Entomostraca of Aldabra, with Special Reference to the Genus Heterocybris (Crustacea, Ostracoda)

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Entomostraca of Aldabra, with special reference to the genus *Heterocypris* (Crustacea, Ostracoda)

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[Plate 19]

1. Introduction

The German geographer Voeltzkow, although he only spent something over a month on Aldabra during April to May 1895, made the first known collection of Entomostraca from the atoll. His lively account includes mention of four species of Ostracoda and also records the occurrence of daphnid cladocerans (Voeltzkow 1897, p. 67; English translation p. 21). Voeltzkow's collection was described by G. W. Müller, who added another ostracode, a *Centrocypris* species which he did not describe because of scanty material, to Voeltzkow's list (Müller 1898, pp. 275–283).

Ostracodes and cladocerans were also recorded by the Bristol University expeditions of 1964 and 1965 but not collected (R. Gaymer, personal communication 1967). The next additions to the known fauna were made by C. A. Wright of the British Museum (Natural History) who cultured ostracodes, an anostracan, *Streptocephalus* sp. and the conchostracan, *Eulimnadia* sp., from mud samples obtained during a September 1966 reconnaissance visit (Stoddart & Wright 1967, p. 1175). Further collections of dried mud from Aldabra were made by J. F. Peake of the British Museum (Natural History) during phase I (August to September 1967) of the Royal Society Expedition to Aldabra. One of these, from a pool between Croix Blanc and Anse Cèdres (the locality of sample 8, see appendix A) has been cultured since 5 December 1967 (see § 8(*d*)).

During phase III of this Expedition (31 December 1967 to 7 April 1968), I collected extensively on Aldabra. Ile Polymnie was not visited but sampling density for the other islands was: West Island, 11 samples; Middle Island, 7 samples; South Island, 74 samples. In addition, the fauna from 100 temporary rainpools on South Island was recorded but, with two exceptions, not sampled. All types of terrestrial aquatic environments were sampled, including saline tide-influenced inland pools, brackish pools and hypersaline pans hostile to the cypridid Ostracoda which formed my special interest on this occasion. The reasons for my heavy commitment to South Island, in particular to its southeast sector, will become apparent later (see § 4 (*i*)).

As a result, the known freshwater Entomostraca fauna of Aldabra (see appendix B) now comprises 23 species, of which 10 are Ostracada, seven Cladocera, one Conchostraca, one Anostraca and four Copepoda. The saline tolerant or marine entomostracans now known consists of a cyclopoid and about 20 harpacticoid copepods (most of the latter sent to J. B. J. Wells for identification) and 10 Cirripedia (identified by W. A. Smith from seven species collected by J. D. Taylor, two by J. Frazier, one by F. R. Fosberg and two by K. G. McKenzie). In addition, there is a diverse fauna of marine Ostracoda.

2. SAMPLING METHODS

Sampling points were located directly onto aerial photographs, or by tape and compass traverses between known locations with later reference to stereo pairs of aerial photographs where these were available, or by compass bearings to known locations and to locations established in the field during phase III. In appendices A to C the Aldabra grid coordinates for each sample are given as are the coordinates for other localities where measurements were made or which were used as field reference points. The error for these various localities is within the limits of grid or map error.

Most faunas were sampled using a home-made plankton net of 160-mesh bolting silk. This was drawn through the water just above substrate level and the catch became concentrated in a small jar at the end of the net. In some instances, marine or salt tolerant specimens were hand collected. All sampling was qualitative only.

The samples were preserved in 5 % formalin as it proved more convenient to carry formaldehyde concentrate into the field than alcohol which suffered from the further disadvantage that it was drinkable.

Although the total fauna observed at the time of collection was recorded on a label, samples were not picked in the field. In a few cases, forms were recorded in the field which could not be found when the samples were picked. These instances are recorded in the appendices as cladoceran, copepod, etc. In many cases, when samples were picked, several forms additional to those originally observed were identified.

Once collected, preserved and labelled, samples were stored in 8 × 2.5 cm glass phials which were kept in reprint boxes fitted with honeycomb-type builder's insulation material at the suggestion of J. F. Peake. This system proved so efficient in the field that no samples were lost through breakage. Later, one phial was smashed in transit to the United Kingdom.

It was planned to measure several ecological parameters of the pools but field conditions on Aldabra were against the convenient portage of glassware and dangerous chemicals and in the event only salinity was measured consistently. In some instances pH was measured by Lovibond Comparator and for a few pools alkalinity and organic matter were determined by titration. Occasional determinations of dissolved oxygen, phosphate and nitrate were also made but these results are considered unreliable.

A National Institute of Oceanography portable salinometer, based upon an original Australian design which has been extensively field tested since the mid-1950s, was used for all salinity and most temperature determinations. The limits of the standard model used are 38‰ (i.e. 38 g l^{-1}) and 31 °C. This range is useful in the tropics as long as measurements are made in the early morning or late afternoon but for series of readings throughout the day a tropical model is required. A disadvantage of the instrument is that the heavy cable is awkward to carry on land.

The salinometer was calibrated before delivery in mid-December 1967. On Aldabra it was twice checked against the Indian Ocean, off Anse Cèdres on 19 January and at Dune Jean-Louis on 18 February. It was also checked against the Indian Ocean on 5 and 6 March at Astove and Cosmoledo respectively, during a collecting trip. The results were consistent (see appendix A). Before leaving Aldabra, I checked it against Standard Sea Water ampoules kindly provided by B. Bell of East African Marine Fisheries Research Organization and found that it was still satisfactory. It is germane to record here that when the salinities of several freshwater and brackish pools, which had first been measured during late January and early February, were rechecked on 21 and 22 March, the later results matched closely those made earlier. Thus, the instrument gave consistent readings over its full range for the entire sampling period.

Air temperatures were measured at the field camps for some weeks with a maximum–minimum thermometer which had been checked for one week against the standard instrument used at the Settlement weather station and found to be accurate within 1 °C.

Some additional water temperatures were taken by ordinary thermometer.

3. Climatic factors

(*a*) *Air temperature*

When it became obvious that the wet season was going to be unseasonably dry, it was decided to measure daily temperature ranges at the field camps to provide more closely applicable field records than those available at the Settlement weather station on West Island. The results for part of February at Wilson's Well are recorded in table 1. They indicate that field shade temperatures in the southeast of South Island, the lee side of Aldabra during the monsoonal season, occasionally exceeded the absolute maximum of 36.3 °C (97.5 °F) recorded at Settlement on 9 January 1968.

Table 1. Air temperature ranges at Wilson's Well during part of February 1968

date (February 1968)	T/°C max.	T/°C min.	T/°F max.	T/°F min.
7	32	22	90	72
8	35	23	95	73
9	37	21	99	70
10	—	23	—	73
11	34	23	94	73
12	34	27	93	80
13	35	27	95	81
14	37	28	98	82
15	35	27	95	80
16	34	27	93	81
17	34	28	94	82
18	35	27	95	81
19	—	26	—	80

(*b*) *Wind*

Wind speed and direction are significant factors when considering the mechanics of the dispersal to isolated islands of some freshwater animals, especially Entomostraca (McKenzie & Hussainy 1968; McKenzie & Norman 1968). The data available for Aldabra have been summarized by G. E. Farrow (this volume, p. 67) and indicate that windborne colonization from Africa is a possibility via relatively light variable westerly winds during the November to March monsoon while colonization from Malagasy is possible during April to October via the somewhat stronger southeasterly Trades. Data on cyclone paths presented by Stoddart (1970) indicate that windborne colonization from the Indo-Malayan Region is also a possibility.

(*c*) *Rainfall*

Although rainfall for the year ending 31 October 1968 was close to the average of about 670 mm (based on 7 years' records, Farrow, this volume, p. 67), January and February 1968, during the summer monsoon, were unusually dry. The rainfall recorded at Settlement during phase III is given in table 2. The figures are significant when considering the recovery of freshwater wells at times of high tide (see § 4 (*a*) iii) and, further, the way in which some entomostracans utilize the temporary aquatic niches which become available on Aldabra following a rain (see § 7(*d*)).

TABLE 2. RAINFALL ON ALDABRA DURING PHASE III

	rainfall/mm		
date	January	February	March
1	1.5	—	2.0
2	0.3	—	—
3	0.3	—	—
4	—	14.0	6.6
5	—	2.6	—
6	—	—	—
7	—	—	8.2
8	—	—	—
9	—	—	3.0
10	—	—	0.3
11	—	0.4	12.0
12	—	—	3.3
13	—	—	—
14	—	—	3.5
15	—	—	2.9
16	2.8	—	6.0
17	2.6	—	—
18	—	—	—
19	—	—	10.0
20	—	—	—
21	0.6	—	5.5
22	—	—	—
23	—	1.6	—
24	—	—	8.7
25	—	3.7	51.0
26	—	0.4	—
27	—	—	5.0
28	—	3.2	—
29	—	0.1	0.1
30	—		2.0
31	—		8.0
totals	8.1	26.0	138.1

4. TERRESTRIAL AQUATIC NICHES

(*a*) *Permanent freshwater reservoirs*

(i) *Introduction*

According to Voeltzkow, the only waterhole on Aldabra which never ran dry was inland from the southeastern end of the lagoon (Voeltzkow 1897, p. 52; English translation p. 9). Clearly, Voeltzkow meant the Cinq Cases area rather than Takamaka and his information presumably came from the Seychellois working for the lessee, J. Spurs. It is difficult to decide which of three small waterholes to the southeast of the Cinq Cases landing stage Voeltzkow referred to. Coordinates for the possiblities are: 3800, 0625; 3860, 0585; and 3905, 0565. The last location is at the present Camp Cinq Cases and is the most likely site based on some details in Voeltzkow's text, namely: (1) the time taken to reach the waterhole, (2) the occurrence and condition of tortoise enclosures *en route*.

Other early references make it clear that the Takamaka area has also long been used for freshwater supplies (Fryer 1910, p. 252).

There are no other known permanent freshwater reservoirs on the atoll (note that Ile Polymnie was not visited during phase III). Voeltzkow mentions (1897, English translation p. 10) that '...there are in the bush behind the settlement cavities in the coral rocks...' which were used by the Seychellois as temporary reservoirs and such small rockbasins are numerous today on West Island, Middle Island and South Island. But Voeltzkow's efforts in 1895 to obtain permanent fresh water on Ile Michel were fruitless and my own attempt at Ile Michel on 15 February met a similar fate at about 2 m below terrain level. On 20 February I dug in the Dune Jean-Louis area near the coast WSW of sample 67 (2565, 0355) but again failed to discover a potable aquifer.

The presence of permanent freshwater reservoirs (figure 1) on Aldabra has obvious significance for freshwater-adapted species and the evidence other than historical for their existence is therefore discussed below in some detail.

(ii) *Elevation of the atoll*

The elevation of Aldabra is well known and has frequently been mentioned as a reason for the wide range of habitats which the atoll presents but its logical corollary appears to have been overlooked. This corollary is that a considerable volume of differentially porous limestone is available for the development of freshwater aquifers above the marine water-table.

(iii) *Tidal influences—freshwater table*

Such aquifers are bound to be influenced by the tides on Aldabra because of the high porosity of limestone even though interstices are likely to be extremely irregular in shape, persistence and size.

At Cinq Cases during early February it was observed, but not measured, that the level of the Cinq Cases well, then under moderate use by about six people, sank during the period of low tides. With high tides the well recovered rapidly. Similar observations were made at Takamaka where Wilson's Well was under heavy use by about a dozen people at the same time. W. Macnae had reported previously that this well was failing and on 12 February it contained barely 4.5 l of water. The first of the next group of high tides was on 13 February. By 15 February we were using the well again and by 17 February it had recovered completely and contained about 1 m of fresh water. The rainfall data for February indicate that these recoveries at Cinq Cases and Takamaka were not due to rains (table 2).

(iv) *Tidal influences—marine water-table*

Rises and falls in the inland marine water-table afford further evidence for the existence of interstices available for freshwater accumulation.

(1) Several observations were made near Anse Cèdres on 19 January. Late that evening (19h30 to 20h00) water had risen appreciably in saline pools, about 400 m inland, the bottoms of which were barely wet that morning. Further, in the vicinity of 3635, 1080 tidewater could be heard running noisily into a pool in a solution chimney in the limestone. The tide had begun to flow off Anse Cèdres at about 14h00.

(2) On 27 January the salinity of the lagoon complex W of Point Hodoul (4025, 0890) was 16‰ at 09h45 when the water-level was low enough for us to wade through easily but 32.9 ‰ at 13h30 when the level of the lagoon was higher and its marine régime obviously well established.

(3) At the locations of samples 29 (3750, 0520), 30 (3755, 0525), and 32 (3755, 0510) comparable observations were made on 2 February. The saltwater level was rising rapidly at all three sites during our visit (17h15 to 18h15). In particular, at the last locality (sample 32), saltwater was racing from one large pool in the complex into another where the water-level was lower, and the first pool was being filled with such force that its surface was markedly disturbed. This rise in the saltwater table again was in rhythm with the rising tide.

(4) On 4 February a large, 8 to 12 m deep, saline pool NW of Point Hodoul (3840, 0950) was sampled and its surface and bottom salinities measured (see appendix A). At 10h00 the water-level of this pool was only about 1 m below terrain level. When we returned at 14h40 the water level had dropped to $2\frac{1}{2}$ to 3 m below terrain level.

(5) On 14 February I measured the changes in salinity near the head of the estuary leading to the camp at Wilson's Well, Takamaka (3390, 0670), as the tide ebbed—also the rates of fall—until both salinity and temperature became too great for my instrument. The measurements confirm the simple observation that saline and hypersaline waters periodically recede from the land into the lagoon, even at high tides. Previously, at Cinq Cases landing stage on 29 January, a maximum rate of the same order (2 to 5 mm min^{-1}) had been obtained for the rising tide (08h00 to 08h30) during the preceding cycle of high tides, indicating a similar situation there.

(6) On 18 February at Dune Jean-Louis pits in the weathered limestone near the base of the dune which had contained some saltwater at 07h30 were barely moist at 18h00, although when one such pit was dug into (18h00) saltwater flowed at 0.3 m depth and its level was obviously rising.

(v) *Inland marine-type faunas*

At many tide-influenced localities on South Island and a few on West Island marine-type faunas were sampled inland (appendix C). These generally included such molluscans as nerites, littorinids, cerithiids, opisthobranchs and tiny pelecypods; aorid amphipods (so determined by M. H. Thurston); eurydicid (= cirolanid) isopods in the genus *Cirolana* (so determined by R. W. Ingle); palaemonid shrimps (determined as *Palaemon debilis* Dana 1852 by L. B. Holthuis); marine worms; marine harpacticoid copepods (sent to J. B. J. Wells for determination); and the marine alga *Caulerpa verticillata* (determined by J. H. Price). In some instances this marine fauna was dwarfed, e.g. the nerites in sample 9 (3640, 1065), south of Anse Cèdres.

At one locality (2715, 0475) several large fish, identified as 'lebine' by the Seychellois who accompanied me, were seen.

Highly saline and hypersaline faunas were also sampled well inland at pools where tidal influences were not obvious, e.g. the large mangrove gastropod, *Terebralia*, at 3470, 0525 (sample 50).

It is conceivable that occasional elements of these diverse faunas were carried in by birds, e.g. frigates or flamingoes, or some other chance agency. But the only possible general conclusions are that these faunas either are relicts of former holomarine or hololagoonal régimes on what is now land, or they represent recent invasions from the sea by subterranean passages, or some combination of both alternatives. In any case, they set limits to the extent of freshwater reservoirs on the atoll, in time as well as spatially (figure 1).

(vi) *Freshwater faunas*

Although the marine-type faunas are limiting factors, the diversity of the freshwater faunas yet suggests a relatively long history for the freshwater reservoirs. For example, of the 23 species of freshwater Entomostraca now known to occur on Aldabra, only three are confined to temporary rainwater rockholes (see § 4(*c*) ii) and most of the others characterize the faunas of the large pools in the reservoir areas (a few species were probably introduced by man comparatively recently, see § 6(*b*) iii).

(vii) *Brackish pools*

In the Cinq Cases area, the outcrop pattern of brackish pools such as pool IX (3875, 0550) and Flamingo Pool (3905, 0795) lies broadly in the buffer zone between the saltwater and freshwater tables. Predictably, such pools also have intermediate salinities, e.g. the salinity of Flamingo Pool on 22 January was 15‰.

FIGURE 1. Distribution of freshwater reservoirs on Aldabra. Closed circles = tide-controlled pools and saline lagoon complexes, dotted areas = extent of the reservoirs.

(viii) *Brackish faunas*

The faunas of such pools include species which because of their tolerances or by necessity of their breeding biology can travel inland up the salt–fresh interface zone to colonize brackish pools. Evidence that the journey is subterranean is afforded by *Palaemon debilis* which is whitish overall in pool IX (sample 15) but strongly coloured in the tide-influenced lagoon complex where sample 32 was collected.

The milk-fish, *Chanos* (determined by P. H. Greenwood) has a potanadromous habit during its breeding cycle (P. H. Greenwood, personal communication). It is thus preadapted to colonize brackish pools, and its occurrence on South Island demonstrates that a salt–fresh interface exists in the ground water-table.

On the behaviour of Palaemonidae in this respect L. B. Holthuis has commented: '...Hardly anything is known about the biology of *Palaemon debilis* other than that it is found in water of greatly varying salinities. It certainly might be worth while to study the species in this respect. Several Palaemonidae do travel from water of low salinity to water of high salinity to let the eggs hatch, after which the larvae (or young) evidently go back to the low salinity medium. Only very recently some research has been done in this field (mostly with *Macrobrachium*)' (L. B. Holthuis, personal communication 1969.)

(*b*) *Temporary rainwater pools*

When rain falls small pools form in every depression and crevice which the limestone affords. Soon many of these pools are swarming with life. Some idea of the diversity of this life is given in table 3 which is the result of qualitative observations on the epibenthos of 100 such pools, made on 20 and 21 March around Cinq Cases and on 25 March near Dune d'Messe. The pools had formed as a result of good intermittent rains since 23 February (see table 2) and their dimensions varied from 8 × 7 × 0.5 cm^3 to 140 × 80 × 11 cm^3. The substrate of these adventitious pools usually consisted of organic detritus, e.g. plant debris and tortoise faeces; algal mats; flags and boulders of limestone both large and small; and often the plants *Fimbristylis*, *Cyperus* and *Acrostichum* were associated.

TABLE 3. FAUNAS OF TEMPORARY RAINPOOLS ON ALDABRA

locality	no.	nil	m.	o.	cl.	co.	a.	a.m.	m.l.p.	a.b.	w.b.	i.l.
Camp Cinq Cases	20	2	—	10	1	—	6	7	1	10	2	8
SW pool III	10	2	—	4	—	—	—	1	1	6	—	7
ENE pool IX	20	—	—	13	1	—	3	1	4	13	—	10
nr pool II	12	—	2	5	—	1	1	3	1	10	2	3
SE sample 33	10	2	—	7	2	—	2	1	1	4	—	—
NW sample 33	10	2	—	5	—	—	3	3	3	8	1	—
SW sample 33	5	—	—	4	—	—	3	1	1	3	—	1
NE sample 33	5	—	—	3	—	—	2	1	1	4	—	3
nr sample 107	8	1	—	6	—	—	—	—	1	2	—	—
totals	100	9	2	57	4	1	20	18	14	60	5	32

No., number of pools recorded at each locality; nil, no fauna; m., molluscans; o., ostracodes; cl., cladocerans; co., copepods, a., anostracans; a.m. aquatic mites; m.l.p., mosquito larvae and pupae; a.b., aquatic beetles; w.b., water boatmen; i.l., insect larvae (not mosquitoes).

Seasonal and other niche considerations will be dealt with later (see § 7), but it is worth emphasizing that although Entomostraca were noted in 57 % of the pools examined only three entomostracan species occurred consistently (see § 4 (*c*) ii).

These pools were uniformly very fresh, although when similar pools occur near the coast they can be affected by seaspray, e.g. sample 103 (2565, 1300) near Anse Badamier on Middle Island which had a salinity of 4.6‰ on 16 March. In spite of this relatively high salinity, sample 103 contained an active fauna of ostracodes, anostracans and mosquito larvae.

(*c*) *Niche categories, their salinity ranges, associated faunas and floras*

Concluding this section, it appears that there are five main categories of terrestrial aquatic niches on Aldabra. The parameters which define them are noted below. Characteristic species are those which occur in three or more samples in any one category (Insecta not included).

(i) *Permanent freshwater reservoirs*

The distribution of this platin category is given by figure 1. Its salinity range is 0.6 to 9.4‰. The characteristic Entomostraca are: *Heterocypris giesbrechti*, *Centrocypris horrida*, *Cypris decaryi*, *Limnocythere* sp.; *Macrothrix spinosa*; *Mesocyclops leuckarti pilosa*. *Thespesia*, *Ficus* and *Pandanus* are common associated trees.

(ii) *Temporary rainwater rockholes*

This category occurs all over Aldabra. In some areas, such pools are relatively large or have been covered over with stones by man to form reservoirs of drinking water (see § 8 (*e*)) in which circumstances they border on permanency. Their normal salinity range is 0.1 to 4.6‰ but at Dune Jean-Louis some covered rockholes can range in salinity up to 10.5‰. The characteristic Entomostraca are: *Heterocypris symmetricus*, *Moina dubia pectinata*, and *Streptocephalus proboscideus*; although the last-named species does not occur in covered rockholes.

(iii) *Brackish pools*

This category has a restricted distribution on the Aldabra platin. The salinity range is 6.4 to 15.0‰. There are no characteristic Entomostraca, and *Palaemon debilis*, *P. concinnus* Dana 1852 and *Chanos* sp. are associated malacostracan crustaceans and fish. *Lumnitzera*, a mangrove, is the typical associated plant.

(iv) *Tide controlled pools*

The distribution of those pools and lagoonal complexes in this category which were visited is given by figure 1. Their salinities range from 11.1 to 36.7‰. The characteristic entomostracans are marine harpacticoids but the great diversity of the faunas of these pools—where *Caulerpa verticillata* is a characteristic alga—has been recorded earlier (see § 4 (*a*) v). Champignon or pavé is the characteristic terrain and *Pemphis* scrub the characteristic vegetation.

(v) *Highly saline pools not obviously tide controlled*

For pools in which tidal control is not obvious, e.g. the hypersaline pool at 3190, 0545, salinities range from 24.6 to 37.4‰. Salt-tolerant harpacticoids and the cyclopoid copepod, *Microcyclops* cf. *dengizicus*, are the associated Entomostraca. The terrain is pavé and *Lumnitzera* characteristically borders these pools.

(vi) *Highly tolerant species*

Several species have tolerances which fit them for more than one of the above broad categories (sympatry not considered here but see § 8 (*f*)). These species include:

(1) *Plesiocypridopsis aldabrae* and *Alona* sp. in categories (i) and (ii);
(2) *Palaemon debilis* in categories (iii) and (iv);
(3) a small gobiid fish in categories (i), (ii), (iii) and (v).

5. THE ENTOMOSTRACA

(*a*) *List of species*

The following Entomostraca have been determined from Aldabra.

(i) *Ostracoda*

Heterocypris giesbrechti (Müller), 1898
Heterocypris symmetricus (Müller), 1898
Cypris decaryi Gauthier, 1933
Centrocypris horrida Vávra, 1895
Strandesia vavrai (Müller), 1898
Parastenocypris aldabrae (Müller), 1898
Cypretta cf. *fontinalis* Hartmann, 1964
Plesiocypridopsis aldabrae (Müller), 1898
Zonocypris cf. *madagascarensis* Müller, 1898
Limnocythere notodonta Vávra, 1906

(ii) *Conchostraca*

Eulimnadia cf. *mauritiana* (Guérin), 1837

(iii) *Cladocera*

Moina dubia De Guerne & Richard, 1892,
  pectinata Gauthier, 1955
Ceriodaphnia rigaudi Richard, 1894
Alona sp.
Leydigia propinqua Sars, 1903, *ciliata* Gauthier,
  1939
Macrothrix spinosa King, 1853
Latonopsis australis Sars, 1888
Diaphanosoma sarsi Richard, 1895

(iv) *Anostraca*

Streptocephalus proboscideus (Frauenfeld), 1873

(v) *Copepoda*

Onychocamptus bengalensis (Sewell), 1934
Cletocamptus confluens (Schmeil), 1894, *meridionalis* Kiefer, 1929
Metis holothuriae (Edwards), 1891
Mesocyclops leuckarti (Claus), 1857, *pilosa* Kiefer, 1930
Psammocyclops excellens Kiefer, 1955
Microcyclops cf. *dengizicus* (Lepeschkin), 1900
(plus harpacticoid spp. sent to J. B. J. Wells)

(vi) *Cirripedia*

See list in Taylor, this volume, p. 173

(*b*) *Taxonomic notes*

(i) Centrocypris horrida (*see figure* 2, *plate* 19)

Following his description of *Centrocypris margaritifera*, Müller says, '...From Aldabra came one shell of a species which undoubtedly belongs to this genus but I am unwilling, for this one-shell, to establish a new species' (translated from Müller 1898, p. 281).

The puzzling feature of this comment is that Müller considered his shell to belong in a new species. All the material which I have examined from Aldabra, wild as well as cultured, belongs quite definitely to *Centrocypris horrida*, the type species of the genus described by Vávra (1895, p. 16) in a paper of which Müller was well aware since he refers to it earlier (Vávra 1895, p. 279). Possibly, the armature on Müller's specimen was worn to such an extent that he was unable to identify it with Vávra's species.

The taxonomic position at the tribal level of *Centrocypris* has not been certain hitherto (Hartmann 1963, p. 132). I believe it may belong to the Notodromadini on these grounds:

(1) It has a similar habit of life, including the ability to swim actively upside down on the meniscus of the pools it inhabits.

(2) The general shape, colour and consistency of its shell are typical of such accepted Notodromadini as the Australasian genus *Newnhamia*, especially in such features as the flat, broad ridged ventral keel and the shell armature.

(3) The antennae are six-jointed with long natatory bristles.

(4) There are five Zahnborsten on the third lobe of both maxillules.

Centrocypris differs from other Notodromadini: first in that its maxillae do not lack epipods, instead small but distinct epipods with six Strahlen occur on both males and females; secondly it carries an anterior setule on the furca; thirdly, other Notodromadini have six Zahnborsten on the third lobes of their maxillules. Hartmann's diagnosis for the Notodromadini (1963, p. 129) thus needs to be expanded significantly to accommodate Vávra's genus.

Description of plate 19

Figure 2

(*a*) *Plesiocypridopsis newtoni* from Hickling Broad, Norfolk (B.M. Reg. No. 1969), lateral view right valve (magn × 100).
(*b*) Same specimen as (*a*), posterior detail (magn × 200).
(*c*) *Plesiocypridopsis aldabrae* culture specimen (B.M. Reg. No. 1969), lateral view right valve (magn × 100).
(*d*) Same specimen as (*c*), posterior detail (magn × 200).
(*e*) *Plesiocypridopsis aldabrae* sample 63 (B.M. Reg. no. 1969), posterior detail lateral view right valve (magn × 200).
(*f*) *Centrocypris horrida*, sample 106, lateral view left valve (magn × 33).
(*g*) *Centrocypris horrida*, sample 106, ventral view right valve (magn × 33).
(*h*) *Centrocypris horrida*, sample 106 (B.M. Reg. no. 1969), dorsal view (magn × 33).

All specimens photographed at the Cambridge Stereoscan unit of the Department of Zoology, British Museum (Natural History).

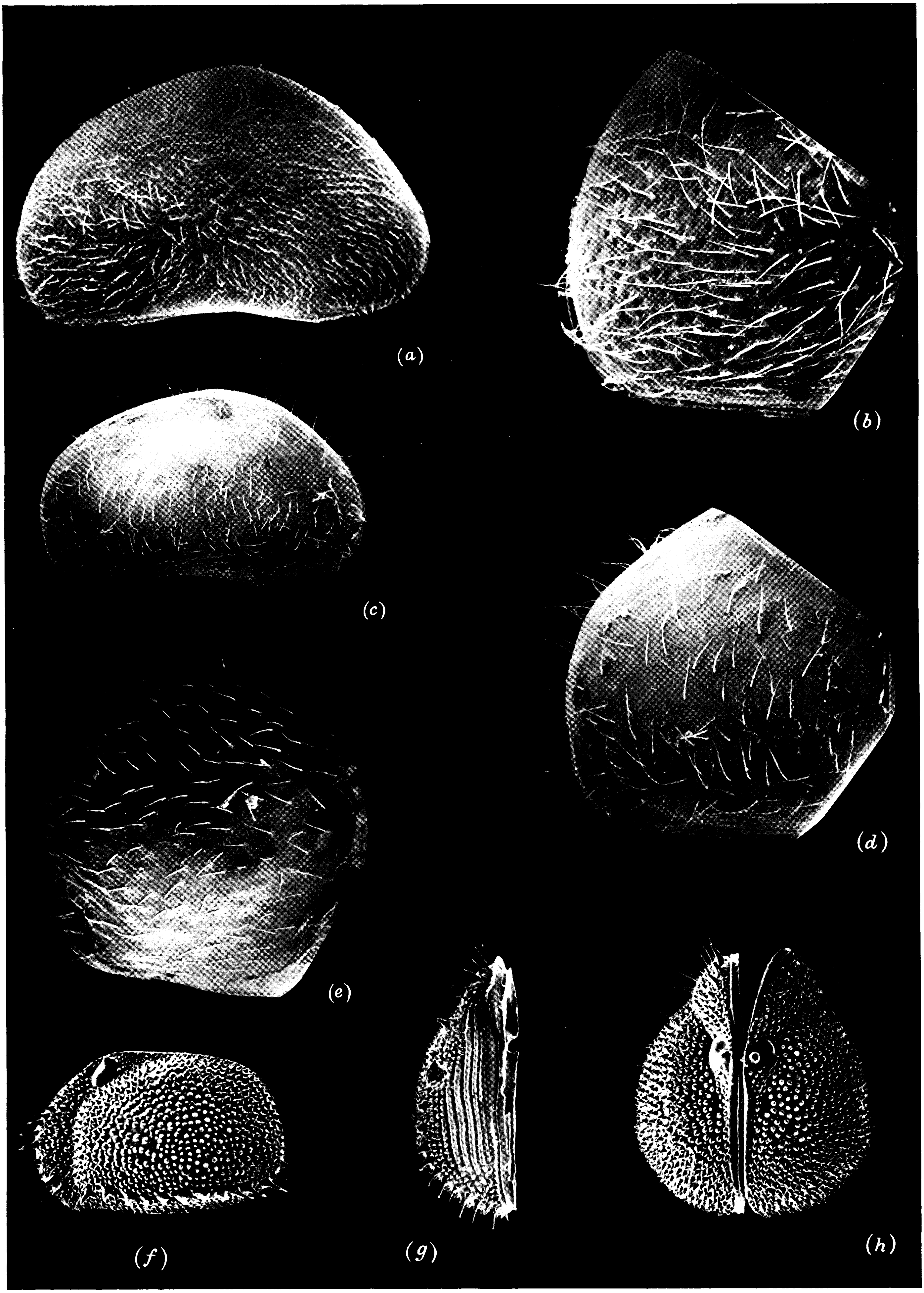

FIGURE 2. For legend see facing page.

(ii) Plesiocypridopsis aldabrae

Many authors have synonymized this species with the English species, *P. newtoni* (Brady, Robertson & Brady 1870) which is also the type species of *Plesiocypridopsis* (Müller 1912, p. 208; Klie 1944, p. 35; Bronstein 1947, p. 158; Rome 1965, p. 50). The 'types' of *P. newtoni* came to the British Museum (Natural History) with the Norman Collection and are registered under no. 1911.11.8, M. 2894. But all that remain on the 'type' slide from Whittlesea Mere are the greenish fragments of part of one valve. Pending the collection of a neotype from the 'Rivers Nene and Cam, and dikes on the site of Whittlesea Mere' (Brady *et al.* 1870, p. 14), material in the spirit collection from Hickling Broad, Norfolk, and from Cheddar, Somerset, has been looked at, as well as specimens in the dry mount slide collection from Loch Ruter, Kircudbrightshire. There is only one male in this material and its penis is missing, a most unfortunate condition. Nevertheless, the following divergences of shell characters between *P. newtoni* and *P. aldabrae* were noted.

(1) *Size. P. aldabrae*; ♂s 0.62 to 0.7 mm, ♀s 0.5 to 0.72 mm; *P. newtoni*: ♂ 0.89 mm, ♀s 0.78 to 0.83 mm.

(2) *Shape*. The left valve of *P. newtoni* is much more obliquely truncate postero-dorsally than is the left valve of *P. aldabrae*.

(3) *Ornament*. The surface punctation on the shell of *P. newtoni* differs from that of *P. aldabrae* (see figure 2, plate 19).

The synonymies noted above, therefore, are not accepted. This means that nothing can be known with certainty about the zoogeography of *P. aldabrae* until all the records of *P. newtoni* have been carefully rechecked.

(iii) Eulimnadia *cf.* mauritiana

This conchostracan was not found during phase III, although it had been observed in great abundance at the margins of pool I (3905, 0560) during phase II (J. D. Taylor, personal communication) (see § 7 (*a*)).

Only two specimens are in the British Museum (Natural History) collections and one of these is badly crushed; fortunately, the other is an ovigerous female. Because of this limitation and because conchostracan species are known to vary greatly, the determination was not easy. I listed several characters for all species and doubtful species of *Eulimnadia* given in the *Zoological Record* and eventually ran down the Aldabra form to *E. mauritiana* and to *E. margaretae* (Bond 1934). The number of growth lines on the Aldabra shell appear to be two or possibly three as recorded for *E. margaretae* whereas shell size and characters of the 'soft parts' anatomy, such as the number of spines on a telson lamina and the dorsodistal armature of trunk segments are close to the descriptions of *E. mauritiana* (Daday 1925, p. 535; Bond 1934, p. 56).

(iv) Streptocephalus proboscideus

The abundant material from Aldabra matches very closely the descriptions given by Daday (1910, p. 395) and Barnard (1929, p. 223) in both adult and juvenile characters. The only difference is that the largest adult male on Aldabra, at 12.8 mm, is slightly smaller than the 13 to 29 mm range quoted by Barnard for males of this species.

(v) Moina dubia pectinata

The Aldabra specimens agree very closely with Gauthier's type description (Gauthier 1955, p. 38). Lately, Goulden (1968, p. 59) has placed *M. dubia pectinata* in synonymy with *M. hartwigi* Weltner, 1898, apparently on the basis of a single character: both have ungrouped setae on the posterior shell rim. In our specimens these setae could be considered ungrouped or weakly grouped and there are no intercalated larger setae. Concerning this character Gauthier wrote: 'The ciliation of the posterior margin generally consists of subequal setae, without intercalated setae of larger size....But I have not examined, in this regard, a sufficient number of specimens to be able to pronounce that it is a constant character in *pectinata*' (Gauthier 1955, p. 41).

FIGURE 3. Distribution of Anostraca on Aldabra. Closed circles = *Streptocephalus proboscideus*.

Since Goulden did not examine any material of *M. dubia pectinata* his synonymization of Gauthier's subspecies with *M. hartwigi* is unsupported by a direct comparison between the two forms. Further, the characters given by Goulden in his diagnosis of *hartwigi* are all, with one exception (the character noted above) common to *M. dubia dubia*, *M. hartwigi* and *M. dubia pectinata*. Goulden does not state in his diagnosis if the claw pecten in *hartwigi* is as well developed as it is in *dubia pectinata*. Weltner's original figure (see Goulden 1968, p. 59) indicates that it may not be. Finally, the type description of *hartwigi* by Weltner (given in Goulden 1968, pp. 59–60) states that the postabdominal claw has 3 to 5 dorsal spines and 12 to 15 spines on the claw pecten. Gauthier's illustrations (1955, plates 22 to 24) show 5 to 8 dorsal spines and 13 to 19 spines on a strongly developed claw pecten (the feature which gives *pectinata* its name).

For these reasons, Goulden's synonymy is not accepted, although the forms *dubia dubia*, *hartwigi* and *dubia pectinata* are evidently closely related.

(vi) Mesocyclops leuckarti pilosa

As noted by Gurney (1933, p. 289) Kiefer's form *pilosa* is the only *M. leuckarti* in which the inner margins of the furcal rami are pilose. All the Aldabra specimens we checked had this character although in one specimen it was only weakly developed. Kiefer's brief note on his new form (1930, p. 45) gives no other details on *pilosa*.

We compared (under oil immersion) the membrane of the 17th antennular segment on our dissected Aldabra specimens with Gurney's illustrations (1933, p. 288) and found that on this character most Aldabra individuals were closest to specimens from Victoria Nyanza.

(vii) Cletocamptus confluens meridionalis

Our dissections of this form showed that it had the characters on which Kiefer established the subspecies (Kiefer 1929, p. 325; 1934, p. 142). On the basis of other evidence (including Gurney 1927, p. 563) Lang (1948, p. 1278) does not accept Kiefer's form as a valid subspecies. The bibliography given in Lang indicates, however, that Kiefer's form is zoogeographically valid and on this ground the subspecific name is retained here.

6. Zoogeography

(a) *Distribution of major groups*

Table 4 gives the zoogeography of 25 species of Aldabra entomostracans, including two which are salt-tolerant, and indicates the wide distribution of four Aldabra cladocerans and of the harpacticoid copepod *Metis holothuriae* (see also Wells 1967, p. 355). Excluding these widespread species and ignoring the questionable records from other subregions of *Heterocypris symmetricus* (Furtos 1936, p. 104) and *Cypris decaryi* (Gauthier 1939, p. 194), 20 species remain of which the taxonomy of one is not yet known and the zoogeography of another requires restudy on taxonomic grounds. Thus, the original list breaks down to fourteen defined species and four tentatively defined species which appear to be zoogeographically sensitive. These species comprise nine Ostracoda, five Copepoda, two Cladocera, one Conchostraca and one Anostraca; of which nine are Malagasy, ten East African, four Indian, two Mediterranean, one Australian and one Indo-Malayan species. Neglecting doubtful records, the provenance of five species is Madagascar, of two species is East Africa, of two species is India, and of one species is Indo-Malaya—at the present state of knowledge.

A second technique for deciding on the zoogeographic affinities of the Aldabra fauna involves studying the distributions on Aldabra of the forms concerned. This is done for four groups in figures 3 to 6—conchostracans were not collected during phase III. The distribution of genera not included in these figures (notably *Heterocypris*) is given in § 4 (*c*). Figures 4 to 6 show a preponderance of records in the southeast of South Island but only isolated records elsewhere on the atoll.

(b) *Conclusions*

The initial conclusion from figures 3 to 6 and § 4 (*c*) is that most Aldabra freshwater Entomostraca originated in the Malagasy subregion, whence they could have dispersed to Aldabra via the dry season southeasterlies. The conclusion is consistent with provenance data extracted from table 4 and is further supported when this data is considered with regard to the total known faunas of the East African, Malagasy, Indian and Indo-Malayan subregions, The relevant percentages for Ostracoda are given in table 5.

Nevertheless, in terms of numbers of species, there are significant East African and Indian elements in the Aldabra fauna as table 4 also makes clear and, as noted, at least one species has an Indo-Malayan provenance.

The dispersal of non-Malagasy forms to Aldabra could be effected from East Africa by birds and monsoonal winds during summer and from India and Indo-Malaya by storm-driven birds and occasional cyclones. Their subsequent concentration at southeast South Island (the area nearest to Madagascar) may be explained by the occurrence there of permanent freshwater reservoirs (see figure 1) for which they became (by inference) preferentially adapted.

These facts indicate that the initial conclusion must be used with some caution. Further caution becomes necessary when the effect of man on Aldabra is considered.

According to Voeltzkow (1897, p. 40) the first European record of Aldabra was in 1511; but man's knowledge of the atoll is likely to have predated this, perhaps by several centuries. The evidence that some Entomostraca have been introduced to Aldabra by human agencies

TABLE 4. SUBREGIONAL ZOOGEOGRAPHY OF SOME ALDABRA ENTOMOSTRACA

species	1	2	3	4	5	6	7	8	9	10
Ostracoda										
Heterocypris giesbrechti	—	? ×	—	—	—	—	—	—	—	—
H. symmetricus	—	×	—	×	—	—	—	—	—	? ×
Cypris decaryi	—	×	—	×	—	—	—	—	—	? ×
Centrocypris horrida	—	×	—	—	×	—	—	—	—	—
Strandesia vavrai	? ×	—	—	× *	—	—	—	—	—	—
Parastenocypris aldabrae	—	×	—	×	—	—	—	—	—	—
Zonocypris cf. *madagascarensis*	—	—	—	× *	—	—	—	—	—	—
Plesiocypridopsis aldabrae				see § 5 (*b*) iii						
Cypretta cf. *fontinalis*	—	—	—	—	× *	—	—	—	—	—
Limnocythere notodonta	—	—	—	—	—	—	× *	—	—	—
Conchostraca										
Eulimnadia cf. *mauritiana*	—	? ×	—	× *	—	—	—	—	—	—
Cladocera										
Moina dubia pectinata	—	—	—	× *	—	—	—	—	—	—
Ceriodaphnia rigaudi	×	×	×	×	—	—	×	—	×	×
Alona sp.				not known						
Leydigia propinqua ciliata	—	× *	—	—	—	—	—	—	—	—
Macrothrix spinosa	—	—	×	—	—	—	? ×	—	×	×
Latonopsis australis	—	×	×	—	—	—	×	×	×	×
Diaphanosoma sarsi	? ×	×	—	—	—	×	×	×	—	×
Anostraca										
Streptocephalus proboscideus	—	× *	—	—	—	—	—	—	—	—
Copepoda										
Onychocamptus bengalensis	—	—	—	—	× *	—	—	—	—	—
Cletocamptus confluens meridionalis	—	×	—	—	—	—	—	—	×	—
Metis holothuriae	×	×	—	—	—	×	×	×	—	×
Mesocyclops leuckarti pilosa	—	×	—	×	—	—	—	—	—	—
Psammocyclops excellens	—	—	—	× *	—	—	—	—	—	—
Microcyclops cf. *dengizicus*	×	—	—	—	×	—	—	—	—	×

1, Mediterranean; 2, East African; 3, South African; 4, Malagasy; 5, Indian; 6, Ceylonese; 7, Indo-Malayan; , Austro-Malayan; 9, Australian; 10, other subregions; * species exclusive to subregions concerned apart from their occurrence on Aldabra (neglecting doubtful records).

TABLE 5. PERCENTAGES OF TOTAL KNOWN FAUNAS OF ZOOGEOGRAPHIC SUBREGIONS OCCURRING ON ALDABRA

subregion	total known fauna	*Aldabra* spp.	*Aldabra*, % of total
East Africa	about 225	0 (5)	0 (< 2.5)
Madagascar	about 25	2 (5)	about 8 (20)
India	about 55	1 (2)	about 2 (4)
Indo-Malaya	about 75	1 (1)	about 1 (1)

Figures outside parentheses refer to Aldabra species otherwise exclusive to provenance indicated; figures inside parentheses refer to total Aldabra species associated with provenance indicated.

depends on the fact that a few species occur only in waterholes used by man and not readily accessible to colonization by winds or birds because they are usually covered over. The likely representatives in this category are: (1) *Strandesia vavrai* (only recorded in Wilson's Well (sample 49) and a small partly covered rockhole (sample 106 near pool II)); (2) *Ceriodaphnia rigaudi* (Wilson's Well and a covered rockhole (sample 7) near Anse Cèdres); (3) *Psammocyclops* excellens (two waterholes, one of them covered (samples 77, 78), on either side of the N–S trail behind the beach at Passe Gionnet). A fourth species which may have been introduced by man is *Cypretta* cf. *fontinalis* which occurs only in a rainwater catchment at the Settlement but an alternative explanation for this occurrence is that the species, which has Indian affinities, arrived during a cyclonic downpour. Their limited known distribution, apart from helping to document human interference on Aldabra also indicates that these species may have been introduced

Figure 4. Distribution of some copepod genera on Aldabra. Closed circles = *Cletocamptus*; open circles = *Mesocyclops*; closed triangle = *Psammocyclops*; closed squares = *Onychocamptus*.

Figure 5. Distribution of some cladoceran genera on Aldabra. Closed circles = *Ceriodaphnia*; open circles = *Macrothrix*; closed triangles = *Moina*; open triangles = *Latonopsis*; closed squares = *Diaphanosoma*; open square = *Leydigia*.

rather recently, perhaps only since the period of more or less permanent occupancy which began in 1888. But it may well be that other species now more widespread on the atoll were introduced in a similar way much earlier.

Figure 6. Distribution of ostracode genera, except *Heterocypris*, on Aldabra. Closed circles = *Centrocypris*; open circles = *Cypris*; closed triangles = *Limnocythere*; open triangle = *Parastenocypris*; closed squares = *Strandesia*; open square = *Cypretta*; half-closed circle = *Zonocypris*.

7. NICHE UTILIZATION

The niches available on islands are limited. It is important, therefore, to understand the variety of mechanisms by which they are occupied spatially and in time.

(*a*) *Staggered life cycles*

Some information on this aspect became available during phase III. The immediately obvious fact about the entomostracan faunas which I collected was that they included no conchostracans although it was known that a species had been cultured successfully by C. A. Wright from dried mud collected during the 1966 reconnaissance. It is possible that January and February 1968 were so dry that Conchostraca were unable to develop but, alternatively, they may well flourish on Aldabra during a different season. Evidence for this alternative is the observation by J. D. Taylor reported earlier (see § 5 (*b*) iii).

Another species, the life cycle of which may be staggered relative to those of wet season faunas is the ostracode *Zonocypris* cf. *madagascarensis*. Only one empty shell of this species was collected at pool III (3895, 0580)—hence the tentative identification. Possibly it is more frequent on Aldabra during the dry season when competition, e.g. with the related species *Plesiocypridopsis aldabrae*, may be less intense.

There are also several records of appearances and absences of species at the same localities when these were visited on different occasions. For example, on 5 January a very small temporary rainwater pool a few metres southeast of Croix Blanc had a fauna of anostracans, ostracodes (*Plesiocypridopsis*) and mosquito larvae, but the anostracans were absent on 22 March when the pool was rechecked. Similarly, several small rainwater pools near Settlement contained anostracans when they were collected on 8 and 9 March (samples 95, 99, 100) but the anostracans had disappeared when they were rechecked on 29 March. In these instances, environmental factors very probably caused the absences recorded. Thus, the pool near Croix Blanc was dry on 20 January and the surfaces of the pools near Settlement were scummed over by algae on 29 March, although they had been clear about three weeks previously.

In other cases, staggering of life cycles seems the probable explanation for such observations. For example, anostracans were not observed in the temporary pools around Cinq Cases during January, although they were known to occur elsewhere at this time, e.g. near Croix Blanc, but were common in temporary pools around Cinq Cases during March (see table 3). Further, *Parastenocypris aldabrae* was collected at pool III on 12 January but was not found at pool II nearby on 24 January, whereas in March this situation was reversed. For large pools such as pool II and pool III it might be argued that a rarely occurring species like *Parastenocypris aldabrae* could be missed during collection but this objection cannot be applied to the results from temporary pools.

(*b*) *Tiered communities*

The most diverse fauna sampled on Aldabra during phase III came from pool III (see appendix B, samples 3 to 5). In all, 10 entomostracans were collected here but field observations were made only on some Ostracoda. Of the six ostracode species: *Parastenocypris aldabrae* was found at the pool's edge crawling slowly over the substrate but not swimming; *Heterocypris giesbrechti* was plentiful on the substrate farther within the pool, grubbed actively into it but also had bursts of swimming in the water column; *Plesiocypridopsis aldabrae* occupied mostly the water column and phytobenthos where it was seen swimming actively and more continuously than *Heterocypris*. When the samples were picked in the laboratory, *Limnocythere notodonta* was identified. From field and laboratory observations on another freshwater cytherid (McKenzie, in press) it is probable that *Limnocythere* has an endobenthic niche on Aldabra emerging during part of the day. Finally, although it was not collected at pool III, *Centrocypris horrida* was observed elsewhere to occupy the lower surface of pools (for its characteristic habit see § 5 (*b*) i). This picture naturally becomes more complicated as other ostracodes, the cladocerans and the copepod are set into their niches but, even as it is, serves to illustrate spatial utilization during the summer wet season of the permanent reservoir niche on Aldabra. Less complex tiered communities, as far as entomostracans are concerned anyway, characterize the temporary pools.

(*c*) *Tolerant species*

The capacity of some species to colonize more than one niche category is an obvious factor bearing on the efficiency of niche utilization on Aldabra. Significant species in this respect are listed elsewhere (§ 4 (*c*) vi).

(*d*) *Opportunism*

Efficiency in colonizing new environments as these become available is a valid means of testing opportunism as a mechanism of niche utilization. Unfortunately, it was not possible to determine which of the temporary pools examined were new environments for one or more elements of the faunas observed. With this qualification, the data in table 3 indicate that *Heterocypris symmetricus* was more opportunistic than *Streptocephalus proboscideus* which was more opportunistic than *Moina dubia pectinata*, at the time observations were made. It is emphasized that only forms which are fit for newly available niches can take up the extra space which these afford.

Another way in which species can behave opportunistically in temporary niches is either by condensing their entire life cycles into the period for which the niche is available or by 'resting' over an unfavourable period, e.g. when a temporary pool dries, and continuing their development when it is refilled by the next rains. One or both of these mechanisms certainly operate on Aldabra. For example, on 14 February I collected a very small temporary pool (sample 56) about 210 m south of Wilson's Well the observed fauna of which consisted of insects (water boatmen and aquatic beetles) and ostracodes. There were numerous adult ostracodes in the pool, so many that it is not conceivable that they all could have been ferried there as adults by the insects in the pool although one or two might have been. Either they developed from egg to adult in this pool within the 10 days since the rain of 5 February (table 2) when it was formed again or else their development had halted at a late stage as the pool dried in Janaury but continued to adulthood after the February rain. Similarly, mature *Streptocephalus* were collected on 16 March near Anse Badamier, Middle Island (sample 103) from a pool which on the rainfall data was probably dry for most of February; and mature *Streptocephalus* were observed on 13 March in a very small temporary pool south of Wilson's Well from which juveniles only had been collected earlier on 8 February (sample 45), but which had dried by 14 February.

8. *HETEROCYPRIS* SPP. (OSTRACODA)

(*a*) *Introduction*

Ostracoda predominated quantitatively as well as qualitatively during phase III. A second point to be emphasized is that, whereas for the other freshwater groups genera on Aldabra are monospecific, in the Ostracoda one genus, *Heterocypris*, is represented by two species. Generally, these two species occupy different niches on Aldabra (see § 4 (*c*) i and ii) and it is the relations between them which form the main record of this part of the paper once data from the culture have been presented.

(*b*) *Culture notes*

The culture, initiated on 5 December 1967, has been observed regularly since 25 September 1968. The community which has developed so far is: *Heterocypris giesbrechti*, *Plesiocypridopsis aldabrae*, *Cypris decaryi*, *Centrocypris horrida*, *Ceriodaphnia rigaudi* and *Alona* sp. *Macrothrix spinosa*, which was collected in the field at the locality from which culture was reared (sample 8), has yet to appear in the aquarium but this blank is more than offset by the records of *Cypris decaryi*, *Ceriodaphnia rigaudi* and *Alona* sp. which were not collected in the field during phase III.

Ceriodaphnia rigaudi was the first species to appear in the culture between mid-December 1967 and mid-April 1968 (R. L. Sayers, personal communication), but has not been observed since. *Cypris decaryi* and *Centrocypris horrida* are known only from a few juveniles and discontinuous records. *Cypris decaryi* first appeared in the culture between mid-December 1967 and mid-April 1968 but did not last long (R. L. Sayers, personal communication). At its second appearance on 3 January 1969 two juveniles were seen and measured (1.25 and 1.3 mm). On 17 February 1969 another juvenile was measured (1.18 mm). There are no subsequent records for the species. *Centrocypris horrida* was first recorded on 16 October 1968 when three juveniles appeared in the aquarium. This group persisted until 9 December when the lone survivor, still immature, measured 1.27 mm. On 6 January 1969 two more juveniles appeared and were measured (0.68 and 0.52 mm). The only subsequent record of *C. horrida* came on 8 April 1969 when a single juvenile measuring 0.61 mm was seen. The three other species have all been persistent and relatively abundant in the aquarium, with *Plesiocypridopsis aldabrae* the dominant among them. *Diaphanosoma sarsi* appeared in the culture on 13 May 1969 (not entered in appendix B).

Particular attention was paid to the ostracodes *Heterocypris giesbrechti* and *Plesiocypridopsis aldabrae*, both of which became well established by September 1968 after some months of dormancy. Their respective colour patterns and behaviour were recorded on 16 October 1968 as follows:

(1) *Heterocypris giesbrechti*—eye red, ovaries green, eggs orange-red to scarlet, digestive system green. Carapace with some greenish markings but generally yellowish in adult females and brownish yellow in mature males;

(2) *Plesiocypridopsis aldabrae*—eye brownish red, eggs orange-red, digestive system dark green. Carapace hirsute, yellowish green in adult females, brighter green in mature males except in the eye region where it is yellowish.

Both species copulated actively during this observation period.

By 12 November, *Heterocypris* females and males became more yellowish orange throughout the whole body and the greenish markings on the valves appeared rather indistinct against this darker background. The males were now much less active and greatly outnumbered by the females but some copulation still took place. Mature females, although also less active, still mostly carried eggs in their brood sacs. Newly hatched juveniles were fewer than in October but still quite common and later instars also occurred.

Some mature females of *Plesiocypridopsis aldabrae* were rather more orange than in October and most carried eggs in their brood sacs. Males were sexually active. (*Plesiocypridopsis* lacks a powerful furca and during copulation males clasp females further up the shell than happens in *Heterocypris* which has a well-developed furca.) This species appeared to be increasing in numbers and many juveniles were present.

In December 1968 mature males of *Heterocypris* seemed to have disappeared and the species as a whole was much less numerous than previously. It was also less active although there were attempts at copulation by immature males. But sexual activity in *Plesiocypridopsis aldabrae* remained unabated, although numbers were down.

On 9 January 1969 a brief resurgence in numbers was noted but both species were much paler with some mature individuals of *P. aldabrae* almost transparent. Sexual activity was very low in *Heterocypris* but still notable in *Plesiocypridopsis*. Numbers have been very low since. Specimens of *Plesiocypridopsis* were becoming greenish again by mid-April 1969.

The culture was sampled at monthly intervals to determine size variation in *Heterocypris* over the 8 months of observations and to provide a standard against which field collections could be compared. The following samples were taken:

(1)	On 25 September 1968	25 mature males and 25 ovigerous females
(2)	On 16 October 1968	16 mature males and 25 ovigerous females
(3)	On 12 November 1968	25 ovigerous females only
(4)	In December 1968	25 mostly ovigerous females only
(5)	On 9 January 1969	45 mature males and 35 mostly ovigerous females
(6)	On 21 February 1969	no collection because of lack of numbers, one ovigerous female measured
(7)	On 19 March 1969	1 mature male and 10 mature females
(8)	On 8 and 25 April 1969	some ovigerous females and one mature male measured, no collection because of lack of numbers

The length of every sampled specimen was measured and these results are recorded in figure 6 which shows that the size of mature *Heterocypris giesbrechti* (both sexes) peaked in October 1968, when the population was largest and in its most vigorous condition, but has declined since. In the field, the size ranges of this species are in very good agreement with the culture ranges (table 6). But Wise (1960, p. 384) has published results indicating differences in size between field and laboratory populations of a species, 'collected from a vernal pond in the spring of 1958 as the pond was nearing the time of complete evaporation.' The significant factor here may be that the American species studied by Wise was adapted to temporary environments whereas *H. giesbrechti* inhabits a permanent natural environment. The reasonable inference is that forms which live naturally under stress conditions might show a size difference under the stable conditions of a culture but forms from relatively stable natural environments might not exhibit such size differences when cultured.

Table 6 also shows that the size ranges at different Aldabra localities vary over the entire seasonal range of cultured animals which may be additional evidence for a staggering of life cycles in the freshwater reservoir areas (see § 7(*a*)).

TABLE 6. SIZE RANGES OF FIELD POPULATIONS OF *HETEROCYPRIS GIESBRECHTI*

sample number	female size/mm		number measured	male size/mm		number measured
	mean	range		mean	range	
1, 2	1.00	0.96–1.04	15	0.84	0.80–0.86	15
3, 4, 5	0.94	0.91–0.96	4	0.82	0.80–0.89	6
10	1.00	0.94–1.04	11	0.85	0.83–0.89	3
11	1.00	0.96–1.08	12	—	—	nil
16	0.93	0.89–0.99	12	0.79	0.76–0.80	3
19	0.95	0.88–1.00	17	0.82	0.80–0.84	9
20	0.95	0.88–1.05	5	—	—	nil
22	0.97	0.92–1.02	8	0.80	0.76–0.84	3
38	0.96	0.92–0.99	8	0.85	0.84–0.86	3
39	0.97	0.92–1.02	9	0.81	0.78–0.84	3
*105	1.00	0.96–1.08	10	0.83	0.83–0.84	8
43	0.97	0.90–1.02	7	0.80	0.77–0.82	5
44	0.92	0.92	1	0.84	0.84	1
46	1.02	0.99–1.05	9	0.85	0.83–0.88	3
47	0.97	0.92–1.02	6	0.88	0.88	1
48	0.97	0.94–0.99	7	0.82	0.81–0.84	5
*107	0.92	0.92	1	—	—	nil
*95	—	—	—	0.83	0.83	1
*99	1.07	1.07	1	—	—	nil
*74	0.92	0.92	1	0.88	0.86–0.89	2
*75	1.00	1.00	1	0.88	0.88	1
*76	1.07	1.05–1.08	2	0.89	0.89	1
77	1.09	1.05–1.14	3	0.83	0.83	1
*78	0.98	0.96–0.99	2	—	—	nil

* Localities of sympatry with *H. symmetricus*.

(*c*) *Differentiating species characters*

(i) *Qualitative characters*

Heterocypris giesbrechti and *H. symmetricus* are easily separated on qualitative characters alone. For instance, their respective colour patterns are quite different. The range of colour patterns in cultured *H. giesbrechti* has been described in the preceding subsection and similar colour patterns were found in the field collections (e.g. sample 16, pool II; 3895, 0560).

The most striking colour pattern for *H. symmetricus* was displayed by the individuals in sample 102 (3345, 0595). In these, the shells were orange-brown all over and the digestive systems were black. In other samples the shells were brownish or dark brown and soft parts also had a brownish tinge. As far as I know, the species has not been cultured. Sometimes (e.g. samples 64, 65, 66 and 67), *H. symmetricus* was whitish (see § 8(*e*) ii).

In general shape the two species are similar except that *H. symmetricus* seems consistently to be relatively higher with respect to its length than *H. giesbrechti* (Müller 1898, pl. 15, figs. 8, 9, 14, 15).

Some striking differences in soft part characters are found in the Zenkers organs, furcae and penes of the two species. On my data, the number of whorls in the Zenkers organ of *H. symmetricus* ranges between 26 and 37, while in *H. giesbrechti* this range is 16 to 21; Müller (1898, pp. 277, 279) noted 31 whorls and 20 whorls respectively. In *H. symmetricus* the furcal shaft is comparatively more slender and the posterior bristle proportionately shorter with respect to the posterior claw than in *H. giesbrechti* (Müller 1898, pl. 14, fig. 19; pl. 15, fig. 16). The anterior flap of the penis in *H. symmetricus* is narrower and more pointed than in *H. giesbrechti* (Müller 1898, pl. 14, fig. 205; pl. 15, fig. 19).

(ii) *Quantitative characters*

An easily assessed quantitative character is overall size which is considered to be represented effectively by carapace length. The field and culture ranges of carapace length for *H. giesbrechti* have already been given (table 6 and figure 6). Müller (1898 p. 277) noted that the size of *H. symmetricus* was very variable, particularly in males and the phase III data not merely support his observations but show further that this variability is much greater than Müller recorded (table 7). The length ranges given by Müller were: males, 0.95 to 1.25 mm and females, 1.3 to 1.45 mm; my data are: males, 1.00 to 1.48 mm and females, 1.23 to 1.80 mm. Thus, the known length ranges for mature individuals in the two species do not overlap.

Although the last comment is a fact, the absolute maximum length for *H. giesbrechti* and the absolute minimum length for *H. symmetricus* are almost contiguous. The figures are: 0.92 mm (*giesbrechti*) and 0.95 mm (*symmetricus*) for males; and 1.15 mm (*giesbrechti*) and 1.23 mm (*symmetricus*) for females. It was decided, therefore, to compare other characters quantitatively for each species in order to observe whether or not this relation between the two species persisted. Measurable characters, relatable to the functioning of the animals, were selected. These characters were:

(1) Length of the five distal joints of the antennule (A_1) which may be used in swimming, stabilizing or, possibly, sensing.

(2) Length of the antennal (A_2) endopod plus its terminal claws which may be used in crawling, grubbing or clasping.

(3) Length of the 'hand' of the mandible coxa (mand.).

(4) Length of the maxillule (M_1) palp plus its terminal claws, used to pass food forward to the mouth.

(5) Length of the maxilla (M_2) endopod in females, on the assumption that since it is a strongly dimorphic character it has some reproductive singificance.

(6) Length of the next two joints of the walking leg (P_1) distal of the 'knee' which by their length partly determine the step of the leg hence have a locomotive significance;

(7) Length of the next two joints of the cleaning limb (P_2) distal of the 'knee' which by their length partly determine the sweep of the limb hence affect its cleaning function.

(8) Length of the shaft of the furca (F) which may be used to assist actual or attempted copulation.

On the above grounds, such selected characters are termed function-related characters. Although some of them are of multi-purpose type this does not affect adversely their usefulness either for the aim noted earlier or for comparing the respective efficiency of the two species.

TABLE 7. SIZE RANGES OF FIELD POPULATIONS OF *HETEROCYPRIS SYMMETRICUS*

sample number	female size/mm		number measured	male size/mm		number measured
	mean	range		mean	range	
6	1.66	1.63–1.72	8	1.38	1.32–1.44	4
26	1.42	1.37–1.48	9	1.20	1.14–1.24	3
*105	1.47	1.46–1.50	6	1.19	1.19	1
52	—	—	nil	1.16	1.16	1
54	1.47	1.47	1	1.16	1.15–1.16	2
56	1.44	1.40–1.47	7	1.20	1.16–1.24	3
102	1.45	1.40–1.50	6	1.15	1.13–1.18	3
57	1.64	1.63–1.66	4	1.32	1.32	2
58	1.41	1.28–1.56	8	1.10	1.07–1.16	4
59	1.34	1.30–1.44	9	1.23	1.21–1.24	3
60	1.55	1.47–1.60	7	1.24	1.18–1.31	3
61	1.59	1.53–1.63	9	1.23	1.08–1.31	3
63	1.55	1.44–1.63	14	1.27	1.21–1.36	8
64	1.47	1.44–1.50	2	1.34	1.34	1
65	—	—	nil	1.17	1.16–1.18	2
66	1.53	1.50–1.63	8	1.29	1.28–1.31	4
67	1.58	1.58	1	1.21	1.18–1.24	2
68	1.40	1.34–1.50	11	1.13	1.05–1.18	9
69	1.75	1.71–1.80	5	1.42	1.40–1.44	2
*107	1.38	1.34–1.42	6	1.13	1.12–1.15	3
70	1.71	1.67–1.75	3	1.42	1.35–1.48	24
94	1.40	1.34–1.47	25	1.11	1.07–1.20	25
*95	1.32	1.23–1.42	10	1.09	1.00–1.18	10
96	1.30	1.23–1.35	16	1.06	1.02–1.12	15
98	1.44	1.44	1	1.23	1.18–1.29	3
*99	1.33	1.28–1.40	9	1.11	1.08–1.15	6
100	1.56	1.56	1	1.24	1.24	1
101	1.62	1.56–1.69	21	1.31	1.20–1.35	12
80	1.47	1.47	1	1.08	1.08	1
*74	1.40	1.40	1	1.24	1.24	1
*75	1.55	1.53–1.56	3	—	—	nil
*76	1.62	1.60–1.63	4	—	—	nil
*78	1.35	1.30–1.40	9	1.12	1.05–1.18	6
103	1.48	1.34–1.58	5	1.17	1.17	1
104	1.44	1.39–1.48	20	1.19	1.13–1.24	20

* Localities of sympatry with *H. giesbrechti*.

Table 8 gives the results. The measurement means are recorded as percentages of mean carapace lengths because carapace length is considered to be representative of the total ostracode organization since in Ostracoda the shell completely encloses the soft body. Figure 8 illustrates the range of the means for each character in both sexes of the two species and indicates that on the average the antennal character (A_2) is proportionately better developed in both sexes of *H. symmetricus*, whereas the female maxilla endopod (M_2) is proportionately better developed in *H. giesbrechti*. But it is apparent that the two species in terms of all the characters measured are about equally efficient.

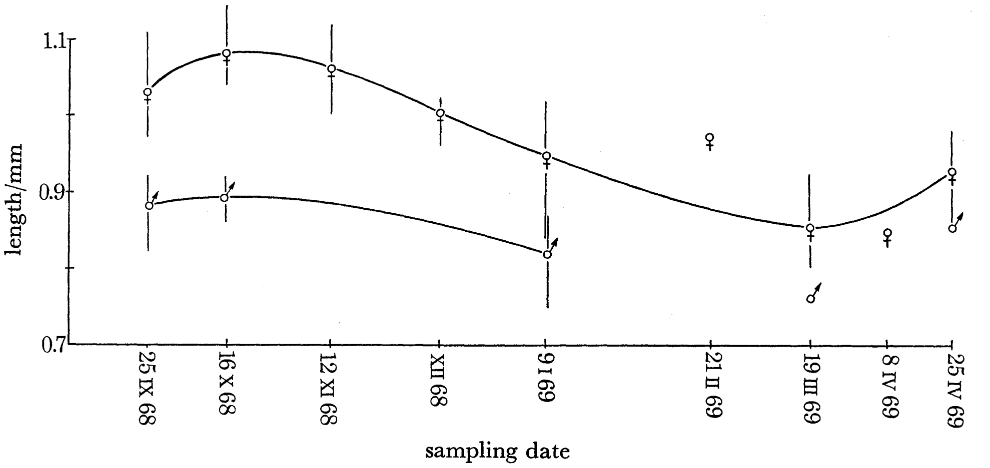

Figure 7. Size variation in both sexes of culture *Heterocypris giesbrechti* between September 1968 and April 1969. Sex symbols are on the means.

Table 8. Means of function-related characters in both sexes of *Heterocypris giesbrechti* and *H. symmetricus* recorded as percentages of mean length

The characters are explained in the text (see §8(*c*) ii).

(1) Females of *Heterocypris giesbrechti*

sample number	number of specimens	A_1	A_2	mand.	M_1	M_2	P_1	P_2	F
culture	95	16.2	19.0	7.3	14.7	11.6	10.6	22.7	19.9
11	12	18.0	20.0	8.0	14.0	12.0	12.0	26.5	23.0
22	9	17.5	19.6	7.7	14.4	11.3	11.3	25.8	22.7
38	9	17.7	19.3	7.3	13.3	10.9	11.5	24.0	20.8
39	9	17.5	19.1	7.2	14.4	11.3	11.3	24.7	22.2
105	1	17.5	19.0	7.5	14.7	11.5	11.5	24.0	21.5
43	7	18.0	19.6	7.7	14.4	11.3	11.3	24.7	22.2
46	9	17.2	19.6	7.8	14.0	11.8	11.8	24.5	22.1
48	7	17.5	19.6	7.7	14.4	11.9	11.3	24.7	22.2
74	1	20.7	20.7	8.4	16.5	13.0	12.0	30.4	23.4

(2) Males of *Heterocypris giesbrechti*

sample number	number of specimens	A_1	A_2	mand.	M_1	P_1	P_2	F	whorls in Zenkers organs
culture	41	17.4	21.3	7.4	13.9	10.7	23.6	20.2	21
11	nil	—	—	—	—	—	—	—	—
22	3	18.1	21.9	8.1	14.5	12.5	26.9	22.5	19
38	3	18.8	22.4	7.6	14.1	11.8	27.1	23.5	20
39	3	17.3	21.6	8.0	14.3	11.7	24.7	21.6	18
105	1	19.3	21.7	8.1	14.5	11.4	25.3	22.9	20
43	5	18.8	21.9	8.1	14.5	11.9	26.3	22.5	18
46	3	18.8	21.2	7.6	13.6	11.8	24.7	23.5	18
48	5	18.3	22.0	7.9	14.1	12.2	25.6	22.0	18
95	1	18.1	21.1	7.8	15.4	11.4	25.3	22.9	18
74	1	19.3	20.5	8.0	13.6	12.5	25.0	22.7	20
76	1	18.0	20.2	7.6	13.9	11.2	24.2	23.0	20

TABLE 8 (*cont.*)

(3) Females of *Heterocypris symmetricus*

sample number	number of specimens	A_1	A_2	mand.	M_1	M_2	P_1	P_2	F
6	8	16.3	22.6	8.2	13.5	9.6	10.2	26.5	20.8
26	11	16.9	24.3	8.2	14.4	9.2	10.6	28.2	21.1
105	1	16.3	23.5	8.7	13.9	9.2	9.9	27.2	20.4
56	11	15.3	21.2	8.3	13.9	10.2	9.8	25.3	20.1
102	3	15.7	21.6	8.0	14.1	9.3	9.3	24.5	19.5
57	4	15.5	22.9	7.3	12.9	9.1	9.8	24.7	20.4
58	8	16.3	22.7	8.2	14.2	10.3	9.9	26.2	21.3
59	9	16.4	23.9	8.4	13.9	9.3	10.8	26.5	20.9
60	7	16.8	22.3	7.5	13.6	9.4	9.7	25.2	21.3
61	9	16.4	22.0	7.5	13.1	8.5	9.7	24.5	18.6
66	8	16.7	23.5	7.8	13.3	8.8	10.5	26.1	20.9
67	1	17.1	24.7	8.4	13.5	9.5	10.8	26.6	21.8
68	11	17.5	21.4	8.6	14.0	9.6	9.6	26.4	21.4
69	5	16.0	21.7	7.3	12.7	9.1	9.7	24.0	20.0
107	1	15.9	22.5	8.1	13.8	10.9	10.1	24.6	21.4
70	3	16.1	22.0	7.3	13.2	8.7	10.0	23.9	19.2
94	7	16.2	21.8	8.0	14.3	10.6	9.5	25.7	20.5
96	1	16.4	21.6	8.1	15.2	10.1	10.1	25.7	20.9
75	3	16.8	22.6	8.0	13.2	8.4	10.3	25.8	19.7
103	5	17.4	22.8	9.3	15.1	11.6	10.4	27.2	20.9
104	8	16.2	23.9	8.1	13.9	9.1	9.8	25.1	19.0

(4) Males of *Heterocypris symmetricus*

sample number	number of specimens	A_1	A_2	mand.	M_1	P_1	P_2	F	whorls in Zenkers organ
6	4	16.6	23.9	8.1	13.8	10.5	27.2	23.9	33
26	4	16.6	24.2	8.1	13.7	10.8	27.5	22.5	31
105	1	16.0	24.8	7.5	13.8	10.1	27.7	22.3	31
56	7	16.5	22.9	8.1	13.3	10.3	25.9	21.5	31
102	2	17.1	24.2	8.3	13.7	10.3	25.8	21.2	28
57	2	19.3	24.2	7.3	12.7	10.2	25.4	22.0	31
58	4	17.3	24.1	8.1	13.6	10.9	27.3	22.7	30
59	3	17.1	24.0	7.9	13.3	10.6	26.4	20.7	30
60	3	17.3	23.4	7.5	13.5	10.5	25.8	22.6	31
61	3	17.4	23.5	7.5	13.3	10.1	25.9	20.3	31
65	2	17.9	24.8	7.6	14.4	11.1	28.2	21.4	—
66	4	17.1	24.8	7.5	13.3	10.5	26.0	20.9	31
67	2	16.5	24.8	8.0	13.9	9.9	27.7	23.1	31
68	9	17.7	23.9	8.6	13.4	10.6	26.5	22.6	31
69	2	16.5	23.6	6.8	12.5	9.5	23.6	21.1	32
106	1	—	—	—	—	—	—	—	31
107	1	17.7	23.9	7.1	14.2	11.5	26.1	22.1	32
70	10	16.5	23.7	7.3	12.8	9.9	23.8	19.7	33
94	7	17.6	23.4	8.0	13.2	10.5	25.7	21.6	29
95	1	17.1	25.9	8.5	14.7	10.5	25.4	21.5	30
96	1	17.3	23.2	8.4	15.1	9.5	25.5	22.7	30
74	1	17.3	25.0	8.1	14.7	10.5	27.0	23.4	26
103	2	19.3	24.0	9.0	15.2	11.5	28.7	22.2	—
104	7	17.5	25.0	8.7	14.1	9.8	25.1	20.8	31

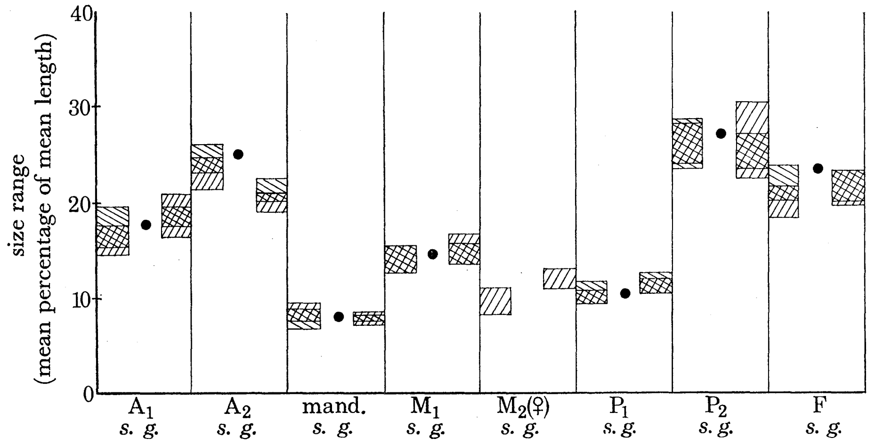

FIGURE 8. Comparison between the ranges of means of function-related characters in both sexes of *H. giesbrechti* and *H. symmetricus*. ▨, males; ▧, females; ●, specimen from sample 74 (see §8(*d*)). *s.*, *H. symmetricus*; *g.*, *H. giesbrechti*. Characters are explained in text (see §8(*c*) ii).

(*d*) *Sympatry*

Tables 6 and 7 show the eight samples in which both *Heterocypris* species occurred and also give the number of mature specimens of each which were collected. Two of the samples came from South Island (Dune d'Messe, Cinq Cases), four from Middle Island (near Camp Gionnet) and one from West Island (near the Settlement).

In three of the four Middle Island samples mature specimens of one sex are lacking and in two of these three, one species is represented by shells only (table 8). In the fourth sample the total number of mature specimens is only five, i.e. only one more than the absolute minimum. In fact, as far as numbers are concerned, only sample 78 had more than ten mature specimens but these did not include mature males of *H. giesbrechti* (tables 6 and 7). It is unlikely that the observed sympatry in the Camp Gionnet area is a contamination effect because: (1) I was careful to clean the net after each sample; (2) the previous sample taken with the net (sample 71) was from a saline lagoon which had been collected four days before I worked near Camp Gionnet.

Samples 99 (West Island) and 107 (Dune d'Messe) each had no mature males of *H. giesbrechti* and only one ovigerous female of this species but contained at least fifteen and nine mature individuals of *H. symmetricus* respectively. In sample 95 only a male of *H. giesbrechti* was found in sympatry with a *symmetricus* population.

It was only in sample 105 (Cinq Cases area, see tables 6 and 7) that adequate numbers of mature individuals of both species were collected. The sample was taken from a small temporary rainwater rockhole, measuring about 40 × 22 cm^2 and about 4 cm deep, located within a few metres of the then western margin of pool II (3895, 0560) and about $\frac{1}{2}$ to 1 m higher than the then level of this pool. The substrate was an organic detritus coated with blue-green algae and there was a clump of dead *Fimbristylis* at one end of the rockhole. The associated fauna consisted of rare anostracans (*Streptocephalus proboscideus*), mosquito and other insect larvae and a land mollusc. The sample contains four species of ostracodes, namely, *Centrocypris horrida*, *Cypris decaryi* and the two *Heterocypris* species. The maximum and minimum air temperatures in the Cinq Cases area for 21 March 1968 (the collection date) were 32 and 25 °C. Salinity and water temperature in this small rockhole were not measured but were recorded for pool II on the next day the result being 3.2‰ at about 33 °C. It is probable that sample 105 was fresher than 3.2‰ and warmer than 33 °C—in this connexion it was noted that faunas of the temporary pools in the Cinq Cases area were active at water temperatures up to about 38 °C (datum from a temporary pool SW of pool III recorded by ordinary thermometer at 16h00 on 20 March 1968; the maximum air temperature, for this day, 33 °C).

This temperature is close to the lethal temperature threshold of 40 °C after prolonged exposure (19 to 24 h) of an American *Streptocephalus* (Moore 1955, p. 9) and to the temperature (about 40 °C) at which an Aldabra *Streptocephalus* died in a test carried out at Dune d'Messe on 25 March 1968 (see also § 8 (*e*) i).

The simplest, and a satisfactory, explanation for the sympatry observed in sample 105 is that *H. symmetricus* invaded by passive dispersal a locality normally colonized by *H. giesbrechti* which became isolated when the margins of pool II retreated during the unusually dry months of January and February 1968. This type of sympatry is of short-term duration and its direction could well be reversed on Aldabra after heavy continuous rains as a result of which the levels of permanent pools may rise until *H. giesbrechti* in turn invades environments normally colonized by *H. symmetricus*. This confrontation between populations of the two species in platin areas has probably persisted as long as they have been on the atoll. It is the more remarkable, therefore, that introgressive forms apparently do not occur.

The other sympatric associations cannot be so explained because the localities are far removed from the permanent reservoir areas. For these the most suitable explanation may be that *H. giesbrechti* was dispersed by chance agencies, such as winds or insect carriers, into environments normally colonized by *H. symmetricus*.

The only specimen which I felt might qualify as an example of introgression between the two species was a mature male in sample 74, from the Camp Gionnet area. The number of whorls on both of the paired Zenkers organs of this male was 26. As in the great majority of specimens (of *H. symmetricus*), excepting sample 94, the lowest number of whorls on any one of the paired Zenkers organs was 28 (in one individual each from samples 58, 95, 102) and since *H. giesbrechti* (number of whorls: 16 to 21) also occurred in sample 74 it seemed worthwhile to test further this peculiar male. Figure 7 gives the results of a test of the specimen's function-related characters and indicates its identity with *H. symmetricus*. The two specimens with 26 whorls from sample 94 tested similarly.

(*e*) *Environmental factors*

(i) *General*

The only ecological factors recorded consistently on Aldabra were salinity and faunal associations (for the latter see appendix B and § 4 (*c*) i and ii). Other results indicated that pH and carbonate content and also organic matter were high in permanent pools.

Temperatures ranged higher in small temporary pools than in large permanent ones (see preceding subsection). Since minimum air temperatures were consistently in the twenties (° C), however, it is not possible that water temperatures were sufficiently high for sufficiently long to be selectively lethal (see also Moore 1955, p. 12).

The temporary environments were invariably shallower and had a much smaller surface area than the permanent pools. The significance of this great difference in size is difficult to assess in view of the records of sympatry but spatial considerations must set an upper limit to the numbers of entomostracans in the temporary pools.

A powerful differentiating ecological factor between the two species is probably the ephemeral nature of environments colonized by *H. symmetricus* and there is evidence that it is adapted for this contingency either by condensing its life cycle or by 'resting' through a dry spell (see § 7(*a*)). Sample 105 indicates that *H. giesbrechti* also has the capacity to survive drying of its environment although evidently it cannot compete in this respect with *H. symmetricus*.

The proper conclusion seems to be that it is the entire complex of ecological factors which determines the fitness of *H. giesbrechti* for a permanent niche on Aldabra and that of *H. symmetricus* for a temporary one. There is, however, a marked distinction between the responses of some *H. symmetricus* and of *H. giesbrechti* generally in regard to salinity and this is treated in the following subsection.

(ii) *Salinity*

Almost undisturbed ecosystems such as Aldabra afford 'natural laboratories' for field experimentation but, as in any laboratory, the experimental conditions need to be selectively controlled. Such a controlled situation exists at Dune Jean-Louis where numerous temporary rainwater rockholes were covered by man to conserve drinking water. The covers of stones not only have fulfilled this function very well but also have had important associated effects in that they cut down sunlight (resulting in white faunas), restricted access to the pools by new animals and exposed the original, now protected, species to relatively simple environmental situations. Some stresses in these environmental situations became intensified with time because: (1) Dune Jean-Louis is on the leeward shore with respect to the summer monsoon so may receive less rain than other parts of the atoll; (2) the pools are not seepage pools, as at Anse Cèdres, nor can they be fed from subterranean reservoirs as at Cinq Cases or Takamaka; (3) the covers of stones tend to exclude most subsequent rain. Thus, once the balance between humidity of the microatmosphere and depth of water had been struck in each pool, changes in its water chemistry should be rather slow, controlled by evaporation to the outside and by substrate development. Under a dry régime, and Aldabra is in the driest part of the Indian Ocean (D. R. Stoddart, this volume, p. 5), there would be a trend in each covered pool towards an increase in salinity.

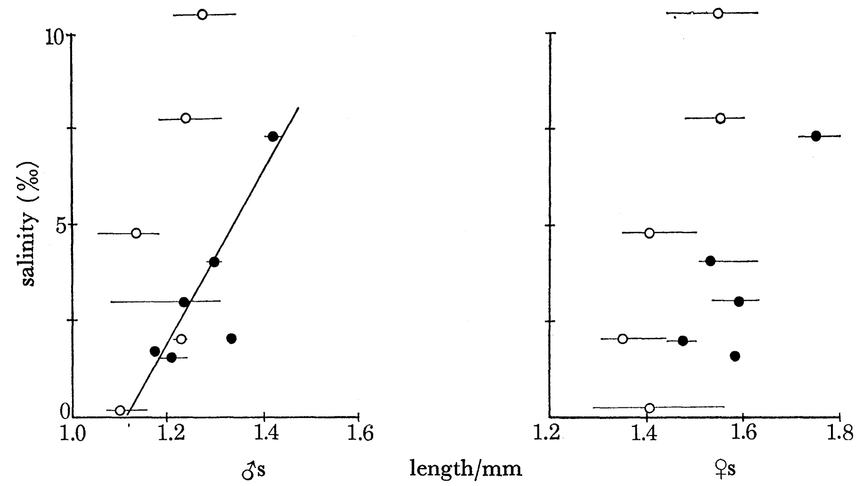

Figure 9. Size variation with respect to salinity in both sexes of *Heterocypris symmetricus* from Dune Jean-Louis. Closed circles = covered pools, open circles = open pools.

The evidence is that these pools differ in salinities and that the sub-populations of *H. symmetricus* which inhabit them differ in size. The probability is good (σ about 0.8) that size of mature males of *H. symmetricus* correlates positively with salinity (figure 8). The figure also shows that this trend is not expressed as well by mature females and that three of the four uncovered pools which were measured in the Dune Jean-Louis area do not aline on the probable trend. When the uncovered pools from all areas are considered the evidence shows a great range in size for *H. symmetricus* but no positive correlation of this factor with salinity.

The sizes of *Heterocypris symmetricus* in the pools which locate on the trend covers almost the entire range of the species on Aldabra and the salinities of these pools cover practically the full range of salinities measured in temporary environments.

In contradistinction, no such trend can be demonstrated for *H. giesbrechti* in the Cinq Cases and Takamaka areas (figure 10). Both males and females of this species show little size variation over a range of salinities similar to those measured for *H. symmetricus* at Dune Jean-Louis.

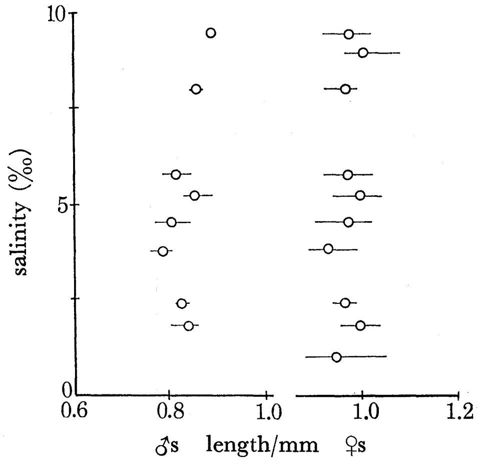

FIGURE 10. Size variation with respect to salinity in both sexes of *Heterocypris giesbrechti* from Cinq Cases and Takamaka. All are open pools.

(*f*) *Zoogeography and taxonomy*

(i) *Distribution of* H. symmetricus *and* H. giesbrechti

H. symmetricus has been recorded from the cenotes of Yucatan but the identification was based on only one female specimen which had a somewhat different furca to that of Müller's species (Furtos 1936, p. 105.) This record has since been reiterated (Tressler 1959, pp. 694 to 695) but is not accepted here.

There are five other records of *H. symmetricus* in the literature (G. Hartmann, personal communication 1969), two of them referring to a subspecies. The localities are: Kilimandjaro (Daday 1910, p. 183), Serengeti Plains (Grochmalicki 1913, p. 524), French West Africa (Gauthier 1938, p. 50), Senegal and southern Madagascar (Gauthier 1951, p. 76) and again Kilimandjaro (Löffler 1968, tables 4 and 5). Löffler's record may be bibliographical only.

It is evident from his descriptions that Gauthier's subspecies *monodi* is very close to the typical form of *symmetricus* from Aldabra. Indeed, apart from minor differences in general shape the distinction rests wholly on characters of the furca. In this respect, the abundant Aldabra material shows that Müller's description and figures did not detail correctly the range in furcal characters. For example, in the furca of an ovigerous female from sample 68 (B.M. 1969. 6.9.250) and in numerous other dissected specimens, the anterior bristle is slightly less than half as long as the anterior claw and the gap between the posterior bristle and the posterior claw is proportionately $1\frac{1}{2}$ times wider than indicated by Müller's illustration. This furca is within the range of Gauthier's subspecies and also accommodates the brief description of the furca of *symmetricus* as identified by Grochmalicki. Thus, there is no longer any reason to retain the subspecies *monodi* Gauthier, 1938, and all the Ethiopian records given above are considered to represent *symmetricus* in the typical sense.

The only other record of *H. giesbrechti* is that by Daday (1910, p. 183) from Kilimandjaro. From Daday's brief discussion it appears, however, that the shell of his form in lateral view resembles that of *symmetricus* as does the accessory part (the anterior flap) of the penis. The latter is an important character at the species level and is constantly different for *symmetricus* and *giesbrechti* as far as the approximately 150 male dissections made during this study are concerned. Daday's record, therefore, is unlikely to be *giesbrechti* in the typical sense.

(ii) *Distribution of related species*

Heterocypris, which includes about 50 extant species, is the largest genus of the tribe Cyprinotini. Fortunately, as regards the closeness of their relation with the Aldabra forms, the great majority of *Heterocypris* species can be discounted quickly, on the grounds given below.

H. symmetricus can be grouped with two other African species, *H. ovularis* Sars, 1924, and *H. obliqua* Lowndes, 1936, also characterized by large size and a narrow penis flap. The latter of these is known from the interconnected Lakes George and Edward (Lowndes 1936, p. 17; Klie 1944, p. 19) and is distinguished by the unusual length of the terminal claws on its antenna and by several peculiarities in its furcal characters (Lowndes 1936, p. 19). *H. ovularis* was described from two localities in Ovamboland and is separated from *H. symmetricus* by its distinctively slender furca (Sars 1924*b*, p. 202).

Other large species occurring in Africa, which, however, do not have a narrow penis flap, are *H. incongruens* (Ramdohr), 1908, *H. aurea* (Sars), 1895 and *H. capensis* (Müller), 1908. *H. aurea* which is the closest of these three to *symmetricus*, it has for example a very similar colour pattern, is known from the Knysna Swamp and Little Namaqualand (Sars 1924*a*, p. 118).

Another species with a narrow penis flap is *H. similis* Klie from Bonaire (Klie 1933, p. 372), but this Neotropic species is a small form and probably closer to the specimen recorded by Furtos as *symmetricus* (see § 8 (*f*) i above).

H. giesbrechti can be grouped with two other Ethiopian species characterized by an oblong shell in which the right valve is denticulated postero-ventrally but not antero-ventrally. These species are *H. oblonga* Sars, 1924, and *H. imus* (Gauthier), 1934. *H. oblonga*, which was described from Damaraland (Sars 1924*a*, p. 201), is much larger than and has a furca unlike that of either *imus* or *giesbrechti* but these two seem to be rather close differing only in some details such as the type of spines on the left male clasping palp and in the penis flap. The provenance of *H. imus* is a temporary pond to the west of Ambovombé, in southern Madagascar and it was also collected from seven other localities in the same district (Gauthier 1934, p. 385).

(iii) *Distribution of* Centrocypris

The most widely distributed species of the Aldabra ostracode faunule is *Centrocypris horrida*. This species is associated with *H. giesbrechti* (sensu Daday) on Kilimandjaro (Daday 1910, p. 199). In Lake George it is associated with *H. obliquus* which is related to *H. symmetricus* (table in

Lowndes 1936). A second species of *Centrocypris*, *C. jakubskii* Grochmalicki occurs with *H. symmetricus* on the Serengeti Plains (Grochmalicki 1913, p. 518). But Müller's Malagasy species, *C. margaritifera* was described from Majunga in NE Madagascar (Müller 1898, p. 279) which is far removed from the provenances of *H. imus* and *H. symmetricus* at the southern end of the island (Gauthier 1934, p. 385, 1951, p. 71).

There are three other records of *C. horrida*, from Zanzibar (Vávra 1895, p. 16), Sudan (Spandl 1924, p. 260) and NE India (Hartmann 1964, p. 140). None of these localities, as far as is yet known, is associated with the Aldabra species of *Heterocypris* or their relatives. On Aldabra, *C. horrida* is associated with *H. giesbrechti*.

(*g*) *General statements on speciation*

The following statements are implicit in the species concept and pertain to the Conclusions which are treated next:

(i) *Time*. In a temporal distribution of related forms, a form which stratigraphically neighbours another is more closely related to it than one which stratigraphically is more separated.

(ii) *Space*. In a spatial distribution of related forms, a form which neighbours another is likely to be more closely related to it than one which is farther away.

(iii) *Morphology*. Like forms in general are more closely related than unlike forms.

(iv) *Ecology*. Species are fit for their environments.

(*h*) *Conclusions*

In terms of the general statements of the preceding subsection, the most interesting entomostracans on Aldabra at the present state of knowledge are the two species of *Heterocypris*.

Nothing is known about the fossil records of these two species and very little about fossils in the entire genus, although information is now beginning to accumulate (e.g. Beasley 1945; Decima 1963; Delorme 1968; Devoto 1965; Dickinson & Swain 1967; Hornibrook 1955; Jordan, Bernstorff & Gründel 1962; Kheil 1965; Mandelshtam & Schneider 1963; Stancheva 1966; Staplin 1963). The only Tertiary African fossil I am aware of which may belong in *Heterocypris* is the Upper Pliocene–Quaternary ostracode K. 560a of Grekoff (1958, p. 27) from Katanga. Thus, the zoogeographic, ecologic and morphologic data given in the preceding subsections afford as yet the only means of tackling the problem of explaining the presence of two species of the same genus on an isolated atoll.

These data show that:

(1) The distribution of typical *symmetricus* is continuous from Senegal to southern Madagascar, whereas that of *giesbrechti*, in the typical sense, is restricted to Aldabra.

(2) The provenance of *symmetricus* on Aldabra is either the Malagasy or the East African subregion, or both; the provenance of *giesbrechti* seems more likely to be Malagasy.

(3) Ecologically, *symmetricus* and its related species are confined to temporary environments whereas *giesbrechti* has a permanent niche on Aldabra but the Ethiopian forms most closely related to it occur in temporary environments.

(4) This difference in ecology has been maintained on Aldabra in spite of considerable fluctuation in the rainfall-controlled boundary region between permanent and temporary pools and the resultant continuous confrontation between the two species at localities of sympatry within this shifting boundary zone.

(5) The two species respond differently to differences in salinity as regards variations in their respective sizes.

(6) Morphologically, the range of characters in Aldabra *symmetricus* lies within the range of the various Ethiopian subpopulations, but the range of at least some characters in *giesbrechti* is discontinuous with ranges of the same characters in populations of related forms.

(7) Several Ethiopian species may be considered close to *symmetricus* but perhaps no more than two or three are close to *giesbrechti*.

(8) In terms of function-related characters both species seem to be about equally efficient.

(9) In many characters, both quantitative and qualitative, *symmetricus* and *giesbrechti* are very distinct species.

Two main conclusions may be drawn. First, '*symmetricus*' and '*giesbrechti*' were already established as distinct entities before they arrived on Aldabra and there has been no breakdown since. Secondly, there are more discontinuities (zoogeographic, ecologic and morphologic) between *giesbrechti* and its closest relatives than between *symmetricus* and its ex-Aldabra subpopulations. Assuming a constant rate of evolution in the two groups, *giesbrechti* is more isolated in a temporal sense than *symmetricus* which leads to the conclusion that the ancestral form of *giesbrechti* reached Aldabra before the ancestral form of *symmetricus*.

(i) *Work points and visualized tests*

Some attempts should be made to core the permanent freshwater pools, especially pool III, near Cinq Cases, and the pool at Takamaka Grove. If obtainable, the cores may well yield datable pieces of wood, recoverable pollen-spore assemblages and a variety of animal remains.

If sufficient ostracode fossils of *Heterocypris* were obtained, measurements of the shell lengths of mature specimens should provide an objective test of the conclusions recorded above. Thus, a trend towards a gradual increase in length with increasing core depth would indicate that *giesbrechti* and *symmetricus* may have speciated on Aldabra from some intermediate ancestral form. Secondly, any sudden marked increase in size, if this persisted for the remainder of the core, would indicate that *symmetricus* may have antedated *giesbrechti* on the atoll.

It would be interesting to test the biologic identities and relations of *symmetricus* and *giesbrechti* by experimental methods such as those used by C. A. Wright on his material for this Discussion meeting.

A successful culture of *H. symmetricus* would allow comparative seasonal-morphological and behavioural laboratory studies to be carried out to test the distinctness of the two species at these levels.

The descriptions of the niches established for *giesbrechti* and *symmetricus* can be implemented by more detailed analyses of their water chemistry and by comparing their respective aquatic insect faunas.

Sampling at different times of year on Aldabra would establish whether or not marked seasonal variations exist in the land aquatic communities.

Further ex-Aldabra sampling, especially in the Malagasy and East African subregions, would indicate the validity or otherwise of the zoogeographic data used here. The extra material thus gathered would also enable fuller and more precise comparisons between the morphologies of the species here grouped with *symmetricus* and *giesbrechti*. Contemporaneous observations of environmental factors would test my ecologic generalizations.

9. Summary

During phase III of the Royal Society's Expedition to Aldabra (31 December 1967–7 April 1968), Entomostraca were collected from all types of terrestrial aquatic environments on West Island, Middle Island and South Island, especially the latter, but Ile Polymnie was not visited. As a result, the known freshwater Entomostraca comprise 23 species, of which ten are Ostracoda, seven Cladocera, one Conchostraca, one Anostraca and four Copepoda. In addition, about 20 saline-tolerant copepods, ten barnacles and a diverse fauna of marine ostracodes occur in the atoll fauna.

Qualitative samples were collected with a fine-meshed hand net. Locations were fixed using aerial photographs or tape and compass traverses between points already located. Salinity was recorded at most sample localities, using a National Institute of Oceanography portable salinometer which gave consistent readings over its full range (0 to 38‰) throughout phase III.

Field records of air temperature indicated that summer shade air temperatures in southeast South Island occasionally exceeded those at the Settlement weather station on West Island (table 1). Rainfall was low during phase III, which covered the normal monsoon season, with January and February, in particular, unusually dry (table 2).

In two areas of South Island, around Cinq Cases and Takamaka, there are permanent freshwater reservoirs (figure 1). They exist because the elevation of Aldabra makes available a considerable volume of differentially porous limestone above the marine water-table. The level of these reservoirs is controlled by rainfall and the fortnightly tidal cycle. The salt-fresh interface reaches the surface in brackish pools such as Flamingo Pool and pool IX. Outside these brackish pools are tide-dominated saline lagoons. At a few localities hypersaline pools and pans occur.

These four types of permanent niches are complemented by a fifth category; the small temporary pools which form everywhere when rain falls and soon are swarming with aquatic life (table 3). The parameters defining all five main niche categories are given in § 4(*c*) which also lists tolerant species.

Some Aldabra entomostracans, in particular the cladocerans, are cosmopolitan, but 18 of the 23 species appear to be zoogeographically sensitive (table 4). Neglecting doubtful records, the indicated subregional provenance of five species is Malagasy, of two each East Africa and India, and one Indo-Malaya. When the distribution of genera on Aldabra is considered (figures 3 to 6) their greatest diversity is seen to be in southeast South Island. The initial conclusion, that most Aldabra freshwater Entomostraca originated in the Malagasy subregion is supported, for Ostracoda at least, by reference to the total known faunas of Madagascar, East Africa, India and Indo-Malaya (table 5).

This conclusion is qualified by the consideration that the diversity of genera at southeast South Island may be due to the presence there of permanent freshwater reservoir areas thus need not necessarily indicate dispersal from Madagascar. Another qualification is imposed by the fact that some species seem to have been introduced by man.

Malagasy species could disperse to Aldabra via birds and the dry season southeasterly Tradewinds. Monsoonal summer winds and birds could account for the presence of East African species, but the Indian and Indo-Malayan forms probably arrived via storm-driven birds or occasional cyclones.

Niches on Aldabra are occupied spatially and in time by such devices as staggered life cycles, tiered communities which vary seasonally, tolerant species and opportunism.

Ostracoda predominated quantitatively as well as qualitatively during phase III and the ostracode *Heterocypris* is the only freshwater entomostracan genus on the atoll which is not monospecific.

A culture of *Heterocypris giesbrechti*, initiated on 5 December 1967, has been observed regularly at the British Museum (Natural History) since 25 September 1968. Size variation in this species over the 8 months of observation was determined by measurement of monthly samples (figure 7), which showed that in both sexes the size of mature individuals peaked in October 1968 when the population was largest and in its most vigorous condition but has declined since. Field size ranges of *H. giesbrechti* (table 6) show good agreement with the culture ranges unlike the results published by Wise (1960).

H. giesbrechti and *H. symmetricus* are easily separated on such characters as colour pattern, shell shape, Zenkers organ, furca and penis. Meristically, they differ in overall length (table 7 gives the field-size ranges of *H. symmetricus*) and in some function-related characters (table 8 and figure 8). It is considered that the characters measured offer an objective way of determining the efficiency of the limbs in question—morphological considerations aside—since the work capacity of a limb distal of any axis is a function of the force applied at that axis and of the distance (= length) over which it operates. This is exemplified, in Ostracoda, by the step of a walking leg, the sweep of a sensing or cleaning limb, the gape of a pair of coxal jaws. In terms of their function-related characters, *giesbrechti* and *symmetricus* are about equally efficient.

Sympatry between *H. symmetricus* and *H. giesbrechti* is thought to be of short-term duration and mainly dependent on rainfall and evaporation which at any time determine the boundary between the two species. Introgressive forms apparently do not occur.

While it seems proper to conclude that it is the entire complex of ecological factors which determine the fitness of *H. giesbrechti* for a permanent niche on Aldabra and of *H. symmetricus* for a temporary one, especially at southeast South Island, there is a marked distinction between the responses of the two species to salinity.

This is best demonstrated in the Dune Jean-Louis area where, under special conditions (see figure 8 and § 8 (*e*) ii), the size of *H. symmetricus* correlates positively with salinity whereas, over the same range of salinities around Cinq Cases and Takamaka, *H. giesbrechti* shows no variation in size (figure 9).

Zoogeographically, the relations of *H. symmetricus* are with several Ethiopian forms and the species in the typical sense extends from southern Madagascar to Senegal. The relatives of *H. giesbrechti*, however, are restricted to a form in the Kilimandjaro area and a species in southern Madagascar and *giesbrechti* in the typical sense seems to be confined to Aldabra. Of the other Aldabra ostracodes *Centrocypris horrida* is the most widely distributed. In Africa it occurs together with *H. symmetricus* or its relatives but on Aldabra it is associated with *H. giesbrechti*.

Following some general considerations on speciation (see § 8 (*g*)) it is concluded (see § 8(*h*)) that '*symmetricus*' and '*giesbrechti*' were already established as distinct species before they arrived on Aldabra and there has been no subsequent interspecific breakdown. Secondly, since there are more zoogeographic, ecologic and morphologic discontinuities between *giesbrechti* and its closest relatives than between *symmetricus* and its ex-Aldabra populations, the ancestral form of the more isolated species, namely *giesbrechti*, reached Aldabra before the ancestral form of the less differentiated *symmetricus*. The date of this dispersal to Aldabra is not known because there is as yet no fossil record of the species or their relatives but future work on Aldabra and elsewhere may enable it to be estimated and at the same time test the validity of my conclusions.

The British Museum (Natural History) and the Aldabra Research Committee of the Royal Society made possible my participation in phase III. The Keeper of Zoology, J. P. Harding, made my time available.

The Cladocera were identified by R. L. Sayers, except for *Moina dubia pectinata* and *Leydigia propinqua ciliata* which were determined by R. L. Sayers and myself. The freshwater and two salt-tolerant copepods were identified by W. A. Smith, except for *Onychocamptus bengalensis*, *Mesocyclops leuckarti pilosa* and *Cletocamptus confluens meridionalis* which were determined by W. A. Smith and myself.

Of the approximately 400 complete dissections of *Heterocypris giesbrechti* and *H. symmetricus* which were made, half were done by W. A. Smith and R. L. Sayers; the remainder by myself. Notes on the *H. giesbrechti* culture were made under my guidance by R. L. Sayers.

Where other determinations are not acknowledged in the text they are mine but I would like to record here a particular debt to F. R. Fosberg of the Smithsonian Institution for his guidance on the Aldabra flora.

Without the help of the Seychellois people on Aldabra my field work would not have been possible.

Field and culture collections and dissections are stored at the British Museum (Natural History) under Registration Numbers 1966.11.21.1 (Conchostraca); 1966.11.21.6 and 1969.6.9.519–527 (Anostraca); 1966.11.21.2–5, 1969.6.9.1–518 and 583–659 (Ostracoda); 1969.6.9.528–582 (Cladocerca); 1969.6.9.660–669 (Copepoda).

APPENDIX A

coordinates (eastings first)	locality descriptions
3905, 0560	pool I. Large freshwater pool fringed with *Acrostichum*, *Fimbristylis*, *Thespesia*. Salinity: 1.4 to 2.15‰. Samples 1 and 2
3895, 0560	pool II. Large freshwater pool fringed with *Fimbristylis*, *Lumnitzera*, *Thespesia*, rare *Acrostichum*. Salinity: 3.2 to 4.4‰. Sample 16. Samples 105, 106 collected very near western margin of this pool
3895, 0580	pool III. Large freshwater pool fringed with *Thespesia*, *Fimbristylis*. Salinity: 1.3 to 1.5‰. Samples 3 to 5
3880, 0580	shallow freshwater pool, *Lumnitzera* fringed, about 150 m W of pool III. Salinity: 4.5‰ (measured shortly after rain)
3860, 0585	small freshwater pool fringed by *Pandanus*, *Thespesia*. Salinity: 1.5 to 2.4‰
3840, 0605	pool VI. Large freshwater pool fringed by *Thespesia*, *Lumnitzera*. Salinity: 3.1 to 3.4‰
3830, 0600	pool VII. Saline tide dominated pool fringed with *Lumnitzera* (some with lichen), *Thespesia*, *Acrostichum*. Salinity: 11.1 to 12.2‰
3810, 0615	pool VIII. Large freshwater pool fringed by *Pandanus*, *Thespesia*, *Lumnitzera*. Salinity: 1.3‰
3800, 0625	small about ½ m deep freshwater pool, last freshwater rockhole on trail to Cinq Cases landing stage from Camp Cinq Cases. Salinity: 1.1 to 2.4‰
3905, 0565	Camp Cinq Cases
3835, 0690	coco. Solitary coconut palm, inland
3745, 0643	Cinq Cases Landing stage
3845, 0525	Peter's Knoll. Low limestone knoll
3875, 0550	pool IX. Large brackish pool fringed by *Lumnitzera*, with *Thespesia* outside the *Lumnitzera*. Salinity: 6.4 to 7.4‰. Sample 15
3890, 0555	freshwater pool NE of pool IX—low limestone ridge between them. Salinity: 1.6‰. Sample 17

coordinates (eastings first)	locality descriptions
3865, 0560	large shallow freshwater pool, about 80 m NW of pool IX. Salinity: 4.4 ‰. Sample 22
3845, 0540	small temporary pool NW of pool with *Avicennia*, near Peter's Knoll. Salinity: 6.3 ‰
3830, 0555	saline pool, fringed by *Lumnitzera* and dead trees, with large colony of *Nephila* on the *Lumnitzera*. Salinity: 14.6 ‰. Sample 18
3800, 0535	large freshwater pool, where Ibis nest in *Lumnitzera*. Salinity: 5.9 ‰. Sample 19
3790, 0530	small freshwater pool, about 120 m SW of Ibis pool. Salinity: 1.0 ‰. Sample 20. About 10 m W of this small pool is a small triangular pool with a *Lumnitzera* bush on its NW edge. Salinity: 7.8 ‰
3770, 0505	saline tide-influenced pool about 400 m SW of Ibis pool. Salinity: 29.7 ‰. Sample 21
3755, 0510	complex of three large tide-influenced saline pools, about 225 m WNW of sample 21. Salinity: 30.5 ‰. Sample 32
3750, 0520	small tide-dominated saline seepage pool NW of sample 32 in *Pemphis* scrub. Salinity: 30.3 ‰. Sample 29
3755, 0525	another small tide-dominated saline seepage pool, N of sample 32 in *Pemphis* scrub. Salinity: 23.5 ‰. Sample 30
3765, 0530	*Acrostichum*—covered fissure pool on edge of *Pemphis* scrub about 100 m E of sample 30. Salinity: 15.4 ‰
3770, 0570	saline arm of Bras l'Eglise where flamingoes feed NW of Ibis pool. Salinity: more than 38 ‰
3955, 0580	covered freshwater rockhole used by Seychellois, on coastal champignon ridge about 150 m W of top of Cinq Cases Dune. Salinity: 1.6 ‰. Sample 33
4030, 0670	coastal terminus of airstrip trace
3960, 0615	freshwater pool N of sample 33 on platin behind coastal champignon ridge. Salinity: 1.9 ‰. Sample 34. Near and N of large freshwater pool with salinity 3.4 ‰
3960, 0675	freshwater pool on platin about 600 m N of sample 34. Salinity: 1.9 ‰
3930, 0685	large freshwater pool slightly E of trail from Camp Cinq Cases to Flamingo Pool. Salinity: 1.3 ‰. Sample 35
3905, 0795	Flamingo pool. Large brackish pool where flamingoes feed fringed by *Lumnitzera* and *Thespesia*. Salinity: 15 ‰. Sample 14
3865, 0775	Dix Neuf. Marker on airstrip trace about 400 m SW of Flamingo pool
3845, 0790	large freshwater pool about 250 m bearing 310° from Dix Neuf, *Thespesia*-fringed with subsidiary *Ficus*, *Pandanus* and *Lumnitzera*. Salinity: 5.7 ‰. Sample 39
3740, 0765	pool X. Large freshwater pool, W margin shaded by *Tamarindus*. Salinity: 1.8 ‰. Sample 31
3920, 0785	second freshwater pool E of Flamingo Pool, fringed by *Thespesia*, *Guettarda*, *Lumnitzera*. Salinity: 5.2 ‰. Sample 10
3915, 0785	first freshwater pool E of Flamingo Pool. Salinity: 8.9 ‰. Sample 11
3875, 0775	freshwater pool about 150 m NE of Dix Neuf. Salinity: 0.9 ‰. Sample 12
3875, 0780	freshwater pool about 30 m N of sample 12. Sample 13
4025, 0890	large tide-dominated saline lagoon complex W of Point Hodoul. Salinity: 16.0 to 32.9 ‰. Samples 23, 24, 25
3985, 0890	very small temporary rainwater rockhole about 350 m W of above saline lagoon complex and about 30 m E of *Acrostichum*-covered brackish pool with salinity 12.7 ‰. Sample 26
3930, 0905	large freshwater pool fringed by *Thespesia* about 1000 m W of saline lagoon complex. Salinity: 4.1 ‰. Sample 27
3840, 0950	large very deep saline tide-influenced pool about 2300 m WNW of Point Hodoul. Salinity (surface): 19.6 to 19.9 ‰. Salinity (bottom): 24.0 to 29.7 ‰. Samples 36, 37
3735, 0960	small shallow freshwater pool about 3 m below terrain level fringed by *Maytenus*, *Ficus* and *Scaevola*. Salinity: 1.3 ‰
3740, 0965	large freshwater pool fringed by *Thespesia* on its southern margin about 1000 m WNW of very deep saline pool. Salinity: 8 ‰. Sample 38
3605, 0925	Croix Blanc, inland terminus of airstrip trace
3580, 0915	Frigate Pool. Large freshwater pool where frigates dive, with *Ficus* and *Pandanus* on N margin. Salinity: 3.9 ‰
3610, 0940	large freshwater pool partly shaded by *Ficus* about 155 m NNE of Croix Blanc. Salinity: 1.8 ‰
3630, 0960	large freshwater pool about 400 m NE of Croix Blanc. Salinity: 0.7 ‰
3655, 0985	large freshwater pool fringed by *Pandanus* about 775 m NE of Croix Blanc. Salinity: 0.6 ‰. Sample 8. This is the pool from which a culture has been reared at British Museum (Natural History)
3655, 1020	small freshwater pool about 1½ m below terrain level about 350 m N of sample 8. Salinity: 5.5 ‰
3650, 1030	several small saline pools on pavé about 2 m below terrain level. Salinity: 22.1 to 22.2 ‰
3645, 1045	more small saline pools on pavé, one covered by scrub with salinity 15.8 ‰

coordinates (eastings first)	locality descriptions
3640, 1065	large saline pool on pavé about 3 m below terrain level and about 1 m deep. Salinity: 23.4‰. Sample 9. N of this *Casuarina* saplings begin to appear
3605, 1118	covered freshwater soak near Anse Cèdres, used by Seychellois. Salinity: 1.2‰. Sample 6
3607, 1120	small covered freshwater rockhole near sample 6. Salinity: 1.5‰. Sample 7
3600, 1130	Anse Cèdres. Salinity (Indian Ocean): 34.1‰
3365, 0640	Camp Takamaka. Wilson's Well. Salinity: 0.5‰. Sample 49
3390, 0670	Takamaka tidal estuary. Salinity: 36.4—more than 38.0‰
3350, 0540	Takamaka Grove. Large freshwater pool shaded by *Ficus*. Salinity: 4.5‰. Sample 43
3375, 0525	large saline pool deepest at its southern margin, fringed by *Acrostichum*, *Pemphis*, *Ficus*, *Pandanus*, *Flacourtia*, about 300 m SE of Takamaka Grove. Salinity: 30.6‰. Sample 42. SW of this pool are two small pools, that farther away with a salinity of 7.5‰, the nearer (which is almost connected to the large saline pool) with a salinity of 11.0‰
3470, 0525	large saline pool fringed by *Pemphis*, *Maytenus*, *Acrostichum*, also *Ficus*, *Pandanus*, *Scaevola*; about 1250 m E of Takamaka Grove. Salinity: 29.7‰. Sample 50
3535, 0545	NE shore of large saline pool about 1850 m E of Takamaka Grove. Salinity: 25.2‰. Sample 51
3585, 0565	saline arm of Bras Takamaka, about 2000 m W of Bras l'Eglise. Samples 40, 41
3605, 0465	small temporary rainwater rockhole about 1000 m S of samples 40, 41. Location approximate
3375, 0620	small temporary rainwater rockhole about 200 m SSE of Wilson's Well. Sample 56
3350, 0620	small temporary rainwater rockhole about 200 m SSW of Wilson's Well. Salinity: 0.1‰. Sample 45
3345, 0595	small temporary rainwater rockhole about 75 m NE of sample 44. Sample 102
3340, 0590	large freshwater pool about 450 m NNW of Takamaka Grove. Salinity: 1.0‰. Sample 44
3325, 0595	large freshwater pool, *Pandanus*-fringed. Salinity: 2.0‰. Sample 46
3310, 0590	large freshwater pool fringed by *Pandanus*, *Ficus*, etc. Salinity: 9.4‰. Sample 47
3285, 0600	large freshwater pool in fairly dense scrub, fringed by *Thespesia*, *Ochna*, rare *Acrostichum*. Salinity: 2.4‰. Sample 48
3235, 0575	small temporary rainwater rockhole about 100 m E of dry *Ficus* and *Pandanus* grove. Sample 53
3190, 0545	large saline pool about 550 m SW of sample 53, fringed by *Lumnitzera* with *Thespesia* and *Flacourtia* beyond this. Salinity: 35.9‰
3180, 0515	small temporary rainwater rockhole shaded by young *Ficus* on edge of pavé about 300 m S of previous locality. Sample 54
3245, 0455	large shallow saline pool about 1300 m SW of Takamaka Grove, fringed by *Lumnitzera* with occasional clumps of *Acrostichum* nearby. Salinity: 26.7‰. Sample 55
3235, 0860	Ile Michel. Small temporary rainwater rockhole shaded by tall *Casuarina*. Sample 57
2625, 0380	Dune Jean-Louis
2650, 0370	Turtler's Hut at Dune Jean-Louis. Salinity (Indian Ocean): 34.5‰
2600, 0360	Dune Patates
2565, 0355	small partly covered rainwater rockhole WSW of Dune Patates. Vegetation includes *Fimbristylis*, *Colubrina*, *Guettarda*, *Maytenus*, *Pemphis*, *Euphorbia abbottii*, *Scaevola*, lone *Pandanus*. Salinity: 1.6‰. Sample 67
2590, 0385	saline pool on pavé, water-level about 3 m below terrain level, about 250 m NNW of Dune Patates. Salinity: 28.1‰
2700, 0425	saline pool on pavé, water-level about 3 m below terrain level, about 80 m W of small isolated copse of *Pemphis* in general low scrub. Salinity: 31.6‰
2715, 0475	two near-by saline pools in fairly dense *Pemphis*, *Maytenus* and *Sideroxylon* scrub. Salinity (smaller): 31.7‰. Salinity (larger): 36.7‰
2730, 0445	Large shallow saline tide-influenced complex about 1250 m NE of Dune Jean-Louis. Salinity: 32.5‰. Sample 62
2642, 0384	small open temporary rainwater rockhole. Salinity: 0.2‰. Sample 58
2644, 0381	formerly covered rainwater rockhole. Salinity: 2.0‰. Sample 59
2650, 0383	two small rainwater rockholes within 1 m of each other; one open (sample 60) with salinity of 7.7‰, the other (sample 61) partly covered with salinity of 3.0‰
2641, 0386	small open temporary rainwater rockhole. Salinity: 10.5‰. Sample 63
2648, 0384	small covered rainwater rockhole. Salinity: 1.9‰. Sample 64
2651, 0383	small covered rainwater rockhole. Salinity: 1.7‰. Sample 65
2656, 0382	small covered rainwater rockhole. Salinity: 4.0‰. Sample 66
2654, 0376	relatively large open rainwater rockhole. Salinity: 4.7‰ (possibly affected by seaspray). Sample 68
2652, 0379	small covered rainwater rockhole. Salinity: 7.4‰. Sample 69
1910, 0145	Dune d'Messe waterhole. Location approximate. Sample 107
0685, 0440	small temporary rainwater rockhole N of beach at Anse Mais. Sample 79

coordinates (eastings first)	locality descriptions
0690, 0430	small temporary rainwater rockhole S of beach at Anse Mais. Sample 80
2565, 1300	small temporary rainwater rockhole on coastal clifftop near and W of Anse Badamier, Middle Island. Salinity: 4.6‰. Sample 103
2815, 1265	small temporary rainwater rockhole on coastal clifftop in fairly dense mixed *Pemphis* scrub, about 2450 m E of Anse Badamier, Middle Island. Salinity: 2.8‰. Sample 104
1400, 1250	Anse Coco, near Passe Gionnet. Collected on beach. Sample 108
1397, 1245	small open rainwater rockpool on ridge behind Camp Gionnet. Sample 74
1396, 1244	small covered rainwater rockhole on ridge behind Camp Gionnet. Sample 75
1392, 1237	open rainwater rockpool marked by cairn on N to S trail SW of Camp Gionnet. Sample 76
1390, 1237	open rainwater rockpool on same N to S trail. Sample 77
1388, 1235	small covered rainwater rockhole at W of same N to S trail. Sample 78
0560, 1050	saline tide-dominated pool N of main Settlement. Sample 28
0575, 1070	small open temporary rainwater rockhole, about 80 m E of northernmost shack at Settlement in fairly dense low scrub. Sample 98
0575, 1070	very small open temporary rainwater rockhole, SE of and very near Sample 98. Salinity: 1.3‰. Sample 99
0585, 1060	rainwater rockpool formerly covered by corrugated sheeting, about 200 m E of the N end of Settlement. Salinity: 0.4‰. Sample 100
0570, 0970	temporary open rainwater rockpool in scrub immediately behind shacks near the southern end of Settlement. Salinity: 0.6‰. Sample 101
0580, 0965	small open temporary rainwater rockhole about 45 m in from W end of trail leading to Bassin Cabri. Salinity: 0.4‰. Sample 95
0615, 0990	small shallow temporary rainwater rockpan at E end of this trail and near W end of Bassin Cabri. Salinity: 0.8‰. Sample 94
0620, 0990	linear rainwater rockhole marked by cairn at Bassin Cabri. Salinity: 1.1‰. Sample 70
0615, 0995	saline tide-influenced pool NW of sample 70. Salinity: 31.0‰. Sample 71
0585, 1055	small temporary open rainwater rockhole in scrub at N end of 'Goat track' behind Settlement. Sample 96
0560, 1010	large rainwater tank immediately SE of guest house (expedition HQ). Sample 97
0555, 1010	waterlogged plank washed up on beach outside guest house. Sample 72
0635, 0920	small clearing in mangroves N of La Gigi. Sample 73. Location approximate

APPENDIX B

coordinates	sample numbers	Entomostracan fauna
3905, 0560	1, 2	*Heterocypris giesbrechti* (G. W. Müller), 1898; *Macrothrix spinosa* King, 1853
3895, 0580	3, 4, 5	*Heterocypris giesbrechti*, *Plesiocypridopsis aldabrae* (G. W. Müller), 1898, *Cypris decaryi* Gauthier, 1933, *Parastenocypris aldabrae* (G. W. Müller), 1898, *Zonocypris* cf. *madagascarensis* G. W. Müller, 1898, *Limnocythere notodonta* Vávra, 1906; *Macrothrix spinosa*, *Alona* sp., *Diaphanosoma sarsi* Richard, 1895; *Mesocyclops leuckarti* (Claus), 1857, *pilosa* Kiefer, 1930
3605, 1118	6	*Heterocypris symmetricus* (G. W. Müller), 1898; cladoceran; copepod
3607, 1120	7	*Ceriodaphnia rigaudi* Richard, 1894
3655, 0985	8	*Heterocypris giesbrechti*, *Plesiocypridopsis aldabrae*, *Centrocypris horrida* Vávra, 1895, *Cypris decaryi*†; *Macrothrix spinosa*, *Ceriodaphnia rigaudi*†, *Alona* sp.†
3920, 0785	10	*Heterocypris giesbrechti*, *Cypris decaryi*
3915, 0785	11	*Heterocypris giesbrechti*, *Cypris decaryi*
3895, 0560	16	*Heterocypris giesbrechti*, *Plesiocypridopsis aldabrae*; copepod
3890, 0555	17	*Plesiocypridopsis aldabrae*; *Macrothrix spinosa*
3800, 0535	19	*Heterocypris giesbrechti*, *Plesiocypridopsis aldabrae*; *Alona* sp.; *Mesocyclops leuckarti pilosa*, *Onychocamptus bengalensis* (Sewell), 1934
3790, 0530	20	*Heterocypris giesbrechti*, *Plesiocypridopsis aldabrae*, *Cypris decaryi*, *Limnocythere notodonta*; *Latonopsis australis* Sars, 1888, *Alona* sp.; *Mesocyclops leuckarti pilosa*
3865, 0560	22	*Heterocypris giesbrechti*, *Plesiocypridopsis aldabrae*, *Cypris decaryi*, *Limnocythere notodonta*; cladocera: ephippia
4025, 0890	23, 24, 25	marine harpacticoids (sent to J. B. J. Wells)

† Culture only.

coordinates	sample numbers	Entomostracan fauna
3985, 0890	26	*Heterocypris symmetricus*, *Plesiocypridopsis aldabrae*; *Leydigia propinqua* Sars, 1903, *ciliata* Gauthier, 1939, *Moina dubia* De Guerne & Richard, 1892, *pectinata* Gauthier, 1955; *Mesocyclops leuckarti pilosa*
3930, 0905	27	*Cletocamptus confluens* (Schmeil), 1894, *meridionalis* Kiefer, 1929
0560, 1050	28	marine harpacticoids (sent to J. B. J. Wells)
3750, 0520	29	marine harpacticoids (sent to J. B. J. Wells)
3955, 0580	33	*Cypris decaryi*, *Plesiocypridopsis aldabrae*
3930, 0685	35	ostracode (sample tube smashed in transit to U.K.)
3740, 0965	38	*Heterocypris giesbrechti*, *Plesiocypridopsis aldabrae*, *Cypris decaryi*; copepod
3845, 0790	39	*Heterocypris giesbrechti*
3585, 0565	40	*Microcyclops* cf. *dengizicus* (Lepeschkin), 1900, marine harpacticoids (sent to J. B. J. Wells)
3585, 0565	41	*Metis holothuriae* (Edwards) 1891
3375, 0525	42	marine harpacticoids (sent to J. B. J. Wells)
3350, 0540	43	*Heterocypris giesbrechti*, *Plesiocypridopsis aldabrae*
3340, 0590	44	*Heterocypris giesbrechti*, *Plesiocypridopsis aldabrae*; *Macrothrix spinosa*
3350, 0620	45	*Plesiocypridopsis aldabrae*; *Streptocephalus proboscideus* Frauenfeld, 1873
3325, 0595	46	*Heterocypris giesbrechti*, *Plesiocypridopsis aldabrae*, *Centrocypris horrida*; *Macrothrix spinosa*
3310, 0590	47	*Heterocypris giesbrechti*, *Plesiocypridopsis aldabrae*; *Cletocamptus confluens meridionalis*, *Onychocamptus bengalensis*
3285, 0600	48	*Heterocypris giesbrechti*, *Plesiocypridopsis aldabrae*
3365, 0640	49	*Plesiocypridopsis aldabrae*, *Strandesia vavrai* (G. W. Müller) 1898; *Ceriodaphnia rigaudi*, *Diaphanosoma sarsi*; *Mesocyclops leuckarti pilosa*
3605, 0465	52	*Heterocypris symmetricus*; *Moina dubia pectinata*; *Streptocephalus proboscideus*
3235, 0575	53	*Heterocypris symmetricus*; *Streptocephalus proboscideus*
3180, 0515	54	*Heterocypris symmetricus*; *Moina dubia pectinata*; *Streptocephalus proboscideus*
3245, 0455	55	*Microcyclops* cf. *dengizicus*, *Cletocamptus confluens meridionalis*
3375, 0620	56	*Heterocypris symmetricus*
3235, 0860	57	*Heterocypris symmetricus*
2642, 0384	58	*Heterocypris symmetricus*; *Moina dubia pectinata*, *Alona* sp.; *Streptocephalus proboscideus*
2644, 0381	59	*Heterocypris symmetricus*, *Plesiocypridopsis aldabrae*; *Moina dubia pectinata*
2650, 0383	60	*Heterocypris symmetricus*, *Plesiocypridopsis aldabrae*; *Moina dubia pectinata*, *Alona* sp.
2650, 0383	61	*Heterocypris symmetricus*, *Plesiocypridopsis aldabrae*; *Moina dubia pectinata*
2641, 0386	63	*Heterocypris symmetricus*, *Plesiocypridopsis aldabrae*.
2648, 0384	64	*Heterocypris symmetricus*, *Plesiocypridopsis aldabrae*; *Alona* sp.
2651, 0383	65	*Heterocypris symmetricus*, *Plesiocypridopsis aldabrae*; *Alona* sp.
2656, 0382	66	*Heterocypris symmetricus*
2565, 0355	67	*Heterocypris symmetricus*, *Plesiocypridopsis aldabrae*; *Alona* sp.
2654, 0376	68	*Heterocypris symmetricus*; *Moina dubia pectinata*
2652, 0379	69	*Heterocypris symmetricus*, *Plesiocypridopsis aldabrae*; *Moina dubia pectinata*
0620, 0999	70	*Heterocypris symmetricus*, *Plesiocypridopsis aldabrae*; *Moina dubia pectinata*
0615, 0995	71	marine harpacticoids (sent to J. B. J. Wells)
0555, 1010	72	*Lepas anatifera* Linnaeus, 1767
1397, 1245	74	*Heterocypris symmetricus*, *H. giesbrechti*, *Plesiocypridopsis aldabrae*; *Moina dubia pectinata*, *Alona* sp.
1396, 1244	75	*Heterocypris symmetricus*, *H. giesbrechti*, *Plesiocypridopsis aldabrae*; ?*Moina*
1392, 1237	76	*Heterocypris symmetricus*, *H. giesbrechti*, *Plesiocypridopsis aldabrae*; *Moina dubia pectinata*
1390, 1237	77	*Heterocypris giesbrechti*, *Plesiocypridopsis aldabrae*; *Moina dubia pectinata*; *Psammocyclops excellens* Kiefer, 1955
1388, 1235	78	*Heterocypris symmetricus*, *H. giesbrechti*, *Plesiocypridopsis aldabrae*; *Moina dubia pectinata*, *Alona* sp.; *Psammocyclops excellens*
0685, 0440	79	*Heterocypris symmetricus*
0690, 0430	80	*Heterocypris symmetricus*; *Moina dubia pectinata*
—	81	*Chelonibia testudinaria* (Linnaeus) 1758, on plastron of ♂ *Chelonia mydas* (collected J. Frazier)
—	82	*Platylepas hexastylos* (O. Fabricius) 1798, on dorsal of tail and flippers and ventral of hind legs, tail and throat of ♂ *Chelonia mydas* (collected J. Frazier)
Islet in Passe Femme	83	*Lithotrya* cf. *valentiana* (Gray) 1825 (collected F. R. Fosberg)
0615, 0990	94	*Heterocypris symmetricus*
0580, 0965	95	*Heterocypris symmetricus*, *H. giesbrechti*; *Moina dubia pectinata*; *Streptocephalus proboscideus*

coordinates	sample numbers	Entomostracan fauna
0585, 1055	96	*Heterocypris symmetricus*; *Streptocephalus proboscideus*
0560, 1010	97	*Cypretta* cf. *fontinalis* Hartmann 1964
0575, 1070	98	*Heterocypris symmetricus*; *Moina dubia pectinata*
0575, 1070	99	*Heterocypris symmetricus*, *H. giesbrechti*; *Streptocephalus proboscideus*
0585, 1060	100	*Heterocypris symmetricus*, *Plesiocypridopsis aldabrae*; *Streptocephalus proboscideus*
0570, 0970	101	*Heterocypris symmetricus*
3345, 0595	102	*Heterocypris symmetricus*
2565, 1300	103	*Heterocypris symmetricus*; *Streptocephalus proboscideus*
2815, 1265	104	*Heterocypris symmetricus*; *Moina dubia pectinata*
3895, 0560	105	*Heterocypris symmetricus*, *H. giesbrechti*, *Cypris decaryi*, *Centrocypris horrida*
3895, 0560	106	*Heterocypris symmetricus*, *Centrocypris horrida*, *Strandesia vavrai*, *Parastenocypris aldabrae*
1910, 0145	107	*Heterocypris symmetricus*, *H. giesbrechti*, *Plesiocypridopsis aldabrae*; *Moina dubia pectinata*, *Alona* sp.; *Streptocephalus proboscideus*
1400, 1250	108	*Balanus* sp.

Appendix C

coordinates	sample numbers	non-Entomostracan fauna
3640, 1065	9	marine molluscs
3875, 0775	12	land molluscs
3905, 0795	14	*Palaemon debilis* Dana, 1852; *Chanos* sp.
3875, 0550	15	*Palaemon debilis*, *P. concinnus* Dana, 1852; *Chanos* sp., gobiid
3830, 0555	18	*Palaemon debilis*
3770, 0505	21	marine molluscs
4025, 0890	23, 24, 25	*Palaemon debilis*; marine molluscs; marine worms
3750, 0520	29	*Palaemon debilis*; *Cirolana* sp.; aorid amphipod; marine molluscs
3755, 0525	30	*Palaemon debilis*; *Cirolana* sp.; marine molluscs
3755, 0510	32	*Palaemon debilis*; marine molluscs
3840, 0950	36, 37	*Palaemon debilis*; gobiid
3375, 0525	42	*Palaemon debilis*; gobiid
3470, 0525	50	*Palaemon debilis*; *Terebralia* sp.
3535, 0545	51	*Palaemon debilis*; gobiid
2730, 0445	62	*Palaemon debilis*; *Cirolana* sp.; marine molluscs
0615, 0995	71	*Palaemon debilis*; *Cirolana* sp.; aorid amphipod; marine molluscs
0635, 0920	73	alphaeid shrimp
3895, 0560	106	land molluscs

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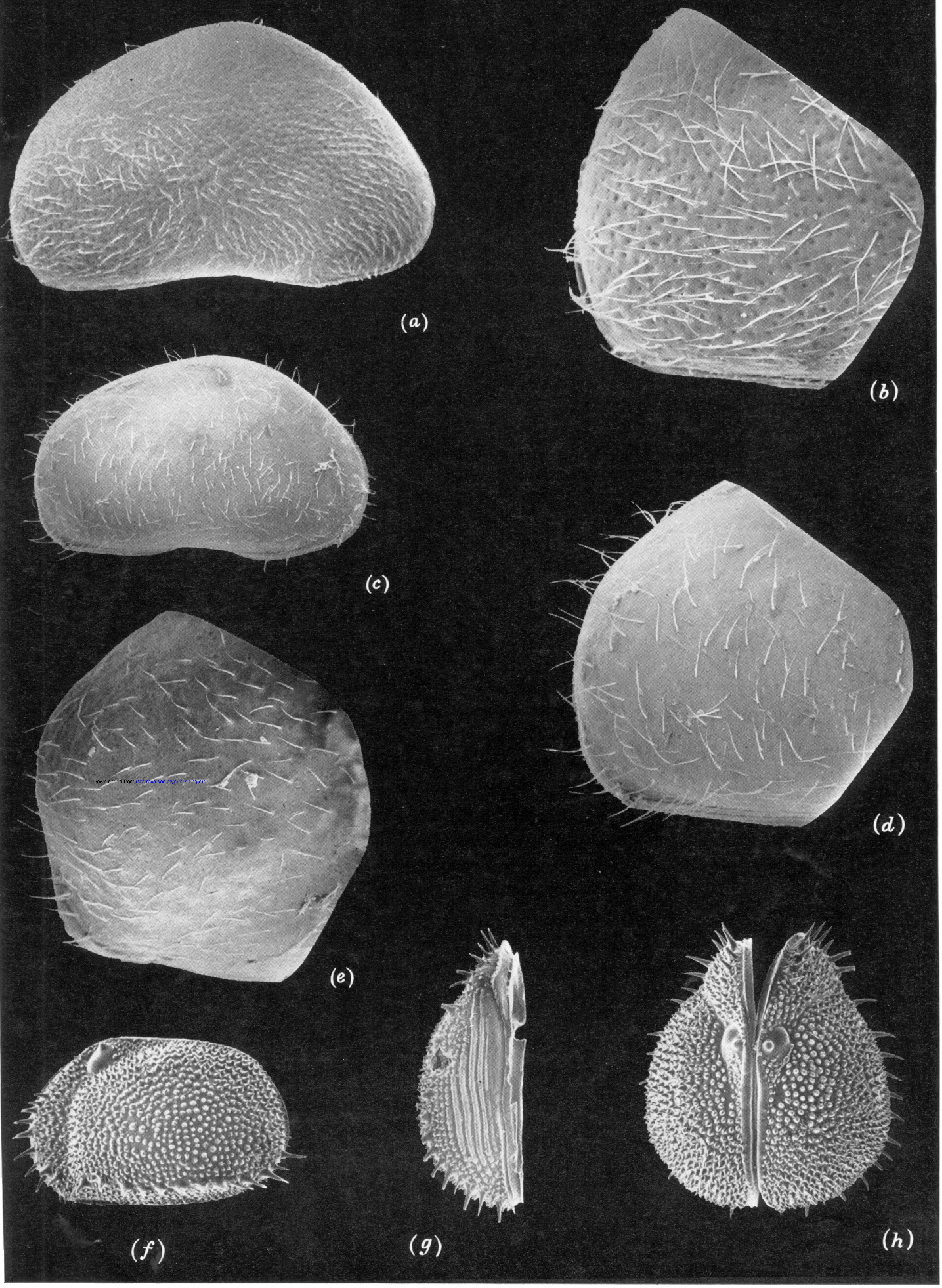

FIGURE 2. For legend see facing page.