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LITTORINIDAE



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THE GENUS LITTORINA IN THE WESTERN ATLANTIC

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The Littorines, or periwinkles, are littoral snails, chiefly herbivorous and normally living near or between the high and low tide marks. Where several species occur in one locality each usually prefers certain types of marine algae, on which it feeds mainly. The intertidal zonation of the northern species has been a favorite topic of study, but does not seem to follow definite rules (J. Colman 1933, Jr. Marine Biol. Assoc. Un. Kingdom, 18, pt. 2, pp. 435-476). When the tide goes out the animal withdraws in the shell and may remain dry and exposed to the sun for many hours. Some species, which live out of water for weeks or months, breathe atmospheric air (P. H. Fischer, M. Duval and A. Raffy 1933, Arch. Zool. Exp. Gén., 74, fasc. 31, p. 629). Many species adhere to rocks, stones or pile-work: a few occur on mud-flats, particularly where there is good drainage, being sometimes common in salt-marshes: and some of the tropical ones live in mangrove swamps, preferably on the roots, branches and leaves of the trees. Periwinkles are a favorite food of many shore birds, particularly ducks.

Littorina Férussac

Paludina subgenus Littorina Férussac 1822, Tabl. Syst. Gén. Moll., p. xxxiv (no description or species; defined on p. xi, where the French vernacular "Littorine" only is used, as containing the marine Paludinae placed by Adanson in Trochus; on p. ix, four such species are listed, without combining them with Littorina, the specific names being those of Gmelin: obtusatus, neritoides, littoreus and muricatus). Genotype by designation of de Blainville (1828, Dict. Sci. Nat., 56, p. 98; only French vernacular "Littorine" used here): Turbo littoreus Linné, 1758, one of the species originally included (see Winckworth 1922, Proc. Mal. Soc. London, 15, p. 95).

Turbo subgenus Littorina "Férussac" de Blainville 1825, Faune Française, Malacozoaires, p. 297 (with definition and species). Genotype by designation of de Blainville (1828): Turbo littoreus Linné, 1758, one of the species originally included.

Litorina "Férussac" Menke 1828, Synopsis Meth. Moll., pp. 24 and 25 (emendation of Littorina). Type by designation of H. Suter (1913, Man. New Zealand Moll., p. 186): Turbo littoreus Linné, 1758, one of the species originally included.

Bucalia "Gray" H. and A. Adams 1854, Gen. Rec. Moll., 1, p. 312 (as a synonym of Littorina). Type by designation of Winckworth (1922): Turbo littoreus Linné, 1758, one of the species originally included. [Gray 1840, Contents Brit. Mus., 42d Ed., p. 147; nomen nudum].

Isonema "Hall" Provancher 1891, Faune Canadienne, Moll. Québec, p. 91 (as a synonym of Littorina; type by present designation: Turbo littoreus Linné, 1758). Not Isonema Meek and Worthen, 1865.

Littorina section Algaroda Dall 1918, Proc. Biol. Soc. Washington, 31, p. 137. Type by monotypy: Turbo littoreus Linné, 1758.

Opinion 46 of the International Commission on Nomenclature seems to cover the case of *Littorina* Férussac. If, however, it were ruled on some technicality that Férussac (1822) cannot be credited with the name, it will date from de Blainville (1825), which will in no way affect its proper use, the genotype remaining the same. A. S. Kennard (1942, Proc. Mal. Soc. London, 25, pt. 3, p. 116) considers that Férussac did not define *Littorina*, but this is open to argument. He regards B.C. Payraudeau's generic definition (1826, Cat. Descr. Ann.

Moll. Corse, p. 114) as the first in date, unaware of de Blainville's earlier definition of 1825. As Payraudeau did not designate his *Littorina basterotii* as the genotype, but merely described it as a new species in the genus, de Blainville's type designation of *Turbo littoreus* in 1828 seems to be the first valid one.

Lithorina Hartmann (1840), Litormia Mörch (1849), Littorrina Gabb (1861), Litorinna Dall (1884), and Littornia Jenkins and Grocock (1891) are misspellings of Littorina.

Shell elongate or rounded turbinate, subglobose, conical, or conico-turriculate, usually rather thick. Spire of few whorls. A deciduous periostracum in some species. Surface either smooth or with spiral engraved lines or grooves, rarely more strongly ribbed or wavy, but never tuberculate; axial sculpture restricted to growth-striae. Aperture entire, ovate or subcircular; outer edge of columellar area continuous with basal lip; outer lip very oblique in profile, simple, sharp-edged, often thickened within. Umbilical slit present in the adult of a few species, more often present in the young and closed later, sometimes absent at all stages. Operculum horny, with a laterally placed, paucispiral (2 or 3 coils, as a rule) nucleus and a low process attaching it to the foot. Animal with one pair only of slender, tapering tentacles; eyes unstalked or on globular expansions at outer bases of tentacles; foot obtuse behind, divided lengthwise, each side progressing alternately; operculigerous lobe without filamentary processes. Radula very long; in *L. littorca* 50 mm. long (twice the length of the animal's body), with some 500 cross-rows of teeth. Oviparous or ovoviviparous. Sexual dimorphism more or less pronounced in the shell.

The 9 species recognized from the western Atlantic may be placed in 5 groups, here given subgeneric rank for convenience, although they do not seem to be of fundamental or phylogenetic importance. The mode of reproduction being known for few species, it is impossible to judge to what extent it is correlated with shell characters.

Littorino, proper, includes snails with a thick, turbinate shell, slightly convex or flattened whorls, a moderately high, pointed spire, and a short, curved inner columellar edge. The type, L. littorea, is oviparous (see under that species). L. irrorata Say also is placed here.

The subgenus Littorivaga Dall (1918, Proc. Biol. Soc. Washington, **31**, p. 137) comprises snails with a thick, turbinate shell, decidedly convex whorls, a moderately high, pointed spire, and a short, curved inner columellar edge. The type is Littorina sitkana Philippi, 1846 (= Litorina sitchana Philippi, 1847, author's emendation). Of our species, only L. saxatilis Linné, an ovoviviparous snail, belongs here.

The subgenus Melarhaphe Menke (1828, Synopsis Meth. Moll., p. 23; monotypic for Melarhaphe glabrata Menke = Turbo neritoides Linné, 1758) comprises snails with a moderately thick, ovate-conical to ovate-turriculate shell, flattened or convex whorls, a high pointed spire, and a long, straightened columellar inner edge. The type species, at first believed to be ovoviviparous, has now been shown to be oviparous, with a pelagic stage similar to that of L. littorea (O. Linke 1935, Zool. Anz., 112, pp. 57-62. M. V. Lebour 1935, Jr. Mar. Biol. Assoc. Un. Kingdom, 20, pp. 373-378). Melarapha Cristofori and Jan (1832), Melaraphis Philippi (1836), Melarhaphis Agassiz (1845), Melaraphe H. and A. Adams (1854), Melarhophe Hall (1867), Melarpha Paetel (1875), Melanorhaphe O. Boettger (1885) and Melarrhaphe v. Martens (1897) are emendations or misspellings of Melarhaphe. Two western Atlantic species belong here: L. nebulosa Lamarck and L. ziczac Gmelin.

The subgenus Neritrema Récluz (1869, Actes Soc. Linn. Bordeaux, ser. 3, 7, pp. 43 and 46; for six species, including Turbo obtusatus Linné, 1758, designated as type by W. H. Dall 1909, U.S. Geol. Surv., Prof. Pap. 59, p. 79) contains subglobular or low-conical snails, with slightly raised spire, a more or less distinct periostracum, a short, concave inner columellar edge, and at least traces of a columellar slit either in the young or in the adult. The type species is oviparous. Neritotrema Wenz (1939, Handb. Paläozoologie, 6, Gastropoda, pt. 4, p. 518) is an emendation. Neritoides T. Brown (1827, Illustr. Conch. Great Britain Ireland, Pl. 43, figs. 14-22, with letterpress; name also on p. iv of Index; monotypic for Neritoides littoralis T. Brown, 1827 = Turbo obtusatus Linné, 1758) is a synonym, the name being antedated by Neritoides Meuschen (1779, Der Naturforscher, 13, p. 85; based on a naticid). I refer to this group the western Atlantic L. meleagris Potiez and

¹ Rang (1829, Manuel Hist. Nat. Moll., p. 185) designated as type of *Littorina*, *Nerita littoralis* Linné, 1758 = *Turbo obtusatus* Linné, 1758; but he had been anticipated by de Blainville (1828), a fact overlooked by Dall and others.

Michaud and L. mespillum v. Mühlfeld, which have at least in the adult an umbilical slit, often as pronounced as in Lacuna. The thick shell and type of markings are, however, as in Littorina, where their nearest relative seems to be L. obtusata. The latter has an umbilical slit in the young, but not in the adult.

The subgenus Littoraria J. E. Gray (in Griffith and Pidgeon 1834, Cuvier's Anim. Kingdom, 12, p. 598 and pl. 1, fig. 3; monotypic for Littoraria pulchra Gray = Littorina pulchra Sowerby, 1824) comprises rather thin, fair-sized snails, with a high, conical, pointed spire, and a long, excavated columellar area, straightened at the inner edge. They are peculiar to tropical and subtropical brackish water. Littorinopsis Mörch (1876, Malak. Blätt., 23, p. 135; type by original designation, Phasianella angulifera Lamarck, 1822, misspelled "subangulata" by Mörch) is a synonym. The only western Atlantic species, L. angulifera, is closely related to the Indo-Pacific L. scabra Linné, which is known to be ovoviviparous.

Aquilonaria turneri Dall, 1886, placed by Tryon in a section of Littorina, is now considered one of the Lacunidae. Littorina adamsii Reeve, 1857 (= L. pulchella "C. B. Adams" Reeve, 1857; not of Dunker, 1845) belongs in Trochidae. Littorina ziczac litterata "Phil.," of some Florida lists, is a fictitious name. Littorina aspera was listed from Mariguana Id., Bahamas, by oversight (W. J. Clench 1937, Proc. New England Zoöl. Club, 16, p. 61).

Littorina littorea Linné, Plate 1, figs. 1-11

Turbo littoreus Linné 1758, Syst. Nat., 10th Ed., 1, p. 761 ("in the European Ocean, common on the coasts of Norway"). Hanley 1855, Ipsa Linnaei Conchylia, p. 326 (type).

Litorina litorea Menke 1828, Synopsis Meth. Moll., p. 25 (emendation of littorea).

Synonymy. This is fully given by P. Dautzenberg and H. Fischer 1912, Rés. Camp. Scientif. Prince de Monaco, 37, pp. 181-187. Littorina communis W. Thompson (1856; not of T. Brown, 1843) is an additional synonym not mentioned by them.

Description. Shell regularly turbinate, higher than wide, thick, opaque, dull, of 7 to 8 gradually increasing and rather flattened whorls: upper part of whorls somewhat concave below the coarsely crenulate, but weak suture: on the body-whorl of adult shells this may become a shallow groove near the mouth: body-whorl about $\frac{2}{3}$ of total height. A light yellowish-brown periostracum, usually lost in the adult: sculpture, when preserved, of many low, irregularly spaced spiral ridges, with finer wavy wrinkles in the intervals, and cut by extremely fine, axial growth-striae. Spire high, more or less pointed, often corroded or destroyed by a worm ($Polydora\ concharum\ Verrill$). Aperture subcircular: outer lip slightly flaring, sharp-edged, smooth within, its upper edge ascending and ap-

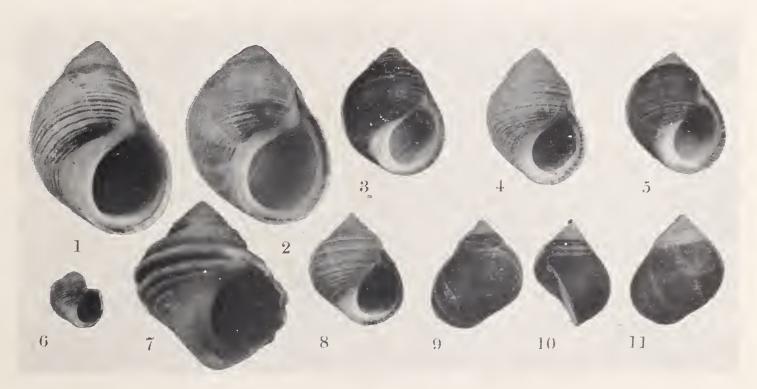


Plate 1. Littorina littorea Linné: 1 and 2, Grand Manan, New Brunswick: 3, Stonington, Connecticut: 4, Salmon Bay, Labrador: 5, Neptune City, New Jersey: 6, Woods Hole, Massachusetts (abnormal): 7, Isle-au-Haut, Maine (young, 8×); 8 to 11, Falmouth, Massachusetts. All, except 7, nat. size.

pressed against the body-whorl, forming a shallow groove within; columellar area broad. thick, slanting inward, smooth, rapidly narrowed at the base, margined outwardly by a sharp but low ridge which merges with the bow-like or rounded-angular basal lip; young shells more angular at the base of the columella; no trace of umbilical depression or pit at any stage. Color fairly constant in America, usually a bistre-gray, the ridges often pale brownish or the shell with dark brown bands; in Europe sometimes entirely reddishorange; mouth within pale chocolate-brown, with whitish outer and basal edge, which is more or less spotted with reddish-brown; columella whitish; operculum yellowish-brown or dark mahogany. Oviparous, as first recognized by W. Clark (1850, Ann. Mag. Nat. Hist., ser. 2, 5, p. 362): from 1 to 9 (usually 2 or 3) eggs enclosed in a chitinous, transparent capsule, which floats away; a first stage ciliate larva (troehosphere) is followed by a second swimming stage (veliger), which produces the shell-bearing, erawling young (M. Tattersall 1908, Irish Naturalist, 17, p. 238; 1920, Fisheries, Ireland, Scientif. Invest., No. 1, pp. 1-11, 1 pl. Caullery and Pelseneer 1910, Bull. Scient. France Belg., 44, pp. 357-360, pl. 9, figs. 1, 2, 5, 6, 9-11). Whorls more convex and aperture relatively larger in female than in male.

length	width aperture	
32.4	$24.5 22 \times 15.8 \text{ mm}.$	Conception Bay, Newfoundland
42	$28.6 26 \times 20.4$	Eastport, Maine
41.5	$28 21.4 \times 17$	Salem, Massachusetts
24.2	$19 17.4 \times 12.5$	Branford, Connecticut
22.7	$19 16.5 \times 13.8$	Neptune City, New Jersey

The largest European shell seen (Clyde, Scotland) is 38 mm. long.

Type. Linné's type is at the Linnaean Society of London. The type locality is Norway.

Range. Coast of western Europe (including the British Isles and the Baltic Sea) from the White Sea (Russia) to the Straits of Gibraltar. Spitzbergen. Not alive in the Mediterranean, specimens reported from there being from ship's ballast. Not positively known to live in Iceland and Greenland, O. Fabricius' (1780) supposed littorea being saxatilis. The few specimens found in Iceland may be subfossil (G. Thorson 1941, Zoology of Iceland, 4, pt. 60, p. 34) or more probably were dumped with ship's ballast.

Introduced by the agency of man on the North American coast of the Atlantic about a century ago and now well established from southern Labrador to southern New Jersey (W. F. Ganong 1886, Amer. Natural., 20, pp. 931-940). It is not known whether the introduction was accidental or intentional. It has not been found fossil nor in Indian shell-heaps. It was unknown to the early American malacologists, not being listed by A. A. Gould (1841, Invertebrates of Massachusetts), J. W. Mighels (1843, for Maine) and J. H. Linsley (1845, for Connecticut). J. W. Dawson stated that he found it at Pictou, Nova Seotia, as early as 1840 (W. F. Ganong 1887, Amer. Natural., 21, p. 287) and E. S. Morse received it in 1855 from Bathurst, Bay of Chaleur, in the Gulf of St. Lawrence (1881, Bull. Essex Inst. for 1880, p. 176). About 1857, however, it was first reported in print by John Willis from Nova Scotia (1860, Proc. Ac. Nat. Sci. Phila., p. 148; 1890, Proc. Trans. Nova Scotian Inst. Nat. Sci., 7, p. 417). From Nova Scotia it spread rapidly southward, its pelagic early stages being carried in the plankton by the Labrador Current. In 1861 or 1862 it occurred in the Bay of Fundy near St. John, New Brunswick (W. F. Ganong 1890, Bull. Nat. Hist. Soc. New Brunswick, 9, p. 47). By 1879 it had reached Connecticut (A. F. Gray 1879, Science News, 1, p. 111; a reprint,

dated April 15, 1879, has added information). Prime found it at Lloyd's Neck, Long Island, in 1881, and Hollick at the Narrows of Staten Island in 1888 (S. Smith 1888, Proc. Nat. Sci. Assoc. Staten Id., 1, part for Jan. 14, p. 61; empty shell; first alive in 1893, see W. T. Davis 1893, op. cit., 3, part for Sept. 9, p. 50). W. A. Stearns collected it in southern Labrador in 1882 (K. Bush 1883, Proc. U.S. Nat. Mus., 6, p. 240). J. Ford reported it in 1892 (Nautilus, 6, p. 27) from Atlantic City. Jeffreys' (1869, Brit. Conch., 5, p. 206) record from "Mexico," after a specimen in the British Museum, was either due to an error in labelling or based on a shell picked up from ship's ballast.

As recognized by Dautzenberg and Fischer (1912), Littorina squalida Broderip and Sowerby (1829, Zool. Journ., 4, p. 370; "boreal Ocean." Gray 1839, Zool. Beechey's Voyage "Blossom," Moll., p. 139, pl. 34, fig. 12; "Icy Cape," Alaska) is the representative, or perhaps subspecies, of L. littorea on the Arctic coast of Alaska, in the Behring Sea, Kamchatka and northern Japan.

Records. Labrador: Salmon Bay. Newfoundland: Conception Bay: Cape Norman; etc. Quebec: Percé Rock; Bonaventure Id. New Brunswick: Grand Manan. Prince Edward Id. Nova Scotia: South Joggins. Cape Breton Id. Maine. Rhode Island: Westerly. Connecticut: Stonington; Branford. New York: Pelham Bay; Oyster Bay, Long Island; Oakwood Beach, Staten Island (W. T. Davis). New Jersey: Neptune City, Monmouth Co.: Atlantic City; Cape May (N. J. State Mus.).

Remarks. L. littorea varies little, particularly in North America, where it is as large as in Europe. Dautzenberg and Fischer (1912) thought that Newfoundland specimens were unusually large, but some British shells are about the same size. H. C. Bumpus (1898, Zool. Bull., 1, pp. 247-259, 14 charts) attempted to show that the species had become more variable in America, being more elongated, lighter, more bulky, and with less pronounced color markings. These differences are slight and not apparent. Moreover, Bumpus' measurements were probably vitiated by the corrosion of the shells (R. P. Bigelow and E. P. Rathbun 1903, Amer. Natural., 37, pp. 171-184).

This periwinkle is a favorite food in Europe and sometimes eaten also in New Brunswick, Nova Scotia and New England (C. W. Johnson 1904, Nautilus, 18, p. 47. W.F. Ganong 1889, Bull. Nat. Hist. Soc. New Brunswick, 8, p. 45). In England pearls have been found in it a few times.

L. littorea prefers rocks and pilings of the lower intertidal zone, near mean sea level, where it thrives in sea-water and is only partially exposed at extreme low tides: but in New England it also occurs on shallow muddy bottoms and among the roots and blades of Zostera, even in water that is only moderately salty (W. J. Clench 1930, Nautilus, 43, p. 105). The habits were studied in New Brunswick by J. N. Gowanloch and F.R. Hayes (1926, Contrib. Canad. Biol. Fish., New Ser., 3, pp. 133-166; 1929, ibid., 4, pp. 413-430). C. H. Batchelder noted that it migrates in early winter 25 to 30 ft. from its summer habitat, to shallower but ice-free basins (1915, Nautilus, 29, p. 45). In parts of Europe it is popularly believed to anticipate changes in weather, moving to higher levels (above high tide mark) before a storm. Its herbivorous habits are sometimes made use of to keep parked oysters free of algal growth. W. T. Davis kept a L. littorea alive from Nov. 23, 1930, to April 1, 1932, in a corked bottle of sea-water with a piece of Ulva lactuca on which it fed (1931, Proc. Staten Id. Inst. Arts Sci., 6, pp. 41, 48 and, 1932, p. 185).

Littorina irrorata Say, Plate 2, figs. 1-7

Turbo irroratus Say 1822 (July?), Jr. Ac. Nat. Sci. Phila., 2, pt. 2, p. 239 (eastern shore of Maryland; coast of Carolina, Georgia, Florida and New Jersey).

Phasianella sulcata Lamarck 1822 (August), Hist. Nat. An. Sans Vert., 7, p. 54 ("coasts of Carolina"). Delessert 1841, Recueil Coq. Lamarck, pl. 37, figs. 13a-b, with letterpress (type).

Littorina lunata H.C. Lea 1845 (March), Proc. Boston Soc. Nat. Hist., 1, p. 205 (Cape May, New Jersey); 1845, Boston Jr. Nat. Hist., 5, pt. 2, p. 287, pl. 24, fig. 3 (type).

Littoriua sayi Reeve 1858, Conchol. Iconica, 10, Littoriua, pl. 17, figs. 96a-b, with letterpress (Florida). Not L. sayi Philippi, 1846.

Littorina carolineusis Conrad 1863, Proc. Ac. Nat. Sci. Phila. for 1862, p. 567 (Pliocene of North Carolina); 1875, Geol. Rept. North Carolina, 1, Appendix, p. 23, pl. 4, figs. 10-11 (types).

Littorina irrorata var. carolinensis M. Smith 1936, Nautilus, 49, p. 136, pl. 9, fig. 1.

Synonymy. T. irroratus and P. sulcata were published about the same time. Lamarck's book is dated "August 1822"; while pt. 2 of vol. 2 of Jr. Ac. Nat. Sci. Phila. was for June 1822 (according to the heading on p. 193). Mörch (1876) believed this to be the actual date of publication; but p. 251 (of this part 2) starts a paper "read July 26, 1822." It seems advisable to adhere to established custom and use Say's name for the species. There is no difficulty about recognizing a young irrorata in Lea's L. luuata.

Description. Shell elongate conical, much higher than wide, thick, opaque, dull, of 8 to 10 gradually increasing, flat whorls; early whorls lost in adult; suture weak, smooth, except behind outer lip of adult, where it is coarsely crenulate. Body-whorl about $\frac{1}{2}$ of total height, rounded at periphery. Surface without periostracum, even in the smallest shell seen (4.5 mm. high); first 3 whorls (lost in adult) apparently smooth; on the 4th traces of spiral engraved lines appear, which become stronger on the succeeding whorls; body-whorl of adult with regularly spaced shallow grooves, separating narrow, low, spiral ridges; uppermost ridge, at suture, wider than the others and slightly ascending; growthstriae very fine, usually obsolete. Spire high, pointed. Aperture pear-shaped; outer lip meeting the body-whorl at a narrowly acute angle, slightly flaring, the edge sharp but slightly wavy or grooved within; farther back the inside is smooth and more or less thickened; inner lip with a strong smooth callus over the body-whorl. Columellar area rather narrow, thick, slanting inward, smooth, even, rapidly narrowed to the basal lip, margined outwardly by a blunt ridge which is somewhat folded back over the much narrowed base of the body-whorl and merges evenly with the bow-like basal lip; no trace of umbilicus at any stage. Color slightly variable, grayish-white, with a bluish tinge in the young, usually with blotches or short streaks of dark purple or reddish-brown on the spiral ridges, rather irregular in young shells, evenly spaced in older shells, often lacking or barely visible. Mouth white or yellowish-white within; outer lip inside with short, hor-



Plate 2. Littorina irrorata Say: 1 and 2, Boca Ciega Bay, Florida; 3 and 4, Pass-a-Grille, Florida; 5, Galveston, Texas; 6, Taunton River, Massachusetts (from Indian shell-heap); 7, Anglesea, New Jersey. All nat. size.

izontal, dark purple streaks, which disappear in very old shells; callus of inner lip and columella pale reddish-brown, fading toward the base; operculum dark mahogany-brown. Reproduction unknown.

length	width	aperture	
29.4	21.3	16.6×12 mm.	Boca Ciega Bay, St. Petersburg, Florida
26	17	15.5×11.5	Little Choptank River, Maryland
24	16.8	15.8×11.9	Cape May, New Jersey
22	16.2	14×11	Galveston, Texas

Types. Say's types of irroratus could not be traced; the type locality is here defined as Little Choptank River, Maryland. The type of P. sulcata is at the Geneva Museum and that of L. lunata should be at USNM, where it is not available at present.

Range. Southeastern United States, from Long Island, New York, to Florida (as far south as Indian River in the East and Charlotte Harbor in the west); on the Gulf of Mexico as far west as Point Isabel, Cameron Co., Texas (north of mouth of Rio Grande; H. B. Stenzel 1940, Nautilus, 54, p. 20). Not taken in Mexico, Central and South America. Very few records from the Antilles, perhaps all based on dead shells, from ballast. Known fossil from the Upper Miocene and Pliocene of North Carolina, South Carolina and Florida, and from the Pleistocene of Louisiana and Texas.

There is no reliable evidence that L. irrorata lives nowadays in New England, all published records from there being before 1880: Stratford, Connecticut ("on high sedge": J. H. Linsley 1845, Amer. Jr. Sci., 48, p. 284); New Haven ("not at all common"; G. W. Perkins 1869, Proc. Boston Soc. Nat. Hist., 13, p. 125); Vineyard Sound and Long Island Sound near New Haven (A. E. Verrill, S. I. Smith and O. Harger 1873, Rept. U.S. Comm. Fish. for 1871-1872, p. 651). H. F. Carpenter saw no specimen in Rhode Island, although he included it in his Catalogue (1885, Random Notes Nat. Hist., 2, p. 46; 1889, Cat. Shell-Bearing Moll. Rhode Id., p. 2). Some of these records may have been based on living snails; others refer to fossils washed up by the waves from old deposits or shell-heaps; and Verrill suggested that in some cases L. irrorata had been brought in with southern oysters. A. Gould (1841) never saw it alive from Massachusetts. It is certain, however, that it was fairly abundant within historic times as far north as Cape Cod. It was reported from an Indian rock-shelter at New Haven (MacCurdy 1914, Amer. Jr. Sci., ser. 4, 38, p. 517). J. B. Knight (1933 Amer. Jr. Sci., ser. 5, 26, pp. 130-133) found it in post-Pliocene deposits underlying a salt-marsh near Branford, Connecticut (one at MCZ received from H. G. Richards), and in Indian shell-heaps nearby. A specimen at the MCZ (Fig. 6) was taken by Mr. R. C. Athearn from an Indian shell-midden at Barnaby's Cove on the Taunton River, Freetown, Massachusetts. Near New York City it was first reported by J. E. DeKay (1843, Zool. New York, 5, Moll., p. 106, pl. 6, figs. 112a-b; "at Harlem, clinging to the stems of salt grass"); later also from Long Island by S. Smith and T. Prime (1870, Ann. Lyc. Nat. Hist. New York, 9, p. 393; "Huntington and Rockaway; a few dead shells were found in the grass above high water mark"), and from Staten Island by S. Smith (1886, Proc. Nat. Sci. Assoc. Staten Id., 1, for June 12, p. 35; 1887, 1, Extra No. 5, p. 50). Mr. Roy Latham informs me that he found a few living specimens near the eastern end of Long Island as late as 1933, but that the species is very rare there. The dying out of L. irrorata at the northern edge of its range may be due to a change in climate for the colder, for which there is a certain amount of evidence (H. M. Raup 1937, Jr. Arnold Arboretum, 18, pp. 79-117).

L. irrorata does not occur in the Pacific. Reeve's irrorata (1857, Conchol. Iconica, 10, Littorina, pl. 11, figs. 56a-b), supposedly from Sitka, Alaska, was L. aspera Philippi, of the Pacific coast of Central America.

Records. New York: Orient, Long Island (R. Latham). New Jersey: Cold Spring Harbor near Wildwood; Anglesea; Cape May. Maryland: Bishop's Head, Dorchester Co.; Little Choptank River. Virginia: Norfolk: etc. North Carolina: Roanoke Id. South Carolina: Charleston. Georgia: St. Simon's Id. Florida: common, as far south as Indian River in the east and Charlotte Harbor in the west. Alabama: Mobile. Mississippi: Cat Id., off Pass Christian: Biloxi. Louisiana: Bayou du Lac: Empire. Texas: Port Aransas; Swan Lake, Galveston. Cuba: Matanzas (3 shells coll. by Sprague; possibly brought in ballast). Hispaniola: Monte Cristi (1 shell collected by Clench, Russell and McLean, 1937; possibly brought in ballast).

Remarks. L. irrorata lives in the brackish water of salt marshes, on grass-stems and around their roots, near and above the high tide mark, often climbing the grass. It is remarkably uniform throughout its range, in shape as well as in color. It could only be confused with L. nebulosa tessellata, which has a different columella and a very convex body-whorl, shouldered at the periphery.

I agree with W. H. Dall (1892, Trans. Wagner Free Inst. Sci., 3, pt. 2, p. 321) that the fossil specimens from the Carolinas and Florida are not separable from Recent ones. Some snails collected alive at Beaufort, North Carolina, are as slender as the fossil figured by M. Smith.

Littorina saxatilis Olivi, Plate 3, figs. 1-10

Turbo suxatilis Olivi 1792, Zool. Adriatica, p. 172, pl. 5, figs. 3a-d (Gulf of Venice, Italy).

Turbo rudis Maton 1797, Observations Nat. Hist. Antiq. Western Counties, 1, p. 277 (Devon, England) [reference checked by H. G. Richards]. Donovan 1800, British Shells, 1, pl. 33, fig. 3.

Turbo davidis "Bolten" Röding 1798, Mus. Bolten., 2, p. 88 (defined by reference to Chemnitz 1781, Syst. Conchy. Cab., 5, pl. 185, figs. 1855a-b, from the Faroë Ids.).

Turbo jngosns Montagu 1803, Test. Brit., 2, p. 586; 1808, Supplement, pl. 20, fig. 2 (Dorsetshire and St. Ives in Cornwall, England).

Turbo tenebrosus Montagu 1803, Test. Brit., 2, p. 303; 1808, Supplement, pl. 20, fig. 4 (Devonshire and Kent, England).

Turbo obligatus Say 1822, Jr. Ac. Nat. Sci. Phila., 2, pt. 2, p. 241 (Portland, Maine).

Turbo vestita Say 1822, Jr. Ac. Nat. Sci. Phila., 2, pt. 2, p. 241 (Maine).

Litorina groenlandica Menke 1830, Synopsis Meth. Moll., 2d Ed., p. 45 (defined by the reference to Chemnitz 1781, Syst. Conchy. Cab., 5, pl. 185, figs. 1855a-b, from the Faroë Ids.).

Littorina nigrolineata J. E. Gray 1839, Zool. Beechey's Voyage "Blossom," Moll., p. 140 (no locality: with description and reference to Chemnitz 1781, Syst. Conchy. Cab., 5, pl. 185, figs. 1854 and; doubtfully, figs. 1855. Dautzenberg and H. Fischer restricted the name to figs. 1854a-b, from the coasts of Europe).

Littorina castanea Deshayes 1843, in Lamarck, Hist. Nat. An. Sans Vert., 2d Ed., 9, p. 206 ("northern seas").

Litorina incarnata "Lovén" Philippi 1846, Abb. Beschr. Conch., 2, p. 103 (Greenland; as a synonym of the red variety of L. groenlandica Menke).

Littorina tenebrosa var. costulata Middendorff 1849, Mém. Ac. Imp. Sci. St. Pétersbourg, ser. 6, Sci. Nat., 6, pts. 5-6, p. 389, pl. 8, figs. 6-8; [1849, Beiträge Malac. Rossica, 2, p. 61, pl. 8, figs. 6-8] (no locality, but evidently from the Arctic coast of Russia; with Turbo obligatus Say and Litorina groenlandica Menke as synonyms).

Synonymy. Only names used for North American shells are listed. For the many Old World synonyms, see P. Dautzenberg and H. Fischer 1912, Rés. Camp. Scientif. Prince de Monaco, 37, pp. 187-201. The following should be added to their list: Litorina macerwinii "Thompson" Philippi (1846), Littorina simplex Reeve (1857), Littorina danieli Locard (1886) and Littorina radis var. alticola Dacie (1917).

Description. Shell turbinate to conical, variable in shape, usually much higher than wide, moderately thick, opaque, dull, of 6 to 8 gradually increasing and convex whorls; suture deep, even or rugulose; body-whorl nearly $\frac{1}{2}$ to $\frac{2}{3}$ of total height. Surface of young with a thin yellowish-brown, minutely wrinkled periostracum, usually lost in the adult, often corroded; sculpture very weak or almost lacking in young and small shells; in larger ones low and broad, rather regularly spaced spiral ridges, which are wider below the periphery; in adult shells they tend to disappear behind the outer lip; the intervals with minute spiral striation; growth-striae very weak; sometimes some of the ridges much stronger, forming widely spaced, sharp ribs. Spire high, pointed. Aperture subcircular; outer lip not flaring, sharp-edged, smooth within and a little thickened some distance from the edge, horizontal or somewhat descending at the body-whorl; columellar area broad, thick, slanting inward, smooth, gradually narrowed to the basal lip, margined outwardly by a sharp ridge, much produced below the base of the body-whorl; in the male, obtusely angular where it meets the bow-like basal lip; a weak umbilical groove outside the edge of the columella in young but no trace of this in adult. Color variable; adult usually a uniform yellowish or brownish-gray, sometimes more reddish or orange-gray, occasionally with one or more spiral white bands, or gray with one or more black or dark purple bands; sometimes the pale bands irregularly interrupted, producing blotching or tessellation; mouth within usually bright reddish-brown, gradually paler toward the edge; columella whitish, pale brown, or dark purple; operculum pale or dark brown. Ovoviviparous; eggs producing shell-bearing, crawling embryos in a brood sac at the lower end of the oviduct. Male smaller than female, with a longer spire in proportion to the body-whorl, and a narrower aperture, somewhat angular at the basal edge.

The largest European shell seen (Brest, France) is 24.3 mm. long and 17.5 mm. wide.

lengtli	width	aperture	
18.3	15.5	13×11.6 mm.	St. Andrews, New Brunswick
18	12	9.5×9.5	Stonington, Connecticut

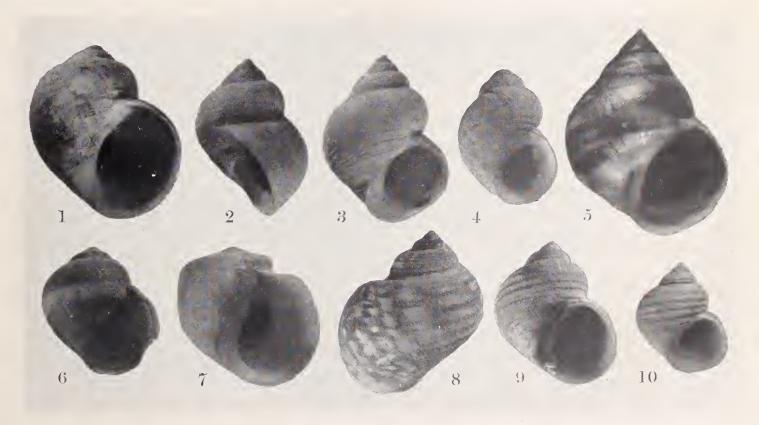


Plate 3. Littorina saxatilis Olivi: 1 and 2, Stonington, Connecticut: 3, St. Andrews, New Brunswick: 4 and 9, Perry, Maine; 5, Isleboro, Maine (young, 8×); 6 to 8, Grand Manan, New Brunswick (7, abnormal); 10, Kennebunk, Maine. All, except 5, nat. size.

Types. Types of savatilis and rudis probably lost. That of castanea may be at the British Museum, as well as those of Montagu's tenebrosus and jugosus. Say's types of obligatus are at the Ac. Nat. Sci. Phila. (No. 18387); those of vestita could not be traced.

Range. Mainly boreal and arctic. In Europe from Nova Zembla (probably even farther east on the coast of Sibcria) and Spitzbergen to the Azores, in the British Isles, the Baltic, the western Mediterranean (Adriatic, Tunisia, etc.) and the Black Sea. Faroë Ids. Iceland. Greenland. Autochthonous in North America from Cape Barrow in Coronation Gulf, 68° 4′ N., 111° W. (W.H.Dall 1919, Rept. Canad. Arctic Exp. 1913-18, 8, pt. A, p. 16), Southampton Id., Hudson Bay, southern Baffin Land (at the Arctic Circle; J. Oughton 1940, Nautilus, 54, pp. 1-6) to southern New Jersey. It is known from Pleistocene deposits in Quebec (J. W. Dawson 1893, Canadian Ice Age, p. 249) and from post-Pliocene deposits underlying a salt-marsh near Branford, Connecticut (J. B. Knight 1934, Amer. Jr. Sci., ser. 5, 28, p. 172). G. F. Matthew (1892, Bull. Nat. Hist. Soc. New Brunswick, 10, p. 23) reports it from Indian shell-heaps at Bocabec, New Brunswick. Published records from the Pacific coast of America, Alaska and Japan were probably all based on forms of L. sitchana Philippi, the Pacific representative, or perhaps subspecies, of L. savatilis. Jeffreys' British Museum specimen (1869, Brit. Conch., 5, p. 206) from Mexico was either wrongly labelled or a shell from ship's ballast.

Records. Greenland: Proven; Frederikshaab; Evigtut. Ontario: Hudson Bay. Labrador: Indian Harbor; Main. Newfoundland: Port Saunders; etc. Quebec: Bonaventure Id.; Gaspé; etc. Nova Scotia: South Joggins; etc. St. Pierre-et-Miquelon. Maine: common. New Hampshire: common. Massachusetts: common. Rhode Island: common. Connecticut: common. New York: common. New Jersey: Sea Isle City; Cape May (N.J. State Mus.).

Remarks. Some of the variations in size, shape, sculpture and color of the proteiform L. saxatilis pass into one another and may be found together under the same conditions: others seem to be due to the direct action of the environment. This was first recognized in England by W. Clark (1850, Ann. Mag. Nat. Hist., ser. 2, 5, pp. 362-364). There appear to be no true geographical races or subspecies. I am unable to distinguish consistently series from Greenland and Labrador (so-called var. groenlandica) from more southern lots. If desired, collectors may sort their specimens into named forms by means of the exquisite figures in Dautzenberg and Fischer's work (1912). Sexual differences are sometimes mistaken for racial ones and monstrosities are not uncommon. The oldest name for our most striking variant, with few, but very strong or sharp ridges, is var. jugosa Montagu. Say's vestita and obligatus were based upon similar shells, but with weaker ridges. More elongate, usually smoother and thinner shells, often found on the mud of brackish crecks or in salt marshes, may be called var. tenebrosa Montagu. Typical saxatilis and var. jugosa prefer rocks or small stones, near high tide mark, where they are exposed for the greater part of every day. According to C. H. Batchelder (1915, Nautilus, 29, p. 46), in northern localities L. savatilis migrates in early winter to deeper water, in order to escape the ground icc. N. R. Bouchard-Chantereaux (1836, Mém. Soc. Agrie. Boulogne-sur-Mcr for 1835, p. 154; erroneously called by him littorea) first noted that the eggs remain in the oviduct until they hatch, producing at once young, crawling snails. These are released one at the time, at intervals of several hours. The lack of a free-swimming stage is correlated with this species living habitually out of the water part of the day, and occasionally remaining dry for several days in succession. It then secretes a sticky slime, which dries up and cements the outer lip to the rock. Being ovoviviparous renders this periwinkle unfit to eat, as noted by W. Clark (1850).

Littorina nebulosa Lamarck, Plate 4, figs. 1-4

Phasianella nebulosa Lamarck 1822, Hist. Nat. An. Sans Vert., 7, p. 54 (Santo Domingo). Delessert 1841, Recueil Coq. Lamarck, pl. 37, figs. 12a-b, with letterpress (type).

Littorina columellaris d'Orbigny 1840, Voy. Amér. Mérid., 5, pt. 3, Moll., p. 392 (Pernambuco; Antilles); 1842, in de la Sagra, Hist. Phys. Pol. Nat. Cuba, Moll., Atlas, pl. 15, figs. 18-20 (binomial on plate); Text, 1, (1842), p. 213 (Martinique; Pernambuco).

Littorina tigrina d'Orbigny 1842, in de la Sagra, Hist. Phys. Pol. Nat. Cuba, Moll., Atlas, pl. 15, figs. 9-11 (binomial on plate); Text, 1, (1842), p. 211 (Havana; Guadeloupe).

Littorina sayi Philippi 1846, Proc. Zool. Soc. London for 1845, p. 140 ("Florida"); 1847, Abb. Beschr. Conch., 3, p. 12, pl. 6 (Litorina), fig. 11 (type).

Litorina exarata Philippi 1848, Abb. Beschr. Conch., 3, p. 63, pl. 7 (Litorina), fig. 8 (no locality).

Litorina angulifera var. minor Weinkauff 1878, Syst. Conchy. Cab., 2, Abt. 9, p. 39 (with nebulosa Lamarck as synonym).

Synonymy. Tryon regarded Lamarck's nebulosa as a variety of L. scabra; but Delessert's figure of the type is certainly L. columellaris. I agree with Weinkauff that Philippi's sayi was this species, not irrorata; the type locality was probably erroneous, as nebulosa is not definitely known from Florida. Tryon supposed that L. tigrina might have been tessellata (here regarded as a form of nebulosa); but, as d'Orbigny's figure does not show the shouldering at the periphery of the body-whorl nor the spotting of the outer lip characteristic of tessellata, I refer it to typical nebulosa.

Description. Shell elongate conical, higher than wide, moderately thick, dull, of 7 to 9 gradually increasing, convex whorls; early whorls lost in adult; suture well marked, smooth or very slightly crenulate behind the outer lip. Body-whorl of adult about $\frac{2}{3}$ of

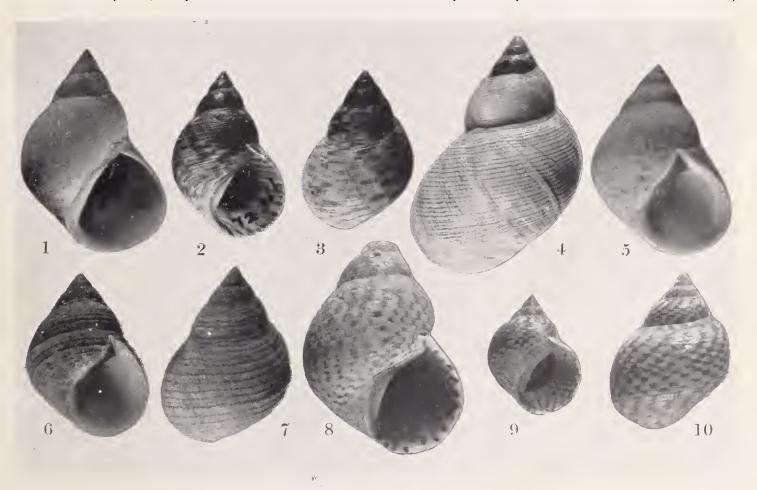


Plate 4. 1 to 4, Littorina nebulosa Lamarck: 1 to 3, Punta de los Colorados, Cienfuegos, Cuba: 4, Chagres River, Panama. 5 to 7, L. n. flava King and Broderip: 5, Proto de Iguapé, Sao Paulo: 6 and 7, La Milpa, Cienfuegos, Cuba. 8 to 10, L. n. tessellata Philippi: 8, West End, Grand Bahama Id.: 9 and 10, Jeremie, Haiti. All 2×.

total height, more convex than earlier whorls. No periostracum. First 2 or 3 whorls worn smooth; traces of spiral engraved lines on the 4th, becoming stronger on the next; on the body-whorl they are numerous, close together, rather regularly spaced, and somewhat wayy, the raised intervals much wider and flat; subsutural area somewhat depressed, with 2 or 3 deeper, more regular grooves; growth-striae strong, more or less decussating the spiral sculpture. Aperture subcircular; outer lip not flaring, the edge sharp, thin, smooth and not thickened within, meeting the body-whorl at a sharp angle; inner lip forming a very slight callus over the body-whorl. Columellar area very long and wide, slanting inward, smooth; the narrow inner edge much thickened, long and nearly straight, ending rather abruptly below, separated by a broad and shallow depression from the sharp outer edge which limits the base of the body-whorl and merges evenly with the bow-like basal lip. Depression of the columella in the position of the umbilicus and more pronounced in young shells; but even in the smallest (5.5 mm.) there is no umbilical slit. Color rather variable in youth, more uniform later; in shells up to 10 mm. long the earliest 2 or 3 whorls are fairly unicolor, pale dirty-yellow; soon white and reddish-brown speckling appears, eventually producing streaks or spots, irregularly scattered or checkered or forming jagged zigzag stripes; in the same lot some young shells may show very few spots or be uniformly dirty- or bone-yellow; spotting usually stops rather abruptly on the 6th or 7th whorl, the remainder being uniformly bone-yellow or white, often with a bluish tinge: occasionally an adult, 21 mm. long, may be blotched over part of the body-whorl. Mouth uniformly yellowish-brown to pale-purplish within; outer lip whitish; columellar area with the swollen inner edge white, the depression pale purplish-brown; operculum pale mahogany-brown. Reproduction unknown.

length	width	aperture	
24	16.2	13.8×12.6 mm.	Cienfuegos, Cuba
23	14.2	14×11.1	Colón, Panama
21	13.2	12.8×9.8	Sta. Barbara de Samana, Hispaniola
24	16.1	14×11.8	Fullerton Bay, Trinidad
21.6	14	13×10.4	Tampico, Mexico

Types. The type of nebulosa is in Lamarck's collection at the Geneva Museum. The types of d'Orbigny's columellaris and tigrina, and of Philippi's sayi and exarata may all be at the British Museum. The type locality of columellaris is herewith designated as Pernambuco and that of tigrina as Havana.

Range. Greater and Lesser Antilles, Gulf of Mexico (from Tampico southward) and Caribbean coast of Central and South America to Trinidad and the Guianas.

Records. Cuba: Matanzas; Cienfuegos; Havana; Manzanillo, Oriente; etc. Jamaica: Bowden; Kingston Harbor. Hispaniola: Sanchez; Sta. Barbara de Samana. Puerto Rico: San Juan Harbor. Trinidad: Mayaro; Moruga; Pointe-à-Pierre; Otaheite Bay; Fullerton Bay. Mexico: Tampico; Vera Cruz. Guatemala: Livingston: Puerto Barrios. Nicaragua: Waunta Haulover. Panama: Porto Bello; Chagres River; Colón (Aspinwall). Specimens at MCZ labelled "Charlotte Harbor" (west coast of Florida), probably an erroneous locality. Reported from Yucatan, Honduras, Costa Rica, Venezuela, French Guiana (Cayenne), Guadeloupe and Martinique. Dall's records from Brasil (1891, Nautilus, 5, p. 44; Sta. Catharina. 1901, Proc. Wash. Ac. Sci., 3, p. 144; Parahyba) were, I believe, based on L. n. flava.

Remarks. L. nebulosa is most commonly found attached to logs, jetties or wreckage: it seems to avoid rocks exposed to heavy surf.

Throughout most of the range of typical *nebulosa* and farther south some specimens differ rather markedly, yet agree in so many characters that they clearly belong to the same stock. I recognize two such forms by name, giving them subspecific rank, though they are perhaps not geographically segregated.

Littorina nebulosa tessellata *Philippi*, Plate 4, figs. 8-10

Litorina tessellata Philippi 1847, Abb. Beschr. Conch., 2, p. 226, pl. 5 (Litorina), fig. 26 (Martinique; new name for L. undulata d'Orbigny, 1842).

Littorina undulata d'Orbigny 1842, in de la Sagra, Hist. Phys. Pol. Nat. Cuba, Moll., Atlas, pl. 15, figs. 12-14 (binomial on plate); Text, 1, (1842), p. 212 (Martinique). Not Littorina undulata Gray, 1839.

Phasianella lineata Lamarck 1822, Hist. Nat. An. Sans Vert., 7, p. 54 (no locality). Delessert 1841, Recueil Coq. Lamarck, pl. 37, figs. 11a-b, with letterpress (type). Not Buccinum lineatum Gmelin, 1790, which is also a Littorina.

Synonymy. Lamarck's P. lineata has often been regarded as a variant of L. ziczac; but Delessert's figure of the type agrees with d'Orbigny's L. undulata, there being no trace of the inner basal band of the mouth characteristic of L. ziczac. As both Lamarck's and d'Orbigny's names conflict with earlier ones in the genus, Philippi's tessellata is the valid name.

Description. Differs from typical nebulosa in the slightly more swollen body-whorl, often obtusely shouldered or subangular below the suture and at the periphery, but without prominent peripheral rib. Spiral linear grooves more spaced, with broad and flat intervals. Brownish-red spots on a grayish-white background in a fairly regular checker pattern, tending to form oblique axial lines. White inner margin of the sharp outer lip with a series of brownish-red spots.

length	width	aperture	
22.8	16.5	12.8×9.8 mm.	Grand Bahama, Bahamas
18.3	13.6	12.5×9.9	Jeremie, Haiti

Types. The type of undulata may be at the British Museum; that of Lamarck's lineata is at the Geneva Museum.

Range. Bahamas, Antilles and the Caribbean coast of South America. Not known from Bermuda, Florida or east of Venezuela.

Records. Bahamas: Grand Bahama; Mariguana; Great Inagua; Long Island; Eleuthera; New Providence. Cuba: Cienfuegos; Caibarien; Baracoa; Sagua: Gibara; Puerto Padre, Oriente. Hispaniola: Gonave Island; Cape Haitien; Jeremie; Miragoane; Santa Barbara de Samana; Monte Cristi; Puerto Sosua. Jamaica: Port Antonio: St. Ann; Kingston Harbor. Virgin Islands: St. John. Panama: Colón. Venezuela: Guanta; Cumana. Reported from Guadeloupe and Puerto Rico.

Remarks. In color *tessellata* is sometimes much like *L.irrorata*, with which it has been confused; it differs in the shape of the columella and the very convex body-whorl.

Littorina nebulosa flava King and Broderip, Plate 4, figs. 5-7

Littorina flava King and Broderip 1832, Zool. Journ., 5, (1831) p. 345 (Rio de Janeiro). d'Orbigny 1840, Voy. Amér. Mérid., 5, pt. 3, Moll., p. 391, pl. 53, figs. 1-3.

Description. Agreeing essentially with nebulosa. Shell on the average smaller, usually broader, often little higher than wide, with the body-whorl relatively longer. Engraved

spiral lines much more spaced, their intervals often raised and more or less rib-like, particularly one at the periphery and another below this; some specimens in the same lot have the ribs very weak; but they may be pronounced even in very young shells. Outer lip with a sharp edge, but often much thickened within. Color markings, if present, of very faint, small spots; most shells uniformly dirty-yellowish or whitish, sometimes slightly orange. Columellar area extensively reddish-brown, paler at the inner edge, white over the outer edge; outer lip white and unspotted over the thickened area; mouth within pale reddish-brown.

length	width	aperture	
19.6	13.8	11.2×9.7 mm.	Cienfuegos Bay, Cuba
16.2	11	9.5×8.4	Trinidad
19.8	14.8	12×9.3	Proto de Iguapé, Brasil

Types. Probably at the British Museum, at least in part.

Range. Chiefly on the coast of eastern South America, from the Gulf of Paria to São Paulo; but by no means rare near Cienfuegos, Cuba (first recorded by C. G. Aguayo 1935, Mem. Soc. Cubana Hist. Nat., 9, p. 111). One lot from Guadeloupe in the C. B. Adams Collection (now at MCZ). Perhaps these Antillean records are due to relatively recent introductions by man.

Records. Cuba: Cienfuegos, fairly common at several localities in the bay. Guade-Loupe. Venezuela: Soldado Rock, Gulf of Paria. Trinidad: common. Tobago. Brasil: Maranhão; Pernambuco; Bahia; Ilha de Itaparica, Bahia; Praia de Itapoan, Bahia; Rio de Janeiro; Proto de Iguapé, São Paulo; Ilha do Cardoso, Cananéa, São Paulo.

Remarks. The original description was very brief: "L. testa longitudinaliter striata, sub-flava; spira brevi; anfractu basali ventricoso; columellae purpurascentis margine et apertura subflava; operculo nigricante; long. 5/8 paulo plus; lat. 7/10; poll.—In young shells there are a few obscure reddish-brown streaks crossing the striae." This was apparently based on specimens with rather weak spiral ridges, but none of the types have ever been figured. The later figures by d'Orbigny and Philippi (1847, Abb. Beschr. Conch., 2, p. 201, pl. 4 (Litorina), figs. 17) show specimens with some sharp ridges. All transitions occur between these two types, in the same lot. Pilsbry (1907, Nautilus, 21, p. 71) writes: "L. flava is very thick inside the lip, exactly like irrorata. It resembles nebulosa in color, but is evidently a distinct species close to irrorata. I have never seen L. flava from north or west of Trinidad." The thickening inside the lip is well-marked in most full-grown shells only; but in the same lot some large shells hardly show it at all. Our Cuban and Guadeloupan specimens do not differ from those of Trinidad and Brasil; but I suggest that *flava* may be a recent introduction in the Antilles by man. It is now well established in the Bay of Cienfuegos. Sometimes called *irrorata* in collections, but that species has a different columella and flattened whorls.

Littorina ziczac Gmelin, Plate 5, figs. 1-10

Trochus ziczac Gmelin 1790, in Linné, Syst. Nat., 13th Ed., 1, pt. 6, p. 3587 (no locality; based on Chemnitz 1781, Syst. Conchy. Cab., 5, pl. 166, figs. 1599a-b, from the "Zuckerinseln" in the West Indies).

Littorina zic-zak "Chemnitz" Mörch 1876, Malak. Blätt., 23, p. 137 (emendation of ziczac).

Littorina zigzag d'Orbigny 1842, in de la Sagra, Hist. Phys. Pol. Nat. Cuba, Moll., Atlas, pl. 15, figs. 5-8 (binomial on plate); Text, 1, (1842), p. 210 (Havana; Martinique; emendation of ziczac).

Littorina zigwag Arango 1880, Contrib. Fauna Malac. Cubana, p. 160 (misspelling of ziczac).

Turbo dispar Montagu 1815, Trans. Linn. Soc. London, 11, p. 195, pl. 13, fig. 4 (supposedly from Poole, England; recognized by E. Forbes and S. Hanley 1853, Hist. Brit. Moll., 3, p. 54, as not British, but probably West Indian).

Littorina lineata d'Orbigny 1842, in de la Sagra, Hist. Phys. Pol. Nat. Cuba, Molf., Atlas, pl. 14, figs 24-27 (binomial on plate); Text, 1, (1842), p. 208 (Havana; Martinique; Rio de Janeiro). Not Buccinum lineatum Gmelin, 1790, or Phasianella lineata Lamarck, 1822.

Littorina lineolata d'Orbigny 1840, Voy. Amér. Mérid., 5, pt. 3, Moll., p. 392 (Rio de Janeiro; with description and reference to Chemnitz 1781, Syst. Conchy. Cab., 5, p. 69, pl. 166, figs. 1600*a-b*, from the "Zuckerinseln" in the West Indies).

Littorina carinata d'Orbigny 1842, in de la Sagra, Hist. Phys. Pol. Nat. Cuba, Moll., Atlas, pl. 15, figs. 1-4 (binomial on plate); Text, 1, (1842), p. 209 (Havana; Martinique). Not Turbo carinatus Sowerby 1819, which is also a Littorina.

Littoriua debilis Philippi 1846, Proc. Zool. Soc. London for 1845, p. 140 (no locality); 1847, Abb. Beschr. Conch., 3, p. 11, pl. 6 (Litoriua), fig. 7 (type).

Litorina d'orbignyana Philippi 1847, Abb. Beschr. Conch., 2, p. 162, pl. 3 (Litorina), fig. 12 (Cuba; Jamaica; Mte. Christi in western Colombia [probably Hispaniola]).

Littorina orbiguyana "Philippi" G. Nevill 1885, Hand List Moll. Ind. Mus., 2, (1884), p. 139 (as a synonym of L. ziezae; emendation of d'orbignyana).

Litorina pusilla Philippi 1847, Abb. Beschr. Conch., 2, p. 164, pl. 3 (Litorina), fig. 23 (Brasil or Sandwich Ids.). Not Littorina pusilla F. M'Coy, 1844.

Litorina mauritiana var. crassior Philippi 1847, Abb. Beschr. Conch., 2, p. 165, pl. 3 (Litorina), fig. 15, only (Cuba).

Litorina columna "Jonas" Philippi 1847, Abb. Beschr. Conch., 3, p. 14, pl. 6 (Litorina), fig. 15 (no locality). Littorina cingulata ["Pfeiffer" C.B.Adams 1847, Cat. Rec. Shells Coll. C.B.Adams, p. 19 (Jamaica; nomen uudum)] Mörch 1876, Malak. Blätt., 23, p. 138 (as a doubtful synonym of L. floccosa). Not Littorina cingulata Philippi, 1846.

Littorina jamaicensis C.B. Adams 1850, Contrib. to Conchology, No. 5, p. 71 (Jamaica).

Litorina lineata var. interrupta "Adams" Philippi 1856, Syst. Conchy. Cab., 2, Abt. 9, p. 24, pl. 3, figs. 14-15 (Jamaica).

Littorina angustior Mörch 1876, Malak. Blätt., 23, p. 139 (Havana; St. Croix; St. Thomas).

Littorina floccosa "Beck" Mörch 1876, Malak. Blätt., 23, p. 138 (St. Thomas).

Littorina glaucocincta "Beck" Mörch 1876, Malak. Blätt., 23, p. 138 (St. John; listed as a variety of L. floccosa).

Littorina riisei Mörch 1876, Malak. Blätt., 23, p. 140 (Havana).

Littorina cubaua Weinkauff 1882, Syst. Conchy. Cab., 2, Abt. 9, p. 68, pl. 9, figs. 2-3 (Cuba).

Synonymy. L. ziczac, of the Antilles, has sometimes been confused with L. mauritinna Lamarck, a closely related or representative species of the Indo-Pacific. Gmelin had no specimen and gave no locality; but he referred to a figure of a West Indian shell, the "Sugar Islands" being an old name for the Windward Islands. The extensive variation in size (for the same number of whorls), shape and color, as well as the pronounced sexual dimorphism, led to a multiplicity of names. Without the types, it is not easy to recognize either L. ziezac or L. nebulosa in the published figures and descriptions. Each case was carefully studied, sometimes with results disagreeing with those of earlier authors. Male shells are often labelled L. ziezac var. lineatu, but I regard Lamarck's P. lineata as L. nebulosa tessellata and Gmelin's B. lineatum as a form of L. scabra. Montagu's T. dispar was a small, unicolor ziezac; he mentions the inner pale band near the base of the mouth.

Description. Shell with marked sexual dimorphism, elongate-conical to short-turriculate and much higher than wide in the female, broadly-conical and nearly as wide as high in the male; moderately thick, dull, of 6 to 8 gradually increasing, convex or moderately flattened whorls; summit as a rule little or not corroded, exceptionally decollate (Philippi's pusilla); suture well-marked, smooth. Body-whorl of adult slightly over $\frac{1}{2}$ of total height, much more convex than earlier whorls (particularly in male), as a rule shouldered or obtusely carinate at the periphery and, near the outer lip, somewhat depressed below the suture. In some senile shells the body-whorl uncoils partly, producing a subsutural carina below a sutural groove or channel (pl. 5, fig. 1). No periostracum. First 2 whorls

worn smooth; sculpture of remainder variable and differing in both sexes: female usually with moderately deep, engraved spiral lines, either few (10 or less) and far apart or many and close, when they may be wavy or irregular, sometimes obsolete; male more strongly sculptured, often with broad and deep spiral grooves, the intervals flat or obtusely ribbed; sculpture sometimes weaker below the periphery; peripheral shoulder either smooth, narrow or barely set off, or forming (particularly in the male) a strong and broad, blunt ridge, sharply delimited above and below; growth-striae very weak or lacking. Aperture broadly pear-shaped; outer lip not flaring, the edge sharp, thin, not thickened within, usually smooth but sometimes wavy in more strongly sculptured (male) shells, meeting the bodywhorl at a sharp angle which is often somewhat channelled inside; inner lip forming a very slight callus over the body-whorl. Columellar area moderately long and wide, slanting inward, smooth, even or barely concave; inner edge bluntly rounded, nearly straight, gradually curving at the base; outer edge weak above where it touches the body-whorl directly or with an intervening very narrow, crescent-shaped, dull lunule; farther down the outer edge is stronger, somewhat produced beyond the base of the body-whorl, either very bluntly angular or evenly rounded into the bow-like basal lip; no trace of umbilical depression or slit even in the smallest shell seen (2 mm.). Color very variable, even in the same lot; typical pattern of fine, oblique, wavy or zigzag, chestnut-brown or purplishbrown, axial lines or stripes on a white or bluish-white background; earliest whorls uniformly pale reddish-brown; the stripes vary in number and width; they may fuse over part or most of the surface, but usually leave prominent whitish spots or streaks below the suture and on the peripheral shoulder; the network pattern of Philippi's pusilla is a modification of this; finally some shells are almost unicolor chestnut or mahogany-brown, faintly paler below the suture and at the periphery, while at the other extreme the

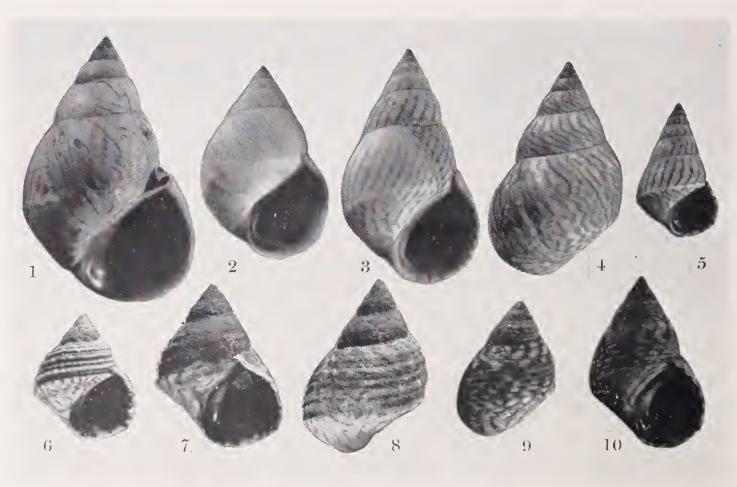


Plate 5. Littorina ziczac Gmelin: 1, Bermuda: 2 to 5, 9 and 10, Bimini Ids. (female shells): 6 to 8, Governor's Harbor, Eleuthera Id. (male shells). All 2 ×.

brown stripes may be lacking or barely visible on the nearly white or pale bluish shell. In addition, 2 or 3 pale bluish spiral bands may be discerned, particularly when the axial pattern is faded. Mouth within somewhat purplish, dark mahogany-brown, with 1 or 2 whitish spiral bands; one, close to the base, always present in larger shells and at least indicated in the young; the other, between the periphery and the suture, sometimes lacking or obliterated; outer lip white, more or less blotched with reddish-brown; columellar area either entirely mahogany or blackish-brown or with the outer edge paler; operculum dark mahogany-brown. Reproduction unknown.

	length	width	aperture	
Female	25.3	15.6	13.3×9 mm.	Bermuda _.
Male	15.8	11	9.8×7.8	New Providence, Bahamas
Female	21.4	12.2	9.6 imes7.2	Cienfuegos Bay, Cuba

Types. Barbados, one of the two so-called "Sugar Islands" cited in Chemnitz's references to Lister and Favanne, is here selected as the type locality of T. ziczac and L. lineolata; but Chemnitz's types are probably lost. The British Museum may have the types of Montagu's T. dispar, Philippi's debilis, d'orbignyana, pusilla and mauritiana var. crassior, and d'Orbigny's carinata. Mörch's types of angustior, floccosa, glancocineta and riisei should be at the Copenhagen Museum. L. columna Philippi was described from the Jonas collection, which I have not traced.

Range. Florida (south of Jupiter Inlet on the east and as far north as Cedar Keys on the west coast). Bermuda and the Antilles to Trinidad, Atlantic coast of southern Texas, Central and South America to Uruguay. Established on the Pacific coast near Panama City, which it reached by means of the Canal.

Records. Florida: common in the south; northernmost locality on the east coast, Giebert's Bar, Martin Co., just above Jupiter Inlet (P. P. McGinty), and on the west coast, Cedar Keys. Texas: Galveston. Bermuda. Bahamas: New Providence; Long Island; Grand Bahama; Cat Id.; Little San Salvador; Great Inagua; N. Bimini Id.: Great Abaco; Eleuthera; Mariguana. Cuba: Havana; Cienfuegos; Caibarien; Guantanamo. Hispaniola: Puerto Plata; Santa Barbara de Samana; Beata Id.; Puerto Sosua; Miragoane; Cape Haitien; El Canal, Cabo Macoris; Gonave Id. Puerto Rico: Borinquen; Guanica Harbor; San Juan; Aricibo; San Geronimo; Veja Baja; Ponce. Ja-MAICA: Montego Bay; Southwest Cay, Pedro; mouth of Dunn's River; St. Ann; Port Antonio. Virgin Ids.: Guana Id., Tortola: Virgin Gorda; St. Croix; St. John; St. Thomas. Lesser Antilles: Guadeloupe; Antigua; Martinique; Grenada; Barbados. Trinidad: Pointe-a-Pierre; Mayaro: Toco; Pelican Id. Caribbean Islands: Swan 1d.; Navassa Id.; Cayman Brac, Cayman Ids. Mexico: Tampico; Vera Cruz. Guate-MALA: near Cavech; Puerto Barrios. Honduras: Roatan Id.; Utilla Id. Costa Rica: Limon. Panama: Porto Bello; Chagres River; Colón (Aspinwall); Panama City (J. Zetek, 1933); Naos Id., Bay of Panama (T. Hallinan, 1914). Venezuela: Soldado Rock, Bay of Paria. Brasil: Manguinhos, Ilha de Itaparica, State Bahia: Pedra Furada, Bahia; Rio de Janeiro; São Paulo. Uruguay: Cabo Polonio; Puerto Paloma, Rocha. Recorded from Nicaragua, St. Kitts, St. Martin, Curação and Colombia (Cartagena).

Remarks. L. ziczac is the most common West Indian species, living in the intertidal zone on rocks, jetties or pilings, sometimes in large colonies in crevices. When few specimens are compared, it is relatively easy to distinguish varieties corresponding to some of the names listed in the synonymy; but a study of a large lot from one spot shows the

fallacy of such attempts, particularly if proper allowance be made for sexual dimorphism. The same lot contains large and small female snails, apparently for the same number of whorls, the smaller snails usually gaudily marked.

Littorina obtusata Linné, Plate 6, figs. 1-6

Turbo obtusatus Linné 1758, Syst. Nat., 10th Ed., 1, p. 761 ("in the northern Ocean"). Hanley 1855, Ipsa Linnaei Conchylia, p. 325, pl. 3, fig. 6 (type).

Neritu littoralis Linné 1758, Syst. Nat., 10th Ed., 1, p. 777 ("on the coasts and in the estuaries of the European sea"). Hanley 1855, Ipsa Linnaei Conchylia, p. 399 (type).

Turbo palliatus Say 1822, Jr. Ac. Nat. Sci. Phila., 2, pt. 2, p. 240 (New England States).

Littorina arctica H.P.C.Möller 1842, Index Moll. Groenlandiae, p. 9 (Greenland; without description, but defined by the reference to Nerita littoralis O. Fabricius 1780, Fauna Groenlandica, p. 402).

Littorina neritoides J.E. DeKay 1843, Zool. New York, 5, Moll., p. 105, pl. 6, figs. 109-111. Not of Linné 1758.

Littorina peconica S. Smith 1860, Ann. Lyc. Nat. Hist. New York, 7, p. 156 (Peconic Bay, Long Island, New York).

Synonymy. For European synonyms, see P. Dautzenberg and H. Fischer 1915, Jour. de Conchy., 62, (1914), pt. 2, pp. 87-128. Turbo veritoides Pulteney (1813) is an additional synonym not mentioned by them.

Description. Shell subglobular or slightly wider than high, thick, opaque, dull, of 4 to 5 rapidly increasing whorls; sutures little or not impressed; body-whorl over $\frac{3}{4}$ of total height. Surface with many minute, wavy, spiral raised lines of the thin periostracum, usually worn off in older specimens, which are either smooth or very finely spirally striate. Spire low, either flattened or obtusely raised in adult shells, sometimes pointed in the young. Aperture subcircular, slightly expanded; outer lip sharp-edged, thickened but smooth within; columellar area broad, thick, smooth, flat or slightly concave, margined outwardly (at the base of the body-whorl) by a low but sharp ridge which merges with the bow-like basal lip; newly hatched snails have a narrow umbilicus, more or less preserved as a pit in older shells; below this pit a roughened lunule often separates the edge of the columella from the body-whorl, but this is not constant even in the same locality. Young shells have the base of the columellar area somewhat rounded-angular. Color variable, usually a uniform yellowish-fulvous or dirty-yellow, rarely more chestnut-brown; young, unworn shells may have the early whorls whitish or bluish; sometimes 2 broad pale chestnut spiral bands, one above and the other below the periphery; more rarely black with spiral lines of obscure whitish or bluish spots, or chestnut-brown with a white band. Mouth within colored like the outside; edge of outer lip unspotted; columella white or dirty-white. Operculum bright yellow to orange-brown. Oviparous: 90 to 180 eggs agglomerated within a gelatinous mass, attached to sea-weed; upon hatching the veliger larva is completely developed and remains in the spawn, emerging in the crawling stage (Caullery and Pelseneer 1910, Bull. Scient. France Belg., 44, p. 357). Male smaller than female, with a more produced spire and narrower body-whorl, the aperture smaller and less expanded.

length	width	aperture	
12	12	10×7.5 mm.	Port Clyde, Maine
10.8	10	7×6	Gaspé Peninsula, Quebec
11.5	13	10×7.5	Rockport, Massachusetts
12.3	11	9×7.2	Rye, New York

The largest European shell seen (Plymouth, England) was 15.5 mm. long and 15.2 mm. wide.

Types. Linné's types of T. obtusatus and N. littoralis are at the Linnaean Society of London. They bear no localities, but obtusatus came probably from the coast of Lapland (Norway), which may be taken as the type locality. One of Linné's obtusatus was figured by Hanley. The type of Say's palliatus is at Ac. Nat. Sci. Phila. (No. 18420). Where the type of L. peconica went is unknown.

Range. Coast of western Europe (including the British Isles) from Nova Zembla (72° 30′ N.) and Spitzbergen to the Straits of Gibraltar; also in the Baltic Sea. Records from the western Mediterranean (Malaga; Corsica) and the Azores are open to question. Faroë Ids. Jan Mayen Id. Iceland. Greenland. Autochthonous in America, from Newfoundland and southern Labrador to southern New Jersey. It was found in Indian shell-heaps in Casco Bay, Maine (J. Wyman 1868, Amer. Natural., 1, p. 565), in the Back Bay area of Boston below a layer of pit in silt deposited several centuries before Colonial times (W. J. Clench 1942, in F. Johnson, The Boylston Street Fishweir, p. 46), and in post-Pliocene deposits underlying a salt-marsh near Branford, Connecticut (J. B. Knight 1934, Amer. Jr. Sci., ser. 5, 28, p. 172). W. H. Dall reported it as a Pliocene fossil from Nome, Alaska (1920, U. S. Geol. Surv., Prof. Pap. 125C, p. 29, pl. 5, fig. 12).

Records. Labrador. Newfoundland: Ferryland. Quebec: Trois Pistoles, Gaspé Peninsula. New Brunswick: Grand Manan. Nova Scotia: Bird Id. Maine: common. New Hampshire: Newcastle. Massachusetts: common. Rhode Island: Westerly; Newport. Connecticut: Stonington; Pine Orchard. New York: Rye; Fort Hamilton, Brooklyn. New Jersey: Cape May (N. J. State Mus.).

Remarks. Jeffreys and Tryon believed that L. obtusata of the British Isles and western Europe was specifically distinct from the more boreal and North American shells which they called L. littoralis (with L. palliata Say as a synonym). Tryon even placed them in different sections of the genus. Others restricted the name palliata to North American specimens. The problem has been thoroughly studied by J. Colman (1932, Biol. Bull., 62, pp. 223-243), who concluded that it is impossible to differentiate between European and North American shells. The species is not very variable and none of its forms appear to merit subspecific rank. They are discussed and figured by Dautzenberg and Fischer (1915).

L. obtusata is usually found on seaweeds attached to intertidal rocks, where its color often blends with that of the surroundings. In New England it may occur sometimes among the low coarse grass of salt marshes. C. H. Batchelder (1915, Nautilus, 29, p. 46) states that it migrates to deeper water in early winter, so as to escape the ground ice of the shore, returning to higher levels in the spring.

Littorina meleagris Potiez and Michaud, Plate 6, figs. 17-19

Phasianella meleagris "Beck" Potiez and Michaud 1838, Gal. Moll. Douai, 1, p. 311 (no locality).

Littorina meleagus "Beck" Rush 1891, Nautilus, 5, p. 67 (St. Thomas; misspelling of meleagris).

Phasianella (or Littorina) punctata Pfeiffer 1840, Arch. f. Naturg., 6, pt. 1, p. 255 (Cuba). Not Turbo punctatus Gmelin, 1790, which is also a Littorina.

Litorina guttata Philippi 1847, Abb. Beschr. Conch., 2, p. 197, pl. 4 (Litorina), fig. 7 (Antilles; Cuba; new name for Phasianella punctata Pfeiffer, 1840).

Littorina hidalgoi Arango 1880, Contrib. Fauna Malac. Cubana, p. 159 (Havana and La Chorrera, Cuba; with brief description). Azpeitia Moros 1925, Rev. R. Ac. Cienc. Ex. Fis. Nat. Madrid, 22, p. 165, pl. 1, fig. 5 (cotype).

Synonymy. The foregoing synonymy, first suggested by Azpeitia Moros (1925), was definitely proposed by C. G. Aguayo (1934, Mem. Soc. Cubana Hist. Nat., 8, p. 88). I had reached the same conclusion indepen-

dently. Potiez and Michaud mention expressly the rimation of the columella and describe the characteristic color pattern. Some confusion has arisen from Reeve's figuring the American meleagris as "L. punctata" (1857, Conch. Icon., 10, Littorina, pl. 13, figs. 66a-b) and the true West African L. punctata Gmelin as "L. guttata" (op. cit., pl. 14, fig. 76).

Description. Shell ovate-turriculate, much higher than wide, moderately thick, dull, of 5 or 6 rapidly increasing convex whorls; early whorls little or not eroded: suture well marked, smooth. Body-whorl about \(^2_3\) of total height, much more convex than the earlier whorls, rounded at the periphery. Periostracum very thin, often worn. Surface either smooth or with faint traces of spiral striation at the periphery: growth-striae very weak, irregular. Aperture pear-shaped; outer lip not flaring, the edge sharp and thin, smooth and slightly thickened within, meeting the body-whorl at a sharp angle: inner lip forming a very slight callus over the body-whorl. Columellar area very long and moderately wide, slanting inward, smooth, flat or slightly convex; the inner edge not thickened, long and nearly straight, but not ending abruptly below; a very sharp outer ridge, blunter at the base where it merges evenly with the bow-like basal lip. A crescent-shaped, slightly concave, dull, microscopically striate columellar lunule, of variable width, separates the outer ridge of the inner lip from the base of the body-whorl and extends as a slit or perforation into the axis; the umbilical slit is often scarcely developed in very young shells

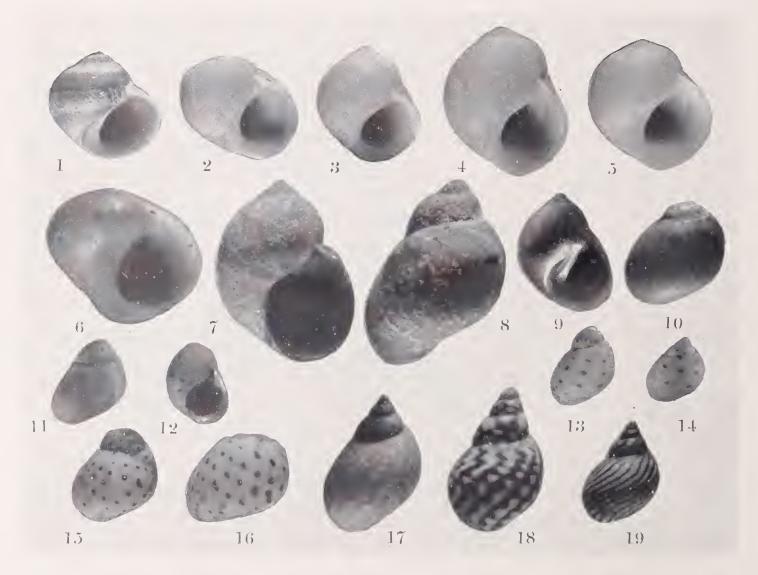


Plate 6. 1 to 6, Littorina obtusata Linné: 1, Rye, New York (2): 2 and 3, Gloucester, Massachusetts (2×); 4 and 5, Port Clyde, Knox Co., Maine (2×): 6, Westerly Rhode Island (young, 8×). 7 to 16, Littorina mespillum Megerlé v. Mühlfeld: 7 and 8, South Cat Cay, Bimini Ids. (4×): 9 and 10, Cayo Frances, Cuba (4×); 11 to 44, Punta Chiva, Samana Peninsula, Hispaniola (2×): 15 and 16, Spanish Water, Curação (4×). 17 to 19, Littorina meleagris Potiez and Michaud: 17, Mariel, Cuba (4×); 18, St. Croix (4×): 19, East Sister Key, Florida (4×).

(3 mm. and less high). Color pattern typically a checkering of large white spots separated by much narrower maliogany or lighter brown intervals, the spots more or less in spiral rows, larger below the sutures: spots sometimes confluent into crenulate spiral bands, or much faded, particularly on the body-whorl. Mouth reddish-brown within; outer lip whitish or reddish-brown, spotted or blotched with white: inner lip whitish or more or less tinged with pale brown; operculum dark mahogany-brown. Reproduction unknown.

length	width	aperture	
7.6	4.7	4.6×3 mm.	Playa del Chivo, Mariel, Cuba
8.9	5.4	5×3.8	Havana, Cuba
7.2	4.2	4×2.8	St. Croix

Types. The present location of the types of P. weleagris and L. guttata (=punctata) is not known. Cotypes of hidalgoi are in Azpeitia Moros' collection, presumably in Madrid. One of the types of weleagris was larger (10 mm.) than any specimen seen.

Range. Southern Florida, Bahamas, Greater and Lesser Antilles, and Caribbean coast of South America.

Records. Florida: Boynton Beach, Palm Beach Co. (P. McGinty). Bahamas: near Matthew Town, Great Inagua: Alicetown, North Bimini. Cuba: Vedado, Havana; Cojimar, Havana Prov.; Playa del Chivo, near Mariel: La Playa, Matanzas; Peñas Altas, Matanzas Prov.: Marianao. Hispaniola: El Canal, Cabo Macoris. Jamaica: (C. B. Adams). Virgin Islands: St. Croix: Guana Id., Tortola: Virgin Gorda: St. Thomas. Lesser Antilles: Guadeloupe; St. Vincent. Recorded from the Tortugas (Florida), Puerto Rico, Vieques Id., Republic of Honduras (Utilla) and Colombia (Cartagena).

Remarks. L. weleagris lives on rocks or pilings in the intertidal zone, in rather quiet water.

Littorina mespillum Megerlé v. Mühlfeld, Plate 6, figs. 7-16

Helix mespillum Megerlé von Mühlfeld 1824, Verh. Ges. Naturf. Fr. Berlin, 1, pt. 4, p. 219, pl. 8, fig. 8 (Antilles) [reference checked by Miss Hazel Gay].

Litorina mespilum Philippi 1847, Abb. Beschr. Conch., 3, p. 16, pl. 6 (Litorina), fig. 20 (Cuba; emendation of mespillum).

Turbo minimus "Gray" Wood 1828, Index Testac., Suppl., pl. 6, fig. 29; with name on p. 19 of letter-press (no description; no locality).

Littorina minima Gray 1839, Zool. Beechey's Voyage "Blossom," Moll., p. 139 (description; no locality). Littorina fusca Pfeiffer 1840, Arch. f. Naturg., 6, pt. 1, p. 254 (Cuba).

Littorina naticoides d'Orbigny 1842, in de la Sagra, Hist. Phys. Pol. Nat. Cuba, Moll., Atlas, pl. 15, figs. 21-23 (binomial on plate); Text, 1, (1842), p. 214 (Havana).

Litorina guudlachi Philippi 1849 (March), Zeitschr. f. Malak., 5, (1848), p. 150 (Cuba).

Synonymy. I am unable to draw the line between spotted minima and unspotted mespillum. Philippi synonymized fusca and naticoides correctly with mespillum. L. gundlachi has not been figured; but the size and "umbilicate-perforate" columella make it either mespillum or meleagris. I have never seen meleagris colored as described for gundlachi, whereas the description agrees well with some unspotted mespillum.

Description. Shell ovate-conical, slightly higher than wide, thick, opaque, dull, of 4 to 7 rapidly increasing whorls: the apex much corroded in older shells: sutures moderately impressed, even, that of the body-whorl deeper: body-whorl over $\frac{2}{3}$ of total height, rounded or weakly shouldered at the periphery. A thin, brownish periostracum, often lost, with microscopic spiral striation in very young shells, later without definite sculpture; beneath this the shell is smooth. Spire low, obtusely pointed. Aperture pear-shaped; outer lip sharp-edged, thickened but smooth within; columellar area narrow,

flat, thick, smooth, slanting inward, with concave inner edge and a thick outer edge. which becomes sharper at the base where it merges with the bow-like basal lip; adults with a distinct, usually narrow, sometimes broader umbilical slit, often continued upward as a distinct perforation of the axis and downward as a narrow, roughened lunule between the outer edge of the columella and the body-whorl: umbilical slit obsolete or absent in very young shells (5 mm. or less long). Color reductible to two types, connected by passages. Some shells (form minima) are pale orange-vellow, straw-vellow or light brown, more rarely almost white, with 5 to 8 rather irregular spiral rows of roundish or dropshaped purplish-brown to blackish spots, very variable in size, and either boldly or weakly marked; sometimes the spots of a row alternate with faint whitish blotches; in the same lot some shells have many spots in distinct rows, others have very few, irregularly scattered or hardly any. Thus we pass to the second type (form mespillum), which is uniformly darker or lighter mahogany-brown, often with a lighter base or paler below the suture, though not distinctly banded, and without spots; in the same lot some shells are unspotted, while others show at least traces of the roundish spots characteristic of the first type. Mouth mahogany-brown within, with spots if these are present outside; outer lip of the same color or paler, in spotted shells often with a few purplish-brown spots; columella uniformly dirty-white or brownish-white: operculum dark mahogany-brown. Reproduction unknown.

length width aperture (summit corroded in all) (spotted) 8 6.5 5.6×4.5 mm. Sta. Barbara de Samana, Hispaniola (unspotted) 10.2 7 6.6×4.8 South Cat Cay, Bimini Ids.

Types. The location of the types of minima, mespillum, fusca and gundlachi is not known; that of naticoides may be at the Paris Museum. As minima was described without locality and mespillum merely from the Antilles, Havana, Cuba, is herewith selected as the type locality for both the spotted and unspotted forms, which are found there together.

Range. Southern Florida Keys, southern Bahamas, and Greater and Lesser Antilles as far as Barbados. Also in Curação, Dutch West Indies. Not known definitely from Trinidad, nor the coast of Central and South America. The reported occurrence in Texas (W.H.Dall 1889, Bull. U. S. N. Mus., No. 37, p. 146) and near Sanibel, Florida (L.M. Perry 1940?, Checklist Mar. Moll. Sanibel-Captiva, p. 14), is doubtful.

Records. Florida: Key West (very young shells: Palmer): East Sister Key near Key Vaca (T. L. McGinty). Bahamas: Andros: Bimini Ids.: Eleuthera: Mariguana: New Providence; Long Island: Great Inagua: Grand Bahama: Cat Id. Cuba: Playa del Chivo and Vedado, Havana: Claude and Peñas Altas, Matanzas Prov.: Nuevitas, Camaguey Prov.: Cienfuegos: Guantanamo Naval Base: Cayo Frances, Caibarien: Gibara. Hispaniola: El Canal, Cabo Macoris: Punta Chiva, 7 miles E. of Santa Barbara de Samana: Puerto Sosua. Puerto Rico: Luquillo Beach. Jamaica: a few specimens without definite locality (C. B. Adams coll.). Guadeloupe. Caribbean Ids.: West side, entrance to Spanish Water, Curação (G. J. H. Molengraaff, 1923). Recorded from St. Martin and St. Croix.

Remarks. W. J. Clench (1938, Nautilus, 51, p. 113) found L. mespillum in Hispaniola in great abundance in the "splash-pools" on limestone rocks, from the high tide line to 6 or 7 feet above. He comments upon the evident kinship of the spotted minima and the unspotted mespillum, which I am unable to distinguish by names. In nearly everyone of the MCZ localities from Cuba, Hispaniola and the Bahamas both occur together, as well as intergrades.

Littorina angulifera Lamarck, Plate 7, figs 1-7

Turbo striatus Schumacher 1817, Essai Syst. Vers Test., p. 198 (based on "Helix scabra Linnaei" of Chemnitz 1795, Syst. Conchy. Cab., 11, p. 283, pl. 210, figs. 2071-2075; fig. 2075 being a shell from Guinea). Not of Vallot, 1801, nor of Brocchi, 1814.

Phasianella angulifera Lamarck 1822, Hist. Nat. An. Sans Vert., 7, p. 54 (Antilles).

Littorina augulifera Maury 1922, Bull. Amer. Paleont., 9, No. 38, p. 106 (misspelling of angulifera).

Littorina subangulata "Lamarck" Mörch 1876, Malak. Blätt., 23, p. 135 (error for angulifera).

Littorina ahenea Reeve 1857, Conch. Iconica, 10, Littorina, pl. 3, figs. 15b-c (Senegal; Reeve's text makes it clear that his name ahenea referred to these only, not to his fig. 15a).

Litorina angulifera var. lineata Philippi 1847, Abb. Beschr. Conch., 2, p. 224, pl. 5 (Litorina), fig. 15 (Loanda, West Africa). Not Buccinum lineatum Gmelin 1790, which is a form of L. scabra Linné.

Litorina angulifera var. flavescens Philippi 1847, Abb. Beschr. Conch., 2, p. 224 (no locality).

Litorina angulifera var. punctata Philippi 1847, Abb. Beschr. Conch., 2, p. 224, pl. 5 (Litorina), fig. 13 (Antilles; Honduras). Not Turbo punctatus Gmelin 1790, which is a Littorina.

Litorina angulifera var. rubra Philippi 1847, Abb. Beschr. Conch., 2, p. 224, pl. 5 (Litorina), fig. 12 (Senegal; Honduras). Not Littorina rubra Anton, 1839.

Litorina angulifera var. strigata Philippi 1847, Abb. Beschr. Conch., 2. p. 224, pl. 5 (Litorina), fig. 14 (Senegambia; Antilles). Not Littorina intermedia var. strigata Philippi, 1846.

Littorina aurea Bonnet 1864, Rev. Mag. Zool., ser. 2. 16, p. 281, pl. 22, figs. 4-4a (no locality).

Littorina scabra d'Orbigny 1842, in de la Sagra, Hist. Phys. Pol. Nat. Cuba, Moll., Atlas, pl. 15, figs. 15-17; Text, 1, (1842), p. 212 (Cuba; Martinique; Guadeloupe; Jamaica). Not Helix scabra Linné, 1758.

Synonymy. Except for L. anrea, from an unknown locality, names listed here were of Atlantic shells, hence referable to variations of one species. Buccinum lineatum Gmelin (1790, in Linné, Syst. Nat., 13th Ed., 1, pt. 6, p. 3493) was based, not on a specimen, but on Knorr's pl. 14**, fig. 4 (1768, Vergnügen der Augen, 3), from an unknown locality. This figure can be matched either amongst Atlantic angulifera or Indo-Pacific L. scabra Linné, 1758. In order to avoid further ambiguity, I suggest referring Knorr's figure definitely to L. scabra, thus making Gmelin's lineatum a synonym or variety of Linné's earlier name.

Description. Shell broadly conico-turriculate, much higher than wide, thin but solid, more or less translucent, slightly shiny, of 6 to 8 gradually increasing, moderately convex whorls; early whorls usually preserved; suture moderately deep, smooth. Body-whorl about ½ or slightly less of total height, slightly descending at the aperture in large shells, rounded or obtusely carinate at the periphery (in the same lot). No periostracum. Rarely corroded; first 2 whorls smooth; remainder with many fine spiral grooves separated by low, flat ribs, much wider than the grooves; one of the ribs stronger at the periphery in carinate shells; grooves sometimes with much finer spiral striation; growth-striae very fine, decussating the ribs. Spire high, pointed. Aperture short oval; outer lip not flaring,

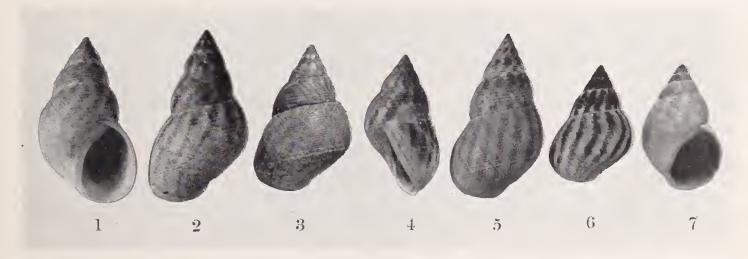


Plate 7. Littorina angulifera Lamarck: 1 and 2, Cape Sable, Florida; 3, Florida City, Florida; 4, Pigeon Point, Tobago Id.: 5, Hungary Bay, Bermuda; 6, Key West, Florida: 7, Ilha de Itaparica, Bahia. All nat. size.

the edge smooth, sharp and not thickened within, nearly horizontal at the body-whorl; inner lip with a very thin deposit over the body-whorl. Columellar area moderately wide, slightly thickened, slanting inward, smooth, slightly depressed or shallowly grooved between the nearly straight inner edge and the much swollen or somewhat reflexed, thick outer edge (at the base of the body-whorl); the outer edge merges evenly with the bow-like basal lip. Smallest shell seen (7 mm. long) without a trace of an umbilical slit. Ground color white (often with a bluish tinge), dirty-yellow, orange-yellow, reddish-brown or grayish-brown; darker markings of elongate spots spaced on the ribs, the spots usually grouped or fused into a more or less distinct pattern of narrow or broad, oblique stripes, either straight or more or less wavy, often best marked on the body-whorl; the early whorls often with a series of vertical white spots, regularly spaced below the suture. Mouth within of the outside color, often with a series of darker blotches at the edge; columellar area whitish at inner and outer edges, pale purplish medially; operculum pale mahogany-brown. Reproduction unknown.

length	width	aperture	
41	23	20.8×16.1	Cape Sable, Florida
33.1	18.2	17×14	Paget, Bermuda
34.5	22.3	18.2×15.2	Caibarien, Cuba
31.6	19.2	17×14	Natal, Brasil

Type. The type of Lamarck's angulifera was apparently not in Delessert's collection and may be at the Paris Museum. Lamarck also referred to his species, correctly, shells figured by Lister (1770, Hist. Conchy., pl. 583, figs. 37-38) from Jamaica and Barbados, Jamaica being here selected as the type locality.

Range. In America on the coast of southern Florida (northward to St. Augustine in the east and at least to Cedar Keys in the west; Dall's record from Texas needs confirmation), Central and South America (from Mexico to São Paulo), Bermuda and Antilles. On the coast of West Africa from Senegal and Cape Verde Ids. to Angola (Lobito Bay). It has reached the Pacific Coast of Panama through the Canal in recent years; C. B. Adams did not find it there in 1850. Other published Indo-Pacific records of angulifera were based on L. scabra.

Records. Florida: common from Jupiter, Palm Beach Co., and Cedar Keys southward; C. W. Johnson found it at St. Augustine about 1883 (1890, Nautilus, 3, p. 115; and 1919, 33, p. 6; possibly no longer living there). Bermuda: common. Bahamas: Long Island; Eleuthera; Cat Island; Bimini Islands; Grand Bahama: Great Inagua: Great Abaco; Little Abaco; New Providence; Mariguana. Cuba: common. Hispaniola: common. Jamaica: common. Puerto Rico: Ponce; San Juan: Guanica. Virgin Ids.: St. Croix; Virgin Gorda; St. John; St. Thomas. Lesser Antilles: Guadeloupe: Tobago. Honduras: Roatan Id. Nicaragua: Waunta Haulover. Panama: Porto Bello; Piriatupo Id., San Blas; Panama City (J. Zetek, 1933); A.P. Brown and H. A. Pilsbry (1913, Proc. Ac. Nat. Sci. Phila., p. 495) report it from Pleistocene deposits at Mt. Hope near Colón. Brasil: Bahia; Ilha de Itaparica, Bahia: Natal; Pernambuco: Maranhão: Rio de Janeiro; São Paulo: Praia de Camocim, Ceará: Fernando Noronha Id. Reported from Curaçao and Colombia. Also seen from Senegal, Liberia, Spanish Guiuea and Gaboon.

Remarks. L. augulifera is the common mangrove periwinkle of the tropical and subtropical coasts, where it prefers the quiet brackish water inlets margined with the thickets

2

3

of *Rhizophora Mangle*, not far from the sea. Here it is attached to the roots, trunks or leaves, sometimes climbing 25 feet above high tide level and spending much of the day out of the water. It may occasionally be found on wharves and pilings. J. S. Gibbons (1878, Quart. Jr. Conch., 1, pt. 15, p. 339) claims that it is more solid where the water is fresher and thinner where it is more saltish. The anatomy was described by J. Leidy, who emphasized the peculiar structure of the branchial chamber (1846, Boston Jr. Nat. Hist., 5, pp. 344-347, pl. 20, figs. 1-3).

The differences between the Atlantic angulifera and the Indo-Pacific Littorina scabra (Linné) are very slight and probably of at most subspecific value, although their ranges nowhere touch. None of the supposedly specific characters hold when many specimens from different localities are compared. L. scabra is, however, more variable, in color as well as in sculpture. It has produced forms with several strong spiral ridges (var. carinifera Menke) or boldly marked with spots at the periphery (var. flammea Philippi), not found in the Atlantic angulifera. West African specimens show no consistent difference from those of tropical America.

R. B. S. Sewell (1924, Rec. Indian Mus., 26, pt. 6, pp. 535-540) found *L. scabra* ovoviviparous, the developing ova filling partially the branchial chamber. No doubt this is also true of *L. angulifera*, although its mode of reproduction has not yet been observed.

Key to Western Atlantic Littorina

- 1. Adult with a more or less distinct umbilical slit or perforation. Small (10 mm. or less)

 Adult without trace of umbilical slit
- 2. Ovate-conical, little higher than wide, unspotted or with roundish dark spots

 L. mespillum
 Ovate-turriculate, much higher than wide, usually with checkered spots, which may fuse more or less

 L. meleagris
- 3. Subglobular, not or little higher than wide, nearly smooth; apex flattened or obtusely pointed; sutures flattened; uniformly colored or with spiral bands. Small (15 mm. or less)

 L. obtusata
 Ovate-conical, turbinate or broadly turriculate, higher than wide; apex sharply pointed; sculpture usually distinct. Often over 15 mm.
- 4. Broadly turriculate, thin and light; spire very high, conical; columellar area hollowed out, with long, straightened inner edge. Up to 41 mm., the mouth about half the height

 L. augnlifera

 Thicker and often heavy, ovate-conical, turbinate, or conico-turriculate
- 5. Conico-turriculate, usually much higher than wide; mouth often much less than half the height; columellar inner edge long and straightened

 6 Turbinate or short conical, moderately or not higher than wide; mouth about half the height or more; columellar inner edge short and strongly curved (concave)
- 6. Columellar area nearly flat; usually with zigzag lines or stripes; mouth inside with a pale basal spiral band and sometimes with a second band above the periphery

 L. ziczac

 Columellar area hollowed out or grooved; unicolor or checkered or blotched with dark; mouth inside without spiral bands

 L. nebulosa
- 7. Broadly ovate-conical, with very convex whorls and deeply impressed sutures; mouth subelliptical, the upper angle nearly square on the body-whorl. Up to 24 mm.

 L. saxotilis

 More turbinate, with flattened or slightly convex whorls and scarcely or not impressed sutures; mouth subovate, the upper angle acute on the body-whorl
- 8. Body-whorl not depressed below the suture; whorls flattened; mouth more elongate; edge of outer lip wavy within. Up to 30 mm.

 L. irrorata
 Body-whorl somewhat depressed below the suture; whorls slightly convex; mouth wider; edge of outer lip smooth within. Up to 42 mm.

 L. littorea

Although the nine species here accepted as valid are very distinct and readily recognized when placed side by side, they show few prominent characters which may be used in a concise key. It may be useful to remember that only three of them (obtusata, saxatilis and littorea) live nowadays on the coast of eastern Canada and New England. Five others (irrorata, ziczac, mespillum, meleagris and angulifera) are found in the southeastern United States, but two of these (mespillum and meleagris) are very rare and restricted to southern Florida. The Caribbean area has also five species (nebulosa, ziczac, mespillum, meleagris and angulifera), but only three of them (nebulosa, ziczac and angulifera) extend beyond Trinidad along the east coast of South America.

The present study lays great stress on the distribution of the several forms, in conformity with the general policy of Johnsonia. The available literature has been carefully combed for information. All records, however, whether based on actual specimens or on published data, were critically examined and only those that appeared fully trustworthy were incorporated. Periwinkles being common shore snails are usually collected in abundance, hence represented in most large collections by a wealth of material. They are an ideal group for students of variation and distribution. Owing to limitations of space, it seemed unwarranted to list all our records of the more common species, so that the main part of their range is given only by states and islands, with the occasional mention of a few selected localities. At the limits of the range, however, all known records are mentioned. It is believed that this method gives a reliable picture, while bringing out the many gaps to be filled by future research.

In areas like the east coast of North America and the Caribbean, where traffic by ships has been intense for several centuries, the student of the geography of marine mollusks should be fully aware of two main sources of error.

There is first the problem presented by the introduction of certain species into new areas through the agency of man. The well-authenticated case of *L. littorea* is very instructive in this connection. If this snail had been brought to the Western Hemisphere one or two centuries earlier, it might have been extremely difficult or perhaps impossible to prove that it was a foreign element in the American fauna. For this reason I have discussed the history of the spread of *L. littorea* rather fully. I have likewise indicated the evidence from which we may safely conclude that our other two northern species (*L. obtnsata* and *L. sawatilis*) are autochthonous in North America at least since the Pliocene or Pleistocene; so that their present occurrence on both sides of the Atlantic is due to natural means of dispersal. The tropical and subtropical *L. angulifera*, which occurs both in the western and the eastern Atlantic, is believed to be autochthonous in both areas. It is known from the Pleistocene of Panama, but has not as yet been found in the fossil state in West Africa. I suggest in this paper that the unusual occurrence of *L. nebulosa flava* at Cienfuegos, Cuba, and possibly in Guadeloupe, may be due to accidental introductions by man.

The frequent dumping of foreign shells with ship's ballast is also likely to lead the student astray. The description of the common West Indian *L. ziczac* as a new British mollusk (*Turbo dispar*) was probably due to this cause. I have pointed out several other aberrant records probably based on material of this type, and which therefore should be disregarded until they can be supported by more positive proof. When a species is found outside the normal range or habitat, the collector should not fail to note whether the specimens were dead or alive.

Some conclusions of more general interest may be drawn from the distribution of the

several species, as known at present. Apart from the introduced *L. littorca*, the western and eastern Atlantic have three species in common, two of them in the northern seas (*L. obtusata* and *L. savatilis*) and one in tropical waters (*L. angulifera*). All three are variable along much the same lines over their entire range and there is no evidence that they have become differentiated into western and eastern geographical races. This is probably due to the similarity of ecological conditions, with the same local differences occurring on both sides of the ocean. It is also worth noting that, except for *L. angulifera*, the Caribbean and South American species are lacking on the African coast of the Atlantic. Most of them have no very close relatives there, as shown by a careful comparative study of the West African species. One possible exception is the West African *Littorina cingulifera* Dunker (1845), which appears to be related to *L. nebulosa*.

On the other hand, it is a remarkable fact that several of the autochthonous Western Atlantic species of *Littorina* are very closely related to forms of the Indo-Pacific area, being sometimes scarcely more than subspecifically distinct. I have called attention to three such cases: *L. savatilis* and *L. sitchana*; *L. ziczac* and *L. mauvitiana*; *L. angulifera* and *L. scabra*. Others may come to light when the Indo-Pacific species are better understood.

It is hoped that the present revision of *Littorina* will be an incentive to further study by the amateur as well as the professional malacologist. Some matters may be investigated by any keen observer, needing no particular training nor laboratory facilities. The distribution of several species should be worked out more carefully at the limits of their ranges, and especially in Central America and the Lesser Antilles. We have as yet little information on the ecology of the tropical species, the habitats they prefer, their daily and seasonal habits, their mode of reproduction, the changes brought about by age, the sexual differences in the shells, etc.

I greatly regret that present disturbed world conditions prevented me from studying the types or from obtaining reliable information about them. This notable defect will have to be corrected when stable conditions return. The location of the types is given after the most reliable published information, except in the case of Say's species, which were looked up for me by Dr. H. G. Riehards. As no types were seen, all synonymies are based on a study of the original descriptions and figures.

Acknowledgments

This study of *Littorina* is based almost entirely upon the very extensive collection of the Museum of Comparative Zoölogy. The unusual circumstances of the times made it impractical to visit other American museums or to draw more information from them. Some unusual specimens were obtained through the kindness of the following private collectors: R. C. Athearn, B. R. Bales, W. T. Davis, Roy Latham, T. L. McGinty, James Miller, Paulo E. de Oliveira and H. G. Richards. I am particularly indebted to Miss Hazel Gay (of the American Museum of Natural History) and to Dr. H. G. Richards (of the Aeademy of Natural Sciences of Philadelphia), who checked up the references to two books not available to me in the originals.

Cienfuegos, Cuba

Cienfuegos is one of Cuba's finest cities. It is built on the eastern shores of Cienfuegos Bay in the Province of Santa Clara on the south coast of the island. The city proper is about ten miles from the harbor entrance.

As a locality name, "Cienfuegos" can be misleading, as it is applied to the general region about the bay. The marine zoölogist would find exceedingly poor collecting in the immediate vicinity of the city, as its situation is far from the open sea and the bay waters are materially freshened by the many small rivers and streams that enter it.

However, excellent marine collecting is to be found near the narrow harbor entrance and along the outer coast nearby. Just above the harbor entrance is situated the little village of Castillo de Jagua where accommodations are to be had at its little hotel and small boats can be obtained for all local trips. On the "Castle" side of the bay (west) a path leads to Punta de la Sabanilla at the harbor entrance. Along the two mile stretch of coast several marine habitats are to be found, mainly however, ledge rock and "diente de perro" the badly weathered dog-tooth limestone. This rock not only extends to this Point, but around it and west for many miles. We followed the shore for over three miles and found this type of rock collecting to be most excellent. The country behind is somewhat level with a low scrub forest with good though limited land shell collecting. Liguus fasciatus goodvichi Cl. and Ceviou iostomum Pfr. are found in fair numbers.

The opposite shore from the "Castle" (east) is by far the better for the shell collector. This can be reached by the little wood-burning boat that makes frequent trips from Cienfuegos and stops at several places about the Bay. La Milpa and Pasacaballos, two very small settlements, are on this side and from the latter, a walk of two miles south along the shore margined with the dog-tooth limestone brings one to the lighthouse at Punta de los Colorados. Backing the coast for a short distance and above the dog-tooth limestone are low red-rocked cliffs which give this Point its name. Less than half a mile east the limestone gives way to a region of flat broken stones and is shallow for many feet seaward. This area offers exceedingly fine collecting. Every flat slab of rock is a home for marine animals, particularly mollusks. We have counted as many as twenty specimens of Livona pica Linné under a single rock slab and Fissurella, Columbella, Conus, Cypraea and a multitude of other genera are to be had for the picking up. Another half mile to the east are short sandy beaches and mangrove areas, both productive for many species not found along the rocky stretches.

North of Castillo de Jagua there are a few small bays which are easily reached by boat. Our method was to hire a man to take us to one of these bays by motor boat, leaving with us a row boat and calling again late in the afternoon. We could then explore at our leisure the entire bay as well as the forest-covered shores about the bay. These bays have a fauna somewhat different from the harbor entrance and the open coast. Near the mouth of small streams several brackish water species were found and elsewhere about the bays we found species that have a tolerance for slightly brackish water.—W. J. Clench