

POPULATION STUDIES ON THE ANTARCTIC COLLEMBOLAN *Gomphiocephalus hodgsoni* CARPENTER

By A. J. Peterson¹

Abstract: The changes in population density of a summer population of *Gomphiocephalus hodgsoni* are correlated with the changing moisture content of the environment. The instar distribution, determined by polymodal analysis and chaetotaxic studies, is described and a model of population growth is postulated.

INTRODUCTION

Gomphiocephalus hodgsoni (Collembola: Hypogastruridae) was first described from specimens collected at Granite Harbor during the British National Antarctic Expedition, 1901-1904 (Carpenter 1908). Subsequent discoveries have extended its range along the South Victoria Land coast from Minna Bluff (78° 15' S) to Mt George Murray (75° 55' S), and to Black, White, Ross and Beaufort Islands in the McMurdo Sound area (Wise 1967). Although there have been several studies on the microclimate of the habitat of antarctic arthropods (Janetshek 1967a; Pryor 1962; Wise, Fearon & Wilkes 1964; Wise & Spain 1967), there has been little previous work on the population dynamics of any single species throughout an entire summer season. Much of the earlier data on changing population levels are concerned with the broad relationships between collembolan and mite species obtained either by irregular sampling throughout the season (Wise et al. 1964; Wise & Spain 1967) or by single surveys of transect lines (Wise & Shoup 1967; Gressitt & Shoup 1967). Consequently nothing is known about the life histories of most antarctic Collembola and there has been only one attempt to determine the life cycle of a species (Janetshek 1967b). The present paper is the first attempt to establish the life cycle and changes in population numbers through the summer from regular sampling of a single population.

DESCRIPTION OF STUDY AREA

The ice-free area at Cape Bird (77° 13' S, 166° 28' E), on the northwestern tip of Ross Island (Fig. 1), occupies a zone some 8 km long and 1 km wide, bordered by sea on one side and the Mt Bird ice cap on the other. Steep scree slopes of deposited moraines rising from sea level to above 150 m border the proximal edge of the beach. From January this beach is usually free of ice and the area surrounded by open water. The zone is free of snow during the summer and surface thawing begins in late November. By late December the snow has melted and apart from streams flowing off the ice cap little seepage water remains. The whole area becomes very dry in the latter part of the season.

The study area was sited in a broad, shallow basin some 60 m above sea level and nearly 300 m south of the northern Adelie penguin rookery (*Pygoscelis adeliae* Hombr. & Jacq.). The skua (*Catharacta macormacki* Saunders) also nests in the vicinity. The whole study area consisted of a mixture of two ecosystems, the chalikosystem and the bryosystem (Janetshek 1963). The former was characteristic of the more exposed areas, whereas the latter characterised more protected and moister sites.

Mosses and lichens are present in the bryosystem on the scree slopes and, as at Cape Hallett,

1. Zoology Department, University of Canterbury, Christchurch, N.Z. Present address: P.O. Box 171, Macdonald College, Quebec, Canada.

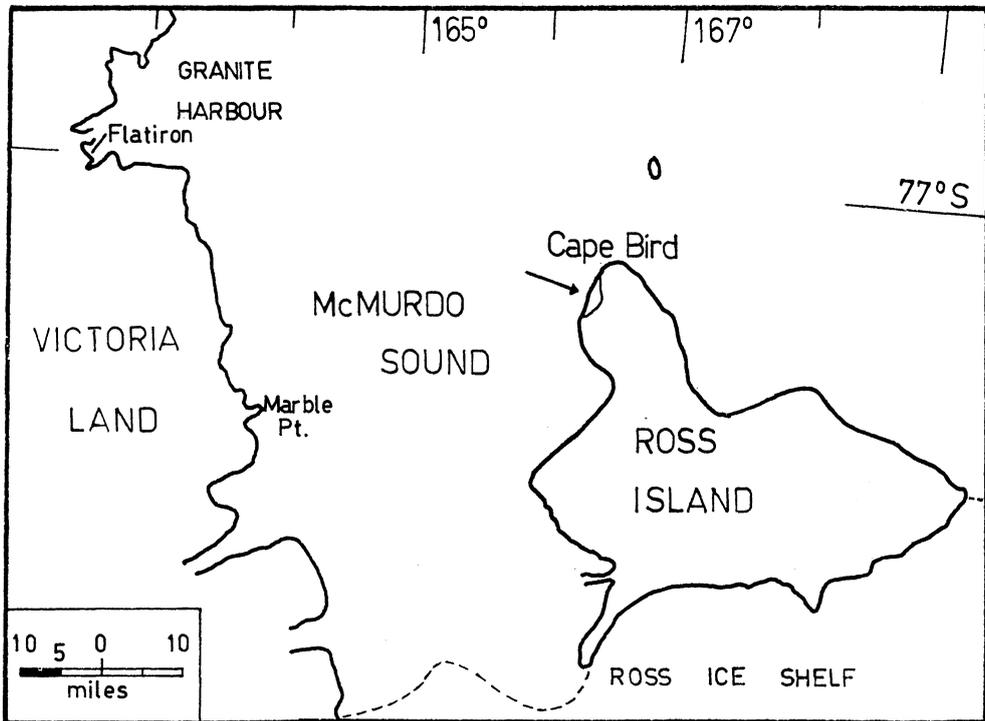


Fig. 1. McMurdo Sound area, Antarctica. Arrow points to the ice free zone of Cape Bird.

the distribution of plant types apparently depends upon the availability of water in particular microhabitats (Rudolph 1963). Algae also grow profusely in the basins that trap the melt water.

Large numbers of ciliates and rotifers are found in association with the algal ponds. Soil nematodes are also present. However, of the soil inhabiting arthropods present on the Antarctic continent only one species of Collembola (*Gomphiocephalus*) and two species of Acarina, *Stereotydeus mollis* Womersley & Strandmann and *Nanorchestes antarcticus* Strandmann, are found.

CLIMATE

Air temperature

Fig. 2a shows the average screen air temperatures over 5-day periods throughout the summer. Minimum daily temperatures were below 0°C throughout the season. Maximum screen temperatures above freezing were recorded on one day in November, 15 days in December, 29 days in January and on one day in February. From 18 December to 26 January the maximum temperatures were consistently above 0°C , the highest being recorded during the first and third weeks in January.

Soil temperature

The relative steepness of the scree slopes and their NW exposures increase the effectiveness of the solar radiation in heating the soil and consistently high maximum temperatures for both surface and subsurface regions were recorded throughout the season. The average surface and

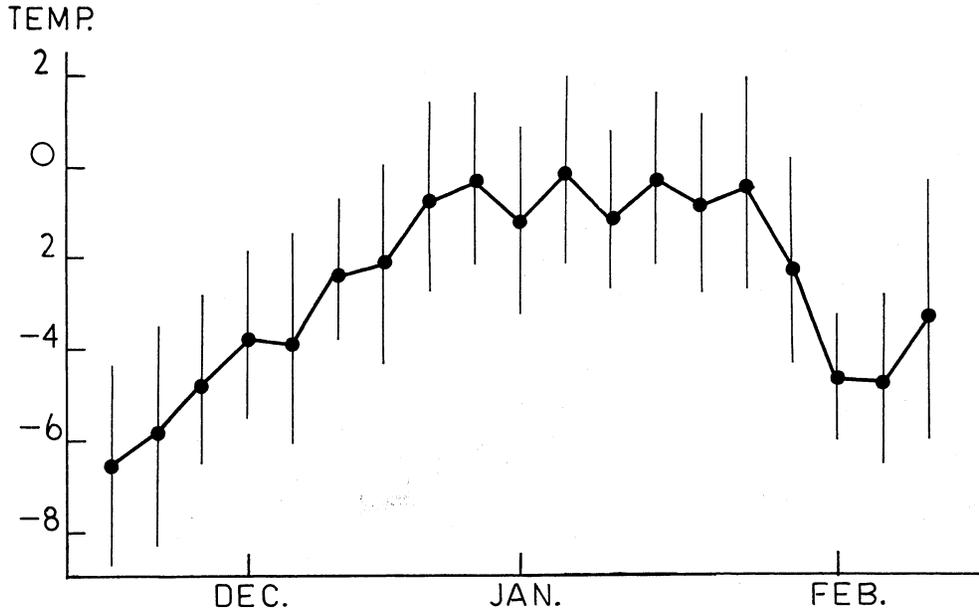


Fig. 2a. Average screen air temperatures (°C) over 5-day periods.

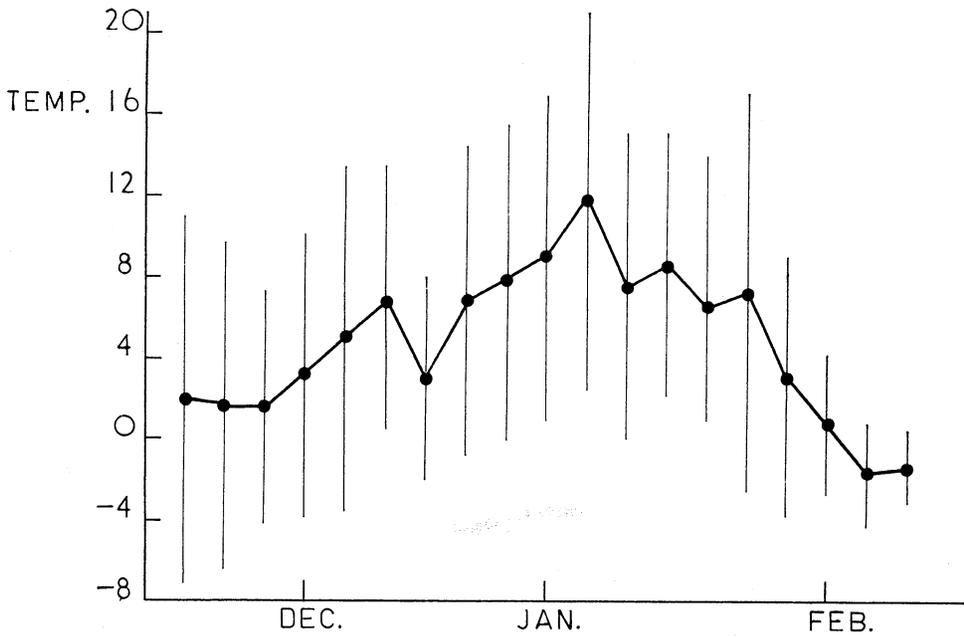


Fig. 2b. Average ground temperatures (°C) over 5-day periods.

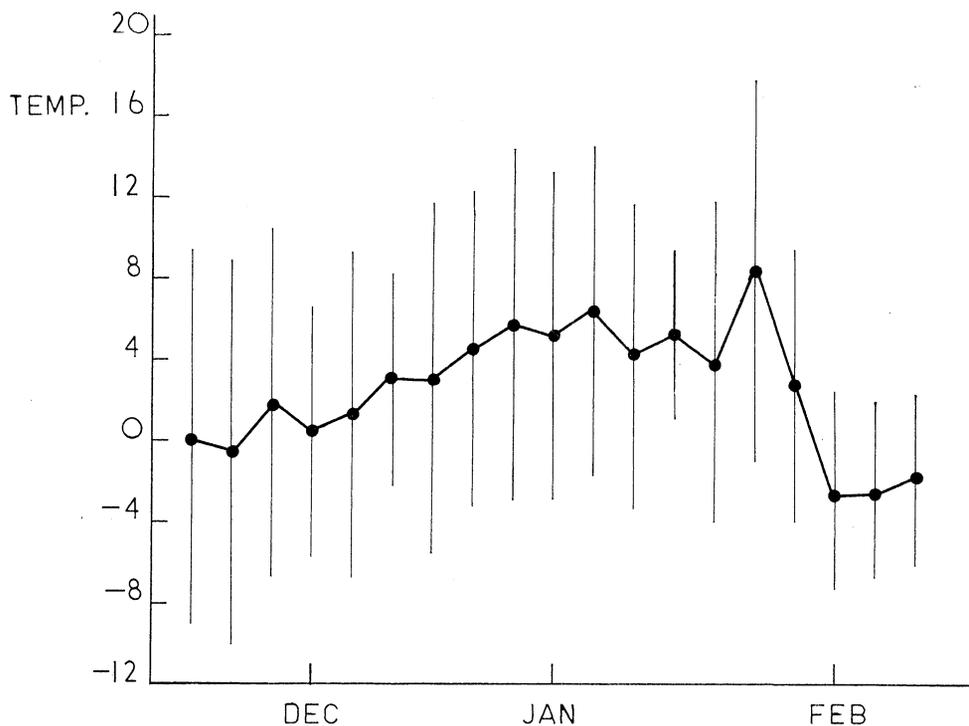


Fig. 2c. Average underground temperatures ($^{\circ}\text{C}$) over 5-day periods.

subsurface temperatures for the 5-day periods are shown in Fig. 2b, 2c. The mean surface temperatures were above 0°C for most of the season, the highest occurring during the third week in January. The highest subsurface temperatures, measured 2 cm below the surface, were recorded during the first week in January.

Wind

Air and soil temperatures are determined not only by the solar radiation levels but also by wind. Fig. 3 shows the monthly average wind speed, in miles per hour, and direction and also the cloud cover, in eighths, during the season.

The study area is particularly well sheltered, especially from southerly winds, which eddy about Ross Island and often appear as a light northerly breeze. Consequently the predominant surface wind is a light to moderate northerly, blowing for 27 days in December and for 20 days in January at an average speed, determined from counting anemometers, of 6.03 m.p.h. The area would often be in a light northerly even when a strong southerly wind was blowing 3 to 4 km off shore. This factor, together with the low general wind levels even further reduced by the dissected terrain, is probably one of the reasons which account for the very high densities of mites and collembola in this ice free area at Cape Bird.

MATERIALS AND METHODS

The field work was carried out at Cape Bird from mid-November 1967 until mid-February 1968, while I was a member of the University of Canterbury Antarctic Unit. Five transect lines

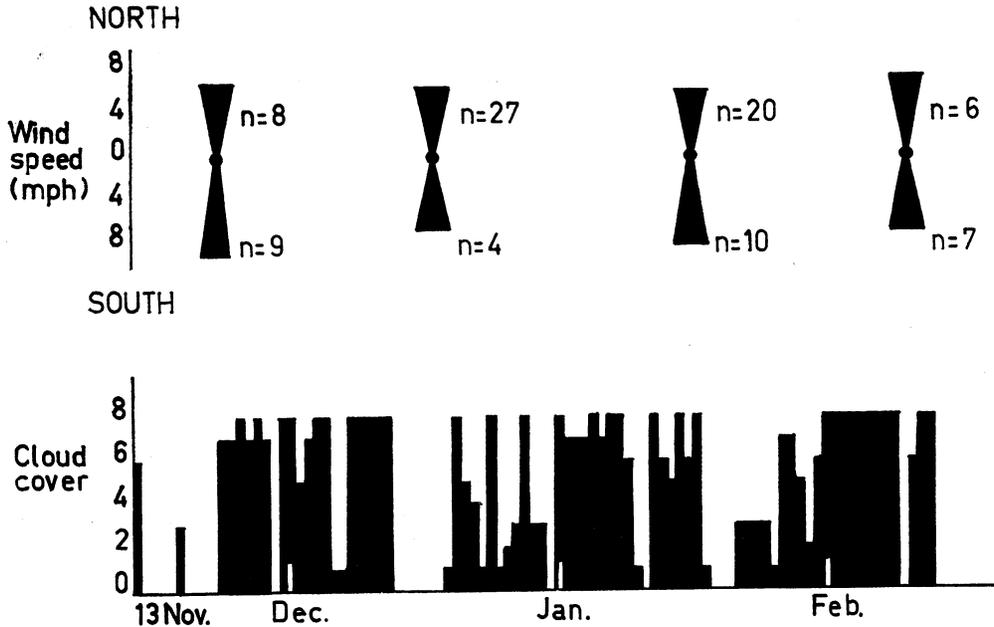


Fig. 3. Cloud cover and wind speed through the summer.

were set up in typical areas within the scree basins and stations of one square foot at yard intervals were established. Each transect line was sampled once a fortnight, weather permitting, the line being shifted 1 ft up the prevailing slope after each visit. A series of tests early in the summer established that few Collembola were present deeper than the surface layer of stones and later sampling was restricted to this depth. All stages of the three species of arthropods at each station were transferred to Weaver's chloral hydrate solution by a small camel hair brush. Weaver's solution caused none of the distortion found with alcohol fixing.

Temperatures throughout the season were obtained from three maximum and minimum thermometers, at 1.2 m above the ground, lying on the ground and buried just beneath the surface layer of stones respectively. Soil moisture content was not measured quantitatively, designations of dry, damp, wet and running water being made at each station when sampled. Cloud cover, wind speed and direction were also noted on each sampling date (Fig. 3).

Because there was no distortion in the fixative, length measurements of *Gomphiocephalus* from the tip of the head to the base of the anal horns, rather than head width or length were taken. The body lengths gave an appreciably greater spread to the measurements. The measurements were made using a binocular microscope with an ocular micrometer inserted into a 5 \times ocular in combination with a 10 \times objective. One ocular micrometer unit was equivalent to 18 μ m.

POSTEMBRYONIC DEVELOPMENT

Introduction

Since all Collembola are ametabolous, newly hatched individuals have the same general appearance as the adults. Postembryonic development is therefore confined to a gradual increase in size, a differentiation of certain imaginal characters and the attaining of sexual maturity. Because

Collembola continue to molt after reaching maturity, they have an indefinite number of instars depending upon length of life and environmental conditions. Growth, however, is not constant throughout their life history.

Agrell (1948) found that the total proportional change during the postembryonic development was reduced with increasing age and that after attaining a maximal size later ecdyses did not cause an increase in growth. Lindemann (1950) noted that size increments decreased once maturity was reached and South (1961) observed that although sexually mature *Entomobrya* continued to increase in size with each molt, their size increments were smaller. Green (1964) found evidence of senile molts in *Folsomia candida distincta* when although the mature individuals continued to molt throughout their entire life, after about the tenth instar their size and form changed very little. Most Collembola, therefore, pass through three growth stages (1) juvenile (2) postmaturity growth and (3) senile molts (Christiansen 1964).

The mature and juvenile forms of Collembola can be readily distinguished by the presence or absence of a fully developed genital plate. However, the distinction between successive instars of both age groups is very slight and it is difficult to determine the instar number, especially in the field. Nevertheless the determination of instars is basic to any life history studies on Collembola, for only then can one resolve such problems as the duration of each instar, the number of stages before sexual maturity, the total number of molts in the life of the species and the changing patterns in population structure throughout the year.

Determination of Instars

Most work on collembolan growth has been with laboratory cultured animals and only Agrell (1948), Hale (1965b) and Janetshek (1967b) have determined the number of instars from material collected in the field. The four methods that have been used in studying the growth of Collembola are: (1) size frequency distributions (Maclagan 1932; Agrell 1948; Hale 1965b; Janetshek 1967b; Pedigo 1967); (2) polymodal analysis using probability paper (Britt 1951); (3) the chaetotaxic development of successive instars (South 1961; Hale 1965b; Betsch 1967; Thibaud 1967) and (4) exuviae counts in cultures of individual animals (Green 1964). In this paper a combination of two methods was used. Mounted specimens of *Gomphiocephalus* were examined to correlate the chaetotaxic development of different instars determined by polymodal analysis.

Polymodal Analysis

Harding (1949) was the first to use normal probability graph paper in the analysis of bimodal, and in some cases trimodal, frequency distributions of biological measurements. Cassie (1950, 1954, 1963) has since extended this method to include all polymodal normal distributions, providing

Table 1. Mean length and observed size range for the first ten instars of *Gomphiocephalus*.

Instar	Mean length (mm)	Observed range (mm)
1	0.495	0.465—0.525
2	0.605	0.545—0.665
3	0.750	0.670—0.830
4	0.920	0.850—0.99
5	1.03	0.98 —1.08
6	1.12	1.08 —1.16
7	1.22	1.17 —1.27
8	1.30	1.27 —1.33
9	1.40	1.35 —1.45
10	1.49	1.46 —1.52

the modes are sufficiently distinct. Taylor (1965) has proposed a new method when the number of observations are small and/or there are many component curves, using moving averages with compensatory formulae to correct the subsequent distortion of parameters. Britt (1951) has been the only worker to apply this polymodal technique to Collembola. By this method he was able to estimate that individuals of *Hypogastrura armatus* 45 days old had passed through six instars.

Length measurements of *Gomphiocephalus* were obtained from a random sample from each transect line throughout the season. The cumulative frequencies of the size classes for each sampling date of the transect were plotted on probability paper. In this way it was hoped to show the numbers of instars, the progression of instars throughout the season and therefore the instar duration.

There were many component curves and a small number of observations for each curve. However, as each mode was clearly distinct, Cassie's method was used in the analysis. The mean length and observed size range of each instar are given in Table 1.

Development of Chaetotaxy in Successive Instars

The value of chaetotaxy in the taxonomy of Collembola has been recognised for some time

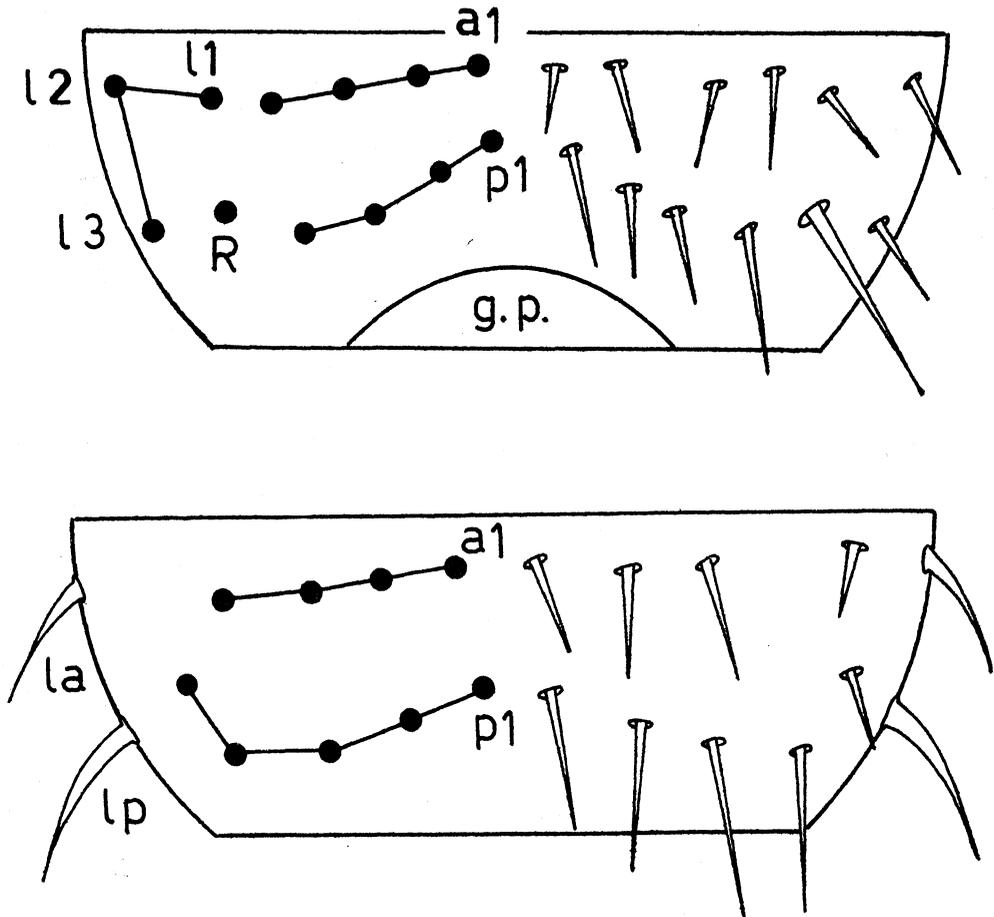


Fig. 4. Adult chaetotaxy on the ventral and dorsal surfaces of abdominal segment 5 (after Yosii 1960).

(Snider 1967), but it is only comparatively recently that chaetotaxic patterns, characteristic of successive instars, have been used in life history studies. South (1961) distinguished the five immature instars in British species of *Entomobrya* on the differing setae arrangements of the trochanteral organ. Hale (1965b) used the progressive development of the fifth abdominal segment to determine the instars in four species of the genus *Onychiurus*. Thibaud (1967) gave an extensive description of the changes in chaetotaxy during the postembryonic development of five species of Hypogastruridae. The basic chaetotaxy of this collembolan family has already been described and the nomenclature in this paper follows that of Yosii (1960).

Other studies have used the progressive development of the genitalia in the same way to determine the instars. Agrell (1948) showed a differentiation in the genital tract in the postembryonic development of *Hypogastrura sahlbergi* and *Folsomia 4-oculata*. Betsch (1967) studied the development of the genital orifice and the anal appendices in distinguishing the differences between male and

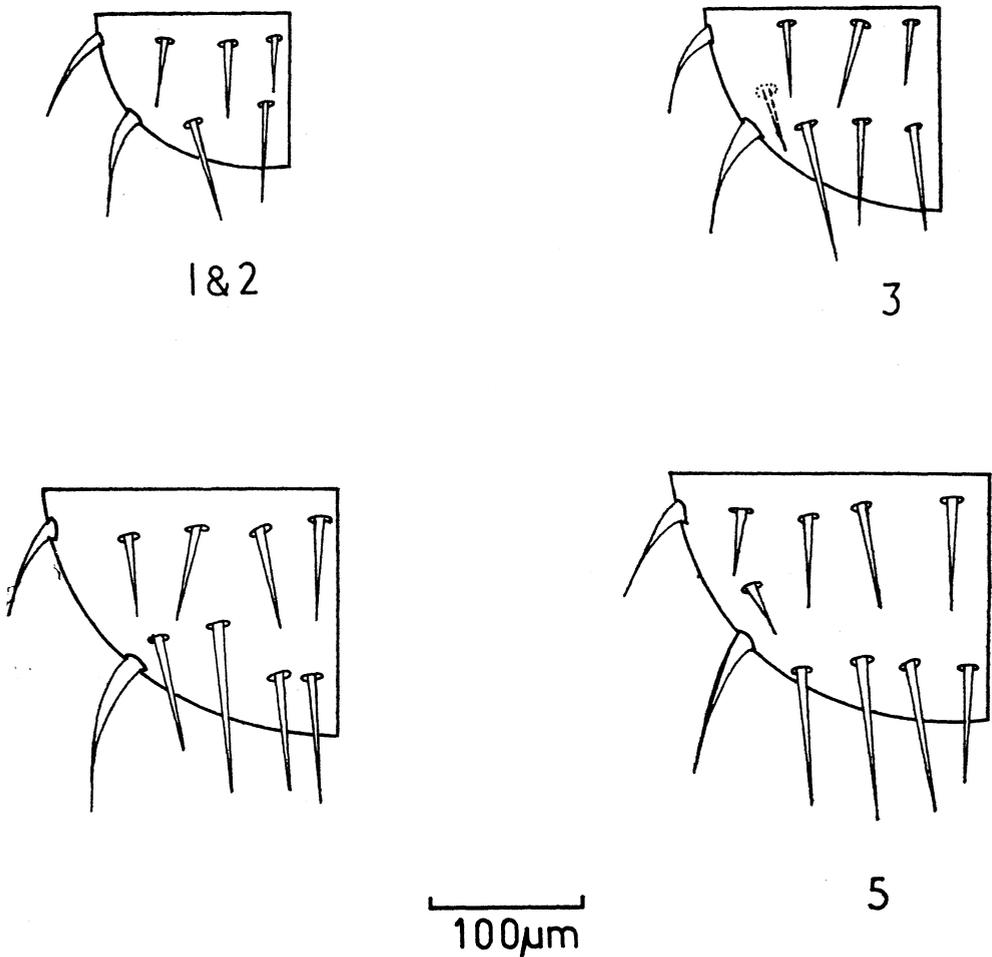


Fig. 5. The successive development of dorsal chaetotaxy on abdominal segment 5 of *Gomphiocephalus*.

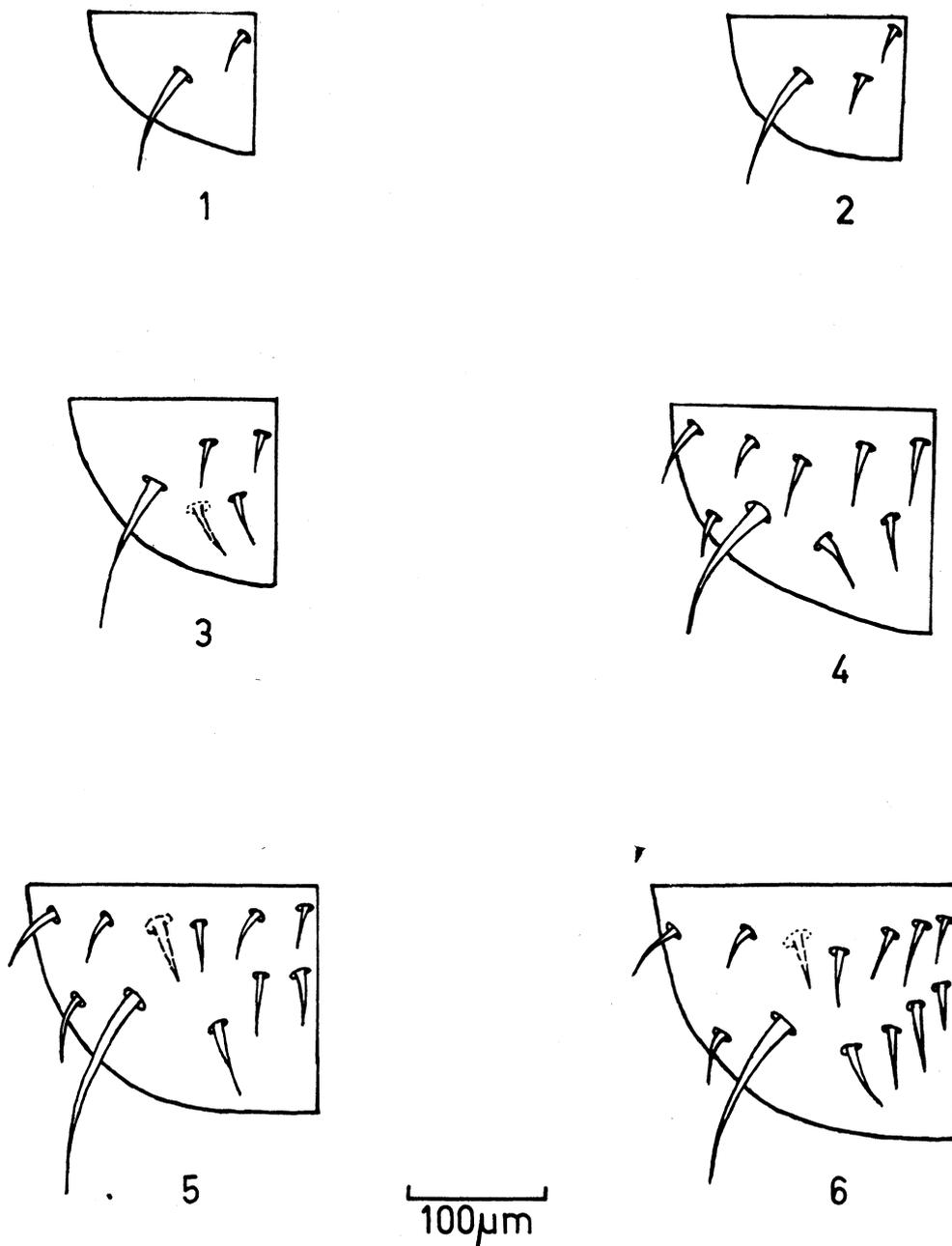


Fig. 6. The successive development of ventral chaetotaxy on abdominal segment 5 of *Gomphiocephalus*.

female instars in *Sphyrtotheca bellingeri*.

Gomphiocephalus varies in color from black to reddish brown and to observe the chaetotaxy the specimens must be cleared before mounting. It was found that specimens cleared sufficiently if the fixative (Weaver's Solution) was simply allowed to evaporate after the sample had been placed in a watch glass. After two to three days they were mounted in a glycerol-carbol fuschin mixture (100 : 1).

Fig. 4 shows the adult chaetotaxy on the ventral and dorsal surfaces of the fifth abdominal segment. The successive development of chaetotaxy, which could be closely related to the successive instars determined by polymodal analysis, is shown in Fig. 5 and 6. The prominent ventral setae (R) are present from the first instar and provide a reference for the subsequent development.

There is an increase in the number of setae from instar 1 until the maximum number is reached

Log. body length

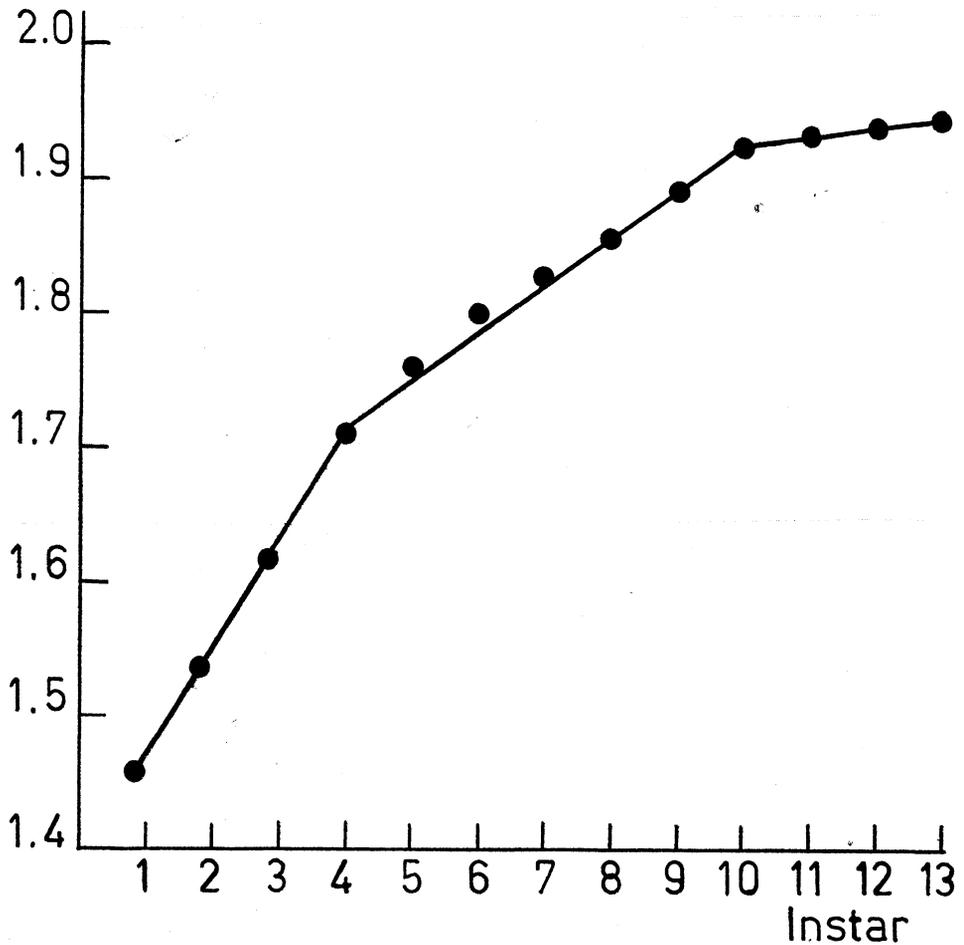


Fig. 7. Dyar's Rule for *Gomphiocephalus* showing the 3 growth phases.

in instar 6. The genital plate appears in instar 5 in both sexes, although in some specimens a few setae were present on the genital area in the fourth stage. After the fifth molt the genital plate has its full complement of setae. Little chaetotaxic variation was observed in the early stages, however considerable individual variations occurred with increasing development. These variations were more numerous on the dorsal surface where many combinations of the basic setae pattern of the instar appeared from the fourth instar onwards. This increase in individual variation with age has been recorded also by South (1961) and Thibaud (1967). The use of chaetotaxy alone in assigning individuals of *Gomphiocephalus* to different instars must therefore be used with caution.

The appearance of both male and female genital plates in the fifth instar suggests that *Gomphiocephalus* becomes sexually mature after the fourth molt.

Growth in Relation to Molting

The regularity of the magnitude of growth during ecdysis in arthropods was discovered first in the Stomatopoda (Brooks 1886) and later by Dyar (1890) in the successive instars of lepidopterous larvae. Subsequent workers on Crustacea have called this relationship Brook's Rule (Fowler 1909; Rice 1968), whereas entomologists have since been calling it Dyar's Rule (Maclagan 1932). This relationship is usually expressed by the equation $Y = K \cdot P^n$ where Y is the length of any measured part after n ecdyses. K and P are constants, P being the progression factor (Brook's or Dyar's factor). The rule is confirmed if a straight line is obtained when the logarithm of the measured part is plotted against the number of instars.

It has been shown that growth in many collembolan species can be described by Dyar's Rule (Maclagan 1932; Agrell 1948; Hale 1965b; Thibaud 1967) and it seems reasonable to assume that it is applicable to Collembola in general. In some cases Dyar's Rule reflects the three growth phases of Collembola. Thus Agrell (1948) showed a diminishing progression factor with increasing development, but there was no distinct decrease at any particular stage. Thibaud (1967) plotting the logarithms of various body measurements against the instar number of six species, found a point of inflexion at the fourth molting. As he was working with laboratory cultures he could correlate directly this change in growth with the appearance of eggs in the fifth instar.

In the present study, when the logarithm of the mean body length was plotted against instar

Table 2. Dyar's Factor and the instar number at which sexual maturity and maximum size is reached in various species of the Family Hypogastruridae.

Species	Dyar's Factor	Sexual Maturity	Max. Size	Reference
<i>Hypogastrura sahlbergi</i>	1.13	—	8	Agrell 1948
<i>H. manubrialis</i>		5-6	—	Ripper 1930
<i>H. purpurescens</i>		5-6	—	Strebel 1932
<i>H. armata</i>		3-4	—	Britt 1951
<i>H. denticulata</i>	1.19	5-6	6	Hale 1965 b
<i>Ceratophysella bengtssoni</i>	1.22	5	6-7	Thibaud 1967
<i>Schaefferia coeca</i>	1.25	5	6	" "
<i>S. willemi</i>	1.24	5	6	" "
<i>Mesogastrura ojcoviensis</i>	1.20	5	6	" "
<i>Mesachorutes quadriocellatus</i>	1.21	5	6	" "
<i>Gomphiocephalus hodgsoni</i>	1.147 (Juv.) 1.075 (Ad.)	5	—	This paper

number for each transect over the season, a straight line was obtained with a point of inflexion at the fourth molt (Fig. 7). There is also some evidence of a senile molt stage above instar 10.

The progression factors for the juveniles and adults of *Gomphiocephalus* were 1.147 and 1.075 respectively. The factor for the juvenile stages is comparable with those recorded for other species in the family Hypogastruridae (Table 2), however the factor for the postmaturity growth stage is somewhat smaller.

Conclusions

A consideration of two inter-related lines of evidence leads to fairly definite conclusions about the postembryonic development of *Gomphiocephalus*. Firstly there is the close correlation between the successive chaetotaxic development and the different instars determined by polymodal analysis. Secondly there is the confirmation of Dyar's Rule and the correlation between a change progression factor, indicative of a change in growth, and the appearance of the genital plate at the same molt. There is also a tendency for a reduction in growth with each molt above the tenth instar.

From these considerations it is concluded that *Gomphiocephalus* becomes sexually mature at the fifth instar and reaches maximum size after the tenth molt. The three phases of postembryonic growth therefore are (1) juvenile, instar 1—instar 4; (2) postmaturity growth, instar 5—instar 10 and (3) senile molts, above instar 11. This agrees well with previous work on the postembryonic growth of Collembola, especially in the family Hypogastruridae (Table 2), the majority requiring from four to six molts to reach sexual maturity (Christiansen 1964). Because no laboratory cultures were reared, nothing can be deduced from these observations about instar duration. This problem is very complex as there are many influencing factors, notably those of temperature and humidity (Thibaud 1968).

Janetschek (1967b), in his work on the growth and maturity of *Gomphiocephalus*, considered that Dyar's Rule was either invalid for the species, or so close to unity it was impossible to demonstrate by his method. He also concluded that *Gomphiocephalus* reached sexual maturity in the sixth instar. However, because of certain circularities of logic, the models upon which he bases his conclusions are suspect. The confirmation of Dyar's Rule in this paper also questions the validity of Janetschek's interpretations.

The different conclusions reached only establish the necessity of rearing larvae of the species or, at least, formally examining them for maturing ova. Either way would determine unequivocally the point of onset of sexual maturity.

THE SUMMER POPULATION

Factors Affecting Summer Populations of Antarctic Collembola

In his extensive review Janetschek (1967a) found that in general the presence of arthropods in South Victoria Land depends upon optimal inter-related conditions of temperature, relative humidity (RH) and soil moisture.

Because of their cutaneous respiration, the humidity of the environment is of immense importance in governing the distribution of Collembola. One must be careful, however, to distinguish between substrate moisture and relative humidity (Christiansen 1964). It has been estimated that 50% RH in the topsoil air could be the lower limit for arthropod life in South Victoria Land (Janetschek 1967a). The importance of soil water content is critical in maintaining an adequate humidity in the topsoil air. This is especially necessary for the survival of juveniles which are very susceptible to a saturation deficiency in the air surrounding them (Pryor 1962, Wallace 1967).

The occurrence of winter population peaks in other regions has been attributed to the direct influence of high soil moisture content and summer minima to the adverse effects of drying (Choudhuri & Roy 1967). Agrell (1941) considered the moisture content of the substrate of prime importance for the distribution of Collembola in different habitats. Hale (1967) and Challet & Bohnsack (1968) also found that the species composition of a collembolan population could be related to the water content of the soil and that changes in populations of Collembola were ultimately related to changes in water content of their habitat. This positive correlation with soil moisture is well documented for many species, including *Gomphiocephalus* (Christiansen 1964).

At Cape Bird, as in most coastal areas of South Victoria Land, the moisture regime of the soil is dependent upon the stored winter snow. Thawing of snow patches and ice along the Antarctic coast during early summer plays an important role in determining the soil moisture levels present at this time. Consequently a decrease in moisture level would be expected during the course of the season as the snow areas disappear, as there are few appreciable snowfalls over the summer. Because of the higher latitude, surface thawing at Cape Bird begins some two to three weeks later than at Cape Hallett (Pryor 1962). During the 1967–68 summer, as in the previous season (E. C. Young, pers. comm.), thawing began in late November—early December. The height of the thaw occurred during mid-December but by the end of the month only some slight seepage water remained except for the definite melt streams flowing off the Mt Bird ice cap, none of which occurred in the study area. During maximal thawing the varied topographical relief caused the expected extremes in patterns of moisture content from dry ridges and hummocks to flooded depressions. At the end of the thaw all parts of the area became very dry.

The interaction between temperature and soil moisture is well documented (Dhillon & Gibson 1962; Wallace 1967). Janetshek (1967a) has determined the limits of the temperature preferendum of *Gomphiocephalus* and it seems that the RH of the top soil air is of greater importance than environmental temperature in controlling the occurrence of free-living Collembola (Pryor 1967).

As in other parts of the world, flooding is a natural disaster which affects the Collembola of South Victoria Land. Various groups of Collembola behave differently on flooding (Kühnelt 1961). Some can migrate to the bank, others can survive submerged for long periods, death presumably ultimately occurring through oxygen lack. Pryor (1962) found that adults of *Isotoma klovstadi* at Cape Hallett could survive up to five days submersion. Although Kühnelt assumed that most Collembola survived flooding in the form of eggs, there are cases where saturated soils cause retardation in egg development and high mortalities (Wallace 1967).

Previous Population Work on *Gomphiocephalus*

Wise et al. (1964) found that peak population densities of *Gomphiocephalus* occurred during late November—early December, more than one month before the period of maximum and minimum mean microclimatic temperature records at each locality. However, Janetshek (1967a) has subsequently found that their data indicated a pronounced general decline in the density of *Gomphiocephalus* with increasing latitude. Furthermore, the first sampling at each locality always yielded the largest numbers and the first sampling of the two southernmost sites occurred one week before the two northern ones, thus inverse to the progress of the season with increasing latitude. Janetshek concluded that for Marble Point (Fig. 1), approximately the same latitude as Cape Bird, a population density in the second week of January comparable with that of the first week in December, if not higher, should be expected.

The results of Wise & Spain (1967) for the 1963–64 season contradict in some respects the results obtained during 1962–1963. The average densities throughout the season of the four quadrats from Granite Harbor and Marble Point have been calculated from the original data of Wise &

Table 3. Previous population numbers recorded for *Gomphiocephalus* in South Victoria Land.
(After Wise et al., 1967 Table 17)

Location	Date	Total Numbers	Density/sq.meter
Marble Point	19.11.63	10	2.5
	15.12.63	—	—
	11. 1.64	188	47
	10. 2.64	2	0.5
Flatiron	15.11.63	6	1.5
	16.12.63	43	10.8
	14. 1.64	750	187.5
	12. 2.64	243	60.8

Spain and shown in Table 3. There is a marked increase during the first two weeks in January followed by a decline to the middle of February. Whether or not much validity can be given to these data is debatable since the numbers of "small" individuals are low, and their percentage of

Density

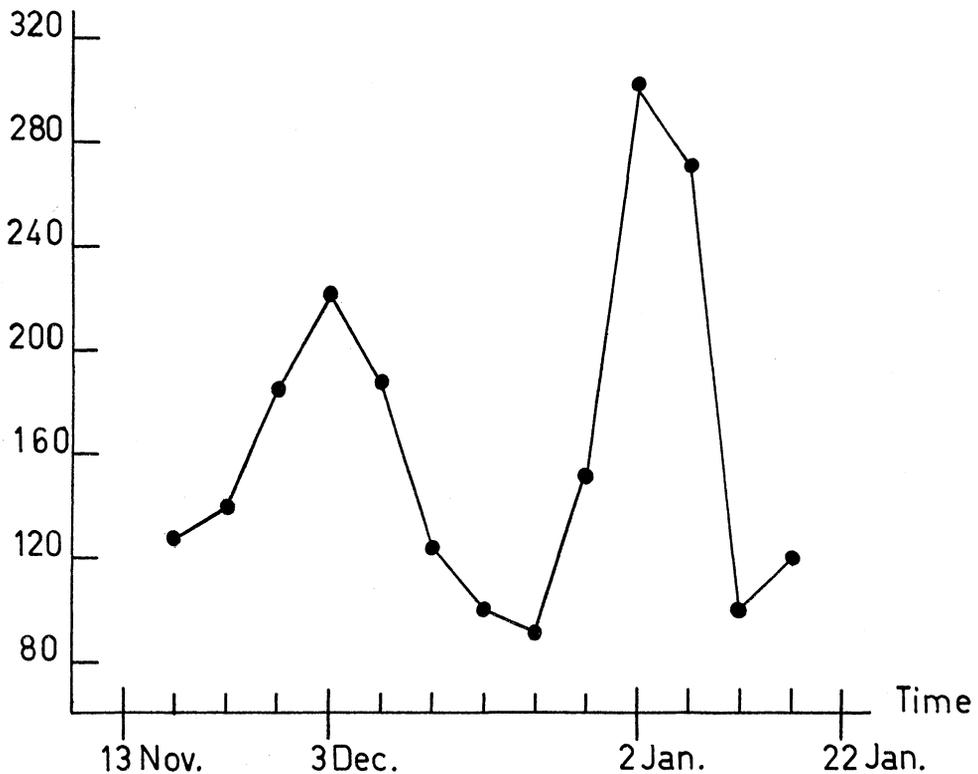


Fig. 8. Total density (per sq. ft) of *Gomphiocephalus* for each 5-day interval over the summer.

the total numbers gives no indication of a growth pattern. However, both sites do give some indication of peak densities during the beginning of January.

The Cape Bird Population

The total density of all the transects for each five-day interval is shown in Fig 8. There is an increase in numbers from the beginning of the season to the end of November. Numbers fall markedly during the middle of December and then increase rapidly from the end of December through to the first week in January. There is a second sharp decline during mid-January but numbers were again increasing at the date of departure from Cape Bird.

Summer Mortality

The variations in soil moisture content of the microenvironment that occur throughout the season are probably the major cause of the observed fluctuations in the numbers of this population of *Gomphiocephalus*. *Gomphiocephalus* tolerates soil moisture levels between 3% and 12%, specimens being found inactive when values are below 3% and absent when values are below 2% or above 12% (Wise et al. 1964).

The decline in numbers during mid-December can be correlated with the increase in soil water due to the melting of the winter snow. During the height of the thaw when the soil water content was well above the upper limit of tolerance for the species, the decrease in numbers is most likely

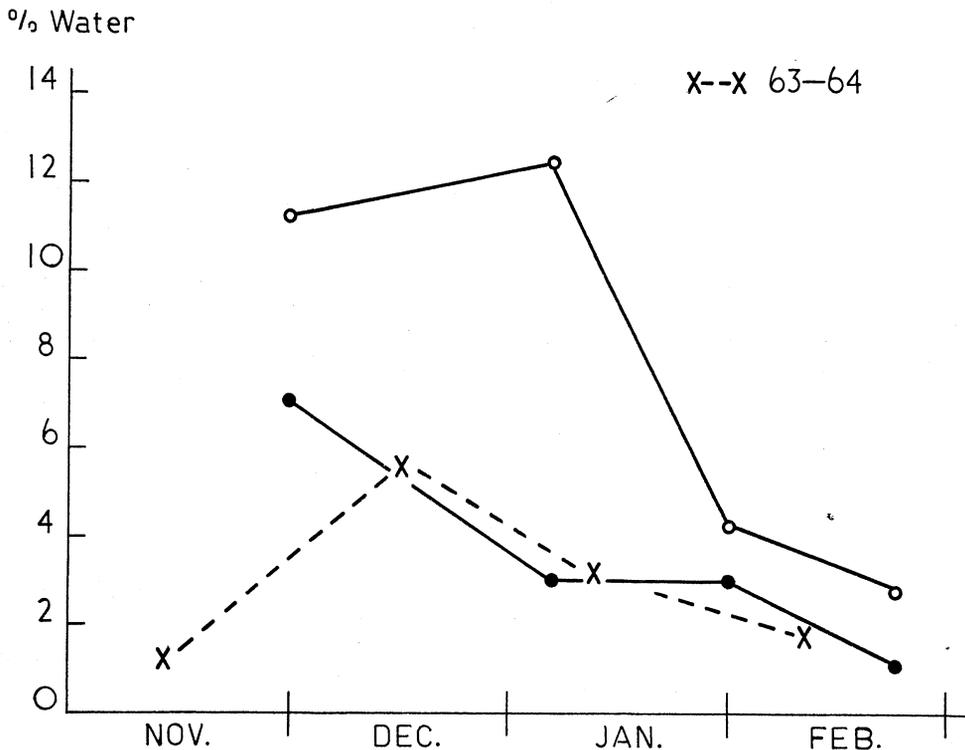


Fig. 9. Percentage soil moisture in the McMurdo Sound area over the summer. ○—○ Marble Point 1962-63, ×---× 1963-64, ●—● Granite Harbor 1962-63 (after Wise et al. 1964).

due to death by drowning. Because of their extremely sluggish motion large numbers of *Gomphiocephalus* become trapped in the surface film of melt-water pools among the surface stones. The mites present, however, can move across the water with consummate ease. As in previous studies (Wise et al. 1964; Janetschek 1967a), mites were found in greatest numbers adjacent to the wetter zones of the transects, and in these wetter areas, the proportion of mites to collembolans was higher than in the drier areas. Although this is probably due to the difference in moisture tolerance between the two species, other factors such as food and the mechanical ability to survive surface flooding are also involved.

While the decrease in numbers during December is due to flooding, the decrease in January is due to the opposite effect, that of the intense drying of the substrate. The overall percentage soil moisture content of coastal South Victoria Land shows a sharp decline towards the end of summer, values dropping below 2% in mid-February (Fig. 9). Maximum mean underground temperatures were recorded at Cape Bird during the beginning of January (Fig. 2c) and although within limits a rise in temperature should be accompanied by an increased reproductive rate, it must be assumed that the favorable effects of increased temperature have been mitigated by the unfavorable influence of reduced soil moisture content. It can be safely concluded that the decrease in population numbers during the period of high temperatures and lowered soil moisture content is due to death of the animals by desiccation. The possibility of either vertical or horizontal migration in relation to changing moisture patterns is discussed later.

Summer Natality

Although Wise & Spain (1967) concluded that with the possible exception of the very beginning of the season, eggs of *Gomphiocephalus* were present and hatched throughout the summer, none were found at Cape Bird until the last week in December. The eggs, with a diameter of 12–14 μm , were lustrous white and occurred in clusters of three or more. Though when present they were very obvious in the substrate and the continual presence of juveniles during the summer would suggest that eggs were hatching throughout the season, it was surprising that none were found before the end of December. However, the large increase in numbers of juvenile instars which occurred at this time can be correlated with the finding of eggs.

At the start of the season, as soon as the ground becomes exposed, topsoil and stone temperatures quickly rise into the preferendum range of *Gomphiocephalus*, during times of radiation influx, due to the low albedo. Moisture content increases with increasing melt processes and it is expected that population densities show a corresponding increase during this "spring" period. However, this increase is curtailed by the onset of flooding. Bellinger (1954) concluded that the great increase in numbers of *Collembola* that occurred during spring was presumably correlated with the combined favorable effects of rising temperatures and abundant moisture supplied by the melting snow cover.

The main regrowth of the Cape Bird population occurred through the last week in December to the first week of January. The increase in numbers towards the end of January was most likely due to increased moisture content in sheltered niches arising from early "autumn" snow at a time when mean underground temperatures were still warm enough to allow melting and offset the general decline in soil moisture. Wise et al. (1964) found numbers of eggs and recently hatched juveniles at Lake Penny (78° 16' S) on 22 February 1963, indicating a gradual increase in numbers towards the close of the season. Similarly Gless (pers. comm.) attributed the rise in collembolan density at Cape Hallett during the latter part of the season to an increase in available water from early autumnal snows coupled with above freezing temperatures.

Conclusions

The large numbers of *Gomphiocephalus* at Cape Bird in the first week of January confirms

Janetschek's (1967a) prediction that peak population densities should occur at this time. It is not clear whether or not there are any inherent reproductive rhythms in *Gomphiocephalus* although Wise & Spain (1967) demonstrated a diurnal rhythm of activity. However, natural populations of soil Collembola in Antarctica, as in other parts of the world (Christiansen 1964) are probably influenced more by environmental fluctuations.

AGE STRUCTURE OF *GOMPHIOCEPHALUS* THROUGHOUT THE SUMMER

Life cycles of Collembola in cold climates

In arctic Sweden Agrell (1941) recorded two generations in one year in *Folsomia quadrioculata*. Workers in subarctic areas of Britain have found that most species have only one, or at the most two, generations per year (Milne 1960, 1962; Hale 1965a, 1966). In coastal South Victoria Land, the extreme low temperatures during the long winter period result in a short reproductive season in the summer. Antarctic Collembola, therefore, are most likely to be restricted to one or two generations a year.

Janetschek (1967b) stated, somewhat ambiguously "that the actual number of generations that can start development and reach maturity within the same season (without hibernation) is nine at the Cape Crozier site." However, as he had previously postulated a period of 38.5 days to reach sexual maturity, and as he considered the length of the breeding season to be no more than 90 days, his data predict that there must be no more than two generations of *Gomphiocephalus* a year.

Fecundity and egg development

In cold climates, probably fewer than 100 eggs are laid by most species of Collembola during the life time of a single female (Hale 1965a). Egg development is dependent upon temperature and at optimal temperatures the eggs require between five and ten days to hatch although the observed range is from 2 to 40 days (Christiansen 1964). Hale (1965a) found that the development of eggs of subarctic species varied from 16 to 50 days depending upon the species and the time of oviposition. Because no laboratory cultures were reared in the present study, the fecundity and time for egg development of *Gomphiocephalus* is not known. However, by considering the changes in population structure through the summer the time for egg development can be estimated.

A Physiological time scale for *Gomphiocephalus*

The properties of antarctic collembolan populations, as for all poikilothermic organisms, cannot be expressed in terms of time alone because temperature, at least, must also be considered. Consequently, homologous measurements of the populations have to be expressed as rates per unit of physiological time. Given steady birth and death rates per physiological time unit, a population would be expected to develop a stable instar distribution in the form of a geometric progression of the successive instars (Hughes 1962).

The physiological time scale, PT, can be related to absolute scales by the expression

$$PT = T \left(\frac{R_T}{R_0} \right) \quad (i)$$

where T is the absolute time. The respiratory rates R_T and R_0 at temperatures T and T_0 respectively, are related by the Respiratory Quotient, Q_{10} , defined as

$$Q_{10} = \left(\frac{R_T}{R_0} \right) \frac{10}{T - T_0} \quad (ii)$$

from (i) and (ii)

$$PT = T \cdot Q_{10} \frac{T - T_0}{10} \quad (\text{Duncan 1969})$$

Hence if Q_{10} for the species is known then a physiological time scale can be calculated.

Unfortunately no Q_{10} value for *Gomphiocephalus* has been recorded. However Zinkler (1966) found that Q_{10} values of five species of Collembola lay within the range of 2 to 3 and a mean value of 2.6 has been tentatively assumed for *Gomphiocephalus*. A mean underground temperature value of $+5^\circ\text{C}$ has been taken as the base temperature (T_0). This lies within the temperature preferendum limits of $+2.5^\circ\text{C}$ to $+16.5^\circ\text{C}$ of *Gomphiocephalus* determined by Janetschek (1967a).

Fig. 8 has been replotted using the calculated physiological time scale as shown in Fig. 10. This gives a better representation of the effect of temperature on the changes in numbers over the season.

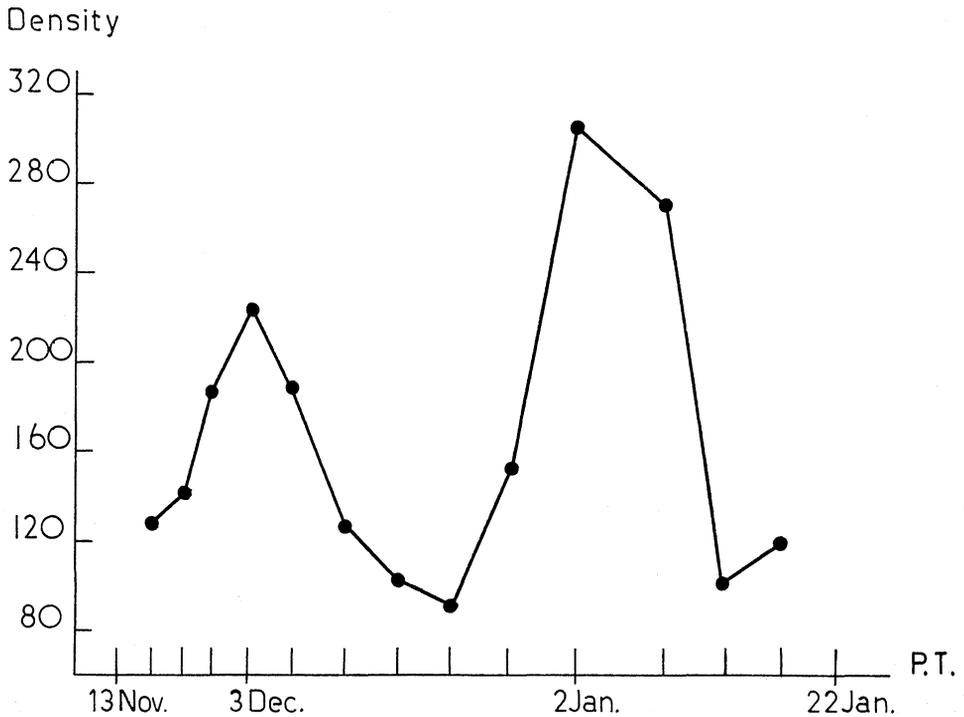


Fig. 10. Population density (per sq. ft) over the summer in relation to physiological time.

Progression of instars throughout the summer

From the frequency percent changes determined by polymodal analysis, the instar distribution of the population at equal intervals of PT, from Fig. 10, has been calculated and shown in Fig. 11. The main recruitment came at PT_6 and PT_7 (end of December—beginning of January) as indicated by the large percentage of juveniles and by the rise in total numbers. This variation in age distribution with population growth has been shown in other collembolan species (Milne 1962). The increase in numbers at PT_2 and PT_3 (end of November—beginning of December) can also be related to an increased percentage of juveniles. There is an indication that the decrease in numbers occurring during the summer may be due to a differential mortality of the juveniles and also of the

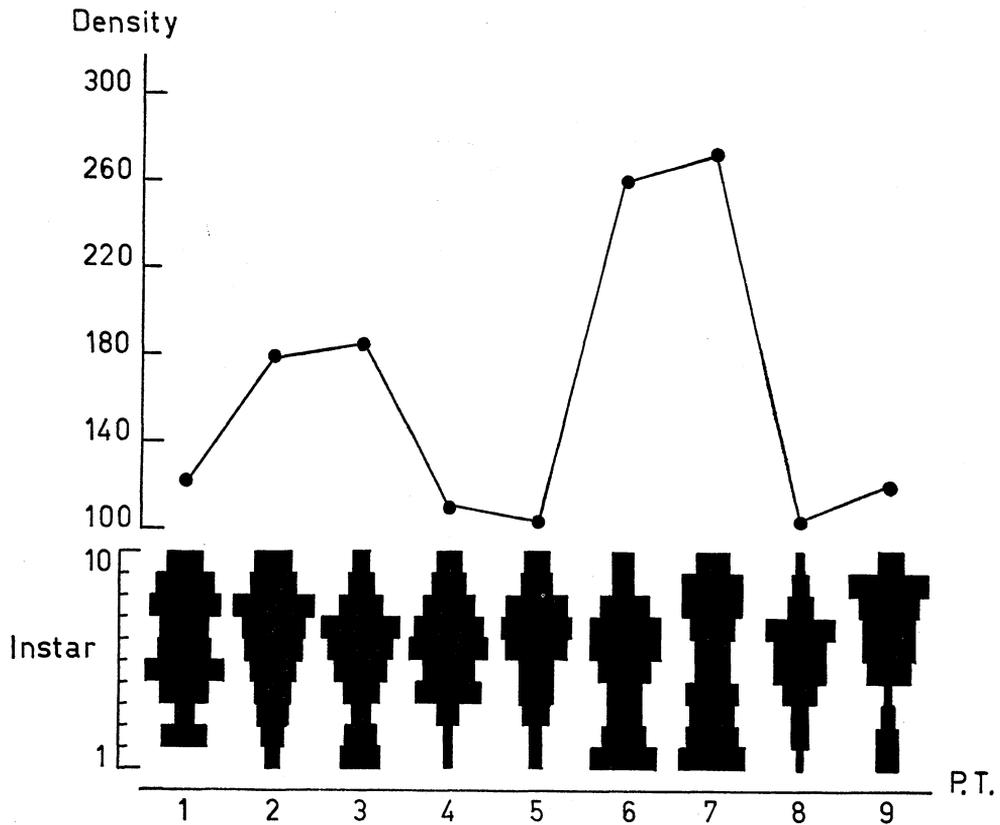


Fig. 11. Changes in population structure of *Gomphiocephalus* over the summer.

older instars. This is especially evident during the drought conditions in January (PT₈). No estimation of the duration of each instar can be made although Fig. 11 does indicate an increasing rate of development with increasing temperature, an observation that is well documented for other species (Hale 1965a).

Conclusion

Fig. 12 depicts a tentative explanation for the changes in age structure, and numbers of *Gomphiocephalus* throughout the summer. It consists of two inter-locking series of generations and it shows that in 'good' summers there are two generations of *Gomphiocephalus*. However the division between winter and summer is extremely variable and the number of generations depends upon environmental conditions at the beginning and end of summer. If the summer season is shortened either by the early onset of winter or the late arrival of spring then only one generation of *Gomphiocephalus* is possible. The model also shows that *Gomphiocephalus* can over-winter in all stages.

A time of approximately 30 days for egg development has been assumed. Hale (1965a) noted that over-wintering eggs of *Dicrytoma* spp. apparently develop more slowly than summer eggs, but it is not known whether the same thing occurs in *Gomphiocephalus*.

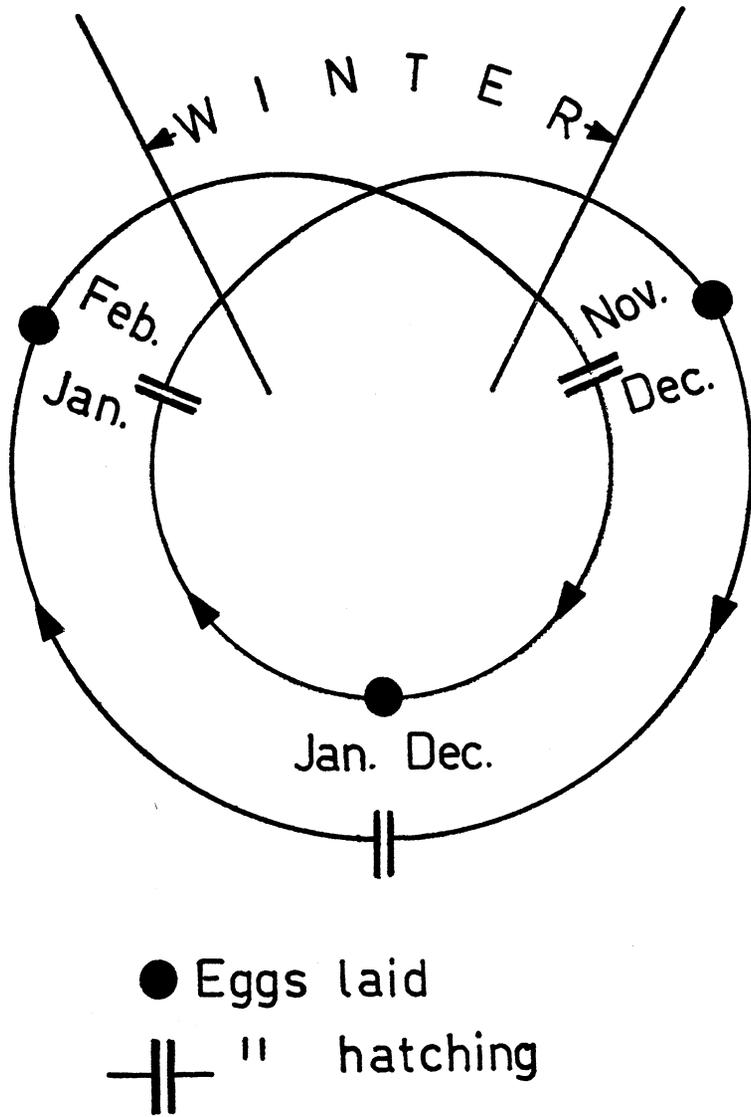


Fig. 12. Postulated inter-relationship of generations of *Gomphiocephalus* at Cape Bird.

GENERAL DISCUSSION

It is generally considered that the harsh climatic conditions of terrestrial Antarctica represent the most stringent conditions for life. Therefore it is not surprising that the terrestrial life is extremely poor, the total fauna consisting of little more than 150 species (Gressitt 1965). This paucity of land fauna is due to three factors—first, the hostile cold-desert climate of the few ice-free areas in which biota can develop; second, the former extensive pleistocene glaciations leaving very few available refugia; and third, the extensive isolation reducing chance colonisation (Janetschek 1967a). However the restrictions of the environment may not be as severe for small animals where differences

between general prevailing conditions and those in the microhabitat are significant. Fig. 2b and 2c show that microhabitat conditions permit collembolan development at times when the external ambient temperature would seem to preclude it.

The high densities of *Gomphiocephalus* at Cape Bird imply that the species is well adapted to the prevailing conditions. Janetshek (1967a) concluded that the lethal cold temperature of *Gomphiocephalus* was $-24 \pm 4^\circ\text{C}$. No records are available for the winter underground temperatures at Cape Bird, however at Cape Hallett the winter minimum was -26.4°C at a depth of 10 cm (Pryor 1962). *Gomphiocephalus* should therefore have no difficulty in surviving the winter especially as over-wintering niches are not so deep in the soil and therefore not subjected to such low temperatures.

Winter hardiness seems to be due to the slowing down of metabolic functions in a conformable way, ultimately to a very low level, and also to the avoidance of intracellular ice formation (Downes 1965). Janetshek (1967a) found a correlation between the rate of ambient cooling and the onset of cold stupor in *Gomphiocephalus*. The slower the rate of cooling the lower was the temperature at which the stupor set in. Also cold stupor could occur above 0°C but with slower cooling rates, the inactivating temperature could be lowered still further, probably close to -4°C with very low gradients. This cold adaption towards the end of the season probably results in an increase in frost resistance before hibernation starts. Intracellular ice formation can be avoided by dehydration or by increasing the concentration of glycerol (Salt 1961), but the situation is not fully understood. There is no doubt that in South Victoria Land dehydration could be operating to some extent to decrease the freezing point of the body fluids of Collembola. Pryor (1962) believed that the great reduction in the adult population of *Isotoma klovstadi* in winter was due to extreme dehydration. The gradual onset of cold hardiness in *Gomphiocephalus* towards the end of the season could be explained if the formation of some physiological mechanism was necessary. Whether or not this is the production of glycerol will not be known until more work on the cold adaption of *Gomphiocephalus* is done.

Gomphiocephalus would be expected to fully exploit the available environmental conditions either by a choice of habitat or by a behavioral response, or both. It is not surprising therefore that the understone niche inhabited by *Gomphiocephalus* possesses a more stable microclimate than either the surrounding soil or upper stone surfaces. Seasonal vertical migration is doubtful. The movement between the under and upper stone surface is a direct response to the prevailing conditions of temperature and humidity, rather than a migration controlled by more remote stimuli. From observations, eggs are laid somewhat deeper, mainly on the lower sides of stones projecting some 6–10 cm into the soil. Climatically this could be a more protected site or it could be that the eggs are laid in areas outside the normal habitat to reduce interference from adult Collembola or possibly from predation by the mites.

Despite the concept that collembolan populations in South Victoria Land shift in relation to a favored moisture belt some distance below snow patches, no proof of this migration was obtained at Cape Bird. During certain days, possibly of higher humidity, many individuals of *Gomphiocephalus* were very active on the surface of stones. However an analysis of the direction of these movements over a period of time when *Gomphiocephalus* occurred in large enough numbers did not indicate a definite directional migration. Rather the movement was found to be completely random. This does not mean that this migration pattern could not occur earlier in the season before all the snow has melted.

Wind is not important in the horizontal distribution of arthropods in South Victoria Land and

the most important factor in the horizontal dispersal of *Gomphiocephalus* is the melt water runoff. This passive mechanism probably influences the entire pattern of distribution at Cape Bird over the seasons. However only when the changing patterns of the isochiones are mapped over a period of some years will the influence of melt processes on the microdistribution of *Gomphiocephalus* be understood.

SUMMARY

Regular samples of the Antarctic collembolan, *Gomphiocephalus hodgsoni*, were taken during the 1967–68 summer from Cape Bird, Ross Island.

Maximum population densities occurred in early January with a minor peak during late November—early December.

Instars were determined by polymodal analysis of the total body length and correlated to the successive development of chaetotaxy of the fifth abdominal segment.

The number of instars to sexual maturity was four and no definite maximum size was reached. Dyar's Rule was found to be applicable to the species.

The instar distribution varied with the population growth over the season and a model of two inter-locking generations was proposed to describe the phenology of *Gomphiocephalus* at Cape Bird.

Acknowledgements: During this study I was privileged to be a member of the University of Canterbury Antarctic Unit under the leadership of Dr E. C. Young and I am greatly indebted to him for his guidance and critical observations. I am also grateful for the cooperation of the Zoology Department, University of Canterbury and the Antarctic Division of the D.S.I.R. (Wellington, New Zealand). The logistic support of the United States Navy Squadron VX-6 is also acknowledged. The investigation was financially supported by a bursary from the Canterbury Branch of the New Zealand Antarctic Society.

REFERENCES

- Agrell, I.** 1941. Zur ökologie der Collembolen. *Opusc. ent. Suppl.* **3**: 1–236.
1948. Studies on the post-embryonic development of Collembola. *Ark. Zool. A* **41**(12): 1–35.
- Bellinger, P. F.** 1954. Studies of soil fauna with special reference to the Collembola. *Bull. Conn. agric. Exp. Stn* **583**: 1–67.
- Betsch, J.-M.** 1967. Remarque sur le développement de l'orifice génital et de l'appendice anal de *Sphyrotheca bellingeri* n. sp. *Rev. Ecol. Biol. Sol* **2**(4): 525–33.
- Britt, N. W.** 1951. Observations on the life history of the Collembolan *Achorutes armatus*. *Trans. Am. microsc. Soc.* **70**: 119–32.
- Brooks, W. K.** 1886. Report on the Stomatopoda. Rep. Scient. Results explor. Voyage Challenger, Zoology **16**(65): 1–116.
- Carpenter, G. H.** 1908. Insecta Aptera. National Antarctic Expedition 1901–1904. Nat. Hist., *IV* (Zool.), 5 pp.
- Cassie, R. M.** 1950. The analysis of polymodal frequency distributions by the probability paper method. *N.Z. Sci. Rev.* **8**: 89–91.
1954. Some uses of probability paper in the analysis of size frequency distributions. *Aust. J. mar. freshwat. Res.* **4**(1): 513–22.
1963. Tests of significance for probability paper analysis. *N.Z. J. Sci.* **6**: 474–82.
- Challet, G. L. & K. K. Bohnsack.** 1968. Distribution and abundance of Collembola at Pt. Barrow, Alaska. *Pedobiologia* **8**: 214–22.
- Choudhuri, D. K. & S. Roy.** 1967. Qualitative composition of the collembolan fauna of some uncultivated fields in Nadia district (West Bengal) with a correlation between monthly population and individual soil factor. *Rev. Ecol. Biol. Sol* **4**(3): 507–15.

- Christiansen, K.** 1964. Bionomics of Collembola. *Ann. Rev. Ent.* **9**: 147-78.
- Dhillon, B. S. & N. H. E. Gibson.** 1962. A study of the Acarina and Collembola of agricultural soils. I. Numbers and distribution in undisturbed grassland. *Pedobiologia* **1**: 189-209.
- Downes, J. A.** 1965. Adaptations of insects in the arctic. *Ann. Rev. Ent.* **10**: 257-74.
- Duncan, K. W.** 1969. The ecology of two species of terrestrial Amphipoda living in waste grassland. *Pedobiologia* **9**: 323-41.
- Dyar, G.** 1890. The number of molts in Lepidopterous larvae. *Psyche* **5**: 420-22.
- Fowler, G. H.** 1909. Biscayan plankton collected during a cruise of H.M.S. 'Research', 1900. Part XII; The Ostracoda. *Trans. Linn. Soc., Lond.* (2) Zool. **10**: 219-336.
- Green, C. D.** 1964. The life history and fecundity of *Folsomia candida* (Willem) var. *distincta* (Bagnell) (Collembola: Isotomidae). *Proc. R. ent. Soc. Lond.* A **39**(7-9): 125-28.
- Gressitt, J. L.** 1965. Terrestrial Animals. In *Antarctica* (ed. T. Hatherton), chap. 14, 351-71. Reed, New Zealand.
- Gressitt, J. L. & J. Shoup.** 1967. Ecological notes on free-living mites in North Victoria Land, Antarctic Res. Ser. **10**: 307-20.
- Hale, W. G.** 1965a. Observations on the breeding biology of Collembola. *Pedobiologia* **5**: 146-52, 161-77.
1965b. Postembryonic development of some species of Collembola. *Pedobiologia* **5**: 228-43.
1966. A population study of moorland Collembola. *Pedobiologia* **6**: 65-99.
1967. Collembola. In *Soil Biology* (ed. A. Burgess & F. Raw), chap. 12, 397-411. Academic Press, London.
- Harding, J. P.** 1949. The use of probability paper for the graphical analysis of polymodal frequency distributions. *J. mar. biol. Ass. U.K.* **28**: 141-53.
- Hughes, R. D.** 1962. A method for estimating the effects of mortality on aphid populations. *J. Anim. Ecol.* **31**: 389-96.
- Janetschek, H.** 1963. On the terrestrial fauna of the Ross Sea area, Antarctica. *Pacif. Ins.* **5**(1): 305-11.
1967a. Arthropod ecology of South Victoria Land. Antarctic Res. Ser. **10**: 205-93.
1967b. Growth and maturity of the springtail *Gomphiocephalus hodgsoni* Carpenter, from South Victoria Land and Ross Island. *Ibid.*, 295-305.
- Kühnhelt, W.** 1961. *Soil Biology*. 395 p. Faber & Faber, London.
- Lindemann, W.** 1950. Untersuchungen zur postembryonalen entwicklung schweizerischer Orchesellen. *Rev. suisse Zool.* **57**: 353-428.
- MacLagan, D. S.** 1932. An ecological study of the 'lucerne flea' (*Smynturus viridis* L.). *Bull. ent. Res.* **23**: 101-45, 151-90.
- Milne, S.** 1960. Studies on the life histories of various species of Arthropleone Collembola. *Proc. R. ent. Soc. Lond.* A **35**: 133-40.
1962. Phenology of a natural population of soil Collembola. *Pedobiologia* **2**: 41-52.
- Pedigo, L. P.** 1967. Selected life history phenomena of *Lepidocyrtus cyaneus* f. *cinereus* Folsom with reference to grooming and the role of the colophore. *Ent. News* **78**(10): 263-67.
- Pryor, M. E.** 1962. Some environmental features of Hallett Station, Antarctica, with special references to soil arthropods. *Pacif. Ins.* **4**(3): 681-728.
1967. Concerning the current status of terrestrial arthropod surveys in Antarctica. *Inform. Byul. Sov. Antarkt. Eksp.* **59**: 231-34.
- Rice, A. L.** 1968. Growth 'rules' and the larvae of decapod Crustaceans. *J. nat. Hist.* **2**(4): 525-30.
- Ripper, W.** 1930. Champignon—Springschwänze—Biologie und Bekämpfung von *Hypogastrura manubrialis* Tullberg. *Z. angew. Ent.* **16**: 547-84.
- Rudolph, E. D.** 1963. Vegetation of Hallett Station area, Victoria Land, Antarctica. *Ecology* **44**(3): 585-86.
- Salt, R. W.** 1961. Principles of insect cold-hardiness. *Ann. Rev. Ent.* **6**: 55-73.
- Snider, R. J.** 1967. The chaetotaxy of North American *Lepidocyrtus* s. str., (Collembola, Entomobryidae). *Contr. Am. ent. Inst.* **2**(3): 1-28.
- South, A.** 1961. The taxonomy of the British species of *Entomobrya* (Collembola). *Trans. R. ent. Soc. Lond.*

113(13): 387-416.

- Strebel, O.** 1932. Beiträge zur Biologie, Ökologie und Physiologie einheimischer Collembolen. *Z. Morph. Ökol. Tiere* **25**: 31-153.
- Taylor, B. J. R.** 1965. The analysis of polymodal frequency distributions. *J. Anim. Ecol.* **34**: 445-52.
- Thibaud, J.-M.** 1967. Contribution à l'étude du développement postembryonnaire chez les collemboles Hypogastruridae épigés et cavernicoles. *Annl. Spéleol.* **22**(1): 1-32.
1968. Contribution à l'étude de l'action des facteurs température et humidité sur la durée du développement postembryonnaire et de l'intermue de l'adulte chez les Collemboles Hypogastruridae. *Rev. Ecol. Biol. Sol.* **5**(2): 265-81.
- Wallace, M. M. H.** 1967. The ecology of *Sminthurus viridis* (L.), (Collembola). (1) Processes influencing numbers in pastures in Western Australia. *Aust. J. Zool.* **15**: 1173-1206.
- Wise, K. A. J.** 1967. Collembola (Springtails). Antarctic Res. Ser. **10**: 123-48.
- Wise, K. A. J., C. E. Fearon & O. R. Wilkes.** 1964. Entomological investigations in Antarctica, 1962-63 season. *Pacif. Ins.* **6**(3): 541-70.
- Wise, K. A. J. & J. Shoup.** 1967. Distribution of Collembola at Cape Hallett. Antarctic Res. Ser. **10**: 325-30.
- Wise, K. A. J. & A. V. Spain.** 1967. Entomological investigations in Antarctica, 1963-64 season. *Pacif. Ins.* **9**(2): 271-93.
- Yosii, R.** 1960. Studies on the collembolan genus *Hypogastrura*. *Amer. Mid. Nat.* **64**: 257-81.
- Zinkler, D.** 1966. Vergleichende untersuchungen zur atmungsphysiologie von Collembolen (Apterygota) und anderen boden Kleinarthropoden. *Z. vergl. Physiol.* **52**: 99-144.