A REVISION OF THE FAMILY PODACARIDAE GRANDJ. (ACARI : ORIBATEI)

BY

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The Podacaridae appear to be restricted, for the most part, to the Antarctic and sub-Antarctic regions of the world. GRANDJEAN (1955) created the family to emphasize the distinction between the species *Podacarus auberti* Grandj. and members of the Ameronothridae. According to this author the main distinguishing characters of *P. auberti* include the presence of large porose hysterosomal sclerites in larval and nymphal stages, the presence of pedotecta, the complete separation of prodorsum and notogaster in the adult, the bideficient notogaster in the adult, the presence of interlamellar setae in all stages and the absence of setae *it* on legs IV.

Using these characters as a guide, the species *Notaspis antarctica* Michael 1903, re-designated *Alaskozetes antarcticus* (Mich.), has also been assigned to this family (WALLWORK 1962). Michael's species shows certain strong similarities to *P. auberti*, particularly in the immature stages. The two species are compared in some detail later.

A third genus having strong affinities with the Podacaridae is *Halozetes* Berl., with *H. marinus* (Lohmann) as the type. This species has been re-described and the genus re-defined recently (WALLWORK 1963). The genus contains several species, some of which were placed originally in the genera *Anarea* Dalenius and *Pertogunia* Dalenius [1]. The inclusion of *Halozetes* in the Podacaridae is warranted on the basis of the presence of porose hysterosomal sclerites in the immature stages, the presence of pedotecta and interlamellar setae, and the absence of setae *it* on tarsus IV. Although *Halozetes* differs significantly in certain respects from *Podacarus* and *Alaskozetes* the range of variability within the genus renders a strict definition difficult.

The purposes of the present paper are to formulate a definition of the family

1. The reasons for placing *Anarea* and *Pertogunia* in synonymy with *Halozetes* have been given previously (WALLWORK 1962, 1963).

Podacaridae on the basis of the three genera presently included within it, to define the genera *Podacarus, Alaskozetes* and *Halozetes* as far as this is possible and to investigate various morphological trends which may serve as useful indicators of generic and specific differences. The discussion presented below is based on observations of material from several collections made in the Antarctic and sub-Antarctic regions. I am indebted to Mr. K. WATSON and members of the Australian National Antarctic Research Expedition, to Dr. J. L. GRESSITT of the Bernice P. Bishop Museum, Hawaii, and to Dr. G. O. EVANS of the British Museum for the opportunity to study these collections.

Characters of the family Podacaridae. — The following characters apply to adults of both sexes unless stated otherwise.

1. Integument of immature stages pleated, with porose sclerites.

2. Labio-genal articulation of ventral region of gnathosoma incomplete (*Podacarus, Alaskozetes*) or complete (*Halozetes*).

3. Pedotecta present.

4. Notogaster of immature stages is unideficient, of adults is usually bideficient, occasionally uni- or tri-deficient.

5. Neotrichy on coxisternal fields III and IV may be present (*Podacarus, Alaskozetes*) or absent (*Halozetes*).

6. Aggenital neotrichy may be present in males, very occasionally in females, or lacking in both sexes.

7. Interlamellar setae are present in all stages.

8. Prodorsal/notogastral separation may be complete (*Podacarus, Alaskozetes, Halozetes* pars) or interrupted in the mid-line (*Halozetes* pars).

9. Setae *it* are lacking on tarsus IV.

10. Sexual dimorphism is present, strongly (*Podacarus, Alaskozetes, Halozetes* pars) or weakly (*Halozetes* pars) developed.

It is evident that the majority of characters listed above show some variability, i.e. a given morphological condition may be present or it may be lacking; if it is present the degree to which it is expressed may be variable. This variability may occur at the generic level and also, in the case of *Halozetes*, at the specific level. Nevertheless the separation of this family from the Ameronothridae (to which it appears closely related morphologically and ecologically) is justified by such constant differences as the presence of porose sclerites in immature stages, pedotecta and interlamellar setae and the absence of setae *it* IV.

The variability noted above can be analyzed as a series of morphological trends in various characters. Before considering these in more detail, short surveys of each of the three genera concerned are given.

The genus *Podacarus*. — Type species : *P. auberti* Grandj. 1955. Type locality : Kerguélen Island. To the present date this genus is monotypical. Grandjean's detailed description, supplemented by my observations on a large collection from

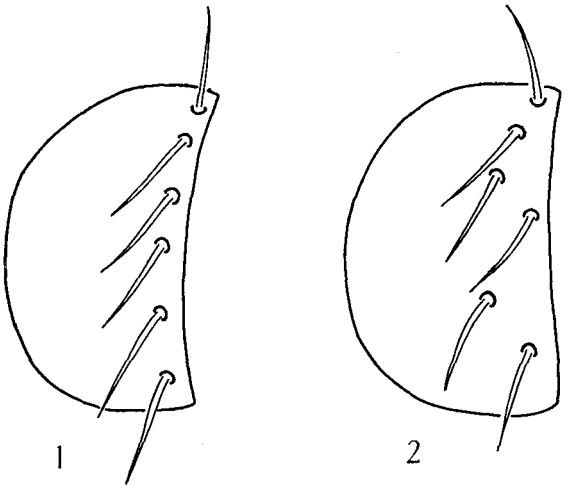
Macquarie Island (WALLWORK 1963), provides the basis for the following list of generic characters which apply to adults of both sexes unless stated otherwise :

1. Larva with 6 pairs of porose hysterosomal sclerites, nymphs with 7 pairs.
2. Prodorsal/notogastral separation complete in all stages, anterior margin of notogaster pointed in adult.
3. Interlamellar setae short in nymphal and adult stages.
4. Sensillus well developed, clavate, in all stages.
5. Aggenital neotrichy present as a relatively constant feature in males ; occasionally present in females.
6. Coxisternal neotrichy generally present in males ; very occasionally present in females.
7. All genital setae arranged in a linear row medially on each plate (fig. 1).
8. Labio-genal articulation incomplete.
9. Legs, particularly legs III and IV, relatively larger in males than in females.

The genus *Alaskozetes*. — Type species : *A. coriaceus* Hammer 1955. Type locality : Lat. 68° N, Long. 160° W. Arctic slope. The original description is based on a female specimen ; the male has not yet been described.

Comparisons between this species and *A. antarcticus* (Mich.) are difficult owing the absence of the male specimens of *A. coriaceus*. Females of the two species, examined at the British Museum, are very similar and it is possible that the two forms are conspecific.

The designation of a sub-species, *A. antarcticus* (Mich.) ssp. *Grandjeani* (Dalenius), for the Macquarie Island forms appears to be justified on the basis of two relatively constant adult features, differing from the nominate form, namely the shorter and thicker interlamellar setae (these are slender and tapering in the nominate form) and the relatively longer setae ps_1 on the posterior part of the notogaster.



FIGS. 1-2. — 1. Genital setae, *Podacarus auberti* ; 2. Genital setae, *Alaskozetes antarcticus*.

There is also a slight difference in the expression of aggenital neotrichy in males of the two forms (see later). The following characters may be used to define genus ; these are applicable to adults of both sexes unless stated otherwise :

1. Larva with 6 pairs of porose hysterosomal sclerites, nymphs with 7 pairs.

2. Prodorsal/notogastral separation complete in all stages, anterior margin of notogaster rounded in adult.

3. Interlamellar setae long and tapering in all stages (*A. coriaceus*, *A. antarcticus* ssp. *antarcticus*) or shorter (i.e. only as long as mutual distance) and thickened (*A. antarcticus* ssp. *Grandjeani*).

4. Sensillus well developed, clavate, in all stages.

5. Aggenital neotrichy well developed in males ; usually lacking in females.

6. Coxisternal neotrichy generally present in males ; frequently present but weakly developed in females.

7. Genital setae arranged in 2 rows of 3 setae each, paraxially and antiaxially respectively on each plate (fig. 2).

8. Labio-genal articulation is incomplete.

9. No size difference in legs between the two sexes.

The genus *Halozetes*. — Type species : *Notaspis marina* Lohmann 1908. Type locality : Kerguélen and/or St Paul Islands. Previously I have described or re-described the five species presently constituting this genus, and have compiled a definition of the genus based on these species (WALLWORK 1963). The main points of this definition are given below for comparison with *Podacarus* and *Alaskozetes*.

1. Larva with 6 pairs of porose sclerites, nymphs with a maximum of 6 pairs and an unpaired sclerite medio-posteriorly.

2. Prodorsal/notogastral separation complete or incomplete in adult ; when complete the anterior border of notogaster is pointed.

3. Interlamellar setae variable in length and form.

4. Sensillus may be strongly developed, clavate, in all stages, weakly developed in all stages, or weakly developed in immature stages only.

5. Aggenital neotrichy may be lacking or weakly or strongly developed in adult males.

6. Coxisternal neotrichy is lacking.

7. Genital setae arranged in 2 rows of 3 setae each, paraxially and antiaxially respectively, on each plate in adults.

8. Labio-genal articulation is complete.

9. No size difference in legs between the two sexes.

Morphological trends in the family Podacaridae. — The lists of characters given above may serve to distinguish the three genera within this family, but they provide little information regarding the relative affinities of the three groups. It is of interest, in this respect, to determine apparent morphogical trends and to analyze the extent to which these are realised in the various genera and species. This analysis does not seek to establish phylogenetic lines of descent, for there is no

fossil record of this family, but rather to determine possible relationships between contemporaneous groups.

The premise on which this analysis is based is that the Ameronothridae and Podacaridae have diverged from a common ancestral group. Both families are represented in the marine littoral fauna, the Ameronothridae being distributed in the temperate and sub-Arctic regions, the Podacaridae in the Antarctic and sub-Antarctic. As far as I am aware the geographical distribution patterns of the two families do not overlap. The Podacaridae includes species which appear to be more strongly specialized morphologically than the Ameronothridae, as evidenced by the possession of porose sclerites in the immature stages and the development of sexual dimorphism, particularly in the adults. The investigation of these specialized trends should indicate the extent to which the Podacaridae have diverged from the Ameronothridae and also how far contemporaneous species within the former family have diverged from each other. This analysis is a first step in an attempt to explain the distribution of representatives of the Podacaridae in the Antarctic and sub-Antarctic regions, a distribution which must take into account not only general faunal comparisons and the implications of the theory of Continental Drift, but also trends in speciation. These trends will now be considered.

1. Porose hysterosomal sclerites.

The significance of these dorsal plaques, which are characteristic of the immature stages of the Podacaridae, is not immediately apparent. They are not present in the Ameronothridae. It is of interest to note that similar sclerites are present in the immature stages of the totally unrelated genus *Holonothrus* Wallwork (superfamily Nothroidea), which is also found in the sub-Antarctic. This is probably an example of convergent evolution ; the sclerites in the latter genus differing from those in the Podarariidae in that they bear the insertions of at least one pair of setae.

The porose sclerites show the strongest development in *Podacarus* and *Alaskozetes* ; in these genera the sclerites are strongly chitinized and clearly delimited. In *Halozetes* the plaques are weakly developed in larva and protonymph, more strongly developed in the later nymphal stages, although the 3 pairs posteriorly and the unpaired medio-posterior sclerite are poorly defined in *H. crozetensis* and *H. belgicae*. In these latter species porose areas on the posterior half of the notogaster are rather diffuse. The complete development of sclerites is not realised, then, in *H. crozetensis* and *H. belgicae*, and the primitive condition of the hysterosoma in which dorsal plaques are lacking (a condition obtaining in the Ameronothridae) is retained in part. In *H. marinus* and *H. intermedius* the development of plaques in immature stages is much stronger. It is possible that the posterior unpaired sclerite, characteristic of *Halozetes*, has developed from the fusion of a pair of sclerites such as are present in *Podacarus* and *Alaskozetes*. In this respect *Halozetes* would appear to be more highly developed morphologically than these two genera.

2. Labio-genal articulation.

This articulation on the ventral surface of the gnathosoma is easily overlooked, but yet may provide the most fundamental difference between *Podacarus* and *Alaskozetes* on the one hand, and *Halozetes* on the other. In *Podacarus* and *Alaskozetes* this articulation does not extent to the lateral limits of the gnathosoma and is therefore incomplete (this same condition obtains in members of the Ameronothridae) ; in *Halozetes* the articulation is complete. Complete development of this articulation, resulting in the complete separation of the hysterostome and maxillary elements of the gnathosoma, is considered to be more advanced than the incomplete condition.

3. Notogastral chaetotaxy.

Nymphal forms are unideficient, i.e. they possess 30 notogastral setae, as a general rule in the Podacaridae. There is some variation in the adult chaetotaxy and this applies at the generic, specific and individual level. Characteristically the adults of *Podacarus* and *Alaskozetes* lack setae c_3 on both sides and are bideficient. Occasionally this seta is present on one or both sides, bringing the number of setae to 29 or 30, the latter condition resembling that in the Ameronothridae which are unideficient. The genus *Halozetes* shows a range of variation ; in *H. crozetensis* there is a strong disposition towards unideficience ; this condition is less strongly expressed in *H. belgicae* where it occurs with a frequency of about 50 %. *H. marinus* is bideficient in all cases examined ; *H. macquariensis* is variable, the number of setae varying between 25 and 28 ; this results from the complete loss of setae c_3, the frequent absence of setae c_1 and the occasional absence of setae c_2. The regression sequence for setae in this series is then : $c_3 : c_1 : c_2$; the same sequence has also been described for *P. auberti* (see GRANDJEAN 1955). This trend in the reduction in number of setae in the *c* series finds its maximum expression in *H. macquariensis* ; it is expressed to a lesser extent in *H. marinus*. *H. crozetensis* demonstrates the least tendency toward regression in this respect ; between these two extremes are located the conditions present in *H. belgicae*, *Podacarus auberti* and *Alaskozetes antarcticus*.

4. Prodorsal/notogastral separation.

Much confusion centres around this morphological feature owing to the fact that the cerotegument covering the adult body in the Podacaridae is frequently confluent in the mid-dorsal line between prodorsum and notogaster, whereas the actual margin of the notogaster may be complete beneath this cerotegument *(Halozetes crozetensis* and *H. macquariensis)*. The true extent of prodorsal/notogastral separation can only be determined after removal of the cerotegument in this region.

According to GRANDJEAN (1955) the absence of a distinct line of demarcation between prodorsum and notogaster is a primitive feature in the Ameronothridae.

As a general rule in the Podacaridae the anterior notogastral border is well defined and complete ; this border may be produced into a strong peak *(Podacarus auberti, Halozetes macquariensis)* or it may be rounded *(Alaskozetes)*. In *Halozetes marinus* the anterior notogastral border is usually incomplete and there is a narrow zone of continuity between prodorsum and notogaster. *H. intermedius* also shows this primitive condition, but to a lesser extent ; in some individuals of this species the border is incomplete, in others it is complete. These two last-named species would then appear to be more primitive than other members of the family with respect to this character.

5. The sensillus.

The sensillus and pseudostigma are always present in the Podacaridae, as far as we know ; the former structure is usually well developed with short stem and clavate head. Occasionally a tendency to regression is evident, as in *Halozetes marinus*. In the adult and tritonymph of this species the sensillus is attenuated and is frequently broken off in captured specimens ; the pseudostigmata are reduced to small pits in the prodorsum. The significance of this regression is not immediately apparent although it may possibly be associated with the specialized conditions of life encountered by this species in the marine littoral zone. The ecologically similar species *H. intermedius* shows this morphological trend to a lesser extent ; regression of sensillus and pseudostigmata to an attenuated condition occurs in the nymphs but not the adults of this species. It is of interest to note in this connection that the family Ameronothridae contains an inter-tidal genus, *Hygroribates,* which is characterized by the complete loss of sensillus and pseudostigma. This regression tendency would then appear to be a parallel development in these two related families, although it is carried to a greater extreme in the Ameronothridae.

6. Interlamellar setae.

The absence of these setae in the Ameronothridae affords a useful point of distinction between this family and the Podacaridae in which these setae are characteristically present and usually well developed. A trend towards reduction is present however in some members of the Podacaridae ; in *P. auberti* there is a progressive reduction in the relative length of these setae during development, until in the adult they are very short and occasionally lacking. Interlamellar setae are generally strongly developed in *Alaskozetes* and *Halozetes,* although in the geographically distinct sub-species *Alaskozetes antarcticus* ssp. *Grandjeani* and *Halozetes belgicae* ssp. *brevipilis* these setae are distinctly shorter than those in the nominate forms. The regressive tendencies of the interlamellar setae in the Ameronothridae and Podacaridae may be another example of parallel evolution in the two families. Again, this tendency has been carried to greater lengths in the Ameronothridae than in the Podacaridae.

7. Sexual dimorphism.

This rather uncommon phenomenon in the Oribatei is a characteristic feature of the Podacaridae. It is lacking, as far as I am aware, in the Ameronothridae, and its absence is regarded as primitive. An immediate distinction can be made between the two sexes of the former family on the basis of the size of the genital aperture ; this is relatively larger in females than in males. Dimorphism is also expressed in several other, less conspicuous, ways, e.g. the relatively larger size of legs III and IV in males in *P. auberti,* the presence of a pre-genital ridge in females of *H. macquariensis* and *H. belgicae* (this ridge is present in both sexes in *H. crozetensis* and is lacking in both sexes in *H. marinus*) and the development of aggenital and coxisternal neotrichy to a different extent (more strongly developed in males than in females) in the majority of species in this family. The various expressions of neotrichy and their possible significance in distinguishing between related species and sub-species are considered below.

8. Aggenital neotrichy.

This condition, represented by the multiplication of the aggenital seta, is lacking in both sexes of *Halozetes marinus, H. intermedius* and *H. macquariensis* ; it is weakly developed in adult males, occasionally expressed in females, in *Podacarus auberti, Halozetes crozetensis* ; it is strongly developed in males, lacking or weakly developed in females in *Alaskozetes antarcticus* and *Halozetes belgicae.* There is, then, a progressive development of this character among the contemporaneous species in this family.

Generally speaking, in a species population showing this character, be it weakly or strongly developed, there are variations in the number of aggenital setae from individual to individual. These variations are, of course, greater in males than in females, and the following discussion is restricted to the condition in adult males. The frequency distribution of these variations within the species and sub-species forms a characteristic pattern for each group. These patterns are shown in figs 3 & 4 in which the frequency of occurrence, expressed as a percentage, of given numbers of aggenital setae is plotted for *P. auberti, Alaskozetes antarcticus* (nominate form), *A. antarcticus* ssp. *Grandjeani, H. crozetensis* and *H. belgicae* ssp. *brevipilis.* Data have not been assembled up to the present for the nominate form of *H. belgicae,* although the indications are that the curve for this form would be displaced to the right of that for the sub-species *brevipilis,* indicating a stronger development of neotrichy. Several interesting points emerge from the observations depicted in figs 3 & 4. In the first instance, although the frequency distributions tend to be slightly skewed, they have the essential configuation of a normal curve, in all species considered. Secondly, if the two figures are super-imposed, there is a close approximation between the curve for *P. auberti* and that for *H. crozetensis* ; similarly there is a close approximation between *Alaskozetes antarcticus* (nominate form) and *H. belgicae* ssp. *brevipilis.* It is suggested that these simi-

larities are due to parallel trends in the genera concerned. Thirdly, the steeper curve of *Alaskozetes antarcticus* ssp. *Grandjeani*, as compared with that of the nominate form, indicates a slightly greater constancy in form in the sub-species *Grandjeani*.

In comparing the frequency distribution curves for the various species there is a strong temptation to consider the derivation of one from the other. Thus,

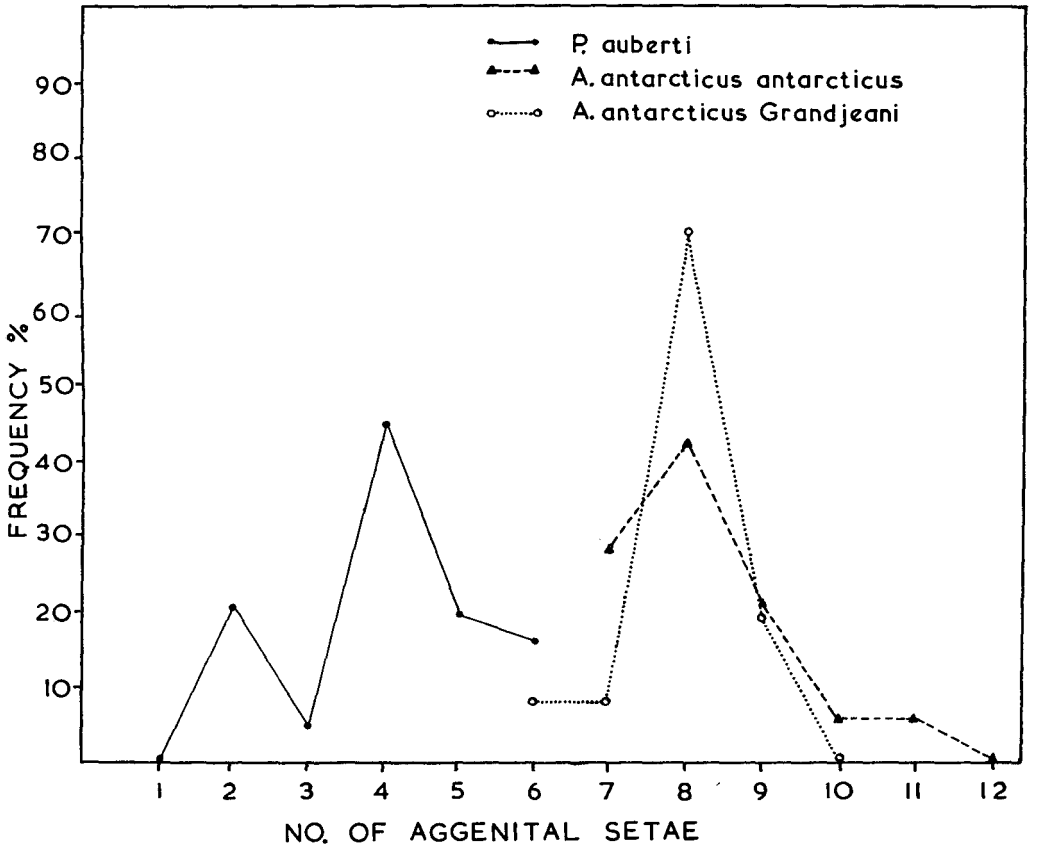


FIG. 3. — Frequency distributions of 2 species of Podacaridae : *P. auberti* and *A. antarcticus*.

comparing the curves for *H. crozetensis* and *H. belgicae* ssp. *brevipilis*, it is noted that these are separated by only a short distance and that the latter curve may be considered as an extension of the former. There is an indication, in this case, of homology and close relationship between the two conditions. In evolutionary terms this means that *H. crozetensis* demonstrates a more primitive condition than *H. belgicae*, the latter species having diverged more strongly from the primitive, i.e. ancestral, condition than the former. This conclusion may not be generally applicable, however ; in the case of *P. auberti* and *A. antarcticus* (nominate

form) a linkage similar to that between *H. crozetensis* and *H. belgicae* ssp. *brevipilis* is indicated from the curves. The comparison can be taken little further however, for the insertion pattern in *P. auberti* is quite different from that in *A. antarcticus* ; in the latter species the aggenital setae on each side are arranged in a linear row, whereas in *P. auberti* they have a random grouping. Homology between these two conditions is more difficult to establish.

9. Coxisternal neotrichy.

The presence of this condition serves as a point of distinction between *Halozetes* and the genera *Podacarus* and *Alaskozetes* ; it is lacking in all of the species of *Halozetes* so far examined. The occurrence of neotrichy on coxisternal fields III/IV

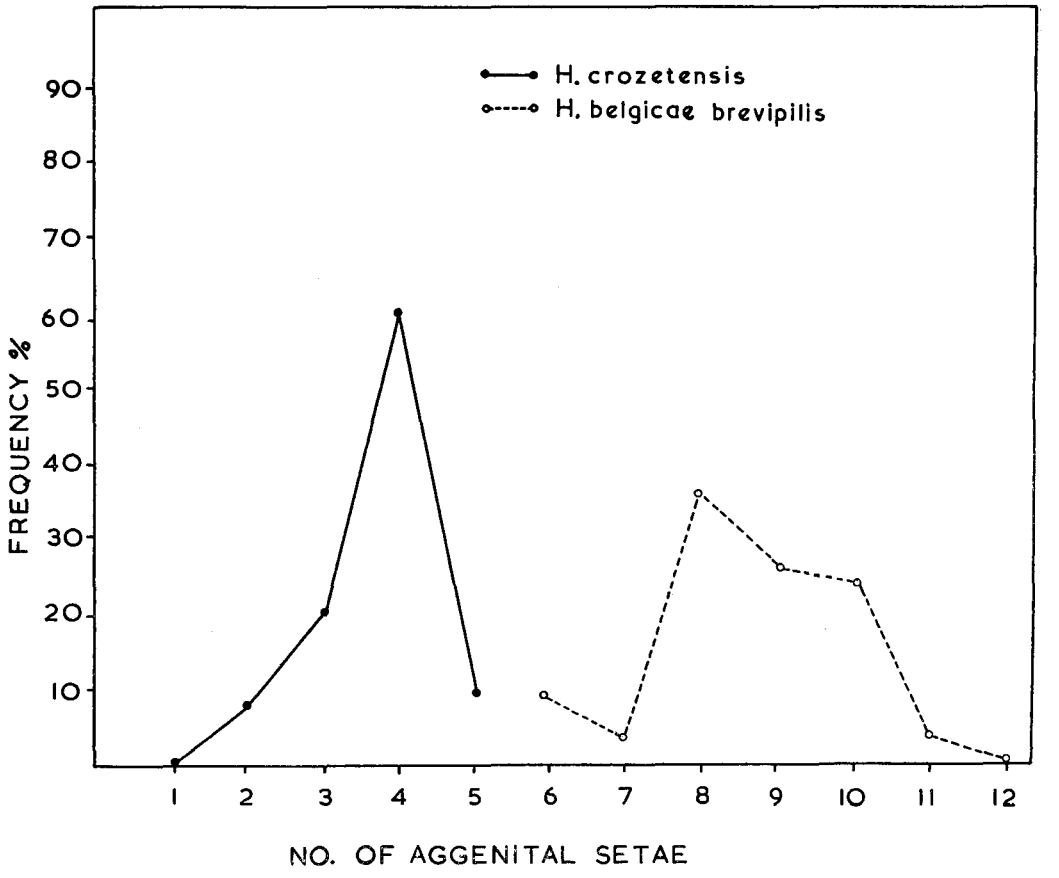


FIG. 4. — Frequency distributions of 2 species of Podacaridae : *H. crozetensis* and *H. belgicae* ssp. *brevipilis*.

in *Podacarus* and *Alaskozetes* may be a further indication of the relationship between the two genera, although ,as in the case of aggenital neotrichy, the pattern of chaetotaxy differs in the two genera. In *P. auberti* secondary setae are located between

coxisternal setae 3b and 4b in a manner such that the setae in this region form a linear row which parallels the ventro-sejugal ridge, i.e. the row extends laterally towards the side of the body ; in *Alaskozetes* the secondary setae are located between coxisternal setae 3a and 4b, the setal pattern forming an arc surrounding, and parallel with, the rim of the genital aperture. Again, the question of homology is uncertain. A frequent feature of *P. auberti* is the duplication or triplication of coxisternal seta 4c ; this condition is rare or lacking in *Alaskozetes*. It may be noted that the expression of coxisternal neotrichy is more strongly developed in males than in females in both *Podacarus* and *Alaskozetes*.

The development of coxisternal neotrichy is regarded as a morphological specialization ; in this respect *Halozetes* is the most primitive of the three genera, *Alaskozetes* the most specialized.

Discussion

Two main points emerge from the analysis given above. Firstly, in all of the three genera considered, morphologically primitive and advanced characters occur simultaneously, i.e. a given genus (and species) will be primitive in some respects, advanced in others. Thus *Halozetes* is primitive with respect to coxisternal neotrichy, while it shows an advanced development in the character of the labio-genal articulation ; conversely *Alaskozetes* retains the primitive condition of the labio-genal articulation, but has become morphologically specialized in the development of coxisternal neotrichy. At the specific level, *H. macquariensis* lacks aggenital neotrichy (a primitive feature), but shows an advanced stage of notogastral regression ; *H. marinus* is primitive in having incomplete separation of prodorsum and notogaster, advanced in the regression of the sensillus. This mixture of primitive and advanced conditions indicates perhaps a differential speed of evolution, not only between different characters in the same genus and species, but also between the same characters (i.e. homologues) in different genera and species.

The second conclusion is that certain similar traits have developed independently in related genera and species. Examples of such parallelisms include the tendency to regression of the interlamellar setae in *Podacarus* and *Ameronothrus*, regression of the sensillus in some members of the genus *Halozetes* and in *Hygroribates*, the development of aggenital neotrichy in some members of *Halozetes*, in *Alaskozetes* and in *Podacarus*, and possibly the development of coxisternal neotrichy in *Alaskozetes* and *Podacarus*. The effect of considering these similarities as parallel developments is to render less strong the relationships between the groups concerned. The alternative is to consider these similarities as strict homologies ; in which case there would be a strong argument for placing all of the species in this family within a single genus, which would, for reasons of priority, be *Halozetes*. In the present analysis I have not been able to do this without ignoring the significance

of such fundamental characters as the development of the hysterosomal sclerites and the labio-genal articulation of the gnathosoma. The differential expression of these two characters separates *Halozetes* from the genera *Podacarus* and *Alaskozetes*, and I have chosen to recognize this separation for these reasons. The question of the identity of the genera *Podacarus* and *Alaskozetes* must now be considered. These two genera appear to be more closely related to each other than either does to the genus *Halozetes* ; this observation is based on evidence from the immature stages. The point at issue is whether or not this relationship is close enough to warrant the two species *Podacarus auberti* and *Alaskozetes antarcticus* being placed in the same genus. Any decision on this question must involve, to some extent at least, a subjective interpretation of the character differences between the two species. I have chosen to separate the two at the generic level for a number of reasons. Firstly because it would appear that the patterns of neotrichy are parallel developments and not strict homologues ; secondly because of the strong tendency to regression of the interlamellar setae in *Podacarus* which is not evident to the same extent in *Alaskozetes* ; thirdly because of the distinctive pattern of insertion of the genital setae in *Podacarus*, and lastly because of the strong dimorphism of legs III and IV in *Podacarus*, a character unique in this family.

The various differences discussed above may be used as the basis for a key to the genera and species of this family. The discovery of new species at some future date will doubtless necessitate modifications. At this time it is believed that the distinctions recognized in this key are indicated by the evidence available. The key is provided below.

Key to genera and species in the Family Podacaridae

1a. Nymphs with less than 7 pairs of well defined porose hysterosomal sclerites ; coxisternal neotrichy absent in adult ; labio-genal articulation of gnathosoma complete in adult. (Genus : *Halozetes* Lohmann)..... 4

1b. Nymphs with 7 pairs of well defined porose hysterosomal sclerites ; coxisternal neotrichy present in adult ; labio-genal articulation incomplete in adult..... 2

2a. Aggenital neotrichy strongly developed (i.e. a total of 6-12 setae) in males, with setae arranged in a linear row ; secondary setae on coxisternal regions III/IV in a row parallel to rim of genital aperture ; interlamellar setae well developed ; legs III and IV no larger in males than in females. (Genus : *Alaskozetes* Hammer. Monotypical ?).. 3

2b. Aggenital neotrichy weakly developed (i.e. a total of 2-6 setae) in males, with setae arranged in a random manner ; secondary setae on coxisternal regions III/IV in a row parallel to the sejugal ridge ; interlamellar setae minute or lacking in adult ; legs III and IV more strongly developed in males than in females. (Genus : *Podacarus* Grandj. Monotypical ?)..... *P. auberti* Grandj.

3a. Interlamellar setae at least 3x as long as mutual distance ; notogastral setae ps_{1-3} all same length..... *A. antarcticus* (Mich.) ssp. *antarcticus*

3b. Interlamellar setae shorter than their mutual distance, strongly thickened ; notogastral setae ps_1 longer than ps_3 and ps_2.... *A. antarcticus* (Mich.) ssp. *Grandjeani*

4a. Prodorsal/notogastral separation incomplete in adult 5

4b. Prodorsal/notogastral separation complete in adult 6

5a. Sensillus and pseudostigmata weakly developed in nymphs and adult ; coxisternal seta 4c present ..... *H. marinus* (Lohmann).

5b. Sensillus and pseudostigmata weakly developed in nymphs, strongly developed in adults ; coxisternal seta 4c lacking ..... *H. intermedius* Wallwork.

6a. Aggenital neotrichy lacking or weakly developed in adult males (i.e. a total of 2-5 setae) 7

6b. Aggenital neotrichy strongly developed in adult males (i.e. a total of 6-12 + setae). (*H. belgicae* Mich.) 8

7a. Aggenital neotrichy lacking ; notogaster of adult bi- or tri-deficient ; setae ps_1 relatively long and smooth ..... *H. macquariensis* (Dalenius)

7b. Aggenital neotrichy usually present in adult males ; notogaster of adult unideficient ; setae ps_1 only as long as the other notogastral setae, strongly barbed ..... *H. crozetensis* (Richters)

8a. Lamellar and interlamellar setae longer than their mutual distance ..... *H. belgicae* (Mich.) ssp. *belgicae*

8b. Lamellar and interlamellar setae shorter than their mutual distance ; interlamellar setae frequently very short ..... *H. belgicae* ssp. *brevipilis*

Summary

Definitions are given of the family Podacaridae and the three genera, *Podacarus*, *Alaskozetes* and *Halozetes*, presently included within it. Observations on several collections from the Antarctic and sub-Antarctic regions are discussed in an attempt to determine various morphological trends which may serve as useful indicators of generic and specific differences within the family. The three genera are separated on the basis of well defined differences, and parallel trends in the development of ventral neotrichy, regression of the sensillus and pseudostigmata and regression of interlamellar setae are discussed. A key to the genera and species within the family is given.

REFERENCES

Grandjean (F.), 1955. — Sur un acarien des îles Kerguélen. *Podacarus auberti* (Oribate). *Mém. Mus. Nat. Hist. Nat. Paris*, sér. A, *Zool.* 8 (3) : 109-150.

Hammer (M.), 1955. — Alaskan Oribatids. *Acta Arctica* 7, 36 pp.

Lohmann (H.), 1908. — Die Meeresmilben der Deutschen Südpolar-Expedition 1901-1903. Deutsche Südpolar Expedition 1901-1903. Bd. IX, Zool. I : 361-413.

Michael (A. D.), 1903. — Acarida (Oribatidae). Résultats du voyage du S. Y. Belgica en 1897-1899. Rapports scientifiques (Zoologie). Acariens libres. R. 17 : 1-7. Anvers.

Wallwork (J. A.), 1962. — A redescription of *Notaspis antarctica* Michael, 1903 (Acari : Oribatei). *Pacific Insects* 4 (4) : 869-880.

Wallwork (J. A.), 1963. — The Oribatei (Acari) of Macquarie Island. *Pacific Insects* 5 (4) : 721-769.