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The marine mollusk fauna of the Virginian area as a basis for defining Zoogeographical provinces*)

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INTRODUCTION

The littoral fauna of the Atlantic coast of North America may be divided by the zoogeographer into several provinces. To the north is the circumpolar Arctic province, whose southern boundary differs according to several authors: Labrador (SVERDRUP c.s., 1954); Newfoundland (JOHNSON, 1934); or northern Nova Scotia (P.-H. FISCHER, 1950). The STEPHENSONS' (1954) recognize a sub-arctic area, the Syrtensian province, extending from Labrador to the Gulf of St. Lawrence. The next zoogeographical region is the cold-temperate Boreal province, whose southern boundary is Cape Cod. It is also called the Acadian or Nova Scotian province (Map 1).

South of Cape Cod is the so-called Transatlantic province, which extends to Florida: Cape Canaveral (STEPHENSON and STEPHENSON, 1952); Jupiter Inlet (CLENCH, 1945); or the southern tip of Florida (FISCHER, 1950). The northern coast of the Gulf of Mexico, from Texas to Cedar Keys (or Tampa Bay or Sanibel Island), Florida, is sometimes considered to be an extension of the Transatlantic province (JOHNSON, 1934; REHDER, 1954; ABBOTT, 1957a), but, according to other authors (EKMAN, 1935, 1953; P.-H. FISCHER, 1950), all of the Gulf of Mexico is part of the Caribbean province, which extends south to Rio de Janeiro. The latter is also called the Antillean, West Indian, or Tropical Western Atlantic province. PULLEY (1952) recognizes six provinces for the Gulf of Mexico only, but this rather extreme number is criticized by HEDGPETH (1953).

RELATION OF THE VIRGINIAN AREA TO THE TRANSATLANTIC PROVINCE

The greater part of the eastcoast of the United States belongs to the Transatlantic province. ABBOTT (1957 a) feels that the name „Transatlantic“, created by WOODWARD in 1856, is unsuitable; he proposes a new name:

*) Received January 3, 1962.

the Appalachian province. Another name for this area is Pennsylvanic province, which has been used by BRONN (1862), TRYON (1882), FISCHER (1887) and SCHILDER (1956). Since Pennsylvania has no connection with the Atlantic Ocean, the name "Pennsylvanic" province is rather strange for a marine area, and the same objection might be made for the Appalachian province.

The Transatlantic province may be divided into several subprovinces: the Virginian (Cape Cod to Cape Hatteras); Carolinian (south of Cape Hatteras); and Texan (north coast Gulf of Mexico). (N.B. North Carolina, north of Cape Hatteras, does not belong to the Carolinian). ABBOTT (1957 a) creates a fourth subprovince for the area around Tampa Bay, the Conradian, since several endemic species are found there.

The opinions concerning the so-called Transatlantic province are rather different. TRYON (1882), P. FISCHER (1887) and P.-H. FISCHER (1950) do not accept a splitting of the Transatlantic province, as was first proposed by E. FORBES. According to EKMAN (1935, 1953) the Virginian is considered to be part of the Boreal province, and the Carolinian should be a transition between the Boreal and Caribbean provinces. SCHILDER (1956) includes the Carolinian into the Caribbean province, for a number of tropical species range north to Cape Hatteras, distributed by the warm Gulf Stream. STEPHENSON and STEPHENSON (1952) consider the Carolinian as an autonomous province (warm-temperate), but they do not accept the Virginian as a separate zoogeographical province, for in their opinion, it is a transition between the warm-temperate and cold-temperate provinces. It is doubtful whether the north coast of the Gulf of Mexico can be considered a special subprovince, it has a mixture of West Indian and Transatlantic species, with a low endemic component (HEDGPETH, 1953). The Conradian also is a doubtful subprovince. MOORE (1961) considers the coast from Texas to Cape Hatteras, except southern Florida, to be a single biogeographic area, the Carolinian province. He states that the tropical element is scanty in this area. WARMKE and ABBOTT (1961) include the area from Rio de Janeiro as far as Cape Hatteras and Bermuda into the Caribbean province, but they exclude the northern and western coasts of the Gulf of Mexico.

A solution to the problem of defining zoogeographical boundaries, may be found in the concept of overlapping zones, as has been suggested for this area by BOUSFIELD (1960), who recognizes the Subarctic (Arctic Ocean to Gulf of Maine), Boreal (Labrador to Cape Hatteras) and Virginian (Gulf of St. Lawrence to northern Florida) provinces. HEDGPETH (1957, pl. 1) also suggests overlapping areas between the Transatlantic and Caribbean provinces: Florida south of Cape Canaveral; Tampa Bay to Cedar Keys; and the coast of southern Texas.

It is remarkable there is so much difficulty concerning the character of the Virginian area, for there is no doubt as to its boundaries, viz. Cape Cod and Cape Hatteras. Both Capes are temperature-barriers, as has been demonstrated by PARR (1933), and, especially for Cape Hatteras, by WELLS

and GRAY (1960). It is clear that the character of this area, depending on the temperature of the waters, is rather sharp cut.

We will discuss here the littoral and sublittoral (down to 100 fathoms) malacofauna of the Virginian area, and try to find out what the Mollusks may add to the knowledge of the zoogeographical provinces of the eastcoast of the United States. For this purpose a list has been compiled of the Mollusks of the Virginian area (table 1), with their distribution in America and Europe. The data are from several literature sources (ABBOTT, 1958, 1961; JACOBSON, 1953; JACOBSON and EMERSON, 1961; JACOT, 1919, 1924; JOHNSON, 1934; "JOHNSONIA", 1941—1960; MORRIS, 1958; SLATER, 1960; SMITH, 1937). The pelagic Mollusks, Pteropods and the Cephalopod *Spirula spirula* Linné, are excluded, although their shells can be found at the beaches of the Virginian area. Also *Congerina leucophaeata* Conrad and *Lasaea rubra* Montagu are not in table 1; the first is a brackish water species, the latter has lately been found alive at Rockaway Beach, New York City, by members of the New York Shell Club, but the distribution in America is not yet known.

TABLE 1.

Littoral and sublittoral Mollusks of the Virginian area, their distribution in the other Western Atlantic provinces and their occurrence in the corresponding Celtic province on the Eastern side.

		Western Atlantic					Celtic in Europe		
		Arctic	Boreal	Virginian	Carolinian	Caribbean	Species	Genus	Family
Class GASTROPODA									
Fam. PATELLIDAE									
	Helcion						×	×	
1	<i>H. pellucidus</i> Linné	—	—	×	—	—	×		
Fam. ACMAEIDAE									
	Acmaea						×	×	
2	<i>A. testudinalis</i> Müller	×	×	×	—	—	×		
Fam. TROCHIDAE									
	Solariella						×	×	
3	<i>S. obscura</i> Couthouy	—	×	×	—	—			
Fam. LACUNIDAE									
	Lacuna						×	×	
4	<i>L. vincta</i> Montagu	×	×	×	—	—	×		
Fam. LITTORINIDAE									
	Littorina						×	×	
5	<i>L. littorea</i> Linné	×	×	×	—	—	×		
6	<i>L. obtusata</i> Linné	—	×	×	—	—	×		
7	<i>L. saxatilis</i> Olivi	×	×	×	—	—	×		
8	<i>L. irrorata</i> Say	—	—	×	×	—			

(TABLE 1)

		Western Atlantic					Celtic in Europe		
		Arctic	Boreal	Virginian	Carolinian	Caribbean	Species	Genus	Family
Fam. HYDROBIIDAE								X	
	Hydrobia						X		
9	<i>H. minuta</i> Totten	—	X	X	—	—			
10	<i>H. laevis</i> DeKay	—	—	X	—	—			
11	<i>H. salsa</i> Pilsbry	—	—	X	—	—			
12	<i>H. stimpsoni</i> S. Smith	—	—	X	—	—			
Fam. RISSOIDAE								X	
	Cingula						X		
13	<i>C. castanea</i> Möller	—	X	X	—	—			
14	<i>C. aculeus</i> Gould	—	X	X	—	—			
	Alvania						X		
15	<i>A. exarata</i> Stimpson	—	X	X	—	—			
Fam. SKENEOPSISIDAE								X	
	Skeneopsis						X		
16	<i>S. planorbis</i> Fabricius	X	X	X	—	—	X		
Fam. CAECIDAE								X	
	Caecum						X		
17	<i>C. pulchellum</i> Stimpson	—	—	X	X	X			
18	<i>C. johnsoni</i> Winkley	—	—	X	—	—			
19	<i>C. cooperi</i> S. Smith	—	—	X	X	—			
Fam. CERITHIIDAE								X	
	Bittium						X		
20	<i>B. alternatum</i> Say	—	X	X	—	—			
21	<i>B. virginicum</i> Henderson & Bartsch	—	—	X	—	—			
Fam. CERITHIOPSISIDAE								X	
	Cerithiopsis						X		
22	<i>C. greeni</i> C. B. Adams	—	X	X	X	X			
23	<i>C. subulata</i> Montagu	—	—	X	X	X			
	Seila								
24	<i>S. adamsi</i> Lea	—	—	X	X	X			
Fam. TRIPHORIDAE								X	
	Triphora						X		
25	<i>T. perversa nigrocincta</i> C. B. Adams	—	X	X	X	X			
Fam. EPITONIIDAE								X	
	Epitonium						X		
26	<i>E. angulatum</i> Say	—	—	X	X	—			
27	<i>E. humphreysii</i> Kiener	—	—	X	X	—			
28	<i>E. rupicolum</i> Kurtz (= <i>lineatum</i> Say)	—	—	X	X	—			
29	<i>E. multistriatum</i> Say	—	—	X	X	—			
30	<i>E. championi</i> Clench & Turner	—	—	X	—	—			
Fam. MELANELLIDAE								X	
	Stilifer								
31	<i>S. stimpsoni</i> Verrill	—	—	X	—	—			

(TABLE 1)

	Western Atlantic					Celtic in Europe		
	Arctic	Boreal	Virginian	Carolinian	Caribbean	Species	Genus	Family
	Fam. CALYPTRAEIDAE							
	Crucibulum							
32	—	×	×	×	—	—	—	×
	Crepidula							
33	—	×	×	×	—	×	—	—
34	—	×	×	×	×	—	—	—
35	—	×	×	×	×	—	—	—
	Fam. APORRHAIIDAE							
	Aporrhais							
36	—	×	×	—	—	—	×	×
	Fam. NATICIDAE							
	Natica							
37	×	×	×	—	—	—	—	—
	Tectonatica							
38	—	—	×	×	×	—	—	—
	Polinices							
39	—	×	×	—	—	—	×	—
40	—	—	×	×	—	—	—	—
	Lunatia							
41	—	×	×	—	—	—	—	—
42	×	×	×	—	—	—	—	—
43	—	×	×	—	—	—	—	—
	Amauropsis							
44	×	×	×	—	—	×	—	×
	Sinum							
45	—	—	×	×	×	—	—	—
	Fam. PURPURIDAE							
	Thais							
46	—	—	×	×	×	—	×	×
	Nucella							
47	—	×	×	—	—	×	×	—
	Urosalpinx							
48	—	×	×	×	—	×	×	—
	Eupleura							
49	—	—	×	×	—	—	—	—
	Fam. COLUMBELLIDAE							
	Anachis							
50	—	—	×	×	—	—	×	—
51	—	—	×	×	—	—	—	—
	Mitrella							
52	—	×	×	×	×	—	—	—
53	—	×	×	—	—	—	—	—
	Fam. BUCCINIDAE							
	Buccinum							
54	—	×	×	—	—	×	—	×
	<i>B. undatum</i> Linné							

(TABLE 1)

	Western Atlantic					Celtic in Europe		
	Arctic	Boreal	Virginian	Carolinian	Caribbean	Species	Genus	Family
							X	
55	—	X	X	—	—	—		
56	—	X	X	—	—	—		
57	—	X	X	—	—	—		
								—
58	—	—	X	X	—	—		—
59	—	—	X	X	—	—		
								X
							X	
60	—	—	X	X	X	—		
61	—	X	X	X	—	—		
62	—	X	X	X	—	—		
								—
63	—	—	X	X	—	—		—
64	—	X	X	—	—	—		
								X
							X	
65	—	X	X	—	—	—		
66	—	—	X	X	—	—		
67	—	—	X	X	—	—		
								X
							X	
68	—	—	X	X	X	—		
								X
							X	
69	—	X	X	—	—	—		
								X
							X	
70	X	X	X	—	—	X		
71	—	X	X	X	X	—		
								X
72	X	X	X	X	X	—		—
73	—	X	X	—	—	—		X
								X
							X	
74	X	X	X	—	—	—		

(TABLE 1)

	Western Atlantic					Celtic in Europe		
	Arctic	Boreal	Virginian	Carolinian	Caribbean	Species	Genus	Family
	Fam. PYRAMIDELLIDAE							
	Odostomia							
92			X				X	X
93		X	X					
94			X	X				
	Chrysallida							
95		X	X	X			X	
	Turbonilla							
96			X				X	
97			X					
98		X	X	X				
99		X	X	X	X			
100			X					
101			X					
102			X					
	Fam. ELLOBIIDAE							
	Ovatella							
103		X	X	X	X	X	X	X
	Melampus							
104		X	X	X				
	Class PELECYPODA							
	Fam. NUCULIDAE							
	Nucula							
105		X	X	X			X	X
106			X					
107		X	X					
108		X	X					
	Fam. NUCULANIDAE							
	Nuculana							
109			X	X	X		X	X
110			X	X	X			
	Yoldia							
111		X	X					
112	X	X	X					
113	X	X	X					
	Fam. SOLEMYACIDAE							
	Solemya							
114		X	X	X				
	Fam. ARCIDAE							
	Anadara							
115			X	X				X
116			X	X	X			

(TABLE 1)

	Western Atlantic					Celtic in Europe		
	Arctic	Boreal	Virginian	Carolinian	Caribbean	Species	Genus	Family
117	Noetia							
	<i>N. ponderosa</i> Say	—	—	×	×	—	—	
	Fam. MYTILIDAE							
	Mytilus							×
118	<i>M. edulis</i> Linné	×	×	×	—	—	×	
	Brachidontes							
119	<i>B. recurvus</i> Rafinesque	—	—	×	×	×	—	
	Modiolus							
120	<i>M. modiolus</i> Linné	×	×	×	×	—	×	
121	<i>M. demissus</i> Dillwyn (= <i>plicatulus</i> Lamarck)	—	×	×	×	—	—	
	Crenella							
122	<i>C. decussata</i> Montagu	×	×	×	—	—	×	
123	<i>C. glandula</i> Totten	—	×	×	—	—	—	
	Musculus							
124	<i>M. discors</i> Linné	×	×	×	—	—	×	
125	<i>M. niger</i> Gray	×	×	×	—	—	×	
126	<i>M. corrugatus</i> Stimpson	×	×	×	—	—	—	
	Fam. PECTINIDAE							
	Aequipecten							
127	<i>A. irradians</i> Lamarck	—	×	×	×	—	—	×
	Placopecten							
128	<i>P. magellanicus</i> Gmelin	—	×	×	—	—	—	
	Fam. ANOMIIDAE							
	Anomia							
129	<i>A. simplex</i> Orbigny	—	×	×	×	×	—	
130	<i>A. aculeata</i> Müller	—	×	×	—	—	×	
	Fam. OSTREIDAE							
	Crassostrea							
131	<i>C. virginica</i> Gmelin	—	×	×	×	×	×	
	Fam. ASTARTIDAE							
	Astarte							
132	<i>A. subaequilaterata</i> Sowerby	×	×	×	×	—	—	
133	<i>A. undata</i> Gould	×	×	×	—	—	—	
134	<i>A. quadrans</i> Gould	—	×	×	—	—	—	
135	<i>A. castanea</i> Say	—	×	×	—	—	—	
	Fam. CRASSATELLIDAE							
	Gouldia							
136	<i>G. mactracea</i> Linsley	—	—	×	—	—	—	
	Fam. CARDITIDAE							
	Venericardia							
137	<i>V. borealis</i> Conrad	—	×	×	—	—	—	
	Fam. CYPRINIDAE							
	Cyprina							
138	<i>C. islandica</i> Linné	×	×	×	—	—	×	

(TABLE 1)

		Western Atlantic					Celtic in Europe		
		Arctic	Boreal	Virginian	Carolinian	Caribbean	Species	Genus	Family
	Fam. DONACIDAE							X	
	Donax						X		
159	<i>D. fossor</i> Say	—	—	X	—	—	—		
	Fam. PSAMMOBIIDAE							X	
	Tagelus						—		
160	<i>T. plebeius</i> Solander (= <i>gibbus</i> Spengler)	—	—	X	X	X	—		
161	<i>T. divisus</i> Spengler	—	—	X	X	X	—		
	Fam. SEMELIDAE							X	
	Abra						X		
162	<i>A. lioica</i> Dall	—	—	X	X	X	—		
163	<i>A. aequalis</i> Say	—	—	X	X	X	—		
	Cumingia						—		
164	<i>C. tellinoides</i> Conrad	—	X	X	X	—	—		
	Fam. TELLINIDAE							X	
	Angulus						X		
165	<i>A. tenera</i> Say (= <i>agilis</i> Stimpson)	—	X	X	—	—	—		
166	<i>A. tenella</i> Verrill	—	—	X	—	—	—		
167	<i>A. versicolor</i> DeKay	—	—	X	X	X	—		
	Macoma						X		
168	<i>M. balthica</i> Linné	X	X	X	X	—	X		
169	<i>M. calcarea</i> Gmelin	X	X	X	—	—	—		
170	<i>M. tenta</i> Say	—	—	X	X	X	—		
171	<i>M. brevifrons</i> Say	—	—	X	X	X	—		
	Fam. SOLENIDAE							X	
	Solen						X		
172	<i>S. viridis</i> Say	—	—	X	X	—	—		
	Ensis						X		
173	<i>E. directus</i> Conrad	—	X	X	X	—	—		
	Siliqua						—		
174	<i>S. costata</i> Say	—	X	X	—	—	—		
	Fam. SAXICAVIDAE (= HIATELLIDAE)							X	
	Saxicava						X		
175	<i>S. arctica</i> Linné (= <i>rugosa</i> Linné)	X	X	X	X	X	X		
	Panomya						X		
176	<i>P. arctica</i> Lamarck	X	X	X	—	—	X		
	Fam. CORBULIDAE (= ALOIDIDAE)							X	
	Corbula						X		
177	<i>C. contracta</i> Say	—	—	X	X	X	—		
178	<i>C. swiftiana</i> C. B. Adams	—	—	X	X	X	—		
	Fam. MYIDAE							X	
	Mya						X		
179	<i>M. arenaria</i> Linné	X	X	X	—	—	X		

(TABLE 1)

	Western Atlantic					Celtic in Europe		
	Arctic	Boreal	Virginian	Carolinian	Caribbean	Species	Genus	Family
	Fam. PHOLADIDAE							
	Cyrtopleura							
180	—	—	×	×	×	—	—	×
	Barnea							
181	—	×	×	×	—	—	×	
	Zirfaea							
182	—	×	×	—	—	×	×	
	Martesia							
183	—	—	×	×	—	—	—	
184	—	—	×	×	×	—	—	
	Fam. TEREDINIDAE							
	Teredo							
185	×	×	×	×	—	×	×	×
186	—	—	×	—	—	—	—	
187	×	×	×	—	—	×	—	
188	—	×	×	—	—	—	—	
189	—	×	×	×	—	×	—	
190	—	—	×	×	—	—	—	
191	—	×	×	—	—	—	—	
	Bankia							
192	—	—	×	×	×	—	×	
	Fam. LYONSIIDAE							
	Lyonsia							
193	—	×	×	×	—	—	×	×
	Fam. PANDORIDAE							
	Pandora							
194	—	×	×	—	—	—	×	×
	Fam. THRACIIDAE							
	Thracia							
195	—	×	×	—	—	—	×	×
	Fam. PERIPLOMATIDAE							
	Periploma							
196	—	×	×	—	—	—	—	×
197	—	×	×	—	—	—	—	
198	—	×	×	—	—	—	—	
	Fam. VERTICORDIIDAE							
	Verticordia							
199	—	—	×	×	×	—	—	—
	Fam. POROMYIDAE							
	Poromya							
200	—	—	×	×	×	×	×	×

(TABLE 1)

		Western Atlantic					Celtic in Europe		
		Arctic	Boreal	Virginian	Carolinian	Caribbean	Species	Genus	Family
Class AMPHINEURA									
Fam. ISCHNOCHITONIDAE									
	Ischnochiton						×	×	
201	<i>I. ruber</i> Linné	×	×	×	—	—	—	×	
	Chaetopleura						—		
202	<i>C. apiculata</i> Say	—	—	×	×	—	—		
Class SCAPHOPODA									
Fam. DENTALIIDAE									
	Dentalium						×	×	
203	<i>D. occidentale</i> Stimpson	—	×	×	—	—	—		
Class CEPHALOPODA									
Fam. SEPIOLIDAE									
	Rossia						—	×	
204	<i>R. tenera</i> Verrill	—	×	×	×	—	—		
Fam. LOLIGINIDAE									
	Loligo						×	×	
205	<i>L. pealei</i> Lesueur	—	×	×	×	—	—		
Fam. OMMASTREPHIDAE									
	Ommastrephes						×	×	
206	<i>O. illecebrosus</i> Lesueur	×	×	×	×	—	—		
Fam. OCTOPODIDAE									
	Octopus						×	×	
207	<i>O. vulgaris</i> Lamarck	—	—	×	×	×	×		

RELATION OF THE MOLLUSKS OF THE VIRGINIAN TO THE BOREAL AND CAROLINIAN PROVINCES

Altogether there are 207 species of littoral and sublittoral Mollusks in the Virginian area. Of these:

- 22 species (10½ %) are endemic;
- 129 species also live in the Boreal province, north of Cape Cod;
- 39 species are living in the Arctic province;
- 101 species are to be found in the Carolinian; and the range of 44 species extends southwards into the West Indies.

It would appear that in the Virginian the boreal element is larger than the element common to the Virginian and Carolinian areas. These results differ from those of the STEPHENSONS' (1954), who assert that the southern (Carolinian) element in the Virginian area is dominant. Their study, however, is not confined to Mollusks.

Altogether 101 of the Virginian species also live in the Carolinian. Table 2 gives numbers of each class of Mollusks.

TABLE 2.
Virginian Mollusks and their distribution in terms of Cape Hatteras.

	Virginian species	Not south of Cape Hatteras	Also south of Cape Hatteras
Gastropoda	104	62	42
Pelecypoda	96	42	54
Amphineura	2	1	1
Scaphopoda	1	1	—
Cephalopoda	4	—	4
Total	207	106 (51%)	101 (49%)

Thus less than half of the Virginian species are also Carolinian.

Many new species appear south of Cape Hatteras. HACKNEY (1944) gives a species list of the Mollusks from Beaufort, North Carolina, just south of Cape Hatteras. From her publication is made up table 3, from which it is seen that the mollusk fauna 100 kilometers south of Cape Hatteras is completely different from the fauna north of the Cape, with 103 new, non-Virginian species and subspecies.

TABLE 3.
Marine Mollusks from Beaufort, North Carolina, and their distribution in terms of Cape Hatteras.

	Beaufort	also Virginian	not Virginian
Gastropoda	74	33	41
Pelecypoda	97	39	58
Amphineura	1	1	—
Scaphopoda	3	—	3
Cephalopoda	2	1	1
Total number of species	177	74	103

Further to the south the number of Carolinian species is even larger. The mollusk faunas of the Virginian and Carolinian appear to be quite different, although TRYON (1882) asserted there is no reason to make a division of the Transatlantic province, since the distribution of the shells does not warrant it. The number of Boreal and Virginian species, living in the Carolinian, is diminished by the fact that many live in deeper and cooler water in the Carolinian. So these species do not really belong to the Carolinian province, which is based on the littoral and sublittoral (down to 100 fathoms) fauna only. Some of the Carolinian species, *Sinum perspectivum*, *Thais haemastoma floridana* (SIELING, 1960), *Prunum roscidum* (ABBOTT, 1957 b), both species of *Labiosa*, and *Martesia cuneiformis*, have only penetrated into the Virginian area at the most southern part, and hardly can be considered to be Virginian species.

COMPARISON OF THE AMERICAN AND EUROPEAN ATLANTIC PROVINCES

The zoogeographical provinces of the eastern Atlantic are (Map 2): to the north, the Arctic province (east and north of North Cape in northern Norway, and the north coast of Iceland); the Boreal province reaches from North Cape to southern Norway, and includes the south coast of Iceland, the Faroe and Shetland Islands; the temperate Celtic province includes the North Sea, the Baltic and the Atlantic coast of Britain, Ireland, France and northern Spain. The boundary with the Lusitanian province is indistinct: the Straits of Dover; the most western point of France; or Cape Finisterre in northwest Spain. The subtropical Lusitanian (or Mediterranean) province includes the Mediterranean, Black and Caspian Seas. The northern and southern Atlantic boundaries of the Lusitanian province are indistinct, to the south: Cape Juby (TRYON, 1882); Cape Blanco (EKMAN, 1953; FISCHER, 1950); or Cape Verde (SCHILDER, 1956). The West African province (= Tropical Eastern Atlantic province) extends to the south as far as Cape Frio. Table 4 compares the zoogeographic provinces of the eastern and western Atlantic.

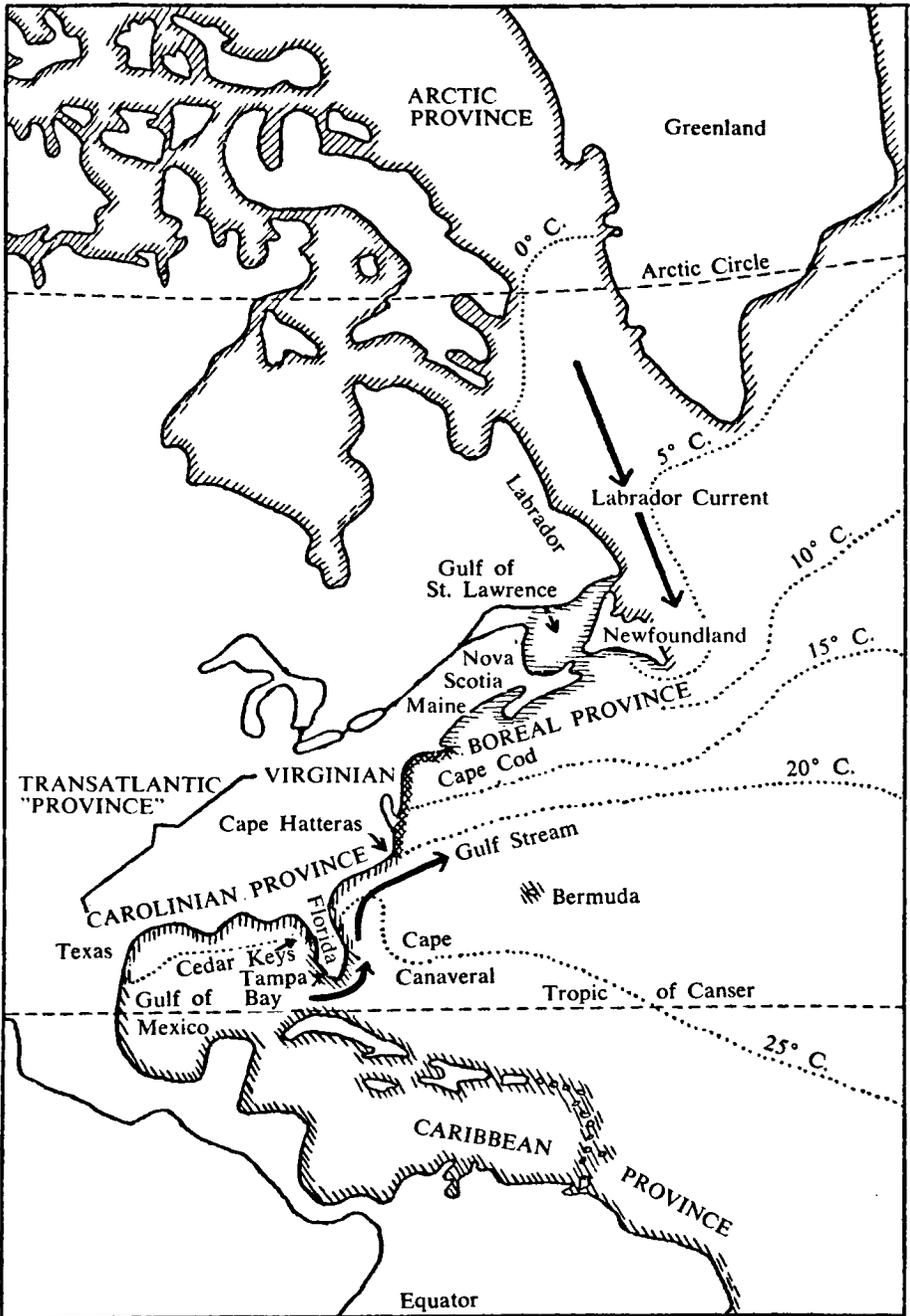
TABLE 4.
Comparison of the northern Atlantic provinces.

climate	western Atlantic	latitude	eastern Atlantic	latitude
arctic	Arctic	83° —47°N	Arctic	83° —71°N
cold-temperate	Amer. Boreal	47° —42°N	Europ. Boreal	71° —58°N
temperate	Virginian	42° —35°N	Celtic	58° —43°N
warm-temperate or subtropical	Carolinian	35° —28°N	Lusitanian	43° —15°N
tropical	Caribbean	28°N—23°S	West African	15°N—18°S

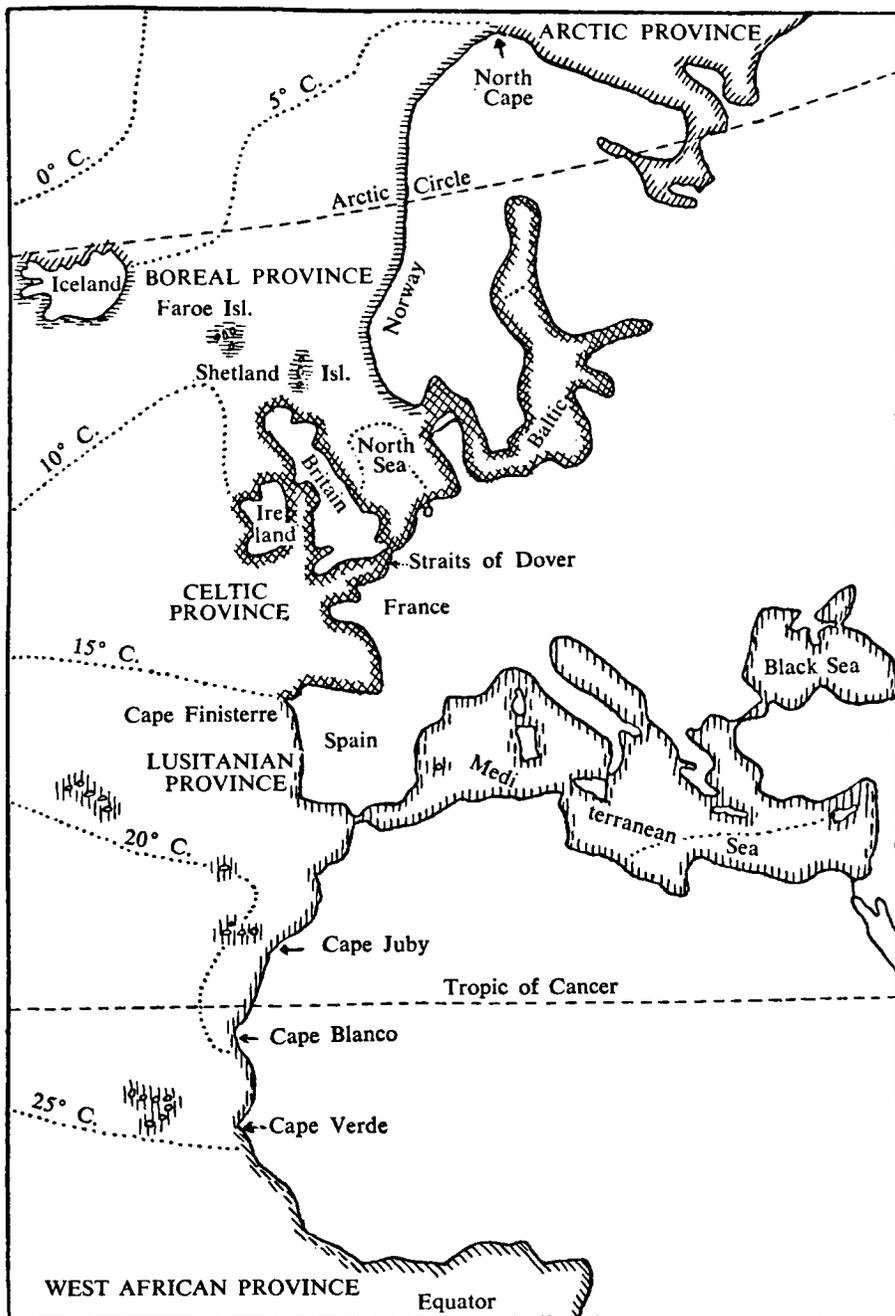
Since the Arctic province is circumpolar, there is no species-difference between the American and European Arctic, but on the American east coast the Arctic province reaches far more south (Newfoundland, Lat. 47° N.) than in Europe (North Cape, Lat. 71° N.), because of the cold Labrador Current, running far south along the American coast, while on the European side of the Atlantic the warm Gulf Stream extends its influence far north. So at about the same latitude where, in America, the Boreal province begins (Lat. 47° N.), the subtropical province begins in Europe (Cape Finisterre, 43° N. Lat.).

On the American Atlantic coast the Arctic and Caribbean provinces are extensive, and between them only 19 degrees of latitude (Newfoundland to Cape Canaveral) comprise the temperate provinces. On the European-African coast the Arctic and Tropical provinces are smaller, and three temperate provinces cover 56 degrees of latitude (three times that in America). Of these latter three provinces, the Lusitanian is the largest (28 degrees of latitude), and the Celtic and Boreal are rather small (15 and 13 degrees respectively).

The American and European Boreal provinces have many species in com-



MAP 1. American northern Atlantic coast with zoogeographical provinces and annual mean isotherms.



MAP 2. European-African northern Atlantic coast with zoogeographical provinces and annual mean isotherms.

mon, thus they are often considered as a single zoogeographical province. The Virginian area is comparable to the Celtic, and the Carolinian to the subtropical Lusitanian (cf. table 4 and maps 1 and 2).

The boundaries of littoral zoogeographical provinces are, for the most part, defined by the surface temperature of the seawater. The southern boundary of the Arctic province is coincident with the annual mean isotherm of 5° C, which is about the southern limit of floating ice. The Boreal province in Europe lies about between the annual mean isotherms of 5° and 10° C; the tropical provinces are bounded by annual isotherms of 25° C, this is the lower limit of reef-building corals. Since the 25° C isotherm runs from North Mexico to Cedar Keys, this is yet another reason to exclude the northern coast of the Gulf of Mexico from the tropical Caribbean province.

In the eastern Atlantic the Celtic province lies approximately between the isotherms of 10° and 15° C, and the Lusitanian province between 15° and 25° C. However, the 15° C isotherm is not the boundary between the Virginian and the Carolinian, for at Cape Hatteras is found the annual mean isotherm of 20° C. Thus a comparison of temperatures of the temperate provinces of the northern Atlantic adds little to an exact definition of the east American temperate provinces. Reason for this is that at the American Atlantic coast the isotherms between 25° and 5° C are close together (between Lat. 30° and 46° N.), but they diverge widely towards the eastern Atlantic coast (between Lat. 12° and 72° N. respectively).

A comparison of the mollusk faunas of the Virginian and the Celtic province might be more useful for an exact definition of the boundaries. Such a comparison has been made by TOBLEMAN (1959), who compared the marine shells of Great Britain with those of the coast from New Jersey to Maine. In our opinion these two areas are not comparable, for Britain has at its southern coast a number of subtropical species, and the American coast from Cape Cod to Maine is pure boreal. It is for this reason that TOBLEMAN finds a number of non comparable shells; however, he does mention many genera and species common to both coasts.

From table 1 it can be seen that many species are to be found both in the Virginian and Celtic. Altogether there are 46 species common to both areas, but 5 species were imported from the United States to Europe (*Crepidula fornicata*, *Urosalpinx cinerea*, *Crassostrea virginica*, *Venus mercenaria*, *Petricola pholadiformis*), and 4 species were imported from the Celtic province to America (*Helcion pellucidus*, *Littorina littorea*, *Ovatella myosotis*, *Teredo navalis*). The latter, the shipworm, now has a wide distribution, but according to BARTSCH (1922) it might have originated in Europe.

Many Virginian mollusk genera and families are present in the Celtic province, table 5 shows the numbers and percentages, the imported species are included.

TABLE 5.

Virginian Mollusks and their distribution in Europe, the imported species are included.

	Virginian	also Celtic	not Celtic
Species	207	46 (22%)	161 (78%)
Genera	132	93 (70%)	39 (30%)
Families	84	78 (93%)	6 (7%)

Thus if the Celtic is an autonomous zoogeographical province, there is some reason for the Virginian also to be considered as such.

DISCUSSION

Although some facts have been mentioned to demonstrate that the Virginian could be compared to the Celtic province, the similarity between the two areas is not as great as table 5 seems to indicate. For the Celtic possesses a number of families, genera and species, which are not to be found in the Virginian.

If we consider the endemic *species*, it is agreed that this should be at least 50% for an autonomous zoogeographical province. In the Virginian area it is 10½%, so far too less. Besides, there are no endemic *genera*.

As the mollusk faunas north and south of Cape Hatteras are very different, the Transatlantic province is an unnatural creation. Only the Carolinian part might be considered a province of its own, comparable to the warm-temperate (subtropical) Lusitanian province in Europe and Africa.

In total there are 129 arctic and boreal species living in the Virginian area, that is 62 % of the Virginian mollusk fauna. This may provide the basis for extending the Boreal province as far as Cape Hatteras, as has been done by EKMAN (1935, 1953), SVERDRUP c.s. (1954) and SCHILDER (1956). However, the mollusk fauna of the Virginian is different from the Boreal area north of Cape Cod, as it is poor in number of species. The temperature-barrier at Cape Cod will be the reason for this, it withholds many boreal species to live in the somewhat warmer Virginian. But this poorly developed boreal fauna in the Virginian area is not enough reason to exclude the Virginian from the Boreal province. This situation is comparable to that in the Bermuda-Islands, their fauna belongs to the Caribbean province, although it is poor in the species-number compared to the rich West-Indian fauna.

When the Virginian is considered to be boreal, the 10½ % of endemic Virginian species become boreal too, which will give the Virginian a total of 72½ % northern (boreal and arctic) species, and only 27½ % southern (Carolinian) species. So there is more reason to consider the Virginian belonging to the Boreal province, than to call it a transition between the warm-temperate (Carolinian) and cold-temperate (Boreal) provinces, as is proposed by the STEPHENSONS' (1952).

When we accept the Virginian to be part of the Boreal province, this means there is no province between the cold- and warm-temperate provinces, like in Europe the Celtic between the Boreal and Lusitanian provinces. This

is a consequence of the rather sharp transition between the cold Labrador Current and the warm Gulf Stream. There is no space left for a temperate province. In Europe only the Gulf Stream is important, there is no cold current that prevents the existence of an autonomous temperate province. However, some authors (EKMAN, 1935, 1953; SVERDRUP c.s., 1954) also deny the existence of a temperate province in Europe, they place the Celtic in the Boreal province. In that case the American and European Atlantic coasts are completely comparable, both having a boreal and subtropical province only between the arctic and tropical provinces. Although we do not agree with this opinion, we stress the fact that there is a great similarity between the faunas of the southern (Virginian) part of the American Boreal and the European Celtic province. It is our opinion that the facts ask for one more zoogeographical province in the European than in the North American coast of the Atlantic.

SUMMARY

The marine fauna of the American Atlantic coast between Cape Cod and Cape Hatteras, the Virginian area, is placed by zoogeographers in different provinces: in the Transatlantic, or in the Boreal province. It is sometimes considered to be a province of its own, or only a transition between the Boreal and Carolinian province.

The mollusk fauna of the Virginian area is compiled and compared with the faunas north and south of the area. As endemism is low, there is no reason to consider the Virginian area an autonomous zoogeographical province. The fauna is too much different from that of the Carolinian area, to combine both in one Transatlantic province. As most of the species are of boreal origin, there is less reason to consider the Virginian area as a transitional region between the Carolinian and the Boreal provinces than as belonging to the Boreal province, the percentage of boreal mollusks is large enough to include it in the Boreal province.

A comparison of the northern Atlantic provinces of America and Europe shows that a different zoogeographical division of both areas is necessary, as a consequence of the currents: the transition between Labrador Current and Gulf Stream suppresses a temperate province on the American East coast, such as the Celtic province is on the European West coast.

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