BASTERIA 45: 143-166, 1982

On the taxonomy and variability of Recent European and North African marine species of the subgenus Rissostomia Sars, 1878, of the genus Rissoa Desmarest, 1814 (Mollusca, Gastropoda, Prosobranchia)

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INTRODUCTION

As is not unusual among groups of closely related variable species, the taxonomy of the subgenus *Rissostomia* is chaotic. Quite a number of specific names has been published, of most of which it is by no means clear whether they represent good species, geographical races (subspecies), or phenotypical habitat forms[1] only. Mars (1956) gave a valuable account of most of these forms. Priolo (1954: 204) summarized part of the problems various authors had with the subgenus.

The situation has been complicated still more by the fact that in the Roskildefjord in Denmark two forms of *R. membranacea* s.l. must be distinguished, of which the shells are very similar, but which show marked differences in the apical dimensions of the shells and in the larval phase (Rehfeldt, 1968). Mrs. Rehfeldt surmised that the forms are to be considered separate species.

MATERIAL EXAMINED

The investigation underlying this paper is based on shells only. Material from the following collections was examined: (1) Ph. Dautzenberg, in the Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels; (2) Naturhistorisches Museum, Vienna; (3) Natur-Museum Senckenberg, Frankfurt/Main; (4) British Museum (Natural History), London; (5) Smithsonian Institution, including J.G. Jeffreys, Washington, D.C.; (6) Royal Scottish Museum, Edinburgh; (7) Universitetets Zoologiske Museum, Copenhagen; (8) Montagu, in the Royal Albert Memorial Museum, Exeter; (9) Rijksmuseum van Natuurlijke Historie, Leiden; the private collections of (10) Dr. J.J. van Aartsen, (11) Mr. H. van Haren, and (12) myself.

GENERAL REMARKS

As shown in fig. 1 of this paper, a sample from St. Lunaire, Bretagne, France (colln. 1), also proved to clearly fall apart into two forms as regards apical dimensions. When the longitudinal ribs on the shells of both forms were counted, the results shown in fig. 2

[1] These notions are used in the sense of Mayr (1964: 193 sqq.).

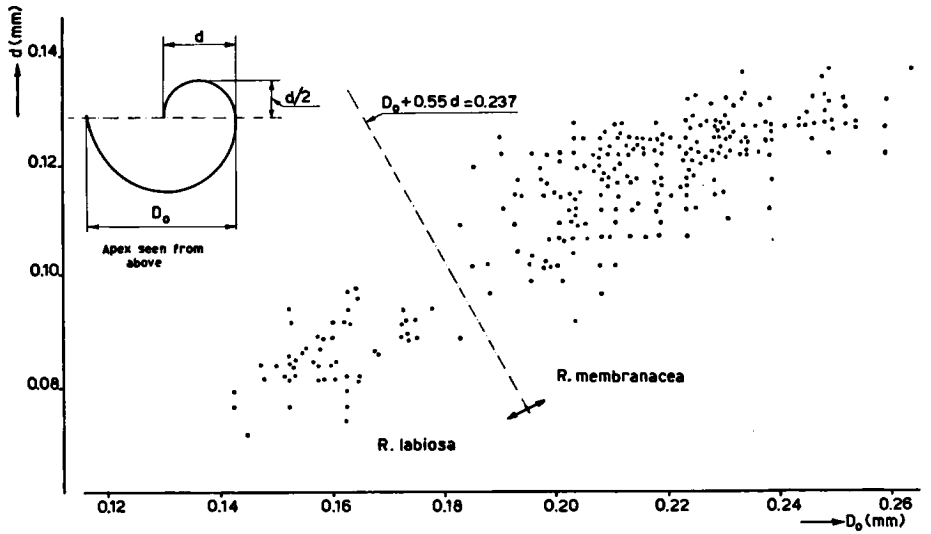


Fig. 1. Apical dimensions of the shells in a mixed sample of *R. membranacea* and *R. labiosa* from St. Lunaire, Bretagne, France. Representative shells are shown in figs. 23 and 45.

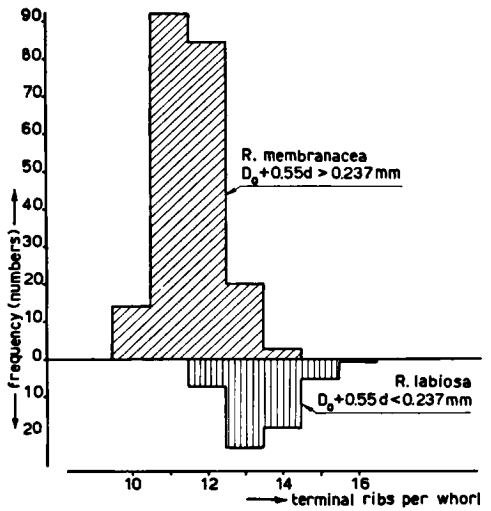


Fig. 2. The number of terminal ribs per whorl differs in the two species in the sample of fig. 1. Terminal ribs are counted backward from the last well developed longitudinal rib, not the labial rib.

were obtained. Fig. 3 shows that the correlation between the apical dimensions and the number of ribs per whorl is about non-existent in each of the forms, and by no means sufficient to explain fig. 2. Both forms in the sample are very homogeneous and, as far as I can see, completely similar to each other, apart from the differences shown in figs. 1 and 2. Figs. 23 and 45 show a good representative of each form. The sample obviously has been dredged. In combination with the striking similarity of both forms, this makes it

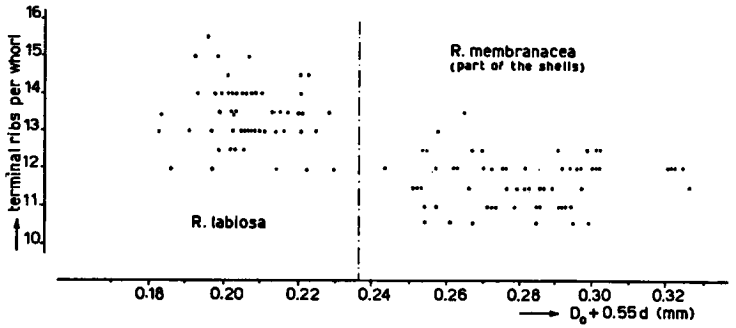


Fig. 3. For each of the two species in the sample of fig. 1 the correlations between the number of terminal ribs per whorl, as shown in fig. 2, and the apical dimensions, as shown in fig. 1, is about completely zero.

very improbable indeed that the two forms represent phenotypical adaptations of only one species to two neighbouring, but sharply separated habitats. Sexual dimorphism as an explication seems to be excluded by the fact that in samples from other localities more often than not only one of the two types of apex distinguished above occurs. Other cases of discontinuous variable characters are quite rare among shells and usually only affect the colour. It certainly is not an attractive explanation of a simultaneous discrepancy of two, apparently independent, characters. In this connection it should be remembered that a comparable case of twofold discrepancy, this time affecting the apical dimensions and the percentage of ribbed shells, has been observed before among other representatives of the genus *Rissoa* (Verduin, 1976: 36). Therefore, figs. 1 and 2 are strongly in support of the conclusion that the sample from St. Lunaire consists of two good species, which can be separated by the apical dimensions along the line $D_o + 0.55d = 0.237$ mm. As will be discussed below, shells with the smaller type of apex belong to *R. labiosa*, those with the larger type of apex to *R. membranacea* s.s.

I started this investigation by separating the shells in all samples according to the criterion derived from the above mentioned sample from St. Lunaire. Most of the samples proved to contain shells with one type of apex only, and thus confirmed the general validity of the criterion (fig. 10). The separation of the shells in the mixed samples did not give much problems either, though among the samples from Tunisia a slightly modified criterion, i.e. $D_o + 0.55d = 0.227$ mm, proved to give the best separation (figs. 38, 51). Only very occasional shells had apical dimensions so close to the criterion that it was difficult to decide which type of apex was involved.

With apices in excellent condition, the measuring accuracy of D_o is estimated to be about 0.003 mm at best, and that of d about 0.005 mm. The accuracy of $D_o + 0.55d$ which corresponds with these numbers is about 0.006 mm.

Shells of *Rissostomia* with the smaller type of apex proved to occur at many localities all along the Mediterranean, Black Sea and European Atlantic coasts, including those of the North Sea and the Baltic Sea. As will be discussed below, they all seem to belong to one species only, *R. labiosa*. Shells with the larger type of apex, however, proved to be restricted[2] to two, geographically rather distant, areas. One of these areas covers the

[2] p.t.o. for footnote 2.

Baltic Sea, the North Sea, and the northern European Atlantic coasts as far south as Bretagne, France. Shells with the larger type of apex in this area all belong to *R. membranacea*. The other area seems to be limited to Tunisia. The great majority of the shells examined from that area have the larger type of apex, the lower limit of the dimensions being about $D_0 + 0.55d = 0.227$ mm (fig. 51). The few shells examined with apices below this limit, clearly have the smaller type of apex (fig. 38). In Tunisia, both the former Lagoon of Tunis and the Golfe de Gabès are well known for the many endemic forms (see e.g. Pallary, 1912), which may have developed there rather recently from species which are still widely spread in the Mediterranean. For this reason, and because of the great distance to the area occupied by *R. membranacea*, I consider shells with the larger type of apex from Tunisia to belong to a distinct species, *R. paradoxa*. As regards the shells with the smaller type of apex from that area, I feel that the conchological differences with *R. labiosa* do not justify considering them to be a distinct species, and probably not even a subspecies (see below).

The conclusions reached in this paper are based on, among others, the conchometrical analysis of 25 selected samples of shells. In the following pages, this analysis will be presented and discussed. Throughout this discussion the biological species concept has been used, as advocated by Mayr (1964: 106, 120).

Rissoa (Rissostomia) labiosa (Montagu, 1803)

Figs. 5-14 contain the results of the conchometrical analysis of 17 samples of shells with the smaller type of apex. The origin of the samples is shown in fig. 4. The text of the labels accompanying the samples and the numbers of shells measured is given in table 1. Representative specimens from each sample are shown in figs. 17-33. Together, the 17 samples properly represent all shells of *R. labiosa* examined, with the exception of a few shells from Tunisia (which, because of their extreme slenderness, will be discussed separately) and of a few shells from the Lofoten Is., Norway, which in my opinion certainly belong to *R. labiosa*, but which by their large dimensions are distinctly outside the normal range of variability of the species (fig. 34).

The choice of most of the characters involved in the analysis is self-evident. As regards characters $A = D_n/D_{n-1}$ and W_n/D_n, figs. 8 and 9 respectively, the reader is referred to the previous paper (Verduin, 1982). Formula 5 of that paper shows that at least one of these quantities must be correlated with slenderness $1/D_{N-1}$. In order to obtain more information about this, fig. 16 has been drawn. It suggests that in *R. labiosa* both A and W_n/D_n are somewhat correlated with the slenderness.

[2] Actually, I found three shells with the larger type of apex among a small sample in colln. 2, labelled: 'Rissostomia membranacea A. Ad./Marenigrum/com. Blume/Smlg. Edlauer No. 1088'. These shells are so different from each other that I am convinced that they are from different populations. Though all three shells may well be of NW. European origin, one in particular strongly recalls certain forms from that area. This is even more true for a fourth shell in the sample, with the smaller type of apex. For this reason, the shells concerned may well be wrongly labelled, and cannot be considered sufficient proof of the occurrence of the larger type of apex in the Black Sea, particularly because colln. 2 contains many more shells from the Black Sea, though all from Varna, among which no shells with the larger type of apex are found. Neither do such shells occur among a sample of six shells in colln. 1, labelled: 'Rissoa venusta Ph./Sébastopol/Milacuevitch 3 96'.

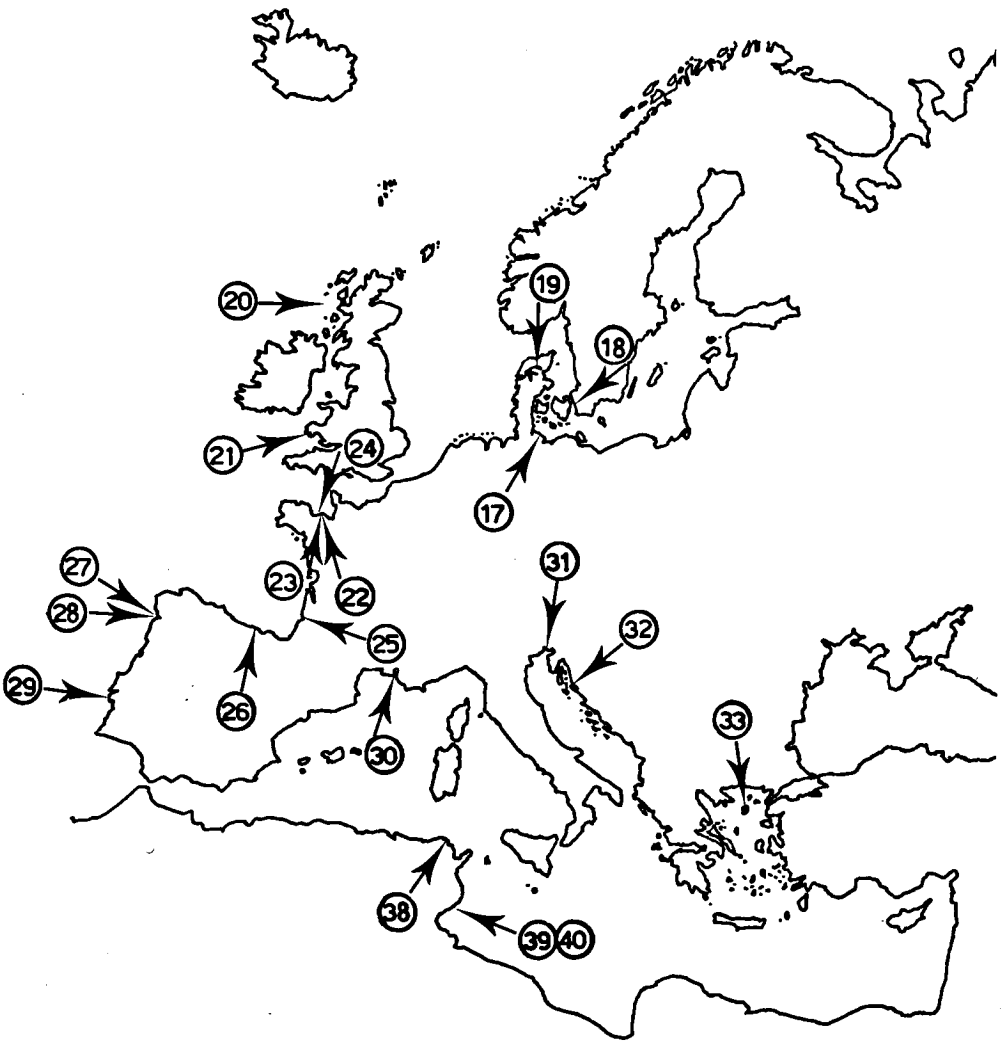
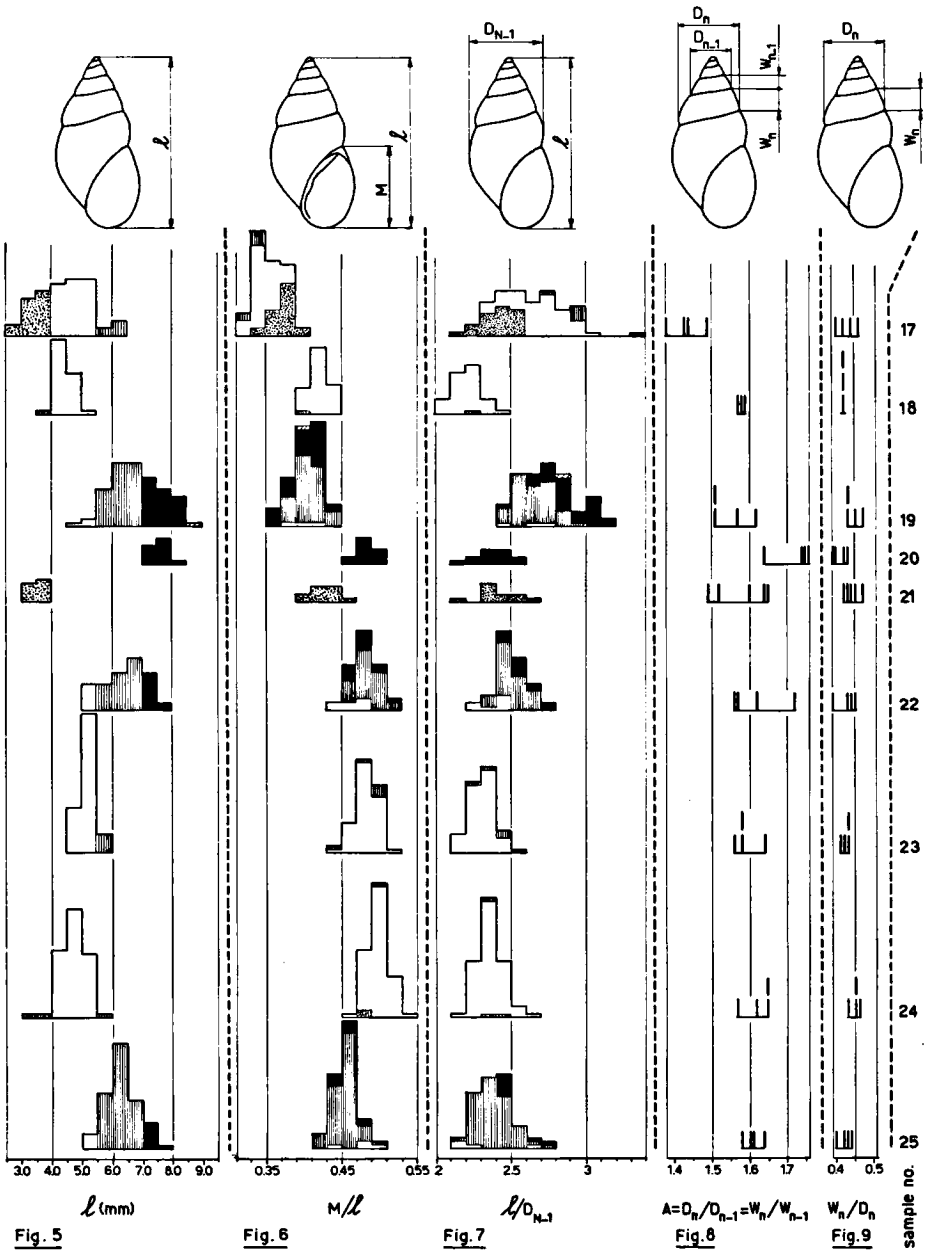
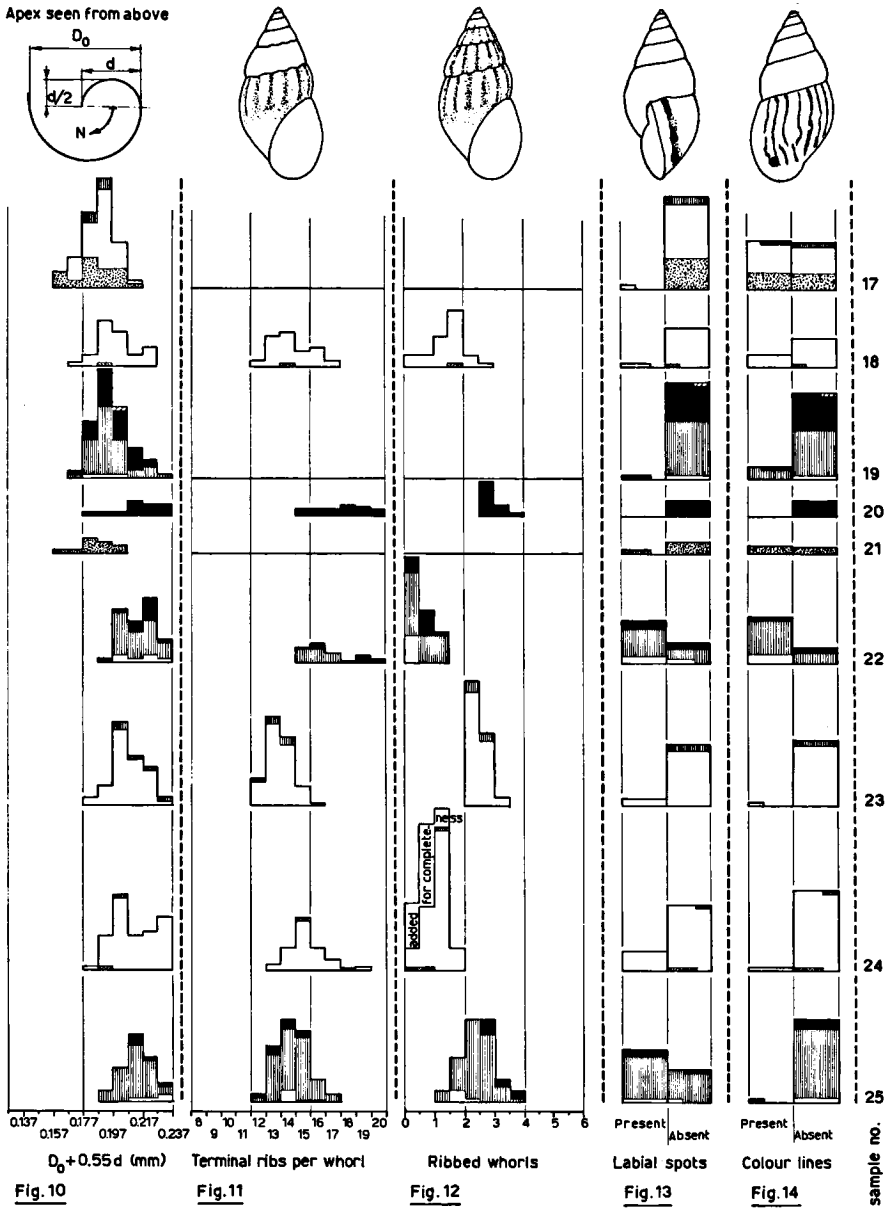


Fig. 4. Origin of the samples 17-33 and 38-40 of *R. labiosa* analyzed in figs. 5-14 and 38. A representative shell of each sample is shown in figs. 17-33 and 39-40, which numbers correspond to those of the samples. For the labels, see table 1.

All shells, except those which are more or less heavily worn, proved to possess a slight umbilical chink, caused by the lower left edge of the aperture being reflected on the lower part of the columella. Therefore, this character has not been accounted for in figs. 5-14. Similarly, the extremely fine spiral sculpture mentioned by Jeffreys (1867: 31) has not been considered, because it is very susceptible to wear and does not seem to convey much information. Generally, this sculpture seems to be about absent on almost all shells from the Mediterranean, Denmark and the Baltic. On the other hand it is present on the



Figs. 5-14. Analysis of samples 17-33 of *R. labiosa*. As regards samples 24 and 27, most of the shells of which the ribs per whorl could not be counted because of few ribs, have been left out of the analysis, except for fig. 12. Representative shells of each sample are shown in figs. 17-33, which numbers correspond to those of the samples. For the origin of the samples, see fig. 4. For the labels, see table 1.


Apex seen from above
D0
d
d/2
N
17
18
19
20
21
22
23
24
25
sample no.
0.137
0.157
0.177
0.197
0.217
0.237
D0+0.55d (mm)
Fig. 10
8 9 10 11 12 13 14 15 16 17 18 19 20
Terminal ribs per whorl
Fig. 11
0 1 2 3 4 5 6
Ribbed whorls
Fig. 12
Present
Absent
Labial spots
Fig. 13
Present
Absent
Colour lines
Fig. 14

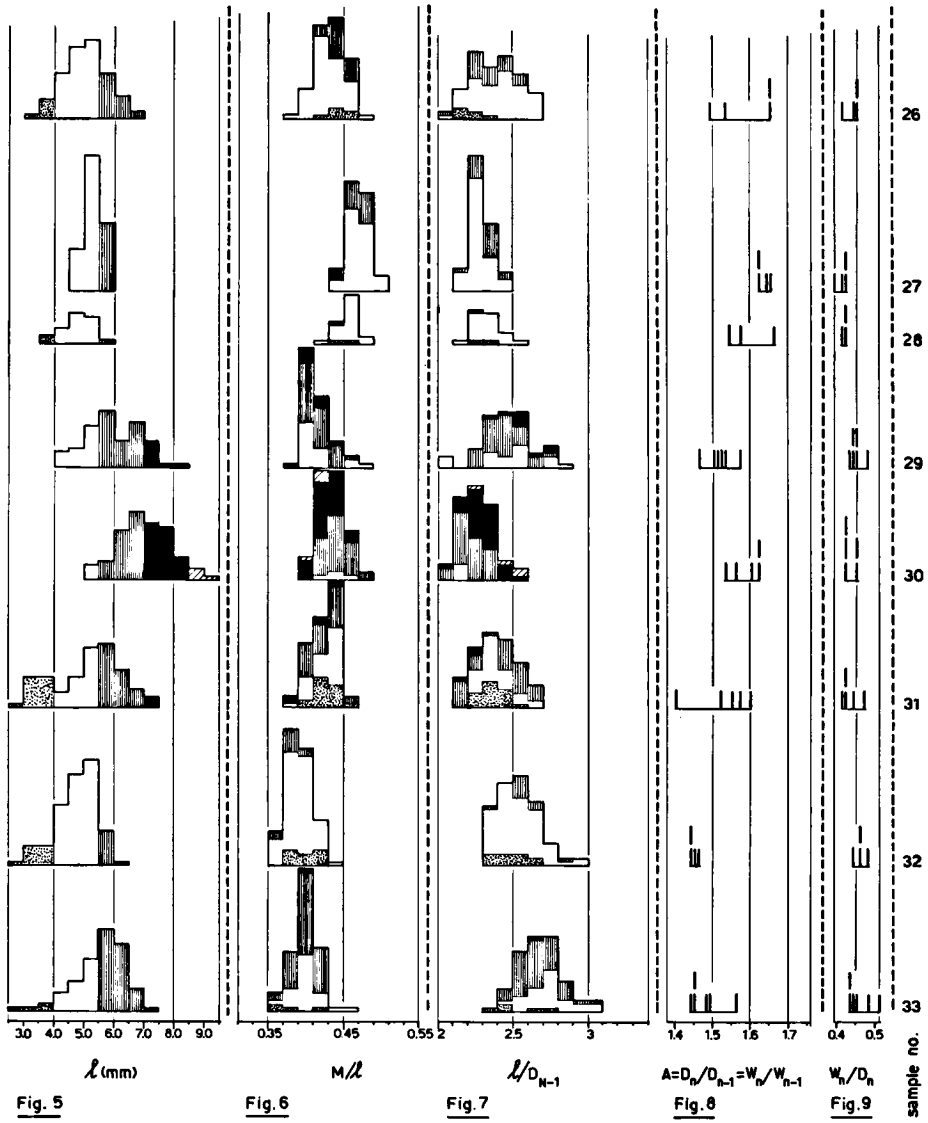
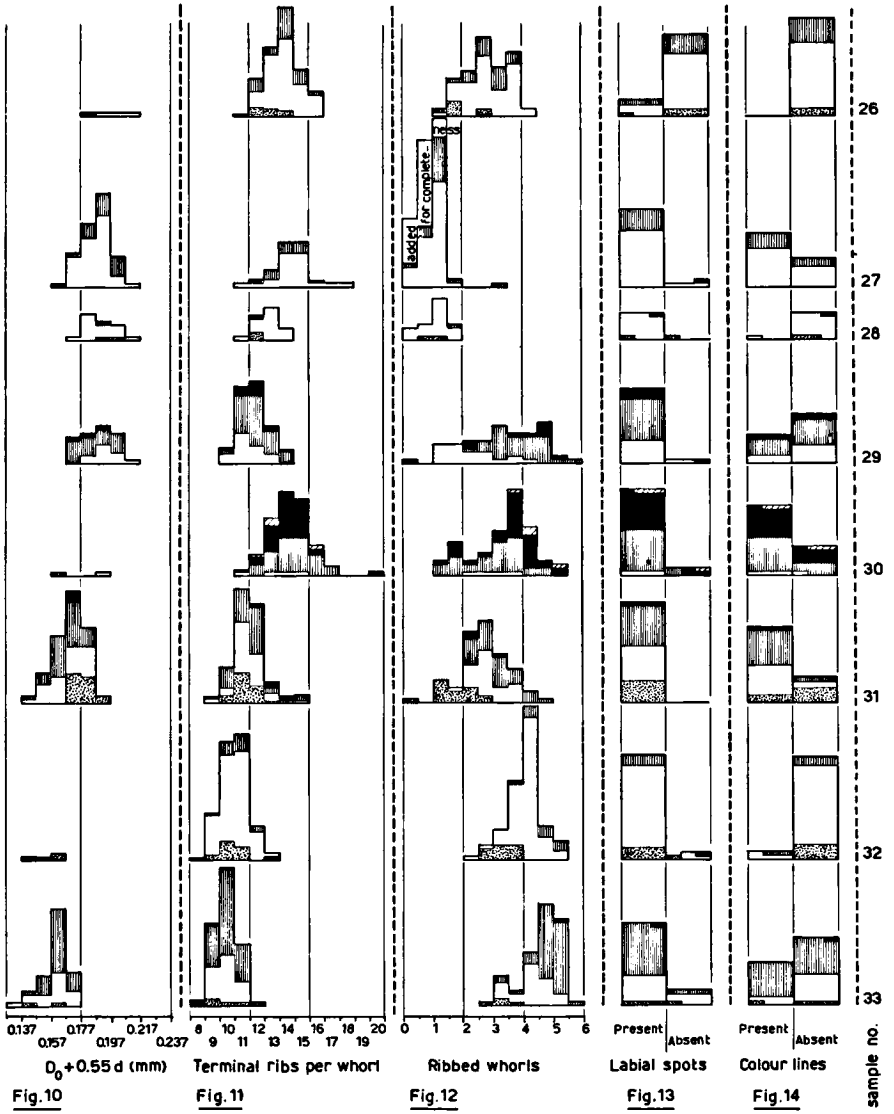


Fig. 5 Fig. 6 Fig. 7 Fig. 8 Fig. 9


26
27
28
29
30
31
32
33
ladder
for complete
0.137
0.157
0.177
0.197
0.217
0.237
D_0+0.55 d (mm)
Fig.10
8 9 10 11 12 13 14 15 16 17 18 19 20
Terminal ribs per whorl
Fig.11
0 1 2 3 4 5 6
Ribbed whorls
Fig.12
Present
Absent
Labial spots
Fig.13
Present
Absent
Colour lines
Fig.14
sample no.

Sample no.	Data from the label	Colln. no.	Number of shells measured	Condition
17	Schönberger Strand/Seegras 5-7 m/Com. Jaeckel/ Smlg. Edlauer 34665	2	75	fresh
18	Nord for Saltholms Flakfort, Øresund/8-10, 5m Skr./ 22-6-1922/Legit: Fiskeker unds. St. 13. A.C.J. Danmark	7	33	do.
19	Nibe Bredning, Limfjorden Danmark/Coll. C.M. Steenberg/14-12-1946	7	81	do.
20	W. Coast of Scotland/1847/Barlee/Jeffreys colln. 183539	5	13	do.
21	Tenby, Pembroke (Wales)/T.A. Verkrüzen/No. 9^3a	9	11	bleached
22	Réservoir du bassin de St. Malo/IX.00	1	50	fresh
23	St. Lunaire/(Zostères)/dd. 13.8.01	1	54	do.
24	Val André/dd. VII-IX-1919	1	67(+39)	do.
25	Bassin d'Arcachon/de Boury Stn. 61	1	68	do.
26	Santander/28/29-5-1959/No. 0193	12	78	fresh?
27	Ria de Arosa, Playa Laganon, baai van Rianjo, Spanje, Gallicië/10-8-1964/Reg. no. 2174. - Sta. 0.148	9	65(+40)	fresh
28	Ria de Arosa, Ensenada de El Grove/wad, verzameld op zeegras/Spanje, Gallicië/10-7-1962/ Reg. no. 2174. - Sta. 0.3	9	22	do.
29	Alfarim/19-7-1977/No. 0003	12	63	do.
30	Marignane/6-6-1961/No. 0002	12	80	do.
31	Grado/30-5-1962/No. 0016	12	79	do.
32	Punta Mika/8-6-1962/No. 0148	12	80	do.
33	Ins. Limnos, Bucht von Mudros/Seegraswiese 9m t./Aegaeis/lg. A. Papp/Smlg. Edlauer Nos. 44432, 44434, 44457, 45320 and 45322	2	78	bleached
34	Lofoten Is., Norway/G.O. Sars/Jeffreys colln. 183557	5	0	fresh
35	Udfor Øregård, Hellerup/1-2m, Ketcher/Danmark/ 20-8-1925/leg. & det. A.C. Johansen	7	2	do.
36	Kiel Bay/Meyer/Jeffreys colln. 183561	5	0	do.
37	Rissoa membranacea (J. Adams)/Mont. coll. 4210	8	1	bleached
38	Bizerte/drag. rade 10m/Chevreux No. 79/7.X.92	1	1	fresh
39	Sfax, Tunesië/No. 9616	10	1	do.
40	Sfax, Tunesië/No. 9180a	10	3	do.
41	Fleet (or Flech?) near Weymouth/Aug. 29.1894/ 1911.10.26.20984.21003	4	0	do.
42	Orwell R., England/Clark's coll./Jeffreys colln. 183540	5	1	do.
43	Horsens Fjord, Jylland, Danmark/legit O.G. Jensen	7	0	do.
44	Lough Larne, Ireland/Jeffreys colln. 183540	5	0	do.
45	St Lunaire/Zostères/dd. 13.8.01	1	0	do.
46	Rissoa tunetana Pallary/Tunis/Pallary ded.	1	1	fossil
47	Salambo, Tunesië/No. 9040	10	9	fresh
48	Zippora paradoxa Monts./Sfax, Tunis/Monterosato No. 332270	5	1	do.
49	Sfax, Tunesië/No. 9180b	10	1	do.
50	Eponges/Coll. Bouvier	1	1	do.

Table 1. Labels of the samples measured and the shells pictured, with additional information. In parentheses: shells of which only the number of ribbed whorls has been counted. The number of the figures of the shells pictured correspond to those of the samples.

shells in most samples from the European Atlantic coasts, though it is weak in sample no. 24 from Val André, and about absent in sample no. 22 from St. Malo, both in Bretagne, France. I fail to see any correlation between this sculpture and one of the other characters analyzed.

From a close examination of the shells the conclusion was drawn that not one of the samples analyzed contains more than one species[3]. This conclusion agrees well with the histograms in figs. 5-14. The slight bimodality which occurs in a few of these may be explained satisfactorily by the restricted number of shells involved. The only inhomogeneity which cannot be explained along these lines, is to be found in the N versus l diagram of sample no. 31 from Grado, northern Adria, shown in fig. 15. The larger shells in this diagram seem to fall apart into two groups, separated by an oblique zone with relatively few shells. Except for this phenomenon, which does not occur in any of the other samples analyzed, there is no reason whatsoever to believe that in the sample from Grado more than one species is present. On the contrary, the opposite is true. All this strongly re-

[3]However, a few aberrant shells have been removed from samples 19, 20 and 21. These will be discussed below.

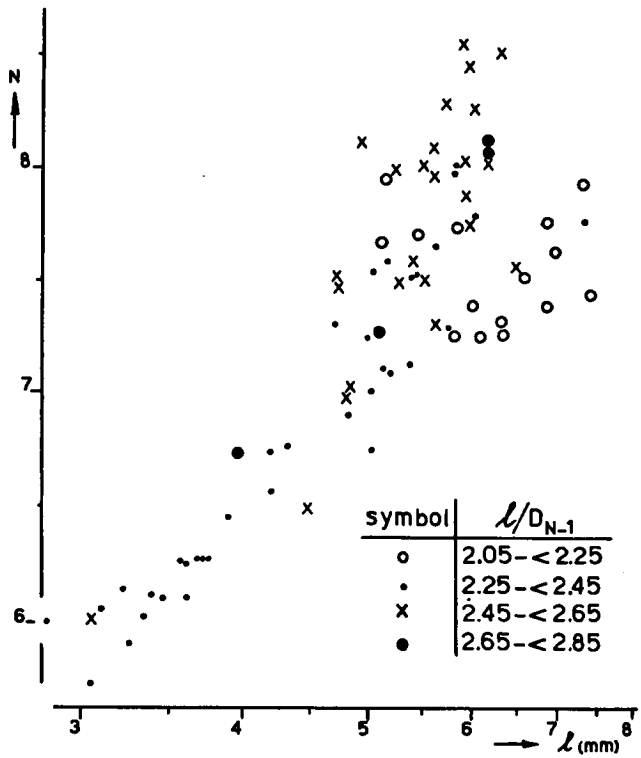


Fig. 15. Number of whorls N versus length l in sample 31 of *R. labiosa* from Grado, N. Adria. Number of whorls counted as shown in fig. 10; slenderness l/D_{N-1} measured as shown in fig. 7.

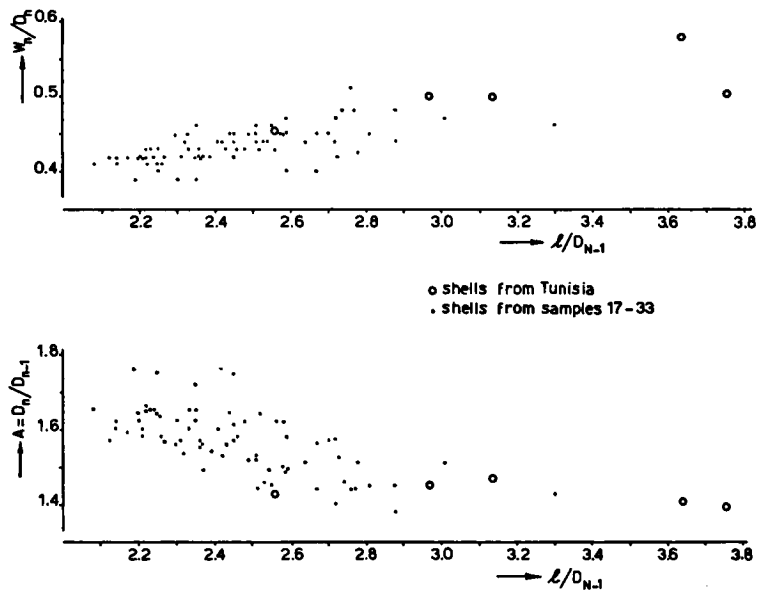


Fig. 16. Correlation between A and W_n/D_n on the one hand, and slenderness l/D_{N-1} on the other hand, among *R. labiosa*. Slenderness measured as shown in fig. 7. For A and W_n/D_n, see figs. 8 and 9, and Verduin, 1982.

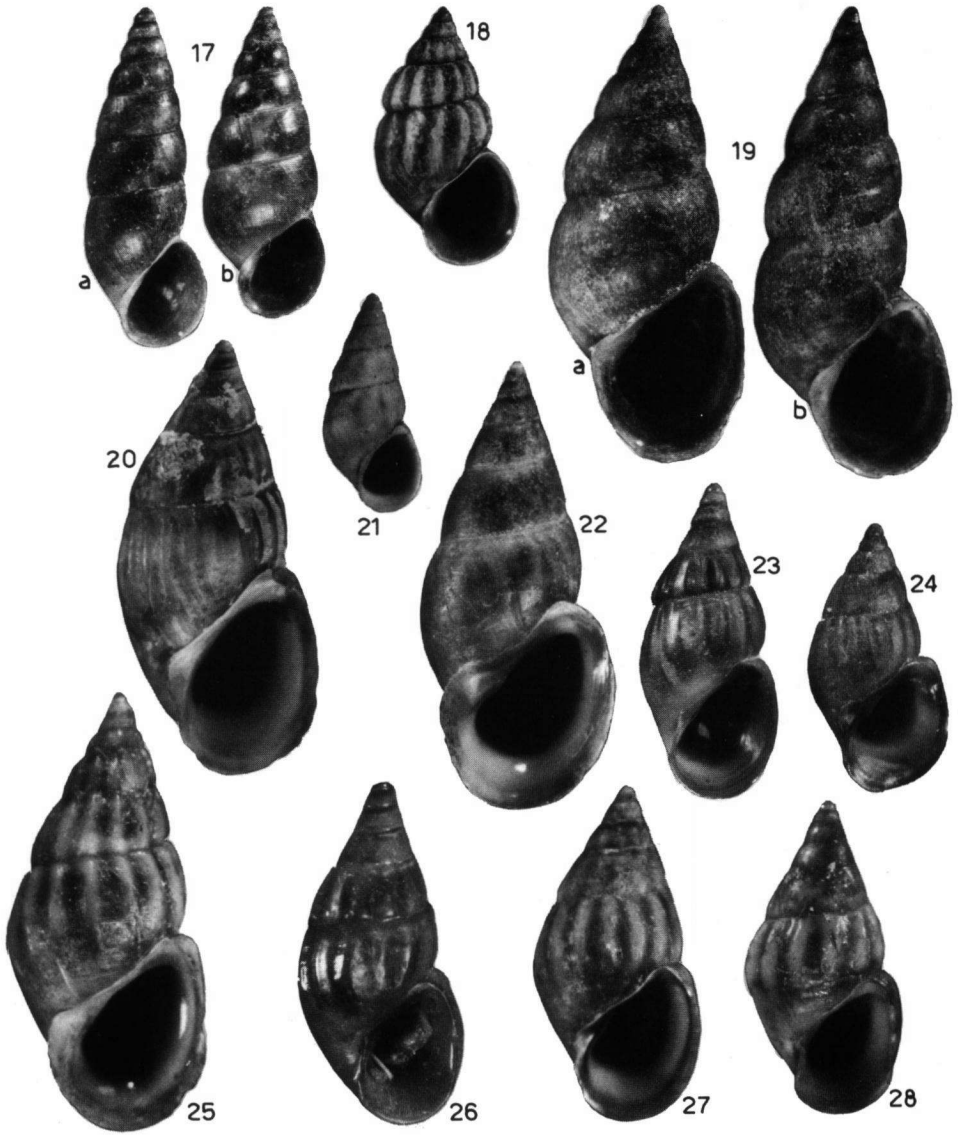
minds one of a similar phenomenon in a sample of *Cingula turriculata* (Monterosato, 1884) (Van Aartsen & Verduin, 1978: 35). The only explanation seems to be that sexual dimorphism which is usually hidden, becomes visible in the shells of occasional samples.

Different as the samples may be, it seems utterly impossible to find any character or combination of characters by which the samples themselves might be satisfactorily arranged into more than one species. Rather, the samples give the impression all to belong to the same species, which morphologically responds strongly to different living conditions at different localities. This point of view is supported by fig. 36, which represents a small sample, which, because of the ribs on the upper whorls, is intermediate between samples as different as those represented by figs. 17 and 18. It should also be mentioned that Fretter & Graham (1962: 474, 685) report the larvae of *R. membranacea* s.l. to have a short free phase among *Zostera* leaves, but not in 'open plankton'. Obviously, little exchange of genetic material (gene flow) is therefore to be expected between even almost adjoining populations, as long as these are separated by a small area inhospitable for the species.

The tentative conclusion drawn from samples 17-33, that shells of *Rissostomia* with the smaller type of apex from the area studied all belong to the same species, implies the essential assumption that nowhere populations of *Rissostomia* exist among which two taxa with the smaller type of apex may be distinguished. Therefore, all evidence to the contrary must be examined before the tentative conclusion may be accepted more definitely. As far as I am aware, the relevant literature contains no factual evidence with regard to the simultaneous occurrence of two forms of *Rissostomia*, which cannot be explained

Fig.no.	l(mm)	A	W_n/D_n	M/l	l/D_{N-1}	N
17a	5.96	1.43	0.46	0.33	3.30	8.5
17b	5.47	1.44	0.40	0.34	2.69	7.8
18	4.60	1.62	0.37	0.46	2.22	6.5
19a	8.05	1.57	0.45	0.42	2.67	7.8
19b	8.34	1.51	0.47	0.38	2.98	8.5
20	7.75	1.64	0.43	0.44	2.52	7.0
21	3.86	1.49	0.47	0.40	2.59	6.7
22	7.94	1.57	0.44	0.41	2.72	7.6
23	5.63	1.58	0.43	0.43	2.50	7.0
24	4.78	1.65	0.46	0.47	2.35	6.1
25	7.74	1.61	0.44	0.43	2.45	7.5
26	6.20	1.53	0.44	0.39	2.42	-
27	5.92	1.65	0.42	0.45	2.24	6.8
28	5.56	1.57	0.42	0.44	2.27	7.1
29a	5.43	1.53	0.44	0.42	2.32	7.3
29b	7.21	1.50	0.45	0.40	2.58	8.3
30a	6.60	1.60	0.44	0.43	2.20	7.4
30b	7.85	1.56	0.45	0.41	2.30	-
31a	3.24	1.55	0.42	0.40	2.36	6.2
31b	5.94	1.52	0.44	0.40	2.51	7.8
31c	6.89	1.57	0.42	0.44	2.12	7.8
32	5.40	1.44	0.46	0.39	2.51	-
33a	6.24	1.44	0.51	0.38	2.76	8.4
33b	5.92	1.48	0.43	0.41	2.50	ca.8
34	13.40	-	-	0.42	2.43	9.2
35a	4.22	1.59	0.40	0.39	2.11	6.5
35b	5.07	1.43	0.43	0.32	2.52	7.7
36	-	-	-	-	-	-
37	6.9	1.68	0.42	0.47	2.50	6.7
39	6.03	1.45	0.50	0.43	2.97	7.7
40	7.91	1.39	0.51	0.38	3.77	9.0
41	-	-	-	-	-	-
42	7.9	1.48	0.51	0.40	2.85	7.7
43	-	-	-	-	-	-
44	-	-	-	-	-	-
45	-	-	-	-	-	-
46	7.8	1.46	0.51	0.40	3.05	7.7
47a	4.21	1.44	0.47	0.40	2.91	6.5
47b	6.90	1.50	0.49	0.40	2.92	7.7
47c	5.80	1.59	0.44	0.45	2.41	6.6
48	6.9	1.41	0.64	0.36	3.94	7.6
49	5.82	1.43	0.60	0.36	3.53	ca.7
50	8.80	1.40	0.59	0.37	4.01	8.2

Table 2. Numerical data of the shells pictured.



Figs. 17-33. Representative shells of samples 17-33 of *R. labiosa*. The numbers of the shells figured correspond to those of the samples. For the origin of the shells, see fig. 4; for the labels, see table 1; for numerical data, see table 2. Other shells from samples 22 and 27 have been figured in Verduin, 1982. Magnification 7.5x.

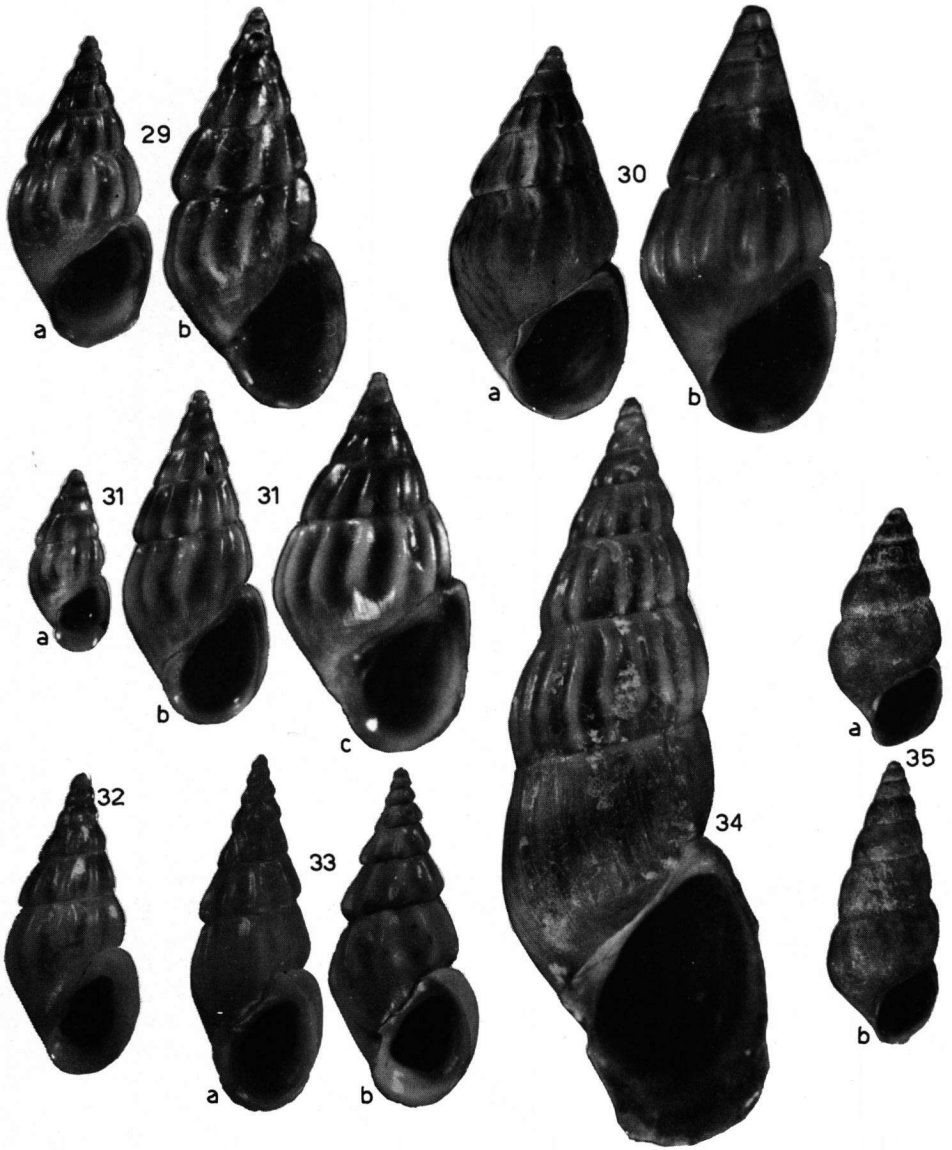


Fig. 34. Very large shell of *R. labiosa* from the Lofoten, Norway. See also no. 34 in tables 1 and 2. Magnification 7.5x.

Fig. 35. Representative shells of two different forms from a sample of *R. labiosa* from Udfor Øregård, Hellerup, Denmark. See also no. 35 in tables 1 and 2. Magnification 7.5x.

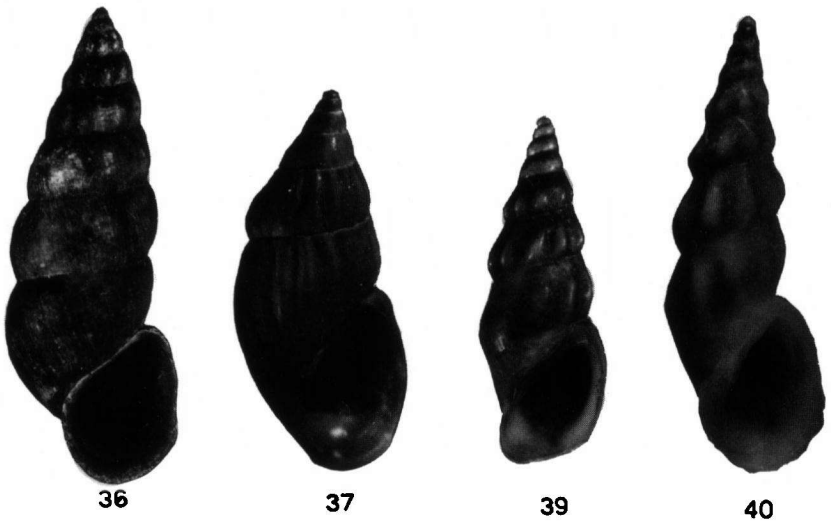


Fig. 36. Representative shell of a sample of seven shells of *R. labiosa* from Kiel Bay, Baltic Sea. The ribbed upper part of the shells strongly resembles shells in sample 18. Thus, the sample unites the rather different forms shown in figs. 17 and 18. For the labels, see table 1. Magnification 7.5x.
Fig. 37. *R. labiosa*, lectotype. Locality unknown. Selected from among sample 37 in table 1. See also table 2. Magnification 7.5x.
Figs. 39-40. Shells from samples 39-40 respectively of *R. labiosa* from Sfax, Tunisia. For the labels, see table 1; for numerical data, see table 2. Magnification 7.5x.

satisfactorily by the presence of *R. labiosa* and *R. membranacea* in one population. Some of the many forms published have been widely accepted as good species, but this in itself, of course, is not sufficient evidence of the presence of more than one species in the sense of the biological species concept.

More substantial evidence is to be found among the samples examined which are not represented in figs. 5-14. Generally, these samples support satisfactorily the tentative conclusion. In the Jeffreys collection, however, nearly every sample of *Rissostomia* from the British Isles with shells with the smaller type of apex contains two or three forms. One of these forms is shown in fig. 20 and is represented by sample no. 20 in figs. 5-14. The shells are solid and morphologically rather constant, and generally have been collected in a very fresh state. This form closely meets the original diagnosis of *R. labiosa*. The second form is shown in fig. 21 and is represented by sample no. 21. Shells of this form are morphologically also very constant and, though well preserved, always have a subfossil appearance. The third form is always fresh, slender, smooth and rather fragile. It much resembles the shell from Nibe Bredning, Denmark, shown in fig. 17, and is morphologically also rather constant. Samples 183536 (Loch Fyne, Scotland), 183540 (Larne Lough, Ireland), 183542 (Tenby, Wales) and 183545 (Weymouth, S. England) contain all three forms. Samples 183537 (Inverary, Scotland), 183538 (Loch Carron, Scotland), 183539 (W. coast of Scotland) (= sample no. 20 in figs. 5-14), 183541 (Bertraghbury Bay, Connemara, Ireland) and 183546 (Poole, S. England) contain the first and the second forms, while samples 183535 (Loch Fyne, Scotland), 183544 ('Southton', abbre-

viation of Southampton?), 183548 (Eymouth, E. Scotland) and 183549 (Eymouth) contain the first and the third forms. Numerically, the first form dominates in all samples concerned. The second and third forms are never represented by more than a few shells, and often by only a single shell.

I carefully examined all other samples, including those from the British Isles in colln. 4. Apart from a few stray samples, which contain one or two aberrant shells which possibly have been wrongly labelled or otherwise[4], I found only one other sample, in colln. 7, which contains two, slightly different, forms. It is from Udfor Øregård, Hellerup. Representatives of both forms are shown in fig. 35. I cannot see any connection between this dimorphism and the dimorphism and even trimorphism in the samples in the Jeffreys collection. I rather believe that the sample from Denmark has been dredged at two nearby localities with slightly different living conditions, which may have resulted in slight differences in the form of the shells.

All this results in the curious situation that the great majority of the British samples in the Jeffreys collection are in favour of the view that at least two taxa occur among the shells of *Rissostomia* with the smaller type of apex, while it proved to be impossible to find any serious support for this view among the many other samples examined. Jeffreys himself (1867: 30) obviously saw no reason to distinguish more than one species among his material, possibly because he was aware that his samples could contain shells from more than one population. Yet, we cannot be sure about this. Therefore, it would be interesting to have reliable information about age and stratigraphical origin of the second form, and about the possible simultaneous occurrence of the first and the third form in the British Isles. As long as such data are not available, however, it does not seem justified to recognize more than one species among the material studied.

We now come to the nomenclatorial problems. The oldest name available is *Turbo membranacea* J. Adams, 1800. Neither the original diagnosis and figure (Adams, 1800: 2), nor any subsequent publication known to me contains information on the apical dimensions. The type specimens have probably been lost. Anyhow, the Adams collection is not in Dance's list (1966: 275 sqq.), and in the British Museum (Natural History) nobody knew about the possible whereabouts of the original material of *R. membranacea*. No shells from the type locality, the Wash, are present among the samples examined, nor are they in the Royal Albert Memorial Museum, Exeter. A request for assistance in 'The Conchologists' Newsletter' of June 1980, in which I asked for the loan of shells from the Wash for the purpose of selecting a neotype, evoked no response. Among the material available, however, two English samples agree remarkably well with the original description, i.e. a sample from Fleet (or Flech?) near Weymouth and a sample from the Orwell River. Figs. 41 and 42 show representative specimens. The shells in both samples have the larger type of apex. Because there are no samples among the material from the British Isles with the smaller type of apex which agree as closely with the original diagnosis of *R. membranacea*, it is probable that the name applies to the form with the larger type of

[4] Among others, this refers to two shells which have been removed from sample no. 19, mainly because they proved to be slightly but distinctly outside the range of variation of the other shells in the sample as regards the number of whorls in relation to the length, and to one shell which has been removed from sample no. 21, because it is distinctly larger than the remaining shells, and because it is the only one which had been glued to a piece of paper.

apex. In order to put an end to all incertainty, I have selected a neotype of *R. membranacea* from among the sample from the Orwell River (no. 42 in table 1), which is closest to the Wash. It is shown in fig. 42, and has the following characters: length l = 7.9 mm; slenderness l/D_{N-1} = 2.85; relative height of the aperture M/l = 0.40; number of whorls N = 7.7; apical dimensions d = 0.12 mm, D_0 = 0.24 mm; there are no longitudinal ribs, nor a labial rib; there are no fine spiral striae; A = 1.48 and W_n/D_n = 0.51. The longitudinal colour lines mentioned in the original diagnosis are absent on the shells in the sample from the Orwell River, but are well developed on the shells in the sample from Fleet. There are 7 paraneotypes with undamaged tops in the sample from the Orwell River.

For the sake of completeness I have selected a lectotype of *R. labiosa* from two samples in the Montagu collection, now in the Royal Albert Memorial Museum, Exeter. One of the samples contains four shells glued to a piece of paper, labelled 'labiosa' written by hand. The apices of two of these shells are damaged, one shell has the smaller, and one the larger type of apex. The other sample contains 50 shells, i.e. 22 with damaged apices, 4 with the smaller, and 14 with the larger type of apex. It is not labelled, but I received both samples in a plastic box which contains two labels: one reading 'labiosa' in a handwriting different from that on the label of the first sample, and one typed label, reading 'Rissoa membranacea (J. Adams)/Mont. coll. 4210'. Because the original diagnosis (Montagu, 1803: 400) applies very satisfactorily to the form shown in fig. 20, which is present in many samples from all over Great Britain, and which has the smaller type of apex, I decided that the specific name which is second in seniority, i.e. *labiosa*, should be connected to the species with the smaller type of apex, notwithstanding its relatively weak numerical representation in Montagu's samples. Therefore, I selected the lectotype from among the four shells mentioned above with the smaller type of apex in the second sample. It is shown in fig. 37, and has the following characters: length l = 6.9 mm; slenderness l/D_{N-1} = 2.50; relative height of the aperture M/l = 0.47; number of whorls N = 6.7; apical dimensions d = 0.08 mm, D_0 = 0.17 mm; 17 terminal ribs per whorl; $2^1/_4$ ribbed whorls; strong labial rib; there are no fine spiral striae; A = 1.68, W_n/D_n = 0.42.

Because the malacofauna in the Golfe de Gabès, Tunisia, is known to have a distinctly endemic character, I prefer to discuss the material from that area separately. With regard to this fauna, Pallary (1904: 214) wrote: 'D'une manière générale tous les Gastropodes ont la coquille bien plus allongée que dans les formes similaires du reste de la Méditerranée. Cette tendance à l'allongement de la spire est un caractère bien constant et bien spécial à la faune du golfe de Gabès'. Later (1906: 116) he explained: 'C'est à la grande densité de ces zostères qu'il faut attribuer l'allongement de la spire dont nous avons déjà fait mention'. Indeed, the main problem with regard to the systematic position of shells of *Rissostomia* with the smaller type of apex from the Golfe de Gabès is the extreme slenderness of most shells. Among the material examined I found only twelve shells with this type of apex. Four of these, belonging to samples 39 and 40, are shown in graphs 16 and 38. The remaining eight shells have not been measured, but they are as slender as, or slightly more slender than, the specimen shown in fig. 40, which itself is the most slender shell in graphs 16 and 38. Otherwise they only differ from the four shells measured in that they are bleached, whitish and opaque, instead of fresh.

For ease of comparison, the lowermost row of histograms of figs. 5-14, representing sample 33 from Mudros, Greece, has been reproduced on a small scale at the top of fig. 38. The shell in sample 38, from Bizerte, about 50 km NW. of Tunis, which is outside the

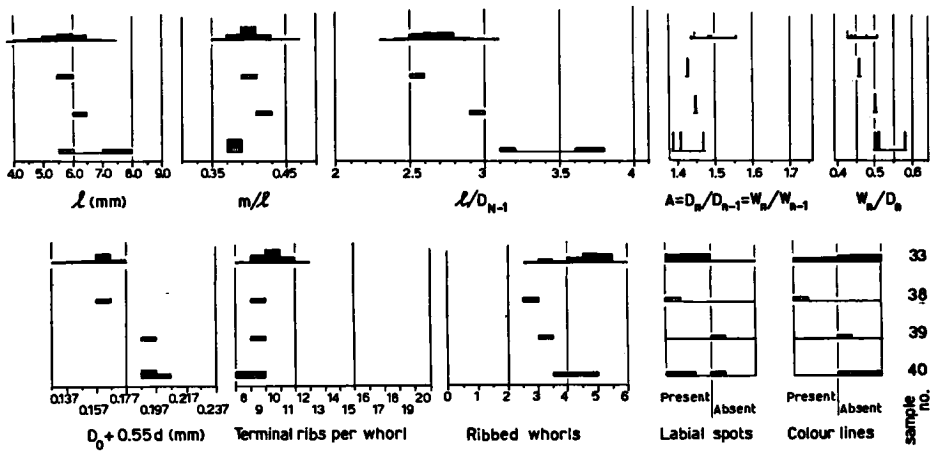


Fig. 38. Analysis of the samples 38-40 of *R. labiosa* from Tunisia. The shells of figs. 39-40 belong to samples 39-40 respectively. For the origin of the samples, see fig. 4. For the labels, see table 1.

Golfe de Gabès, does not really differ from the sample from Mudros. Similarly, some of the shells in samples 39 and 40, from the Golfe de Gabès, are not, or hardly, outside the range of variation known from other Mediterranean samples of *R. labiosa*. Thus, there seems to be no good reason to consider these a separate species. On the other hand, there is no reason to surmise that they are not conspecific with the more slender specimens from the Golfe de Gabès. As long as so little material is available for study, it therefore seems best to attach no special taxonomic status to the shells examined, but to consider them to belong to another local form, or possibly a subspecies, of *R. labiosa*.

I have seen no shells with the smaller type of apex from the former Lagoon of Tunis.

Rissoa (Rissostomia) membranacea (J. Adams, 1800)

Shells of *R. membranacea* differ from those of *R. labiosa* in the larger apical dimensions, i.e. $D_0 + 0.55d > 0.237$ mm. For the remainder, the variability of both species shows a remarkable similarity. Because shells of *R. labiosa* have been investigated intensively in this paper, those of *R. membranacea* have not been worked out in detail. A few forms are shown in figs. 41-45.

R. membranacea is common at many localities in and around the Baltic, the North Sea, the Irish Sea and the Channel. I have seen no specimens from Norway, nor from localities south of Bretagne, France.

Rissoa (Rissostomia) paradoxa (Monterosato, 1844)

Many collections contain well preserved samples of mostly bleached, whitish and opaque shells of *Rissostomia* with the larger type of apex from Tunisia. Such shells seem to be as clearly separated from those with the smaller type of apex in Tunisia as are *R.*

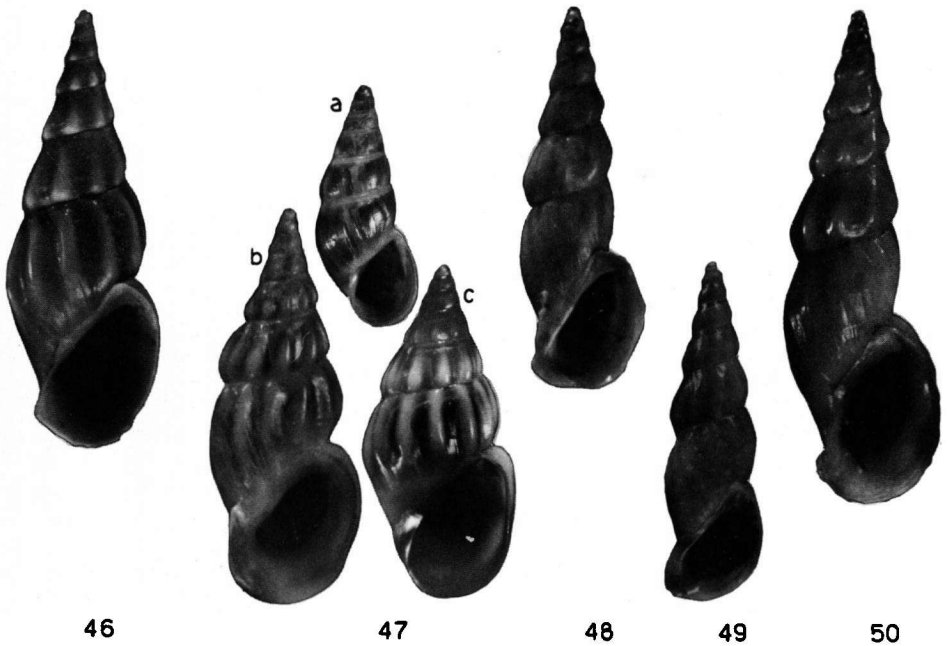
Figs. 41-45. Shells of *R. membranacea* from different localities. Figs. 41 and 42 represent samples which agree well with the original description. The shell shown in fig. 42 is the neotype, from the Orwell River, SW. England, selected from among sample 42. Sample 41 from Fleet (or Flech?) near Weymouth, S. England; sample 43 from Horsens Fjord, Denmark; sample 44 from Larne, Ireland; sample 45 from St. Lunaire, Bretagne, France. For the labels, see table 1. Magnification 7.5x.

membranacea and *R. labiosa* in NW. Europe[5]. Therefore, I am convinced that the shells with the larger type of apex from Tunisia, which meet the slightly modified criterion $D_o + 0.55d > 0.227$ mm, do not belong to *R. labiosa*. Because of the great geographical distance to the range of *R. membranacea*, it also seems to be improbable that they belong to that species. Consequently, they must belong to a third species.

Colln. 5 contains four samples, nos. 332269-332272, which, with variations, are labelled: 'Zippora paradoxa Monts./Sfax, Tunis/Monterosato'. One of these, no. 332272, is accompanied by a handwritten label reading: 'Zippora paradoxa Monts. 1884 Typ. = auriscalp. var. expansa, BDD typ. Eponges de Sfax'. The tops of the shells in this sample, however, are all damaged. The shells in the remaining samples, as far as undamaged, have the larger type of apex. I selected a lectotype from among the shells of sample no. 332270. It is fresh, with an operculum still visible in the aperture. It is shown in fig. 48, and has the following characters: length l = 6.9 mm; slenderness $l/D_{N-1} = 3.94$; relative height of the aperture M/l = 0.36; number of whorls N= 7.6; apical dimensions d = 0.12 mm, $D_o = 0.21$ mm; 10 terminal ribs per whorl; $3^3/_4$ ribbed whorls; slight labial rib; weak and very fine spiral sculpture; A = 1.41, $W_n/D_n = 0.64$. There are six paralectotypes with undamaged apices in the sample, and 13 in the remaining samples.

As is illustrated by the numerous varieties mentioned by Pallary (1906: 96-97), *R. paradoxa* is a variable species. Figs. 47-50 show fresh specimens from the Golfe de Gabès as well as from other Tunisian localities; see also fig. 51. Again, specimens from the Golfe

[5]The number of shells with the smaller type of apex examined from Tunisia is too low to write with certainty.



Figs. 46-50. Shells of *R. paradoxa* from different Tunisian localities. Fig. 46 - lectotype of forma *tunetana* Pallary, 1912, fossil from the former Lagoon of Tunis, selected from among sample 46; sample 47 from Salambo, a few km NO. of Tunis; fig. 48 - lectotype of *R. paradoxa* from Sfax, Golfe de Gabès, selected from among sample 48; sample 49 from Sfax; sample 50 from unknown locality, in my opinion from the Golfe de Gabès. For the labels, see table 1; for numerical data, see table 2. Magnification 7.5x.

de Gabès (i.e. those from Sfax) tend to be much more slender than those from other areas (e.g. those from Salambo). As in *R. labiosa*, it is difficult to believe that all these different forms do not belong to only one species. It does seem to be improbable indeed that such a small area would harbour two species of *Rissostomia* with the larger type of apex, while no such species are found elsewhere in the Mediterranean.

Pallary (1912: 9) considered his species *R. tunetana*, described from fossil material from the former Lagoon of Tunis, to be distinct from *R. paradoxa*, without giving convincing reasons for his opinion. Because information about the apical dimensions is absent, *R. tunetana* can no more be identified from the original diagnosis as can *R. paradoxa*. Colln. 1, however, contains a sample labelled: 'Rissoa tunetana Pallary/Tunis/ Pallary ded.'. All shells with undamaged tops in the sample have the larger type of apex. As is illustrated by the great number of varieties mentioned by Pallary, *R. tunetana* is also a very variable form. Because I can see no good reason why *R. tunetana* should be considered to be distinct from *R. paradoxa*, I consider them to be synonyms. I have designated a lectotype of *R. tunetana* from among the sample mentioned above. It is shown in fig. 46 and has the following characters: length l = 7.8 mm; slenderness $l/D_{N-1} = 3.05$; relative height of the aperture M/l = 0.40; number of whorls N = 7.7; apical dimensions d =

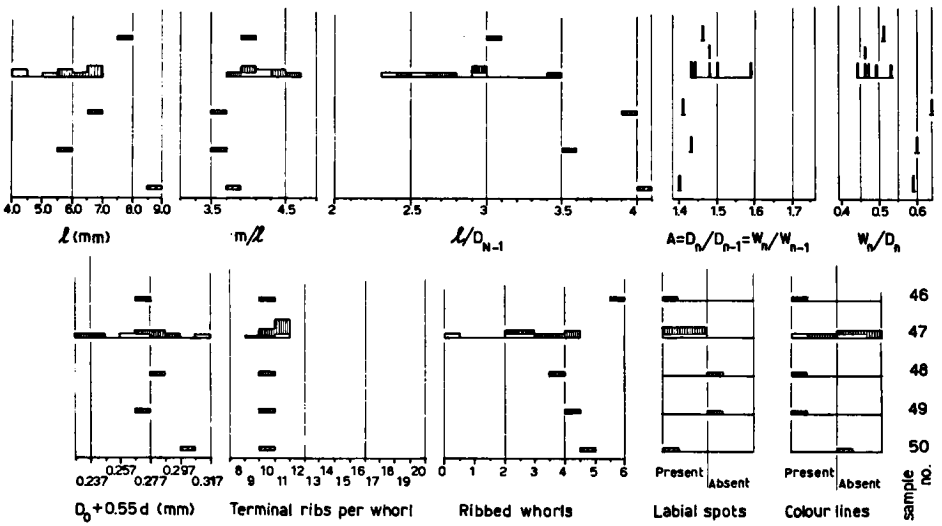


Fig. 51. Analysis of samples 46-50 of *R. paradoxa* from different Tunisian localities. These include the lectotypes of *R. paradoxa* and its forma *tunetana*. Representative shells are shown in figs. 46-50.

0.1 mm, D_0 = 0.21 mm; 10 terminal ribs per whorl; $5^3/_4$ ribbed whorls; weak labial rib; traces of weak and very fine spiral sculpture; A = 1.46, W_n/D_n = 0.51; narrow dark longitudinal colour lines. There are 12 paralectotypes with undamaged top in the sample.

Attention is drawn to the fact that some of the samples from the Golfe de Gabès have been collected from sponges, which is not the usual habitat of *Rissostomia*. Because the shells involved usually look far from fresh, I am inclined to believe that *R. paradoxa* generally does not live in sponges.

SYNONYMS

As far as I am aware, this investigation covers all taxa of the subgenus *Rissostomia*. With regard to the species which belong to that subgenus, however, I cannot agree with Nordsieck (1972). Because of the little factual evidence available, we can, of course, but guess at the true phylogenetical relationships among the genus *Rissoa* s.l. As to these, therefore, everyone is entitled to his own opinions. Yet, it does not seem to be reasonable to place *R. lineolata* Michaud, 1832, in another subgenus than *R. radiata* Philippi, 1836, as it is sometimes next to impossible to separate the shells of both species (Verduin, 1976: 42). Similarly, I can see no reason to remove *R. oblonga* Desmarest, 1814, *R. elata* Philippi, 1844, *R. paradoxa* and *R. tunetana* from *Rissostomia*, and to place them in a taxon of which *R. auriscalpium* (Linné, 1758) is the type species. From this investigation it is evident that the slenderness of the shells, a character which seems to have led Nordsieck to his views, is not of much taxonomic importance among *Rissostomia*. Personally, I am inclined to attach more value to the characteristic spiral sculpture

on the lower part of the body whorl of *R. auriscalpium*, which is completely absent in *Rissostomia*, and to the projection on the inner lip of the aperture, which is a character of *Rissostomia*, and which is absent in *R. auriscalpium*.

I have made no attempt to examine type material of synonymous species. Information about the apical dimensions is absent in all diagnoses and pictures of these species. Therefore, I could only identify those species which have been described from regions where only one species occurs, i.e. *R. labiosa*. This applies to *R. oblonga*, *R. elata*, *R. fragilis* Michaud, 1832, *R. venusta* Philippi, 1844, and *R. pontica* Milachewitch, 1916. In my opinion, Philippi created *R. elata* because he misunderstood *R. oblonga*. Anyway, in 1836 he did not yet mention the very common species *R. similis* Scacchi, 1836, but only mentioned *R. oblonga* as 'satis frequens'. In 1844 the description of *R. oblonga* had been slightly changed and had become very similar indeed to that of *R. similis*, which is mentioned as 'rarior'. In my experience, however, *R. similis* and the closely related species *R. lia* (Monterosato, 1884) and *R. guerinii* Récluz, 1843, are far more frequent on the coast of Sicily than *R. labiosa* (see also Priolo, 1954). All this supports the view that Philippi considered *R. oblonga* as a form closely related to *R. similis*.

The type localities of *R. grossa* Michaud, 1832, are south France and Great Britain. I consider shells from the former locality synonymous with *R. labiosa*. The British specimens cannot be identified as long as the apical dimensions are unknown. The same is true with regard to *R. cornea* Lovén, 1846, *R. octona* (Nilsson, 1822), *R. souleyetana* Récluz, 1843, *R. costata* (Pulteney, 1813), and *R. pulla* Brown, 1844. Nordsieck (1972) described *R. transitans* and *R. paradoxissima* from Tunisia. Probably these are also synonyms of *R. paradoxa*.

I most sincerely thank all persons and institutions which have contributed to this paper by the loan of material; I am also indebted to Dr. J. van Goethem, Brussels, for his hospitality.

ABSTRACT AND CONCLUSIONS

From an extensive conchological investigation it is concluded that the Recent forms of the subgenus *Rissostomia* Sars, 1878, probably belong to three species only. Of these, *Rissoa labiosa* (Montagu, 1803) is represented by a great number of local forms from the Black Sea to the North Sea and the Baltic. Shells of *R. membranacea* (J. Adams, 1800) and of *R. paradoxa* (Monterosato, 1884) can often only be separated from those of *R. labiosa* by the larger apical dimensions. *R. membranacea* occurs in many local forms in north and north-west Europe. It seems to have its southern limit in south Bretagne, France. *R. paradoxa* seems to be restricted to Tunisia.

A neotype of *R. membranacea* and lectotypes of *R. labiosa*, of *R. paradoxa* and of *R. tunetana* Pallary, 1912, a junior synonym of *R. paradoxa*, have been selected.

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SAMENVATTING

Over de taxonomie en de variabiliteit van recente Europese en Noordafrikaanse soorten van het subgenus *Rissostomia* Sars, 1878, van het geslacht *Rissoa* Desmarest, 1814

Op grond van een uitgebreid conchologisch onderzoek wordt geconcludeerd dat de recente vormen van *Rissostomia* tot slechts drie soorten behoren. *Rissoa labiosa* (Montagu, 1803) is door een groot aantal plaatselijke vormen vertegenwoordigd in een gebied dat zich uitstrekt van de Zwarte Zee tot de Oostzee. Schelpen van *R. membranacea* (J. Adams, 1800) en van *R. paradoxa* (Monterosato, 1884) kunnen gewoonlijk slechts van die van *R. labiosa* onderscheiden worden aan de hand van de grotere topwinding. De grens tussen *R. labiosa* en *R. membranacea* blijkt bij $D_O + 0{,}55d = 0{,}237$ mm te liggen (zie fig. 1, die de top weergeeft, van bovenaf gezien). De grens tussen *R. labiosa* en *R. paradoxa* ligt bij $D_O + 0{,}55d = 0{,}227$ mm. *R. membranacea* komt in veel plaatselijke vormen voor in Noord- en Noordwest-Europa. De zuidelijke grens van het verspreidingsgebied lijkt in Zuid-Bretagne, Frankrijk, te liggen. Het verspreidingsgebied van *R. paradoxa* lijkt zich te beperken tot de kust van Tunesië.