A new lucinid bivalve from the Niger Delta and an appraisal of the Loripes group (Bivalvia, Lucinacea)

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INTRODUCTION

From a survey of part of the Niger Delta, Nigeria (Oil Pollution Research Unit, abbreviated OPRU, Orielton: Confidential Report), numbers of bivalves were found living in intertidal mangrove peat. These belong to two easily distinguishable species; *Cyrenoida rosea* (d'Ailly, 1896) (Cyrenoidacea) and an undetermined lucinacean.

This paper reports on the identity of this lucine and leads to a discussion of the "Loripes group". The "Loripes group" has been variously delimited by Chavan (1937, 1969) and was only briefly considered by Bretsky (1976), the most recent review of the Lucinidae.

Abbreviations for collections are as follows: IRNSB = Institut Royal des Sciences Naturelles de Belgique, Brussels; MHNP = Muséum National d'Histoire Naturelle, Paris; NMW = National Museum of Wales, Cardiff.

Loripes (Keletistes n. subg.) rhizoecus¹ n. sp.

Material examined. — 24 specimens from the Odeama area of the Niger Delta, Nigeria (4°22'N 6°30'E), type locality. This species was also recorded from the Bodo West area (4°33'N 7°13'E) and from the Forcados area (5°23'N 5°27'E). The material was collected by Dr. John Hartley on 21.I.1983. Holotype: NMW Z.1983.034.1; paratypes: NMW Z.1983.034.2-10.

Habitat. — This lucine was found in intertidal mangrove root peat up to 80 m from creek edges. The preferred habitat, where densities of about $300/m^2$ occurred, was of moist peat on accreting creek banks amongst stands of *Rhizophora racemosa* G.F.W. Mey which were 30-40 m high. The bivalve was present in the top 3 cm of the peat where this was loose and not compacted. The salinity recorded at the time of collection, which was in the dry season, varied from $13^{\circ}/_{00}$ to $32^{\circ}/_{00}$, the greatest densities occurring where the salinity was greater than $17^{\circ}/_{00}$. Where more estuarine conditions occurred, i.e. where salinity varied from $1^{\circ}/_{00}$ to $20^{\circ}/_{00}$, the lucine was replaced by *Cyrenoida rosea*.

Other fauna present with the lucine included the crabs Goniopsis pelli (Herklots), Sesarma alberti Rathbun, Upogebia sp., and the prosobranch Tympanotonus fuscatus (L., 1758). Goniopsis pelli appeared to be a predator of the lucine, which it found by burrowing through the surface layer of peat. Crushed valves were seen in the shredded peat thrown up by the burrowing crab.

The habitat requirements of the lucine are apparently rather narrow. Densities declined rapidly away from the zone where the *Rhizophora* trees were most dense, i.e.

¹ Rhizoecus (Greek: rhizo = roots, oikos = oecus = home), referring to the preferred habitat of Rhizophora peat.

where the peat became drier and similarly it did not occur in the mud of the creek banks.

This information was supplied by Dr. J. Hartley of OPRU.

Description. — The shell (figs. 1, 2a, b). — Equivalve; outline quadrate, anteriorly reduced, the posterior margin is rounded, becoming straight, the ventral margin also becoming straight, occasionally sinuous, the anterior margin angulate, usually with a sinuation dorsal to the anterior pointed extremity. Moderately inflated, some almost globose, but this is variable; length: tumidity ratio 1.25-1.89, mean 1.54. Umbos small, opisthogyre. Lunule small, longer than wide, ovoid, but in the inflated specimens becoming chordate. Escutcheon very narrow. Ligament wholly internal in a pit angled away from the umbo. Sculpture predominantly of irregularly spaced concentric, but sinuous lines and narrow ridges. Faint radial ridges are present to varying degrees on the anterior and posterior dorsal areas. The obsolescence of the radial sculpture is not related to shell size and therefore doubtfully to corrosion. Hinge (figs. 3a-f) weak, RV initially with single laterals and a single cardinal, LV with double laterals and two cardinals, but in most specimens the laterals are obsolete and the cardinals appear single in both valves. Formula initially AI, 3b, AI/AII, AIV, 2, 4b, PII, PIV but usually "AI", 3b "PI"/"A?", 2, "P?". Adductor scars subequal, the anterior is narrowly oval with half its length free from the pallial scar, the posterior is narrowly ovoid. The anterior pedal retractor scar is separate from the anterior adductor scar. There is no pallial blood vessel scar. The inner edge is weakly and variably crenulate. For dimensions see table 1.

Anatomy (fig. 4). — The mantle edges are unfused for the most part, except postventrally and for a narrow junction between the posterior inhalant aperture and the exhalant siphon. The free inner lobe is frilled, especially ventrally, and around the posterior inhalant aperture there are four to six small papillae. The exhalant siphon is short in its inverted state and appears to show a rolled-back collar, but this may not reflect any functional differentiation. The gills consist of single demibranchs only. The palps are very small and no ridging could be discerned. The foot is vermiform, but short in the contracted state, the heel is just discernable as a feature. The digestive pouches are moderately developed. The gut follows a simple S-shaped curve, the oesophagus is very short, leading to a cylindrical stomach.

SYSTEMATICS

Family level. — The anatomy of *L. rhizoecus* is typical of the Lucinidae in that the gills consist of single demibranchs and an exhalant siphon is present (Allen, 1958; Bretsky, 1976). Anatomically there is a close affinity with *Loripes lucinalis* (Lamarck, 1818) (fig. 5).

Species level. — The deeply inset ligament implies that this species belongs to the "Loripes group". The only Atlantic species of the "Loripes group" which possesses an inner crenulated margin and obsolete radial costae is Loripes aberrans Dautzenberg, 1910. This species is also figured by Nicklès (1950).

This species was originally described from subfossil beds from Mauritania. For comparison this paper reports on 73 valves from the type locality "Nouakchott, Tranche A ^b, Mauritania" collected by Gruvel 7.XI.1908 with *Senilia senilis* (L., 1758) (Arcacea), Reg. No. IRNSB I.G.10.591, and MHNP. These are part of the type series reported upon by Dautzenberg (1910). The specimens are similar to *L. rhizoecus* in the

	Height	Length	Tumidity
	9.1	9.8	5.4
	6.9	7.35	4.5
	× 5.7	5.9	3.3
	5.05	5.4	3.15
	5.0	5.0	3.35
	4.9	5.1	3.3
	4.7	5.0	3.2
	4.5	4.9	3.3
	4.5	4.75	3.1
	4.0	4.1	3.1
	4.0	4.1	2.6
	3.8	3.9	2.5
	3.6	3.7	2.85
	3.5	3.6	2.5
	3.2	3.25	2.6
	3.0	3.4	2.5
	2.85	3.4	1.8
	2.6	3.0	2.4
Holotype —	8.95	10.05	5.8
Height : Length Ratio	0.94 ± 0.04		
Length : Tumidity Ratio	1.54 ± 0.19		

Table 1. Dimensions in mm of Loripes (Keletistes) rhizoecus n. sp. shells.

presence of an internal ligament and obsolete radial costae. However, it is apparent that within the series there are two morphological forms. The majority of specimens are relatively compressed, anteriorly angulate with a weak hinge. The other form is relatively tumid, anteriorly rounded, umbonate with a strong hinge. Table 2 gives the height to length and length to tumidity ratios and the latter are expressed graphically in fig. 6. The outline differences are illustrated by comparing figs. 8 and 9. The hinge differences are illustrated by comparing figs. 15a-b and 16a-b. The differences are most extreme at the upper end of the size range, but below approximately 7 mm it can be difficult to assign specimens to one of the two forms. Subfossil assemblages are seldom representative of single habitats and one could interpret the above variation as indicative of two distinct species. However, in such circumstances ecophenotypic variation cannot be ruled out. In an attempt to clarify the situation, recent material assigned to L. aberrans has been examined from a number of localities from Senegal to the Ivory Coast. The relative shell dimensions are listed in table 2 and examples are illustrated in fig. 17. The majority of this material, although variable, is most like the compressed weak-hinged variety, although one valve from the Ivory Coast and two valves from French Guinea can be associated with the tumid strong-hinged variety. Unfortunately these specimens were not live-collected and were presumably taken from the strand line where mixing of "populations" is very likely. However, these varieties can be recognized in Dautzenberg's (1910) original figures. Fig. 15 represents the compressed form and figs. 16 and 17 the tumid form.

Dautzenberg's (1910) differential diagnosis was based upon comparison with Loripes lucinalis and states that L. aberrans is "ovate-trigonal" with "much stronger teeth" and

Locality	Size range	Height: length	Length: tumidity	Number of specimens
Mauritania (syntype series)	3.95-11.5	0.96	1.97	48
	* 4.55-8.85	1.0	1.54	25
Senegal, Sine Saloum	4.5-7.8	0.97	1.93	7
Senegal	10.65-13.1	0.92	2.05	3
Iles Tristao	4.0-7.75	0.95	1.94	4
	•	1.0	1.55	1
Lagune d'Azurette	7.5-11.7	0.90	2.16	6
Abidian	•	0.97	1.59	2

* Refers to turnid form of aberrans series.

Table 2. Comparison of phenetic data from six samples of the Loripes (Keletistes) aberrans Dtzbg. series.

thus implies that he regarded the tumid, strong hinged variety as typical. In the future I would therefore suggest that a lectotype similar to Dautzenberg's fig. 16 should be chosen to represent L. aberrans.

However, the possibility that L. rhizoecus could be part of the aberrans series either as an ecophenotypic or geographic variety is of greater relevance to this paper. Morphologically the Niger material is distinct, note the reduction of the anterior area, the straight ventral margin and the irregular concentric corrugations. None of these characters are present in the L. aberrans series. Variation of these characters within the Niger material is small and this is so for all the localities sampled. Without genetic data ecophenotypic variation cannot be conclusively excluded but the majority of taxonomic decisions remain based on morphological grounds alone. Consequently, the constant differences between the Niger material and the aberrans series warrant separate nomenclatorial status.

Generic level. — Generic systematics have been the subject of two reviews (Chavan, 1937, 1938; Bretsky, 1976). These have attempted to create a phyletic classification but are based solely on shell characters. Both reviewers expressed the shortcomings of this approach as exemplified by the consideration of certain characters as indicative of monophyletic lineages, e.g. the divaricate sculpture of the Divaricellinae. This study does not intend to review the phylogeny of any lineage and must take the approach from a purely phenetic position. This is not ideal, but the material available is no greater than that seen by Chavan or Bretsky and, like those works, the conclusions would largely be a matter of opinion.

From the phenetic position the shell characters of an internal ligament and nondivaricate sculpture clearly link *L. rhizoecus* with the "Loripes group" as defined by Bretsky (1976). Unfortunately she was unable to review the genera in this group and recourse must be made to the works of Chavan (1937, 1938, 1969). The "Loripes group" as defined by Chavan has been variable.

Chavan, 1937	Chavan, 1938	Chavan, 1969
genus Loripes	genus Loripes	genus Loripes
subg. Microloripes	subg. Microloripes	genus Parvilucina

subg. Wallucina	subg. Wallucina	subg. Microloripes
subg. Sydlorina (?)	subg. Pillucina	genus Pillucina
	(syn. Sydlorina)	subg. Sydlorina
		genus Wallucina

An examination of species belonging to the "Loripes group" reveals some of the reasons why this variation has occurred.

Loripes s.s. Poli, 1791

Type species Tellina lactea Poli, 1791 (non L., 1758) = Amphidesma lucinalis Lamarck, 1818, also L. clausus (Philippi, 1850), L. cryptellus (d'Orbigny, 1846).

This is one of the more stable genera. The shells (fig. 10) are circular with some angulation of the anterior margin and straightening of the posterior margin (see the variety *desmaresti* Payraudeau, 1826), and not inflated. The sculpture is of fine incremental growth lines giving a virtually smooth surface in unworn shells. The hinge (figs. 18a, b, 19a, b) is moderately developed, initially of the formula AI, 3b, PI/AII, AIII, 2, 4b, PII, PIV, but the laterals frequently become obsolete. The inner margin is smooth.

Wallucina Iredale, 1930

Type species Lucina jacksonensis Smith, 1885, also Lucina icterica Reeve, 1850, Lucina erythraea Issel, 1869.

Orbicular tumid forms (figs. 11 and 12), somewhat expanded anteriorly with a noticeable lunule. The sculpture consists of uneven concentric lines and ridges crossed by numerous very fine radial striae. However, these radial striae are part of the infrastructure of the shell and are not surface features, so that this has not been noted previously. The hinge (fig. 20a-b), especially the cardinal teeth, is well developed. Cardinal 3b is large and 2 is stronger than 4b. The laterals as in *Loripes* are variable, although the anterior in both valves are typically obsolete. The posterior laterals are better developed, with both PII and PIII visible in some specimens and PI in most specimens. The inner margin is minutely crenulated.

Pillucina Pilsbry, 1921

Type species Pillucina spaldingi Pilsbry, 1921, also Lucina pisidium Dunker, 1860, Lucina hawaiiensis (Smith, 1885).

Very similar in form to *Wallucina*, i.e. orbicular and tumid (fig. 13). Sculpture of concentric lines and ridges crossed by low radial costae, which are obsolete on the median area of the shell. Pilsbry (1921) in his original description stated that the hinge (fig. 21a-b) consists only of cardinal teeth and this was restated by Chavan (1938, 1969). However, Kay (1979) states that very small laterals are present in both valves. Therefore the hinge is identical to that of *Wallucina*. The inner margin is crenulated.

Sydlorina Iredale, 1930

Type species Sydlorina symbolica Iredale, 1930.

These shells are identical to species of *Pillucina* and *Sydlorina* is regarded as a synonym.

Parvilucina Dall, 1901

Type species Lucina tenuisculpta Carpenter, 1864.

The genus *Parvilucina* possesses a marginal ligament and therefore cannot be included in the "Loripes group" as defined by Bretsky (1976).

Microloripes Cossmann, 1910

Type species Lucina dentata Defrance, 1823.

Orbicular and tumid shells. Sculpture of uneven concentric lines and ridges. Hinge well developed as in *Loripes*, but also with 3a. The inner margin is finely crenulated. These are all Tertiary fossils.

Both Wallucina and Microloripes have been cited as having recent representatives in the tropical eastern Atlantic. Chavan (1937, 1938) placed L. aberrans in Wallucina, but as shown above Wallucina lacks the radial surface sculpture. This species is considered in more detail below. Microloripes contrarius Dunker, 1846 (Chavan, 1937; Dell, 1964) has an unusual sculpture. Specimens seen and the original figures and the descriptions given by Chavan (1937) and Lamy (1920) clearly indicate a concentric sculpture of incremental lines crossed by a few wavy transverse faint ridges. The specimens concerned are all rather small, i.e. less than 5 mm, and are typical of juvenile specimens of a Divaricella. Those cited by Dell (1964) are referable to Lucina s.s. and in no way belong to the "Loripes group".

Chavan also included in *Pillucina, Lucina fischeriana* Issel, 1869 (fig. 14) from the Red Sea. This species is cricular, not tumid, and has a sculpture of broad radial costae with fine concentric undulating striae. The hinge (fig. 22a-b) is not strong, but has a complete dentition of AI, 3b, PI/AII, AIV, 2, 4b, PII. The ligament is deeply inset. The inner margin is fluted. This species has a sculpture resembling that of juveniles of *Ctena divergens* (Philippi, 1850) and has a similar hinge. The ligament is, however, rather deeper than the submarginal ligament of *Ctena*.

The conflicting definitions of genera have therefore probably arisen through a misinterpretation of the radial sculpture and through the variability of hinge structure which is subject to obsolescence in most species.

Having outlined the current genera of the "Loripes" group, they can be seen to fall into two sections; Loripes and the Indo-Pacific Wallucina-Pillucina combination. The West African L. aberrans-rhizoecus complex is most akin to Pillucina in sculpture, but to Loripes in overall form, except for the tumid form of aberrans. Thus the ovate trigonal form of aberrans is closest in form to Pillucina, the compressed form in outline to Loripes, and rhizoecus unlike either in form. Microloripes possesses an extra cardinal and is therefore not of immediate significance and may well not belong to the "Loripes group". As with the decisions on specific status, those on generic status are open to opinion.

The "Loripes group" has a dentition which is constant, except for obsolescence in larger specimens, especially in those with expanded and rounded anterior margins, e.g. Wallucina and Pillucina. Differences are therefore only in the form of the sculpture. Loripes species are known from the Atlantic Ocean and African coast of the Indian Ocean, Pillucina/Wallucina from the Indo-Pacific. The variation in form of the West African species is surely part of a single phylogenetic line, perhaps from the wellsculptured ovate-trigonal aberrans to the quadrate rhizoecus. On sculptural terms, this series would appear to derive from something akin to Pillucina but it has considerably altered from the Indo-Pacific *Pillucina* species. For this reason I would recognize the sculptured West African species as representing a separate phylogenetic line and consequently give it subgeneric status: *Keletistes*.

Keletistes² new subgenus

Type species Loripes (Keletistes) rhizoecus n. sp., included species L. aberrans.

Shell small, to 15 mm, subcircular becoming quadrate or trigonal with a nonexpanded anterior area, which has an angulate outline. Umbo medium to low, opisthogyre. Sculpture consisting of concentric incremental lines or low ridges crossed especially on the anterior and posterior areas by a few weak or obsolete radial costae, which are not always present. Inner margin crenulate. Hinge obsolete to moderate. Dentition initially AI, 3B, PI/AII, AIV, 2, 4b, PII, PIV, but becoming obsolete.

The phenetic arrangement of the "Loripes group" now includes:

Genus Loripes Poli, 1791 Subgenus Loripes s.s. (synonym Lucinida d'Orbigny, 1846) Subgenus Wallucina Iredale, 1930 Subgenus Pillucina Pilsbry, 1921 (synonym Sydlorina Iredale, 1930) Subgenus Kelestistes nov.

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SUMMARY

A new species of lucine bivalve, Loripes (Keletistes) rhizoecus, is described from the Niger Delta. The "Loripes group" is discussed and the subgenus Keletistes is introduced. The "Loripes group" is considered to contain only four recent valid subgenera: Loripes s.s., Wallucina, Pillucina (syn. Sydlorina) and Keletistes.

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 2 Keletistes, Greek = one who changes, referring to the variety of form seen in the outline and hinge of the two species assigned to that genus.

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Fig. 1. Loripes (Keletistes) rhizoecus n. sp. Holotype NMW Z.1983.034.1, exterior of left valve, length 10.05 mm.



Fig. 2. Loripes (Keletistes) rhizoecus n. sp. Holotype NMW Z.1983.034.1. (a) (top). Hinge line of left valve; (b) (bottom). Interior of right valve.



Fig. 3. Hinge lines of specimens of Loripes (Keletistes) rhizoecus n. sp. to show degeneration of teeth. Left valves on left side; all backscattered SEM images. (a,b). NMW Z.1983.034.2, scale bar 0.5 mm; (c,d). NMW Z.1983.034.3; (e,f). NMW Z.1983.034.1. Scale bars c-f 1 mm.



Fig. 4. Loripes (Keletistes) rhizoecus n. sp. Gross anatomy viewed from the left side after removal of the left mantle and ctenidium. Abbreviations: AA = anterior adductor muscle, CT = ctenidium, DP = digestive pouch, EA = exhalant aperture, FT = foot (toe), FH = foot (heel), HG = hind gut, IA = inhalant aperture, LP = labial palps, ME = mantle edge, PA = posterior adductor muscle, PG = pedal gape, SP = siphon.



Fig. 5. Loripes (Loripes) lucinalis (Lam.). Gross anatomy viewed from the left side after removal of the left mantle and ctenidium. NMW Z.1980.198.16, Guernsey. For abbreviations used see fig. 4.



Fig. 6. Plot of valve tumidity against valve length for specimens from the syntype series of *Loripes (Keletistes)* aberrans Dtzbg., IRNSB IG.10.591 and MHNP. Circles - umbonate form, triangles - compressed form.



Figs. 7-14. Right valves of a variety of species assigned to Loripes. 7. L. (Keletistes) rhizoecus n. sp., Nigeria, NMW Z.1983.034.1 (width of shell 10.05 mm); 8. L. (K.) aberrans Dtzbg., compressed form, Mauritania, IRNSB 1G.10.591; 9. L. (K.) aberrans Dtzbg., umbonate form, Mauritania, IRNSB 1G.10.591; 10. L. (L.) lucinalis (Lam.), Guernsey, NMW Z.1980.198.16; 11. L. (Wallucina) icterica (Rve.), Australia, NMW Z.1955.158; 12. L. (W.) erythraeus (Issel), Suez, NMW Z.1955.158; 13. L. (Pillucina) pisidium (Dkr.), Japan, NMW Z.1955.158; 14. "Loripes" fischerianus Issel, Red Sea, NMW Z.1955.158.



Figs. 15-16. Hinge lines of Loripes (K.) aberrans Dtzbg., left valves on left side, backscattered SEM images 15a, umbonate form; 15b, compressed form. Scale bars 1 mm.



Fig. 17. Loripes (K.) aberrans Dtzbg. from various localities throughout West Africa (a-i), all MHNP; j. L.
(K.) rhizoecus n. sp., Nigeria, NMW. a-f. Compressed form - (a) Mauritania, subfossil; (b) Sine Saloum,
Senegal; (c) Senegal; (d) Is. Tristao; (e) Abidjan; (f) Lagune d'Azurette. g-i. Umbonate form - (g) Mauritania, subfossil; (h) Abidjan; (i) Is. Tristao. Width of bottom right hand shell 10.05 mm.



Figs. 18-22. Hinge lines of five species of Loripes's.l., left valves on left side, all backscattered SEM images.
18. L. (L.) lucinalis (Lam.); 19. L. (L.) clausus (Phil.); 20. L. (Wallucina) erythraeus (Issel); 21. L. (Pillucina) pisidium (Dkr.); 22. "Loripes" fischerianus Issel. Scale bars all 1 mm.