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Application of the dendrite analysis in the discussion on the biogeography of the Antarctic

ABSTRACT: The method of construction and division of dendrites proposed by Florek et al. (1951) was used for defining of the Antarctic biogeographic areas. The affinity matrices of Knox and Lowry (1977) resulting from the analysis of the distribution of Antarctic *Polychaeta* and *Amphipoda* were taken as a basis for dendrite construction. The results of the present analysis are compared with the conclusions of these authors and similarities and differences are discussed on the background of the hitherto published biogeographic divisions of Antarctica.

Key words: Antarctica, biogeography.

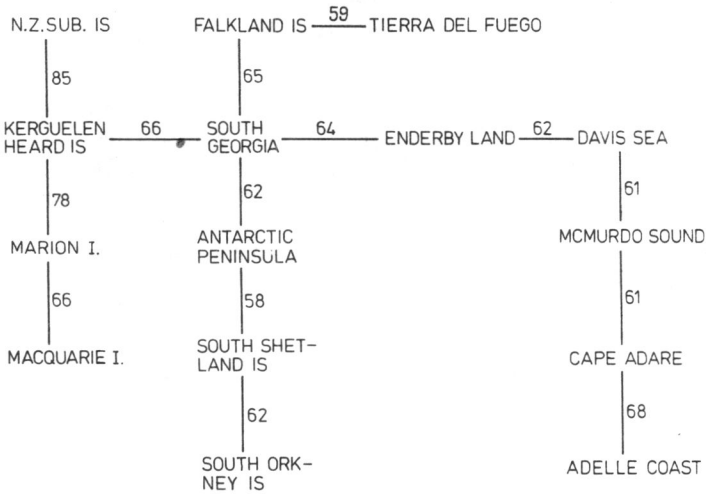
1. Introduction

The Southern Ocean distincly differs from other parts of the World Ocean in its specific benthos, plankton and nekton communities. Particular animal groups inhabiting this area have a high percentage of endemic species, genera and even families. Open to debate, on the other hand, is the division of this area into biogeographical regions. A proposal of such dividing was put forward for instance by Knox and Lowry (1977) who have used a comprehensive knowledge of the distribution of two groups of benthos rich in species, namely *Amphipoda* and *Polychaeta*. The basis of such an analysis were the affinity matrices of selected Antarctic localities. These matrices enabled to group biogeographical areas separately for *Amphipoda* and for *Polychaeta* (Knox and Lowry 1977, Figs 3 and 7, pp. 438 and 444).

According to the present author, there is a possibility of grouping the localities by means of the mathematically objective method proposed by Florek et al. (1951). Using such a method of ordering information included in affinity matrices of Knox and Lowry (1977) the aim of the present author was to answer the following questions: 1) is the grouping of localities into biogeographical areas, which is proposed by the above cited authors, the only possible one and the best one ?; 2) will conclusions drawn from the dendrite analysis be in agreement with the conclusions of the above cited authors?

2. Methods

On the basis of information on the mutual affinity between the localities in question (Knox and Lowry 1977) their shortest dendrites have been constructed according to Florek et al. (1951) separately for *Amphipoda* and *Polychaeta* (Figs 1 and 2). In such ordering of the

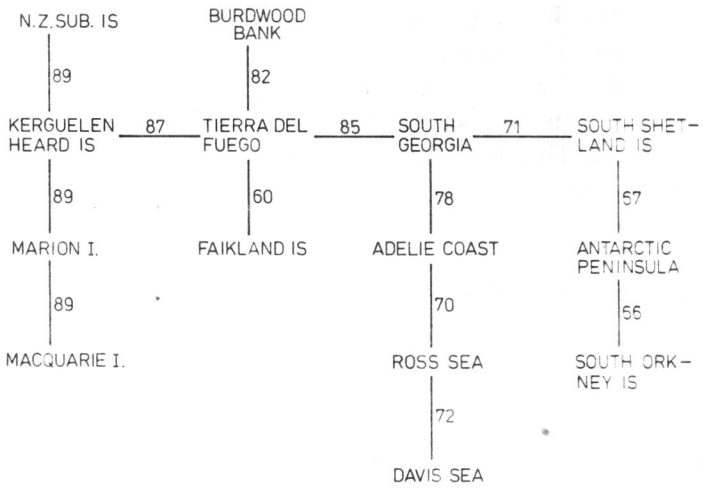


d	w′	w″
85		
78	1,0897	0,9500
68	1,1471	
66	1,0303	
65	1,0154	0,9998
64	1,0156	0,9838
62	1,0323	
61	1,0164	0,9831
59	1,0339	
58	1,0172	

Fig. 1. Dendrite of localities constructed on the basis of the affinity matrix of Knox and Lowry (1977) for *Polychaeta* (affinities are substituted by distances; in the table within the figure the natural division of the dendrite is presented, where d stands for distances expressed in percent, w′ — quotients of neighbouring distances, w″ — quotients indicating the mathematical strength of given divisions)

localities those of the highest affinity are neighbouring each other. Then, the natural division of the dendrites into parts was carried out using the Florek et al. (1951) method which these authors present as follows: "The number of parts, k, into which the set Z built of n elements is divided in natural way, may be estimated by the following method: all sections (distances = d; J. S.) occurring in the dendrite F (Z) are arranged

in decreasing order. Let $d_1, d_2, \ldots d_{n-1}$ stand for the lengths of these sections. We set the quotients of lengths (distances; J. S.) between adjacent sections: $w_2 = \frac{d_1}{d_2}$, $w_3 = \frac{d_2}{d_3}$, ..., $w_{n-1} = \frac{d_{n-2}}{d_{n-1}}$. We can say that the set Z falls in the natural way into k parts, if $w_k < w_{k+1}$ for every $k = 2, 3, \ldots n-1$. Of the two natural divisions the division into k parts is better (stronger) than the division into m parts when $w_k < w_m$." Because Knox and Lowry (1977) have estimated the affinities and the method of Florek et al. (1951) is based on the distances, the affinities in dendrites were



d	w'	w''
89		
87	1,0230	0,9995
85	1,0235	0,9874
82	1,0366	0,9860
78	1,0513	0,9705
72	1,0833	
71	1,0141	0,9998
70	1,0143	0,9708
57	1,0448	
56	1,0152	0,9229
60	1,1000	

Fig. 2. Dendrite of localities constructed on the basis of the affinity matrix of Knox and Lowry (1977) for *Amphipoda* (symbols as in Fig. 1)

substituted by distances calculated from the equation: $d = 100 - s$, where "d" stands for distance, and "s" — affinity in percent. The values w'' (Figs 1—4) correspond to the mathematical strength of each division, indicating the value of discontinuity in the series of quotients w' (Figs 1, 2). The lower is this value, the stronger is the division. Some informations on the dendrite division are to be found also in the paper by Romaniszyn (1970). Dendrites constructed in this way and their mathematically acceptable divisions, constitute the basis of the present analysis.

3. Results

There are several possibilities of dividing of both dendrites (Figs 3, 4); each of these divisions has a different mathematical strength. As the mathematically strongest division may be not necessarily the most proper for biogeographical divisions it is necessary to discuss each of them.

Polychaeta

Division 1 of the dendrite ($w'' = 0.9500$) (Fig. 3) is the strongest of the four and exhibits a highest degree of generalization. It distinguishes three groups of areas, of which the first comprises Auckland and Campbell Islands, the second Macquarie and Marion Islands, the third — all the remaining localities. This division indicates to a considerable homogeneity of the fauna of *Polychaeta* within all the localities of the Antarctic including Kerguelen and Heard Islands and the Magellanic area, and at the same time it indicates to significant differences between the three so distinguished groups. However, this division does not contribute much to solving the problem of biogeographical division of the Antarctic. On the other hand divisions 2 and 3, and particularly the latter can be well used for this purpose. In respect to mathematical strength, both these divisions are equivalent. The latter, which seems to be more justified from the biogeographical point of view, distinguishes 7 biogeographical areas:

1) East Antarctic
2) West Antarctic (Scotia Arc with the Antarctic Peninsula)
3) Magellanic
4) Kerguelen and Heard Islands
5) Marion Island
6) Macquarie Island
7) Auckland and Campbell Islands.

Division 2 stresses additionally a strong affinity between Tierra del Fuego and Falkland Islands on the one hand and the Antarctic Peninsula and South Shetland Islands on the other. Division 4 ($w'' = 0.9998$), which is mathematically very weak, distinguishes the Scotia Arc, the Antarctic Peninsula and the Eastern Antarctic as one separate area. Being very weak in comparison with the others, this division may be ignored.

Amphipoda

In the case of *Amphipoda* biogeographical division carried out on the basis of the distribution of *Amphipoda* is less univocal than in the case of *Polychaeta*. There are as much as 7 possible divisions of the dendrite (Fig. 4). The strongest one (division 1, $w'' = 0.9229$) combines Tierra del Fuego with Falkland Islands, leaving other localities as separate groups. This division indicates to considerable differences among the faunas of *Amphipoda* of all localities in question and consequently, in contrast to *Polychaeta*, to the higher variability of the amphipod fauna as a whole. As in the case of *Polychaeta*, this strongest division contri-

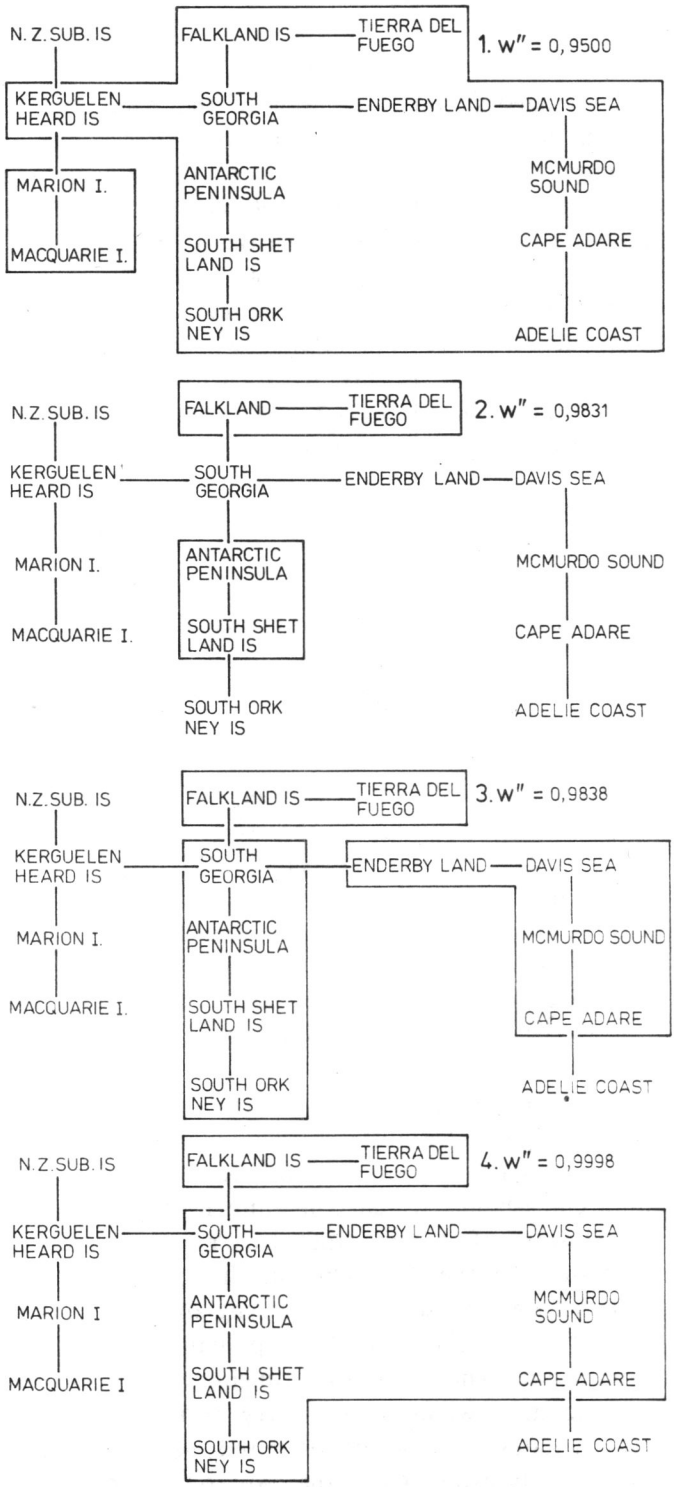


Fig. 3. Four possible divisions of the dendrite from Fig. 1. (Explanations in the text and in Figs 1 and 2)

butes little to the biogeographical dividing of the Antarctic. In this case each locality forms a separate group. Divisions 2 and 3 have similar mathematical strengths and are very similar to divisions 2 and 3 of the dendrite based on the distribution of *Polychaeta* (Fig. 3). Division 2 (Fig. 4) distinguihes similar areas, and division 3, similarly as in the case of *Polychaeta*, stresses the faunistic similarity of two smaller areas. Divisions 4 and 5, which are mathematically slighty weaker, are very similar. They differ only in respect to Burdwood Bank, which may result from the insufficient knowledge of this locality as it was pointed out by Knox and Lowry (1977). Divisions 6 and 7 are very weak and seem to be little justified from the biological point of view.

4. Discussion

An analysis of an affinity matrix of the localities which was proposed on the basis of the distribution of *Polychaeta* inclined Knox and Lowry (1977) to distinguisch three areas: A. Subantarctic (with King Edward Island, Macquarie and possibly Auckland and Campbell Island), B. Antarctic (with the whole coastline of the continent together with the Scotia Arc, Kerguelen and Heard Islands), and C. Magellanic (including Tierra del Fuego and Falkland Islands). From the viewpoint of the dendrite analysis, such a division is weakly justified. Division 4 (Fig. 3), which, as it was mentioned earlier, is mathematically very weak, is closest to such a conception. According to this division 4, Kerguelen and Heard Islands constitute a separate area; the subantarctic islands — Marion, Macquarie and Auckland and Campbell, should be then considered as three independent areas as well. Division 3 is the most justified one (Fig. 3) from the biological point of view.

In the case of *Amphipoda*, the division 2 (Fig. 4), which is mathematically strong, should be considered the best one in biogeographical terms. It accords with the division proposed by Knox and Lowry (1977), except the subantarctic islands, which constitute here separate areas.

The final conclusion of Knox and Lowry (1977) concerning the biogeographical division of the Antarctic on the basis of the distribution of *Polychaeta* differs from the scheme appearing directly from the affinity matrix. They state: "... we believe they group mainly as a large Antarctic area which includes the whole coastline, including the Scotia Arc and a smaller Magellanic area which is not very convicingly separated. The Subantarctic area includes only Macquarie and Marion Islands, both of which show some relationship with the Antarctic, and Auckland and Campbell with New Zealand". At the same time Knox and Lowry (1977) stressed that the regionalization on the basis of the distribution

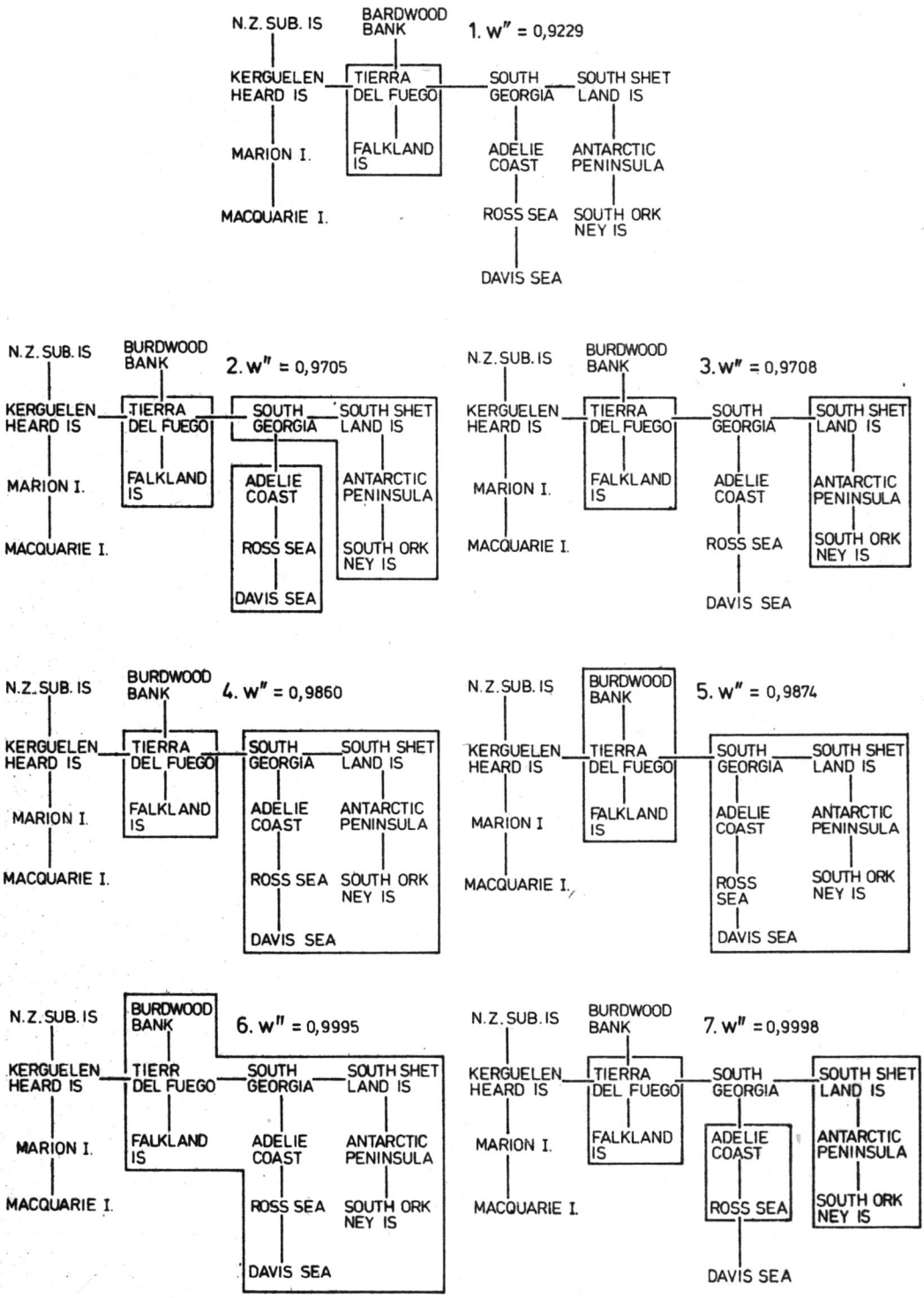


Fig. 4. Seven possible divisions of the dendrite from Fig. 2
(Explanations in the text and in Figs 1 and 2)

of *Polychaeta* differs from the grouping of localities resulting from the distribution of *Amphipoda*. In the opinion of the present author this conclusion seems to be controversial. It appears that the grouping of localities in the case of both animal groups can be similar. The difference between the two divisions of Knox and Lowry (1977) results from the accepted affinity limit value of 25% (localities of the affinity equalling or exceeding this value are combined in groups by these authors). However, this value must not be an essential and only one for each matrix taken separately and for both matrices taken together. It seems that a natural division of dendrites which is based on a mathematically objective criterion evidences for the concept of similar regionalization for both animal groups. The following remarks can be put forward. The final division of Knox and Lowry (1977) based on the fauna of *Polychaeta* is almost identical with the mathematically strongest division of the dendrite (Fig. 3—1). If, however, such a grouping was to be accepted then, consequently, the zoogeographical division made on the basis of the fauna of *Amphipoda* should correspond to the division 1 of the dendrite presented in Fig. 4, because only these two divisions are camparable as regards their mathematical strength. Nevertheless, these strongest divisions indicate rather to the difference in the faunas of the two groups (homogeneity of the fauna of *Polychaeta* and heterogeneity of the fauna of *Amphipoda*), then the possibility of different biogeographical divisions. In respect to the mathematical strength, the division 1 is followed in both dendrites by divisions 2 and 3. In view of the present consideration important divisions are division 2 for *Amphipoda* (Fig. 4) and division 3 for *Polychaeta* (Fig. 3) In both cases the grouping of localities is almost identical (the separate position of Burdwood Bank in the case of *Amphipoda* and of Adelie Coast in the case of *Polychaeta* may be ignored, taking into account the remark of Knox and Lowry (1977) about the insufficient knowledge of these regions. The peculiarities of the faunas of both animal groups cause that the divisions of both dendrites are different, especially in the case of the mathematically strongest divisions. Nevertheless the more detailed regionalization on the basis of polychaete fauna is possible, although it has to be based obviously on more subtle criteria. Consequently, to the present author's mind, the grouping of localities can be the same, with biogeographic distinction between East and West Antarctic, in the case of both animal groups. This is in accordance, in respect to *Polychaeta*, with the conclusions of Averincev (1972) from the distribution of *Polychaeta Errantia*.

The majority of authors dealing with biogeographic regionalization of the Southern Ocean consider the West Antarctic and East Antarctic as separate regions (Ekman 1953, Knox 1960, Andriashev 1965, Kusakin 1967, Hedgpeth 1969, Kott 1969, Averincev 1972, Cantera and

Arnaud 1984) and only few authors regard the whole Antarctic as one region (Powell 1965, Dell 1972).

There are different opinions on the biogeographic status of South Georgia. Ekman (1953), Knox (1960), Andriashev (1965) and Powell (1965) are treating this island as a province of the equal rank as an Antarctic province, encompassing the continent together with Scotia Arc and Bouvetøya and Heard Island. Kusakin (1967) and Averincev (1972) proposed to separate South Georgia subregion equivalent to the West- and East-Antarctic subregions. Hedgpeth (1969, 1970) and Dell (1972) suggested for South Georgia a particular rank — a district in the Scotia subregion. Finally Kott (1969) divided the Antarctic region in two provinces — a continental one and a South Georgia province. This last one would encompass the Antarctic Peninsula and the whole Scotia Arc. Biogeographic rank of South Georgia resulting from the dendrite analysis (Figs 3 and 4) fits the best to the concept of Kott (1969). It seems that basing on the distribution of *Polychaeta* and *Amphipoda* South Georgia should be included to the West Antarctic. It is to be stressed, however, that South Georgia faunistically shows similarities on one hand to the Magellanic area and to the East Antarctic area on the other, and in the case of *Polychaeta* also to the Kerguelen Islands (Figs 3 and 4).

The faunistic affinities of the subantarctic islands are very interesting. From the analysis of the dendrites divisions (Figs 3 and 4) it follows that Macquarie Island, Kerguelen and Heard Islands, Marion Island and Auckland and Campbell Islands constitute four separate biogeographic areas. Such a division is near to the concept of Kusakin (1967) resulting from the analysis of the distribution of *Isopoda*. This author distinguished the Kerguelen region, dividing it however in three subregions: Macquarie, Kerguelen and Marion. Knox and Lowry (1977) are stressing as well that the said islands because of their amphipod fauna specifity make them difficult for grouping. In general, however, most of the authors join Prince Edward, Marion, Crozet, Kerguelen, Heard and Macquarie islands in one unity (Knox 1960, Andriashev 1965, Powell 1965, Hedgpeth 1969, Averinvev 1972, Dell 1972, Cantera and Arnaud 1984). Most of the authors are of the opinion that the Auckland and Campbell Islands should be considered as an area separate from all other subantarctic areas. Only Kott (1969) included these islands into the Kerguelen province together with Macquarie, Kerguelen and Heard Islands.

5. Conclusions

I. The dendrite analysis of data included in the matrices of Knox and Lowry (1977) allowed to group objectively particular Antarctic

localities; this grouping confirms and illustrates a number of conclusions of these authors regarding the biogeographical division of the Antarctic and also the conclusions about the pecularities of the faunas of both animal group analysed. On the other hand this dendrite analysis makes part of their conclusions disputable.

II. The mathematically strongest divisions of both dendrites and their structure confirm and illustrate the homogeneity of the Antarctic fauna of *Polychaeta* and a considerable variability of the fauna of *Amphipoda*.

III. The natural divisions of both dendrities with several possibilities of grouping illustrates well the idea of Knox and Lowry (1977) that the subantarctic islands (Kerguelen and Heard, Marion, Macquarie as well as Auckland and Campbell) should be considered four distinct zoogeographic areas. This is especially clear in the analysis of the distribution of *Amphipoda*.

IV. The structure of the dendrites illustrates well the concept of the exceptional position of South Georgia as a transitional area, which is particularly obvious in the case of *Polychaeta*. This area is a place in which the dendrite branches into four different biogeographical areas.

V. The proposal of distinguishing biogeographical areas on the basis of *Polychaeta* distribution which is here presented differs from the concept of Knox and Lowry (1977). The grouping of localities in the case of both animal groups discussed would be similar with a reservation that the differences in the case of polychaete fauna are only more subtle. Thus the presently proposed division of the Antarctic into areas is in general in agreement with Averincev's (1972) division based on the distribution of *Polychaeta Errantia*.

VI. The opinion of Knox and Lowry (1977) that in the case of the analysis of the distribution of *Polychaeta* the Magellanic area cannot be distinctly enough separated from the Antarctic area, seems to be controversial, and, consequently, the combining the two areas is also disputable. As it is shown in Fig. 3 the Magellanic area is distinctly separated.

VII. Disregarding the strongest divisions of both dendrites as contributing little to the problem of the Antarctic biogeographical regionalization as well as the weakest divisions, the present author proposes the following division identical for *Amphipoda* and for *Polychaeta* (Fig. 5):

A. Magellanic area
B. West Antarctic area (= Scotia Arc with the Antarctic Peninsula)
C. East Antarctic area
D. Marion Island

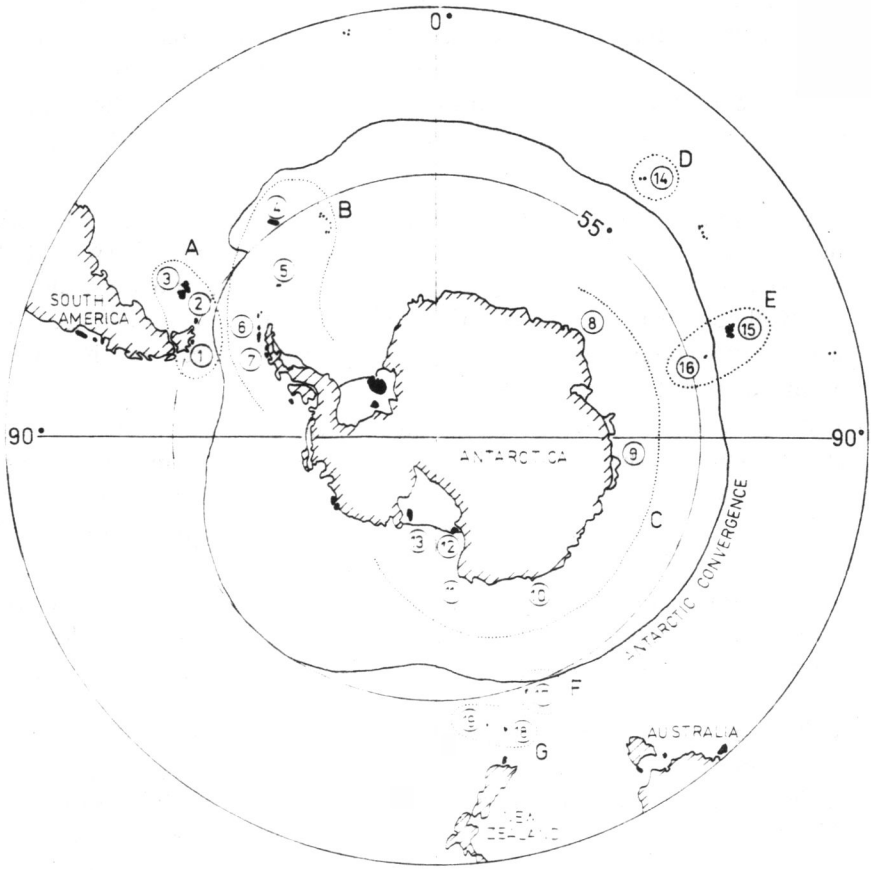


Fig. 5. Map of the Antarctic with proposed biogeographic areas
(1 — Tierra del Fuego, 2 — Burdwood Bank, 3 — Falkland Islands, 4 — South Georgia, 5 — South Orkney Islands, 6 — South Shetland Islands, 7 — Antarctic Peninsula, 8 — Enderby Land, 9 — Davis Sea, 10 — Adelie Coast, 11 — Cape Adare, 12 — McMurdo Sound, 13 — Ross Sea, 14 — Marion Island, 15 — Kerguelen Island, 16 — Heard Island, 17 — Macquarie Island, 18 — Auckland Island, 19 — Campbell Island; A — Magellanic area, B — West Antarctic area, C — East Antarctic area, D — Marion Island, E — Kerguelen and Heard Islands, F — Macquarie Islands, G — Auckland and Campbell Islands)

E. Kerguelen and Heard Islands
F. Macquarie Island
G. Auckland and Campbell Islands

VIII. Separating the East Antarctic from the West Antarctic as distinct zoogeographical units is more justified than combining them into one area.

6. Резюме

Используя таблицы сходства Нокса и Лоури (1977), разработанные на основе распределения антарктических *Polychaeta* и *Amphipoda*, представлены предложения для математической группировки антарктических районов. При помощи метода Флорка и др. (1951) были составлены самые короткие дендриты районов и проведено их математическое разделение (рис. 1, 2, 3, 4).

С математической точки зрения самые сильные разделения обоих дендритов подтверждают и хорошо обосновывают гипотезу Нокса и Лоури (1977) об однородности фауны антарктических *Polychaeta* и о значительном разнообразии фауны *Amphipoda*. Из анализа обоих дендритов следует, что субантарктические острова (Кергелен, Хёрд, Марион, Маккуори, а также Окленд и Кэмпбелл) нужно считать независимыми зоогеографическими провинциями, что хорошо совпадает с мнением авторов выше указанной работы. Группировка районов в случае обеих рассматриваемых групп животных является аналогичной, что, в свою очередь, отличается от предложения Нокса и Лоури. Сомнительным кажется также подчеркивание авторами того факта, что в случае *Polychaeta* магелланская провинция не отделяется отчетливо от остальных антарктических провинций.

По мнению автора настоящей статьи необходимо принять следующее разделение, одинаковое для обеих групп бентоса (рис. 5):

Провинция восточной Антарктиды
Провинция западной Антарктиды (Дуга Скотия с Антарктическим полуостровом)
Магелланская провинция
Острова Кергелен и Хёрд
Остров Марион
Острова Маккуори
Острова Окленд и Кэмпбелл.

Разделение восточной и западной Антарктиды, как отдельных зоогеографических провинции, в соответствии с принятыми принципами анализа данных, является более обоснованным, чем объединение их в одну область.

7. Streszczenie

Wykorzystując tabele podobieństw Knoxa i Lowry'ego (1977) opracowane na podstawie rozmieszczenia antarktycznych *Polychaeta* i *Amphipoda*, przedstawiono propozycję matematycznego grupowania rejonów szelfu antarktycznego. Posługując się metodą opisaną przez Florka i innych (1951) ułożono najkrótsze dendryty rejonów oraz dokonano ich naturalnego podziału (rys. 1, 2, 3, 4).

Najmocniejsze podziały obu dendrytów potwierdzają i dobrze uzasadniają tezę Knoxa i Lowry'ego (1977) o jednorodności fauny antarktycznych *Polychaeta* i o dużym zróżnicowaniu fauny *Amphipoda*. Z analizy obu dendrytów wynika, że wyspy subantarktyczne (Kerguelen i Heard, Marion, Macquarie oraz Auckland i Campbell) należy traktować jako niezależne obszary zoogeograficzne, co jest zgodne z zapatrywaniem autorów oryginalnej pracy. Grupowanie rejonów w przypadku obu rozpatrywanych grup zwierzęcych jest podobne, co z kolei

różni się od propozycji Knoxa i Lowry'ego. Dyskusyjnym wydaje się podkreślenie tych autorów, iż w przypadku *Polychaeta* obszar magellański nie jest zbyt przekonywująco oddzielony od obszaru antarktycznego.

Zdaniem autora niniejszych uwag należy przyjąć następujący podział, jednakowy dla obu grup bentosu (rys. 5):

Obszar Antarktydy Wschodniej
Obszar Antarktydy Zachodniej (Łuk Scotia z Półwyspem Antarktycznym)
Obszar magellański
Wyspy Kerguelen i Heard
Wyspa Marion
Wyspy Macquarie
Wyspy Auckland i Campbell.

Rozdzielenie Antarktydy Zachodniej i Wschodniej jako osobnych obszarów zoogeograficznych jest, w myśl przyjętych założeń analizy danych, bardziej uzasadnione niż łączenie ich w jeden obszar.

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