, 1957, Mem. Soc. Cubana Hist. Nat. 23: 124, pl. 1, fig. 10 (type-locality, Los Acostas, Luiz Lazo, Provincia Pinar del Río; holotype, MP 5520).

Description. Shell reaching 8.2 mm in diameter, imperforate, depressed and polished; color pale lemon yellow or white; whorls 4–5, barely inflated, rapidly increasing in size, the last whorl twice the width of the penultimate; body whorl narrowly but evenly rounded at the periphery and somewhat shelved in mature specimens; suture indicated but barely impressed; umbilical area shallowly excavated, somewhat more translucent than rest of shell; spire low, dome-shaped, apex barely raised above succeeding whorl; aperture oblique, with two entering lamellae: the upper (parietal) lamella strong, well raised, the lower (columellar) weaker, rising directly from the evenly rounded, concave columella; palatal lamellae wanting; outer lip thin, entire, somewhat retreating centrally; sur-

According to Baker (1934a: 63), *linguifera* aestivates under rocks but rapidly climbs rockfaces during rains; the localities he lists for the species, all presently preserved as samples in the Academy of Natural Sciences of Philadelphia, show that the species lives mainly at altitudes between sea level and 600 ft. In contrast *P. nitida* lives at higher elevations in more eastern sections of the island.

Specimens examined: JAMAICA: *Westmoreland:* Bluefield (USNM); Grange Hill (Goodfriend); Mt. Pleasant; Orange Hill (both USNM); Retreat; Sweetwater; Waterwheel (all ANSP). *St. Elizabeth:* Luana Spring (MCZ); near Black River (USNM).

Subgenus **Despoenella** H. B. Baker

Odontostoma Orbigny, 1848. Mollusques [in] Sagra, Histoire Physique, Politique et Naturelle de l'Ile de Cuba 1:237 (type-species, *Odontostoma depressa* Orbigny, 1842, by subsequent designation H. B. Baker, 1923: 84) *non* Turton 1830 (Moll.), *nec* Agassiz 1846 (Moll.), *nec* Mörch 1852 (Moll.).

Odostoma Orbigny. Gray, 1856. Proc. Zool. Soc. London, pt. 24, p. 99, error for *Odontostoma.*

Despoenella H. B. Baker, 1923. Nautilus 36: 85 (type-species, *Odontostoma depressa* Orbigny, 1842, new name for *Odontostoma* Orbigny, 1842, *non* Turton 1830 *etc.*

Despaenella H. B. Baker. Neave, 1939. Nomenclator Zoologicus 2: 51, error for *Despoenella.*

Description. Aperture with one columellar and one parietal lamella; no palatal lamellae.

Remarks. As discussed under *Zoogeography* in the *Introduction* (*q.v.*), *Despoenella* is found in Jamaica, Cuba, and Hispaniola. Like *Proserpina s.s.*, the subgenus does not occur on the mainland. *Despoenella* probably originated in Jamaica from an ancient continental parental stock and subsequently dispersed to Cuba, and, perhaps, later to Hispaniola. In Cuba and Hispaniola, it is the only subgenus of *Proserpina s. l.* present.

5 subequal lamellae: one columellar and 2 parietal, evenly spaced, reaching to or slightly projecting beyond the apertural margin; and 2 palatal, narrower than the parietal and more widely spaced and originating somewhat inside the aperture; shells smooth; the surface weakly punctate at 50 ×, marked by fine, regularly spaced internal lineations and irregular growth lines under the surface glaze; protoconch 1½ whorls, minutely punctate, slightly raised; periostracum and operculum lacking.

Height	Width	
3.8 mm	5.7 mm	Westmoreland
3.5	5.5	lectotype of *pulchra*
3.4	4.6	Luana Spring, St. Elizabeth

Remarks. *Proserpina linguifera* with its complement of apertural lamellae clearly belongs to the nominate subgenus and is closely related to *P. nitida*, the type-species of *Proserpina*. In his original description of *linguifera* (as the synonym *pulchra*), C. B. Adams (1850: 81) expressed doubt about the distinctness of the species though indicating that a series of 30 specimens which he had at hand showed consistent differences in shell shape. In the samples available to us, *linguifera* and *nitida* may be distinguished by features which were pointed out by Pfeiffer (1850: 12). *P. linguifera* is principally smaller in size than *nitida*. Its shape is more conical and the outline of the shell higher than in *P. nitida*. Further, even in individuals only 3–4 mm in diamter, its lamellae are more strongly developed and more stout. Incidentally, the color of the spire which was mentioned by Adams (1850: 81) is no longer detectable in his specimens, a fact which lends credence to his suggestion that such coloration would bleach out upon exposure.

P. linguifera is also ecologically and geographically separated from its close relative, *P. nitida* (Map 1). Occupying a range in the extreme southwest of the island of Jamaica, *P. linguifera* is found in the hilly and less montane areas of Westmoreland and St. Elizabeth's Parish.

Trelawny: Mahogany Hall, W of Hastings, Burnthill Road (all FM); Windsor Cave (MCZ). *St. Ann:* White Cliff and Pedro River, Lillyfield; Schwallensburgh (all FM); Mt. Diablo, 1500-2600 ft. (MCZ). *St. Elizabeth:* Ipswich; Aberdeen; Redgate; Quick Step (all Goodfriend); Mt. Alta; near Bullett Hall; Balaclava Station (ANSP). *Manchester:* Bloomfield; Bloomsville Cave; Cabbage Hall; Crawl Hill, Bellfield (all FM); Cedar Hill; Comfort Hall (both ANSP); Endeavor; Calway; Heartsease; Knockpatric; Martin Hill (all FM); vicinity of Mandeville (ANSP); Spitzbergen; Topshan; Upper Lincoln (all FM). *Clarendon:* Cumberland; Spaldings, Kyle Hill (both FM). *St. Catherine:* Camperdown and Holly Mountain (both (FM). *St. Andrew:* Long Mountain (FM). *St. Thomas:* Yallahs (MCZ).

Proserpina (Proserpina) linguifera (Jonas)
Plate 10, figs. 6–7; Map 1

Helicina linguifera Jonas 1839. Wiegmann's Archiv Naturgesch. 1: 341 (Patriam ignoro).

Proserpina allognota Jonas 1846. Zeitschrift für Malakozoologie 3: 12, new name for *H. linguifera* Jonas 1839.

Proserpina pulchra Adams 1850, Contribution to Conchology No. 5: 81 (Jamaica; lectotype, MCZ 275999, selected by Jacobson and Boss 1973: 409, pl. 85, figs. 5–6).

Proserpina linguifera Jonas. Pfeiffer 1850. [in] Martini and Chemnitz, Conch. Cab. (2) 1: pt. 12, sect. 2, p. 12, pl. 103, figs. 12–15 (wahrscheinlich Jamaika).

Description. Shell reaching 5.7 mm in diameter, 3.8 mm in height, imperforate, raised discoidal, smooth, glossy; color white, spire frequently pale lemon yellow; whorls about 4-5, barely inflated, the last more than twice the width of penultimate; body whorl wellrounded, the periphery central; suture visible but barely impressed, bordered with opaque white line; umbilical area sunken; spire weakly raised, domelike, the last whorl in adult individuals shelved so that the outline of the spire does not form a straight line; aperture oblique, narrowly semilunate with

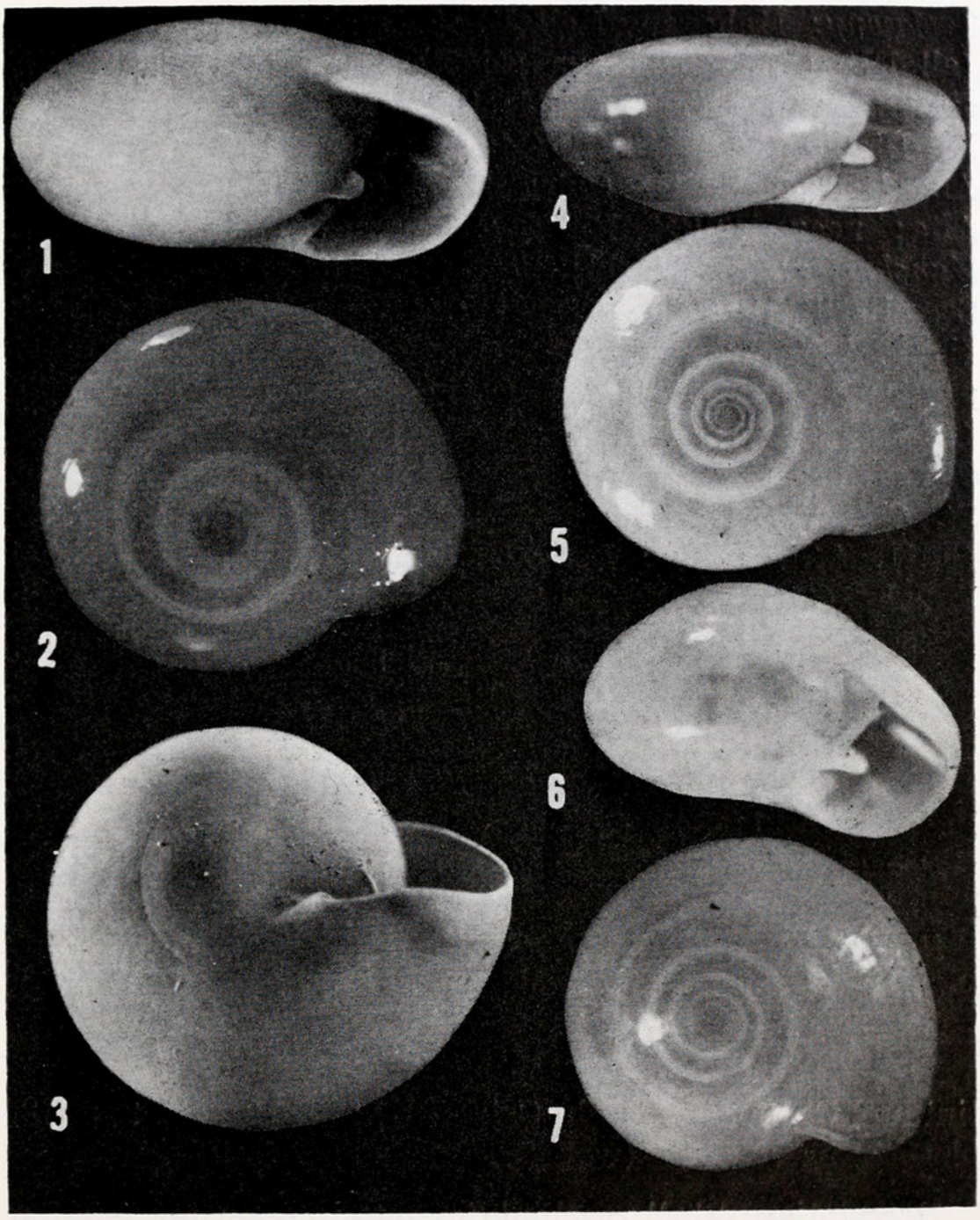


Plate 10

Figs. 1–3. *Proserpina* (*Proserpina*) *nitida* Sowerby. Windsor Cave, Trelawny, Jamaica, 8.1 mm × 3.9 mm, MCZ 94053.

Figs. 4 and 5. Lectotype of *Proserpina nitida planulata* C. B. Adams selected by Jacobson and Boss 1973: 405, pl. 85, figs. 3–4, Jamaica, 10.4 mm × 4.4 mm, MCZ 276092.

Figs. 6 and 7. *Proserpina* (*Proserpina*) *linguifera* (Jonas). Lectotype of *Proserpina pulchra* C. B. Adams, selected by Jacobson and Boss 1973: 409, pl. 85, figs. 5–6, [Westmoreland], Jamaica, 5.5 mm × 3.5 mm, MCZ 275999.

retreating centrally; sculpture of barely impressed growth lines under surface glaze; protoconch 1½ whorls, glassy, minute punctations (50 ×); periostracum and operculum lacking.

Height	Width	
4.4 mm	10.4 mm	lectotype of *planulata*
5.4	9.4	Mandeville, St. James
5.2	9.1	Windsor Caves, Trelawny
5.2	8.9	Spring Mount, St. James
4.5	7.8	Mocho, St. James

Remarks. P. nitida, the type-species of the genus *Proserpina,* is most closely related to *P. linguifera.* Both species inhabit the island of Jamaica and are characterized conchologically by the development of numerous apertural lamellae: one columellar, 2 parietal and 2 palatal. In *nitida,* these lamellae tend to be less strongly developed or thickened, especially in smaller individuals. Additionally, the uppermost of the parietal lamellae is usually set further back in the aperture. *P. nitida* is larger in overall size, has a less conic, more sublenticular shape and has a proportionately lower outline than *linguifera.* Further, the species have distinct ecological niches and geographic ranges on the island. *P. nitida* is widely distributed from around Montego Bay in St. James' Parish east to the vicinity of Yallahs in St. Thomas'. Data concerning altitudinal preferences show that the species is found principally in elevations above 1000 ft. and extending to 2600 ft. In contrast, *P. linguifera* is restricted to the southwestern portion of the island and usually lives at elevations below 600 ft. (Map 1). Baker (1934a: 63) pointed out that the species aestivates under rocks but rapidly climbs rockfaces during rains. Gloyne (1872: 45) cited the common widespread occurrence of this species and noted the existence of variations in size and color.

Specimens examined (selected). JAMAICA: *Westmoreland* (MCZ). *St. James:* Orange Hill and Spring Mt., Montego Bay (ANSP; MCZ); SE of Catadupa Station (ANSP); Mocho (MCZ); Retreat and Phoenix (FM).

Subgenus *Proserpina s.s.*

Description. Shell depressed or subglobose, with 2 or 3 parietal and 2 palatal lamellae.

Remarks. As noted in the *Introduction,* the nominate subgenus is confined geographically to Jamaica where it is represented by 2 allopatric species.

Proserpina (Proserpina) nitida Sowerby
Plate 10, figs. 1–5; Map 1

Proserpina nitida Sowerby 1839. Conchological Manual, 1 Ed., p. 124, fig. 274; 1842, 2 Ed., p. 237, fig. 274 Pfeiffer 1848, Monographia Heliceorum Viventium 1: 12 (Habitat in insula Jamaica; type, ? BMNH).

Helix Proserpina (sic) Pfeiffer 1845. Zeitschrift für Malakozoologie 2: 84 (Jamaica; type, destroyed, Clench and Jacobson 1971a: 101).

Odontostoma nitidum (Sowerby). Pfeiffer 1848. Monographia Heliceorum Viventium 1: 12.

Proserpina nitida planulata C. B. Adams 1850. Contributions to Conchology, No. 9: 174 (Jamaica; lectotype, MCZ 276092, selected by Jacobson and Boss 1973: 405, pl. 85, figs. 3–4.

Description. Shell reaching 10.4 mm in diameter, 5.4 mm in height, imperforate, depressed, polished; color very pale lemon yellow or white, apex and earlier teleoconch frequently darker; whorls 5–6, almost flat, the last one twice the width of the penultimate; body whorl narrowly rounded, almost obtusely keeled, periphery somewhat above the center; suture barely impressed, bordered by an opaque white line; umbilical area weakly sunken, translucent; spire very low to almost flat, gently and weakly rounded; aperture oblique, widely subtriangular, with 5 lamellae: a thin thick upward directed one on the columella, a thick horizontal one just above, both projecting somewhat beyond the apertural margin, and a third, still higher in the aperture and more deeply set in the body whorl, and a thin basal and palatal lamella beginning somewhat within the aperture; outer lip entire, slightly thickened, somewhat

tents British Museum, ed. 42, p. 129, 153, *non Proserpinus* Hübner 1816 (Lepidoptera).

Procerpena Gray, 1847. Proc. Zool. Soc. London, pt. 15, p. 182, cited as misprint for *Proserpina.*

Despoena Newton, 1891. Systematic List British Oligocene and Eocene Mollusca in the British Museum, p. 255, new name for *Proserpina* Sowerby 1839, *non* Hübner 1816.

Description. Shell ranging from 3 to 10 mm in diameter, imperforate, globose to depressed, smooth and polished; suture perceptible but barely impressed, umbilical region moderately sunken; aperture with one to 3 parietal denticles or lamellae and with zero to 2 palatals; outer lip thin, entire, usually retreating centrally.

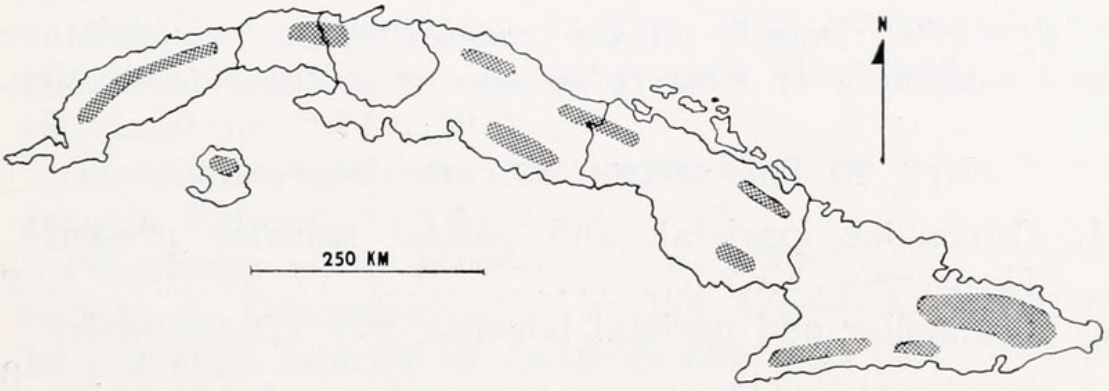
Remarks. Details on the zoogeography, nomenclature and subgenera of *Proserpina* appear in the *Introduction.*

Key to Proserpina s.s. and Despoenella

1. Columellar, parietal, and palatal lamellae present (*Proserpina s.s.*) 2
   Columellar and parietal lamellae only (*Despoenella*) 3
2. Shell larger, diameter to 10 mm, somewhat depressed, apertural lamellae less strongly developed .... *nitida*
   Shell smaller, diameter to 6 mm, somewhat globose, apertural lamellae more strongly developed. . *linguifera*
3. Shell depressed 4
   Shell globose 6
4. Shell larger, diameter to 8 mm; Cuba ..... *depressa*
   Shell smaller, diameter to 5 mm; Jamaica and Hispaniola 5
5. Proportionately less postembryonic growth; Jamaica ..... *bidentata*
   Proportionately greater postembryonic growth; Hispaniola ..... *marcanoi*
6. Slightly smaller size, diameter to 5 mm; profile lower; Cuba ..... *globulosa*
   Slightly larger size, diameter to 6 mm; profile higher; Jamaica ..... *pisum*

globulosa has reached the Isle of Pines while *depressa* has not.

The distinctive ranges of both species of Cuban *Despoenella* lend credence to the following hypothesis: the Cuban species of *Despoenella* were derived from Jamaica by hurricane borne propagules, which in becoming separated from the mother stocks in Jamaica, speciated and spread widely in Cuba. During the Pleistocene, they became locally extinct or contracted their ranges to emergent refugia (Map 4) as did some reptiles (Schwartz, 1970) and possibly such other helicinids as *Alcadia, Idesa* and *Hjalmarsona* (Boss and Jacobson, 1973b: 315-318), leaving disjunctive populations in Pinar del Río, Oriente, and the



Map 4. Pleistocene refugia in Cuba (modified from Schwartz 1970).

Isle of Pines. Apparently *globulosa* was derived from *pisum* of southwestern Jamaica earlier than Cuban *depressa* was from *bidentata* of the montane regions of northeastern Jamaica. Considering the distances involved, it is most probable that the invasion took place from Jamaica to Oriente.

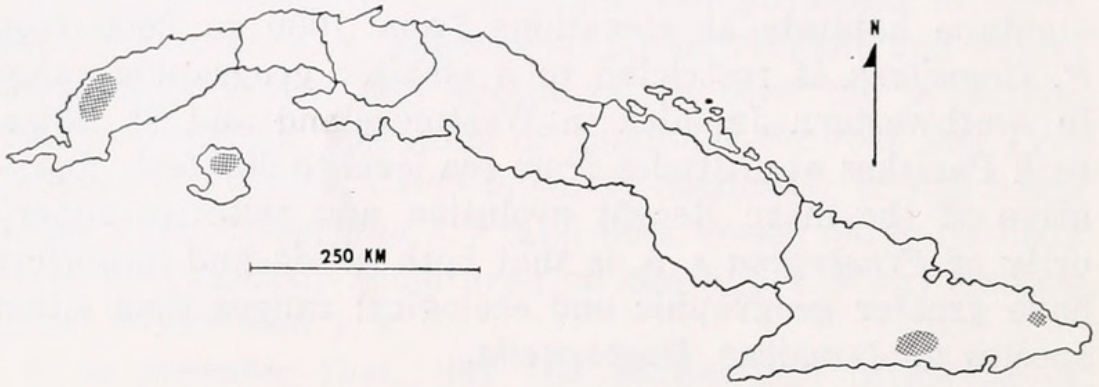
Family HELICINIDAE Latreille, 1825

Subfamily PROSERPININAE Gray, 1847

Genus **Proserpina** Sowerby

Proserpina Sowerby, 1839. Conchological Manual, 1st Ed., p. 124, fig. 274 (type-species, *Proserpina nitida* Sowerby 1839, by monotypy); Gray, 1840. Synopsis Con-

species, *P. depressa* occupies a similar range, including Oriente, Pinar del Río and Habana Provinces but excluding the Isle of Pines (Map 3).

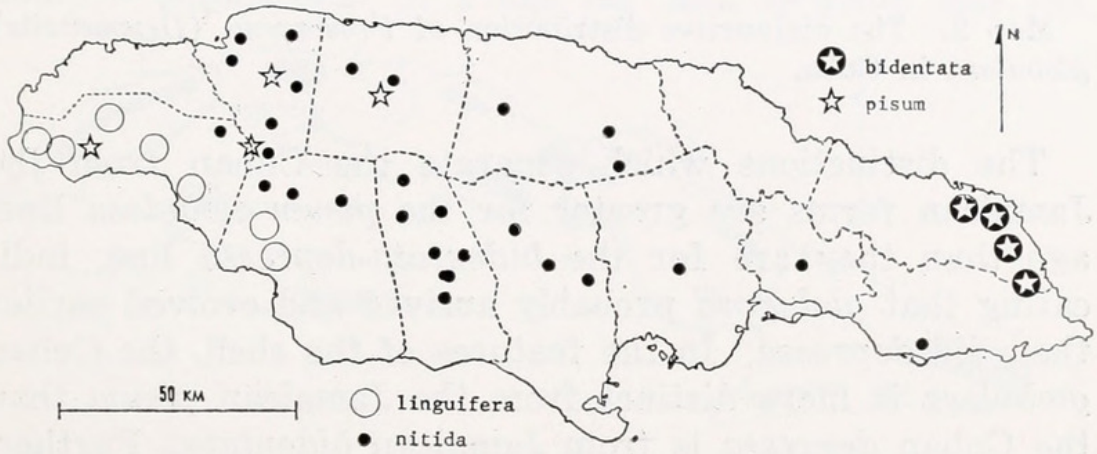


Map 2. The disjunctive distribution of *Proserpina* (*Despoenella*) *globulosa* in Cuba.

The distinctions which separate the Cuban from the Jamaican forms are greater for the *pisum-globulosa* lineage than they are for the *bidentata-depressa* line, indicating that *globulosa* probably arrived and evolved earlier than did *depressa*. In the features of the shell, the Cuban *globulosa* is more distinct from the Jamaican *pisum* than the Cuban *depressa* is from Jamaican *bidentata*. Further, zoogeographic fact supports the supposition of *globulosa's* earlier arrival and evolution. Having had longer to expand geographically, an older invading stock should have a greater range, even after the exigencies of the Pleistocene. This assumption is apparently true in this case since *P.*

Map 3. The disjunctive distribution of *Proserpina* (*Despoenella*) *depressa* in Cuba.

The species are allopatric and have distinct ecological niches in Jamaica. *P. nitida* has a wider distribution extending from the vicinity of Montego Bay in the northwest to St. Thomas' Parish in the southeast and it lives in more montane habitats at elevations from 1000 to 2600 feet. *P. linguifera* is restricted to a smaller geographic range in southwestern Jamaica in Westmoreland and St. Elizabeth Parishes at altitudes from sea level to 600 feet. Indicative of the more Recent evolution and selective superiority of *Proserpina s. s.* is that both *nitida* and *linguifera* have greater geographic and ecological ranges than either species of Jamaican *Despoenella.*



Map 1. The distribution of the 4 Jamaican species of *Proserpina. P. linguifera* and *P. nitida* belong to the nominate subgenus *Proserpina* while *P. bidentata* and *P. pisum* belong to *Despoenella.* The species of each subgenus are allopatrically distributed.

Both Jamaica and Cuba have two representative species of the subgenus, *Despoenella.* On Jamaica (Map 1), the globose species, *P. pisum* is geographically restricted to the western end of the island occurring in, as far as is known, the Parish of Westmoreland, St. James and Trelawney. While the eastern portion of the island, especially in the John Crow Mountains of Portland Parish, harbors *P. bidentata.*

In Cuba, the two species of *Despoenella* have disjunctive distributions which are very similar. The globose species, *P. globulosa* occurs in Pinar del Río and Isle of Pines in the west and Oriente in the East (Map 2) ; the depressed

Hispaniola and Cuba while *Proserpina s. s.* appears to have evolved autochthonously in Jamaica to a more specialized condition with a fuller complement of 5 apertural lamellae.

Thus, the similarity of apertural configurations in *Ceres* and *Proserpina s. s.* appears to be convergent and represents advancement and specialization over the primitive, weakly protected apertures of *Linidiella-Staffola* and *Proserpinella.* Further, *Ceres* is surely dissimilar in size being larger than *Proserpina s. s.* and both keeled along its body whorl and radially sculptured on the upper whorl surface unlike *Proserpina s. s.*

It is probable that, like the mammalian invasions of South America which have taken place principally since the closure of the Isthmus of Panama in the Pliocene just a few million years ago, the South American proserpinine snails are relatively new arrivals. All of them are referable to the primitive *Linidiella-Staffola* lineage having just a single apertural lamellae on the columella. There has probably not been time for a multiply lamellate form to have arisen in South America.

The distribution of the Proserpininae in the West Indies is more restricted than most other groups of the Helicinidae, especially such genera as *Alcadia, Lucidella* and *Helicina s. s.* Only two subgenera, *Proserpina s. s.* and *Despoenella* represent the proserpinine lineage in the Greater Antilles, including 2 species on Cuba, 4 on Jamaica and 1 on Hispaniola. The fact that the subfamily is restricted to 3 of the 4 Greater Antilles and does not occur on Puerto Rico or any of the Lesser Antilles seems to suggest a relatively late arrival of the group from the mainland. Unfortunately, no definite time-scale can be postulated for either the arrival of a proserpinine propagule on Jamaica, which was the center of the Antillean radiation in proserpinines, or the subsequent invasions of the group in Cuba and Hispaniola.

Proserpina s. s. is represented by two species, *P. nitida* and *P. linguifera,* both of which arose on the island of Jamaica (Map 1), probably from a *Despoenella*-like precursor which already had at least 2 apertural lamellae.

serpinella. The Mexican *Ceres* has a total complement of 6 denticles: 1 columellar, 2 parietal, and 3 palatal. The West Indian groups are divisible into *Proserpina s.s.* limited to Jamaica, with 5 lamellae: 1 columellar, 2 parietal and 2 palatal; and *Despoenella* in Jamaica, Hispaniola and Cuba, all with 2 lamellae: 1 columellar and 1 parietal.

Without any substantive fossil evidence, the zoogeographic and phyletic relationships of the Proserpininae must be based on inferential evidence and assumption. Zoogeographically, the West Indies are essentially receivers of immigrants from the mainland areas of North-Central America and South America. As Darlington with his own emphases surmises (1938: 288): "I think it is safe to conclude . . . that the Greater Antillean fauna is an *accumulation* of immigrants, not a *residue* of a larger fauna." Occasionally West Indian propagules have invaded Florida or the Bahamas (*e.g.*, *Lucidella tantilla*, Boss and Jacobson 1974 a: 23) or have radiated within the Antilles themselves.

Phylogenetically, it may be assumed that the loss of the operculum in the Proserpininae was a specialization diverging from the fundamental prosobranchiate structure of the Helicinidae, specifically, and the Neritacea, in general. The elaboration of apertural lamellae may be considered a further specialization so that the ultimate in their development is the elaboration of numerous lamellae, a condition reached in *Proserpina s.s.* with 5 lamellae and *Ceres* with 6. The stem, or most primitive, proserpinine stock, on inferences both geographic and phyletic, must be the lineage comprising *Linidiella*, *Staffola* and *Proserpinella* of Mexico and South America, each with only a single lamella, be it columellar or parietal.

One line of this primitive stock gave rise to *Ceres* with its full complement of lamellae and another to the Antillean representatives including both *Proserpina s. s.* and *Despoenella*. Of the Antillean representatives, *Despoenella* is the more primitive and older, having two apertural lamellae and a wider geographic range, including Jamaica,

TABLE I

The species and generic units of the Proserpininae (for more specific data on the nomina, see Boss and Jacobson 1975).

1. Ceres Gray (Spire sculptured, not glossy; 6 denticles).

eolina Duclos	Mexico
salleana Gray	Mexico
nelsoni Dall	Mexico

2. Proserpina s. s. Sowerby (Parietal, columellar, and palatal lamellae present).

nitida Sowerby	Jamaica
linguifera Jonas	Jamaica

3. Despoenella Baker (Parietal and columellar lamellae only).

bidentata C. B. Adams	Jamaica
pisum C. B. Adams	Jamaica
depressa Orbigny	Cuba
globulosa Orbigny	Cuba
marcanoi Clench	Hispaniola

4. Staffoia Dall (Heavy columellar lamella only).

blandiana H. Adams	Peru
cousini Jousseaume	Ecuador
orbignyi Ancey	Bolivia
derbyi Dall	Bahia, Brazil

5. Linidiella Jousseaume (Thin columellar lamella only).

swifti Bland	Venezuela
cinnamomea Sykes	Ecuador
sulfureus Thompson	Chiapas, Mexico

6. Proserpinella Bland (Shell fragile, parietal denticle only).

berendti Bland	Mexico
hannae Dall	Tres Marías Ids., Mexico

tural lamellae have a place in such an arrangement, being referable to the subfamily Proserpininae.

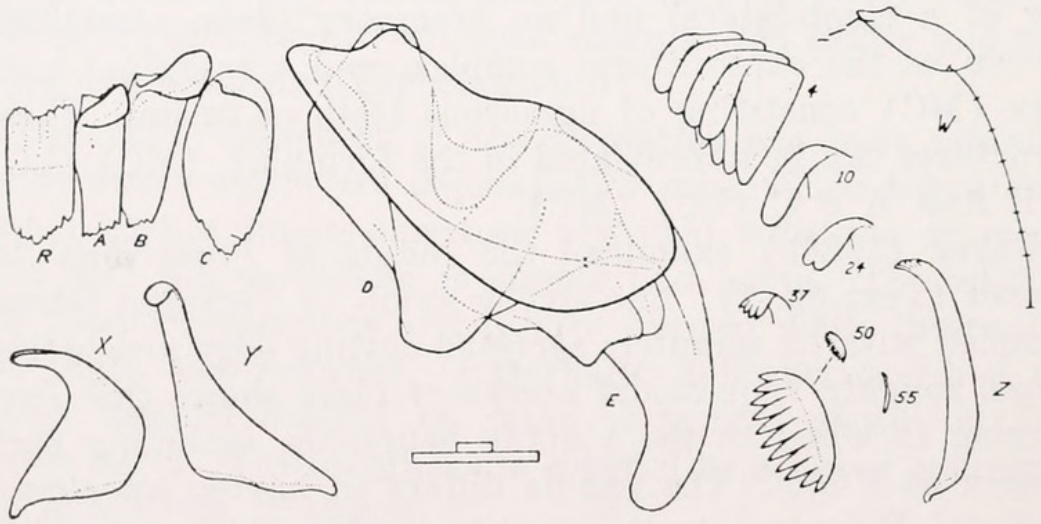
Gray (1856) figured the radula of *Ceres salleana* from Cordera, Vera Cruz, Mexico, showed it to be typically rhipidoglossate, and was followed by Troschel (1857: 84, pl. 6, fig. 2). Although Gray stated that the teeth were unlike *Helicina*, further investigations have shown that the radula of *Ceres* is indeed very similar to *Helicina* (Baker, 1922). Baker (1926b) went so far as to suggest that the radula which Gray figured was a *Helicina* rather than a *Ceres*. That the original shell specimen of *Ceres salleana* was not a *Helicina* is indicated by Gray's statement that his specimen lacked an operculum. Evidently, as Baker suspected, there was some sort of mixup at the time of Gray's description since the figure provided by Gray is more like *Helicina* and rather unlike *Proserpina* in that the A- and B- centrals are cusped, the lateral complex (which is mounted in reverse position in Gray's figure) multiply cusped, the innermost uncinus tricuspid and the next 10-11 bicuspid. The cusped nature of these teeth is similar to what is found in several species of *Helicina* while. with the exception of some outer marginals, *Proserpina* does not have multiply cusped cardinals, laterals or inner marginals. As Baker (1926b: 461) suggested: "if Gray's figure be even approximately correct, *Ceres* would belong in a different family [i.e. subfamily, according to the present system], from *Proserpina*, as it would evidently be derived from a quite different helicinid stock."

Zoogeography

The Proserpininae (Table 1) are solely New World in distribution with four groups occurring on the mainland in Mexico and South America and two other groups in the Greater Antilles, with the exception of Puerto Rico, in the West Indies. The groups are mainly distinguished by the development of apertural teeth. Most of the mainland forms have a single apertural denticle, on the columella in *Linidiella* and *Staffola* and on the parietal surface in *Pro-*

longer to about the 12th tooth. The outer marginals are narrow and elongate (ligulate), the outermost with broad, reflected tips and numerous cusplets. The A-, B-, and C-central teeth are otherwise similar to those of the vianine helicinids with simple, heavy, cutting edges.

Baker (1926b: 451) noted a remarkable resemblance of the radula of *Proserpina depressa* from Cuba to *Calybium mouhoti* Pfeiffer from Indo-China which he had studied earlier (Baker, 1922: 59, 64, pl. 6, fig. 29). *Calybium*, by its radular structure, also shows affinities with such West Indian genera as *Viana* and *Eutrochatella*. Further, *C. massiei* Morlet, which is related to *C. mohouti*, has parietal lamellae and a degenerate, linear, horny operculum, for which reason Morlet (1892: 326) took it to be an intermediate form between *Eutrochatella* and the Proserpininae. The Paleocene *Dimorphoptychia arnoudii* (Michaud) from outcrops near Rheims, France may by its shape and aper-



Text-figure 1. The radula of *Proserpina depressa*. Diagram (W) in upper right hand corner represents positions of highly refractive backs of teeth in right half of a transverse row. Both scales represent lengths of 50 microns (.05 mm); upper one is for diagram (W), lower one for remainder of drawings. In detailed figures, intervals between R and A, between B and C, and between C and D are increased so as to free edges of teeth. Block of first 4 marginals (foreshortened), and tips of 10th, 24th, 37th, 50th (also shown enlarged), and 55th (cusps omitted) are oriented simply with respect to long axis of ribbon. X is an isolated second marginal; Y probably about the 25th; Z probably about the 40th (after Baker 1926b).

time seemed to cover the shell only partially, leaving the central portion and the apex frequently uncovered. Baker (1934b) added the following remarks on the animals: "In *P. nitida* Swby., *P. linguifera* Pfr. (*sic*) and *P. bidentata* C. B. A. [the mantles] are yellowish green with black maculations, but in *P. pisum* C. B. A. are bright green. The foot, which is similarly colored, is very long, slender and carinate; progression is relatively rapid and is mainly accomplished by lateral, snake-like undulations, although some vague movement appears to take place in the very narrow middle zone of the sole. The animals are very active; when disturbed, they quickly draw in the mantle-flaps and lash their tails back and forth with remarkable strength for small snails."

The radula. The radula of *Proserpina* exhibits the essential rhipidoglossate features of a helicinid (Troschel, 1857): a single central rachidian tooth (R), flanked by A-, B-, and C-centrals and a lateral complex (LC) consisting of a comb-lateral and an accessory plate, sometimes known as the capituliform complex, and a marginal complex (MC) consisting of numerous teeth or uncini. These structures can be abbreviated in the formula: (MC) (LC) C B A R A B C (LC) (MC).

Baker (1926b) examined the radula of *Proserpina depressa* (Text-fig. 1). The strong anvil- or T-shaped lateral complex with its minutely serrated cutting edge and rather large, roughly rhomboidal accessory plate shows that *Proserpina* is allied to the vianine helicinids, including such genera as *Viana*. The radula differs in having an almost vestigial R-central tooth consisting of a thin plate with parallel sides and a weakly notched anterior edge without a reflection. The A-central is more elongate and smaller and the accessory plate is relatively larger than in vianine helicinids. Additionally, the A-central is smaller than the B-central which is just the reverse in the vianine taxa.

The first 22 uncini are unicuspid, the innermost tooth being broadly triangular, basally thickened, twisted posteriorly and reflected at the upper angle. The teeth increase in length from the inside outwardly and the blades become

in its own monotypic subfamily, the Dimorphoptychinae (Wenz, 1938; Keen, 1960).

These taxa and the inclusive species are appended in the following paper (Boss and Jacobson, 1975).

Morphology

General anatomy. No thorough anatomical study of any member of the Proserpininae has been published and only two reports on radulae have appeared. The general prosobranch and helicinid affinities were indicated by Gray (1856) and followed by Pfeiffer (1859). The animal possesses a mantle capable of some extension about the shell but without lateral membraneous fringes or "beards" typical of neritids. Only two subulate tentacles are present on the head, and the sessile eyes, not set on separate peduncles, are on the outer bases of these tentacles. The proboscis is short, broad and annulated. The foot is short, anteriorly truncated, dorsally keeled, and pointed posteriorly. Respiration is facilitated by an open vascularized cavity and the sexes are separate (gonochoristic).

The shell. Members of the Proserpininae have spirally coiled shells which are depressed to subconic in shape and which have a lunate aperture provided with one or more lamellae; the peristome is simple and acute. The whorls are totally contiguous and tightly pressed while internally the septa are resorbed. Externally a highly polished or glossy enamel coating or wash is typical except in the genus *Ceres*. The umbilicus is covered by a heavy callosity. An operculum is absent.

The mantle. The mantle in the Proserpininae is unique in its extension and covering of the shell. Jacobson (1956: 3) observed that the mantle of *P. nitida* of Jamaica, when the animal is active, completely covers the shell, an observation made previously by Baker (1934b: 151) who also noticed the same characteristic in other Jamaican proserpinines: *linguifera* Jonas, *bidentata* C. B. Adams and *pisum* C. B. Adams. Jacobson explained that in the case of *P. depressa* of Cuba, however, the mantle at any one

Keen (1960) utilized two subfamilies, Proserpininae for *Proserpina* and *Despoenella,* and the Proserpinellinae for *Proserpinella, Ceres* and *Linidiella.*

Unfortunately, as has been shown, there has been little consensus of opinion concerning the suprageneric taxa of the Helicinidae. Many different subfamilial and even tribal nomina have been used. For example, in 1922 Baker listed 2 subfamilies, but in 1926 he employed 3 and later he (1956) reverted to two subfamilies with 5 tribes in one and 3 in another. The original subfamilial units introduced by Wagner (1907-1911) have seldom, if ever, been employed subsequently. Recently, Thompson (1967) recognized the group as the family Proserpinidae but shortly thereafter considered it as a tribe, the Proserpinini (Thompson, 1968). A thorough review of the various subfamilies of the Helicinidae and their usages being improper to the scope of this paper, we have utilized the taxon Proserpininae as a distinct subfamily, much as the early application of this nomen as a familial unit (Gray, 1847; Pfeiffer, 1857).

The Proserpininae may be defined as follows: Helicinid prosobranch terrestrial gastropods having a depressed to subconic shell which is usually exceptionally glossy and smooth, being covered with an enamel-like polished coating or wash, and over which the mantle may completely or partially extend. Peristome simple and acute; aperture lunate with one or more lamellae, be they either columellar, parietal or palatal. Umbilicus covered with a callous deposit; septa of inner whorls resorbed. Operculum none. Radula rhipidoglossate, very similar to other helicinids (e.g. *Viana*) but with central teeth somewhat reduced.

According to this definition, the following generic and subgeneric nomina are included in the Proserpininae: *Ceres, Chersodespoena, Cyane, Despoena, Despoenella, Linidiella, Odontostoma, Proserpina, Proserpinella,* and *Staffola.* If the radular structure of the European Paleocene *Dimorphoptychia* were known, it might well be referable to this subfamily; however, at present it remains

Systematic Position

The true placement of *Proserpina* with the Helicinidae was suggested by Orbigny (1842: 237) when he wrote that *Odontostoma* (=*Proserpina*) was closer to *Helicina* because of the "encroûtment columellaire" and probably formed "le passage entre les deux familles, Helicidae et Helicinidae." He doubtfully referred the genus to the family Cyclostomidae. In 1847, Gray recognized the phylogenetic affinities of *Proserpina* by establishing the distinct unit, the family Proserpinidae, and placing it in association with the Oligyridae [= Helicinidae], a procedure which he followed subsequently (Gray, 1857) as did Poey (1854) and H. and A. Adams (1856). Such an arrangement was arrived at by a further knowledge of the anatomy of the animal and the structure of the shell. In a personal communication from Shuttleworth in Basel, Gray was informed that *Prosperpina* had two subulate tentacles with subsessile eyes at their outer bases, a prosobranch feature. Further, as in *Helicina* and other genera, notably the Auriculidae [= Ellobiidae = Melampidae], *Proserpina* absorbs the walls of the whorls internally (Bland, 1858). Pfeiffer (1848; 1850; 1853; 1859) placed the group in the Helicidae or in juxtaposition with the Ellobiidae or Auriculacea (1856; 1857). Later (1876) he grouped the genera *Ceres, Proserpina, Proserpinella* and *Cyane* as the Proserpinacea in the prosobranchs, relating them to the Helicinidae.

Newton (1891) erected the family Despoenidae with prosobranchiate placement on his new name *Despoena*, an unnecessary replacement name for *Proserpina*.

Wagner (1905-1911) did not treat *Proserpina* as a member of the Helicinidae but Thiele (1929) and Wenz (1938) both recognized a helicinid subfamily, the Proserpininae, for *Proserpina, Ceres, Cyane* and *Proserpinella*. Earlier for *Proserpina* and *Ceres*, Thiele (1925) had introduced the subfamilial nomen, Cererinae, which is synonymous with the Proserpininae.

The name *Proserpina* was first introduced by G. B. Sowerby II (1839: 124, fig. 274) when he published the binomen *Proserpina nitida* and a recognizable figure. Under the International Code of Zoological Nomenclature (1964), this constitutes sufficient indication both for the genus and its type-species. In 1842, Sowerby repeated the name (p. 237) and the figure (fig. 274) and stated that this was "a small shell belonging to the Helix tribe, to which, it is believed, Mr. Gray has applied the name *Prosperpina nitida*. We do not know how the genus is defined." Earlier, listing the species in *Helicodonta*, he (1839: 124) had also thought the species had affinities with the pulmonate helicids. Gray had indeed used the name *Proserpina* in 1840 (pp. 129, 153, or 125 and 149), also placed in the Helicidae, and subsequently misspelled as *Procerpena* (Gray, 1847: 182), but Sowerby's published figure and binomen has priority, notwithstanding that several authorities have credited it to Gray or even Guilding.

Odontostoma was introduced by Orbigny in 1842 for the two Cuban species of *Proserpina* but since that name is preoccupied by Turton 1830, H. B. Baker (1923) substituted the name *Despoenella*, with *O. depressa* Orbigny as type-species. The misspellings, *Odostoma* and *Despaenella* are errors in Gray (1856) and Neave (1939), respectively.

Newton (1891), supposing that *Prosperpina* Sowerby 1839 was preoccupied by *Proserpinus* Hübner 1816, introduced the substitute name *Despoena*. But since *Proserpina* is not really preoccupied, *Despoena* falls into synonymy.

Proserpina nitida is the type-species of *Proserpina* by monotypy (Sowerby 1839, p. 124). Gray (1847: 182) incorrectly selected *Helicina linguifera* Jonas as the type-species, a procedure in which he was followed by several authors including Wenz (1938: 448). It is clear that the designation is incorrect and subsequent to that of Sowerby, but, fortunately, the generic characteristics of both *P. linguifera* (= *pulchra* C. B. Adams) and *P. nitida* are the same, so that no serious problem was created.

As in the previous series of papers on the Helicinidae, especially of Cuba (*e.g. Viana, Priotrochatella, Emoda, Glyptemoda, Calidviana, Ustronia, Troschelviana, Semitrochatella* (Clench and Jacobson, 1968; 1970; 1971 a & b) and *Ceratodiscus, Alcadia,* and *Lucidella* (Boss and Jacobson, 1973 a; 1973 b; 1974 a), we herein treat the species of the Greater Antilles and add remarks on the mainland forms. As in the case of our study of *Lucidella* (Boss and Jacobson 1974 b) we append a list of all the nominal taxa of the Proserpininae.

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Abbreviations

ANSP — Academy of Natural Sciences, Philadelphia
MCZ — Museum of Comparative Zoology, Cambridge
USNM — National Museum of Natural History, Washington
FM — Field Museum, Chicago

Historical Remarks

Proserpina has a complicated nomenclatorial history. The correct authorship of the genus, the valid designation of a type-species, the introduction of unnecessary substitute nomina and the exact familial placement of the genus contribute to this complexity.