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The Magnitude of Islands and the Size of Bats (*Chiroptera*)

[Pp. 281—348]

Wielkość wysp a wielkość form nietoperzy (*Chiroptera*)
Величина островов и размеры летучих мышей (*Chiroptera*)

Abstract: The study covers the suborder *Megachiroptera*, with its sole family *Pteropidae*, and the suborder *Microchiroptera*, for which representatives of 9 families have been chosen. In the *Megachiroptera* a decrease in the size of insular forms was found in 15 cases, an increase in 6 cases, whereas in 16 cases there were either no changes in size or they were too complicated for analysis. In the *Microchiroptera* the insular forms showed a decrease in size in 59 cases and an increase in 26. The cases of the third category (see *Megachiroptera*) have not been included in the study. The result for both suborders together is 32 increases against 74 decreases, which indicates that the tendency towards reduction in measurements prevails evidently over the opposite tendency. The main cause of the diminution of measurements in the insular *Chiroptera* is probably the promotion of quantitatively strong populations by selection, which, on the other hand, on account of the limitation of space and, in consequence, among other things, of food supply, is possible by reduction in body size. Inbreeding (less harmful than was supposed before and of rare occurrence owing to the strong dispersal of bats), reduced selection, genetic drift, pleiotropism and gene linkage (these act ambivalently), and Bergmann's rule (which rather holds good for the temperate zone, where however there are not many islands; besides, it only partly relates to the bats living there because of their slight homeothermy) seem to be of minor importance.

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I. INTRODUCTION

No studies on the dependence of the size of bats upon the magnitude of the islands inhabited by them have hitherto been published, though some works of this sort were given to other orders of mammals as well as to other classes of vertebrates, e. g., RENSCH (1930) and other workers carried out investigations on birds and MERTENS (1934) brought out an excellent work on reptiles.

The opinion that mammals always dwarf on islands was commonly held by the investigators of the 19th century. Its origin was favoured by the fact that older zoologists took much more interest in large mammals than in small ones. At first these studies were poor in respect of method; hence, as early as the beginning of the 20th century objections were raised to the procedure based on comparison of remotely related forms, the ignoration of influences of domestication and geological history, etc. (ANTONIUS, 1914; HILZHEIMER, 1909). It is another matter that in their argumentation the critics themselves used to forget about Bergmann's rule as that usually associated with the changes in size caused by isolation. Even in some conspicuous modern works the authors do not remember to be cautious in this respect. Thus, ALLEE and SCHMIDT (1951) refer for an example of dwarfism in insular mammals to the paper by KRAUSSE (1914), who states that some mammals of Sardinia are smaller than the same species in Thuringia, and yet they live there under completely different climatic conditions, especially so far as the thermal minima are concerned, and these are believed to play a conclusive part in Bergmann's rule.

It was not until some time later that the authors took interest in small insular mammals (BERRY, 1964; CORBETT, 1961; DEGERBØL, 1940; STEVEN, 1953), which usually appeared to be larger than the forms from the mainland. This induced FOSTER (1964) to make a comparative survey of 116 insular forms representing 6 orders of mammals. He found an evident tendency towards gigantism in insular rodents and towards dwarfism in the *Lagomorpha*, *Carnivora* and *Artiodactyla*. The insular marsupials turned out to be larger and insectivores smaller, but the material for these orders was a little too scanty to make any definite conclusions.

Two trends can be distinguished in the interpretation of these changes. The first of them is represented by ALLEE and SCHMIDT (1951), who explain the dwarfing of mammals on islands simply by the limitation of space, without taking up further analysis of the causes. MERTENS represents the second trend; he analysed in detail these phenomena and arrived at the conclusion that it is not the restriction of space alone but rather its consequences that cause the changes in size.

An investigation of bats in this respect seems particularly instructive on account of an interesting peculiarity of this group: on the one hand, they have extensive individual ranges like large mammals and, on the other hand, they are of small size like many rodents. Another peculiarity consists in their power of flight, which makes them biologically convergent with birds and these last, unlike the majority of mammals, show a tendency towards increase in size on islands (RENSCH, 1930). Finally, the lack of knowledge how this order of mammals, which comes second in number of forms, behaves in this respect seems to be rather a serious gap.

In my study I included both suborders of bats, the *Mega-* and *Microchiroptera*. The first of them form only one family and are generally larger than the members of the other suborder. This last, in turn, exceeds the first suborder in number of forms by several times and consists of as many as 16 families, out of which 9 were chosen for study. All in all, 106 comparisons have been obtained for the order *Chiroptera*.

I wish to express my heartfelt gratitude to Dr E. RAYMOND HALL, Distinguished Summerfield Professor of the Kansas University, Lawrence, U.S.A., who by providing facilities for my stay in the U.S.A. and during his talks with me inspired me with the idea of working out the problem which has become the subject of this paper and to Prof. K. KOWALSKI, Head of the Institute of of Systematic Zoology, Polish Acad. Sci., Kraków, Poland, for his valuable criticism and edition of the paper. I am also indebted to Dr A.N. KURSKOV, the Institute of Zoology, Byelorussian Acad. Sci., Minsk, U.S.S.R., for the translation of the Summary into Russian, Dr V. HANÁK, Charles' University, Prague, Czechoslovakia and Dr P.P. STRELKOV, the Institute of Zoology, Acad. Sci., Leningrad, U.S.S.R., for lending me the undispensable literature and to Mr J. ZAWADZKI for his painstaking translation of this paper into English.

II. MATERIAL AND METHOD

On account of the scope of the present work and the lack of suitable collections in the museums, I used only the materials derived from literature. As regards taxonomy, I brought the data from the old works up-to-date, basing myself on the papers by CABRERA (1957), CHASEN (1940), ELLERMAN and MORRISON-SCOTT (1951), HALL and KELSON (1959), LAURIE and HILL (1954), TROUGHTON (1954) and on other smaller revisions.

I compared only closely related forms, i. e., those belonging to the same species or superspecies. It is therefore of lesser importance for the ends of this work whether a given form should be considered to be a closely related species or merely a subspecies.

Size differences are, for the most part, given after the authors mentioned.

Whenever I have established them myself, I mark it. I did not, as a rule, analyse the cases characterised by lack of size differences, as they are considerably less reliable and also less important to the general conclusions.

For comparisons within the *Megachiroptera* I adopted the method of establishing the smallest and the largest form of the whole group of related forms. The introduction of this method was necessary, seeing that the centre of the *Megachiroptera* lies in the most complicated regions of the world as regards zoogeography, with primary and secondary centres of radiation (SIMPSON, 1961), where the origin of one form from another is very often obscure. I made only one exception, in the case of *Rousettus angolensis,* because of the geographically uncomplicated area of its occurrence, and I treated this form in the same manner as I did the *Microchiroptera.*

Having regard to the difficulties of this method, for studies on the *Microchiroptera* I chose mainly regions which were geographically much less complicated and in these I compared insular forms only with the nearest continental forms (or the forms from smaller islands with those from larger islands). To save room I desisted from giving the measurements and omitted the list of islands, which, besides, I regarded as dispensable for these geographically simple regions. In the handling of the *Microchiroptera* I left out all the cases which were too complicated for analysis and those showing no size differences. In addition, for this group I applied the method of multiple comparisons (with few exceptions), which made it possible to achieve a great increase in the number of results. This method consists in comparing, within particular groups, each insular form with each form living on the coast of the mainland. Thus, *Peropteryx macrotis*, having 3 insular forms, compared with 1 continental form provides 3 (1 × 3) results, *Hipposideros commersoni* (2 insular forms × 3 continental) 6 results, etc. Discussing the results, I marked the number of comparisons as follows: *H. commersoni* (6 ×).

Abbreviations used in this paper: f — length of forearm; sk — greatest length of skull; bc — width of brain-case; zyg — width of skull between zygomatic arches; teeth — length of upper tooth-row from C to the last M. The symbol „- -8·3" denotes maximum measurements and „8·3- -" minimum measurements. All the measurements are given in millimetres.

III. LIST OF ISLANDS MENTIONED IN THE SECTION ON THE *MEGACHIROPTERA*

Admiralty Islands — N of eastern New Guinea, often included in the Bismarck Archipelago, 2072 km². Largest island: Manus — 1787 km². Ruk — 16 km long.

Alcester Islands — 40 km SW of Woodlark I. Isolated island and islet, both together some dozen square kilometres in area.

Aldabra Islands — 402 km NW of Madagascar. They consist of 4 main islands, which form an atoll, 34 km long by 13 km wide. Area of lagoon — 130 km^2.

Alor — eastern Little Sunda Is., N of Timor, 2098 km^2.

Anambas Islands — E of the state of Pahang, Malaysia. These are very numerous small islands. Largest island: Djemadja — 16 × 24 km.

Andaman Islands — Indian Ocean; 200 islands and islets with a total area of 6496 km^2. Five main islands are poorly isolated from each other. Narcondam, 6 km^2 in area, is strongly isolated, about 110 km from the main islands.

Aru Islands — S of western New Guinea, 8563 km^2. Five main islands, surrounded by 80 small ones, constitute as if one large island. Wokam is one of the main islands.

Aur — 70 km E of the state of Johore, Malaysia, 6 × 3 km.

Babi — W of Sumatra, 30 km SE of Simalur, is the largest island of the Babi group, 5·5 × 5·5 km. It lies 2·8 km from Lassia, 5·5 × 1·8 km.

Balambangan — 22 km from the N point of Borneo, 22 × 5·5 km. Separated from larger Banguey by a 5·5-kilometre strait.

Bali — 3·2 km E from Java, 32 km from Lombok, 5809 km^2.

Banda Islands — S of Ceram. One larger and 10 small islands. Total area — 104 km^2.

Banguey (= Banggi) — see Balambangan, 33 × 22 km.

Bangka (= Banka) — off the E coast of southern Sumatra, separated from it by a strait 13 km wide, 11 942 km^2.

Batu Islands — W of Sumatra, between Nias and Siberut. They consist of some larger islands (9·7 × 48, 22·5 × 40, 11·3 × 37, 3·2 × 8 km) and numerous small islets. Total area — 1199 km^2.

Bawean — 106 km N of Java, strongly isolated, 199 km^2.

Belitung — between Sumatra and Borneo, 4833 km^2.

Berhala — in the Strait of Malacca, 46 km from Sumatra. Less than 1 km^2 in area.

Bismarck Archipelago — NE of New Guinea, 50 919 km^2. New Ireland — 9842 km^2, New Britain — 37 814 km^2. It includes the Duke of York group, 60 km^2 in area, composed of 13 islets between New Ireland and New Britain; one of them is Mioko. Another small island of the archipelago is Makupa.

Bonerato — 11·2 × 9·7 km; 130 km N of Flores and 1·8 km away from Kalao, which is twice as large.

Borneo — 746 000 km^2.

Caroline Islands — Micronesia, 1194 km^2. Largest isolated islands: Kusaie — 109 km^2, Ponape — 334 km^2. Main groups of islands: Palau (= Pelew) — 487 km^2, 8 islands and 1 atoll, Yap — 101 km^2, 4 large and 10 small islands (largest island — 16 × 4·8 km), Truk (= Ruk) — 101 km^2, 57 islets, of which the largest has an area of 23 km^2. Here belongs also the Mortlock (= Nomoi) group, 241 km SE of the Truk group, with 3 atolls formed by 93 islets. The largest islet is about 2·6 km^2 in area.

Celebes — 189 035 km^2.

Ceylon — 65 600 km^2.

Christmas Island — Indian Ocean, 370 km S of the western point of Java. Strongly isolated, 155 km^2.

Claremont Islands — 65 km E of the Cape York Peninsula (Australia). Five islets with a total area of about 1 km^2, poorly isolated from other, also small, islands which form the Great Barrier Reef.

Comoro Islands — between northern Madagascar and Africa, 2150 km^2. Largest island: Grande Comoro — 1145 km^2. Anjouan — 357 km^2, Moheli — 290 km^2, Mayotte — 354 km^2.

Condore Islands — 90 km S of the Indo-China Peninsula, 104 km^2; 12 islands, the largest of which is $16 \times 4{\cdot}8$ km.

Conflict Islands — a large atoll between the Louisiade Archipelago and the E point of New Guinea. It consists of 10 main islets.

D'Entrecasteaux Islands — just off the E point of New Guinea, 3108 km^2. Largest island: Fergusson — 1342 km^2. Goodenough — 32×24 km.

Duff Islands — 111 km NE of the Santa Cruz group; 22 islets, of which the largest is 1·6 km long.

Dyampea (= Tanahdjampea, etc.) — 148 km N of Flores, 19×16 km.

Enggano — 110 km W of southern Sumatra, isolated, 444 km^2. Pulo Dua — a very small islet situated close to it.

Fiji Islands — in eastern Melanesia; 250 islands and islets. Total area — 18 804 km^2. Viti Levu — 10 386 km^2, Vanua Levu — 5535 km^2, Ovalau — 101 km^2, Taviuni — 435 km^2, Moala — 62 km^2, Totoya — 28 km^2, Nauai — some dozen km^2, Namena — several km^2, Nairai — some dozen km^2, Yasawa — 3×15 km.

Flores — 14 273 km^2.

Gebe — between Halmahera and New Guinea, just on the equator. $7{\cdot}5 \times 40$ km.

Heath (also Rogeia) close to the E point of New Guinea, several km^2.

Jarak — in the Strait of Malacca, 1 km^2.

Java — 126 500 km^2.

Kangean Islands — 120 km N of Bali, isolated from large islands. They consist of one larger island and a few smaller ones. Total area — 668 km^2. Kangean — 487 km^2, Paliat — $4{\cdot}8 \times 14{\cdot}5$ km, Sepanjang — 8×16 km.

Karkar (= Dampier) — 15·5 km from the NE coast of New Guinea. 363 km^2.

Kai Islands — S of western New Guinea, 1437 km^2. Largest island: Great Kai — 624 km^2, the second largest island is 48 km long by 16 km wide.

Koh Pennan — 50 km E of the middle Malay Peninsula, with numerous islands in the strait, 129 km^2.

Koh Samui — 9 km E of the middle Malay Peninsula, near Koh Pennan, 272 km^2.

Labuan — off the NW coast of Borneo, 32 km from the town of Brunei, 91 km^2.

Laccadive Islands — Indian Ocean; 14 islands with an area of 26—207 km^2. Minicoy atoll, 8·7 × 5·2 km and up to 1·1 km wide, belongs to this group.

Lantinga — a small islet off the E coast of the Malay Peninsula, between the groups Redang and Tioman.

Laurot Islands — 120 km S of Borneo; 3 islands and a few islets with a total area of some dozen square kilometres. One of them is Mata Siri.

Lingga Archipelago — 37 km from the E coast of Sumatra; 2181 km^2. Lingga — 932 km^2, Singkep — 829 km^2.

Lombok — Little Sunda Islands, 4729 km^2.

Louisiade Archipelago — 232 km SE of the eastern point of New Guinea; 10 larger islands, the remaining ones are small. Largest island: Tagula — 24 × 80 km. Panniet is the largest in the Deboyne group (6 islands) — 8 × 4·8 km. Russel — 16 × 32 km, Misima — 259 km^2.

Loyalty Islands — E of New Caledonia, Melanesia; 2072 km^2. Largest islands: Lifu — 16 × 64 km, Mare — 29 × 35 km, Uvea — 5·6 × 37 km.

Madagascar — 590 000 km^2.

Madura — off the N coast of Java, 14 175 km^2.

Maldive Islands — Indian Ocean; 19 atolls, which extend meridionally over the space of 870 km; 298 km^2. Male is one of the atolls.

Manam (= Manumudar, Vulcan) — 83 km^2, situated 14 km from the N coast of New Guinea.

Mangalum — a very small island, 48 km from NW coast of Borneo.

Mantanani — a very small island in the group of the same name, 22 km from the NW coast of Borneo.

Marianas Islands — Micronesia, sometimes included in the Caroline Islands; 958 km^2. Largest island: Guam — 559 km^2.

Marshall-Bennett Islands — 5 islets, 39 km W of Woodlark, Melanesia. The largest island is several square kilometres in area.

Mascarene Islands — E of Madagascar. Mauritius — 1865 km^2, Reunion — 2512 km^2, Rodriguez — 109 km^2. They are all strongly isolated.

Mergui Archipelago — along the W coast of the proximal half of the Malay Peninsula. Kuda, Muntia, Panjang and Paya are small islands; Panjang, the largest of them, is 3·2 × 24 km.

Micronesia — out of the vast number of islands of this group of archipelagos, the Volcano (= Kazan Retto) Islands are referred to in this paper. They are 3 islets, 5·2, 21 and 3·9 km^2 in area, isolated from each other and from the Bonin Is., situated next to them. The Bonin Islands, lying N of them, consist of 20 islets, of which the largest is 25 km^2. Total area — 104 km^2.

Misool (Mysol) — 64 km SW from the W point of New Guinea, 71 × 50 km.

Moluccas — between Celebes and New Guinea. Largest island: Halmahera — 17 793 km^2. Ambon group: Ambon — 813 km^2, Buru — 9500 km^2, Ceram — 17 151 km². Panjang (11·3 × 3·2 km), 48 km SE of Ceram is one of the 3 islands of the Gorong Is., the two others being Gorong — 12·9 × 4·8 km and Manawoka — 17·7 × 3·2 km. Other islands of the Moluccas: Ternate — 29 km W of Halmahera, 106 km², Morotai — 24 km NE of Halmahera, 1813 km², Batjan — 2365 km², Rau — 2·5 km W of Morotai, 14·5 × 6·4 km. Obi Is. — largest island: Obir, 84 × 45 km; other islands much smaller. Boano — off the W coast of Ceram, 148 km²; Saparua — 8 km from the S coast of Ceram, 189 km²; Arsilulu — a small island near Ambon; Keffing — as above; Watubela Islands — between the Kai Is. and Ceram; 8 islands, of which two are 14·5 × 3·2 and 9·6 × 4·8 km.

Murray Islands — 3 islets with a total area of several km², 185 km NEE of the Cape York Peninsula (Australia), isolated from large islands.

Natuna Islands — between Borneo and Sumatra. In the North Natuna group North Natuna (= Laut), 4·8 ×11 km, is the largest and surrounded with numerous small islets; 64 km S of it is Great Natuna (= Bunguran), 40 × 64 km, the largest of the Natuna Is. Close to its N point is very small Pulo Panjang (= Pandjang). The largest islands of the Southern Natuna Is. are Sirhassen (= Serasan), 6·4 ×16 km and Subi Besar, 8 ×19 km.

New Caledonia — Melanesia, 22 139 km².

New Guinea — 772 000 km².

New Hebrides — Melanesia, 14 763 km². Largest island: Espiritu Santo — 3846 km². Efate — 129 × 32 km, Epi — 365 km², Aore — 52 km², Aurora — 350 km², Lopevi — 7·5 × 4·5 km, Malekula — 37 × 72 km, Pentecost — 492 km², Aneityum — 65 km², isolated; Malo — just close to Espiritu Santo, beside smaller Tanna — 557 km², Aoba (= Leper) — 246 km², Ambrym — 596 km², Erromanga — 894 km².

Nias — W of Sumatra, 4064 km².

Nicobar Islands — Indian Ocean, N of Sumatra; 19 islands with a total area of 1645 km². Great Nicobar, 862 km², is the largest; Little Nicobar, 207 km², is 7·5 km from it. Car Nicobar — 127 km², strongly isolated; Nancowry — 65 km²; close to it is Camorta, 129 km², and near this is Trinkut, 10 × 5 km. Tillanchong lies 25 km from Camorta, 17 × 0·5—2 km.

Pagai Islands — W of Sumatra; 2 larger islands and small islets. North Pagai — 27 × 40 km, South Pagai — 19 × 68 km.

Pantar — Little Sunda Is., between Alor and Lomblen, 728 km².

Peleng — 19 km E of Celebes, 2406 km².

Pemanggil — E of the Malay Peninsula, between Tioman and Aur, 4·5 × 2·7 km.

Pemba — 64 km E of Africa, 984 km².

Percy group — 80 km from the coast of Queensland (Australia), 12 islets, the largest of which measures 8 × 4 km.

Perhentian Islands — 16 km E of the state Trengganu (Malaysia) 2 islets, situated beside each other, with a total area of several square kilometres.

Philippines — 7083 islands, 299 700 km². Basilan — 1279 km², Cagayan

Sulu — 67 km² (strongly isolated), Catanduanes — 1430 km², Cebu — 4408 km², Cuyo — 57 km² (isolated from larger islands), Dinagat — 800 km², Guimaras — 578 km², Jolo — 894 km² (isolated from larger islands), Lamboyan — very small, near the southern end of Palawan, Leyte — 7198 km², Luzon — 105 700 km² (the largest in the group), Malanipa — very small, near Basilan and Mindanao, Mindanao — 97 968 km², Mindoro — 7146 km², Negros — 12 699 km², Palawan — 11 525 km², Palmas — 77 km SE of Mindanao, several km², isolated, Panay — 11 519 km², Polillo — 606 km², Samar — 13 079 km², Sibutu — isolated from large islands, the largest in the Sibutu group, Sulu Islands — 101 km², Tablas — 686 km².

Phu Quoc — close to the coast of Cambodia, 596 km².

Pinon — a small island off the NW coast of New Guinea.

Pisang, Pulau — 1·5 km², in the Strait of Malacca, 13·5 km from the coast of the state of Johore; there are 3 other smaller islets in its close neighbourhood.

Redang Islands — 24 km from the coast of Trengganu, Malaysia. Babi — 4 × 1·8 km, Great Redang — 23 km², Sri Buat (= Siribuat) — 3·5 × 2·5 km, Tinggi — 7 × 4 km.

Riau Archipelago — S of the Malay Peninsula, 5903 km².

Salajar (Salayer) — 16·7 km S of the SW point of Celebes, 671 km².

Salawati — between Halmahera and New Guinea, 48 km in diameter.

Samao (= Semaoe) — close to the W point of Timor, 27 × 13 km.

Samoa Islands — western Polynesia, 10 larger islands and many islets, total area — 3131 km². Largest island: Sawaii — 1821 km². Upolu — 1114 km², Tutuila — 104 km², isolated; Tau — 34 km² and near it 2 small islets with an area of several square kilometres, which form the Manua group with it.

Sangihe Islands — between the NE point of Celebes and Mindanao, 813 km². Largest island: Sangihe — 562 km². Siau — 155 km², Tahulandang — 62 km², Biaro — 11 × 4·8 km.

Santa Cruz Islands — Melanesia, 958 km². Largest island: Santa Cruz (= Ndeni) — 24 × 56 km. Vanikoro (double island) — 16 × 48 km, Tapoua (probably Utupua) — 24 × 16 km (ring).

Sawu Island — between Sumba and Timor. Sawu 414 km², Raijua — 36 km².

Schouten Islands — in Geelvink Bay, NW of New Guinea, 3188 km². Largest island: Biak — 80 × 40 km.

Sembilan group — 9 islets, 18·5 km W of the state of Perak, in the Strait of Malacca. Total area less than 5 km².

Seychelles — Indian Ocean. Total area — 407 km². Largest island: Mahe — 142 km².

Siberut — W of Sumatra, 113 × 40 km.

Simalur (= Simeulue) — W of Sumatra, 1844 km².

Sipora — W of Sumatra, 48 × 19 km.

Solombo Besar — in the Java Sea, probably in the Laurot group and very small.

Solomon Islands — Melanesia; total area — 40 430 km². Alu — close to Shortland, several km², Banika — in the Russell group, 31·5 km NWW of Guadalcanal, near Pavuvu, 1·6 × 9·6 km, Bougainville — 101 km², Buka — just by the N point of the previous, 777 km², Choiseul — 5853 km², Fauro — 12 km from the SE point of Bougainville, 9·6 ×16 km, Florida — between Malaita and Guadalcanal, 34 × 7 km, Ghizo — 13 km SE of Vella Lavella, 3·2 × 8 km, Gover (= Ndai) — 44 km N of Malaita, 2·5 × 6·5 km, Guadalcanal — 65 km², Kulumbangra (= Kolombangara) — 8 km NW of New Georgia, 32 × 24 km, Malaita — 6216 km², Malapa — 4·5 km E of the E point of Guadalcanal, 5 km², Mono — one of the islands of the Treasury group, S of Bougainville, 9·6 km in diameter, Navoro (= Narovo, Simbo) — 10 km SSW of Ronongo, 3 × 7 km, New Georgia — main island in the group of the same name, 32 × 80 km, Rendova — some dozen kilometres SW of the previous islands, 8 × 24 km, Rennell — isolated, 19 × 80 km, Ronongo (= Ganongga) — 3 km SSW of Vella Lavella, 24 × 8 km, Rubiana — a small islet close to the S coast of New Georgia, Russell group — see Banika; besides, Pavuvu — 8 ×16 km, San Christoval — 65 × 207 km, Shortland — main island in the Shortland group, 10 km S of Bougainville, 16 ×13 km, Tukopia — ? km², Ugi — 8·4 km from the NE coast of San Christoval, 3 ×10 km, Vella Lavella — 52 km SW of Choiseul, 40 ×16 km, Sta Ysabel — 4662 km².

South Twin — in the Mergui Archipelago, W of the Malay Peninsula. At most several square kilometres in area.

Sula Islands — E of Celebes, 3 islands and small islets. Total area — 4851 km². Mangole — 116 ×16 km, Sanana (= Sulabesi) — 56 ×16 km, Taliabu — 109 ×40 km.

Sumatra — 433 795 km².

Sumba — Little Sunda Islands, 11 152 km².

Sumbawa — Little Sunda Is., 15 449 km².

Swallow Islands — 40 km NE of Santa Cruz; five small islands, the largest of which is 6·4 km long.

Talaud Islands — between Halmahera and Mindanao, 3 islands and several small islets, 1282 km². Kaburuang — 93 km², Karakelong — 984 km², Salebabu — 155 km².

Tambelan Islands — 150 km W of the W point of Borneo. Several tens of square kilometres.

Tanimbar Islands — E of Timor, 5625 km². Largest island: Jamdena — 113 × 45 km. Selaru — 48 ×16 km, Larat — 32 × 8 km.

Thursday Island — 12 km W of the northernmost point of the Cape York Peninsula (Australia); surrounded by 3 smaller islands; 2·4 ×1·6 km.

Timor — 34 907 km².

Tioman — 56 km E of the state of Johore, Malaysia, 137 km².

Togian Islands — in the Gulf of Tomini, eastern Celebes, 803 km². Batudaka — 29 ×13 km, Togian — 21 ×11 km, Talata Ko — 16 × 8 km, Una Una — 9·6 km in diameter.

Tonga Islands — western Polynesia, S of Samoa Is., 65 km². Niue (= Savage) — 259 km², isolated; Tonga-Tabu (= Tongatapu) — 34 × 8·5 km, the largest; Namouka — the largest in its group, several km². Besides, a large number of other islands and islets.

Trobriand Islands — 5 islands and islets, N of D'Entrecasteaux Is., E. New Guinea. Largest island: Kiriwina — 16 × 56 km.

Waigeo — N of the W point of New Guinea, 48 × 113 km.

Wallis Islands — W of the Samoa Is. Uea (= Uvea) — 11·2 × 6·4 km, isolated except for small islets which surround it.

Wetar (= Wetter) — 64 km N of Timor, 3626 km².

Willis group — 450 km E of Queensland, Australia; three small islands. Total area — about 5 km².

Woodlark — Melanesia, E of the D'Entrecasteaux Is., 64 × 16 km.

Yule — close to the coast of the eastern part of the Gulf of Papua, New Guinea.

IV. SUBORDER: *MEGACHIROPTERA*

Family: *Pteropidae*

This family is the only one of the suborder *Megachiroptera*. It consists of phytophagous bats distributed widely in the tropics of the Old World.

The basic work that I used in this part of my investigations was the catalogue by ANDERSEN (1912).

1. *Rousettus leschenaulti*. *R. l. leschenaulti* DESMAREST, 1820 occurs probably in whole India (Rajasthan, Coorg, Western Ghats, Kumaon, Bengal), Nepal, Bhutan, Burma (including Tenasserim), northern Thailand, Tonkin (northern Vietnam) up to the Fukien Province (S. E. China). ANDERSEN examined 11 specimens from the Himalayas, Nepal, Bengal, middle Burma and northern Thailand. In 7 specimens (India, Himalayas, Burma, N. Thailand) f = 80·5—87·5. Six skulls (Himalayas, Bengal, Burma, N. Thailand) had sk = 37—41·5; bc = 15·5—17; zyg = 22·3—23·7; teeth = 14—15·7.

R. l. shortridgei THOMAS and WROUGHTON, 1909 has been recorded only from Java. It is bigger than the previous subspecies. F = 91; sk = 42·5; bc = 17; zyg = 26·5; teeth = 16·3.

Java is known for its mild climate and its thermal minima are undoubtedly far higher than those on the Asiatic continent, especially in Nepal or Bhutan, where even 0°C is not uncommon in winter. Consequently, the larger size of the Javan form disagrees with Bergmann's rule. The influence of insularity may have prevailed here, though this supposition is not certain because of the large area of Java.

2. *Rousettus amplexicaudatus* is divided into 3 size groups. *R. a. hedigeri* POHLE, 1953 from the Solomon Is. belongs to the first, smallest group. Six

specimens of this subspecies, derived from Fauro and Guadalcanal, were examined by ANDERSEN as *R. brachyotis*. F = 69·8—75; sk = 33—36·2; bc = 13·8—14·8; zyg = 20—23·7. Some data on *R. a. hedigeri* have been published also by SANBORN (1931), who examined 4 specimens from Santa Ysabel. In 2 males f ranged between 74 and 76, in one female it was 68·2. The difference in size between *R. a. hedigeri* and *R. a. brachyotis* must be very small, since SANBORN, too, numbered his specimens in *brachyotis*. However, POHLE (1953) asserts — in truth, on the basis of only one specimen, from Bougainville — that it is slightly smaller than *R. a. brachyotis*, from which it has only recently individuated. As LAURIE and HILL (1954), after all, acknowledge the distinctness of *R. a. hedigeri*, it has been included in this paper as a separate form.

Size group II consists of *R. a. brachyotis* (DOBSON, 1877) and *R. a. minor* (DOBSON, 1873). The first of them occurs on Halmahera and Ambon (Moluccas), New Guinea and on the Bismarck Archipelago. It is much smaller than *R. a. amplexicaudatus* and resembles *R. a. minor* in size or is only slightly smaller. ANDERSEN found f = 73—81 in a big sample of specimens; in 2 specimens sk = 33—36·2; bc = 13·8—14·8; zyg = 20—23·7; teeth = 11·8—13. *R. a. minor* is known from Java. ANDERSEN collected 22 specimens, of which 18 had f = 73—81, on the average 76·9. In 11 skulls the measurements were as follows: sk = 34—37 (35·6), teeth = 12—13·3 (12·7) (mean values are given in brackets). SODY (1940) records f = 70—81·5 (76·5) for 90 specimens and teeth = 12·0—13·3 (12·7) for 15 skulls.

The third and last size group includes only *R. a. amplexicaudatus* (E. GEOFFROY, 1810). It has a large range, covering the eastern part of the Little Sunda Is. (Flores, Sumba, Sawu, Alor, Timor), Peleng, the southern Malay Peninsula, Sumatra, Enggano, Borneo, the Philippine Is. (from Luzon to Mindanao), N. Thailand, Cambodia and Tenasserim. ANDERSEN examined 14 specimens from Cambodia, Luzon, Borneo, Alor, Sumatra, Enggano, Flores, Sawu and Timor. In 10 specimens f = 77—87; sk = 35—39, bc = 14—15·8, zyg = 21—24·5, teeth = 12·8—14·2. SODY (1940) gives the measurements of 2 males and 1 female from Enggano: f = 76—81, sk = 35·3—37·6 (1 male and 1 female), teeth = 12·5—12·7. Eight specimens from Timor have f = 77—84, teeth = 12·4—13·1.

The geographical continuity in the distribution of these subspecies is, therefore, fairly evident. This continuity is infringed only in *R. a. amplexicaudatus* by its occurrence on Peleng, whereas it is absent (or has not been found yet) from Celebes. The presence of this form in the eastern part of the Little Sunda Is., with its presumable lack on Celebes, makes a similar disjunction. It is also interesting that it is lacking on Java but at the same time occurs west and east of it.

There is some gradient in the distribution of the size groups and the deviations from it are the same as the above-mentioned disjunctions in *R. a. amplexicaudatus*; namely, group I is the easternmost one, the intermediate size group (II) occupies the middle of the range, and group III inhabits farthest west, north and north-east. If the centre of origin of the bats lies, as DARLINGTON (1957) thinks, in south-eastern Asia, then *R. amplexicaudatus* visibly decreased its body size, as it colonized farther and farther areas. It is difficult to find out any obvious relations between the area of an island and the size of the form inhabiting it for these subspecies. However, the clear majority of islands on which the largest subspecies lives, not to mention the continent, are larger than the islands of the Solomon Archipelago, where the smallest form occurs.

An examination of the isotherms (Fiziko-Geogr. Atlas Mira, 1964) shows a great stability of temperatures in these tropical regions, there being no gradient of temperature corresponding to that of body size.

3. *Rousettus angolensis angolensis* (BOCAGE, 1898) is, according to EISENTRAUT (1964), somewhat smaller on Fernando Poo than in Cameroon. This reduction in size affected, above all, the forearm, tibia, metatarsals and phalanges. The measurements of 37 specimens from this island are: f = 70—77 (73·2), sk = 38·9—41·0 (40·2), bc = 14·4—15·9 (15·3), zyg = 22·4—24·0 (23·3), teeth = 14·8—16·2 (15·6), whereas 20 specimens of the same subspecies from Cameroon had f = 72·0—81·4 (77·5), sk = 39·5—42·2 (40·7), bc = 14·5—16·0 (15·3), zyg = 22·3—25·1 (23·4), teeth = 15·4—16·8 (16·1). The length of tibia was 27·0—30·0 (28·6) in the insular specimens and 28·0—34·8 (30·7) in those from Cameroon.

4. *Pteropus hypomelanus* is noted for its quite exceptionally large number of forms. In respect of size they are divided into 4 groups. Group I includes *P. faunulus* MILLER, 1902 from Car Nicobar and Nancowry (Nicobar Is.) and *P. speciosus* ANDERSEN, 1908 from Sibutu (Sulu Is.), Malanipa and Mindanao (Philippine Is.), Solombo Besar and Matasiri (this last belongs to the Laurot Is.). Both these species have been numbered in this group on the basis of their close relationship to *P. hypomelanus*. *P. faunulus* was examined by ANDERSEN on 1 specimen only derived from Nancowry. F = 118, sk = about 54·5, teeth = 19·8. In ANDERSEN'S opinion, *P. speciosus* corresponds in size to the smallest specimens of *P. h. enganus*. He examined 2 specimens from Sibutu and Mindanao, in which f = 120—123, sk = 57, bc = 21·3—21·7, zyg = 31·8—33, teeth = 22·6.

P. h. enganus MILLER, 1906 known from the islands Sipora, Siberut and Enggano, belongs to size group II. According to ANDERSEN, it is the smallest subspecies of *P. hypomelanus*. He examined 14 specimens from Enggano; their f = 121—133·5. In 8 skulls sk = 61·7—64·5, bc = 22·2—23, zyg = 31·5—35·2, teeth (9 spec.) = 22·8—26·2. SODY (1940) gives the following measurements for 8 individuals from the same island: f = 121—143, sk = 54·6—64·6, zyg = 26·9—35·5, teeth = 20·4—24·0.

Group III consists of as many as 12 subspecies, which, according to ANDERSEN, are the same size. In addition, *P. h. vulcanius* must be placed in this group on the basis of THOMAS'S (1915) description and so must *P. h. fretensis*, which was described by KLOSS (1916).

P. h. hypomelanus TEMMINCK, 1853 occurs on Halmahera and Ternate (Moluccas). ANDERSEN examined 7 specimens. Bc = 23, zyg = 35, teeth = 23·5 (measurements of 1 specimen only).

P. h. condorensis PETERS, 1869 is known from Thailand, Cambodia, Cochin China and the Puolo Condore Is. ANDERSEN examined 9 specimens. The measurements of 1 specimen from the Condore Is. are f = 135, sk = 64, teeth = 25·7.

P. h. geminorum MILLER, 1903 lives on South Twin (Mergui Arch.) and on other islands situated farther to the south, such as Panjang, Muntia, Kuda, up to Paya off the coast of the Malay state of Kedah. ANDERSEN examined 6 specimens, 4 of which had f = 134—137, sk = 64·7—68·7, bc = 22·8—23·2, zyg = 32·2—36·2, teeth = 25—26·2.

P. h. satyrus ANDERSEN, 1908 has been recorded from Narcondam (Andaman Is.) only. ANDERSEN examined 2 specimens. Measurements of 1 specimen: f = about 139, sk = 62·5, teeth = 23·8.

P. h. macassaricus HEUDE, 1896 occurs on Celebes, Peleng, and on the Sangihe and Talaud Is. ANDERSEN examined 9 specimens from these islands (except Peleng). In 4 specimens f = 131—145·5 and 3 skulls had sk = 64--, bc = --23·2, zyg = 35--; teeth (5 specimens, of which 2 juveniles) = 23·8—25·8.

P. h. luteus ANDERSEN, 1908 is known from New Guinea and from the D'Entrecasteaux, Conflict, Marshall Bennett, Trobriand and Louisiade Islands. ANDERSEN examined 7 specimens from New Guinea, Kiriwina (Trobriand Is.), Woodlark, and the Conflict Islands. In 4 specimens f = 128·5—135·5, sk = 63·8—65·5, bc = 22·8—23·0, zyg = 33·7—36·8, teeth (3 adults and 2 juveniles) = 23·2—24·8.

P. h. vulcanius THOMAS, 1915 is present only on Manam Island. THOMAS (1915) examined 6 specimens and for the type gave f = about 130, sk = 66.

P. h. fretensis KLOSS, 1916 was found on the islets Jarak and Berhala in the Strait of Malacca. One male and 2 females had f = 138, --130, sk = 67·8, 62·5—63·3, bc = 23, 20·5—22·6, zyg = 37·2, 31·7—34, teeth = 22·3—23.

P. h. robinsoni ANDERSEN, 1909 is known from the islets Rumbia and Lallang (Sembilan group). ANDERSEN examined 4 specimens from Rumbia but he gave no measurements.

P. h. canus ANDERSEN, 1908 has been reported from Pandak, Panjang and Laut in the North Natuna group. ANDERSEN examined 4 specimens from these three islands. In 3 specimens sk = 63·8—67·2, bc = --23·5, zyg = --38·5, teeth = 25—27·5.

P. h. annectens ANDERSEN, 1908 inhabits the islands Sirhassen, Panjang and Subi Besar in the South Natuna group. ANDERSEN examined 5 specimens from Sirhassen. In 2 specimens f = 130—133·5, sk = 61·3—64·5, bc = 22—22·8, zyg = 31·2—33·7, teeth = 24—24·7.

P. h. lepidus MILLER, 1900 is known from the Tambelan and Perhentian Islands, Great Redang (Redang Is.), Lantinga, Tioman, Pemanggil, Aur and Djemadja (the last one in the Anambas Is.). ANDERSEN examined 7 specimens from, among other islands, Big Tambelan, Aur and Tioman, their f being 131—139. Six skulls had sk = 62·5—67·5, bc = 23—24·2, zyg = 34·2–38, teeth = 25—26·2.

P. h. tomesi PETERS, 1868 occurs on the coastal islands of Borneo, from Sarawak to Sibutu (Philippine Is.), and including, among other islands, Labuan, Mangalum, Mantanani, Sibutu. It is also known from Lamboyan (Philippine Is.). ANDERSEN examined 7 specimens. The eighth specimen of this group appeared to be *P. h. robinsoni*, which error the author himself rectified on p. 816. The measurements given by him must be taken with this reserve; f = 128—142·5, sk (7 specimens) = 62·8—67·7, bc = 22—23·7, zyg = 32·5—37·5, teeth = 23·8—26·2.

P. h. cagayanus MEARNS, 1905 lives on the Philippine Is., where it is known from Dinagat, Guimaras, Leyte, Mindanao, Panay, Cagayan Sulu, and Luzon, and so practically from the whole archipelago. ANDERSEN examined 13 specimens from Cayagan Sulu, Luzon, Panay, Dinagat and Mindanao. In 6 specimens f = 135—141·5; 5 specimens had sk = 63·7—65, bc = 21·8—23·2, zyg = 35—37 and in 10 (of which 4 juveniles) teeth = 23·8—25·7.

P. h. simalurus THOMAS, 1923 from Simalur and a few adjacent islets, e. g., Pulu Tapah, belongs to group IV, which is the group of the largest forms. THOMAS examined 20 specimens, in which the forearm exceeded 140 mm in length. The type, from Pulu Tapah, measured: f = 146, sk = 68, zyg = 35. THOMAS emphasizes that this form is larger than the other subspecies of *P. hypomelanus*. According to CHASEN and KLOSS (1927), the length of its forearm ranges from 141 to 149 mm.

The distribution of group I shows the lack of a compact geographic area. It extends from the Nicobar Is. on the west to Malanipa (Philippines) on the east and from this last island on the north to Matasiri (Laurot Is.) on the south, overlapping the ranges of other size groups. It is interesting that they are all small islands, the largest of them being hardly 127 km² in area. The compactness of the range of group II is natural, since it includes only one form. This area lies quite clearly on the western periphery of the range of the species. The area occupied by group III is vast, which is also only natural, if we take into account the large number of its forms. On the west it is bounded by Narcondam (Andaman Is.) and the coastal islands of the Malay Peninsula; its south-eastern boundary is marked out by the archipelagos round the southern point of New Guinea and even the middle group of the Solomon Islands, whereas on the north and north-east it extends over Thailand, Cambodia, Cochin-China and the Philippines. Unlike the previous size groups, this group is represented both on very small islets and on large islands and even on the mainland of Asia. Group IV, which besides consists of only one subspecies, has the smallest range and, as has already been mentioned, inhabits the neighbourhood of the smallest subspecies of *P. hypomelanus*, which is really noteworthy.

To sum up, the distribution of the forms of the superspecies *P. hypomelanus* is characterized by A) a great disjunction in *P. speciosus*, B) the fact that a narrow strait sometimes separates two distinct subspecies from each other, e. g., *P. h. luteus* in New Guinea and *P. h. vulcanius* on Manam at a distance of 14·5 km; on the other hand, a sole subspecies may be distributed very widely on islands which are much more isolated from each other, e. g., *P. h. cagayanus* on the Philippines, and C) the striking lack of clear correlation between the magnitude of an island and the size of the form living on it. However, the islands inhabited by *P. faunulus* and *P. speciosus* with the exception of Mindanao are many times smaller than Simalur, on which the largest form lives.

The phenomenon mentioned in B) might be explained by a difference in the rate of evolution or by its temporary "standstill" (Mertens, 1934).

5. *Pteropus griseus* includes 3 subspecies, but closely related. *P. pumilus* Miller, 1910 from an islet called Palmas in the Philippines must also be counted in here. *P. pumilus* is the smallest form. Andersen examined 1 specimen (teeth = 18·2) and Miller (1910) took measurements of another specimen: f = 109, bc = 19·6, zyg = 29·6, teeth = 18·2.

P. g. griseus E. Geoffroy, 1810 and *P. g. pallidus* Temminck, 1825 belong to size group II. The first of them is known from Timor, Samao, Dyampea and Bonerato. Andersen examined 11 specimens collected from the whole range. In 4 of them f = 114·5—118, in 1 specimen teeth = 21·2. *P. g. pallidus* has been recorded from the Banda Is. Andersen examined 9 specimens. In 5 specimens f = 113·5—119 and 4 had sk = 56—59, bc = 21—22·7, zyg = 31—32·8 and teeth = 20·8—22·2.

P. g. mimus Andersen, 1908 from southern Celebes and Luzon constitutes the third group in respect of size. Three specimens from these islands were examined by Andersen. In 1 specimen from Luzon f = 127·5, sk = 59·8, bc = 22, zyg = 32·2; three specimens had teeth = 20·8—22·7. The disjunction of distribution is strikingly great.

The smallest form comes therefore from the smallest islet, the 2 intermediate forms from very small and medium-sized islands and the largest form from the largest islands.

6. *Pteropus lombocensis* has 2 subspecies. The smaller of them, *P. l. solitarius* Andersen, 1908 is known only from Alor. In the only specimen examined by Andersen f = 108·5, sk = 53, bc = 21·2, zyg = 30·2, teeth = 20·2. The larger subspecies, *P. l. lombocensis* Dobson, 1878 occurs on Lombok and Flores, and 7 specimens from both these islands had f = 113—122, sk = --55, bc = 20·2—22, zyg = 29·7—31·2, teeth = 20—21·2.

As can be seen from these data, the larger form lives on the larger islands. This situation will however change, if 2 closely related species, placed by Andersen in the group *lombocensis*, have been taken into account. *P. rodricensis* Dobson, 1878 from Rodriguez (Mascarene Is.) was examined by Andersen on 8 specimens. Although this investigator did not compare its size with the size of the subspecies of *P. lombocensis*, it will be seen from the measurements given for 3 specimens that it is rather larger: f = 124·5—127, sk = 52·2--, bc = 19·5—20·8, zyg = 28·2—30·8, teeth = 18·5—19·8. On the other hand, *P. molossinus* Temminck, 1853 from Ponapé and the Mortlock group (Carolines), and so also from small islands, is considerably smaller than the abovementioned forms of the superspecies *P. lombocensis*. Andersen examined 19 specimens (17 from Ponapé, 1 from Mortlock and 1 from an unknown locality), of which 6 had f = 94—98·5, sk = 40·4—41·8, bc = 17·2—18, zyg = 24—25, teeth = 13·8—14·8.

It seems that this situation might be explained by applying the interpretation given by Mertens (1934) for insular reptiles, i. e., it should be assumed that Alor, Lombok and Flores are too large to induce insular changes in the forms inhabiting them; then only quite small islands, which bring about extreme reactions, would remain for analysis. In the present case they are bipolar, since in one form *(P. rodricensis)* the size probably increased and in the other *(P. molossinus)* it decreased considerably.

7. *Pteropus admiralitatum* consists of 4 subspecies, but closely related *P. brunneus* Dobson, 1878 should also be reckoned in here. There seem to be two size groups, of which one, that of smaller forms, includes *P. a. goveri* Tate, 1934 from Gover (Solomon Is.), *P. a. solomonis* Thomas, 1904 from the middle and eastern Solomon Is. (from Vella Lavella through Ghizo, Ronongo, Navoro, Banika and Russel to Guadalcanal) and *P. a. colonus* Andersen, 1908 from Alu, Shortland and Mono (western part of the Solomon Is.).

Tate described six specimens of *P. a. goveri*. Five of them had f = 108—111, zyg = 28—32·0, teeth = 20·0—22·1. One specimen of *P. a. solomonis* was examined by Andersen and 3 by Sanborn (1931). F = 107—110 (4 specimens), bc = 20, teeth = 20·5 (1 spec.). These measurements were taken on the specimens from Ghizo, Ronongo, Vella Lavella and Navoro. In addition, Sanborn and Beecher (1947) give the length of forearm for 5 individuals from Guadalcanal and Banika, f = 104—115. *P. a. colonus* was examined by Andersen on 2 specimens from Shortland and Alu. F = 109·5—114, sk = 55, bc = 20·3—20·8, zyg = 29·5—31, teeth = 21—21·2. Sanborn (1931) had at his disposal 8 specimens from Mono and found that their measurements corresponded closely to the data given by Andersen.

The group of larger forms consists of *P. a. admiralitatum* Thomas, 1894 from the Admiralty Is. and *P. brunneus* from the Percy group. Andersen examined 4 specimens of *P. a. admiralitatum*, in which f = 118—126, bc = 21—22, zyg = 31·8—33, teeth = 21·7—22. *P. brunneus* is known from only one specimen. F = 118, bc = 23, zyg = 34·7, teeth = 23·7.

The compactness of the ranges of the subspecies belonging to size group I is evident. A comparison of the islands inhabited by either size group shows no significant differences in area; the members of group I live both on large and on very small islands (Gover) and the same is true of the members of group II. The occurrence of *P. brunneus*, which is a relatively large form, on the very small and, besides, partly barren Percy Is. claims attention.

8. There are two subspecies of *Pteropus ornatus*. One of them, *P. o. auratus* ANDERSEN, 1909 from Lifu and Mare (Loyalty Is.) is, according to FELTEN (1964a), evidently smaller than the other subspecies, and its measurements taken by this author are: sk = 67·4 (64·2—71·8 — 13 specimens), bc = 22·7 (21·5—23·7 — 12 spec.), zyg = 35·6 (34·0—38·4 — 13 spec.), teeth = 25·8 (24·4—28·5 — 18 spec.), f = 146 (140—156 — 14 spec.).

The measurements of *P. o. ornatus* GRAY, 1870 from New Caledonia are, after FELTEN (1964a), as follows: sk = 69·5 (66·7—72·6 — 16 spec.), bc = 23·1 (22·0—23·8 — 22 spec.), zyg = 36·5 (33·8—39·2 — 20 spec.), teeth = 26·3 (24·7—28·0 — 23 spec.), f = 154 (144—163 — 22 spec.).

As will be seen from these data, the considerably larger island is inhabited by the larger form.

9. *Pteropus tonganus* has 4 subspecies, which form 3 size groups. The first group consists of *P. t. vanikorensis* QUOY and GAYMARD, 1830 from Vanikoro (Santa Cruz Is.) and, probably, *P. t. basilicus* THOMAS, 1915 from Karkar I. Four specimens of the first species were examined by ANDERSEN. In 2 specimens f = 136—137, in one sk = 67, bc = 23·8, zyg = 38·2, teeth = 24·8. As to the other subspecies, THOMAS (1915), comparing it, among other forms, with *P. t. vanikorensis*, did not write about any differences in size and the measurements given by him provide no grounds for the supposition that such differences exist at all. Three specimens had f = 136—142, in one sk = 65·6, teeth = 24·7.

Size group II includes *P. t. tonganus* QUOY and GAYMARD, 1830 from the Fiji Is. (it occurs on islands from somewhat more than ten square kilometres in area to 10,386 km^2), Uea (in the Wallis group and not Tonga, as erroneously given by ANDERSEN), Tonga Is. (Tongatabu, Namouka) and the Samoa Is. (also on islands from somewhat more than ten square kilometres in area to 1821 km^2 [Sawaii]; ANDERSEN wrongly used the name Savage for Sawaii, as there is no island of this name in the Samoa group; instead, Savage or Niue lies in the eastern periphery of the Tonga Is.). ANDERSEN examined 22 specimens from the Fiji Is., the Tonga Is., Uea and the Samoa Is. In 15 specimens f = 139—150, in 13 of them sk = 63·2—67, bc = 22—24·5, zyg = 34—38·7, and 14 had teeth = 24·5—26. FELTEN (1964a, b), too, examined *P. t. tonganus* and, what is more, on still more abundant material, which consisted of above 60 specimens from the Tonga Is., the Samoa Is., Uea and the Fiji Is. (from this last group of islands as many as 54 individuals). The data obtained by him are, as follows: sk = 63·7 (60·5—68·3 — 42 specimens), bc = 22·5 (20·5—24·0 — 48 spec.), zyg = 34·7 (31·7—39·4 — 43 spec.), teeth = 23·8 (22·3—25·7 — 61 spec.), f = 141 (133—150 — 48 spec.).

Size group III is represented by *P. t. geddiei* MACGILLIVRAY, 1860 from the New Hebrides (it lives on islands of different magnitudes, e. g., Aneityum, Espiritu Santo and others), the Solomon Is. (Rennell and Tukopia), New Caledonia and the Loyalty Is. In addition, SANBORN and NICHOLSON (1950) recorded it from the Santa Cruz Is. (Ndeni, Vanikoro and Tapoua), the Swallows (Nupani and Matema) and the Duff group (Masurers). ANDERSEN examined 4 specimens from Aneityum and New Caledonia, but both the specimens measured were from Aneityum. One of them had f = 153·5 and in both teeth = 27·8—30. SANBORN (1931) was in possession of 11 specimens from 5 larger islands of the New Hebrides, 13 from 3 islands of the Santa Cruz group, 3 from the Swallows and 2 from the Duff Is., their length of forearm ranging from 150 to 170 mm. FELTEN (1964b) collected numerous specimens from 9 islands of the New Hebrides, which he divided into 4 groups according to their provenance, namely, going from south to north: 1. Aneityum and Tana, 2. Efate, 3. Epi, Ambrym, Malekula and Pentecost, 4. Malo and Espiritu Santo. Generally speaking, the area of particular islands increases from group to group (Malo does not violate this generalization, as it might seem, because lying close to Espiritu Santo, it is hardly isolated from it). As will be seen from the data given in Table I, some samples number only

Table I

Pteropus tonganus geddiei MACGILLIVRAY, 1860

	Group I	Group II	Group III	Group IV
Sk	10 69·9 (68.3—72·1)	4 70·1 (66·7—73·4)	6 72·6 (69·0—75·9)	4 70·3 (70·0—70·9)
Bc	11 22·7 (23·1—24·4)	5 23·9 (22·9—24·9)	8 24·0 (22·0—25·2)	5 23·6 (23·2—24·5)
Zyg	11 37·2 (37·5—38·9)	4 37·8 (36·4—39·7)	8 38·4 (35·5—41·0)	5 37·1 (36·3—37·8)
Teeth	17 27·0 (26·1—28·8)	8 27·1 (25·7—28·3)	9 28·1 (26·8—30·9)	6 27·6 (26·5—28·7)
F	14 153 (149 — 158)	8 160 (156 — 163)	8 162 (155 — 176)	6 157 (152 — 167)

Explanation: The data presented for each group are the number of specimens measured, the mean measurement and, in brackets, the extreme measurements.

4 specimens and, therefore, they cannot be regarded as a reliable evidence of the existence, or lack, of the dependence of measurements in bats upon the magnitude of island. An analysis of this table, however, suggests the lack of such relations within this subspecies and FELTEN emphasizes the great morphological uniformity of *P. t. geddiei* all over the extensive area of the New Hebrides. In his later work (FELTEN, 1964a) this investigator had still richer material at his disposal, since it had been increased with specimens from New Caledonia and additional ones from the New Hebrides and Uea, but his measurements are arranged in a fashion which is unfit for the subject of the present study. Thus, I can only report after him that in 45 specimens from New Caledonia, from the New Hebrides and from the Loyalty Is. sk = 65·2—75·9, in 48 specimens bc = 22·0—25·2, in 49 specimens zyg = 33·1—41·1, in 65 specimens teeth = 24·8—30·9 and in 54 specimens f = 147—167.

In conclusion, the distribution of the subspecies of *P. tonganus* seems to be controlled by topogeographical factors. The smallest subspecies inhabit the islands of medium magnitude, whereas 2 larger subspecies dwell on islands varying enormously in area. It is impossible to find out whether the islands inhabited by *P. t. tonganus* are, on an average, larger or smaller than the islands on which larger *P. t. geddiei* lives.

10. *Pteropus caniceps* splits into 2 subspecies. The smaller subspecies, *P. c. caniceps* Gray, 1870 occurs on Morotai, Halmahera, Ternate, Batjan (Moluccas), Sulabesi (Sula Is.) and Siau (Sangihe Is.). Andersen examined 16 specimens from the whole area. Three of them had f = 135—139·5, 2 specimens had bc = 24—24·2, zyg = 37—37·5, teeth = 26·7—27.

P. c. dobsoni Andersen, 1908 is known from Celebes. Andersen collected only 1 specimen with f = 144·5, bc = 23·7, zyg = 33·8, teeth = 26·6. In this case, therefore, the larger form inhabits the considerably larger island.

11. *Pteropus rufus* has 2 subspecies. In addition, 5 species, closely related to it, may be included in the superspecies *P. rufus*.

P. r. rufus E. Geoffroy, 1803 occurs in northern and middle Madagascar. Eight specimens of this subspecies, which is smaller than the next, were examined by Andersen. In 6 of them f = 158·5—165·5, and in 5 specimens sk = 69—73·8, bc = 24·2—26, zyg = 37·7—40, teeth 26—27·8.

P. r. princeps Andersen, 1908 is known only from 1 specimen from the southernmost part of Madagascar (Fort Dauphin). F = 170·5, sk = 77, bc = 26·8, zyg = 42, teeth = 28·7.

It seems that these differences in size may be explained by Bergmann's rule; southern Madagascar has lower temperatures than the rest of the island. For example, the mean minima for particular months range from 18° to 23° on Nossi-Bé Island situated close to the west-northern coast of Madagascar, whereas in Tulear, a port on the south-western coast, these values are 8—18° (Pilot, vol. 39, 1946).

The species discussed below occur on islands, which are so much inferior to Madagascar in area that this last may be treated as a continent in comparison with them.

Pteropus aldabrensis True, 1893 from Aldabra is the smallest of the insular species. Andersen examined only 1 specimen with f = 134, sk = 58·3, bc = 21·8, zyg = 32·8, teeth = 21·7.

Three species, which resemble each other in size, must be numbered in group II: *Pteropus comorensis* Nicoll, 1908 from Mayotte, Anjouan, Moheli and Grande Comoro (Comoro Is.), *P. seychellensis* Milne-Edwards, 1887 from all the islands of the Seychelles and *P. voeltzkowi* Matschie, 1909 from Pemba. Andersen had 19 specimens of *P. comorensis* from different islands. In 12 specimens f = 151—157 and in 10 skulls sk = 65·5—68 bc = 23—24·8, zyg = 35—39. Teeth = 24—25·5 in 18 specimens. Eight specimens of *P. seychellensis* were examined by Andersen and 5 of them had f = 143—154. However, the minimum value is somewhat lowered, because not all the specimens were quite adult. No measurements of skull were given for this species. Andersen examined 7 specimens of *P. voeltzkowi*, in which sk = 63·7—68·5, bc = 22·7—25, zyg = 32—36·5, teeth = 24·8—26·5, whereas f = 151—161 in 4 specimens.

It seems that *P. niger* KERR, 1792 from Reunion and Mauritius (Mascarene Is.) ought to be included in size group III of the insular forms (ANDERSEN did not declare his opinion in this respect). He examined 10 specimens of this form and found f = 159—171 in 2 of them, and sk = 67, bc = 23·8, zyg = 35·5 and teeth = 25·8 in one.

It thus appears that the species from the larger islands are generally larger and, in turn, the species from the mainland of Madagascar is larger than the insular forms, perhaps except *P. niger*.

12. *Pteropus melanotus* is divided into 5 subspecies, which form 4 size groups. *P. m. natalis* THOMAS, 1887 from Christmas Island (Indian Ocean) belongs to group I. Eighteen specimens were examined by ANDERSEN and 12 of them had f = 125—135, sk = 54·5—56, bc = 19·3—20·7, zyg = 27·2—30·2, teeth = 21·5—22·8.

Group II is made up of *P. m. modigliani* THOMAS, 1894 from the islands Enggano and Pulo Dua. The measurements of 7 specimens examined by ANDERSEN are f = 134·5—141, sk = 61·7—66·8, bc = 22—23·7, zyg = 33—37 and teeth (6 specimens) = 24—26·5. SODY (1940), who also measured 7 specimens, found f = 122—152, sk = 57—65·1, zyg = 29·6—36·7, teeth = 22·8—25·3, but he remarked that 1 specimen was much smaller than the rest and that after its exclusion the minimum values would have been: f = 136, sk = 61·2, zyg = 35·2, teeth = 24·2.

Group III includes *P. m. tytleri* MASON, 1908 from the Andaman Is. In one of the three specimens examined by ANDERSEN f = 149·5, sk = ±66, teeth = 26·8.

P. m. melanotus BLYTH, 1863 from Car Nicobar, Tillanchong, Trinkut and Great Nicobar (Nicobar Is.) belongs to size group IV. ANDERSEN examined 10 specimens from these islands; in 8 of them f = 153—165, and 9 had sk = 72—75·5, bc = 23·8—25·5, zyg = 37·2—40·2, teeth = 27·3—29·6. *P. m. niadicus* MILLER, 1906 from Nias resembles the last species in size. ANDERSEN measured 3 specimens. F = 153—160, sk = 72—75, bc = 23·8—24·8, teeth (2 specimens) = 27·5—27·8.

As will be seen from these data, the smaller subspecies inhabit the smaller islands, but the larger subspecies live both on large and on very small islands.

13. *P. melanopogon* comprises 3 subspecies. Besides, *P. livingstonei* GRAY 1866, as a close relative, will be considered together with them. This last belongs to size group I. It is said to be a mountain species inhabiting the large forest on the summit (1600 m, always in clouds) of Anjouan (Comoro Is.); it has not been recorded from lower regions. In 3 specimens collected by ANDERSEN f = 162—172, sk = ±72—±75, bc = —25, zyg = —±39, teeth = 28—29.

P. m. keyensis PETERS, 1867, which occurs on Great Kai, Kai Doulan, Little Kai and Koor (Kai Is.), represents group II. ANDERSEN examined 21 specimens. F = 167—187·5 (9 specimens), sk = 77—81·5 (5 spec.), zyg = --48·7 (6 spec.), teeth = 29—33·3 (7 spec.).

The third group includes *P. m. aruensis* PETERS, 1867, which lives on the Aru Is. ANDERSEN examined 6 specimens, of which 2 had f = 190—191; he published no measurements of the skull.

Group IV consists of *P. m. melanopogon* PETERS, 1867 and *P. m. sepikensis* SANBORN, 1931, which are probably equal in size. The first of these species has been recorded from Ambon, Buru, Ceram and small islets, such as Boano, Saparua, Goram and Manovolka (= Manawoka) (Moluccas), as well as from the Banda Is., Jamdena (Tanimbar Is.) and Siau (Sangihe Is.). Thirteen specimens from all the above-mentioned islands were examined by ANDERSEN. In 3 of them f = 196—204 and in 2 specimens sk = --90, bc = 27·2—29·2, zyg = 44—49, whereas 4 specimens had teeth = 32·5—34·5. *P. m. sepikensis* has been described from only 1 specimen collected near the northern coast of New Guinea. Its f = 204, sk = 90·9, bc = 29, zyg = 49 and teeth = 35.

As can be seen from the foregoing, the first four forms, *P. livingstonei*, *P. m. keyensis*, *P. m. aruensis* and *P. m. sepikensis*, mentioned here in the order in which their size increases, inhabit the islands, which also increase in area. This regularity is, however, violated by *P. m. melanopogon*, which occurs both on relatively large islands (Ceram) and on quite small ones (Banda, Siau, Goram and Manovolka).

14. *Pteropus rayneri* is a greatly differentiated species, though its range, confined to the Solomon Is., is comparatively small. Size group I comprises *P. r. cognatus* ANDERSEN, 1908 from San Christoval and Ugi and *P. r. rennelli* TROUGHTON, 1929 from Rennell. ANDERSEN examined 3 incompletely grown-up specimens of *P. r. cognatus* from San Christoval, in which he found f (minimum) = 121, bc = 22, zyg = 33·2, teeth = 23. The measurements of *P. r. rennelli*, after HILL (1962), are: f = 130, sk = 58·7, bc = 21·2, zyg = 33·0, teeth = 21·7.

P. r. rayneri GRAY, 1870 from Gaudalcanal and Malaita forms the second group. The 6 specimens examined by ANDERSEN, not all of them complete, were derived only from the first of these islands. In 3 specimens f = 137·5—140·5, in 2 skulls bc = 23—23, zyg = 33—33 and 3 skulls had teeth = 23·8—24.

Group III includes *P. r. lavellanus* ANDERSEN, 1908 from Vella Lavella, Ghizo and Ronongo and *P. r. monoensis* LAWRENCE, 1945 from Mono. ANDERSEN had 3 specimens of the first form from Vella Lavella; in 2 of them f = 151—155·5; 3 specimens from the 3 above-mentioned islands, measured by SANBORN (1931), had f = 151—158·8, and the measurements taken by ANDERSEN on 2 skulls were: sk = 65·8—69, bc = 24·5—24·8, zyg = --40, teeth (3 spec.) = 27—27. According to LAWRENCE (1945), *P. r. monoensis* resembles *P. r. lavellanus* in size. In 3 males the radius ranged between 145·4 and 148·3 mm, sk = 64·1—69·4, bc = 24·4—25, zyg (2 spec.) = 37·1—39·2, teeth = 23·8—26·9.

P. r. grandis THOMAS, 1887, recorded from Alu, Bougainville, Choiseul and Sta Ysabel, *P. r. rubianus* ANDERSEN, 1908 from Rubiana and Navoro and *P. chrysoproctus* TEMMINCK, 1837 — included in this group on the basis of its close relationship to *P. rayneri* — from Ambon, Buru, Ceram, Arsilulu, Keffing, Pulo Panjang, Goram, Watubella (Moluccas) and Siau (Sangihe Is.) belong to group IV.

ANDERSEN measured 3 specimens of *P. r. grandis* from Alu and Bougainville and found f = 167—172 in 2 specimens and sk = 72·8—76, bc = 26—27·5, zyg = 40—42·5, teeth = 28—30. He measured only 1 specimen of *P. r. rubianus* from Rubiana, its f = 163 and teeth = 27·7, and SANBORN (1931) another specimen from Navoro, f = 166·1. ANDERSEN examined 10 specimens of *P. chrysoproctus*, of which 4 had f = 163—176·5 and teeth = 29—31·7.

As HILL (1962) has already noticed, it is evident that the size of the subspecies of *P. rayneri* increases, as we move from south-east to north-west. However, some islands of the Solomon group do not show such a gradient of size.

15. *Pteropus samoensis* PEALE, 1848, known from Sawaii, Upolu, Tutuila and the Manua group (Samoa Is.) and *P. nawaiensis* GRAY, 1870 from Vanua Levu, Viti Levu, Ovalau and Nauai (Fiji Is.), closely related to the first species, form a separate group. ANDERSEN examined 6 specimens of *P. nawaiensis* from the 4 islands mentioned and 4 of them had f = 124—131·5, sk = ±55—±60, bc = 21·2—23, zyg = 31·2—35·5, teeth = 21·2—23·8. *P. samoensis* is somewhat larger than *P. nawaiensis*. Out of the 5 specimens examined by ANDERSEN 1 had f = 143·5, sk = ±61 and teeth = 23·2.

There are no remarkable differences in area between the islands inhabited by both these species. The smallest islands of both archipelagos correspond to each other in area. It may well be that the largest islands of the Fiji Archipelago are too large to have, from the viewpoint of the present considerations, insular characters.

16. *Pteropus anetianus* (GRAY, 1870) from the New Hebrides has been recently worked out in detail by FELTEN (1964b). *Pteropus vetulus* JOUAN, 1863 should be classified in the same group, since, according to this author (1964a), it is very closely allied to *P. anetianus*. FELTEN claims that *P. vetulus*, which occurs in New Caledonia, is the smaller species. The measurements are: in 13 specimens sk = 49·3 (48·0—50·5), bc = 19·2 (18·0—19·9); in 14 specimens zyg = 27·3 (25·6—28·5), teeth = 17·2 (16·8—18·1); in 10 specimens f = 106 (100—114).

P. a. anetianus (GRAY, 1870) from Aneityum belongs to group II. Its measurements, according to FELTEN (1964b) are sk = 57·6 (1 specimen), bc = 21·1—21·4 (2 spec.), zyg = 32·1 (1 spec.), teeth = 20·5 (20·2—20·8 — 5 spec.), f = 121 (114—127 — 4 spec.). This group comprises also *P. a. eotinus* ANDERSEN, 1913 from Aurora, Lopevi, Malekula and Pentecost and *P. a. bakeri* THOMAS, 1925 from Efate and Epi. The measurements of *P. a. eotinus* are as follows (after FELTEN): sk = 60·7 (57·9—62·9 — 16 spec.), bc = 21·9 (21·1—22·9 — 15 spec.), zyg = 35·4 (33·8—38·1 — 14 spec.), teeth = 22·2 (21·3—

23·2 — 17 spec.), f = 127 (122—132 — 14 spec.). The skull of *P. a. eotinus* is somewhat larger than that of *P. a. bakeri* and the forearm is shorter on an average by 1 mm. FELTEN published the following data concerning *P. a. bakeri*: sk = 60·0 (58·5—61·5 — 12 spec.), bc = 21·6 (20·0—22·3 — 14 spec.), zyg = 34·3 (32·8—35·8 — 12 spec.), teeth = 21·5 (20·7—22·5 — 18 spec.), f = 128 (119—134 — 17 spec.).

Group III is composed of 1 subspecies, *P. a. aorensis* LAWRENCE, 1945 from Aore and Espiritu Santo. Its measurements, after FELTEN (1964b): sk = 61·2 (59·5—63·3 — 8 spec.), bc = 22·0 (20·8—22·9 — 10 spec.), zyg = 35·8 (33·0—37·7 — 10 spec.), teeth = 22·3 (21·3—23·1 — 12 spec.), f = 130 (123—136 — 11 spec.).

As will be seen from the foregoing data, the smallest form, *P. vetulus*, occurs on the decidedly largest island, since the area of New Caledonia considerably exceeds that of all the islands of the New Hebrides taken together, and the largest form, *P. a. aorensis*, dwells on the largest island of the New Hebrides, Espiritu Santo (Aore may be left out of consideration on account of its situation just close to Espiritu Santo). It deserves noticing that no farther than 1·5 km from Aore, on Malo, there lives another subspecies, which is also recorded from the remarkably remoter (14·5 km) Malekula Island. If *P. vetulus*, as a separate though closely related species, has been excluded, it will appear that small Aneityum is inhabited by the smallest subspecies and the largest island of the group, Espiritu Santo, by the largest form. However, the intermediate form, *P. a. eotinus*, occurs both on large Malekula and on very small Malo. On the other hand, it would be a naiveté to suppose that the magnitude of islands will be exactly reflected in the sizes of bats, if such a correlation exists at all. Though it is difficult to find — in view of the case of *P. vetulus* — whether the sizes of *P. a. anetianus* and *P. a. aorensis* are associated with the magnitude of islands inhabited by them, yet in some cases the geographical correlations are evident, e. g., the pairs Aurora — Pentecost and Espiritu Santo — Aore. The causes of geographical inconsequences, such as the occurrence of different forms on islands situated very near each other (Aore and Malo), may lie in the geological history of these islands, but this is obscure (DARLINGTON, 1957).

FELTEN (1964b) emphasizes the great differences between 2 species, which belong to the same genus and have the same range; one of them, *P. tonganus*, occurs all over the New Hebrides and out of them in the form of a single and, what is more, morphologically very uniform subspecies, *P. t. geddiei*, whereas the other, *Pteropus anetianus*, has split into 4 subspecies in these islands. Here, as in some other cases, we may be concerned with a temporary "standstill" in evolution.

17. Several closely allied species form a separate group, referred here to as the group of *Pteropus pselaphon*. ANDERSEN does not generally compare their sizes.

Size group I includes *P. tokudae* TATE, 1934, described by TATE (1934a) from 2 specimens from Guam (Marianas). F = --95, zyg = 8·7—9·2, teeth = 13·6—13·9.

Pteropus insularis HOMBRON and JACQUINOT, 1842 from Ruk and Uala (not Ualan, which lies in the eastern Carolines) in the Truk group in the central Carolines and *Pteropus phaeocephalus* THOMAS, 1882 from the Mortlock group in the central Carolines have been numbered in group II. In TATE'S (1934) opinion, *P. insularis* is next of kin to *P. tokudae* and it may well be that this last is nothing but a subspecies of *P. insularis*, to which it is however inferior in size. Seven specimens of *P. insularis* from Uala and Ruk were examined by ANDERSEN. In 5 specimens f = 101—109 and 3 had sk = 45·2—46, bc = 17·8—18·2, zyg = 25·5—26, teeth = 15·8—16. ANDERSEN had only 1 specimen of *P. phaeocephalus*. F = 105, sk = 45·2, bc = 18·2, teeth = 15·7.

Group III has 1 species, *Pteropus tuberculatus* PETERS, 1869 from Vanikoro (Santa Cruz Is.). ANDERSEN had at his disposal only 2 incomplete specimens. F = 119·5, sk = 56·8, bc = 22·8, zyg = 33, teeth = 21·5.

Pteropus pselaphon LAY, 1829 from the Bonin and Volcano Islands (Micronesia) and *Pteropus leucopterus* TEMMINCK, 1853 from Luzon (Philippines) belong to group IV. ANDERSEN examined 11 specimens of *P. pselaphon*, of which 7 had f = 132·5—141 and in 6 specimens sk = 63·5—69, bc = 23·8—23·8, zyg = 35·8—38·2, teeth = 23—24·2. Three specimens of *P. leucopterus* examined by ANDERSEN had f = 136(?)—142·5; in 2 skulls bc = 24·5—25·8, zyg = 37—38.

Pteropus pilosus ANDERSEN, 1908 from the Palau group (Carolines) constitutes group V. ANDERSEN possessed only one specimen, in which f = 151·5, sk = 69, bc = 24, teeth = 25.

It will be seen from these data that the smallest and the largest form come from islands, which are more or less equal in area. These islands belong to the largest of those on which the group *P. pselaphon* occurs except for Luzon, whereas the species similar to each other in size (*P. leucopterus* and *P. pselaphon*) live on islands which differ extremely in size, i. e., on Luzon and on the Bonin and Volcano Islands.

The course of the January isotherms of the range of the group *P. pselaphon* suggests that the situation corresponds to Bergmann's rule, as the species of group IV live in areas having considerably lower minimum temperatures than those inhabited by smaller species. The largest species, however, lives in the hot climate.

At any rate, the generally small numbers of specimens measured in the group of *P. pselaphon* make any speculations difficult.

18. *Pteropus vampyrus* splits into numerous subspecies, distributed in south-eastern Asia, in the Sunda Archipelago and on the Philippines. These subspecies are divided into 6 size groups.

Group I includes *P. v. ariel* G. M. ALLEN, 1908, which lives all over the Maldive Islands but is absent from Minicoy, the nearest island of the Laccadives situated north of them. This subspecies is somewhat smaller than

P. v. giganteus and *P. v leucocephalus.* Andersen examined only one specimen, in which f = 160, sk = 71·5, bc = 26, zyg = 44·5, teeth = 27. He adds that the measurements of this specimen correspond well to the measurements of the holotype.

Group II is made up of *P. v. giganteus* (Brunnich, 1782) and *P. v. leucocephalus* Hodgson, 1835. The first of them occurs on Ceylon, on the Indian Peninsula (up to Punjab on the north) and probably as far to the east as Sikkim, Butan and Pegu. Andersen had 19 specimens from India and Ceylon. In 16 of them f = 163·5—176·5 and 20 skulls had sk = 70·8—76, bc = 24—26·8, zyg = 36·2—43, teeth = 26·8—29·8 (25 specimens).

P. v. leucocephalus lives in Nepal and Assam, among other regions, in Manipur. Twelve specimens from these areas were examined by Andersen, who gives no measurements but states that this subspecies is similar to *P. v. giganteus* in any respect only that it has evidently longer and softer hair. Its hair on the back is 15—18 mm long, whereas for *P. v. giganteus* this value amounts only to 8—12 mm.

P. v. intermedius Andersen, 1908 known only from Amherst (Tenasserim) forms group III. According to Andersen, this subspecies is somewhat larger than *P. v. giganteus* and *P. v. leucocephalus*, but this investigator had only one specimen at his disposal. F = about 180 (dry skin), sk = 72·5, bc = 26·7, zyg = 40, teeth = 27.

Group IV consists of 3 subspecies of similar size. *P. v. edulis* E. Geoffroy, 1810 is known from Timor and Sawu. Andersen examined 4 specimens from both these islands. In 2 specimens f = 185—187, one had sk = 76, bc = 26·7, teeth = 30. *P. v. natunae* Andersen, 1908 occurs on Bunguran and Pulo Panjang (North Natuna Is.), Borneo, Balambangan and Banguey. Twelve specimens from Bunguran, Pulo Panjang and Sarawak were examined by Andersen, who found f = 182·5—196 in 7 specimens and sk = 72·8—77·7, bc = 25·5—26·8, zyg = 40·8—43, teeth = 28·2—30·2 in 8 skulls. The last member of this group is *P. v. lanensis* Mearns, 1905 from the Philippines, from Luzon to Mindanao, the smallest island from which it is known being Tablas. Andersen examined 7 specimens from Catanduanes, Leyte, Cebu, Panay and Dinagat. In 6 of them f = 185—201, sk = 73·5—78·5, bc = 25·8—27·5, zyg = 39—45, teeth = 28·8—30·8.

The fifth size group is represented by *P. v. malaccensis* Andersen, 1908 from the southern part of the Malay Peninsula, Sumatra, Riau and Lingga Archipelagos, Sipora, Pagai Is., Bangka, Siantan (Anambas Is.), Tenasserim, Annam and Phu Quoc. Andersen examined 26 specimens from the Malay Peninsula, north of Pattani and Jalor, and from Sumatra and Bangka. In 9 specimens f = 195—209, in 13 specimens sk = 76·5—86·5, bc = 26·8—28·5, zyg = 44·3—50 and 21 specimens had teeth = 29·2—33·8. Andersen stated that this subspecies is much larger than *P. v. edulis*, *P. v. natunae* and *P. v. lanensis*, but smaller than *P. v. vampyrus* and *P. v. pluton*.

P. v. vampyrus Linnaeus, 1758 from Java and *P. v. pluton* Temminck, 1853 from Lombok, Sumbawa and Bali belong to group VI, i. e., that of the largest subspecies. They are the largest forms of the order *Chiroptera* at all, their wing span reaching 160 cm, and sometimes even more. ANDERSEN examined 27 specimens of *P. v. vampyrus*, of which 8 had f = 208—220, in 11 specimens sk = 82—91, bc = 27—28·5, zyg = 43·8—50 and in 25 specimens teeth = 31—35·7. The same investigator had 3 specimens of *P. v. pluton* from Bali and Lombok. In 2 of them f = 214—217, in 1 specimen sk = about 86, bc = 29·5, zyg = 47·5, teeth = 33·8.

A comparison of two extreme size groups, i. e., I and VI, shows clearly that the range of small *P. v. ariel* is many times smaller than the ranges of *P. v. vampyrus* and *P. v. pluton*. It must be also taken into considerations that the Maldives are greatly dismembered and scattered over a large area, whereas the islands inhabited by group VI are poorly isolated from each other, which in a way still increases their area. An analysis of the isotherms of these islands does not suggest any significant differences in temperatures. It may be supposed though that the amplitudes on the large islands are greater and, consequently, the minima lower than those on the small islands. This would favour the increase of body size in group VI. However, even if this fact plays any role, the huge difference in area between the islands may certainly be of far greater importance in this respect. The fact that the same result will be obtained from the comparison of the islands on which *P. v. ariel* lives with those inhabited by any other group of this species but group VI seems to support this supposition; all the islands, to say nothing of the mainland, inhabited by groups II—V are generally many times as large as the Maldives.

This picture will change completely, if we compare group VI with group II instead of group I. Then, it turns out that the mainland is inhabited by small forms, which would indicate that the restriction of space on islands brings about an increase in the body size of their inhabitants. Besides, the occurrence of smaller forms in a climate with distinctly lower minima of temperatures is, as it were, the reverse of Bergmann's rule: in the winter the temperatures at the foot of the Himalayas sometimes fall even below 0°, whereas, for example, on Java the isotherms of the coldest and the warmest month are those of 21° and 27°, respectively.

In turn, a comparison of the geographical distribution of groups IV and VI does not lead to any hypotheses which might explain the still conspicuous difference in size between the subspecies of these groups. The members of group IV dwell on the islands from Luzon on the north to Sawu on the south, and so approximately between 18°30'N and 10°30'S. These islands represent a wide scale of magnitude, from Sawu to Borneo. On the other hand, the differences in magnitude between the islands inhabited by group VI are much smaller, but there are no essential differences of this kind between the islands of both these groups. The geographical latitudes and climates are also quite similar.

But enough of these fruitless comparisons! We can find another sort of correlations here, the geographical ones. It is evident that groups I and II, and so the smallest subspecies, inhabit the western and north-western part of the range of *P. vampyrus*, both the mainland and extremely small islands. The eastern subspecies are larger, but the situation is more complicated there, which is probably due to the exceptional dismemberment of the area. There is therefore no gradient of size in the eastern or south-eastern direction and the farthest north- and south-eastern islands are inhabited only by members of size group IV and not VI, for group VI occupies almost the southernmost but not the easternmost part of the range of this species, and smaller subspecies, those of groups IV and V, occur north, east and west of it. The size gradient is also disturbed by the range of group V, which is situated west of the smaller fourth group.

Another geographical dependence is the distinct compactness of the ranges of particular subspecies, which is particularly well seen in the subspecies inhabiting large areas. This may be exemplified by *P. v. malaccensis*, which occurs both on the mainland and on numerous, very small and very large, adjacent islands. A similar situation may be found in *P. v. natunae* and *P. v. lanensis*. This compactness sometimes goes so far that the subspecies belonging to the same size group neighbour upon each other, e. g., *P. v. leucocephalus* and *P. v. giganteus*, *P. v. vampyrus* and *P. v. pluton*. In other cases this compactness is only partial, e. g., *P. v. lanensis* neighbours upon *P. v. natunae*, but *P. v. edulis* shows a great disjunction. However, it should be kept in mind that these regions have not been explored sufficiently well yet and, consequently, *P. v. edulis* may still be found, e. g., on Celebes.

The neighbouring of subspecies from the same size groups suggests the existence of some other, not only geographical, laws.

19. *Pteropus alecto* has 4 subspecies classified in 3 groups. *P. a. morio* Andersen, 1908 from Sumba and Sawu belongs to group I. It is considerably smaller than the nominative subspecies. Andersen examined 4 specimens. The measurements of one of them are as follows: f = 141·5, sk = 65·5, bc = 23·7, zyg = 36·2, teeth = 23·8. Group II contains *P. a. aterrimus* Matschie, 1899 from Bawean and the Kangean Is. Twelve specimens from Bawean were examined by Andersen and in 3 of them f = 152·5—160, sk = 69—71·7, bc = 23·8—25, zyg = 35·2—39, teeth = 26·8—27. Andersen claims that the six specimens that he had from the Kangean Is. resembled the Bawean specimens so much, that they were undistinguishable. In 4 specimens from the Kangean Is. f = 160—165, sk = 70·2—75, teeth = 27·5—28·7. These data would, however, indicate the larger size of the members of this population. It should be added that the Kangean Is., too, are considerably larger than Bawean (see the List of Islands).

Group III consists of *P. a. alecto* Temminck, 1837 and *P. a. gouldi* Peters, 1867. *P. a. alecto* is known from Celebes, Salajar and Lombok. Andersen examined 9 specimens, of which 5 had f = 160—175, whereas in 6 skulls sk = 70·5—73·8, bc = 25—25·8, zyg = 38—39, teeth = 26·7—29·7. *P. a. gouldi* occurs in northern and north-eastern Australia (Queensland, at least as far to the south as Rockhampton, and the Northern Territory). Besides, it has been recorded from the islands in Torres Strait and off the eastern coast of Queensland. ANDERSEN collected 28 specimens. In 10 of them f = 153—180 and 11 specimens had sk = 68—75·5, bc = 24·5—26·5, zyg =37—42·5, teeth = 25—27·8.

As will be seen from these data, the smallest form lives, among other islands, on Sumba, which is much larger than most of the islands inhabited by the larger forms. The same subspecies lives in Australia and on the small adjoining islands. Therefore the relations within *P. alecto* are rather dependent on geographical neighbourhood.

20. *Pteropus conspicillatus* GOULD, 1850 splits into 2 subspecies, which seem to be the same size. The typical form occurs in the eastern part of New Guinea and on the islands situated north-east of it, e. g., Woodlark, Kiriwina (Trobriand Is.) and the Alcester Is., on the islands in Torres Strait, and in Australia, on the coast of northern Queensland as far as Cardwell on the south and in Arnhem Land. ANDERSEN examined 9 specimens from the whole range of this subspecies. In 7 specimens f = 157—181, sk = 70—72, bc = 25·8—29·5, zyg = 40—47, teeth = 27·5—31.

P. c. chrysauchen PETERS, 1862 occupies the western part of the range of the species; it occurs on the Moluccas from Morotai to Obi, on the islands between New Guinea and Halmahera: Gebe, Salawati and Misool, as well as in north-western New Guinea, on the Schouten Is. and on Pinon. ANDERSEN examined 9 specimens from Ternate, Batchian and Misool, of which 4 had f = 175—180 and in 3 specimens sk = about 74—78·5, bc = 27—27·8, zyg = 46·8—46·8, teeth = 28·8—31·2.

On account of the equal size of both subspecies, *P. conspicillatus* may be compared with its close relative, *P. ocularis* PETERS, 1867, which inhabits Ceram and Buru. Ten specimens from both these islands were examined by ANDERSEN and 9 of them had f = 129—141, sk = 62·5—66·5, teeth = 24—25·7. *P. ocularis* is thus far smaller, which was emphasized by ANDERSEN.

The relations between these forms are therefore those of geographical neighbourhood, for 2 adjacent islands are inhabited by the same form. On the other hand, there is no evident correlation between the size of animal and the magnitude of island.

21. *Pteropus neohibernicus* PETERS, 1876 divides into 3 subspecies, of which *P. n. hilli* FELTEN, 1961 from Manus in the Admiralty Is. is the smallest. FELTEN (1961) gave measurements for 2 specimens: bc = 24·8—25·2, zyg = 40·7—41·3, teeth = 28·2—28·4, f = 175—175.

The measurements taken by FELTEN show that *P. n. neohibernicus* PETERS, 1876 from the Bismarck Archipelago is larger than the previous subspecies. The largest island of the Bismarck Archipelago reaches 37 814 km^2 in area. FELTEN does not write from which of the islands his specimens came, but ANDERSEN'S catalogue shows that this subspecies inhabits even quite small islands, e. g., Mioko in the Duke of York group. Measurements of FELTEN'S specimens: sk = 83·8 (81·9—87·5 — 9 specimens), bc = 27·1 (25·7—29·0 — 10 spec.), zyg = 43·9 (41·7—46·0 — 11 spec.), teeth = 32·8 (31·5—34·9 — 14 spec.), f = 189 (172—200 — 7 spec.).

P. n. papuanus PETERS and DORIA, 1881 from New Guinea, Gebe and Misool is the largest subspecies. The measurements of specimens examined by FELTEN (1961) are as follows: sk = 88·3 (81·0—97·0 — 22 spec.), bc = 27·6 (25·4—29·4 — 25 spec.), zyg = 45·9 (39·3—50·3 — 22 spec.), teeth = 34·2 (30·0—38·7 — 27 spec.), f = 198 (190—210 — 14 spec.).

In this case the size of the subspecies increases with the increase of the area of islands. The presence of the largest form on such small islands as Misool and Gebe makes a breach in this situation. It is easy, however, to explain it by historico-geographical factors, for, according to DARLINGTON (1957), New Guinea was connected with these islands in the Pleistocene.

22. *Pteropus macrotis* PETERS, 1867 occurs on southern New Guinea and on Wokam in the Aru Is. *P. m. macrotis* PETERS, 1867 has been recorded only from Wokam. ANDERSEN measured 1 specimen, in which f = 121, teeth = 19·8. In his opinion, this form is smaller than *P. m. epularius* RAMSAY, 1878 from southern New Guinea in any respect. Two specimens examined by ANDERSEN from this island and from a small islet, Yule, situated close to the coast in the eastern part of the Gulf of Papua, had f = 136—141, sk = 55·8–-, bc = 22·5—22·7, zyg = 32·8—32·8, teeth = 21·7—22.

P. poliocephalus TEMMINCK, 1825, which is closely related with these forms is the largest. It inhabits the eastern coast of Australia, from middle Queensland to the frontier of Victoria, and reaches as far as Melbourne during its migrations. ANDERSEN examined 20 specimens. In 3 of them f = 161—162, sk = 65·8–-, bc = 25·2–-, zyg = 36·8—39·8, teeth = 24·8—26·8.

Thus, the subspecies from the small island of Wokam is smaller than that of New Guinea, which is many times larger, but the problem of the causes of the very great difference in size between *P. macrotis* and *P. poliocephalus* is, besides, complicated by the fact that the range of this last species virtually stretches beyond the Capricorn Tropic, as, according to TROUGHTON (1954), it becomes rare north of the tropic. The range of *P. macrotis* lies whole in the tropics, between 5° and 10° S latitude. In consequence, the range of *P. macrotis* has the July isotherm of 24°C and the range of *P. poliocephalus* only 8—16°C. Hence, the remarkable increase in size of *P. poliocephalus* may be explained by Bergmann's rule. It is worth noticing that the hair of this species is rough and much longer and denser. The length of hair on the back is 31 mm and the leg is hairy down to the ankle, whereas in *P. macrotis* the corresponding value is only 10 mm, the smooth hair clings to the body and the lower part of the leg is bare.

23. The group of *Pteropus scapulatus* consists of 2 species. *P. woodfordi* THOMAS, 1888 occurs on the central and eastern Solomon Is.: New Georgia,

Guadalcanal, Florida, Kulumbangra and the Russell group. ANDERSEN examined 6 specimens from the first two islands. Their f = 92·5—99 and 4 specimens had sk = 42—44·5, bc = 17·5—18, zyg = 24·8—26·7, teeth = 13·8—14·8. SANBORN and BEECHER (1947) measured 18 specimens from Guadalcanal and 1 from Banika and obtained the following results: f = 92·7—99, sk = 42·3—45·4, zyg = 24·9—27·9, bc = 18—18·8.

P. scapulatus PETERS, 1862 is considerably larger and inhabits northern and north-eastern Australia: from Thursday Island at least as far to the south as Rockhampton, besides, in Arnhem Land and Kimberley Division. ANDERSEN examined 21 specimens from the whole range, among other localities, from Thursday Island and from the small Claremont Is. In 15 specimens f = 131—143 and 14 specimens had sk = 54—59·5, bc = 21·5—23, zyg = 33—35·8, teeth = 17—19·5 (19 specimens).

In this group, the species from the mainland is much larger than the insular one, but is should be emphasized that the larger form lives also on small islands, some dozen square kilometres in area, isolated from the mainland of Australia.

24. The two smallest forms of the group of *Acerodon mackloti* (TEMMINCK, 1837) are *A. m. gilvus* ANDERSEN, 1909 and *A. celebensis* (PETERS, 1867). The first of them lives on Sumba. One specimen measured by ANDERSEN had f = 135, sk = 66, bc = 24·8, zyg = 36, teeth = 27·7. *A. celebensis* inhabits Celebes, Mangole (Sula Is.) and Salajar. As can be seen from the data given by ANDERSEN, it is the same size as *A. m. gilvus*. Nine specimens from these three islands were examined by him, and in 3 of them f = 130—140; five skulls had sk = 62·5—63, bc = 23·5—24·8, zyg = 33·8—36, teeth = 24·8—25·8.

A. m. floresi (GRAY, 1870) from Flores and Sumbawa and *A. m. mackloti* (TEMMINCK, 1837) from Timor belong to size group II. ANDERSEN examined 2 specimens of *A. m. floresi* from Flores, of which one had f = 140, sk = 71, bc = 25·7, zyg = 40·8, teeth = 29·7. He possessed also 8 specimens of *A. m. mackloti*. Seven of them had f = 139—146, in 2 skulls sk = 69—70, bc = 25·7—25·8, zyg = 40—40·2, teeth = 28·2—28·3.

Size group III contains *A. m. alorensis* ANDERSEN, 1909 from Alor. ANDERSEN examined only 1 specimen. F = 156, sk = 71·8, bc = 25·7, zyg = 40·8, teeth = 29·7.

Before drawing conclusions it should be noted that the ranges of some forms may be more extensive than those suggested by the material given above. *A. celebensis* may well fly from Mangole to Taliabu (the strait is less than 2 km wide) and Sanana (over a strait 3·5 km in width). For this reason it is safer to assume that this species lives all over the Sula Is. It is possible for bats to fly over the 16·5-km-wide strait which separates Salajar from Celebes, the more so, because there are 2 islets in the strait. Similarly, *A. m. alorensis* may fly over to Pantar, 13 km away, particularly so since it will find 4 islets on its way.

The foregoing data show that the largest form inhabits the smallest area, even if Pantar is added to Alor. The smallest forms live on islands, which range from small to large, and the medium-sized forms occupy islands with a middle and large area.

25. ANDERSEN places *Acerodon jubatus* ESCHSCHOLTZ, 1831, *A. humilis* ANDERSEN, 1909 and *A. lucifer* ELLIOT, 1896, as closely related species, in one group. The smallest of them, *A. humilis*, is known only from 1 specimen from Salebabu in the Talaud group. Its f = about 140, sk = 63·2, bc = 22·2, zyg = 34, teeth = 24·8. Salebabu is however poorly isolated from Karakelong, which is 1·5 km away, and Kaburuang, 4 km away. Consequently, particular individuals of *A. humilis* probably fly from island to island so that its range may include the whole group of Talaud.

A. lucifer, known from 1 specimen from Panay (Philippines) is larger. Its measurements, after ANDERSEN, are: f = 165, sk = 71·8, bc = 26·2, zyg = 38·5, teeth = 30·8.

The largest is *A. jubatus*, which splits into 2 subspecies. The forma typica is smaller and occurs on the Philippines, north of Mindanao. ANDERSEN had 20 specimens, among other islands, from Luzon, Negros and Dinagat. In 15 specimens f = 182—198, sk = 77·2—84, bc = 26·7—27·5, zyg = 41·3—47, teeth = 32—36. *A. j. mindanensis* ANDERSEN, 1909 from Mindanao and Basilan is larger. ANDERSEN measured only 1 specimen from Mindanao, its measurements being f = 205, sk = 85, bc = 29·5, zyg = 46·8, teeth = 34. TAYLOR (1934, after LAWRENCE, 1939) and LAWRENCE herself (1939) examined far richer material, and so the larger size of this subspecies in relation to the typical form cannot be questioned. It is seemingly hard to find any relations between the magnitude of islands and the size of the form in this case. It is enough to show that *A. humilis* and *A. j. mindanensis*, which live under similar climatic conditions and on islands of similar areas (Talaud Is. and Basilan), differ extremely from each other in size. However, Basilan is poorly isolated from Mindanao by a strait, 15·7 km wide, in which, besides, there are some islands. Hence, it may be assumed that these two islands make a whole. It follows that the increase in size of these bats generally accompanies the increase in area of the islands.

26. *Dobsonia peroni* (E. GEOFFROY, 1810) is divided into 2 subspecies. The evidently smaller subspecies, *D. p. sumbana* ANDERSEN, 1909, lives on Sumba. ANDERSEN measured only 1 specimen, in which f = 106, sk = 46·6, bc = 19, zyg = 28, teeth = 18·8. The other subspecies, *D. p. peroni* (E. GEOFFROY, 1810) occurs on Timor, Alor, Wetar, Flores, Sumbawa and Bali. ANDERSEN examined 11 specimens from the first 3 islands. Eight specimens from Timor and Alor had f = 108·5—117; in 6 specimens from the same islands sk = 48·8—51·7, bc = 19·5—20·8, zyg = 29·7—32·2, teeth = 20—22.

Sumba does not differ from the other islands mentioned either in area or in climate and the cause of the difference in size between these two subspecies is not clear.

27. The subspecies of *Dobsonia moluccensis* together with closely related

D. exoleta ANDERSEN, 1909 are divided into 5 size groups. Group I includes *D. m. pannietensis* (DE VIS, 1905) from the Trobriand Is. (Kiriwina), D'Entrecasteaux Is. (Fergusson), Louisiade Archipelago (Panniet) and probably other islands south-east of New Guinea. ANDERSEN examined 5 specimens from Kiriwina and Fergusson. Two specimens from Kiriwina had f = 109—112, sk = 47—48, bc = 20—20, zyg = 28, teeth = 19·8—19·8.

Group II is made up of somewhat larger *D. exoleta* from Celebes and from the Togian Is. Seven specimens from Celebes were examined by ANDERSEN. In 3 of them f = 112·5—116, sk = 52, bc = 20, zyg = 32, teeth = 20·5—21·3.

D. m. anderseni THOMAS, 1914 from Manus and Ruk (southern Bismarck Arch.) belongs to group III. THOMAS (1914) examined 3 specimens from either of these islands. F = 123—125. In the holotype from Manus sk = 54·5, zyg = 33·6, teeth = 20. According to this investigator this form is smaller than *D. m. moluccensis* but larger than *D. exoleta.*

D. m. moluccensis (QUOY and GAYMARD, 1830) from the Ambon group (Ambon, Buru, Ceram) and the Aru Is. is reckoned in group IV. ANDERSEN examined 16 specimens from the whole range of this subspecies. Ten specimens from the whole range had f = 133·5—141; in 7 specimens from Buru, Ambon and Aru bc = 22·8—23·5, zyg = 36—38, teeth = 24·5—26·3.

Group V consists of *D. m. magna* THOMAS, 1905 from New Guinea, Misool, Waigeo and the York Peninsula (Australia). ANDERSEN examined 13 specimens from the whole range but York. Nine specimens from New Guinea had f = 146—152·5 and in 6 specimens sk = 62—63·8, bc = 23—24·3, zyg = 36—38, teeth = 25·2—27·8.

As in many other cases, the relations observed here are those resulting from geographical neighbourhood irrespective of the area of island. The smallest form occurs on islands which are considerably smaller than those inhabited by the largest form.

28. *Dobsonia viridis* and the species which are closely related to it split into 4 size groups. *D. inermis* ANDERSEN, 1909, whose 2 subspecies equal in size inhabit the Solomon Is., from the smallest, Rubiana, to the largest one, Bougainville, belongs to group I. ANDERSEN examined 5 specimens of both these subspecies from San Christoval, Ugi, Shortland and Rubiana. In 3 specimens f = 105·5—109·5, bc = 18·7—19·2, teeth = 17—18·5, and 2 specimens had sk = 41·3—45·5, zyg = 26·8—27·8.

The second size group consists of *D. viridis viridis* (HEUDE, 1896) from the Kai Is., Banda Is., Ambon, Buru and Ceram (Moluccas) and *D. praedatrix* ANDERSEN, 1909 from New Ireland, New Britain and Duke of York, all in the Bismarck Arch. ANDERSEN examined 15 specimens of the first form, which he collected from its whole range. Ten specimens had f = 111—118, in 8 of them sk = 46·5—49, bc = 18·7—19·5, zyg = 28·5—31, teeth = 18·2—19·8. The same author stated that 12 specimens from the Ambon group and the Banda Is. do not differ in size from 18 specimens from Kai (in this comparison ANDERSEN based himself on additional material). He also examined 5 specimens of

D. praedatrix, of which 3 had f = 111·5—121·5, sk = 49—51·8, bc = 19·8—20·2, zyg = 30·3—33, teeth = 18·3—20·8.

Group III comprises *D. crenulata* ANDERSEN, 1909 from the Halmahera group (Rau, Morotai, Halmahera, Ternate and Batjan). ANDERSEN examined 11 specimens from these islands except Halmahera. In 5 of them (from Morotai and Batjan) f = 125—128·5 and in 4 specimens sk = 49—51·2, bc = 19·7—20, zyg = 30·5—30·8, teeth = 20—21.

D. chapmani RABOR, 1952 constitutes the fourth size group. SANBORN (1952), on the basis of 19 specimens from Negros (Philippines), regards it as the largest in *Dobsonia viridis* group. RABOR (1952) measured 11 specimens from this island. Their f = 124—128, sk = 49·9—53·5, bc = 20—21·5, zyg = 31·6—32·9, teeth = 20·5—22·3.

A comparison of these groups shows that the smallest form *(D. inermis)* inhabits smaller islands than the largest one *(D. chapmani)*. The size differences cannot be explained by Bergmann's rule, because the temperatures of both these regions are similar. However, if we try to relate these facts to the magnitude of islands, further comparisons command caution, because, for example, the forms which belong to size group II occur on islands varying in size, from small ones, some dozens of square kilometres in area, to large islands with an area of several dozen thousand square kilometres. If these comparisons are confined to the most closely related forms, i. e., to *D. v. viridis* and *D. chapmani*, it is also hard to find any correlations between the area of island and the size of the given form; some islands inhabited by *D. v. viridis* are larger than Negros, others are many times smaller.

On the other hand, a certain geographical gradient of size can be distinguished here: the two smallest forms live farthest to the east, in the Solomon Is., *D. praedatrix* and *D. v. viridis*, which are somewhat larger occur more to the west, on the Bismarck Arch. and southern Moluccas, whereas the still larger form, *D. crenulata*, inhabits the northern Moluccas and the largest one, *D. chapmani*, lives on Negros. There is thus a strong progression in size from the east toward the west and toward the north.

29. *Cynopterus sphinx* has 5 subspecies. The smallest of them, *C. s. sphinx* (VAHL, 1797) lives in a part of India, on Ceylon, in Burma and in northern Thailand. ANDERSEN examined 32 specimens from Ceylon, India, Assam and northern Thailand. In 21 specimens f = 66—73·5 and 17 of them had sk = 31·5—34·5, bc = 13·8—15, zyg = 20—22·8, teeth = 10·8—12·2.

C. s. gangeticus ANDERSEN, 1910, known from Uttar Pradesh, Madhya Pradesh, and Palanpur in India, belongs to size group II. It is larger than *C. s. sphinx*, and its large specimens are said to be equal in size to the small specimens of *C. s. titthaecheilus*. Three specimens examined by ANDERSEN were from Lucknow and Nasik and had f = 73—78, sk = 33—36, bc = ––15·5, teeth = 11·8—12·3.

Group III is made up of *C. s. titthaecheius* (TEMMINCK, 1825) from Lombok, Bali, Java, Sumatra and Lower Thailand, *C. s. major* MILLER, 1906 from

Nias, and *C. s. terminus* SODY, 1940 from Timor. ANDERSEN examined 62 specimens of *C. s. titthaecheilus* from Sumatra, Java, Bali and Lombok. In 17 of them f = 74·5—83 and in 15 specimens sk = 35·5—38·5, bc = 14·2—15·8, zyg = 22·8—24·5, teeth = 12·2—13. Twelve specimens of *C. s. major* were measured: f = 75·5—82, sk = 34—35·8, bc = 14—15·5, zyg = 22·8—24·2, teeth = 11·7—12·4. Having examined 6 specimens of *C. s. terminus*, SODY (1940) stated that externally it is exactly like *C. s. titthaecheilus* from Java only that its skull is considerably shorter. The measurements of the type are f = 83, zyg = 21·9, teeth = 10·8.

The subspecies of *C. sphinx* may be also divided in another manner, into a northern continental group of the smaller forms, *C. s. sphinx* and *C. s. gangeticus*, and a southern insular group including the remaining three larger subspecies. Hence follows that the distribution of these subspecies disagrees with Bergmann's rule, for the smaller forms live in a cooler climate; in India and Ceylon the January isotherms range from 12° to 16° and in northern India the minimum temperatures are below 0°, whereas the islands inhabited by forms of the third size group have winter isotherms of 24—28°. It might be inferred that the influence of small areas of the islands prevails here over Bergmann's rule, if the insular forms were really as a rule larger. However, that is not the case: the smallest form lives on Ceylon. Neither can we apply the rule which RENSCH (1930) established for the birds of the Little Sunda Is., whose subspecies become the larger, the farther towards the east they live. RENSCH interpreted this phenomenon as a sign of Bergmann's rule in the tropics, because these islands become dryer towards the east and, consequently, their minimum temperatures are lower. In the case of *C. sphinx*, however, the forms of the same size are distributed over an area of 30 degrees of geographical longitude, from Nias to Timor. In the end, it is difficult to find any influence of climate on the increase in size of the subspecies of *C. sphinx*. The influence of space restriction on islands is also doubtful, because on Nias there lives as large a form as that on more than a hundred times larger Sumatra, and the form living on large Ceylon is smaller than those on other islands. Of all the factors having a bearing upon the size and distribution of the forms of this species, the historico-geographical factors seem to be the most important.

30. The subspecies of *Cynopterus brachyotis* are very numerous. They may be classified in 5 size groups, of which group I contains *C. b. minutus* MILLER, 1910 from Nias. Five specimens examined by ANDERSEN had f = 54·5—59, sk = 25·8—28·7, bc = 11—12·2, zyg = 16—18, teeth = 8·8—9·5.

C. b. brachyotis (MÜLLER, 1838), *C. b. concolor* (SODY, 1940), *C. b. ceylonensis* (GRAY, 1870) and *C. b. brachysoma* DOBSON, 1871 are numbered in group II. *C. b. brachyotis* has a very large range; it occurs in Lower Thailand, on Sumatra, Borneo, Celebes, the Philippines and on many small islands and archipelagos among them, such as Pulau Pisang, the Redang Is. (the islets of Tinggi, Babi and Sri Buat), the Riau Arch., the Batu Is., Bangka, Belitung, Peleng, Bawean and the Talaud Is. *C. b. concolor* is known only from

Enggano, *C. b. ceylonensis* from Ceylon, and *C. b. brachysoma* from the Andaman Is.

The abundant series of *C. b. brachyotis* (ANDERSEN, 1912 and CHASEN, 1940) have f = 57—67·7. These great fluctuations, reaching 18·8%, if the value 57 is assumed to be 100%, occur even in specimens from the same locality. On the other hand, the mean lengths of forearm in the state of Kedah (Malay Peninsula) and on Borneo are almost equal, as they amount to 62·7 and 63, respectively (CHASEN, 1940). On the basis of his rich material ANDERSEN emphasizes the strict likeness of the specimens from the Philippines, Celebes (2 of which come from an altitude of 1067—1220 m), Borneo, the Malay Peninsula and Sumatra, which he illustrates with the following table (abridged):

	Lower Thailand, Malay Pen., Sumatra	Borneo	Philippines	Celebes
	36 skulls 37 specimens	24 skulls 31 specimens	3 skulls 5 specimens	2 skulls 2 specimens
sk	27·2—30·6	27—30·7	29 —30	28—28·8
teeth	8·8—10·2	9—10·4	9·5— 9·8	9—9·8
f	57 —65.5	58—66	62 —64	60—63·5
tibia	21·5—24·5	21—25·5	22 —23·5	22

ANDERSEN examined a total of 100 specimens, out of which 8 were from the Philippines (Luzon and Mindanao), 4 from Celebes, 38 from Borneo, 27 from the Malay Peninsula, 12 from the Riau Arch., 5 from Sumatra and 6 from other localities, which have not been defined exactly. The measurements of skulls of 65 specimens are: sk = 27—30·7, bc = 12—13·6, zyg = 17·8—20, teeth = 8·8—10·4.

C. b. concolor is known from 5 specimens, the size of which corresponds to that of *C. b. brachyotis* from Borneo. F = 63—66, sk = 28·8—29·4, teeth = 9·3—9·7 (SODY, 1940). Seven specimens of *C. b. ceylonensis* were examined by ANDERSEN. In 6 of them f = 59—64 and 4 had sk = 28—30·8, bc = 12·5—14, zyg = 18—20·2, teeth = 9·7—11. Three specimens of *C. b. brachysoma* had f = 59—66, sk = 28·5—31, bc = 11·7—13·6, zyg = 16·7—18·6, teeth = 10—10·8.

C. b. javanicus ANDERSEN, 1910 from Bali, Madura and Java is in size group III. According to ANDERSEN, it is somewhat larger than *C. b. brachyotis*, which belongs to the previous group. This author examined 23 specimens from Java, of which 17 had f = 61·5—68 and in 16 specimens sk = 28·3—30·8, bc = 12·2—13·5, zyg = 18·2—20·3, teeth = 9·5—10·5.

The fourth group consists of *C. b. insularum* ANDERSEN, 1910, *C. b. sche-*

rzeri (ZELEBOR, 1869) and *C. b. babi* LYON, 1916. *C. b. insularum* occurs on Kangean (Kangean Is.) and Pulo Mata Siri (Laurot Is.). ANDERSEN considers it to be larger than *C. b. javanicus* and much larger than *C. b. brachyotis*, as the length of forearm of its smallest specimens is equal to that of the largest specimens of *C. b. brachyotis*. ANDERSEN examined 7 specimens from both islands, of which 6 had f = 66·5—69·5, sk = 29·5—31·2, bc = 13·2—13·8, zyg = 19·2—20, teeth = 9·8—10·6.

C. b. scherzeri is known from Car Nicobar and Great Nicobar (Nicobars). ANDERSEN examined 3 specimens, in which f = 69·5 (or less) — 70·5. Two skulls had sk = -- 31·2, bc = 12·6—13, zyg = 19—19·5, teeth = 10·4—10·7. In ANDERSEN'S opinion, this subspecies is larger than *C. b. brachysoma*.

C. b. babi has been recorded only from Babi. In 3 specimens examined by LYON (1916) f = 66—68. The skull of the type had sk = 30, zyg = 19, bc = 13, teeth = 10·2. According to LYON, this subspecies is equal in size to *C. b. scherzeri* and, what is surprising, more closely related to this form than to *C. b. brachyotis* from Sumatra.

C. b. angulatus MILLER, 1898 and *C. b. pagensis* MILLER, 1906 are included in the last, fifth, size group. *C. b. angulatus* has a wide range, as it occurs in Burma, Thailand, Cambodia, Annam, Assam, the Anambas Is., the Natunas and on many small islands off the coast of Lower Thailand. ANDERSEN examined 42 specimens from Assam, Lower Thailand, the southern Malay Peninsula, Upper Burma, Thailand, Cambodia, Annam and the Natuna Is. In 34 specimens f = 65—72, sk = 30·5—33·2, bc = 13·2—14·2, zyg = 19·8—21·8, teeth = 10·2—11·3.

C. b. pagensis is known from the Pagai Is., Siberut and Sipora. ANDERSEN examined 4 specimens from North Pagai and Sipora, which, according to him, have nothing to distinguish it from *C. b. angulatus*. Here are the measurements of 2 specimens from North Pagai given by ANDERSEN and MILLER (1906) (in brackets): sk = 32·8 (30·8), mandibula = 24·5 (23), teeth = 10·8 (---), f = 69·5 (69·8).

A comparison of 2 groups, extreme in respect of size, that is, group I represented by *C. b. minutus* from Nias and group V represented by *C. b. angulatus* and *C. b. pagensis* from the mainland of south-eastern Asia, the Pagai Is., Sipora, Siberut, the Natuna Is., the Anambas Is. and numerous small islands off the coast of Lower Thailand, shows no evident relations between the size of these forms and the areas inhabited by them. If we compare group I with group IV, we shall find that the smallest form lives in a considerably larger area than the large forms do. On the other hand, one might arrive at quite contrary conclusions, when comparing group I with group III.

Let us come to another sort of comparisons and confine ourselves to the forms inhabiting the row of islands west of Sumatra, from Enggano to Babi. Enggano is inhabited by bats of size group II, the Pagai Is., Sipora and Siberut by group V, the Batu Is. by group II, Nias by group I and, finally, Babi by group IV. This situation is not clear, either. Both group I and group V occur on the largest islands and group IV is found on the extremely small island, Babi.

It must also be stressed that *C. b. brachyotis* lives, on the one hand, on the Malay Peninsula and Borneo and, on the other hand, on fairly isolated islets, which are hardly some dozen square kilometres in area.

It is also difficult to find any gradient of size in the area inhabited by *C. brachyotis*, as we pass from east to west or in any other direction. Instead, we can observe, to a degree, some geographical influences, e. g., the huge area of the Philippines is inhabited by only one subspecies, though some islands of this archipelago are strongly isolated. The same form lives on the adjacent islands, Madura, Java and Bali.

31. *Cynopterus horsfieldi* splits into 4 subspecies classified in 3 size groups. Group I contains *C. h. horsfieldi* Gray, 1843 from Java. Andersen examined 25 specimens, of which 15 had f = 64·5—71 and in 16 specimens sk = 30·5—33·3, bc = 12·7—14, zyg = 20·8—22·2, teeth = 10·5—11·5.

Two considerably larger subspecies make up the second size group. *C. h. lyoni* Andersen, 1912 occurs on Sumatra and in the southern part of the Malay Peninsula. Andersen examined 6 specimens from Sumatra; 3 of them had f = 71·5—77·5, sk = 33·5—35·8, bc = 15—15·5, zyg = 22·7—23·8, teeth = 11—12. *C. h. persimilis* Andersen, 1912 is known only from Borneo. Measurements of 1 specimen: f = 79·5, teeth = 12.

C. h. princeps Miller, 1906 from Nias belongs to group III. It exceeds the previous subspecies in size remarkably. Two specimens were examined by Andersen, one by Miller (1906); the measurements taken by Miller are given in brackets. F = 87—89·5 (84·4), sk = 38·5—39·3, bc = 15·8—16, zyg = 25·3-- (25·4), teeth = 13·2—13·5 (12·2).

Thus, the subspecies from the 2 largest islands (Borneo and Sumatra) are of medium size, the species from Java, which is intermediate in respect of size, is the smallest and the largest subspecies comes from comparatively very small Nias. Since, in all probability, it came to Nias from Sumatra, it might be supposed that the decrease in area has caused an increase in the size of the bat.

32. *Nyctimene albiventer* has 2 subspecies. The smaller subspecies, *N. a. albiventer* (Gray, 1863) lives on Morotai, Halmahera and Ternate (Moluccas). In 4 specimens from Morotai and Ternate examined by Andersen f = 50—54·5. The specimen from Morotai had teeth = 8·7.

N. a. papuanus Andersen, 1910 is known from New Guinea, the Kai Is., New Britain (Bismarck Arch.), the Admiralty Is. and the York Peninsula (Australia). Andersen examined 15 specimens from the whole range of this subspecies. In 13 specimens f = 54·5—59 (on the average 56·3) and 9 specimens had sk = 28·5—29·8, bc = 12·5—12·8, zyg = 18·7—19, teeth = 9·7—10·3.

There are no clear-cut differences between the ranges of these subspecies either in climate or in magnitude of particular areas. Hence, it is impossible to state anything but that the western form is smaller than the eastern one.

33. *Nyctimene minutus* has been recorded from Celebes and Buru (southern Moluccas). Celebes is inhabited by the subspecies *C. m. minutus* ANDERSEN, 1910. The only specimen examined by ANDERSEN had f = 51, bc = 11·8, zyg = 17·5, teeth = 8·8.

N. m. varius ANDERSEN, 1910 is known only from Buru. ANDERSEN, again, had only 1 specimen at his disposal. In his opinion, these two subspecies do not differ in size. F = 55, sk = 28·8, bc = 12·2, zyg = 17·5, teeth = 10.

Therefore, the subspecies seem to be the same size in spite of the enormous difference in area between the two islands.

34. *Nyctimene major* is divided into 4 subspecies, which form 3 size groups. *N. m. lullulae* THOMAS, 1904 from Woodlark is in group I. In one specimen examined by ANDERSEN f = 69, sk = 33·2, bc = 14·5, zyg = 22, teeth = 11·5.

Group II includes *N. m. geminus* ANDERSEN, 1910 and *N. m. scitulus* ANDERSEN, 1910. *N. m. geminus* occurs in eastern New Guinea and on the adjacent islands and archipelagos: the Trobriand Is., the D'Entrecasteaux Is., the Louisiade Is., and Heath. ANDERSEN examined 4 specimens from New Guinea, Kiriwina, Fergusson and Goodenough. F = 70·5—77, sk = ‒‒36·5, bc = 14·8‒‒, zyg = ‒‒23·2, teeth = 12·2—13·5.

N. m. scitulus is known from the Solomon Is.: Shortland, Alu, Florida, New Georgia, Guadalcanal, Choiseul and Malapa. ANDERSEN examined 5 specimens from Shortland, New Georgia, Florida and Guadalcanal. F = 71·5—80, sk = 36·8—37·2, bc = 14·3—14·8, zyg = 22·8—23, teeth = 12·7—13·2.

Group III contains *N. m. major* (DOBSON, 1877) from New Ireland, New Britain, Duke of York and Makupa (Bismarck Arch.). Ten specimens from these islands were examined by ANDERSEN. In 8 of them f = 78—85·5 and in 2 specimens sk = 37, bc = 15—16, zyg = 23·5—23·8, teeth = 13·5—14·2.

In this series the lack of a size gradient in any direction and the lack of correlation between the size of a form and the area of the island are seemingly evident. However, Duke of York and Makupa, though very small, are poorly isolated from New Britain and New Ireland, between which they are situated, e. g., they are hardly a few kilometres away from New Britain. As a result, they may be regarded as parts of these two large islands. Then, it will appear that there is some correlation between the magnitude of the form and that of the island. Besides, there is some, though slight, influence of geographical neighbourhood, as New Guinea and the adjacent islands are inhabited by the same subspecies, but this is not the case in so far as the Bismarck Archipelago is concerned.

35. *Macroglossus minimus* splits into 3 subspecies. *M. m. minimus* (GEOFFROY, 1810) inhabits Java, Madura, Bali and the Kangean Is. It is much smaller than the next subspecies, *M. m. sobrinus*. ANDERSEN examined 39 specimens from Java and Madura and one from the Kangean Is. Thirty-one specimens from these three regions had f = 40—44·5 and in 18 specimens from the same regions sk = 24·8—27·5, bc = 10·5—11·2, zyg = 13·6—15·8, teeth = 8·2—9.

M. m. sobrinus ANDERSEN, 1911, which in the Malay Peninsula reaches as far to the north as Tenasserim, is besides known from Sumatra, Nias and Java. ANDERSEN examined 26 specimens from the whole range. In 19 specimens from the Malay Peninsula, Sumatra and Java f = 42—48·5 and in 14 from the Malay Pen. and Java sk = 28·5—29·5, bc = 10·8—11·5, zyg = 14·8—15·8, teeth = 9·2—10.

M. m. fraternus CHASEN and KLOSS, 1927 is the largest. It lives on Siberut and Sipora. The authors of this form examined 4 specimens from both the islands and 3 of them had f = 49—52, sk = 31·5—32·9, teeth = 10—10·6; zyg (in 2 specimens) = 16·9—17.

It is remarkable that 2 subspecies which differ in size occur on the same island. The distribution of these forms shows fairly evident influences of geographical neighbourhood, but it is hard to notice any correlation between the size of a form and that of the island. The forms of different sizes on the islands west of Sumatra may exemplify the genetic drift.

36. *Macroglassus lagochilus* is divided into 2 size groups. Group I consists of *M. l. nanus* MATSCHIE, 1899, *M. l. microtus* ANDERSEN, 1911 and *M. l. pygmaeus* ANDERSEN, 1911.

M. l. nanus occurs on New Guinea, Misool, the Aru Is., the Kai Is., the Admiralty Is. and the Bismarck Arch. ANDERSEN examined 19 specimens mainly from New Ireland (12) and from the Aru Is. (5). In 18 specimens from nearly the whole range f = 37—39, 10 specimens had sk = 24—26, bc = 10·1—10·6, zyg = 12·8—15, teeth = 7·8—8·9.

M. l. microtus inhabits the Solomon Is. (Florida, Guadalcanal, Bougainville and San Christoval). Three specimens from Florida and Guadalcanal were examined by ANDERSEN and 2 of them (Guadalcanal) had f = 37·5—38·5, sk = 23·8—24·6, bc = 10·5—10·7, zyg = 13·2—15·8, teeth = 8—8·5.

M. l. pygmaeus, 2 specimens of which were examined, lives on the Murray Is. One of these specimens had f = 37·5 and teeth = 7·8 (ANDERSEN, 1912).

Group II contains only *M. l. lagochilus* MATSCHIE, 1899, which is much larger than the subspecies of the previous group. Its range is wide and includes Celebes, Peleng, the Sangihe Is., the Moluccas (Ambon, Buru, Ceram), the Banda Is., the Malay Pen., Nias, Borneo, Sirhassen (southern Natuna Is.), the Philippines (Tablas, Cagayan Sulu, Samar, Panay, Cuyo, Negros, Mindanao). ANDERSEN examined 21 specimens from Borneo, Cagayan Sulu, the Philippines, Buru, Ceram and the Banda Is. The specimens from Borneo, Celebes, the Philippines, Buru and Ceram did not differ from each other, which is illustrated by the data tabulated by ANDERSEN. In 17 specimens f = 38—44·5 and 14 specimens had sk = 24·8—27·2, bc = 9·8—11, zyg = 12·8—15·8, teeth = 8—9·2.

It is thus evident that the smaller subspecies occur in the eastern part of the range of the species and the larger subspecies lives nearer to the supposed centre of radiation of the *Pteropidae*. Some geographical influences, e. g., the presence of one and the same form all over the Solomon Is. etc., are also obvious. On the other hand, it is difficult to find any correlation between the size of these forms and the area of island; it is enough to remind of the fact that the forms of the same size live on New Guinea and on the Murray Is.

37. *Syconycteris crassa* has 5 subspecies in 4 size groups. *S. c. finschi* (MATSCHIE, 1899) from the Bismarck Arch. belongs to group I. ANDERSEN had only one specimen, from New Britain, in which f = 39, sk = 25, bc = 10·7, zyg = 15, teeth = 7·2.

Group II consists of *S. c. papuana* (MATSCHIE, 1899) from New Guinea and the Aru Is. and *S. c. keyensis* ANDERSEN, 1911 from the Kai Is., which in ANDERSEN'S opinion, are somewhat larger. In the materials of this author *S. c. papuana* was represented by 17 specimens, which came from both regions in nearly equal parts. In 16 specimens f = 40—44 and in 12 skulls sk = 25·7—27·3, bc = 10·2—11·8, zyg = 14·5—16·8, teeth = 7·6—8·8. ANDERSEN compared the material from New Guinea with that from the Aru Is. and obtained the following results (the measurements of the specimens from the Aru Is. in brackets): sk = 25·8—27·3 (25·7—27·3), teeth = 7·6—8·8 (7·8—8·8), f = 40—43 (40—44). These measurements, as well as 4 additional ones, do not form a basis for the supposition that the two populations differ in size.

S. c. keyensis is, according to ANDERSEN, exactly the same size as *S. c. papuana*. This opinion is, however, based on only one specimen. F = 42·5, sk = 25·8, bc = 10·2, zyg = 15·2, teeth = 7·1.

Group III includes only *S. c. crassa* (THOMAS, 1895) from the Trobriand Is. and the D'Entrecasteaux Is., where it inhabits Kiriwina and Fergusson. ANDERSEN examined 4 specimens from both these islands. He claims that this form is larger than *S. c. papuana* in all respects. The smallest specimen of *S. c. crassa* is said to be equal in size to the largest specimen of *S. c. papuana*. Three specimens from both islands had f = 43·5—47, sk = 27·6—28·8, bc = 11·2—11·7, zyg = 16·2—17, teeth = 8·7—8·8.

S. c. major ANDERSEN, 1911 from Ambon and Ceram is the only subspecies of group IV. ANDERSEN examined 5 specimens from both islands. In 4 of them f = 46—49, 3 skulls from both islands had sk = 28·8—29·8, bc = 11·5—11·7, zyg = 17·3—18·2, teeth = 8·8—9·7.

A comparison of the areas of islands inhabited by the smallest and the largest form shows that that of the smallest form is much larger. Special attention should be given to Kiriwina, which, as the smallest island, might exert the greatest influence on the size of the form which lives on it. This form, *S. c. crassa*, is one of the larger subspecies, but it occurs also on the considerably larger island, Fergusson, adjacent to it. Another island, Ambon, as small as Kiriwina, is inhabited by the largest subspecies. However, this island is separated from much larger Ceram only by a 5-kilometre-wide strait, its isolation is therefore doubtful, and the same form lives also on Ceram. The largest subspecies occurs farthest to the west and the smallest is one of the two easternmost forms, but it must be kept in mind that the other eastern form is one of the larger subspecies. In addition, there is no size gradient between the forms which have outermost positions.

V. SUBORDER: *MICROCHIROPTERA*

Family: *Emballonuridae*

This pantropical insectivorous family is the most primitive of the *Microchiroptera* except for the *Rhinopomidae*.

1. *Peropteryx macrotis* (WAGNER, 1843). The typical form from the tropics of the American mainland is larger than the insular forms: a) *P. m. trinitatis* MILLER, 1899 from Trinidad (SANBORN, 1937, after HUSSON, 1960; GOODWIN and GREENHALL, 1961), b) *P. m. phaea* G. M. ALLEN, 1911 from Grenada (SANBORN, 1937, after HUSSON, 1960), c) the population of *P. m. macrotis* from Margarita I. (HUSSON, 1960) ($1 \times 3 = 3$).

Family: *Noctilionidae*

Small primitive neotropical family of fish- and insect-eaters.

2. *Noctilio leporinus leporinus* (LINNAEUS, 1758). According to HUSSON (1962), the members of the population from Surinam are considerably smaller than those from Trinidad. This will also be seen from the measurements given by other authors, such as GOODWIN and GREENHALL (1961) and DALQUEST (1951). For this reason HUSSON calls the subspecific membership of the Trinidad population into question.

Family: *Rhinolophidae*

In the Old World, partly also in the temperate zone. Insectivorous.

3. *Rhinolophus alcyone* TEMMINCK, 1852. In EISENTRAUT'S (1964) opinion, the members of the population from Fernando Po are larger than those from Cameroon.

Family: *Hipposideridae*

In the tropics and partly subtropics of the Old World. Insectivorous.

4. *Hipposideros bicolor* (TEMMINCK, 1834). Out of the 8 subspecies distinguished by HILL (1963), the smallest, as may be inferred from his data, is *H. b. gentilis* ANDERSEN, 1918 from northern India, Assam, Sikkim and Burma. The largest forms are *H. b. atrox* ANDERSEN, 1918 and *H. b. major* ANDERSEN, 1918, which are, besides, probably identical. They occur on the Malay Peninsula and on the islands Terutau, Tioman, Sumatra and Enggano.

5. *Hipposideros ater* TEMPLETON, 1848. The data given by HILL (1963) and TATE (1941) show that the typical form from Ceylon and India is the smallest, whereas the largest subspecies is *H. a. nicobarulae* MILLER, 1902 from Little Nicobar.

It is worth notice that the whole area of the Philippines is inhabited by only one subspecies, *H. a. antricola* (PETERS, 1861). The distribution of *H. a.*

saevus ANDERSEN, 1918 is also instructive. It covers the whole Malay Peninsula and the Condor Is., Terutau, Tioman, the Mergui Arch., Sumatra, Java, Bali, Celebes, Peleng, the Kai Is., Buru and Ceram.

6. *Hipposideros cineraceus* BLYTH, 1853. The remarks on this species (typical form) published by CHASEN (1940) are very interesting. The specimens from the Riau Arch., the southern part of the Malay Peninsula, small islands in the Strait of Malacca, the larger islands Terutau and Langkavi, western Thailand north of the town of Rahaeng and the Anambas Is. form a very even large series. The largest, however, judging by the forearm, are the members of the series from the small island Pulau Pisang.

7. *Hipposideros turpis* BANGS, 1901. According to HILL (1963), out of the two subspecies the nominative one from Ishigaki (Sakishima Gp.) east of Formosa is much smaller. The larger subspecies, *H. t. pendleburyi* CHASEN, 1936, is known from Malay Peninsula from 8°30'N latitude. These two forms are therefore separated by a zone of 16 degrees of geographical latitude, which suggests that the smaller form lives in a cooler climate. As a matter of fact, in nearby Taipei in northern Formosa the mean daily minima of particular months are 12—24 (18)°C, the mean monthly minimum temperatures range from 7 to 22°C, the mean annual minimum temperature is 5°C and the absolute minimum temperature 0°C. On the other hand, in Cape St. Jaques near Saigon, over 2° farther to the north than the place from which *H. t. pendleburyi* has been described, these values were, respectively, 22—24 (23)°C, 19—23 (19)°C and 17°C (Pilot).

8. *Hipposideros larvatus* (HORSFIELD, 1823). It follows from the data published by HILL (1963) that the smallest subspecies is probably *H. l. barbensis* MILLER, 1900 from the small island St. Barbe, situated just close to the equator between Sumatra and Borneo. It is also known from Aur. The largest subspecies is *H. l. grandis* G. M. ALLEN, 1936 from Burma, Thailand and Indochina.

It should be added that HILL (1963) found a gradient of decreasing size among the numerous subspecies of *H. larvatus* in south-east Asia in passing south-east from the mainland to the islands of the Malay Archipelago. OEI claims (1960) that the bats and other animal groups of the Indonesian Archipelago become smaller from the west towards the east.

9. *Hipposideros lankadiva* KELAART, 1850. *H. l. mixtus* ANDERSEN, 1918 from India is smaller than the typical form from Ceylon, which will be seen from HILL'S data (1963).

10. *Hipposideros diadema* (GEOFFROY, 1813). It splits into 16 subspecies and is being mentioned here for an interesting remark of HILL (1963). According to this author, the larger subspecies are met with in south-east Asia, on the Nicobars, Sumatra, Java, Borneo and smaller islands situated among them. On the other hand, the smaller subspecies occur east of Celebes and the Philippines to the Solomon Is. and northern Australia. Thus the western part of the range of the species is occupied by the larger forms.

11. *Hipposideros commersoni* (GEOFFROY, 1813). HILL'S (1963) and BOCAGE'S (1891) data suggest that *H. c. thomensis* (BOCAGE, 1891) from Sao Tomé (826 km²) off the coast of Africa in the Gulf of Guinea is the smallest subspecies. The typical form from Madagascar is larger and again all the three subspecies from the African continent — *H. c. marungensis* (NOACK, 1887), *H. c. gigas* (WAGNER, 1845) and *H. c. niangarae* J. A. ALLEN, 1917 — are larger than the Madagascan form. ($2 \times 3 = 6$).

12. *Hipposideros dinops* ANDERSEN, 1905. The results published by HILL (1963) show that *H. d. pelingensis* SHAMEL, 1940 from Celebes and Peleng is somewhat smaller than *H. d. dinops* from Rubiana and Bougainville (Solomon Arch.). Since Peleng is poorly isolated from Celebes and Rubiana from New Georgia, we may assume that the smaller form lives in a larger area.

13. *Hipposideros caffer guineensis* ANDERSEN, 1906. According to EISENTRAUT (1964), the specimens from Fernando Poo are smaller than those from adjacent Cameroon. The decrease in size affects, above all, the forearm, the leg, the phalanges of the wing and, to a somewhat lower degree, the skull.

14. *Coelops frithi* BLYTH, 1848. The data published by ALLEN (1938) and HARRISON (1964) indicate that *C. f. formosanus* HORIKAWA 1928 from Formosa is larger than *C. f. inflatus* MILLER, 1928 from the neighbouring Fukien Province.

Family: *Phyllostomatidae*

It is the third largest chiropteran family, confined to the tropics and subtropics of America. Plant- and flesh-eaters.

15. *Chilonycteris parnelli* (GRAY, 1843). Insect-eaters. In KOOPMAN'S (1955) opinion, the 2 largest subspecies, *C. p. rubiginosa* WAGNER, 1843 and *C. p. mexicana* MILLER, 1902, occur on the American mainland. All the insular subspecies are smaller than those from the mainland. They are *C. p. parnelli* (GRAY, 1843) from Jamaica, *C. p. boothi* GUNDLACH, 1861 from Cuba, *C. p. portoricensis* MILLER, 1902 from Puerto Rico, *C. p. pusillus* G. M. ALLEN, 1917 from Hispaniola and *C. p. gonavensis* KOOPMAN, 1955 from Gonave. They are arranged in order of size, from the largest form to the smallest. As will be seen, the subspecies from the smallest island is the smallest. ($2 \times 5 = 10$).

16. *Mormoops blainvillii* LEACH, 1821. It inhabits the Greater Antilles: Cuba, Jamaica, Hispaniola, Puerto Rico, Mona. *M. megalophylla* (PETERS, 1864) occurs from the southernmost region of the United States to Colombia and Venezuela. The data offered by HALL and KELSON (1959) and HALL and DALQUEST (1963) suggest that the subspecies from the continent is larger. The members of this genus are insectivorous.

17. *Mormoops megalophylla* (PETERS, 1864). The data presented by HUSSON (1960) as well as by GOODWIN and GREENHALL (1961) reveal that *M. m. intermedia* WAGENAAR HUMMELINCK, 1940 from Aruba, Curacao and Bonaire is

the smallest subspecies, whereas the largest one is *M. m. tumidiceps* MILLER, 1902 from Colombia and Trinidad.

The poor isolation of Trinidad from the mainland permits this comparison; besides, Trinidad is many times as large as Aruba, Curacao and Bonaire.

18. *Glossophaga longirostris* MILLER, 1898. It feeds on nectar and pollen of flowers and on fruit. According to GOODWIN and GREENHALL (1961), the typical form from Venezuela and northern Colombia is much smaller than *G. l. major* GOODWIN, 1958 from Trinidad and Tobago.

19. *Glossophaga soricina* (PALLAS, 1766). Food as in the previous species. In MILLER'S opinion (1913), *G. s. leachii* (GRAY, 1844), which occurs from Mexico to South America, is smaller than *G. s. mutica* MERRIAM, 1898 from the Tres Marias Is. off the coast of the state of Najarit, Mexico. *G. s. antillarum* REHN, 1902 from Jamaica is probably still larger than *G. s. mutica* (MILLER, 1913). It is interesting that the last two forms are very much like each other. ($1 \times 2 = 2$).

20. *Brachyphylla* GRAY, 1834. Four closely related species of this genus live on the Greater and Lesser Antilles. They are probably fruit-eaters. The observations of HALL and KELSON (1959) show that the 2 smaller species are *B. pumila* MILLER, 1918 from Hispaniola and *B. nana* MILLER, 1902 from Cuba.

The 2 larger species live on considerably smaller islands, *B. minor* MILLER, 1913 on Barbados and *B. cavernarum* GRAY, 1843 on Puerto Rico and on the whole belt of the Lesser Antilles as far to the south as St. Vincent. This last species is considerably larger than *B. minor*; its measurements are given by HUSSON (1960). ($2 \times 2 = 4$).

21. *Chiroderma* PETERS, 1860. Probably fruit-eaters. The two smallest species occur in limited areas: *C. trinitatum* GOODWIN, 1958 on Trinidad (GOODWIN, 1958; GOODWIN and GREENHALL, 1964) and *C. gorgasi* HANDLEY, 1960 in the Isthmus of Panama (HANDLEY, 1960).

The simultaneous occurrence of *C. villosum* PETERS, 1860 from the mainland on Trinidad (and on Tobago) does not complicate this comparison as might be expected, for in all probability it has recently settled on these islands. ($2 \times 1 = 2$).

22. *Ectophylla macconnelli* (THOMAS, 1901). Probably plant-eaters. According to GOODWIN and GREENHALL (1962, 1964), the typical form from the mainland of South America is much smaller than *E. m. flavescens* GOODWIN and GREENHALL, 1962 from Trinidad.

Family: *Natalidae*

This small insectivorous family is confined to the tropics of America.

23. *Natalus major* MILLER, 1902. *N. m. major* MILLER, 1902 from Hispaniola and *N. m. jamaicensis* GOODWIN, 1959 from Jamaica make up a group of smaller subspecies. In GOODWIN'S (1959) opinion, they are exceeded in size by *N. m.*

primus ANTHONY, 1919 from Cuba, which is larger than the former islands. (2 × 1 = 2).

24. *Natalus tumidirostris* MILLER, 1900. The typical form from Curacao off the coast of Venezuela is the smallest (GOODWIN, 1959) and *N. t. haymani* GOODWIN, 1959 from Trinidad the largest.

Family: *Vespertilionidae*

This evolutionarily advanced family includes the largest number of forms of all the chiropteran families. Its range is much more extensive than the range of all the remaining families together, which is connected with the fact that this is the only family that occurs all over the temperate zone. Insect-eaters.

25. *Myotis goudoti* (A. SMITH, 1834). According to DORST (1959), the typical form from Madagascar is much smaller than *M. g. anjouanensis* DORST, 1959 from Anjouan (Comoro Is.).

26. *Eptesicus fuscus* (PALISOT de BEAUVOIS, 1796). On the American continent it is represented, i. a., by *E. f. osceola* RHOADS, 1902 from Florida and *E. f. miradorensis* (H. ALLEN, 1866) from Mexico and Central America. This last form is larger than *E. f. osceola* (RHOADS, 1902; GOODWIN, 1942). The subspecies from the Antilles are smaller (MILLER, 1918) and of these *E. f. bahamensis* (MILLER, 1897) from New Providence (Bahama Is.) is the smallest (MILLER, 1918; SHAMEL, 1945; G. M. ALLEN, 1911). *E. f. hispaniolae* MILLER, 1918 from Hispaniola and Jamaica and *E. f. dutertreus* (P. GERVAIS, 1837) from Cuba are larger (MILLER, 1897, 1918; SHAMEL, 1945; JONES, 1964). Judging from the data presented by ANTHONY (1918), MILLER (1918) and SHAMEL (1945), the largest of the insular forms is *E. f. wetmorei* JACKSON, 1916 from Puerto Rico. (2 × 4 = 8).

27. *Lasiurus borealis* (MÜLLER, 1776). *L. b. borealis* from the southern and eastern parts of the United States (MILLER, 1931), *L. b. teliotis* (H. ALLEN, 1891) from Mexico and Central America and *L. b. frantzii* (PETERS, 1871) from Panama and the northern part of South America are smaller than their close insular relatives, *L. pfeifferi* (GUNDLACH, 1861), from Cuba and *L. degelidus* MILLER, 1931 from Jamaica (HANDLEY, 1960). (2 × 3 = 6).

28. *Lasiurus cinereus* (PALISOT de BEAUVOIS, 1796). SANBORN and CRESPO (1957) state that *L. c. semotus* (H. ALLEN, 1890) from the Hawaiian Is. is a smaller form. It probably has evolved from *L. c. cinereus* from the mainland of North America. The reduction in size may have been caused by both mild winters on the Hawaiian Is. (Bergmann's rule) and inbreeding. *L. c. semotus* has very likely sprung from a single fertilized female which strayed from the mainland.

29. *Nycticeius cubanus* (GUNDLACH, 1861) lives on Cuba. According to HALL and KELSON (1959) it is smaller than its close relative, *N. humeralis* (RAFINESQUE, 1818) from the mainland. *M. humeralis* splits into three subspecies, of which the nearest form is *N. h. subtropicalis* SCHWARTZ, 1951 from southern Florida.

30. *Antrozous* H. ALLEN, 1862. ORR and SILVA-TABOADA (1960) claim that *A. koopmani* described by them from Cuba is remarkably larger than *A. pallidus* (Le CONTE, 1856) from the mainland, which was probably its ancestral form.

Antrozous dubiaquercus VAN GELDER, 1959 from the Tres Marias Is. off the coast of the state of Najarit, Mexico, is also, according to VAN GELDER, larger than the continental ancestral form, *A. pallidus*. $(2 \times 1 = 2)$.

Family: *Mystacinidae*

This endemic family from New Zealand has only one species. Insect-eaters.

31. *Mystacina tuberculata* (GRAY 1843). DWYER (1962) states that the typical form, which occurs on the northern island and in the northern part of the southern island, is smaller than *M. t. robusta* DWYER, 1962 from STEWARD I. 32 km south of the southern island. *M. t. robusta* shows, besides, some differences in body proportions, e. g., its ears and forearms are shorter and the nostrils less projecting. For this reason DWYER explains these differences by Bergmann's rule and by Allen's rule, connected with this first. Namely, Stewart I. is situated in a much cooler climate than both the New Zealand islands.

Family: *Molossidae*

This evolutionarily most advanced chiropteran family lives mainly in the tropics and subtropics. Insect-eaters.

32. *Tadarida brasiliensis* (I. GEOFFROY, 1824). SHAMEL (1931) writes that the forms of the genus *Tadarida* from the Antilles are smaller than those from the mainland. If only the subspecies of *T. brasiliensis* are taken into consideration, not to compare remotely related forms, it will be found that *T. b. antillularum* (MILLER, 1902) from Puerto Rico and the Lesser Antilles, *T. b. muscula* (GUNDLACH, 1861) from Cuba, *T. b. murina* (GRAY, 1827) from Jamaica, *T. b. constanzae* SHAMEL, 1931 from Hispaniola and *T. b. bahamensis* (REHN, 1902) from the Bahamas are smaller than continental *T. b. cynocephala* (LE CONTE, 1831) and *T. b. mexicana* (SAUSSURE, 1860) from the United States and Mexico, *T. b. intermedia* SHAMEL, 1931 from Central America and *T. b. brasiliensis* from Central and South America.

The insular subspecies listed above are arranged in order of magnitude, from the smallest to the largest. Within the Antilles there are no correlations between the size of a form and the magnitude of the island inhabited by it. $(4 \times 5 = 20)$.

VI. SUMMARY OF RESULTS

Megachiroptera: In 6 cases the insular form (or that from a smaller island) is of larger size. These are *Rousettus leschenaulti*, *Pteropus anetianus*, the group of *Acerodon mackloti*, *Cynopterus sphinx*, *C. horsfieldi*, *Synonycteris crassa*.

In 15 cases the form from the mainland or from a larger island is of larger size. These are *Rousettus amplexicaudatus*, *R. angolensis*, *Pteropus hypomelanus*, *P. griseus*, *P. lombocensis*, *P. ornatus*, *P. caniceps*, *P. rufus*, *P. vampyrus*, *P. macrotis* *P. scapulatus*, the group of *Acerodon jubatus*, *Dobsonia viridis*, *D. moluccensis* and *Nyctimene major*.

In 16 cases no differences in size were found, or they were too complicated to analyse. These cases include *Pteropus admiralitatum*, *P. tonganus*, *P. melanotus*, *P. melanopogon*, *P. rayneri*, *P. samoensis*, *P. pselaphon*, *P. alecto*, *P. conspiciliatus*, *P. neohibernicus*, *Dobsonia peroni*, *Cynopterus brachyotis*, *Nyctimene albiventer*, *N. minutus*, *Macroglossus minimus* and *M. lagochilus*.

Microchiroptera: In 26 cases the insular form (or that from a smaller island) is of larger size. These are *Noctilio leporinus*, *Rhinolophus alcyone*, *Hipposideros bicolor*, *H. ater*, *H. cineraceus*, *H. lankadiva*, *H. dinops*, *Coelops frithi*, *Glossophaga longirostris*, *G. soricina* (2 ×), *Brachyphylla* (4 ×), *Ectophylla macconnelli*, *Myotis goudoti*, *Antrozous* (2 ×), *Lasiurus borealis* (6 ×) and *Mystacina tuberculata*.

In 59 cases the form from the mainland or from a larger island is of larger size. These are *Peropteryx macrotis* (3 ×), *Hipposideros turpis*, *H. larvatus*, *H. commersoni* (6 ×), *H. caffer guineensis*, *Chilonycteris parnelli* (10 ×), *Mormoops blainvillii*, *M. megalophylla*, *Chiroderma* (2 ×), *Natalus tumidirostris*, *N. major* (2 ×), *Lasiurus cinereus*, *Eptesicus fuscus* (8 ×), *Nycticeius cubanus*, *Tadarida brasiliensis* (20 ×).

The result obtained by adding the corresponding groups together (keeping in mind the differences between the methods used to investigate either suborder) is 32:74, which indicates that the *Chiroptera* living on islands more often decrease in size than increase.

VII. DISCUSSION

The studies on the hypothetical dependence of the size of particular forms upon the magnitude of the areas inhabited by them are especially difficult in so far as the *Chiroptera* are concerned. The difficulties are due to the following circumstances:

1. I venture the statement that there are no fully isolated islands and the exact degree of isolation is scarcely known, since isolation is conditioned, among other things, by the nature of the prevailing winds, though, again, it is unknown to what extent. Besides, it is also dependent on the biology of the given chiropteran form.

The ignorance of the degree of isolation is of little importance, if the form studied inhabits a large island as compared with a few adjacent small islets, for from our point of view it does not make a great difference whether we assume only the area of this large island, e. g., 500 km², as the range of the population, or the area of the whole group of islands, e. g., 520 km². These difficulties increase in significance, as the value of the ratio of the area of the island under study to the area of the adjacent islands becomes smaller.

2. Though some phenomena of "insularity" may occur even on very large islands (e. g., impoverishment of the fauna on Borneo; Darlington, 1957), yet it is obvious that the smaller the island, the more intense these phenomena should be. In practice, however, the smaller an island is, the less is known of it and the less available are the adequate sources of information. It is only too natural that the scientific, economic and even navigational significance of islands decreases with their area.

3. Not unlike other flying animals, particular forms of bats often have very extensive ranges. This impedes an analysis very much and limits the number of comparisons that can be drawn, which has been pointed out above in the considerations on the *Megachiroptera*.

4. Rensch (1933) has shown that the *Chiroptera*, as flying mammals, have fewer subspecies to one species than, e. g., the *Insectivora* and more species which are not differentiated into subspecies. This fact, too, limits the possibility of comparisons.

5. The taxonomy of bats is less well known than that of other mammals. All these circumstances certainly contribute to the fact that in the hitherto conducted investigations of the influence of insular environment, bats, which in respect of quantity and quality form an outstanding though specific group of mammals, have been left out.

In order to illustrate the difficulties in question, particular cases have been discussed in the section on the *Megachiroptera*. As will be seen from this discussion, there are generally no evident relations between the magnitude of an island and the size of the chiropteran form inhabiting it. It was not until the method of comparing only forms with extreme sizes had been applied that I managed to arrive at decisive conclusions in 21 cases, but in the remaining 16 cases even this method failed.

So far as the *Megachiroptera* are concerned, the mean lengths of forearm were calculated (assuming that they are proportional to the body size) for the group of forms which increase in size on islands and separately for the group of forms which behave contrariwise. In each group of comparisons the mean was calculated by adding together the minimum measurement of the smallest form and the maximum measurement of the largest form and dividing the sum by 2. It appeared that in 6 cases in which the size increased on islands the mean lengths of forearm (f) ranged from 44·0 to 143·0 mm and the mean from these 6 means was 90·4 mm. To improve the homogeneity of the material under study the genus *Nyctimene*, as at least partly insectivorous, was excluded from the group of 15 cases with decreasing sizes. For the remaining forms of this group these values are 75·7—190·0 mm and 130·6 mm, respectively. As the difference between these two means (90·4 mm and 130·6 mm) is very great, its significance was examined by Student's test. Since t amounts to about 6 with the probability equal to 0·05, the difference cannot be regarded as statistically significant. No such calculations were carried out for the *Microchiroptera*, because this group is much less uniform in respect of both systematics and food. In addition, the data offered by different authors often concern other measurements than the length of forearm.

The results of the present work are based in part on the measurements of small samples of specimens, which may arouse objections as to their being representative. However, it is less important to the ends of this work to investigate whether and, if so, to what extent a particular form of bats differs in size from another related form than to find how the order *Chiroptera* as a whole behaves in this respect, for casual deviations from the actual state, caused by the scarcity of material, must, according to the calculus of probabilities, be equally frequent in both directions and, consequently, cancel each other. The same arguments applied Rensch (1936) anticipating any possible objections to his results concerning the climatic rules, obtained on the basis of much scantier material than that used for the present study. Moreover, in the case of formation of a new population with a very small number of individuals, as often happens under insular conditions (Rensch, 1954), individual variation decreases. To tell the truth, Van Valen (1965) points to opposite tendencies in at least some of birds and explains the increased morphological variation of insular populations examined by him by their adaptation to the broadened ecological niches on islands. This broadening of niches is due, according to him, to the faunistic impoverishment of islands and to the resultant lack of competition from the species that live only on the mainland. It is well known that both individual and geographical variation is exceptionally small in bats (Miller, 1897; Kuzyakin, 1950), and therefore the sufficient number of specimens to characterize a form is much smaller here than in other mammals.

Let us survey the factors which may induce an increase in the size of insular bats:

Ia: As regards rather isolated islands, it is probable that, above all, the stronger and so, for the most part, bigger specimens of the original population managed to cover the distance separating these islands from the mainland. So far as these characters are hereditary, they were transmitted to the offspring. As a result, a variety larger than the initial form may have sprung up.

The increase of size brought about in this way does not seem to have taken place frequently. The dispersal of bats is strong, as very small and so rather weak species have reached such isolated and often small islands as the Hawaiian Is., Norfolk and Lord Howe (E of Australia), Iceland, the Cocos Is. (Indian Ocean) and the Galapagos Is. Of the relatively large islands which have not been colonized by bats as yet, though they provide very favourable local conditions, I can name only the Tahiti Is. It is worth while to mention a strange fact that the land birds of the most isolated oceanic islands are not good flyers, neither are they derived from good flyers (Darlington, 1957). However, the bats of isolated islands are, for the most part, good flyers *(La-*

siurus, *Nyctalus verrucosus* BOWDICH, the *Molossidae)*, though there are some examples of hardly moderate flyers that reached remote islands, e. g., *Myotis lucifugus* (LE CONTE) in Iceland and *Lasionycteris noctivagans* (LE CONTE) on the Bermudas.

Ib: Both pleiotropism and the gene linkage may bring about the formation of a larger form. The *Chiroptera* have not been examined in this respect at all, owing to the difficulties encountered in laboratory breeding and to their very low reproductive power. However, the enormous frequency of both these phenomena in other animals suggests that they may often be the cause and the mechanism of size changes in insular bats. Nevertheless, the action of these agents is ambivalent and therefore they may promote an increase in size as well as a decrease.

Ic: When colonizing an island, the initial populations often have incomplete gene pools. In this case it comes, even without selection, to the rise of a new form. Such "split-off" forms often show an extreme evolution of some characters (MERTENS, 1934), the occurrence of which in large populations is prevented by panmixia. Such a character may be "excessive" size, but on account of the strong dispersal of bats, i. e., the strong exchange between populations, the increase of size in this way seems rare.

Id: Weak selection on islands may permit of the formation of particularly large varieties as a result of genetic drift. Stress should be laid, among other things, on the fact, pointed to by many authors, that there is a relative lack of snakes on islands, and in the tropics these reptiles are main enemies of bats. On the other hand, more recent and exact investigations show that genetic drift is a remarkably rarer phenomenon than was supposed earlier and its place is usually taken by selection (MAYR, 1963). Genetic drift increases in weight, when the population is small and its reproductive power and degree of isolation are great. The reproductive power of the *Chiroptera* is exceptionally small and the degree of isolation of particular populations on various islands is considerably lower than in the huge majority of animals (power of flight). Only on small, exceptionally strongly isolated islands genetic drift might be of major importance to the evolution of these mammals. However, there are hardly any islands of this sort. The importance of genetic drift is still diminished by the fact of the uncommonly slow evolution of the *Chiroptera* (from the Eocene, after the radiational explosion, which probably took place in the Palaeocene). On the other hand, the extremely low reproductive power of this group indicates its equally low mortality rate or similarly poor selection even on the mainland and, the more so, on islands where selection is weakened. To sum up, selection and, particularly, genetic drift seem to play only a minor part in the changes of size in insular bats.

Ie: Large organisms withstand short-lived hunger better than the small ones owing to their less intense metabolism; the larger organism uses less food per gram body weight, though its food requirements are larger. Hence, it better endures a short-lived hunger caused, e. g., by a typhoon or gale, which unables them to obtain food. This is not contrary to the thesis that small organisms get along better during a lasting shortage of food (see IIe).

If: If the climate of an island is cooler than that of the region inhabited by the initial population, a larger form may evolve in accordance with Bergmann's rule. This phenomenon is well exemplified by *Mystacina tuberculata* from New Zealand, discussed more closely in another place. However, as will be shown in item IIj, Bergmann's rule applies here rather rarely.

Ig: A number of advantages which a large organism has over a small one may favour the rise of a larger form. According to Rensch (1954), the brain and sense organs of larger animals function more efficiently, because they consist of a larger number of sensory cells and the dendrites of the brain have more branches. The larger an animal is, the more well-developed are, on the principle of positive allometry, the temporal lobes of its brain, which are the most progressive parts determining its intelligence. The organs of defence and attack also grow in a positively allometric manner. Larger animals live longer and, therefore, they have more time to amass experience and develop different antibodies. Their physical advantage often assures victory to them in the intra- and interspecific competition.

Nevertheless, it is doubtful whether the benefits resulting from increased intelligence are so great on islands as they are on the mainland. It is a known fact that islands are not satiated biocenotically and, as a result, the bats have fewer enemies there and interspecific competition is less intense. See also item Id.

Ih: It is well known that the danger of overheating is greater in larger organisms. For example, Prater (1948) saw specimens of some large species of the *Megachiroptera* fall dead off trees in the Madras region, when the damp wind from the ocean had changed to the hot and dry wind from the inside of the land. The maximum temperatures are lower on islands than on the mainland. It follows that on an island an organism can "allow itself" an increase in size more safely than on the mainland.

The danger of overheating is the greatest in large species that spend the daytime in the full sunshine, and then only in few megachiropterans. Temperatures of 130°—135°F (= 54·4°—57·2°C) were also found under the roofs of buildings in which bats took shelter (Goodwin and Greenhall, 1961; Greenhall and Stell, 1960). However, most species spend the daytime in the shade, in considerably lower temperatures. The huge majority of these mammals are very small and remarkably thermophilous (out of the 17 families, 14 are limited to the tropics and subtropics and of the remaining 3 families one has only 1 species and another occurs only in the warmer part of the temperate zone). It may be supposed that even on the mainland overheating is dangerous to only very few species, the less so on islands. Hence, it is rather doubtful whether the lower maximum temperatures on islands may promote an increase in the size of these mammals.

In turn, I shall discuss the factors which may be responsible for a decrease in the size of insular chiropterans.

IIa: Pleiotropism and gene linkage may bring about the origin of smaller forms. See item Ib.

IIb: A deficient gene pool in individual specimens colonizing an island may result in a decrease in size. RENSCH (1954), however, thinks that the origin of new forms in the way of elimination of alleles is very rare and he seems to be right in this respect. For example, DAMMERMAN (1948) shows in his work how often the trials for colonization of even very small and isolated islands (Cocos Is., Indian Ocean) are made and that these islands are downright invaded by large numbers of bats from other remote small islands (Christmas Is., Indian Ocean).

IIc: In some cases dwarfism is caused by inbreeding and the deterioration of living conditions on the peripheries of the range of a given form.

Inbreeding occurs rather rarely (see the preceding item and Ia). Moreover, as MAYR (1963, pp. 530—531) has shown, it often has no negative effects on the population. An example of the negative consequences of inbreeding is probably *Lasiurus cinereus semotus*, an endemic form from the Hawaiian Islands discussed in another place, and perhaps both the endemic species from New Zealand, the only bats and, at the same time, the only native mammals of this country. At any rate, the enigmatic rare occurrence of all these 3 species, in spite of the probably favourable environment and the lack of competition from other bats, is striking. It may well be that the cause of this rare occurrence is inbreeding, especially in the initial phase of the colonization of these islands.

On the other hand, the deterioration of living conditions is certainly a much more frequent phenomenon, which, above all, takes place on very small isolated islands and atolls. Owing to the limitation of space the number of ecological niches is considerably reduced. Caves are especially often lacking on islands. If a cave species reaches such an island, it must be satisfied with a worse shelter. A relative floral and faunal poverty results in the sameness of diet and even in temporary food deficiency. The winds, not to mention typhoons, are stronger on islands than on the mainland. They hamper the flight of bats and especially their pursuit of prey, being probably responsible also for a remarkable decrease which can be observed in the number of flying species of insects on some islands. Insular insects often do not fly at all, or again they may be endowed with very great faculty for flight. Such a situation is naturally unfavourable to insectivorous bats. Typhoons, which carry the insects off and destroy trees, fruits and flowers, may cause a food shortage lasting for a number of years. It must, however, be kept in mind that the weakened selection on islands diminishes the negative effects of the poverty of ecological niches to some degree.

IId: Weakened selection may entail the origin of particularly small forms on islands. See item Id.

IIe: Dwarfism is advantageous during a lasting food deficiency, as it is easier for a smaller form to satisfy its wants. It is a well-known fact that the smaller organism needs a smaller amount of food, though its energy requirements per gram of body weight are larger, that is, its metabolism is intenser. The lasting food deficiency may be brought about either by climatic conditions (gales, rain, coldness) or by the excessive density of bat populations. In this last case the large form must be less numerous, which in the presence of such normal fluctuations in numbers as occur in all populations may lead to extinction or to the impoverishment of the genetic pool.

IIf: Small organisms reach sexual maturity earlier, have litters more frequently and more young ones in a litter. There is no need to discuss the advantage of this to the preservation of species.

Bats have not yet been studied in this respect sufficiently well, but the following facts suggest that they are not exempted from this rule: in the small *Vespertilionidae* the pregnancy lasts 44—73 days, and in the large *Megachiroptera* even 6 months. The former reach their final measurements in 6 weeks, the latter in 8 months, and equally long they are dependent on their mothers (ASDELL, 1964; EISENTRAUT, 1957; GRASSÉ, 1955). The largest species give birth to 1 young, other to 2 and rarely more than 2 young ones.

IIg: The limitation of space determines the maximum amount of biomass which an island can hold. The more numerous a population is, the better chance it has to survive quantitative depressions, which are so common in the animal kingdom. Hence it becomes clear that evolution must favour the quantitatively strong populations. The smaller the specimens of an insular population are, the more of them an island is capable of supporting. In this aspect, evolution very likely favours the speciation of small forms on islands. It is known that in the process of faunal impoverishment of islands the large mammals disappear first. It the bats, which like large mammals demand large areas, do not vanish, it happens owing to their considerably more numerous populations and the strong dispersal from other islands and the mainland. Dispersal makes the recolonization of an island possible in the event of the complete extinction of its previous population. As for the selection on islands, see also item Ic.

IIh: Small forms have better chances of finding suitable shelter. It is obvious that many hollows of trees, crevices and other places of refuge are not spacious enough to hold large forms, whose superior bodily power will be no good in such cases. The forms which take shelter in hollows and crevices attempt to find hiding-places with as narrow openings as possible so as to be safe from enemies. In this respect the small forms also have the advantage of the large ones. It comes to this that some forms are able to squeeze in through a crack 6 mm in width. In connection with this fact some species have particularly flattened skulls (*Tylonycteris*, *Platymops* and others).

Many forms willingly spend the daytime in trees, among branches and leaves, which habit is common in the tropical *Chiroptera*. It is more difficult for an enemy to find a small form than a large one under these conditions.

IIi: Smaller forms of bats seem to get food more easily than the larger ones. Most of these mammals are insectivorous and a vast majority of insects are very small. The smaller the size of bats, the greater their mobility (LEHMANN, 1956) and faculty for manoeuvering, evading an enemy and catching prey. A decrease in size does not entail a decrease in the maximum speed, which is the same in all geometrically similar animals, that is, does not depend on the size of animals (LEHMANN, 1956). The large size of some flowers and fruits does not prevent small bats from feeding on them, unless the peel of fruits is very thick or hard as happens in exceptional cases. On the contrary, in all probability, the seeking and consumption of flowers and fruits which are below some size limit is difficult, does not pay, or even is quite impossible for large forms. This is often caused by purely mechanical factors, e. g., the strength of stalks is to little to bear the weight of a bat. Hence, cauliflory, frequently encountered in the tropics, is regarded as an adaptation to chiropterophily and chiropterochory.

IIj: Bergmann's rule favours the development of small insular forms, but this happens rather in the temperate zone where the number of islands is small. Moreover, the temperate zone is inhabited almost exclusively by the *Vespertilionidae* and *Rhinolophidae*, whose homeothermy is the weakest of all the chiropteran families. Therefore, as will be shown below, Bergmann's rule only partly applies to these families. For example, KUZYAKIN (1950) did not find any signs of Bergmann's rule in the *Vespertilionidae* in the Palaearctic, whereas the *Rhinolophidae* of this region, according to him, increase in size with the altitude, which seems to fall under Bergmann's rule.

As may be judged by the laboratory experiments on mice and chicks (SUMNER, 1911; ALLEE and LUTHERMAN, 1940), this rule acts directly, i. e., a change is already observable in the F_1 generation grown in a different temperature from that of its parents. The minimum temperatures on islands are, as a rule, higher than those on the mainland. These minima, in RENSCH'S (1933, 1954) opinion, are decisive as far as Bergmann's rule is concerned. However, if the minima really govern the phenomena described by Bergmann's rule, RENSCH goes wrong in explaining the origin of giant forms of birds on islands by it (it is a fact that in another place [1930] he explains the increased size of insular birds by the lower mean temperatures on the islands), for it will be seen from Table II that the minima on islands are remarkably higher than those on the coast of the mainland, with which they are compared in most cases, let alone the minima in the inland regions of the mainland, where they must be still much lower and the differences between them and the minima for islands greater. Table II shows that in 35 out of the 38 comparisons presented the higher minimum temperature occurs on islands, though the abovementioned lack of the data concerning the inland regions of the mainlands handicaps the distinctness of the results (with the exception of NoNo 6, 8, 9, 17, 18 and 26, in which, in addition, the same locality occurs three times).

It will be seen from this table that only in 3 cases (NoNo 19, 33, 34) the

Table II

Comparison of minimum temperatures (in °C) on islands with those on mainlands

No	1	2		3	4	5
1	San Miguel, Azores, 746 km² Bahía Blanca, Argentina	0°59′	37°44′N 38°43′S	12—19 (15,5) 4—17 (10)	9—17 (8) —3—+9 (—5)	5,5 —8
2	Ascension, Atlantic O., 88 km² Luanda, Angola, Africa	0°53′	7°56′S 8°49′S	22—23 (22) 18—24 (22)	20,5—22 (20) 16—22 (15)	18 14
3	St. Helena, Atlantic O., 122 km² Moçamedes, Angola, Africa	0°43′	15°55′S 15°12′S	17—22 (19) 13—20,5 (17)	15—19 (15) 9—17 (9)	14 8
4	Fernando de Noronha, Atlantic O., 15,5 km² Mayumba, Gabon, Africa	0°25′	3°50′S 3°25′S	23—24 (17) 20—23 (22)	21—23 (20,5) 18—22 (17)	18 16
5	Norfolk, E. Australia, 34 km² Tor, Sinai Pen.	0°44′	28°58′S 28°14′N	13—20 (17) 9—24 (17)	10—17 (9) 5,5—21 (4)	7 2
6	Lord Howe, E. Australia, 13 km² Parana, Argentina	0°13′	31°31′S 31°44′S	13—19 (16) 7—19 (13)	8—15 (7) 0—13 (—1)	6 —4
7	Willis, E. Australia, 5 km² Cairns, E. Australia	0°37′	16°18′S 16°55′S	22—25,5 (24) 17—24 (21)	19—23 (19) 11—22 (10)	17 7
8	Table, northern Andaman Is., 1,3 km² Riyan, Red Sea	0°28′	14°11′N 14°39′N	24—27 (25) 19—26 (23)	22—24 (23) 17—23 (16)	18 15
9	Car Nicobar, Nicobar Is., 128 km² Zungeru, central Nigeria, Africa	0°33′	9°15′N 9°48′N	24—25,5 (25) 17—24 (21)	22—23 (21) 14—20,5 (13)	19 11
10	Cuyo, Philippines, 57 km² Lindi, E. Africa	0°51′	10°51′N 10°00′S	24—25,5 (24) 19—24 (22)	22—24 (21) 16—22 (15)	18 12
11	Cocos, Indian O., 3,9 km² Porto da Baia, Brazil	0°55′	12°05′S 13°00′S	24—25,5 (24) 20,5—23 (22)	22—23 (21) 19—22 (19)	20 17
12	Christmas, Indian O., 155 km² Lindi, E. Africa	0°25′	10°25′S 10°00′S	23—24 (24) 19—24 (22)	21—23 (20,5) 16—22 (15)	19 12
13	Mahe, Seychelles, Indian O., 142 km² Mombasa, E. Africa	0°34′	4°37′S 4°03′S	23—25,5 (25) 22—25 (23)	22—24 (23) 20—23 (20)	20 16
14	Diego Garcia, Chagos Arch., Indian O., 28,5 km² Dar es Salam, E. Africa	0°24′	7°14′S 6°50′S	24—25,5 (25) 19—25 (23)	———— ————	22 15
15	Rodriguez, Indian O., 104 km² Beira, E. Africa	0° 9′	19°41′S 19°50′S	19—24 (22) 16—24 (20,5)	17—23 (17) 13—20,5 (12)	15 9
16	Minicoy, Indian O., a dozen km² or so Kilwa Kivinje, E. Africa	0°27′	8°18′N 8°45′S	21—27 (24) 20,5—25 (23)	22—24 (20,5) 18—23 (18)	17 15
17	Yap, Carolines, Pacific O., 225 km² Zungeru, central Nigeria, Africa	0°18′	9°30′N 9°48′N	24—25 (25) 17—24 (21)	22—24 (22) 14—20,5 (13)	19 11

Table II (continued)

No	1	2		3	4	5
18	Ponapé, Carolines, Pacific O., 334 km²	0°48′	7°00′N	23—24 (23)	21—22 (20,5)	20
	Lokoja, central Nigeria, Africa		7°48′N	19—24 (22)	14—20,5 (13)	6
19	Guam, Marianas, Pacific O., 526 km²	0°37′	13°24′N	23—25 (24)	22—23 (21)	18
	Aden, Arabian Peninsula		12°47′N	23—30 (26)	20,5—28 (20)	16
20	Tana, New Hebrides, Pacific O., 557 km²	0°16′	19°30′S	18—23 (21)	14—20,5 (14)	12
	Townsville, E. Australia		19°14′S	14—24 (19)	7—21 (6)	1
21	Rotuma, Polynesia, 47 km²	0°30′	12°30′S	23—24 (24)	21—23 (20,5)	19
	Porto da Baia, Brazil		13°00′S	20,5—23 (22)	19—22 (19)	17
22	Tongatapu, Polynesia, 388 km²	0° 1′	21°08′S	18—23 (20)	13—20 (12)	11
	Mackay, E. Australia		21°09′S	12—23 (18)	5—20 (4)	0
23	Niue, Polynesia, 259 km²	0°12′	19°02′S	19—23 (20,5)	15—20 (12)	12
	Townsville, E. Australia		19°14′S	14—24 (19)	7—21 (6)	1
24	Funafuti, Micronesia, 2,6 km²	0°18′	8°31′S	25—25,5 (25,5)	23—24 (22)	21
	Luanda, Angola, Africa		8°49′S	18—24 (22)	16—22 (15)	14
25	Ocean, Micronesia, 5,7 km²	0°29′	0°52′S	25—25 (25)	23—23 (22)	20
	Libreville, Gabon, Africa		0°23′N	20—23 (22)	19—20,5 (18)	17
26	Ujelang, Marshall Is., Micronesia, a dozen km² or so	0° 2′	9°46′N	25—25,5 (25)	23—24 (23)	22
	Zungeru, central Nigeria, Africa		9°48′N	17—24 (21)	14—20,5 (13)	11
27	Pitcairn, Polynesia, 5,2 km²	0°10′	25°04′S	18—23 (20)	14—20,5 (12)	10,5
	Carnarvon, W. Australia		24°54′S	10,5—22 (17)	6—18 (5,5)	3
28	Easter, Polynesia, 128 km²	0°18′	27°10′S	15—20 (17)	11—18 (10,5)	10,5
	Brisbane, E. Australia		27°28′S	9—20,5 (15)	4—17 (4)	2
29	Rarotonga, Polynesia, 67 km²	0° 3′	21°12′S	18—23 (20,5)	14—20 (13)	9
	Mackay, E. Australia		21°9′	12—23 (18)	5—20 (4)	0
30	Malden, Polynesia, 39 km²	0°36′	4°3′S	24—24 (24)	22—23 (20,5)	18
	Loango, Kongo Brazzaville		4°39′S	19—24 (22)	17—22 (17)	15
31	Pukupuka, Polynesia, 5,2 km²	0°53′	10°53′S	24—25,5 (25)	23—23 (22)	21
	Lindi, E. Africa		10°00′S	19—24 (22)	16—22 (15)	12
32	Fanning, Polynesia, 32 km²	0° 8′	3°55′N	24—25 (25)	22—23 (22)	20
	Douala, Cameroon, Africa		4°3′N	22—23 (22)	20,5—21 (20)	19
33	Antigua, Caribbean Sea, 280 km²	0°37′	17°5′N	21—24 (22)	19—22 (18)	12
	Vizagapatam, E. India		17°42′N	19—27 (24)	17—24 (16)	14
34	Barbados, Caribbean Sea, 430 km²	0°16′	13°8′N	21—23 (22)	18—22 (18)	16
	Mangalore, E. India		12°52′N	22—26 (23)	19—23 (18)	17
35	Bermuda, Atlantic O., 54 km²	0°21′	32°18′N	14—23 (18)	9—20,5 (8)	5,5
	Perth, W. Australia		31°57′N	9—17 (13)	4—12 (3)	1

Table II (continued)

No	1	2	3	4	5
36	New Providence, Bahamas, Atlantic O., 150 km² Taihoku, China	0° 3′ 25°5′N 25°2′N	18—24 (21) 12—24 (18)	13—22 (22) 7—22 (5)	5 0
37	Grand Turk, Caribbean Sea, 24,5 km² Phu Lien, China	0°41′ 21°29′N 20°48′N	21—25,5 (23) 14—25,5 (20,5)	18—22 (17) 9—22 (8)	15 6
38	Key West, Gulf of Mexico, 10,3 km² Amoy, China	0° 7′ 24°33′N 24°26′N	18—25,5 (22) 11—27 (19)	12—22 (10,5) 6—24 (5,5)	5 4

Explanation: Column 1 — localities; in the first place the name of the island and its area. Column 2 — difference in geographical latitudes and latitudes themselves. If the localities are situated on both sides of the equator, the difference between their distances from the equator is given instead of the between the latitudes. The criterion of comparison was a distance smaller than 1° of geographical latitude. Column 3 — mean daily minimum temperatures for the warmest and coldest months; in brackets are the mean daily minimum temperatures calculated from the data for all months. Column 4 — mean minimum temperature in the warmest and coldest months; in brackets is the mean annual minimum temperature. Column 5 — absolute minimum temperature. After Pilot (see References).

temperatures from column 3 were higher on the continents than on the islands. The differences ranged from −1·7°C to +5·6°C, so in favour of the islands in the whole column; the mean temperature from column 3 is 2·2°C higher than the mean temperature from the continental localities. In column 4 only in one case (No. 34) the temperature on the mainland is slightly higher and the range of all the differences is from −0·6°C to +12·8°C, and so in favour of the islands. The mean temperature of the islands calculated from column 4 is on the average 5·7°C higher than that of the mainlands.

Since Rensch limits Bergmann's rule to homeothermous animals, it seems just to consider which of the chiropteran families discussed are homeothermous. According to Kulzer (1965), the members of the families *Vespertilionidae* and *Rhinolophidae* examined so far have the least well-developed homeothermy and are positioned, as it were, half-way between the homeo- and heterothermous animals (N. B., this enabled them to penetrate into the interior of the temperate zone). The *Molossidae* show a better thermoregulation, and the members of the *Pteropidae*, *Emballonuridae* and *Hipposideridae* studied hitherto are fully homeothermous. The analogy of climates allows the assumption that the remaining tropical families discussed in this paper, i. e., the *Noctilionidae*, *Phyllostomidae* and *Natalidae*, are homeothermous. As may be inferred from Dwyer's data (1962), the thermoregulation of the *Mystacinidae* resembles that of the *Vespertilionidae* and *Rhinolophidae*, though it may be somewhat better, as the *Mystacinidae* do not seem to hibernate.

To sum up, the arguments based on the results of this work are rather for the dwarfism than gigantism of the insular *Chiroptera*. The most important agent which brings about the decrease in the size of insular *Chiroptera* is probably the fact mentioned in item II g that evolution favours quantitatively strong populations. Items II c (partim), II e, II f, II h and II i or the deterioration of living conditions, the greater facility of smaller specimens in satisfying their necessities of life, the greater reproductive power and the greater chances of finding shelter and hiding from predators stand in a close connection with this fact.

It seems that the variety of sizes of the insular chiropteran forms cannot be explained by their different phylogenetic age, because there is no rule of the phylogenetic increase of size in bats (Rensch, 1954).

The high percentage of the cases in which there was an increase in size or lack of any changes, or the cases too complicated to analyse, points to the complexity of the problem and the reciprocally neutralizing tendencies of the factors which go to make the final resultant. In sum, the selection for the decrease in size in the insular *Chiroptera* does not seem to be strong.

If these results are added to the data presented by Foster for other orders of mammals, the prevalence of forms which decrease their size is still greater. This corroborates the studies of the nineteenth century, though they were carried out by wrong methods. On the whole, the small size of insular mammals is the rule (Hesse, 1925). It may appear surprising that the *Chiroptera* behave here like large mammals and quite unlike, e. g., rodents. These differences, however, become only natural, if one gets acquainted with the discussion concerning the causes of the increase in size in insular rodents (Berry, 1964). The question arises why birds also differ in this respect from bats. The essential difference in so far as this problem is concerned is the comparative lack of "nesting" and feeding territoriality in bats. Territoriality is an important element assuring food supply. In addition, birds show a greater plasticity in obtaining food than bats. Both these agents diminish the harmful consequences of the deterioration of living conditions on islands. It is therefore possible that birds have, as it were, "more" food on islands than bats and for this reason they "can afford" to increase their size more readily than these last. Naturally, it must be kept in mind that these "laws" are statistical in character and the exceptions to them are only too frequent.

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STRESZCZENIE

Do badań wybrano rząd *Chiroptera*, jako ważny, bo drugi pod względem ilości form rząd ssaków. Interesujące było porównanie go z innymi, zbadanymi już pod tym względem rzędami ssaków, szczególnie z gryzoniami, jako ssakami podobnej wielkości. Także zachęcające było porównanie ich z ptakami ze względu na konwergencje biologiczne obu tych grup. Inną ciekawą okolicznością był fakt, że nietoperze mając małe wymiary ciała, mają wielkie areały osobnicze, jak wielkie ssaki. Ponieważ gryzonie zwiększają wymiary na wyspach, zaś duże ssaki — zmniejszają, interesujące było stwierdzenie, jak się pod tym względem zachowują nietoperze.

W tym celu z rzędu *Chiroptera* zbadano na zależność między wielkością wyspy a wielkością formy oba podrzędy, tj. *Megachiroptera* i *Microchiroptera*. Badania oparto wyłącznie na literaturze. *Megachiroptera* badano drogą porównywania wielkości wysp z kontynentami (lub większych wysp z mniej-

szymi wyspami) zamieszkałymi przez 2 formy ekstremalnej wielkości. Porównywano tylko blisko spokrewnione formy, tj. należące do tego samego gatunku lub nadgatunku. *Megachiroptera* mają tylko 1 rodzinę i z wyjątkiem co najmniej częściowo owadożernej *Nyctimene*, są roślinożerne. Zbadano przedstawicieli rodzajów: *Rousettus*, *Pteropus*, *Acerodon*, *Dobsonia*, *Cynopterus*, *Nyctimene*, *Macroglossus* i *Syconycteris*.

U *Microchiroptera* zbadano przedstawicieli 9 rodzin spośród 16. Były to: *Emballonuridae* (*Peropteryx*, owadożerny), *Noctilionidae* (*Noctilio* — owadożerny i rybożerny), *Rhinolophidae* (*Rhinolophus* — owadożerny), *Hipposideridae* (*Hipposideros* i *Coelops* — owadożerne), *Phyllostomatidae* (*Chilonycteris* i *Mormoops* — owadożerne; *Glossophaga*, *Brachyphylla*, *Chiroderma*, *Ectophylla* — roślinożerne), *Natalidae* (*Natalus* — owadożerny), *Vespertilionidae* (*Myotis*, *Eptesicus*, *Nycticeius*, *Antrozous* i *Lasiurus* — owadożerne), *Mystacinidae* (*Mystacina* — owadożerna), *Molossidae* (*Tadarida* — owadożerna). Były to porównania blisko z sobą sąsiadujących geograficznie, pokrewnych form (ten sam gatunek lub nadgatunek), z których jedne zamieszkiwały wyspę, drugie zaś wybrzeże przyległego kontynentu, albo jedne zamieszkiwały mniejszą wyspę, drugie zaś większą. Tu jednak, w przeciwieństwie do *Megachiroptera*, porównywano ze sobą wszystkie formy danego gatunku czy nadgatunku, mnożąc ilość form wyspowych przez ilość najbliższych geograficznie form kontynentalnych etc. W ten sposób, zamiast jednego wyniku, z danej grupy porównań uzyskiwano czasem nawet do 20 wyników. U *Microchiroptera* pomijano wypadki braku różnic wielkości oraz wypadki zbyt skomplikowane.

U *Megachiroptera* forma wyspowa (lub z mniejszej wyspy) miała większe wymiary w 6 wypadkach, w 15 wypadkach była mniejsza, w 16 zaś wypadkach brak było różnic wielkości lub wypadki były zbyt skomplikowane do analizy.

U *Microchiroptera* forma wyspowa (lub z mniejszej wyspy) miała większe rozmiary w 26 wypadkach, a w 59 była mniejsza.

Wynik łączny u obu podrzędów nietoperzy wynosi 32:74, co wskazuje, że nietoperze na wyspach najczęściej zmniejszają wymiary jak wielkie ssaki, odwrotnie do gryzoni i ptaków, u których panuje tendencja przeciwna. Najważniejszą przyczyną zmniejszania wymiarów przez wyspowe *Chiroptera* jest zapewne popieranie przez selekcję populacji ilościowo silnych, to zaś pociąga za sobą zmniejszanie wielkości ciała wobec ograniczenia przestrzeni i tym samym możliwości, między innymi, wyżywienia, czyli występuje ogólne pogorszenie się warunków życiowych (zmniejszenie się ilości nisz ekologicznych). Mały organizm ma mniejsze potrzeby pokarmowe, łatwiej znajduje pokarm dzięki większej ruchliwości i łatwości manewrowania, osiąga szybciej dojrzałość płciową i rodzi więcej młodych oraz ma częstsze mioty, łatwiej znajduje dogodne kryjówki i łatwiej mu się ukryć przed wrogami. Natomiast podrzędną rolę w zmniejszaniu wymiarów przez wyspowe *Chiroptera* ma chów w pokrewieństwie (nie tak szkodliwy, jak dawniej sądzono, i rzadko zachodzący wobec silnego dispersalu nietoperzy), osłabiona selekcja i dryf genetyczny (działają ambiwalentnie), reguła Bergmanna (bardziej aktualna w klimacie umiarkowanym, lecz tam jest mało wysp, nadto, do żyjących tam nietoperzy reguła ta stosuje się tylko częściowo ze względu na słabe wykształcenie ich homotermii), oraz plejotropizm i sprzężenie genów (działają ambiwalentnie).

Znaczny procent przykładów zwiększenia wielkości, braku jej zmiany i wypadków zbyt skomplikowanych do analizy wskazują na złożoność i wzajemnie się neutralizujące tendencje czynników składających się na ostateczny wynik. W sumie, selekcja na zmniejszenie się wymiarów u wyspowych *Chiroptera* nie wydaje się silna.

РЕЗЮМЕ

Для исследований взят отряд *Chiroptera*, как один из наиболее важных, являющийся вторым по численности отрядом млекопитающих. Представляет интерес сравнение его с другими, уже исследованными в этом отношении, отрядами млекопитающих, в особенности с грызунами, имеющими такие же размеры, и с птицами в виду биологической конвергенции в этих двух группах. Другим интересным обстоятельством явилось то, что имея малые размеры тела летучие мыши, обладают, подобно крупным млекопитающим, большим ареалом. Поскольку грызуны увеличивают размеры тела на островах, в то время как крупные млекопитающие — уменьшают, представляет интерес установить, как в этом отношении ведут себя летучие мыши.

Для выяснения зависимости между величиной островов и размерами особей из отряда *Chitroptera* исследовано оба подотряда: *Megachiroptera* и *Microchiroptera*. Исследования базировались только на литературных данных. *Megachiroptera* исследовали путем сравнения величины зверьков на островах и континенте, (или же форм больших островов с формами меньших островов) заселенными 2 формами крайней величины. Сравнивали только близко родственные формы, т. е. принадлежащие к одному и тому же виду или надвиду. *Megachiroptera* имеют только 1 семейство и, за исключением по крайней мере частично насекомоядной *Nyctimene*, являются растительноядными. Исследовали представителей родов: *Rousettus, Pteropus, Acerodon, Dobsonia, Cynopterus, Nyctimene, Macroglossus, Syconycteris.*

У *Microchiroptera* исследовали представителей следующих 9 семейств из 16: *Emballonuridae (Peropteryx,* насекомоядные), *Noctilionidae* (*Noctilio* — насекомоядные и рыбоядные), *Rhinolophidae* (*Rhinolophus* — насекомоядные), *Hipposideridae* (*Hipposideros* и *Coelops* — насекомоядные), *Phyllostomatidae* (*Chilonycteris* и *Mormoops* — насекомоядные), *Glossophaga, Brachyphylla, Chiroderma, Ectophylla* — растительноядные), *Natalidae* (*Natalus* — насекомоядные), *Vespertilionidae* (*Myotis, Eptesicus, Nycticeius, Antrozous* и *Lasiurus* — насекомоядные), *Mystacinidae* (*Mystacina* — насекомоядные), *Molossidae* (*Tadarida* — насекомоядные).

Сравнивали по соседству расположенные родственные формы (тот же вид или надвид), из которых одна заселяла остров, а другие — побережье прилегающего континента, или одни располагались на малом, а другие на большем острове. В данном случае в отличие от *Megachiroptera* сравнивались все формы данного вида или надвида, умножая количество островных форм на количество ближайших к ним в географическом отношении континентальных форм и т. д. Таким

образом, вместо одного результата из данной группы сравнений получали иногда даже 20 результатов. У *Microchiroptera* отбрасывались случаи отсутствия разницы размеров или случаи слишком сложные.

У *Megachiroptera* островные формы (или же с меньших островов) имели большие размеры в 6 случаях, в 15 случаях были меньшие, в 16 случаях не было разницы в размерах или же были случаи слишком сложные для анализа.

У *Microchiroptera* островная форма (или с меньшего острова) имела большие размеры в 26 случаях, а в 59 случаях была меньшей. Общий результат в обоих подотрядах летучих мышей составляет 32:74, что указывает на то, что летучие мыши на островах чаще уменьшают размеры (как крупные млекопитающие) в противоположность грызунам и птицам, у которых отмечается обратная тенденция. Самой главной причиной уменьшения размеров островных летучих мышей, по-видимому является то, что естественный отбор поддерживает количественно крупные популяции, а это тянет за собой уменьшение размеров тела, в силу ограниченности пространства и тем самым, между прочим, возможностей прокормления, иначе говоря, наступает общее ухудшение условий жизни (уменьшение количества экологических ниш). Малый организм имеет меньшие кормовые потребности, легче находит корм благодаря большей подвижности и легкости маневрирования, быстрее достигает половой зрелости, производит большее количество молодых, имеет большее количество помётов в году, легче находит благоприятные укрытия и легче может спрятаться от врагов. Второстепенную роль в уменьшении размеров островных летучих мышей играет родственное спаривание (не так уж вредное, как раньше предполагали и редко имеющее место в виду сильной дисперсии летучих мышей), ослабленный отбор и генетический дрейф (действующие амбивалентно), правило Бергмана (более актуальное в умеренном климате, но там имеется мало островов, кроме того к живущим там летучим мышам это правило применимо только частично в виду слабого формирования их гомотермии), а также плейотропизм и сцепление генов (действуют амбивалентно).

Значительный процент примеров увеличения размеров или отсутствия их различия и случаев слишком сложных для анализа указывают на сложность и тенденцию взаимной нейтрализации факторов, дающих окончательный результат. В сумме, отбор на уменьшение размеров у островных летучих мышей не предоставляется сильным.

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