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**Pycnogonid higher classification and a revision of the genus
Austropallene (family Callipallenidae)**

Bain, Bonnie Allison, Ph.D.

City University of New York, 1992

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A

PYCNOGONID HIGHER CLASSIFICATION AND A REVISION OF THE
GENUS AUSTROPALLENE (FAMILY CALLIPALLENIDAE)

by

BONNIE ALLISON BAIN

A dissertation submitted to the Graduate Faculty in Biology
in partial fulfillment of the requirements for the degree
of Doctor of Philosophy, The City University of New York.

1992

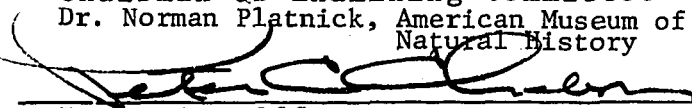
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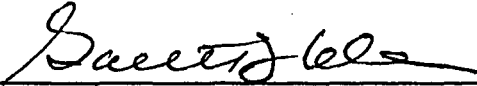
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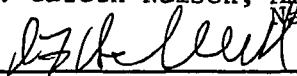
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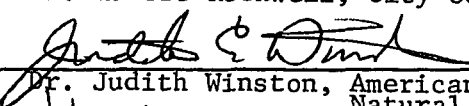
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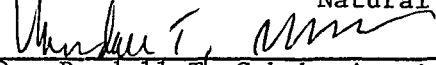

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Abstract

PYCNOGONID HIGHER CLASSIFICATION AND A REVISION OF THE GENUS AUSTROPALLENE (FAMILY CALLIPALLENIDAE)

by

Bonnie Bain

Adviser: Norman Platnick

This thesis is presented in two parts. In part I, a brief introduction to and a history of previous work on the pycnogonids is given. The discussion on morphology which follows concentrates on three topics which are seldom given a thorough discussion: ovigerous legs, extra pairs of walking legs, and larval development. Included in each discussion is the relevance of these topics to phylogenetic analysis of the Class Pycnogonida. The cladistic analysis section begins with a discussion of methods, choice of outgroup, and a presentation and discussion of characters used. The analysis used 86 pycnogonid genera and 57 characters. Data on the 86 genera were obtained from published type descriptions. A complete list of the genera and all references used to obtain type descriptions will be found in Appendix I. Results of the analysis are presented next and a comparison is made between the cladogram and previous ideas of relationship within the pycnogonids. Part II is a revision of the genus Austropallene. A brief history of previous work on this genus is given, followed by methods, choice of outgroup (the genus Nymphon), and character discussions for the cladistic analysis. Fourteen

characters and 8 taxa were used and 1 tree was produced both by Hennig86 and PAUP (version 3.0q). On the basis of this tree and the accompanying character support for it, Austropallene is split into two genera: Tarapallene and Austropallene. This discussion is followed by diagnoses and descriptions of the genera and diagnoses and descriptions of 8 species of Austropallene. In addition, two previous species, A. australis and A. turqueti, which had been considered synonyms of A. cornigera, are restored to species status on the basis of their ovigerous leg spines. Ovigerous leg spines are used here for the first time as the basis for separating species within Austropallene. Use of ovigerous leg spines in this manner should prove to be useful in other pycnogonid genera also. All ovigerous leg spines were examined under the SEM. Species specific differences were not readily apparent under the lower magnification levels of the light microscope.

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Part I - Pycnogonids

Introduction:

Pycnogonids (Class Pycnogonida, Sub-phylum Chelicerata) are spider-like marine organisms. Hence, their common name: sea spider. They are found worldwide in many different habitats, from benthic waters to the deep sea. Although quite common in many places, they are seldom seen due to their retiring habits and (usually) very good camouflage. There are approximately 86 genera and 1,000 species.

There is some uncertainty about the exact number of genera and species. Estimates range from 500 species and 70 genera (King, 1973) to 1,000 species and 84 genera (Arnaud & Bamber, 1987). In an attempt to address this problem, I have compiled a list of genera from the primary literature and have removed all synonyms which have been well documented by previous workers. 124 generic names have been proposed for pycnogonids and 86 of these remain after all well documented synonyms have been removed.

The exact number of species is a more difficult problem. There is no published pycnogonid species catalog and new species are constantly being described by various authors. The exact number of species is known for some of the smaller genera (for example, Cheilopallene has 6 species). However, for many of the larger genera (Nymphon, Anoplodactylus, Pallenopsis), one can only estimate the total number of described species. For example, Nymphon probably has 200+ currently described species and

Anoplodactylus and Pallenopsis each have between 50-100 described species.

Pycnogonid Literature:

There have been several major summaries of pycnogonid biology over the years. Hoek (1881) wrote an excellent summary along with the species descriptions, etc. from the Challenger Expedition. Next, Schimkewitsch, in two volumes (1929 and 1930), made an attempt to summarize all the generic and species names up to that point in time. This was purely a systematic work and was in Latin and Russian. Helfer and Schlottke (1935) attempted a general summary (in German) of pycnogonid biology, but their work was filled with errors. Fage (1949) gave a brief pycnogonid summary (in French) which seems to have come mainly from Helfer and Schlottke. King (1973) published Pycnogonids which, unlike the others, was intended for a more general audience. Unfortunately, this book is filled with errors, both factual and typographic. Fry and Stock (1978) published the first complete pycnogonid bibliography.

The best recent review of pycnogonid biology is by Arnaud & Bamber (1987). Although the definitive work is yet to be written, their review provides the best recent introduction to the group. Their emphasis is on pycnogonid ecology but they do have a brief (although incomplete) systematic section.

Pycnogonid Morphology:

Like all chelicerates, pycnogonids (fig. 1) have a pair of chelicerae, a pair of palps, and four pairs of

walking legs. In addition, they also have an extra pair of appendages, called ovigerous legs or ovigers, which are located between the palps and the first pair of walking legs.

Since the true affinities of the pycnogonids with other groups of organisms have remained obscure for so long, pycnogonid workers have developed their own terminology for various structures. For example, the first pair of appendages (chelicerae) have been referred to by various authors as cheliphores or chelophores in order to distinguish them from chelicerate chelicerae (See discussion in Cole, 1904). The second pair of pycnogonid appendages were originally referred to as antennae. By 1880, most authors preferred the term palp for this structure. Pedipalp (the second pair of appendages in chelicerates) was not used, by general agreement to avoid implying relationships that may or may not exist. This separate terminology was extended to the names of the various leg joints also. Figure 1 shows the currently accepted names for the pycnogonid leg joints: coxa 1, coxa 2, coxa 3, femur, tibia 1, tibia 2, tarsus, propodus.

The use of a separate terminology for the various pycnogonid structures is no longer necessary. Dencker (1974) examined the "...system of skeleton and muscles..." in Nymphon rubrum and compared this to similar structures in the arachnids. On the basis of this comparison, he applied arachnid names to the various leg joints of the pycnogonid walking leg (Dencker 1974, p. 282, fig. 8). In

addition, his examination of muscle structure in the palps and chelicerae led him to conclude that "the [pycnogonid] chelicerae and palpi are arachnidlike." (p. 272). While the cladistic analysis of all chelicerates which includes the pycnogonids in a realistic manner remains to be done, adoption of Dencker's terminology for the pycnogonid walking legs and replacing chelifore (and chelophore) with chelicerae and palp with pedipalp is recommended as a first step towards a better understanding of pycnogonid-arachnid relationships.

The remainder of this section will cover three topics (ovigerous legs, larval development, and extra pairs of walking legs) which are rarely discussed in much detail in the literature. Two of these topics (ovigerous legs and larval development) may potentially have great impact on our understanding of pycnogonid interrelationships. Ovigerous leg characters have been used in the present cladistic analysis and have proven to be quite useful in sorting out some of the major clades (see character discussion below). Larval characters have not yet been used due to the paucity of information available at the present time. As a first step towards increasing awareness of the potential importance of this topic and encouraging authors to include more information on this subject in future papers, I have put together a brief summary of pycnogonid larval development. The third topic, extra pairs of walking legs in pycnogonids, does not contain as much phylogenetic information as ovigerous legs and larval

development. However, there is often some confusion among non-specialists between presence of extra pairs of walking legs in some pycnogonids with the presence of ovigerous legs in all pycnogonids. It is hoped that this section will clarify this point.

Ovigerous Legs:

The ovigerous legs play a very important role in the systematics of pycnogonids. Figs. 2-6 illustrate the ovigerous leg types found in each of the major groups. The type of ovigerous leg found in the colossendeids, nymphonids, and callipallenids has a number of special structures:

1. The last four joints (7-10) are modified into a characteristic shape often referred to as a strigilis or shepherd's crook (fig. 2).
2. This shepherd's crook has one (callipallenids, nymphonids) or more (colossendeids) rows of compound spines located on the inner margin of the structure.
3. A terminal oviger claw (fig. 2b) may be present. Often it is very small and visible only under the SEM. This terminal oviger claw, if present, may be toothed or serrated.
4. An apophysis is often present at the distal end of the fifth joint in the male. This apophysis can be a plain swelling or ornamented with spines.

Other groups of pycnogonids are characterized by various reductions in these structures. Many ammotheids have ovigerous legs as in fig. 3 or fig. 4 in which the last four joints are reduced in various ways, the terminal claw is absent, and the compound spines are highly modified or completely absent.

The tanystylids have ovigerous legs similar to the ones found in the female Pycnothea in which all of the joints are reduced, no strigilis or other modification is present, and, in addition, instead of a terminal claw, joint 10 has two highly modified compound spines in the terminal position.

In the Phoxichilidiidae (fig. 5), the strigilis is absent and very little specialized structure remains.

Some genera like Austrodecus (fig. 6) and Pantopipetta are characterized by an extreme reduction in the ovigerous legs. For instance, in Austrodecus, "[The] ovigers [are] strongly reduced in both sexes [and] 4-7 jointed. Terminal joint [is] the longest, without indication of a dorsal or a ventral margin, without special spines." (Stock, 1954, p. 151).

Ovigerous legs are used by adult pycnogonids for carrying the egg masses (male only) and by both sexes for grooming. Grooming has only been observed in those genera which have the nymphonid-callipallenid type of ovigerous leg with the fully functional strigilis. According to Nakamura and Sekiguchi (1980) the ovigerous legs seem to

play a role in courtship and mating behavior.

The presence of ovigerous legs has been a major impediment to our understanding of pycnogonid-chelicerate relationships. All chelicerates have the following pairs of appendages (in the following order, from anterior to posterior): 1 pair of chelicerae, 1 pair of pedipalps, and 4 pairs of walking legs. In addition, pycnogonids have a pair of ovigerous legs inserted after the pedipalps and in front of the first pair of walking legs. Previous authors, as a first step in determining relationships among the various arthropods (in this case, chelicerates), usually began by counting appendages from front to back with chelicerae as 1, pedipalps as 2, etc. By counting the ovigerous legs in pycnogonids as #3, this always threw off the rest of the count and rendered impossible any meaningful comparison between the pycnogonids and the other chelicerates.

Instead of viewing the ovigerous legs as unaccountable stumbling blocks, we need to ask, instead, where they came from. Perhaps when we know their origin, then we will be able to deal with them in a more meaningful way.

It seems to me, in light of the advances in molecular biology in recent years, and particularly the discovery of homeotic mutations, that this would be a potentially fruitful area in which to begin the search for the origin of the ovigerous legs. Homeotic mutations are mutations which can cause, for example, an antenna to develop as a leg or a modified leg.

There are several reasons which lead me to believe that the ovigerous legs might be accounted for by a homeotic mutation: 1. Dencker (1974, p. 272) demonstrated that the ovigerous leg is derived from a pycnogonid walking leg on the basis of muscle structure. Furthermore, the last four joints (the strigilis) are shown to be a subdivided tarsus (fig. 9, p. 283). 2. The ovigerous leg and the pedipalp, in some Colossendeis, share the first joint before branching out into their respective structures. This is similar to some of the modified legs produced by some homeotic mutations.

If ovigerous legs were assumed to be the result of a homeotic mutation, then one could construct the following transformation series:

Ovigerous leg + strigilis + terminal claw = 0

Loss of terminal claw = 1

Modification of strigilis = 2

or

Loss of strigilis = 3

Larval Development:

The sexes are separate in pycnogonids and egg-laying and fertilization occur after a series of courtship and mating behaviors in which the male and female end up one on top of the other (Nakamura and Sekiguchi, 1980). At this point, the female lays the eggs and the male picks them up with his ovigerous legs, covers them with a secretion from his cement gland (located on the femur of each walking leg) and attaches them to his ovigerous legs. This has only

been documented well for two species: Pycnogonum littorale (Behrens, 1984) and Propallene longiceps (Nakamura, 1981). The male then carries the eggs around until they hatch. Upon hatching, the larvae usually drop off and disappear to unknown destinations. Various later stages have been found, for example, in hydroids (Hedgpeth, 1947), inside a clam (Paphia) (Ohshima, 1937), attached to nudibranchs (Ohshima, 1933), or attached to a polychaete (Salazar-Vallejo and Stock, 1987). For most species, complete developmental series are unknown.

Many earlier works illustrated the various life stages if by chance they were present in the preserved material. T. H. Morgan's (1891) paper is by far the best example of this. He illustrated the various larval stages of Tanystylum orbiculare, Phoxichilidium maxillare, and Callipallene brevirostris. In addition, he went one step further than other workers and cut sections of the various larval stages. Nothing comparable has been done since.

Nakamura (1981) described, in detail, how he reared a pycnogonid (Propallene longiceps) through all the stages in its life cycle. He described 9 molts from hatching to adult. Behrens (1984), reared Pycnogonum littorale in the laboratory. He described 6 molts from hatching to a juvenile with 3 pairs of legs. Jarvis and King (1972), postulate that there are 9-11 molts total in Pycnogonum littorale based on measurements of trunk lengths of many individuals.

Most known pycnogonid larvae are of the typical protonymphon type. These include Tanystylum (Morgan,

1891), Ammothea hilgendorfi (personal observation), Pycnogonum (Behrens, 1984), and others. However, this is not the only kind of pycnogonid larva. Nakamura (1981) was the first to distinguish between the protonymphon and what he referred to as the "attaching larva" which is the type he found in Propallene.

The attaching larva, in contrast to the protonymphon larva, remains attached to the ovigerous legs of the male for the next few molts. Nakamura's attaching larva left the ovigerous legs of the male Propallene at the beginning of the fourth instar. The attaching larva of Austropallene remained attached to the ovigerous legs of the male through the fourth instar stage (Bain, in prep).

The protonymphon larva has two pairs of larval appendages which it uses for swimming or crawling. Some protonymphons (for example, Phoxichilidium, fig. 1g, p. 147 Lebour, 1945) have long filamentous extensions on these larval appendages, presumably to aid in buoyancy. The attaching larva, on the other hand, has only a pair of chelicerae and two pairs of limb buds. They remain attached to the male by means of long thin strands of an unknown clear substance which issue forth from glands located immediately below the chelicerae.

Ohshima (1933), found several stages of two different pycnogonids which differ from the typical protonymphon larva in that all the limb buds appeared at once. He referred these to the genus Ammothea. The adults remain unknown to this day. Only one other pycnogonid,

Nymphonella tapetis, has been described as having this kind of larva (Ohshima, 1937).

It appears, then, that there are three lines of development within the pycnogonids, two major and one minor:

1. Protonymphon larva:

Hatches out as a protonymphon. As development proceeds, the body elongates, limbs (walking legs) are added one at a time. Examples: Tanystylum orbiculare (Morgan, 1891); Pycnogonum littorale (Behrens, 1984). Appendages 2 and 3 (larval appendages) eventually are replaced by adult pedipalps and ovigerous legs respectively in Tanystylum and appear to be lost between molts V and VI in Pycnogonum.

2. Attaching larva:

No larval appendages, larva has only chelicerae and first two limb buds (first two walking legs). As development proceeds, the two limb buds develop into walking legs one at a time and the additional limb buds appear and also develop into walking legs one at a time. Pedipalps and ovigerous legs appear and develop during the last few molts. Examples: Propallene, Austropallene.

3. Atypical protonymphon larva:

Hatches out as a protonymphon. After the first molt, all resemblance to a protonymphon ends. At

this time, all the limb buds (for walking legs) appear at once. Appendages 2 and 3 as in 1. above for Tanystylum. Examples: Nymphonella, Ammothea sp. (Ohshima 1933).

The attaching larva seems to be characteristic of the callipallenids. Both the protonymphon larva (example: Nymphon leptocheles, fig. 3A in Bamber, 1983) and the attaching larva (example: Nymphon hirtipes, plate VI in Wilson, 1878) have been described for the genus Nymphon.

The protonymphon larva seems to be much more widespread, being found in the various ammotheids and tanystylids and in Anoplodactylus and Phoxichilidium. No larval stages have ever been reported for some groups such as the colossendeids and many of the little known and seldom seen pycnogonids such as Queubus, Pycnofragilia and others.

It is not known how widespread the atypical protonymphon larva will turn out to be. For now it is known definitely only from Nymphonella tapetis and from Ohshima's Ammothea sp.

Extra Pairs of Walking Legs:

The vast majority of known pycnogonid species all have eight walking legs. Several genera of pycnogonids are known which have 10 and in one case 12, walking legs. In each case, the extra-legged species are reported to be identical to the eight-legged species in all other aspects.

These extra-legged species have for now been classified as separate genera (Hedgpeth, 1947, p. 9-33). Whether this separation of very similar organisms into separate genera on the basis of one character only (extra pairs of walking legs) will stand on closer scrutiny remains to be seen. Again, the first question to be answered here is where these extra legs came from.

The extra legs do not seem to be developmental abnormalities that appear sporadically. The literature on this subject indicates that there are entire populations of extra-legged pycnogonids. Closer scrutiny of 8 and 10 (or 12) legged individuals may well reveal previously unreported differences between the two. For now, in the cladistic analysis of the Class Pycnogonida, they are left as separate genera.

Higher Classification - A Brief History:

Modern pycnogonid classification comes from Hedgpeth (1947). In this paper, after a re-examination of all previous classifications, he divided the Class Pycnogonida into 8 families (note: no orders designated) mainly on the basis of the presence or absence of chelicerae, pedipalps, and ovigerous legs (and various combinations thereof). He also used number of segments in the pedipalps and number of segments in the ovigerous legs as characters where applicable. Table 1 gives a complete summary of Hedgpeth's classification. With a few modifications (see below), this remains the classification in use today.

Hedgpeth (1954) proposed dividing the Class Pycnogonida into two orders: Pantopoda for all living forms

and Palaeopantopoda for fossil forms. This suggestion has not been put into general use.

Fry (1978) examined 45 characters and 73 genera of pycnogonids and proposed a scheme with 5 orders and 30 families in it. Unfortunately, he used phenetic methods and his results have not met with much acceptance. There are several other problems with the work: First, it was not based on examination of type specimens or on the use of type descriptions from the literature. Instead, "Data were collected for 45 characters from all of the published descriptions of 73 genera of living pycnogonids." (p. 35). [underlining mine]. Nor does the author cite the specific references that were used. Instead, he refers the reader to the published bibliography for the group: Fry and Stock (1978).

The following from Fry (1978) essentially summarizes the current state of affairs:

Not only is classification of the modern Pycnogonida Latreille, 1810 (sensu Hedgpeth, 1955) unstable above the familial level, but there also remains some disagreement amongst specialists as to what is the most satisfactory number of families and where their boundaries lie.... D'Arcy Thompson (1909) concluded that the pycnogonids are ill-suited for arrangement into the higher categories of the Linnean hierarchy. Some more recent authors have supported this view tacitly by their avoidance of categories above the familial, or even the generic, level. (p. 35-36).

Currently recognized families are given in Table 2. All three authors recognize the families Nymphonidae and Callipallenidae. Pallene is a pre-occupied name according to Flynn (1929, p. 252), so the family Pallenidae has been changed to the family Callipallenidae. All three authors

recognize this family, but differ to some extent in the genera placed within it. See Table 3 for a comparison among Hedgpeth, Child, and Arnaud & Bamber.

All three authors recognize a family Phoxichilidiidae and two of the three recognize a family Endeidae. This family contains only the genus Endeis, a small, slender, long-legged pycnogonid which lacks chelicerae and pedipalps in the adult. Juvenile Endeis one molt away from the adult stage, according to Stock (1974, p. 1016) have chelicerae reminiscent of those found in Anoplodactylus (family Phoxichilidiidae). For this reason, Stock places the genus Endeis into the family Phoxichilidiidae.

Again, all authors recognize a family Ammotheidae. This family is characterized by having 6- to 10-jointed pedipalps; chelicerae usually reduced in some manner, or in some cases absent; and ovigerous legs as in fig. 3 or fig. 4.

The family Tanystylidae was created for some ammotheid-like pycnogonids which tend to be very small (1 or 2 mm), have circular bodies, 4- to 7-jointed pedipalps, and have the chelicerae reduced to a knob. Because the tanystylids share so many characters with the ammotheids, there seems to be general agreement that they belong in the family Ammotheidae. (For example, see the discussion in Stock (1954, p. 16).

There is no disagreement among the various authors in recognizing the families Colossendeidae and Pycnogonidae. The Colossendeidae contain the very large (up to 50 cm leg

span) deep-water genera such as Colossendeis and Rhopalorhynchus and the bizarre 10- and 12-legged Decolopoda and Dodecolopoda from the Antarctic. In addition, Pantopipetta, a very tiny deep-water pycnogonid with a very long, thin, curved proboscis is included in this family.

The family Pycnogonidae contains only the genera Pycnogonum and Pentapycnon. Pycnogonum is a short, squat, very atypical pycnogonid which lacks chelicerae and pedipalps in the adult. It is one of the more commonly seen pycnogonids due to its very slow movements and its habit of feeding exclusively on sea anemones. It is often found with its proboscis inserted into its host and offers no resistance to being collected. Pentapycnon is a ten-legged Pycnogonum.

The family Austrodecidae was created for the genus Austrodecus by Stock (1954, p. 151). Austrodecus is very similar to Pantopipetta. Both share the very small size and the very long, thin, curved proboscis. For these reasons and others, Hedgpeth and McCain (1971, p. 217) added the genus Pantopipetta to the family Austrodecidae.

The family Rhynchothoracidae appears twice in the literature: first in Thompson (1909) and then in Fry (1978). C. A. Child and other authors use Thompson (1909), or they include the genus Rhynchothorax with the family Ammotheidae. Arnaud and Bamber (1987) use Fry (1978). Rhynchothorax is another very small, very bizarre pycnogonid with no obvious affinities to any of the

traditional families. It occupies the interstitial habitat and every investigator of this habitat, it seems, finds a new Rhynchothorax. More and more new Rhynchothorax species are being described each year. This creates an immediate problem of how to classify them. Much has been written (none of it satisfactory) about what to do with this genus. The best that traditional classifications have been able to do is to isolate it in its own family for now.

Cladistic Analysis - Methods:

For the cladistic analysis of the Class Pycnogonida, 86 genera and 57 characters were used. Due to a complete lack of any previous comprehensive attempt at a phylogenetic analysis of the entire class (omitting Fry's phenetic analysis for the reasons stated above), this analysis was based entirely on the type descriptions in the literature. In certain cases, due to some very inadequate early type descriptions, it was necessary to search the literature for later, more comprehensive descriptions. Appendix I contains a complete list of genera and the literature sources used for each genus.

The cladistic analysis was run on Hennig86 using the mh* and bb* tree search commands. Due to the large size of the data set, it was impossible to search for an exact solution. Each run produced a total of 743 trees (overflow) and the Nelson consensus tree of these 743 trees is included here. The data set was also run on PAUP (version 3.0q), but it failed to find any trees shorter than the tree produced by the mh* option in Hennig86.

Throwing out all the jargon, what the above paragraph means is the following: A cladistic analysis takes character information presented in the form of a data matrix (see Appendix II) and groups the characters together on the basis of shared derived characters (coded as 1 in the matrix). Shared primitive characters (coded as 0 in the matrix) do not provide any information about group relationships and are therefore not used to form groups here. For small data sets (below 20 taxa), it is possible to find an exact solution in a short period of time. The `ie` command in Hennig86 will deliver an exact solution by implicit enumeration. The data in Appendix II were run on Hennig86 using the `ie` command. After 3 days, the program was still running. For cases like this, Hennig86 provides one with faster, heuristic options. The following (from the Hennig86 manual) explains the `mh*` and `bb*` options selected for analyzing this particular data set:

`mhennig (mh)`: This command constructs several trees, each by a single pass through the data, adding terminals in several different sequences. The shortest trees found are retained.

`mhennig* (mh*)`: This command constructs trees as outlined in `mhennig` above and then applies branch-swapping to each of the initial trees, retaining no more than one tree for each initial one.

`bb`: This command applies extended branch-swapping to the trees in the current tree file. It cannot be used alone because it requires an initial tree or trees to begin

with. The shortest trees found are retained. It will retain no more than 100 trees.

bb*: Adding an asterisk to the initial bb command means that all available tree space will be used to store results. In other words, all trees found will be retained, depending on how much tree space is available to hold them.

Nelson tree: Hennig86 produces a Nelson consensus tree which summarizes in one tree all the non-conflicting information found in (in this case) the 743+ most parsimonious trees produced by the mh* and bb* options. In other words, this data set produces, using these options, 743+ trees of equal length. The topology of the individual trees may vary, but the lengths are all the same.

Choice of Outgroup:

Historically, pycnogonids have been viewed as an appendix to the chelicerates. Some earlier authors even went so far as to put them in a separate phylum by themselves. The main reason for such extreme actions has been an over-reliance on pycnogonid autapomorphies and, as a result of this, an overlooking of the similarities that pycnogonids share with the chelicerates and specifically with the arachnids. For example, they both share a very similar nervous system (Barnes, 1980, p. 658) and very similar leg musculature (Dencker, 1974).

Pycnogonids and arachnids together share some features that separate both from the horseshoe crabs. For instance, arachnids and pycnogonids each have quite distinct chelicerae and pedipalps and these in turn are quite

distinct from the walking legs. In horseshoe crabs, all of these structures are very similar.

For this cladistic analysis, an opilionid was used as the outgroup. Any of the other arachnids would have been just as satisfactory at this stage in our understanding of the relationships between these two groups. The next step here will be to include all of the arachnids and the other chelicerate taxa as outgroups in any subsequent analysis. Until this is done, the choice of any one of these will remain arbitrary at best.

Character Descriptions:

Pedipalp:

1. Number of segments: This character (and character 2, see below) contains lots of phylogenetic information. It has ten states (coded 0-9) and was run as unordered. The states ranged from pedipalp completely absent to present as a bud to present with 10 segments. One genus, Nymphonella has a pedipalp with up to 17 segments due to segment 10 being very finely subdivided. This number of segments turns out to be an autapomorphy for the genus. Any recoding here resulted in a loss of resolution on the cladogram. States for character 1: 0 = absent; 1 = present as a bud; 2 = 2 segments; 3 = 4 segments; 4 = 5 segments; 5 = 6 segments; 6 = 8 segments; 7 = 9 segments; 8 = 10 segments; 9 = more than 10 segments.

Chelicerae:

2. Shape of entire structure: This character also contains lots of phylogenetic information. Again, any recoding here resulted in a loss of resolution. This character has 9 states (0-8) and was run as unordered. The different states reflect the different kinds of chelicerae found in pycnogonids. States for character 2: 0 = Movable finger equal or nearly equal in length to palm; palm squarish; both fingers curved (example - Anoplodactylus allotrius in Child, 1979). 1 = Movable finger equal or nearly equal in length to palm; palm squarish; fingers straight, not curved (example - Callipallene panamensis in

Child, 1979). 2 = Movable finger elongated, often longer than palm; palm elongated (example - Nymphon lituus in Child, 1979). 3 = Movable finger shorter than palm; movable finger fits into notch on immovable finger (example - Austropallene calmani in Gordon, 1944). 4 = Palm much longer (more than 2x) than movable finger; both fingers at right angle to palm (example - Pallenopsis virgata in Nakamura, 1987). 5 = Like state 0, but one finger absent (example - Hemichela micrasterias in Stock, 1954b). 6 = Palm present, fingers reduced; fingers often reduced to knobs or missing altogether (example - Decachela dogieli in Hong and Kim, 1987). 7 = Entire structure reduced to a bud (example - Ammothea hilgendorfi in Nakamura, 1987). 8 = Movable finger longer than palm; palm small, squarish; fingers resemble ice-tongs (example - Decolopoda australis in Bouvier, 1906b). 9 = Chelicerae (fingers + palm) absent (example - Pycnogonum tenue in Nakamura, 1987).

3. Number of scape segments: The scape is the shaft of the chelicera. It has two states: 1-segmented or 2-segmented.

4. Chelicerae retract into scape: In some pycnogonids, the chelicerae, being small, can be retracted into the scape. This character has two states: retractable and not retractable.

5. Orientation of the chelicerae: Some pycnogonids hold the chelicerae in a vertical position and some hold them in a horizontal position.

6. Size of chelicerae: Most pycnogonid chelicerae are the same relative size in relation to their body. Others,

for example Pycnothea, have miniature chelicerae in proportion to their body.

7. Movable finger: This character has two states: curved (state 0) or straight (state 1).

8. Immovable finger: This character has two states: curved (state 0) or straight (state 1).

9. Palm: This character has two states: palm short (state 0) or palm long (state 1). Most pycnogonids have a short palm. Some, like Nymphon have a long palm.

10. Teeth on movable finger: The two states for this character are: movable finger not toothed or serrated (state 0) and movable finger toothed or serrated (state 1).

11. Teeth on immovable finger: This character is the same as character 10 except that it applies to the immovable cheliceral finger.

12. Position of fingers relative to palm: This character has two states, fingers parallel (state 0) or fingers perpendicular (state 1) to palm.

13. Tips of fingers: Most pycnogonid chelicerae have tips which meet (state 0). Some others have tips which overlap (state 1).

14. Finger and palm lengths: This character has two states: fingers longer than palm (state 0) and palm longer than fingers (state 1).

15. Reduction series for chelicerae: Within the pycnogonids one can find a variety of states for the chelicerae ranging from fully functional (Nymphon, Callipallene, Anoplodactylus, Anoropallene, etc.) to one

finger missing (Hemichela only) to palm present, fingers reduced or absent (Decachela, some Achelia, etc.) to entire chelicera reduced to a bud (Ammothea hilgendorfi, Mimipallene) to entire chelicera absent (Pycnogonum). This character was run as unordered and coded as follows:

0. Chelicera with palm, movable finger, immovable finger.
1. Palm present, fingers reduced or absent.
2. Entire structure reduced to a bud; fingers and palm absent.
3. Entire structure absent.

Ovigerous Legs:

16. Oviger segment 5: In a number of genera (Callipallene, Austropallene, Anoropallene, etc.), the males have a distinct apophysis at the distal end of the fifth oviger segment. 0 = apophysis absent; 1 = apophysis present.

17. Distribution of spines on segments 7-10: Compound spines on the strigilis of ovigerous legs, if present, are either randomly distributed (state 1) or arranged in a regular pattern (state 0) (one or several rows).

18. Spine type on segments 7-10: These are of two types: compound (state 0) or simple (state 1).

19. Terminal oviger claw: This character has two states, present (state 0) or absent (state 1).

20. Ovigerous legs: Some pycnogonids (for example Austrodecus) have very minute ovigerous legs. This character has two states: ovigerous legs standard size in

relation to body (state 0) or ovigerous legs miniaturized (state 1).

21. Number of segments (ovigerous legs): This character has the following states: 10 segments, 9 segments, 7 segments, 6 segments, or 5 segments. This character was run as unordered.

22. Comparison of male and female ovigerous legs: Often, male and female ovigerous legs are quite different. In Nymphon, Callipallene, etc., the difference is only in the presence or absence of the apophysis on the fifth joint. In other genera, there are more dramatic differences. For instance, in Ammothea hilgendorfi, the male has a large swollen segment 6 and segments 7-10 are reduced to a tiny string suspended from the swollen segment. In Pycnothea, segment 7 is swollen and segments 8, 9, and 10 are reduced to a very tiny size. In both of these examples, the female has an ovigerous leg in which all of the segments are reduced in size and none are greatly swollen. In genera such as Anoplodactylus and Phoxichilidium, males have ovigerous legs of 5 or 6 segments only and females lack ovigerous legs.

23. Segments 7-10 (ovigerous legs): This character has two states: strigilis present (state 0) or strigilis absent (state 1).

24. Terminal oviger claw: Character 19 is coded as present or absent for this structure. The present character provides more information on this structure when it is present. It is coded as smooth (state 0) or serrated (state 1).

25. Segment 6 (ovigerous legs): See character 22 for an explanation. This character is coded as swollen (state 1) or not swollen (state 0).

26. Segment 7 (ovigerous legs): See character 22 for an explanation. This character is also coded as swollen (state 1) or not swollen (state 0).

27. Pair of spines at tip of ovigerous leg: absent (state 0) or present (state 1).

Eggs:

28. Shape of egg mass: This character has the potential to be quite informative. In the current data matrix, only a few taxa could be included because this information is missing from the vast majority of published type descriptions. The few descriptions containing this character proved it to be quite diverse: egg mass in the shape of a solid ball, hollow ball, ribbon, bracelet, and egg mass strung between the ovigers. It was run as unordered.

29. Egg size: This has 3 states, small, medium, and large and was run as unordered.

Walking Leg:

(Count legs from front to back: first = front pair, etc.)

30. Genital pores: These are located on the second coxal joint in pycnogonids. This character is informative in the male only. In all females except one (Pycnogonum), it is found on all four pairs of legs. In the male, there are four states: on all four pairs of legs (state 0), on legs two, three, and four (state 1), on legs three and four

(state 2), and only on the last pair (fourth pair) of legs (state 3). The character is run as unordered.

31. Genital pore structure: This character has two states: Genital pore on small, raised mound (state 0) or on a spike (state 1).

32. Cement gland size and number: The data matrix contains many question marks for the cement gland characters. Cement glands are often inconspicuous and are easily overlooked, especially in smaller taxa. In spite of the large amount of missing data for these characters, they do contain phylogenetic information. Removal of cement gland characters from the matrix causes a conspicuous loss of resolution. This character has two states: A single large gland (state 0) or multiple small glands (state 1).

33. Cement gland opening: This character has two states: opening flush with surface (state 0) or opening on a raised mound or spike or tube (state 1).

34. Cement gland location: This character has three states: femur only (state 0), femur and tibia (state 1), and femur and 3rd coxa (state 2). Femur only is the most common state. It was run as unordered.

35. Location of cement gland opening: This character has two states: located on dorsal surface (state 0), or located on ventral surface (state 1).

36. Extra pairs of walking legs: This character has two states: 4 pairs of walking legs (most pycnogonids) (state 0) and 5 or 6 pairs (Pentanymphe, Dodecolopoda, Pentapycnon, etc.) (state 1).

37. Lateral processes: Lateral processes are the extensions from the body to which the walking legs are attached. They can either be close together (state 1) or widely separated (state 0).

Propodus and Tarsus:

38. Tarsus length: This character has two states, short (state 1) and long (state 0). The vast majority of taxa had a short tarsus.

39. Propodal heel projection: The proximal end of the propodus (the heel) often has a projection. In a number of taxa, this projection is absent.

40. Dorsal terminal propodal projection: This structure is a projection at the distal end of the propodus opposite to the beginning of the terminal claw. It is coded as present (state 1) or absent (state 0).

41. Spines on propodus: This has two states, spiny (state 0) or smooth (state 1).

Auxiliary claws: Much has been written about whether or not auxiliary claws provide any information about pycnogonid relationships. The results have, until now, been inconclusive. Auxiliary claws, when coded in the traditional manner, as simply present or absent, do not provide any phylogenetic information whatsoever. They greatly contribute to the homoplasy of the data and unite no groups when coded in this manner. A better approach than coding as present or absent is to examine whether or not they are paired or single (character 42), their point of origin (character 43), their location (character 44),

their length relative to the main claw (characters 47 and 48), and organize them into a reduction series (character 46).

42. Auxiliary claws: This character has two states: paired (state 0) or single (state 1). Most pycnogonids have paired auxiliary claws.

43. Auxiliary claws - origin: This has two states: origin at base of main claw (state 0) and origin out on main claw (state 1).

44. Auxiliary claws - location: This character has two states: located one on each side of main claw (state 0) or both located in center-line of main claw (state 1).

45. Main claw (propodus): This character has two states: not serrated (most pycnogonids) (state 0) and serrated (state 1).

46. Reduction series for auxiliary claws:

0. Auxiliary claws longer than 1/2 the length of the main claw.

1. Auxiliary claws shorter than 1/2 the length of the main claw.

2. Auxiliary claws even shorter.

3. Auxiliary claws absent.

This character was run as unordered.

47. Main claw compared to auxiliary claws: This character has two states: main claw long (longer than auxiliaries) and thin (state 0) or main claw short (shorter than auxiliaries) and thick (state 1).

48. Auxiliary claws compared to main claw: This character has two states: auxiliaries shorter than main

claw (state 0) or auxiliaries longer than main claw (state 1).

Abdomen:

49. Abdomen articulation: In most pycnogonids, the abdomen is as in figure 1. Some pycnogonids (for example, Colossendeis) have a different kind of abdomen. It is very reduced in size, extends straight out from between the fourth pair of lateral processes, and is articulated to the body. This character has two states: abdomen not articulated (state 0), and abdomen articulated (state 1).

Paired Ventral Ganglia:

50. Paired ventral ganglia: Pycnogonids have a variety of states for this character (information based on personal observations) ranging from having all four pairs of ganglia separate (one pair per walking leg), to having all ganglia bunched up together (but still distinguishable as separate) at the anterior end. Unfortunately, it was only possible to code this for several taxa. The vast majority of type descriptions did not mention it. For those that did, the following coding was used: all four pairs of ganglia separate (one pair per walking leg) (state 0); and 3rd and 4th pairs of ganglia close together (state 1). When better material becomes available, this character has the potential to be very informative.

Eyes:

51. Number of eyes: This character was coded as 2 pair of eyes present (state 0) or 1 pair of eyes present (state 1). Most pycnogonids have 2 pair.

52. Size of eyes: Pycnogonid eyes are usually all the same size and shape, but some genera (for example, Pallenopsis) have unequal eyes. The character has two states: eyes all equal in size (state 0) or eyes not all equal in size (state 1).

Body Outline:

53. Body outline: Many pycnogonids (Nymphon, Austropallene, Ammonothea, etc.) are longitudinal in outline. Some are circular (Tanystylum, some Achelia) and one (Chonothea) is triangular in outline. The character has two states: body longitudinal in outline (state 0) or body circular (or triangular) in outline (state 1).

Hood:

54. Hood: This structure is a cover or hood enclosing the chelicerae in several genera (for example, Austroraptus and Oorhynchus). It may prove to be more widespread than is currently indicated in the data matrix. In the type descriptions, unless the author specifically mentioned the presence of a hood, or drew an outstanding illustration of the anterior end of the pycnogonid, it was impossible to tell if some of the more poorly known pycnogonids had this structure. It was coded as present (state 1) or absent (state 0).

Neck:

55. Pre-neck: This character is defined as a neck-like extension of the body from the first pair of walking legs to the eye tubercle. It has two states: absent (state 0) or present (state 1).

56. Post-neck: This character is defined as a neck-like extension of the body from the eye tubercle forward to the chelicerae. It has two states: absent (state 0) or present (state 1).

57. Overhanging neck: This character is defined as a neck-like extension of the body which extends up over the proboscis, chelicerae, and pedipalps. The eye tubercle is located on top of this extension. It has two states: absent (state 0) or present (state 1).

Cladistic Analysis:

The data matrix is shown in Appendix II. It contains 86 taxa and 57 characters. The data were run on Hennig86 using the options outlined in the Methods section above.

Comparison with Current Classification:

The cladogram from the present study (fig. 7) is compared with Hedgpeth's (1947) classification (Table 1). Several of the more traditional groupings can be recognized on the cladogram. Going from right to left, first of all we find the group containing all of the family Nymphonidae plus most of the family Callipallenidae. This group is supported by characters 1, 2, 5, 9, 10, 11, 13, 24, 35, and 38. (see individual character descriptions for details). This grouping is given the new name: Order Nymphoniformes. Nymphon J. C. Fabricius 1794 was chosen here instead of Callipallene Flynn 1929 because Nymphon is the older name. This order contains two families and three genera which are presently incertae sedis.

All of the rest of the pycnogonid genera are included in the second order which is given the name Ammotheiformes. This new order contains six families and eight subfamilies. Also included in this grouping are a number of genera that are, for the present, incertae sedis. Among these are Pentapycnon and Pycnogonum (Hedgpeth's family Pycnogonidae); Rhynchothorax (Fry's family Rhynchothoracidae; and Austrodecus (one half of Hedgpeth and McCain's family Austrodecidae).

Next are two smaller groups of two genera each. The first containing Hedgpethius and Prototrygaeus is held together by having ovigerous legs composed of 9 segments only and auxiliary claws longer than main claw. This grouping is given the name family Hedgpethidae. The second, family Nymphonellidae, contains the genera Calypsopycnon and Nymphonella. It has two synapomorphies: characters 4 (chelicerae which retract into the scape) and 6 (miniaturization of the chelicerae).

The next major group, family Hannonidae is supported by the following characters: 5, 6, 17, 23, 25, and 30. The genera which comprise this new group come from either the traditional family Ammotheidae or the traditional family Callipallenidae.

Moving along, the next grouping, family Colossendeidae, contains genera from the traditional families Colossendeidae, Ammotheidae, and Austrodecidae. It has the following character support: 3, 13, and 46. This family is split into three subfamilies.

The last major grouping, family Ammotheidae, contains genera from the traditional families Ammotheidae, Tanystylidae, and Phoxichilidiidae. It also contains the genus Endeis (family Endeidae). It is supported by the following characters: 2, 15, 17, 19, 23, 30, and 40. Austroraptus through Magnammothea contain representatives of the first two traditional families and the remaining family, Phoxichilidiidae is found in the grouping Pallenopsis through Anoplodactylus. Interestingly enough, the genus Endeis (Hedgpeth's family Endeidae) comes out well within the group containing the members of the former family Phoxichilidiidae.

This new family Ammotheidae is split into five subfamilies. Two are monotypic (Austroraptinae and Ammothellinae) and one (Achelinae) contains two genera. The subfamily Tanystylinae contains three of the genera (Discoarachne, Tanystylum, and Trygaeus) originally included by Hedgpeth in his family Tanystylidae. The subfamily Ammotheinae surprisingly groups genera from four traditional families (Phoxichilidiidae, Endeidae, Ammotheidae, and Callipallenidae). Endeis has been placed within the Phoxichilidiidae previously by Stock (see discussion above), but genera such as Ammothea and Anoplodactylus have been considered to be distantly related, if at all, and certainly not considered to be sister taxa.

Comparing the cladogram to Hedgpeth's eight families (and the subsequent modifications to these families) one can draw the following conclusions:

1. There is no support for the families Endeidae, Rhynchothoracidae, and Austrodecidae.
2. There may, in the future, be support for a family (or order) Pycnogonidae. Present evidence is inconclusive.
3. The families Nymphonidae and Callipallenidae need to be combined into one larger grouping (order Nymphoniformes).
4. The families Ammotheidae, Tanystylidae, and Phoxichilidiidae need to be combined into one larger grouping (order Ammotheiformes).

Much work remains to be done on the systematics of the Class Pycnogonida. There are still too many gaps in our knowledge of the group. It is hoped that this cladogram, based on type descriptions from the literature, will offer a starting point for future investigations into this topic. It is not meant to be the final answer, but rather a summary of our current knowledge.

Class Pycnogonida Latreille 1810

Order Nymphoniformes nom. nov.

Family Callipallenidae Hilton 1942

Family Heteronymphonidae nom. nov.

incertae sedis: Nymphon, Pentanympion,
Sexanympion

Order Ammotheiformes nom. nov.

Family Paranympionidae Fry 1978

Family Hedgpethidae nom. nov.

Family Nymphonellidae nom. nov.

Family Hannonidae Fry 1978

Family Colossendeidae Hoek 1881

Subfamily Colossendeinae Hoek 1881

Subfamily Ascorhynchinae Hoek 1881

Subfamily Rhopalorhynchinae Fry 1978

Family Ammotheidae Dohrn 1881

Subfamily Ammotheinae Dohrn 1881

Subfamily Tanystylinae Schimkewitsch 1913
Subfamily Achelinae Wilson 1881
Subfamily Ammothellinae Fry 1978
Subfamily Austroraptinae nom. nov.
incertae sedis: Oorhynchus, Scipiolus.
incertae sedis: Austrodecus, Böhmia,
Boreonymphon, Ephyrogymna, Hemichela,
Heterofragilia, Nymphopsis, Pentapycnon,
Pigrogromitus, Pycnofragilia, Pycnogonum,
Queubus, Rhynchothorax.

DIAGNOSES OF NEW AND REVISED HIGHER TAXA

ORDER NYMPHONIFORMES nom. nov.

DIAGNOSIS: Small to medium sized pycnogonids with fully functional chelicerae, usually 5-segmented pedipalps or pedipalps reduced to less than 5 segments. In some genera, pedipalps present only in the male. Ovigerous legs of the nymphonid-callipallenid type, usually with apophysis on fifth segment present in male only. Terminal claw present or absent, often serrated when present. Compound spines on ovigerous legs in a single row only. Post-neck often present.

FAMILY CALLIPALLENIDAE Hilton 1942 STATUS REVISED

DIAGNOSIS: Generally small pycnogonids with fully functional chelicerae; pedipalps often reduced to less than 5 segments and in some genera, present only in the male. Ovigerous legs of the nymphonid-callipallenid type, with apophysis on fifth segment present in male only. Terminal claw can be present or absent. Compound spines on ovigerous legs in a single row only. Post-neck present.

INCLUDED GENERA: Anoropallene, Austropallene,
Callipallene, Cheilopallene, Neonymphon Neopallene,
Oropallene, Pallenella, Parapallene, Propallene,
Pseudopallene, Seguapallene, Siphopallene,
Spasmopallene, Stylopallene.

FAMILY HETERONYMPHONIDAE nom. nov.

DIAGNOSIS: Similar in most characters to the family
Callipallenidae, except that instead of a post-neck,
these two taxa have a pre-neck.

INCLUDED GENERA: Heteronymphon, Safropallene.

INCERTAE SEDIS: Nymphon, Pentanymphton, Sexanymphton

ORDER AMMOTHEIFORMES nom. nov.

DIAGNOSIS: Chelicerae range from fully functional to
completely absent. Many genera have chelicerae
modified in some manner (fingers atrophied, fingers
absent, fingers and palm absent, etc.). Pedipalps
generally present, often 10-segmented. Ovigerous legs
modified in various ways. Pre-neck and post-neck both
absent. Overhanging neck found in a few genera.

FAMILY PARANYMPHONIDAE Fry 1978

DIAGNOSIS: Chelicerae fully functional, fingers longer
than palm. Pedipalps present in both sexes, 6-7
segmented. Ovigerous legs of the nymphonid-
callipallenid type, lacking apophysis on fifth segment
in both sexes. Short post-neck present.

INCLUDED GENERA: Paranymphon

FAMILY HEDGPETHIDAE nom. nov.

DIAGNOSIS: Ovigerous legs composed of 9 segments only.
Auxiliary claws longer than main claw. Main claw
short and thick.

INCLUDED GENERA: Hedgpethius, Prototrygaeus.

FAMILY NYMPHONELLIDAE nom. nov.

DIAGNOSIS: Characterized by miniature chelicerae which
can be retracted back into the scape.

INCLUDED GENERA: Calypsopycnon, Nymphonella.

FAMILY HANNONIDAE Fry 1978 STATUS REVISED

DIAGNOSIS: Chelicerae often miniaturized, and held
vertically instead of horizontally. Pedipalps
variable. Ovigerous legs 9 or 10 jointed; strigilis
absent; segment 6 often swollen. Gonopores on legs 3
and 4 only.

INCLUDED GENERA: Bradypallene, Cilunculus,
Dromedopycnon, Elassorhis, Hannonia, Kyphomia,
Megarethus, Mimipallene, Pycnothea, Sericosura.

FAMILY COLOSSENDEIDAE Hoek 1881 STATUS REVISED

DIAGNOSIS: Chelicerae can be present or absent,
cheliceral scape 2 segmented. Tips of chelicerae may
overlap. Pedipalps variable. Ovigerous legs similar
to nymphonid-callipallenid type only with two or more

rows of compound spines or ovigerous legs variously modified. Pre-neck, post-neck, overhanging neck absent. Auxiliary claws absent. Abdomen often articulated.

SUBFAMILY COLOSSENDEINAE Hoek 1881 STATUS REVISED

DIAGNOSIS: Generally large pycnogonids with chelicerae absent and pedipalp 10 segmented. Abdomen articulated to body.

INCLUDED GENERA: Colossendeis

SUBFAMILY ASCORHYNCHINAE Hoek 1881 STATUS REVISED

DIAGNOSIS: Generally small pycnogonids with variable chelicerae and 2 segmented scape. Pedipalps variable. Ovigerous legs 9 to 10 segmented. Auxiliary claws located in center line of main claw.

INCLUDED GENERA: Ascorhynchus, Bathyzetes, Eurycyde.

SUBFAMILY RHOPALORHYNCHINAE Fry 1978 STATUS REVISED

DIAGNOSIS: Generally large pycnogonids with functional chelicerae. Pedipalps variable. Ovigerous legs 10 jointed, usually with compound spines. Abdomen articulated. Three of the genera have one or two extra pairs of walking legs.

INCLUDED GENERA: Decolopoda, Dodecolopoda, Hedgpethia, Pantopipetta, Pentacolossendeis, Rhopalorhynchus.

FAMILY AMMOTHEIDAE Dohrn 1881 STATUS REVISED

DIAGNOSIS: Chelicerae variable, ranging from fully functional to completely absent. Pedipalps variable. Ovigerous legs variable, usually 10 segmented; no strigilis but with various other modifications. Pre-neck and post-neck absent. Some taxa with an overhanging neck.

SUBFAMILY AMMOTHEINAE Dohrn 1881

DIAGNOSIS: Small to medium sized pycnogonids with variable chelicerae: the more derived taxa have fully functional chelicerae, the more basal taxa have variable chelicerai states. Pedipalps range from 10 segments to completely absent. Ovigerous legs range from 10 segmented with various modifications to a group of taxa (Pallenopsis to Anoplodactylus) with only 5 or 6 segments. Overhanging neck found in several taxa.

INCLUDED GENERA: Ammothea carolinensis, Anammothea, Anoplodactylus, Athernopycnon, Clavigeropallene, Ecleipsothremma, Endeis, Magnammothea, Pallenopsis, Phoxichilidium, Phoxiphilyra, Pycnosomia, Thaumastopycnon.

SUBFAMILY TANYSTYLINAE Schimkewitsch 1913 STATUS
REVISED

DIAGNOSIS: Generally small pycnogonids with chelicerae reduced, often with only a knob remaining where the original chelicera was located. Pedipalps up to 10

segmented, often with fewer segments. Ovigerous legs 10 segmented, strigilis absent, few or no compound spines present, often with a pair of spines present at distal end of terminal segment. Pre-neck, post-neck, overhanging neck, all absent.

INCLUDED GENERA: Acheliana, Aduncorostris, Ammothea hilgendorfi, Chonothoa, Decachela, Discoarachne, Tanystylum, Trygaeus.

SUBFAMILY ACHELINAE Wilson 1881 STATUS REVISED

DIAGNOSIS: Non-functional chelicerae with fingers reduced, palm present. Pedipalps of 8 segments. Ovigerous legs 10 segmented, strigilis absent. Pre-neck, post-neck, overhanging neck, all absent.

INCLUDED GENERA: Achelia, Austrothea.

SUBFAMILY AMMOTHELLINAE Fry 1978

DIAGNOSIS: Small pycnogonids with non-functional chelicerae (fingers reduced, palm present). Pedipalps of 9 segments. Ovigerous legs of 9 segments, strigilis absent. Pre-neck, post-neck, overhanging neck, all absent.

INCLUDED GENERA: Ammothella

SUBFAMILY AUSTRORAPTINAE nom. nov.

DIAGNOSIS: Chelicerae non-functional (fingers reduced, palm absent). Pedipalps of 6 or 7 segments. Ovigerous legs of 10 segments, strigilis absent. Pre-neck, post-neck, overhanging neck, all absent.

INCLUDED GENERA: Austroraptus

INCERTAE SEDIS: Oorhynchus, Scipiolus.

INCERTAE SEDIS: Austrodecus, Böhmia, Boreonymphon,
Ephyrogymna, Hemichela, Heterofragilia, Nymphopsis,
Pentapycnon, Pigrogromitus, Pycnofragilia, Pycnogonum,
Queubus, Rhynchothorax.

Table 1

Pycnogonid Classification (Hedgpeth, 1947)

FAMILY	OVIGER	CHELIFORE	PALP	PRINCIPAL GENERA
NYMPHONIDAE	M, F	Chelate	5 jt.	Nymphon
Wilson, 1878	10 jt.			Heteronymphon
	comp. sp.			Pentanympion
PALLENIDAE	M, F	Chelate	absent,	Callipallene
Wilson, 1878	10 jt.		or	Pseudopallene
	comp.sp		knoblike,	Cordylochele
			or 3-4jt.	Austropallene
				Oropallene
				Propallene
				Hannonia
				Pycnothea
				Decachela
				Pigrogromitus
				Pallenopsis
PHOXICHILID.	M	Chelate	absent	Phoxichilidium
G. O. Sars,	5-9 jt.		or	Anoplodactylus
1891	simple sp.		knoblike	Halosoma
				Hodgsonia
				Pycnosoma

Table 1 continued

ENDEIDAE	M	absent	absent	Endeis
Norman, 1908	7 jt.			
	simple sp.			
AMMOTHEIDAE	M, F	present,	6-10 jt.	Amothea
Dohrn, 1881	9-10 jt.	usually	(Nympho-	Achelia
	spines	achelate	nella,	Ammothella
	simple	but some-	17-20jt)	Nymphopsis
	or	times with		Ascorhynchus
	compound	small		Nymphonella
		chelae		Eurycyde
				Cilunculus
				Boehmia
				Ephyrogymna
				Pycnofragilia
				Heterofragilia
				Austroraptus
				Lecythorhynchus
				Ainigma
				Paranymphon
TANYSTYLIDAE	M, F	achelate	4-6 jt.	Tanystylum
Schimb., 1913	10 jt.			Clotenia
	comp. sp.			Austrodecus
				Rhynchothorax
				Discoarachne
				Dorhynchus

Table 1 continued

				Trygaeus
				Scipiolus
COLOSSENDEIDAE	M, F	absent or	8-10 jt.	Colossendeis
Hoek, 1881	10 jt.	deciduous		Rhopalorhynchus
	comp.sp.	or		Pentacolossendeis
		chelate		Decolopoda
		in extra-		Dodecolopoda
		legged		? Pipetta
		form		
PYCNOGONIDAE	M	absent	absent	Pycnogonum
Wilson, 1878	6-9 jt.			Pentapycnon
	NO SPINES			

Table 2

Summary of Current Classifications,
A Comparison

Hedgpeth (1947)	Stock (various papers)	Arnaud & Bamber (1987)
Nymphonidae	Nymphonidae	Nymphonidae
Pallenidae ¹	Callipallenidae	Callipallenidae
Phoxichilid.	Phoxichilid. ²	Phoxichilid.
Endeidae		Endeidae
Ammotheidae	Ammotheidae ³	Ammotheidae ³
Tanystylidae		
Colossendeidae	Colossendeidae	Colossendeidae
Pycnogonidae	Pycnogonidae	Pycnogonidae
	Austrodecidae Stock, 1954b	Austrodecidae Hedgpeth & McCain, 1971
		Rhynchothoracidae Fry, 1978

¹ Pallene is a preoccupied name according to Flynn (1929, p. 252).

² Includes Endeis.

³ Includes Tanystylidae.

Table 3

Family Callipallenidae

Hedgpeth (1947)	Child (1982)	Arnaud & Bamber (1987)
Austropallene	Anoropallene	Anoropallene
Callipallene	Austropallene	Austropallene
Cordylochele	Callipallene	Callipallene
Decachela	Cheilopallene	Cheilopallene
Hannonia	Decachela	Clavigeropallene
Oropallene	Hannonia	Hannonia
Pallenopsis	Metapallene	Metapallene
Pigrogromitus	Mimipallene	Mimipallene
Propallene	Neopallene	Neopallene
Pseudopallene	Oropallene	Oropallene
Pycnothea	Pallenella	Pallenella
	Pallenoides	Pallenoides
	Pallenopsis	Parapallene
	Parapallene	Propallene
	Pigrogromitus	Pseudopallene
	Propallene	Pycnothea
	Pseudopallene	Seguapallene
	Pycnopallene	Siphopallene
	Pycnothea	Spasmopallene
	Queubus	Stylopallene
	Seguapallene	
	Spasmopallene	
	Stylopallene	
Total=11	Total=23	Total=20

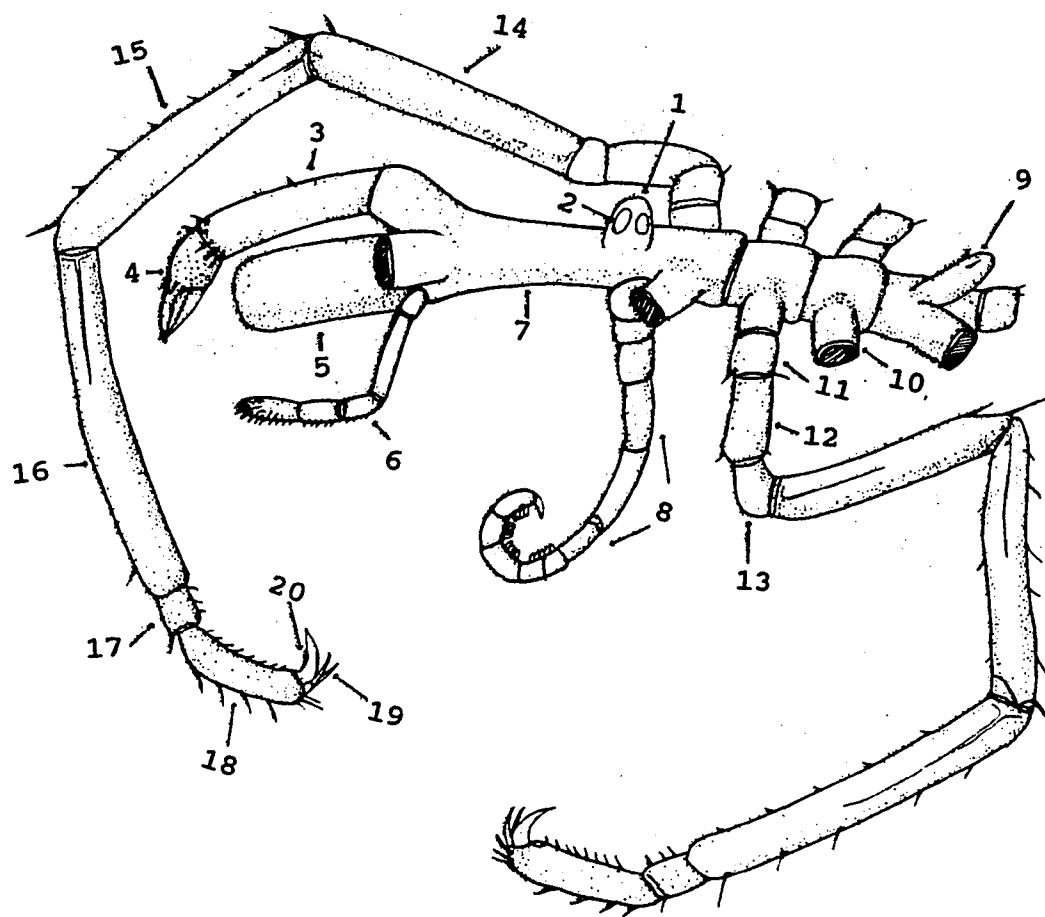


FIGURE 1

PYCNOGONID (after Nakamura, 1987). 1. Eye tubercle. 2. Eye. 3. Cheliceral scape. 4. Chelicera (Cheliphore, Chelophore). 5. Proboscis. 6. Pedipalp (Palp). 7. Post-neck. 8. Ovigerous leg or Oviger. 9. Abdomen. 10. Lateral process. 11. Coxa 1. 12. Coxa 2. 13. Coxa 3. 14. Femur. 15. Tibia 1. 16. Tibia 2. 17. Tarsus. 18. Propodus. 19. Auxiliary claws. 20. Claw.



FIGURE 2

Ovigerous Leg: Nymphonid-Callipallenid Type

This type of ovigerous leg has 10 segments, the strigilis (segments 7-10), the terminal claw, and is identical in both sexes. 2a. Entire structure (segment 6 is solid black for reference). 2b. Terminal claw. Nymphon lituus (from Child, 1979).

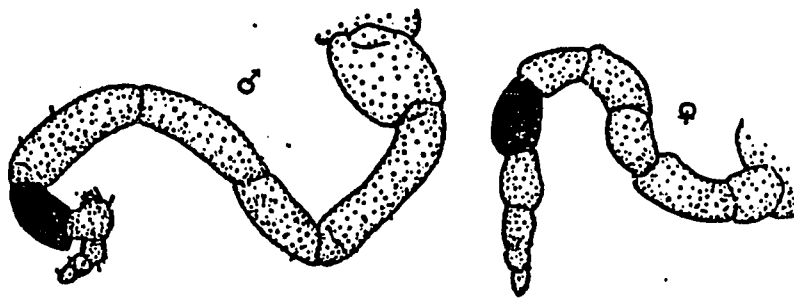


FIGURE 3

Ovigerous Leg: Ammotheid Type

This type of ovigerous leg has 10 segments also, no strigilis, no terminal claw, and male and female are different. In Ammothea hilgendorfi (from Cole, 1904), segment 7 is swollen in the male and segments 8, 9, and 10 are very much reduced in size.

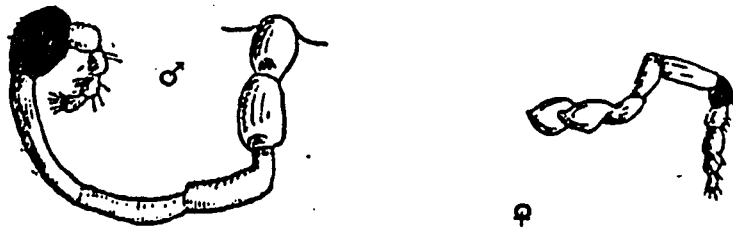


FIGURE 4

Ovigerous Leg: Pycnotheid Type

Similar to figure 3, except that segment 6 is swollen and segments 7-10 are very much reduced in size. Pycnothea (from Loman, 1920).

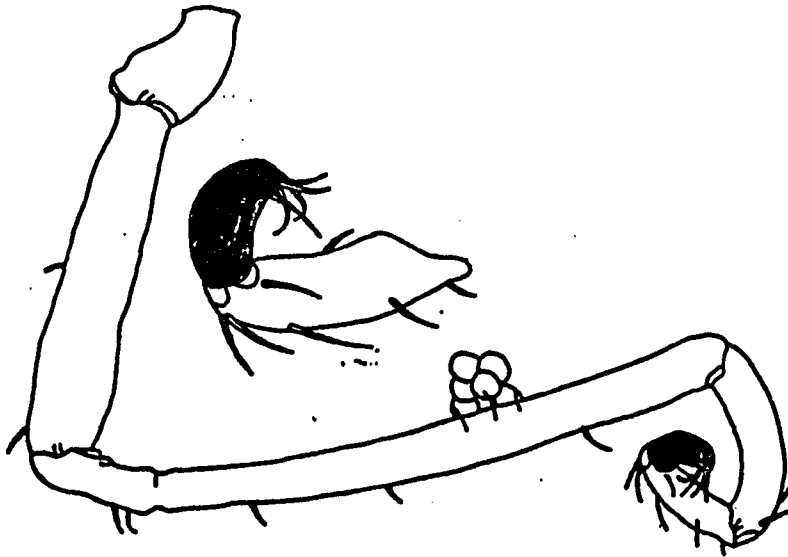


FIGURE 5

Ovigerous Leg: Phoxichilidiid Type

This type of ovigerous leg is present in the male only (completely lacking in the female) and is reduced to either 5 or 6 segments. Anoplodactylus (from Child, 1979).

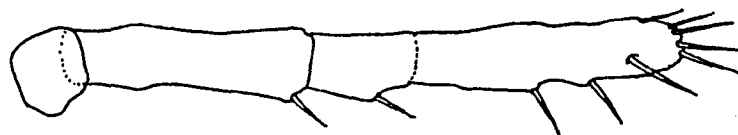


FIGURE 6

Ovigerous Leg: Austrodecus Type

This type of ovigerous leg is characterized by a vast reduction in size (figure not to scale) and by loss of most of the segments and most of the specialized structure found in more typical ovigerous legs.

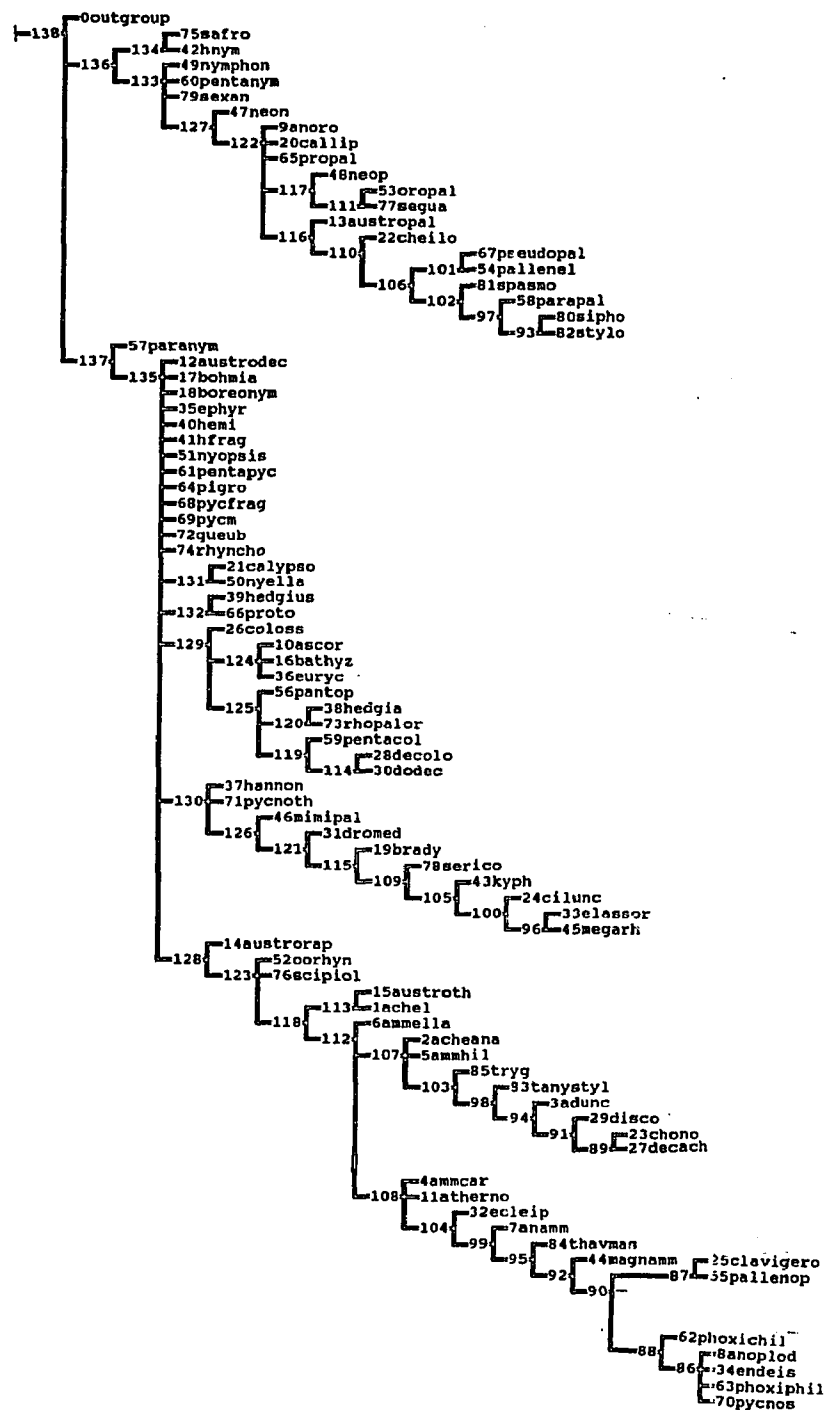


FIGURE 7

Cladogram (Nelson Consensus Tree) of the Class Pycnogonida

Appendix I

List of Genera

These are the genera used in the cladistic analysis. The type description reference is given first followed by other references used for characters not included in the type description. For complete references, please see Fry and Stock, 1978 [references before 1978] and Arnaud and Bamber, 1987 [references after 1978].

Achelia Hodge, 1864

Hodge (1864, p. 114-115; Plate XIII, figs. 7-10)
Other references: Hodgson (1915, p. 147), Hedgpeth (1948, p. 241)

Acheliana Arnaud, 1971

Arnaud, F. (1971, p. 199-204)
Other references: None

Aduncorostris Fry and Hedgpeth, 1969

Fry and Hedgpeth (1969, p. 113)
Other references: Stock, (1954b, p. 109-112 and figs. 52-53)

Ammothea Leach, 1814

Leach (1814, p. 33-34) [Ammothea carolinensis]
Other references: Hodgson (1915, p. 146), Calman (1915a, p. 310-315), Fry and Hedgpeth (1969, p. 73-75 and figs. 106-108)
Cole (1904, plate XV, figs. 1-8) [Ammothea hilgendorfi]

Ammothella Verrill, 1900

Verrill (1900, p. 581-582 and figs. 2-4)
Other references: Marcus (1940b, p. 92-93 and fig. 12), Hedgpeth (1948, p. 246)

Anammothea Fry and Hedgpeth, 1969

Fry and Hedgpeth (1969, p. 97-98 and figs. 150-151)
Other references: Gordon (1932, p. 99-101 and figs. 48-50)

Anoplodactylus Wilson, 1878a

Wilson (1878a, p. 200-202 and fig. 1)
Other references: Hedgpeth (1948, p. 216-226 and fig. 28a-c), Needler (1943, p. 13-14 and fig. 17)

Anoropallene Stock, 1956a

Stock (1956a, p. 46-48 and fig. 7)

Other references: None

Ascorhynchus G. O. Sars, 1877

G. O. Sars (1877, p. 367-368)

Other references: G. O. Sars (1891a, p. 132-136 and plate XIV, fig. 2a-t). Wilson (1881, p. 247-249 and plate II, fig. 3-4)

Athernopycnon Fry and Hedgpeth, 1969

Fry and Hedgpeth (1969, p. 94-96 and figs. 145-147)

Other references: Calman (1915c, p. 53-55 and fig. 12)

Austrodecus Hodgson, 1907b

Hodgson (1907b, p. 52-54)

Other references: Stock (1954b, p. 151), Stock (1957c, p. 45-50 and fig. 19-21)

Austropallene Hodgson, 1915a

Hodgson (1915a, p. 161)

Other references: None

Austroraptus Hodgson, 1907b

Hodgson (1907b, p. 54-56 and plate VIII, fig. 2)

Other references: Calman (1915c, p. 62-63 and fig.

17), Fry and Hedgpeth (1969, p. 113-117 and figs. 174-185)

Austrothea Hodgson, 1915

Hodgson (1915, p. 147)

Other references: Calman (1915c, p. 56-60 and figs. 13-14), Fry and Hedgpeth (1969, p. 109-110 and figs. 168-170)

Bathyzetes Stock, 1955b

Stock (1955b, p. 261-263 and fig. 24)

Other references: Loman, 1908, p. 28-31 and plate V, figs. 52-65), Nakamura and Child (1990, p. 305-307 and fig. 1e-g)

Böhmia Hoek, 1881

Hoek (1881, p. 24)

Other references: Böhm (1879a, p. 192-195 and plate II, fig. 5), Stock (1957b, p. 97 and fig. 14), Flynn (1928, p. 30 and fig. 17), Gordon (1944, p. 61-62 and fig. 23), Barnard (1954, p. 133-136 and fig. 22)

Boreonymphon G. O. Sars, 1888

G. O. Sars (1888, p. 354-355)

Other references: Just (1972, p. 3-6 and figs. 2 and 7c)

Bradypallene Kim and Hong, 1987

Kim and Hong (1987, p. 272-276 and figs. 1-2)

Other references: None

Callipallene Flynn, 1929

Flynn (1929, p. 252)

Other references: Johnston (1837, p. 380), Hedgpeth (1948, p. 202-203 and fig. 18a), Stock (1952b, p. 1-14 and figs. 1-27), Stock (1954b, p. 37)

Calypsopycnon Hedgpeth, 1948

Hedgpeth (1948, p. 263-265 and fig. 48)

Other references: None

Cheilopallene Stock, 1955b

Stock (1955b, p. 230-233 and figs. 8-9)

Other references: Child (1988b, p. 64-66 and fig. 5)

Chonothoa Nakamura and Child, 1983

Nakamura and Child (1983, p. 31 and fig. 10)

Other references: None

Cilunculus Loman, 1908

Loman (1908, p. 54-55 and plate VII, fig. 83-95)

Other references: Stock (1955b, p. 253-257 and figs. 19-21)

Clavigeropallene Pushkin, 1974a

Pushkin (1974a, p. 939-940)

Other references: Calman (1915c, p. 44-46 and fig. 9)

Colossendeis Jarzynsky, 1870

Jarzynsky (1870, p. 319-320)

Other references: Hoek (1881a, p. 61-64)

Decachela Hilton, 1939

Hilton (1939, p. 27-35)

Other references: Losina-Losinsky (1961, p. 88-90 and fig. 16), Hong and Kim (1987, p. 155-158 and figs. 13-14)

Decolopoda Eights, 1835

Eights (1835, p. 203-206 and plate VII, figs. 1-2)

Other references: Hodgson (1905c, p. 35-41 and plates 3-4), Fry and Hedgpeth (1969, p. 54-56 and figs. 75-78)

Discoarachne Hoek, 1881

Hoek (1881, p. 74-76 and plate VII, figs. 8-12)

Other references: Cole (1901b, p. 243-247 and plate 13)

Dodecolopoda Calman and Gordon, 1933

Calman and Gordon (1933, p. 107-110 and fig. 1)

Other references: Fry and Hedgpeth (1969, p. 56-57 and figs. 77-82)

Dromedopycnon Child, 1982c

Child (1982c, p. 15-18 and fig. 5)

Other references: None

Ecleipsothremma Fry and Hedgpeth, 1969

Fry and Hedgpeth (1969, p. 96-97 and figs. 148-149)

Other references: Hodgson (1907b, p. 49-50 and plate VII, fig. 2)

Elassorhis Child, 1982c

Child (1982c, p. 11-14 and fig. 4)

Other references: None

Endeis Philippi, 1843

Philippi (1843, p. 175-177 and plate IX)

Other references: Dohrn (1881, p. 169-174 and plates X, Xa, and XI), Calman (1915c, p. 48-49)

Ephyrogymna Hedgpeth, 1943b

Hedgpeth (1943b, p. 50-52 and plate IX, figs. a-g)

Other references: None

Eurycyde Schiödte, 1857

Schiödte (1857, p. 71-72)

Other references: G. O. Sars (1891a, p. 128-132 and plate XIV, fig. 1), Stock (1955b, p. 260-261)

Hannonia Hoek, 1881

Hoek (1881, p. 92-93 and plate XIV, fig. 8-11)

Other references: Stock (1959, p. 561-562 and fig. 6), Stock (1982, p. 188-189 and fig. 10)

Hedgpethia Turpaeva, 1973

Turpaeva (1973, p. 183-186 and fig. 2)

Other references: Loman (1908, p. 22-23 and plate VI, figs. 66-73)

Hedgpethius Child, 1974

Child (1974, p. 493-497 and fig. 1)

Other references: Child (1982a, p. 360-363)

Hemichela Stock, 1954b

Stock (1954b, p. 90-94 and figs. 42-43)

Other references: None

Heterofragilia Hedgpeth, 1943b

Hedgpeth (1943b, p. 53-54 and plate X, figs. a-i)

Other references: Stock (1954b, p. p. 136-139 and figs. 67-68), Utinomi (1955, p. 28-31 and figs. 17-18)

Heteronymphon Gordon, 1932c

Gordon (1932c, p. 79-82 and figs. 38-39)

Other references: Hodgson (1915a, p. 159), Hodgson (1915b, p. 142), Hodgson (1927, p. 321-322 and fig. 4), Gordon (1938, p. 14 and fig. 2)

Kyphomia Helfer, 1938

Helfer (1938, p. 179-181 and fig. 9)

Other references: Stock (1953a, p. 34), Barnard (1954, p. 144-145 and fig. 28a), Stock (1954b, p. 118)

Magnammothia Fry and Hedgpeth, 1969

Fry and Hedgpeth (1969, p. 90-91 and figs. 137-138)

Other references: Gordon (1932c, p. 97-99 and figs. 46-47)

Megarhethus Child, 1982c

Child (1982c, p. 14-15 and fig. 2f-i)

Other references: Hedgpeth (1948, p. 243, fig. 38h-1)

Mimipallene Child, 1982c

Child (1982c, p. 27-29 and fig. 8)

Other references: None

Neonymphon Stock, 1955b

Stock (1955b, p. 219-223 and figs. 2-3)

Other references: None

Neopallene Dohrn, 1881

Dohrn (1881, p. 199-202 and plate XV, figs. 11-15)

Other references: Stock (1954b, p. 34-36 and figs. 13-14)

Nymphon J. C. Fabricius, 1794

J. C. Fabricius (1794, p. 417)

Other references: O. Fabricius (1780, p. 229-231),
Wilson (1878b, p. 20-22 and plate VII, figs. 1a-q),
Hoek (1881b, p. 12-15 and plate I, figs. 17-21)

Nymphonella Ohshima, 1927a

Ohshima (1927a, p. 257-263)

Other references: Ohshima (1933a, p. 59-60 and figs. 1-4), Ohshima (1935b, p. 95-99 and figs. 1-3)

Nymphopsis Haswell, 1885

Haswell (1885, p. 1025-1026 and plate LV, figs. 1-4)

Other references: Flynn (1919b, p. 83-87 and figs. 18-21), Flynn (1929, p. 256-257 and figs. 4-5)

Oorhynchus Hoek, 1881

Hoek (1881, p. 59-61 and plate VII, figs. 1-7)

Other references: Gordon (1944, p. 60-62 and fig. 22)

Oropallene Schimkewitsch, 1929

Schimkewitsch (1929, p. 291-292)

Other references: Hoek (1898, p. 290-293 and plate II, figs. 1-6), Child (1987c, p. 915-916 and fig. 6)

Pallenella Schimkewitsch, 1909b

Schimkewitsch (1909b, p. 7)

Other references: Hoek (1881a, p. 78-79 and plate XI, figs. 8-12)

Pallenopsis Wilson, 1881

Wilson (1881, p. 250-252 and plates IV and V)

Other references: None

Pantopipetta Stock, 1963

Stock (1963, p. 334-336)

Other references: Loman (1904a, p. 264-266), Loman (1908, p. 27-28 and plate XIII, figs. 190-192 and plate XIV, figs. 193-199)

Paranymphon Caullery, 1896

Caullery (1896, p. 361-362 and plate 12)

Other references: Hedgpeth (1948, p. 253), Stock (1966b, p. 408-409 and fig. 1), Child (1982c, p. 18-19), Hong and Kim (1987, p. 149-153 and fig. 9)

Parapallene Carpenter, 1892c

Carpenter (1892c, p. 553)

Other references: Hoek (1881a, p. 76-78 and plate XI, figs. 1-7), Calman (1937b, p. 530-533), Stock (1954b, p. 50-55 and fig. 24d-e), Child (1975, p. 12)

Pentacolossendeis Hedgpeth, 1943b

Hedgpeth (1943b, p. 56-57)

Other references: Hedgpeth (1948, p. 275-276 and fig. 51)

Pentanymphe Hodgson, 1904

Hodgson (1904, p. 459-462 and plate XIV)

Other references: Calman (1915c, p. 27-28)

Pentapycnon Bouvier, 1910a

Bouvier (1910a, p. 26)

Other references: Bouvier (1913, p. 150-156 and figs. 98-100), Hedgpeth (1947b, p. 11-17 and fig. 5), Hedgpeth (1948, p. 281)

Phoxichilidium Milne-Edwards, 1840

Milne-Edwards (1840, p. 535-536)

Other references: Sars (1891a, p. 20-24 and plate II, fig. 1a-g), Marcus (1940b, p. 36-38), Lebour (1945, p. 146-150 and figs. 1-2), Hedgpeth (1948, p. 216-217), Utinomi (1955, p. 21-22)

Phoxiphilyra Stock, 1974

Stock (1974, p. 957-1092)

Other references: Losina-Losinsky (1961, p. 82-86 and fig. 13)

Pigrogromitus Calman, 1927

Calman (1927, p. 408-410 and fig. 104)

Other references: None

Propallene Schimkewitsch, 1909b

Schimkewitsch (1909b, p. 11-13 and fig. 3)

Other references: Böhm (1879b, p. 59-60), Stock (1975b, p. 89-97 and figs. 1-41)

Prototrygaeus Stock, 1975a

Stock (1975a, p. 979-981 and fig. 9)

Other references: None

Pseudopallene Wilson, 1878a

Wilson (1878a, p. 202-203 and fig. 2)

Other references: Sars (1891a, p. 38-42 and plate III, fig. 3a-h), Schimkewitsch (1930, p. 263-271 and figs. 62-63)

Pycnofragilia Hedgpeth, 1943b

Hedgpeth (1943b, p. 53 and plate X, figs. a-i)
Other references: Loman (1908, p. 56-58 and plate VIII, figs. 112-121)

Pycnogonum Brünnich, 1764

Brünnich (1764, p. 84 and fig. 4)
Other references: O. Fabricius (1780, p. 233), King (1974, p. 56-58 and figs. 24-25)

Pycnosomia Losina-Losinsky, 1961

Losina-Losinsky (1961, p. 86)
Other references: Losina-Losinsky (1933, p. 74-75 and fig. 1)

Pycnothea Loman, 1920

Loman (1920, p. 137-139 and fig. 1)
Other references: None

Queubus Barnard, 1946

Barnard (1946, p. 63)
Other references: Barnard (1954, p. 156-158 and fig. 34), Stock (1959, p. 562-563 and fig. 7)

Rhopalorhynchus Wood-Mason, 1873

Wood-Mason (1873, p. 171-175 and plate XIII)
Other references: Calman (1923, p. 268-270 and fig. 1), Stock (1958b, p. 113-119 and figs. 1-21)

Rhynchothorax Costa, 1861

Costa (1861, p. 7-9 and plate I)
Other references: Dohrn (1881, p. 210-215 and plate XVII, figs. 1-9), Stock (1974, p. 15 and fig. 3)

Safropallene Arnaud and Child, 1988

Arnaud and Child (1988, p. 147-150 and fig. 6)
Other references: None

Scipiolus Loman, 1908

Loman (1908, p. 58-59 and plate XV, figs. 204-212)
Other references: Stock (1957b, p. 91-94 and figs. 9-11)

Seguapallene Pushkin, 1975b

Pushkin (1975b, p. 1404-1406 and fig. 2)
Other references: None

Sericosura Fry and Hedgpeth, 1969

Fry and Hedgpeth (1969, p. 112-113 and fig. 173)

Other references: Child (1982c, p. 19-21 and fig. 6)

Sexanymphon Hedgpeth and Fry, 1964

Hedgpeth and Fry (1964, p. 161-169 and figs. 1-3)

Other references: None

Siphopallene Stock, 1968b

Stock (1968b, p. 44-46 and fig. 17a-b)

Other references: Clark (1963, p. 40-42 and fig. 21),
Stock (1973b, p. 96 and fig. 3d)

Spasmopallene Stock, 1968b

Stock (1968b, p. 39-42 and fig. 15)

Other references: Clark (1963, p. 33-35 and figs. 17a-
h and 18a-b)

Stylopallene Clark, 1963

Clark (1963, p. 35-38 and fig. 19)

Other references: None

Tanystylum Miers, 1879

Miers (1879, p. 213-214 and plate XI, fig. 9)

Other references: Clark (1977c, p. 315-318 and 333-336
and figs. 51-61)

Thavmastopycnon Fry and Hedgpeth, 1969

Fry and Hedgpeth (1969, p. 92-94 and figs. 139-144)

Other references: Möbius (1902, p. 183-184 and plate
XXVI, figs. 7-12)

Trygaeus Dohrn, 1881

Dohrn (1881, p. 164-168)

Other references: Stock (1966b, p. 409-411 and fig. 2)

Appendix III

Key to Generic Names (Figure 7)

Achelia = Achel
Acheliana = Acheana
Aduncorostris = Adunc
Ammothea carolinensis = Ammcar
Ammothea hilgendorfi = Ammhil
Ammothella = Ammella
Anammothea = Anamm
Anoplodactylus = Anoplod
Anoropallene = Anoro
Ascorhynchus = Ascor
Athernopycnon = Atherno
Austrodecus = Austrodec
Austropallene = Austropal
Austroraptus = Austrorap
Austrothea = Austroth
Bathyzetes = Bathyz
Böhmia = Bohmia
Boreonymphon = Boreonym
Bradypallene = Brady
Callipallene = Callip
Calypsopycnon = Calypso
Cheilopallene = Cheilo
Chonothoa = Chono
Cilunculus = Cilunc
Clavigeropallene = Clavigero
Colossendeis = Coloss
Decachela = Decach
Decolopoda = Decolo
Discoarachne = Disco
Dodecolopoda = Dodec
Dromedopycnon = Dromed
Ecleipsothremma = Ecleip
Elassorhis = Elassor
Endeis = Endeis
Ephyrogymna = Ephyr
Eurycyde = Euryc
Hannonia = Hannon
Hedgpethia = Hedgia
Hedgpethius = Hedgius
Hemichela = Hemi
Heterofragilia = Hfrag
Heteronymphon = Hnym
Kyphomia = Kyph
Magnammothea = Magnamm
Megarhethus = Megarh

Mimipallene = Mimipal
Neonymphon = Neon
Neopallene = Neop
Nymphon = Nymphon
Nymphonella = Nyella
Nymphopsis = Nyopsis
Oorhynchus = Oorhyn
Oropallene = Oropal
Pallenella = Pallenel
Pallenopsis = Pallenop
Pantopipetta = Pantop
Paranymphon = Paranyrn
Parapallene = Parapal
Pentacolossendeis = Pentacol
Pentanymphon = Pentanyrn
Pentapycnon = Pentapyc
Phoxichilidium = Phoxichil
Phoxiphilyra = Phoxiphil
Pigrogromitus = Pigro
Propallene = Propal
Prototrygaeus = Proto
Pseudopallene = Pseudopal
Pycnofragilia = Pycfrag
Pycnogonum = Pycrn
Pycnosomia = Pycnos
Pycnothea = Pycnoth
Queubus = Queub
Rhopalorhynchus = Rhopalor
Rhynchothorax = Rhyncho
Safropallene = Safro
Scipiolus = Scipiol
Sequapallene = Segua
Sericosura = Serico
Sexanymphon = Sexan
Siphopallene = Siphon
Spasmopallene = Spasmo
Stylopallene = Stylo
Tanystylum = Tanystyl
Thavmastopycnon = Thavmas
Trygaeus = Tryg

Appendix IV

Synapomorphies of Terminal Taxa (Figure 7)

(Numbers in parentheses indicate the state of a multistate character).

Nymphoniformes: Node 136; Characters 1(4), 2(2), 5, 9, 10, 11, 13, 24, 35, 38, 46(3).

Callipallenidae: Node 127; Characters 1(3), 32, 33, 50, 56.

Heteronymphonidae: Node 134; Characters 32, 33, 50, 55.

Ammotheiformes: Node 137; Characters 15, 17, 19, 23, 30(2), 40.

Paranympthonidae: Node 57; Characters 1(5), 5, 10, 11, 24, 33, 34, 38, 46(3), 50.

Hedgpethidae: Node 132; Characters 1(5), 2(6), 3, 15, 17, 18, 19, 21, 22, 23, 25, 29, 33, 40, 48, 50.

Nymphonellidae: Node 131; Characters 4, 6, 29, 41, 46(3), 50.

Hannonidae: Node 130; Characters 5, 6, 17, 23, 25, 30(2).

Colossendeidae: Node 129; Characters 3, 13, 33, 46(3), 50.

Colossendeinae: Node 26; Characters 15(3), 30(2), 41, 49.

Ascorhynchinae: Node 124; Characters 15, 30(2), 35, 49.

Rhopalorhynchinae: Node 125; Characters 15(3), 35, 38.

Ammotheidae: Node 128; Characters 15, 17, 19, 30(2), 33, 40, 50.

Ammotheinae: Node 108; Characters 22, 23, 26, 39.

Tanystyliinae: Node 107; Characters 22, 23, 26, 27, 39, 46.

Achelinae: Node 113; Characters 1(6), 27, 39.

Ammothellinae: Node 6; Characters 3, 21, 23, 26, 27, 39, 43, 44, 46.

Austroraptinae: Node 14; Characters 1(5), 18, 23, 44, 46(2).

Part II - A Revision of the Genus

Austropallene Hodgson, 1915

Introduction:

Austropallene is a small (seven described species) genus of Antarctic pycnogonids. They are widespread in Antarctica and a few are found by almost every expedition to this region. The largest are approximately 2.5 cm in diameter and the smallest are only a few millimeters in size. Nothing is known about their feeding behavior, preferred foods, preferred habitat, mating behavior, etc. They have an attaching larva instead of a protonymphon (Bain, in prep.) and their larval development is similar, but not identical to that found in Propallene (Nakamura, 1981).

This paper presents a brief taxonomic history of the group, then a character discussion with emphasis on ovigerous leg spines, then a cladistic analysis of the seven currently described species using Nymphon as the outgroup, and finally re-diagnoses and descriptions of existing taxa and diagnoses and descriptions of a new genus and several new species.

Acknowledgments:

Specimens for this revision were borrowed from the following sources: Mr. C. A. Child, National Museum of

Natural History (USNM), Smithsonian Institution, Washington, D.C.; Dr. Jan Stock, Instituut voor Taxonomische Zoölogie - Zoölogisch Museum, Amsterdam, Netherlands; Mr. A. I. Muir, Department of Zoology, British Museum (Natural History) (BMNH), London, England; Dr. M. Moritz, Museum für Naturkunde (ZMB) der Humboldt-Universität zu Berlin, Germany; and Dr. Nguyen Ngoc-Ho, Muséum National d'Histoire Naturelle (MNHN), Paris, France.

I would like to extend thanks to all of the above individuals and institutions for their assistance during this revision. In addition, I would like to thank Peling Fong for her helpful assistance in preparing and photographing various specimens under the SEM and Grayce Bain for her many patient and helpful suggestions.

Materials and Methods:

Type material for all currently described species has been examined. The conditions of the various types are discussed under the appropriate species descriptions. Specimens examined under the SEM were prepared by standard procedures (dehydration through an ethanol series, then critical point dried, gold-coated and mounted on stubs).

History:

Austropallene cornigera, the type for the genus, was originally described as Pseudopallene cornigera by Möbius

(1902). He based his description on three ♀ syntypes. Prior to this, Pseudopallene had included only those species with an Arctic distribution. Following in quick succession, several other Antarctic Pseudopallenes were added: P. australis by Hodgson (1907); and P. brachyura and P. cristata by Bouvier (1911).

Pseudopallene and Austropallene are superficially very similar. The only apparent major difference between the two genera, aside from the different distributions, is the presence in Pseudopallene of a large terminal claw on the ovigerous leg. This terminal claw, under the light microscope, appears to be lacking in Austropallene.

A third genus, Cordylochele, with similarities to both Pseudopallene and Austropallene had been described by Sars (1888). Like Pseudopallene, Cordylochele at first had only an Arctic distribution. The first Antarctic representative of Cordylochele was C. turqueti described by Bouvier (1905). C. turqueti was synonymized with A. cornigera by Hodgson (1907). Stock (1953) synonymized the genus Cordylochele with Pseudopallene.

Hodgson (1915) created the genus Austropallene for those genera which did not fit into either Pseudopallene or Cordylochele. He placed the following species into this new genus: Austropallene cornigera, A. cristata, and A.

spicata (new species). P. australis was made a synonym of A. cornigera.

The following is the original description for Austropallene:

AUSTROPALLENE

A genus established to include those forms which Möbius, Prof. Bouvier, and the present writer [Hodgson, 1915] have included in different genera--Pseudopallene, Cordylochele. The presence of cephalic spurs is a most noticeable feature and is confined to all these southern species.

Body robust or slender, segmentation distinct, lateral processes close together or widely separated. Large and stout cephalic spurs. Eyes well developed. Proboscis tapering, with or without a setose wreath. Cheliferi stout, chelae short and powerful. Palps no trace. Ovigera 10-jointed, without a terminal claw. In the male a distal swelling on the fifth joint. No auxiliary claws. (Hodgson, 1915a, p. 161 and 1915b, p. 144).

Calman (1915) described a new species of Austropallene, A. tibicina; and discovered, "...that Hodgson's Austropallene spicata has been founded on the male sex of the same [Austropallene brachyura] species."

Isabella Gordon (1938) published a key to the 4 described species of Austropallene: A. brachyura, A. cornigera, A. cristata, and A. tibicina. In Gordon (1944), she described two more species of Austropallene, A. calmani and A. gracilipes and revised the 1938 key to include these two.

Fage (1952) described the smallest known Austropallene, A. tcherniai. Fage's species brought the

total number of described Austropallene species to seven, a number which has remained unchanged until the present paper.

Ovigerous leg spines:

Specialists in different groups have come to rely on certain characters for splitting many similar taxa into some number of different species. For instance, entomologists use male genitalia for this purpose and arachnid workers use the male pedipalps. There has not been identified, until now, one particular character within the pycnogonids that can be used in this manner for reliably splitting similar taxa into species. The following discussion proposes the use of ovigerous leg spines, viewed under the SEM, to identify new species, especially in taxa where there are many, many very similar individuals.

Fig. 11 shows an Austropallene strigilis. Each of the four segments of the strigilis contains a single row of compound spines. The number of spines on each segment is species specific according to Loman (1923). Examination of A. williamsi in table 4 demonstrates that this is not always true. The various specimens of williamsi that were examined have similar but not exact spine counts. The

larger specimens had more spines per segment and the smaller specimens had fewer.

A more reliable indicator of separate species is the shape of the individual compound spine itself. This study demonstrates that, under the SEM, each Austropallene species has a unique compound spine shape. In addition, it is shown that, at least for some of the species, spine shape varies according to strigilis segment. For instance, compare figures 38a and 38b with figure 38c.

Ovigerous Leg Spines - Problems:

Ovigerous leg spines seem to take a lot of abuse during the course of their lifetime. Most specimens examined had very badly worn spines (fig. 12, a-c). Many others had spines which were encased in mud or bottom sediment (fig. 13). Very few specimens overall had usable spines. For all of the species except those originally assigned to cornigera, only one or two mature adult specimens were available for study. Often the spines on the few available specimens were so worn or encased in mud as to make them unusable. Various attempts were made to clean the mud-encased spines without success. In order to get usable photos of these spines, more specimens need to be collected. Perhaps rearing some in captivity may yield specimens with clean and usable spines. Using the methods

of Nakamura (1981), it should be possible to rear these species since their development is very similar to Nakamura's Propallene longiceps.

Ovigerous Leg Spines - A specific example:

One lot of A. williamsi contained 4 males and 9 females, allowing a comparison of ovigerous leg spines among adult members of one small population. Of this population, 2 males (labeled J-K) and 6 females (labeled A-F) appeared, under the light microscope, to have usable ovigerous leg spines. One ovigerous leg was removed from each and run up for SEM. Both ovigers were removed from specimen K for a left versus right comparison. Not all spines on each ovigerous leg were intact.

Males: The two ovigerous legs from specimen K (figs. 14a and 14b) proved to be mirror images of each other. The spines curve in opposite directions, thus making it possible to tell right from left. Overall, the ovigerous legs of J and K appear to be identical. Intact spines were found on segment 10 of K (fig. 15) and on segments 8 and 9 of J (fig. 16a and 16b). An inspection of these three figures shows that all three spines, while similar in some ways, are quite different in other ways. A thorough search of the pycnogonid literature reveals only one other reported case of different ovigerous leg spines in the same

species. Fage (1956, p. 291-295) reports that males and females of Propallene stocki have different ovigerous leg spines. This present report is the first record of different ovigerous leg spines (on different segments of the strigilis) of the same sex.

Females: Of the 6 females prepared for the SEM, only 2 (B and C) provided any usable information. Fig. 17 shows the entire segment 10 of B. Typically, all females examined under the SEM had most or all of the end spines broken off. Fig. 18 is a close-up of the end of segment 10 illustrating this point. Figures 19 and 20 show close-ups of the spines on segment 10. These appear to be similar to the male segment 10 spines shown in fig. 15 above, although the female spines show much more wear and tear.

Specimen C illustrates another problem encountered on many of the female specimens. Often, all of the spines and sometimes the entire strigilis were thoroughly encased in mud and debris. In specimen C, the third spine from the end (fig. 21abc) has lost its mud casing, allowing a comparison of it with the other segment 10 spines in figures 19 and 20. Again, all three spines are very similar. It was not possible to compare female spines from segments 8 and 9 due to the poor condition of these segments and spines.

On the basis of the above findings, one can conclude the following:

1. The right and left ovigerous legs of a pair are mirror images of each other.
2. Spine type can vary according to strigilis segment.
3. Male and female spines appear to be identical in this genus.

Thus, ovigerous leg spines should prove to be useful in separating very similar taxa into a number of species. Care should be taken to establish first of all whether or not males and females are identical (if not, use only one or the other) and second, to use only spines from the same segment (example: all comparisons made with segment 10 spines, etc.). Right and left ovigerous legs, at least in Austropallene, are identical. This has not yet been examined in other taxa.

Cladistic Analysis - Introduction and Methods:

Austropallene is the first pycnogonid genus to be revised using cladistic techniques to examine relationships within the genus. Fourteen characters and 8 taxa (Appendix V) were used (7 Austropallene species + Nymphon as the outgroup).

The ie option in Hennig86 was used to analyze the data set. One tree was produced (fig. 22) with a length of 21, a ci of 66, and an ri of 65.

Choice of Outgroup:

Austropallene is nested well within the clade (fig. 7) containing most of what used to be referred to as the family Callipallenidae. A logical first outgroup choice for this analysis would be Callipallene or Anoropallene. However, these share too many of the same states of most of the characters with all of the Austropallene species being examined here. They differ significantly only in characters 3, 12, and 14. Character 3 (cheliceral notch) turns out to be an autapomorphy for the cornigera species group within the redefined genus Austropallene (see below).

Character 12 (pedipalp) has several states within this larger group: Austropallene through Siphopallene all lack pedipalps. Propallene and Anoropallene (callipallenids with pedipalps in the male only) form part of the sister group to all of the above and the various nymphons (pedipalps present in male and female both) form the sister group to all of these.

Character 14 (terminal claw on ovigerous leg) proved to be the most interesting of all of the characters here. The nymphons all have a large, prominent terminal oviger

claw. Moving up the cladogram, Propallene has lost this terminal claw, Anoropallene has lost it, Callipallene has lost it, Austropallene has lost it, and then it reappears in all taxa above Austropallene (the state in Cheilopallene is unknown due to a possibly damaged type according to the type description). Why such a mixed distribution of character states?

One possible explanation presented itself while doing the present analysis. All ovigerous legs of the various Austropallene species were examined under the SEM. This demonstrated quite clearly the absence of a terminal claw on the ovigerous leg in all species but one, Austropallene cristata. A. cristata has a small (not visible under the light microscope) but quite unmistakable terminal oviger claw (fig. 23).

In order to deal with characters 12 and 14 most effectively, Nymphon was chosen as the outgroup. It shares the same state in character 12 with the opilionid outgroup for the higher classification and it is at the base of the clade in which character 14 switches around a lot.

Character Descriptions:

1. Cheliceral scape: The scape is the shaft of the chelicera. In all Austropallene it is one-segmented. It has two states here: smooth = 0, spiny = 1.

2. If scape is spiny: This character is self-explanatory: random scattering of small spines = 0, several large prominent spines = 1.

3. Cheliceral notch: This is an autapomorphy for the cornigera species group. It has two states: absent = 0, present = 1.

4. Tips of cheliceral fingers: This is also self-explanatory: tips of fingers meet = 0, tips of fingers do not meet = 1.

5. Amount of separation between lateral processes: Lateral processes are the extensions from the body to which the legs are attached: widely separated = 0, crowded = 1.

6. Ornamentation on lateral processes: Lateral process ornamentation consists of a pair of side spikes and/or one central spike. This character has two states: ornamentation does not vary from front to back = 0, ornamentation varies from front to back = 1.

7. Pair of prominent spikes on sides of lateral processes: absent = 0, present = 1

8. Central lateral process spike: absent = 0, present = 1

9. Abdomen shape: long and bulbous = 0, short and squat = 1. Most pycnogonids have state 0.

10. Length of abdomen in relation to 4th lateral processes: abdomen as long as 4th lateral processes = 0, much shorter than 4th lateral processes = 1.

11. Length of main claw on propodus: tip does not reach end of heel = 0, tip does reach end of heel = 1

12. Pedipalp: present = 0, absent = 1

13. Auxiliary claws: present = 0, absent = 1. This character was present in the outgroup and absent in all Austropallene.

14. Terminal claw on ovigerous leg: present = 0, absent = 1

Results and Discussion:

PAUP and Hennig86 both produced the tree shown in fig.

22.

A. gracilipes, A. cornigera, A. calmani, and A. tibicina form a group united by character 3 (presence of notched chelicera, fig. 9). Characters 8 and 11 add tcherniai to this group. Characters 9, 10, and 14 unite brachyura with the above taxa. All six of these form the redefined genus Austropallene (see below for diagnosis, etc.). Within Austropallene, cornigera is found to contain 10 additional species, all of which are identical except for the shape of the ovigerous leg spines and the number of ovigerous leg spines on each segment in the strigilis. The other species within Austropallene, in addition to differences in the ovigerous leg spine characters, each have their own unique chelicerae.

A. cristata comes out as unresolved at the base of the tree. We don't currently know enough about the real distribution of character 14 (terminal oviger claw) within the larger clade containing Nymphon and Austropallene to do anything more with A. cristata at the present time. In addition to the presence of the small terminal oviger claw, A. cristata has other unique features (highly modified compound spines, a pair of compound spines near the distal end of segment 10, three large tubercles on the body) which render it impossible to place either within the Austropallene ingroup or within the larger clade containing

Nymphon and the callipallenids. Much more work is required within this larger clade in order to further increase our understanding of the interrelationships among these organisms. I would recommend that much of this investigation take place at the SEM level. I suspect that this is where we will find most of the remaining phylogenetically informative pycnogonid characters.

Based on the above, A. cristata is removed from Austropallene and placed into a new genus: Tarapallene.

Species Descriptions:

Ovigerous leg spines are illustrated for the first time with SEM photos for both the 7 previously described species of Austropallene and 10 new species, all ten of which are in the cornigera species group.

Tarapallene new genus

TYPE SPECIES: Pseudopallene cristata Bouvier 1911 (type #MNHN-PY 301, 1 ♂, in MNHN, examined). The ovigerous legs on the type were covered with too much debris rendering it impossible to examine the spines adequately.

ETYMOLOGY: T. cristata resembles a tarantula. Gender = feminine.

DIAGNOSIS: Tarapallene can easily be distinguished from other genera by the shape of the chelicerae, the presence

of three prominent tubercles on the dorsal surface of the body, the unique, long hairy spines covering the legs, and the presence, on the tenth ovigerous leg joint, of a pair of spines near the distal end (fig. 23b).

DESCRIPTION: Chelicerae massive, without notch on immovable finger; scape one jointed, smooth except for scattering of small spines near base; proboscis long and thin, thicker at base, cone-shaped; pedipalps absent; cephalic spurs low--bulbous at base, pointed at tips; neck very short; eye tubercle low, rounded at tip, four eyes present; body relatively smooth with three tall tubercles along midline; ornamentation on lateral processes does not vary from front to back; lateral processes not widely separated; pair of prominent spikes on sides of lateral processes present; legs covered with two rows of long spines; auxiliary claws absent; main claw extends almost to heel; abdomen erect, large and bulbous; ovigerous legs 10 jointed, last four joints form a strigilis; in male, a very large apophysis on fifth joint, absent in female; short, smooth terminal claw present at end of fifth joint.

INCLUDED SPECIES: Only Tarapallene cristata.

Tarapallene cristata (Bouvier) new combination

Figures 23abc, 24

Pseudopallene cristata, Bouvier, 1911, p. 1138, Bouvier, 1913, pp. 102-105 and figs. 55-59.

Austropallene cristata, Hodgson, 1915a, p. 161; Hodgson, 1915b, p. 144; Hodgson, 1927, pp. 331-332 (key on p. 329); Gordon, 1938, p. 14 (key); Gordon, 1944, p. 36 (key).

DIAGNOSIS: Fig. 23a and c illustrate the ovigerous leg spines and fig. 24, the strigilis for this species. See diagnosis and description for the genus for the other characters. Strigilis spine count, see table 4.

MALE: Described by Bouvier 1913.

FEMALE: Described by Bouvier 1913.

MATERIAL EXAMINED: MNHN-PY 301 (HOLOTYPE, 1 ♂), USNM #233806 (1 juv., Off Lavoisier Island, Antarctic Peninsula, 65 58 --S 066 51 --W, depth: 154 m), USNM # 233808 (1 ♀, Ross Sea, 76 02 06S 179 57 00W, depth: 347-358 m), USNM #233809 (4 juv., Ross Sea, Antarctica, 62 41 --S 054 43 --W, depth: 210-220 m), USNM #233810 (1 juv., Ross Sea, Antarctica, 76 00 --S 176 48 --W, depth: 566-569 m), USNM #233811 (1 juv., off Antipodes Islands, New Zealand, 49 --S 178 -- --E, depth: ?), USNM #233812 (3 juv., Low Island, South Shetland Islands, Antarctica, 63 25 --S 062 15 --W, depth: 119-124 m), USNM #233813 (1 juv., South Shetland Islands, Antarctica, 64 54 --S 053 38 --W, depth:

79-85 m), USNM #233814 (1 juv., South Shetland Islands, Antarctica, 64 47 18S 064 07 24W, depth: 110 m), USNM #233815 (2 juv., South Shetland Islands, Antarctica, 64 47 24S 064 06 54W, depth: 94-165 m), USNM #233816 (1 ♂ ovig., 1 ♀, South Shetland Islands, Antarctica, 64 47 14S 064 07 20W, depth: 90-110 m), USNM #233817 (2 juv., Antarctic Ocean, Antarctica, 66 21 42S 066 47 00W, depth: 70-106 m), USNM #233931 (1 ♂, Anvers Island, Palmer Archipelago, depth: 88-112 m).

DISTRIBUTION: From the Antarctic Peninsula to the Ross Sea; also collected off Antipodes Island, New Zealand.

Austropallene Hodgson, 1915

Austropallene Hodgson, 1915a, p. 161 and 1915b, p. 144 (type species subsequently designated by Helfer and Schlottke, 1935, p. 269, Austropallene cornigera (Möbius, 1902); three female syntypes (ZMB P-206), examined. The 3 females turn out to be a male, a female, and a juvenile. The male is hereby designated as the lectotype).

DIAGNOSIS: Austropallene can be separated from other genera by the massive chelicera as in fig. 9 or various modified versions of this chelicera as in fig. 10a-e. The various species of Austropallene are separated on the basis of the type and number of ovigerous leg spines and the chelicera

type. Within the cornigera species group, only the ovigerous leg spines can be used to separate species.

DESCRIPTION: Chelicerae massive or normal in size, immovable finger notched or not notched; scape one-jointed, smooth; proboscis cone-shaped, can be long and thin or short and thick; pedipalps absent; cephalic spurs large, bulbous at base, pointed at tips; neck long; eye tubercle tall and rounded at tip, four eyes present; body relatively smooth; ornamentation on lateral processes can vary from front to back; lateral processes widely separated; pair of prominent spikes on sides of lateral processes present; central lateral process spike present or absent; legs spiny; auxiliary claws absent; main claw extends to heel; abdomen erect, large and bulbous or short and squat; ovigerous legs 10-jointed, last four joints form a strigilis, in male, an apophysis is present on fifth joint, absent in female.

INCLUDED SPECIES: Currently described: Austropallene brachyura, A. calmani, A. cornigera, A. gracilipes, A. tcherniai, A. tibicina. New (or re-described) species: A. australis, A. turqueti, A. wolfgangi, A. maryae, A. jamesi, A. lanceoli, A. edwardi, A. brandti, A. hermani, A. williamsi.

Austropallene brachyura Bouvier, 1911

Figures 10a, 25abc, 26

Pseudopallene brachyura, Bouvier, 1911, p. 1138, Bouvier, 1913, pp. 98-101 and figs. 51-54.

Austropallene spicata, Hodgson, 1915a, p. 161; Hodgson, 1915b, pp. 144-145.

Austropallene brachyura, Calman, 1915, p. 39 (spicata found to be the male of A. brachyura); Hodgson, 1927, pp. 332-334 (key on p. 329) and fig. 8; Gordon, 1938, p. 14 (key); Gordon, 1944, p. 37 (key) and fig. 14b.

DIAGNOSIS: This species can be easily recognized by the distinctive chelicera (fig. 10a). The ovigerous leg spines are very finely divided at the tip, not flaring as in gracilipes and others. The spines tend to be very dirty.

Male: Described by Calman 1915.

Female: Described by Bouvier 1913.

MATERIAL EXAMINED: MNHN-PY 297 (HOLOTYPE, 1 ♀), USNM #233822 (1 ♀, Antarctic Peninsula, Antarctica, 64 50 42S 063 51 12W, depth: 312-330 m), USNM #233823 (1 ♂, off Cape Hallett, McMurdo Sound, Ross Sea, Antarctica, 72 08 --S 172 10 --E, depth: 433 m), USNM #233827 (1 ♀, South Orkney Islands Slope, South Scotia Ridge, Antarctica, 60 50 00S 042 55 06W, depth: 298-302 m), USNM #233828 (9 ♂, 3 ♀, 4 juv., Scotia Sea, Antarctica, 56 19--S 027 29--W, depth:

148-201 m), USNM #233868 (1 ♀, 1 juv., South Shetland Islands, 62 41 --S 054 43 --W, depth: 210-220 m).
DISTRIBUTION: South Orkney Islands to the Ross Sea.

Austropallene calmani Gordon

Figures 10b, 27, 28

Austropallene calmani Gordon, 1944, pp. 42-45, fig. 13 and 14a.

DIAGNOSIS: Chelicerae as in fig. 10b. Fig. 27 illustrates the ovigerous leg spines and fig. 28, the strigilis for this species. Strigilis spine count, see table 4. The ovigerous leg spines for this species have long thin indentations on them and the tops of the spines are more exploded than in any of the other species. The spines on the type were covered with debris.

MALE: Described by Gordon 1944.

FEMALE: Described by Gordon 1944.

MATERIAL EXAMINED: BMNH--1942:12:30:55 (HOLOTYPE, 1 ♀), BMNH--1942:12:30:56 (PARATYPE, 1 ♂), BMNH--1975:127:2 (PARATYPE, 1 ♀), BMNH--1975:128:1 (PARATYPE, too incomplete to determine sex), USNM #233977 (2 ♂, 1 ♀, South Sandwich Islands, Antarctica, depth: 148-201 m), USNM #233981 (1 ♀, South Sandwich Islands, Antarctica, depth: 130-133 m), USNM #233982 (1 ♂, South Orkney Islands, Antarctica, depth: 115-

132 m), USNM #233986 (1 ♀, Palmer Archipelago, Antarctica, depth: 640-670 m).

DISTRIBUTION: South Sandwich Islands to Palmer Archipelago.

Austropallene cornigera (Möbius)

Figures 8, 9

Pseudopallene cornigera, Möbius, 1902 pp. 186-187 and fig. 14-20, plate XXVII; Hodgson, 1907, pp. 7-9 and plate 1, fig. 3; Bouvier, 1911, p. 1138; Bouvier, 1913, pp. 97-98.

Austropallene cornigera, Hodgson, 1915a, p. 161 and Hodgson, 1915b, p. 144 (in part, excluding australis); Calman, 1915, p. 38; Loman, 1923, p. 22; Hodgson, 1927, pp. 329-330 (key on p. 329) and fig. 7; Gordon, 1932, pp. 85-86 and figs. 42-43; Gordon, 1938, p. 14 (key); Gordon, 1944, p. 36 (key).

DIAGNOSIS: Chelicerae massive, as in fig. 9. It proved to be impossible to get clear pictures of the ovigerous leg spines of Möbius' type specimens. They were in very bad shape. A description of these spines will have to await further collecting from the type locality. Spine count for ovigerous legs, see table 4.

MALE: Described by Möbius 1902.

FEMALE: Described by Möbius 1902.

MATERIAL EXAMINED: ZMB P-206 (1 ♂ HOLOTYPE, 1 ♀, 1 juv.).

DISTRIBUTION: Bouvet Island (depth 450 m).

Austropallene gracilipes Gordon

Figures 10c, 29, 30, 31, 32

Austropallene gracilipes Gordon, 1944, pp. 39-41 and figs. 10a, 11a and c, and 14c and d.

DIAGNOSIS: Chelicerae as in fig. 10c. Figs. 29-30 illustrate the ovigerous leg spines and fig. 32, the strigilis for this species. Strigilis spine count, see table 4. The ovigerous leg spines for this species are very clean and very distinct. They are characterized by having several stout spines near the base and a very regular pattern of deeply sculptured indentations which taper gracefully to a point. The top half of each spine is striated. The ovigerous leg spine formula is 12-9-8-10 (segments 10-7). The ovigerous legs are missing from the type specimen.

MALE: Described by Gordon 1944.

FEMALE: Described by Gordon 1944.

MATERIAL EXAMINED: BMNH--1942:12:30:53 (HOLOTYPE, 1 ♂), BMNH--1942:12:30:54 (PARATYPE, 1 ♀), BMNH--1975:293:1 (PARATYPE, 1 ?), BMNH--1975:294:3 (PARATYPES, 3 ?), USNM #233831 (1 ♀, Wilkes Station, Vincennes Bay, Antarctica, 66 -- --S 110 -- --E, depth: ?), USNM #233832 (1 ♀, N. of Cape Washington, Ross Sea, Antarctica, 74 25 06S 167 00

18E, depth: 732 m), USNM #233835 (1 ♀, South Orkney Islands, Antarctica, 62 05 30S 045 08 --W, depth: 265-267 m), USNM #233840 (1 ♀, Antarctic Peninsula, Antarctica, 65 03 00S 063 55 35W, depth: 260-280 m), USNM #233841 (1 ♀, Antarctic Peninsula, Antarctica, 66 07 42S 066 35 30W, depth: 140-210 m), USNM #233843 (1 ♂ ovig., Antarctic Peninsula, Antarctica, 64 21 24S 061 28 12W, depth: 110-155 m), USNM #233849 (1 ♂, Antarctic Peninsula, Antarctica, No latitude and longitude information on label, depth: ?).
DISTRIBUTION: From the South Orkney Islands to Vincennes Bay (may be circumpolar in distribution).

Austropallene tcherniai Fage 1952

Figures 10e, 33

Austropallene tcherniai, Fage, 1952, pp. 182-184 and fig. 1-2.

DIAGNOSIS: A. tcherniai can be separated from the other genera on the basis of its very small size and its distinctive chelicerae as in fig. 10e. The ovigerous leg spines are similar to those found in gracilipes, only smaller and with fewer sculptured indentations. Segment 10 has a modified terminal spine (fig. 33b). The ovigerous legs are missing from Fage's type and they are missing or

incomplete on the other specimens so it is impossible to provide information on spine counts for this species. Although the ovigerous legs appear to be those of a mature pycnogonid, gonopores were not found on any of these specimens. It is possible that tcherniai may be an immature stage of one of the other Austropallene species. MALE: Unknown--holotype may be a juvenile. FEMALE: Unknown--holotype may be a juvenile. MATERIAL EXAMINED: Holotype (MNHN--PY 284, 1 juv. ?), 3 ?? (Instituut voor Taxonomische Zoölogie-Zoölogisch Museum, Amsterdam--PA 1358), USNM #233974 (1 juv. ?, off Ross Island, McMurdo Sound, Ross Sea, depth: 562-564 m). DISTRIBUTION: Ross Sea.

Austropallene tibicina Calman

Figures 10d, 34, 35

Austropallene tibicina Calman, 1915, pp. 39-41 and fig. 7-8; Gordon, 1938, p. 14 (key), Gordon, 1944, p. 37 (key) and pp. 41-42 and figs. 12b-d and 14e.

DIAGNOSIS: Chelicerae as in fig. 10d. Fig. 34 illustrates the ovigerous leg spines and fig. 35, the strigilis for this species. The spines on segments 9 and 10 were too bent over to see clearly. Strigilis spine count, see table 4. The ovigerous leg spines are similar to the gracilipes

spines, but not as deeply sculptured and they have fewer striations. The figures are grainy because the type specimen was not coated.

MALE: Described by Calman 1915.

FEMALE: Described by Calman 1915.

MATERIAL EXAMINED: BMNH--1915.7.24.158-162 (HOLOTYPE, 1 ♂), BMNH--1915.7.24.158-162 (PARATYPE, 1 ?), USNM #87336 (1 ♂, Cape Royds, Ross Island, Antarctica, depth: 58 fm), USNM #233908 (1 ♀, Anvers Island, Palmer Archipelago, Antarctica, 64 47 42S 064 07 24W, depth: 100 m), USNM #233989 (2 ♀, South Shetland Islands, Antarctica, depth: 210-220 m), USNM #233994 (1 ♀, Palmer Archipelago, Antarctica, depth: 85-130 m).

DISTRIBUTION: South Shetland Islands to the Ross Sea.

Each of the following species are identical to A. cornigera for all characters except ovigerous leg spine type and strigilis spine count. These ten species plus A. cornigera now constitute the cornigera species group.

Austropallene australis Status Revised

Figure 36

Pseudopallene australis, Hodgson, 1907, pp. 10-11 and plate 1, fig. 2. Hodgson 1915a, p. 161 and 1915b, p. 144 (australe incorrect subsequent spelling).

DIAGNOSIS: Fig. 36 illustrates the ovigerous leg spines for this species. A. australis is unique in that it has long thin spines near the distal end of segment 10 and more typical spines on the rest of the segment. Strigilis spine count, see table 4.

MALE: Unknown

FEMALE: Described by Hodgson 1907b.

REMARKS: Based on a comparison of ovigerous leg spines, A. australis (and A. turqueti, see below) should be re-established as valid species.

MATERIAL EXAMINED: BMNH--1907.6.24.8 (HOLOTYPE).

DISTRIBUTION: 78 25 40S 185 39 06E, depth: 300 fm.

Austropallene turqueti Status Revised

Figure 37

Cordylochele turqueti Bouvier, 1905, pp. 297-298; Bouvier, 1906, pp. 33-39 and figs. 7-18 and plate III, figs. 1-2; Bouvier, 1913, p. 97 (as synonym of Pseudopallene cornigera).

DIAGNOSIS: Fig. 37a illustrates the ovigerous leg spines and 37c, the strigilis for this species.

MALE: Unknown

FEMALE: Described by Bouvier 1906b.

MATERIAL EXAMINED: MNHN-PY 287 (HOLOTYPE, 1 ♀).

DISTRIBUTION: Carthage Bay.

Austropallene wolfgangi

Figures 38, 39

TYPE: USNM 233887 (1 ♂)

ETYMOLOGY: Named for my friend, Wolfgang Fuchs.

DIAGNOSIS: The holotype is red in color, the paratype is yellow. Fig. 38abc illustrates the ovigerous leg spines and fig. 39, the strigilis for this species. Strigilis spine count, see table 4.

MALE: Trunk length (chelicera insertion to tip of 4th lateral processes), 5.5 mm; trunk width (across 2nd lateral processes), 3.5 mm; proboscis length, 3.3 mm; abdomen length, 0.9 mm; third leg, coxa 1, 1.3 mm; coxa 2, 2.7 mm; coxa 3, 1.0 mm; femur, 5.8 mm; tibia 1, 5.5 mm; tibia 2, 5.5 mm; tarsus, 0.7 mm; propodus, 2.3 mm; claw, 1.7 mm.

FEMALE: Unknown

MATERIAL EXAMINED: USNM 233887 (holotype, Ross Sea, off Cape Adare, 73 02 --S 176 54 --E, Depth: ?), USNM 87352 (1 ♂ paratype, U. S. Navy Antarctic Exp. #43, 65 (or 165 ?) 25 --S 101 13 --E, depth: 100 fm).

DISTRIBUTION: Ross Sea.

Austropallene maryae

Figure 40

TYPE: Holotype USNM 233873 (♀) and 1 ♀ paratype (also USNM 233873). Holotype has 1 ovigerous leg tip missing. Paratype has complete ovigerous legs. Three juveniles also included in vial.

ETYMOLOGY: Named for Mary Bain.

DIAGNOSIS: Color = yellow. Fig. 40 illustrates the ovigerous leg spines for this species. Strigilis spine count, see table 4.

MALE: Unknown.

FEMALE: Trunk length (chelicera insertion to tip of 4th lateral processes), 5.8 mm; trunk width (across 2nd lateral processes), 4.3 mm; proboscis length, 3.2 mm; abdomen length, 1.2 mm; third leg, coxa 1, 0.9 mm; coxa 2, 2.2 mm; coxa 3, 0.8 mm; femur, 6.3 mm; tibia 1, 5.3 mm; tibia 2, 5.7 mm; tarsus, 0.8 mm; propodus, 2.2 mm; claw, 1.8 mm.

MATERIAL EXAMINED: Only USNM 233873 (South Sandwich Islands, Antarctica, 56 19 --S 027 29 --W, depth: 148-201 m).

DISTRIBUTION: South Sandwich Islands.

Austropallene jamesi

Figure 41

TYPE: Holotype USNM 233875 (1 ♀ missing an ovigerous leg tip) and paratype USNM 233875 (1 ♀, ovigerous legs intact).

ETYMOLOGY: Named for James Bain.

DIAGNOSIS: Color = yellowish-brown. Fig. 41ab illustrates the ovigerous leg spines and fig. 41c, the strigilis for this species. Strigilis spine count, see table 4.

MALE: Unknown.

FEMALE: Trunk length (chelicera insertion to tip of 4th lateral processes), 4.9 mm; trunk width (across 2nd lateral processes), 3.2 mm; proboscis length, 2.9 mm; abdomen length, 1.2 mm; third leg, coxa 1, 0.9 mm; coxa 2, 1.6 mm; coxa 3, 1.0 mm; femur, 4.2 mm; tibia 1, 4.0 mm; tibia 2, 4.6 mm; tarsus, 0.6 mm; propodus, 2.0 mm; claw, 1.2 mm.

MATERIAL EXAMINED: Only USNM 233875 (Ross Sea, off Cape Adare, 71 16 --S 171 45 --E, depth: 1565-1674 m).

DISTRIBUTION: Off Cape Adare, Ross Sea.

Austropallene lanceoli

Figures 42, 43, 44

TYPE: Holotype USNM 233892 (1 ♂).

ETYMOLOGY: Named for its long, lance-shaped spines.

DIAGNOSIS: Color = red. Fig. 42 illustrates the ovigerous leg spines and fig. 44, the strigilis for this species. Strigilis spine count, see table 4.

MALE: Trunk length (chelicera insertion to tip of 4th lateral processes), 6.2 mm; trunk width (across 2nd lateral processes), 4.2 mm; proboscis length, 3.0 mm; abdomen

length, 1.4 mm; third leg, coxa 1, 1.1 mm; coxa 2, 3.1 mm; coxa 3, 1.2 mm; femur, 6.0 mm; tibia 1, 6.7 mm; tibia 2, 6.5 mm; tarsus, 0.7 mm; propodus, 2.5 mm; claw, 1.8 mm.

FEMALE: Unknown.

MATERIAL EXAMINED: Only the holotype (Off Ross Ice Shelf, Ross Sea, 77 04 --S 168 19 --E, depth: ?).

DISTRIBUTION: Off Ross Ice Shelf, Ross Sea.

Austropallene edwardi

Figure 45

TYPE: USNM 233896 (1 ♀).

ETYMOLOGY: Named for Edward Bain.

DIAGNOSIS: Color = red. Fig. 45 illustrates the ovigerous leg spines for this species. Strigilis spine count, see table 4.

MALE: Unknown.

FEMALE: Trunk length (chelicera insertion to tip of 4th lateral processes), 6.6 mm; trunk width (across 2nd lateral processes), 4.2 mm; proboscis length, 3.5 mm; abdomen length, 1.3 mm; third leg, coxa 1, 1.6 mm; coxa 2, 2.7 mm; coxa 3, 1.6 mm; femur, 5.9 mm; tibia 1, 6.3 mm; tibia 2, 6.4 mm; tarsus, 0.6 mm; propodus, 2.7 mm; claw, 1.8 mm.

MATERIAL EXAMINED: Only the holotype (Off Ross Ice Shelf, Ross Sea, Antarctica, 77 32 --S 172 32 --W, depth: 468-482 m).

DISTRIBUTION: Off Ross Ice Shelf, Ross Sea.

Austropallene brandti

Figures 46, 47

TYPE: Holotype USNM 233900 (1 ♀) and 2 ♀ paratypes in same vial. Holotype has ovigerous leg tip missing; paratypes have complete ovigerous legs.

ETYMOLOGY: Named for Will Brandt.

DIAGNOSIS: Color = pale yellow. Fig. 46ab illustrates the ovigerous leg spines and fig. 47, the strigilis for this species. Figures 46c and 46d illustrate the split terminal claw characteristic of this species. Strigilis spine count, see table 4.

MALE: Unknown.

FEMALE: Trunk length (chelicera insertion to tip of 4th lateral processes), 7.1 mm; trunk width (across 2nd lateral processes), 4.4 mm; proboscis length, 3.6 mm; abdomen length, 1.3 mm; third leg, coxa 1, 1.1 mm; coxa 2, 2.7 mm; coxa 3, 1.3 mm; femur, 6.4 mm; tibia 1, 5.4 mm; tibia 2, 5.5 mm; tarsus, 0.5 mm; propodus, 2.3 mm; claw, 2.1 mm.

MATERIAL EXAMINED: Only the holotype (Off Ross Ice Shelf, Ross Sea, Antarctica, 76 01 30S 179 49 54E, depth: 388-399 m).

DISTRIBUTION: Off Ross Ice Shelf, Antarctica.

Austropallene hermani

Figures 48ab, 49

TYPE: Holotype USNM 233909 (1 ♀, missing most of the walking legs).

ETYMOLOGY: Named for my good buddy Herman.

DIAGNOSIS: Color = red. Fig. 48ab illustrates the ovigerous leg spines and fig. 49, the strigilis for this species. Strigilis spine count, see table 4.

MALE: Unknown.

FEMALE: Trunk length (chelicera insertion to tip of 4th lateral processes), 5.8 mm; trunk width (across 2nd lateral processes), 3.8 mm; proboscis length, 3.0 mm; abdomen length, 1.2 mm.

MATERIAL EXAMINED: Only the holotype (Anvers Island, Palmer Archipelago, Antarctica, 64 47 24S 064 07 12W, depth: 91-110 m).

DISTRIBUTION: Anvers Island, Palmer Archipelago.

Austropallene williami

Figures 14-21

TYPE: Holotype USNM 233955 (the ♂ labeled J) and paratype (the ♀ labeled A).

ETYMOLOGY: Named for my father, William M. Bain.

DIAGNOSIS: Color = yellow. Figs. 15 and 16ab illustrate the ovigerous leg spines and fig. 14ab, the strigilis for this species. Strigilis spine count, see table 4.

MALE: Trunk length (chelicera insertion to tip of 4th lateral processes), 6.1 mm; trunk width (across 2nd lateral processes), 3.8 mm; proboscis length, 2.6 mm; abdomen length, 1.3 mm (third legs missing on holotype).

FEMALE: Trunk length (chelicera insertion to tip of 4th lateral processes), 6.0 mm; trunk width (across 2nd lateral processes), 3.5 mm; proboscis length, 3.0 mm; abdomen length, 1.1 mm; third leg, coxa 1, 0.9 mm; coxa 2, 2.9 mm; coxa 3, 1.3 mm; femur, 5.6 mm; tibia 1, 5.8 mm; tibia 2, 5.8 mm; tarsus, 0.6 mm; propodus, 2.2 mm; claw, 1.6 mm.

MATERIAL EXAMINED: USNM 233955 contains 15 specimens (4 ♂ and 9 ♀ and 2 juveniles, Little America V, Kainan Bay, Ross Sea; depth: 1640 m).

DISTRIBUTION: Ross Sea

Table 4

Spine Counts--Ovigerous Legs

	segment	segment	segment	segment
	10	9	8	7
<i>T. cristata</i>	11	6	-	9
<i>A. brachyura</i>	8	6	7	10
<i>A. calmani</i>	8	9	10	11
<i>A. cornigera</i>	12	11	11	-
<i>A. gracilipes</i>	12	9	8+	10
<i>A. tcherniai</i>	-	-	-	-
<i>A. tibicina</i>	9	9	8	12
<i>A. australis</i>	16	14	17	-
<i>A. turqueti</i>	-	-	-	-
<i>A. wolfgangi</i>	17	16	18	21
<i>A. maryae</i>	15	13	14	14
<i>A. jamesi</i>	10	8	10	10
<i>A. lanceoli</i>	17	14	16	20
<i>A. edwardi</i>	19	14	15	19
<i>A. brandti</i>	21	18	19	22

Table 4 continued

A. hermani	17	16	17	17
A. williami (A)	15	15	15	17
A. williami (B)	16	17	17	18
A. williami (C)	18	18	20	17
A. williami (D)	16	14	16	17
A. williami (E)	19	15	17	18
A. williami (J)	19	16	18	21

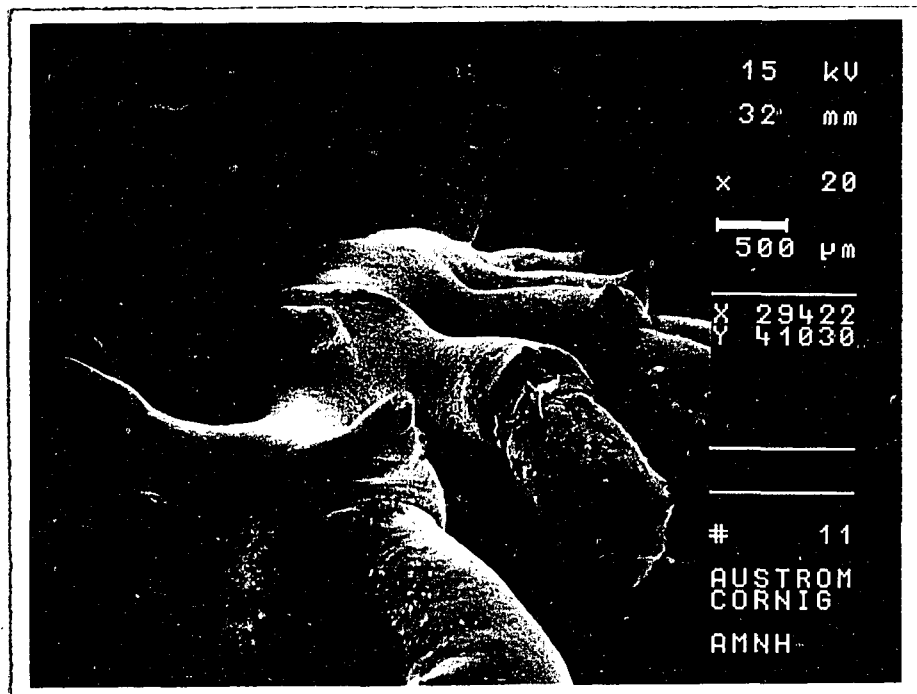


FIGURE 8
Cephalic Spurs

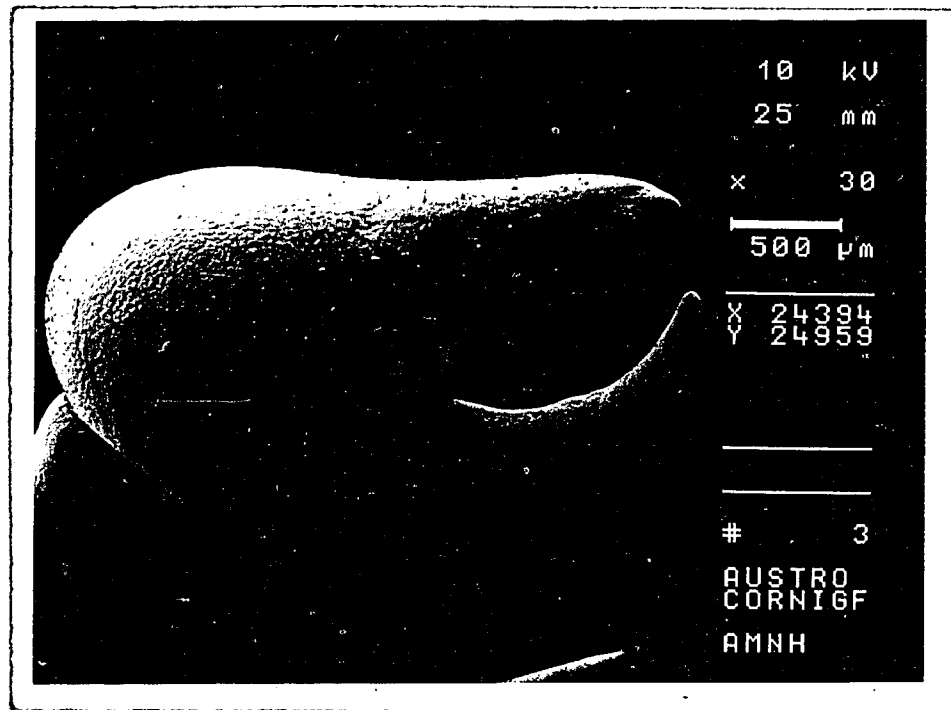
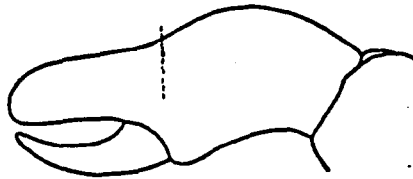


FIGURE 9

Typical chelicera of the Austropallene cornigera species group.

FIGURE 10

10a.



Austropallene brachyura Hodgson. b. Right chela of ♀ from Sta. 90.

10b.

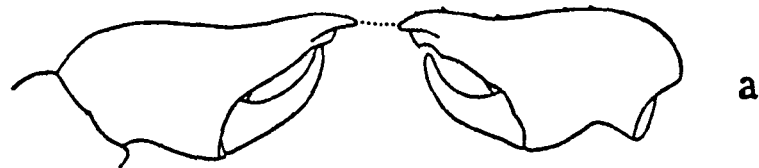
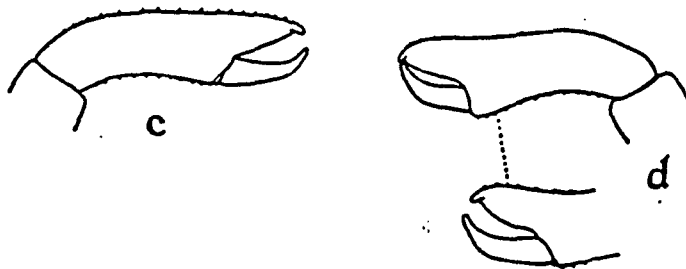


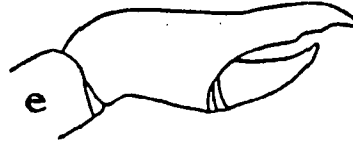
Fig. 14. *Austropallene calmani* n.sp. a. Left and right chela of ♂ paratype.

10c.



Austropallene gracilipes n.sp. c. Right chela of holotype (♂) in ventral aspect. d. Right chela of ♀ paratype from Sta. 103.

10d.



Austropallene tibicina Calman. e. Right chela of young ♂ in ventral aspect. All $\times 54$.

10e.



FIGURE 10

Chelicerae typical of the other (non-cornigera) Austropallene species. 10a. A. brachyura (from Gordon, 1944); 10b. A. calmani (from Gordon, 1944); 10c. A. gracilipes (from Gordon, 1944); 10d. A. tibicina (from Gordon, 1944); 10e. A. tcherniai (from Fage, 1952).

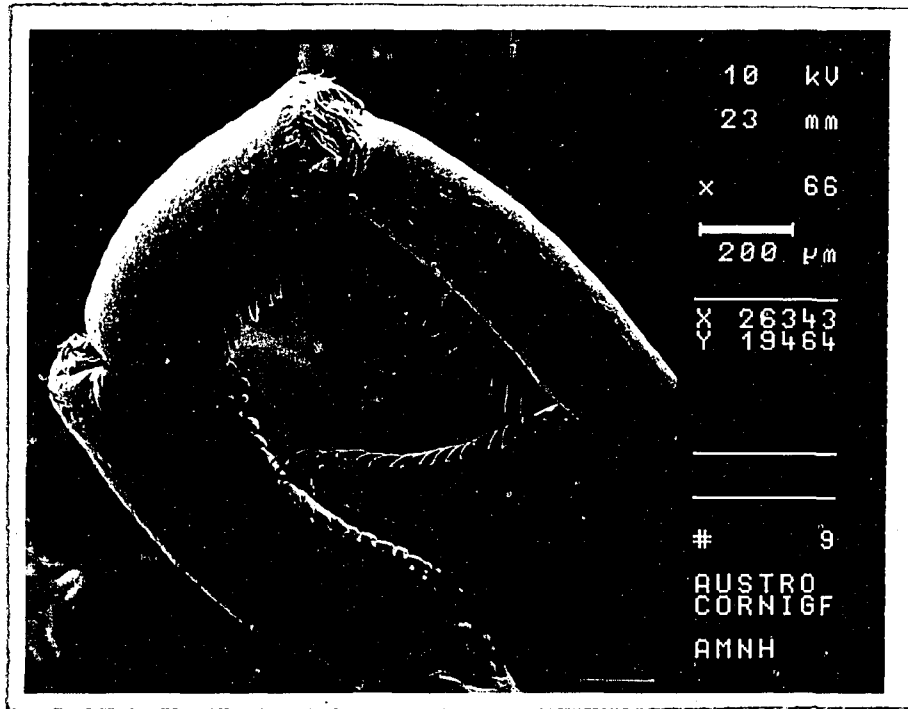
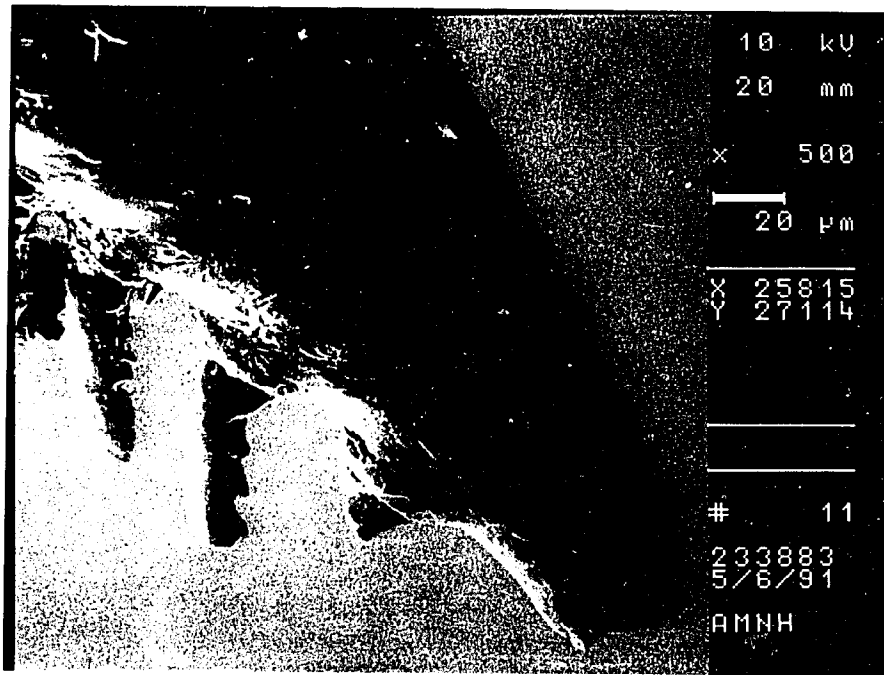


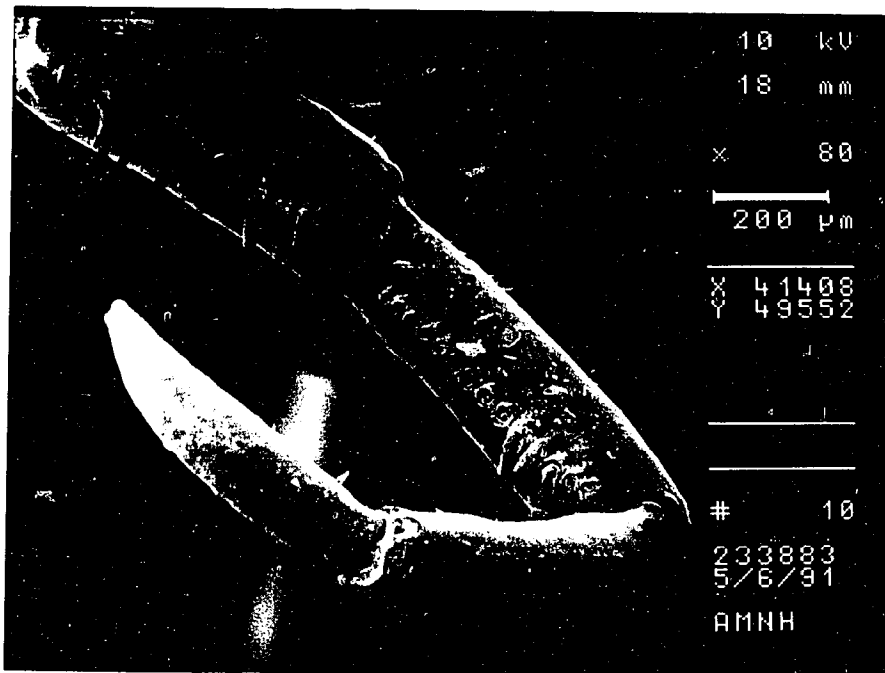
FIGURE 11

Strigilis typical of the Austropallene cornigera species group.

12a



12b



12c

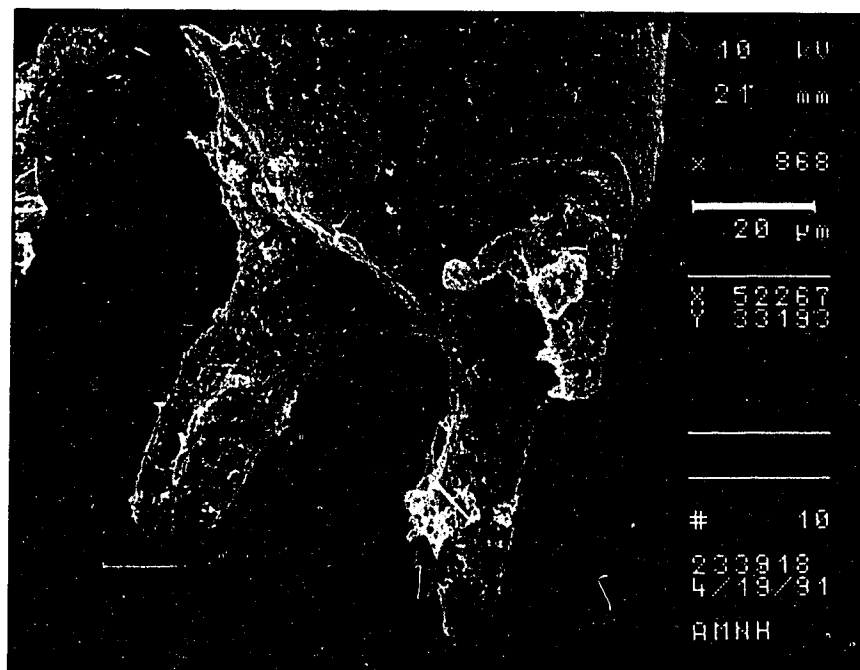


FIGURE 12

Examples of very badly damaged and worn Austropallene compound spines. 12a. Segment 10; 12b. Strigilis; 12c. Segment 10.

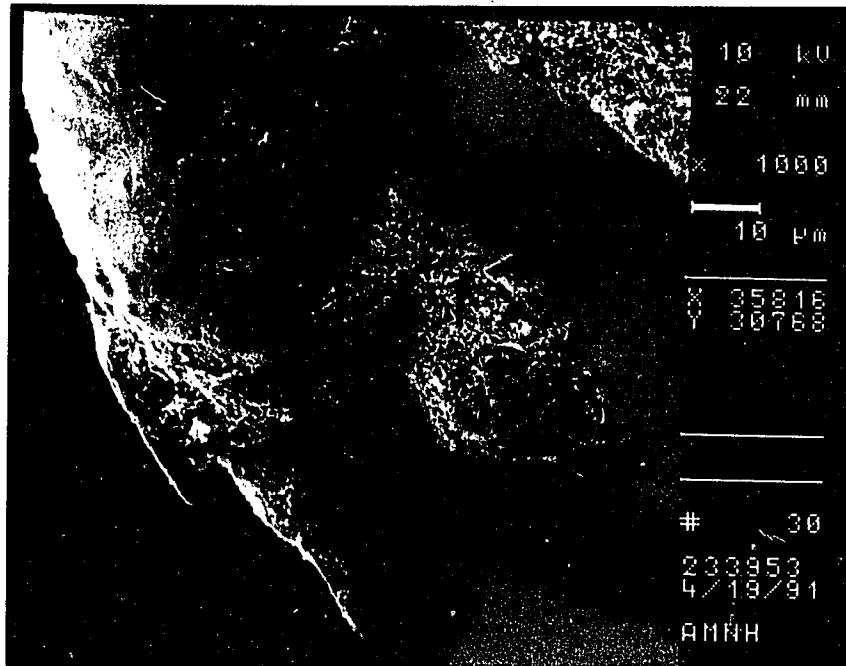
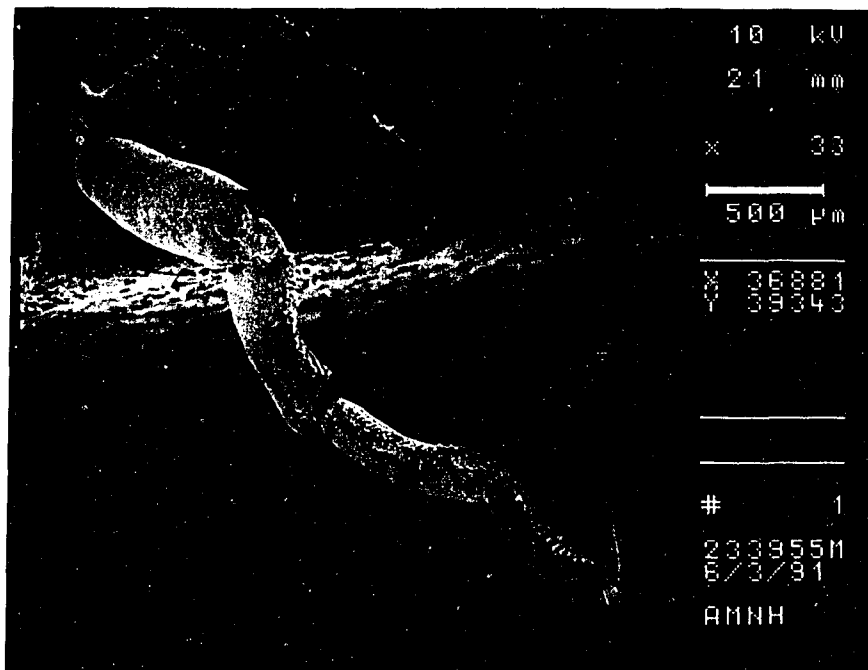


FIGURE 13

Example of mud encased spines. Segment 10.

14a



955K

14b

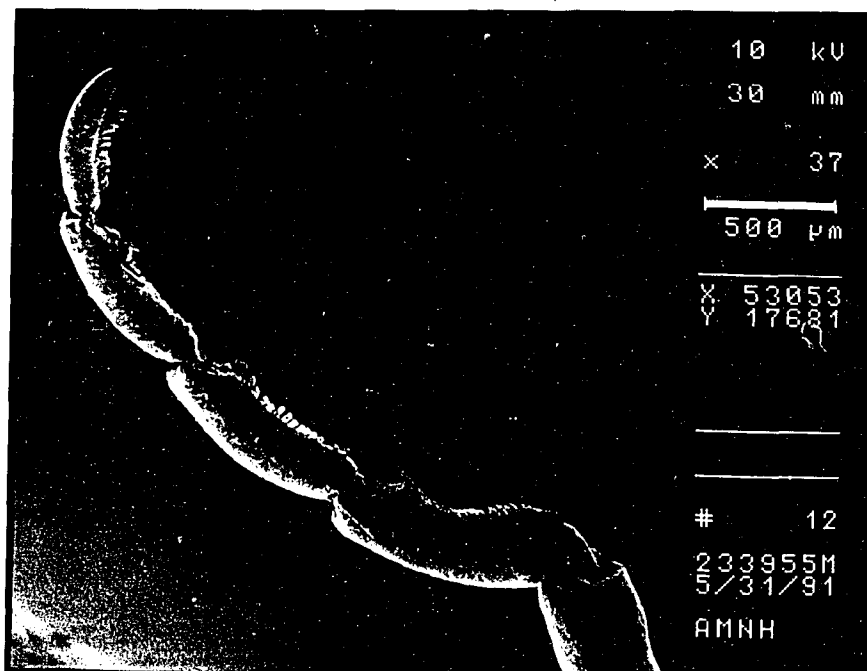


FIGURE 14

Austropallene williamsi, right (14a) and left (14b) ovigerous legs of specimen K (see text for explanation).

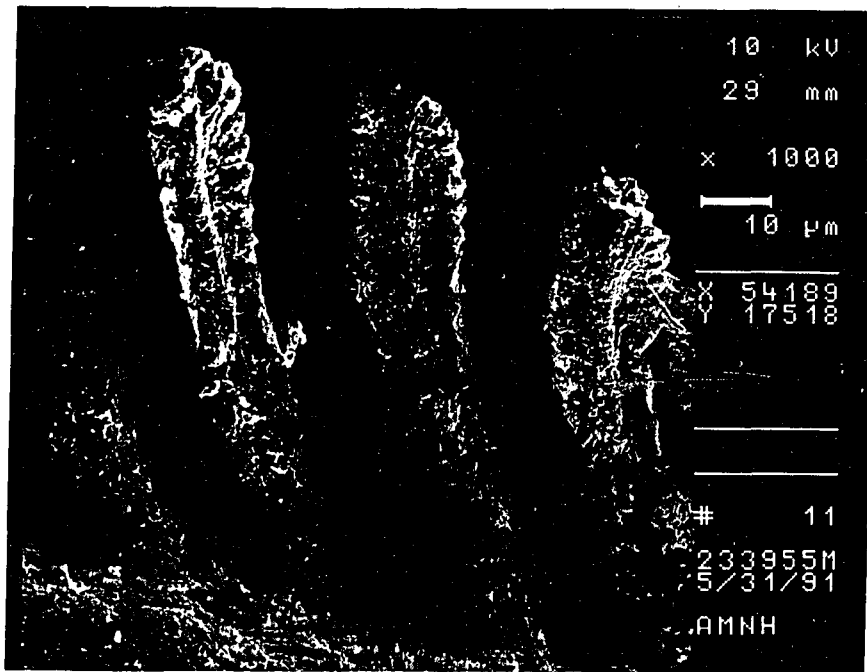
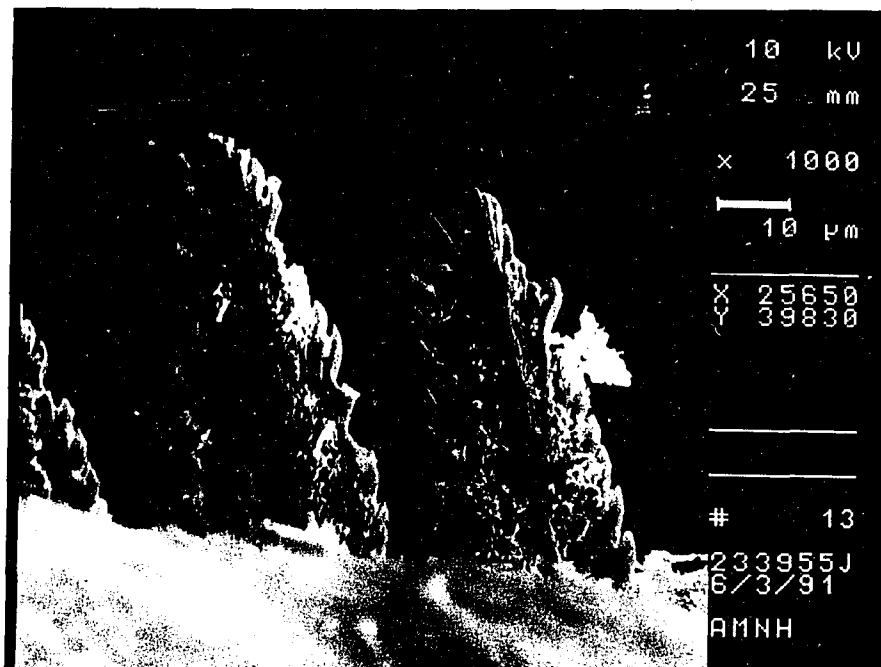


FIGURE 15

Austropallene williamsi, compound spines from segment 10,
specimen K.

16a



16b

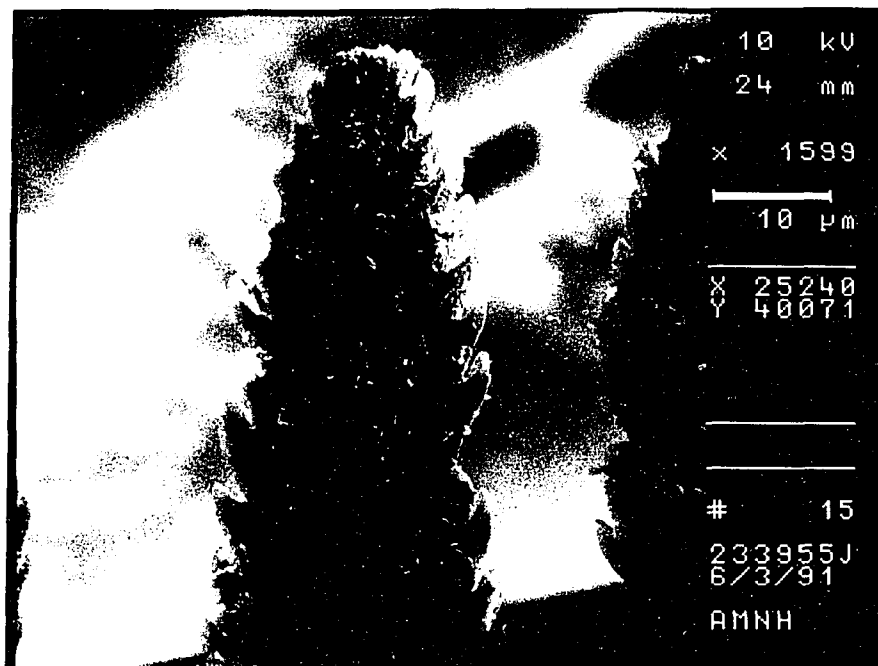


FIGURE 16

Austropallene williamsi, 16a. Compound spines from segment 8; 16b. Compound spines from segment 9. Both from specimen J.



FIGURE 17

Austropallene williamsi, Segment 10, specimen B.

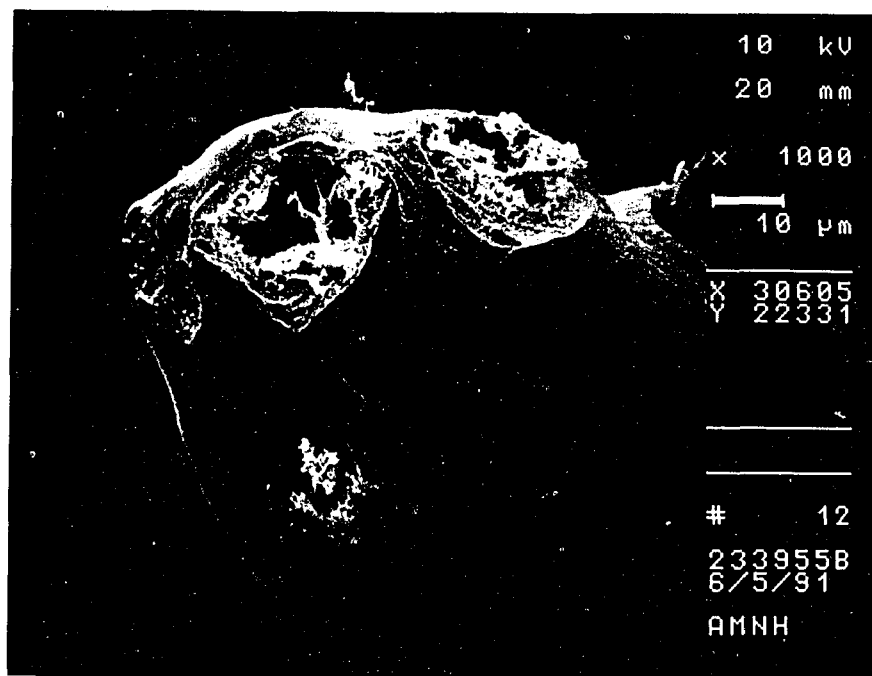


FIGURE 18

Austropallene williamsi, Segment 10, distal end, showing broken spines, specimen B.

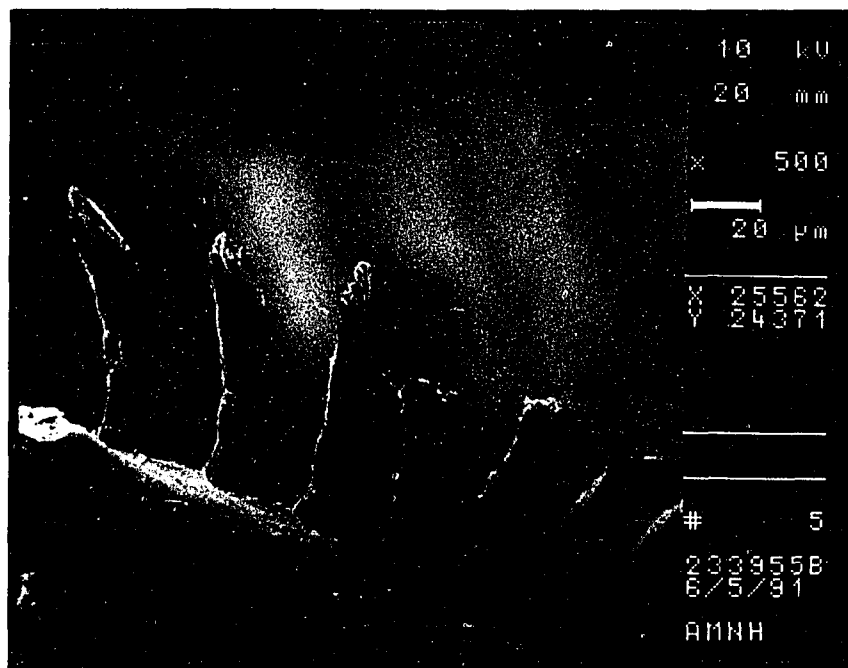


FIGURE 19

Austropallene williamsi, Compound spines on segment 10, specimen B.

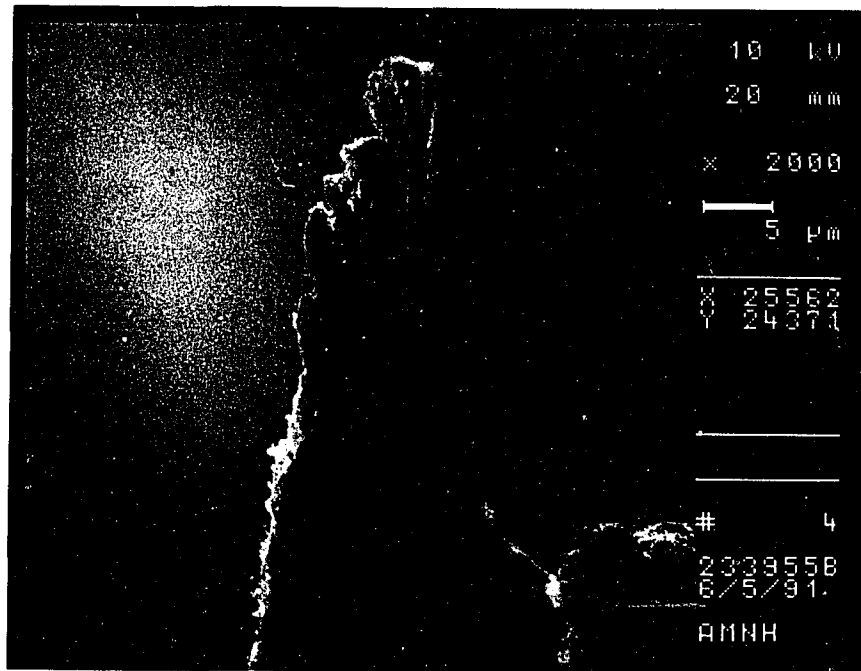
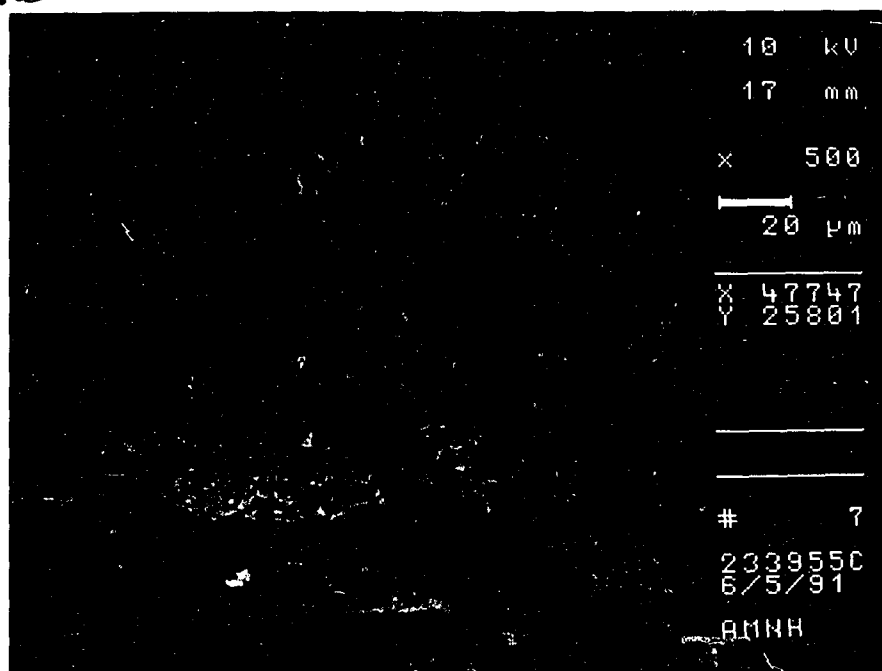


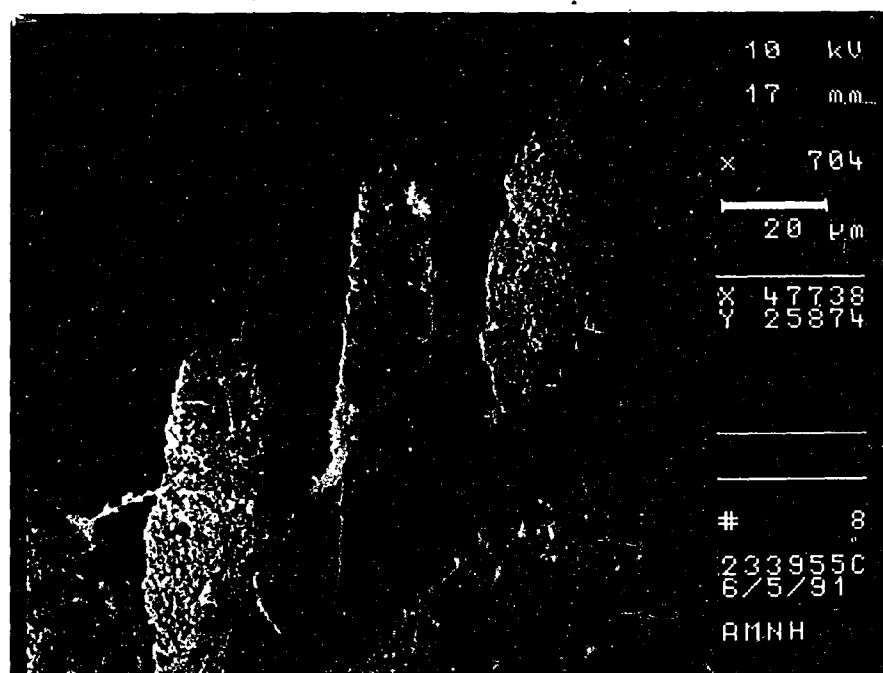
FIGURE 20

Austropallene williamsi, Close-up of compound spines on segment 10, specimen B.

21a



21b



21c

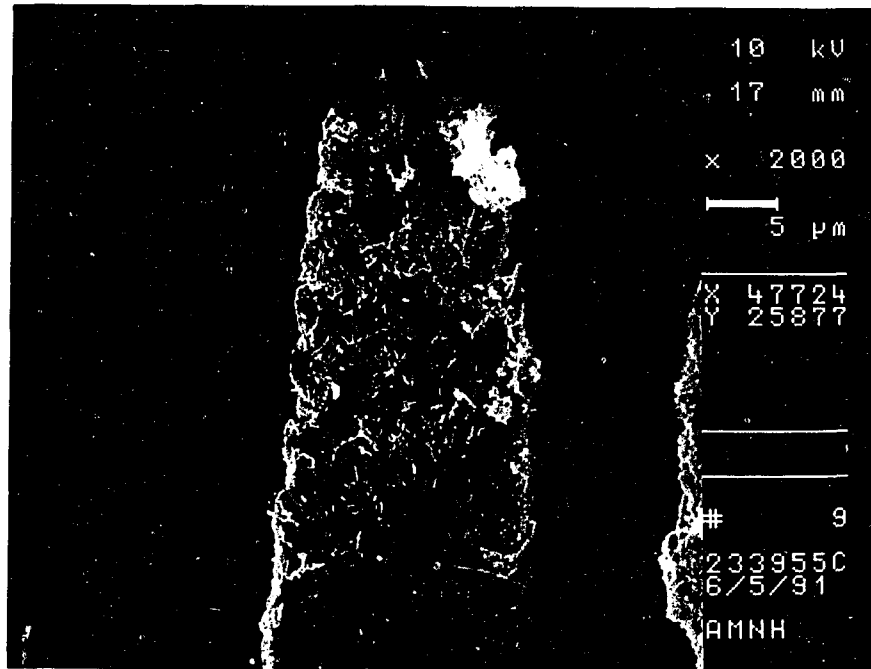


FIGURE 21

Austropallene williamsi, specimen C. 21a. segment 10; 21b. Close-up of spines shown in 21a; 21c. Close-up of the one clean spine. See text for explanation.

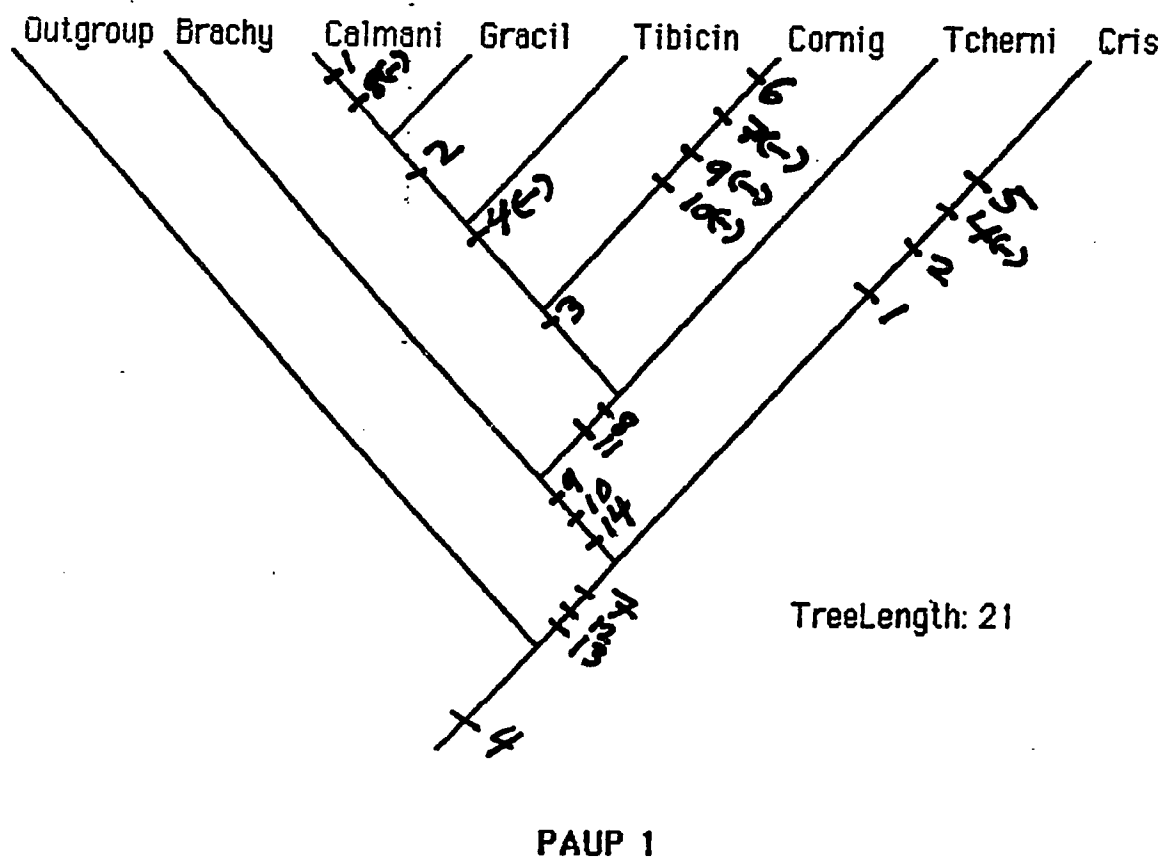
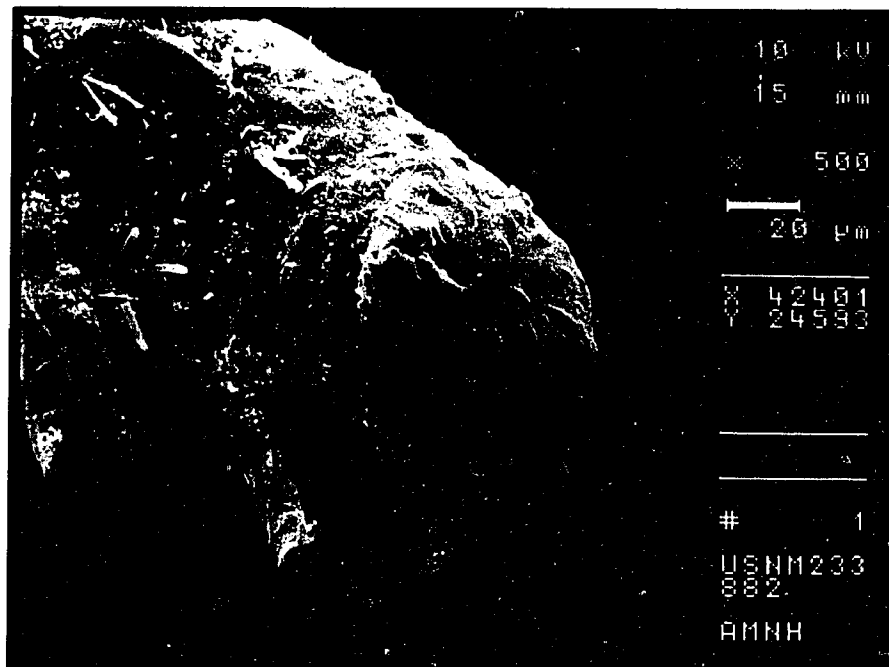


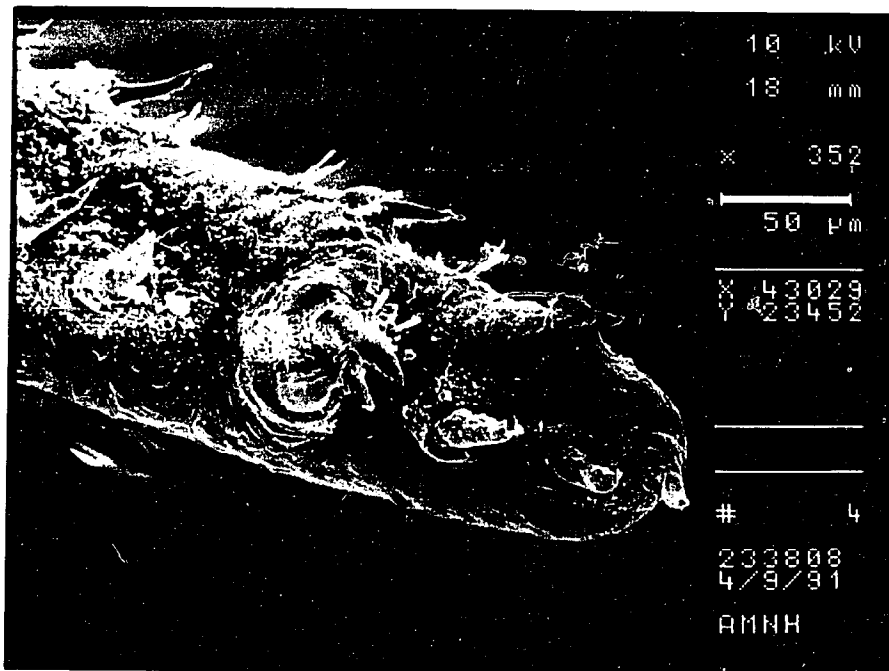
FIGURE 22

Cladogram of the genus Austropallene

23a



23b



23c

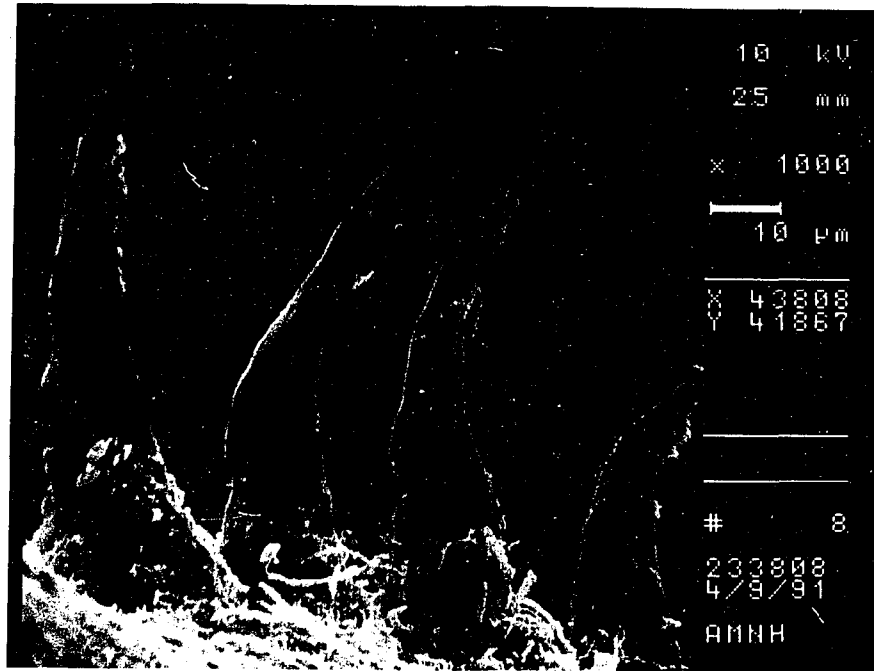


FIGURE 23

Tarapallene cristata, 23a. Distal end of segment 10 showing terminal claw (side view); 23b. Same, ventral view; 23c. Compound spines on segment 10.

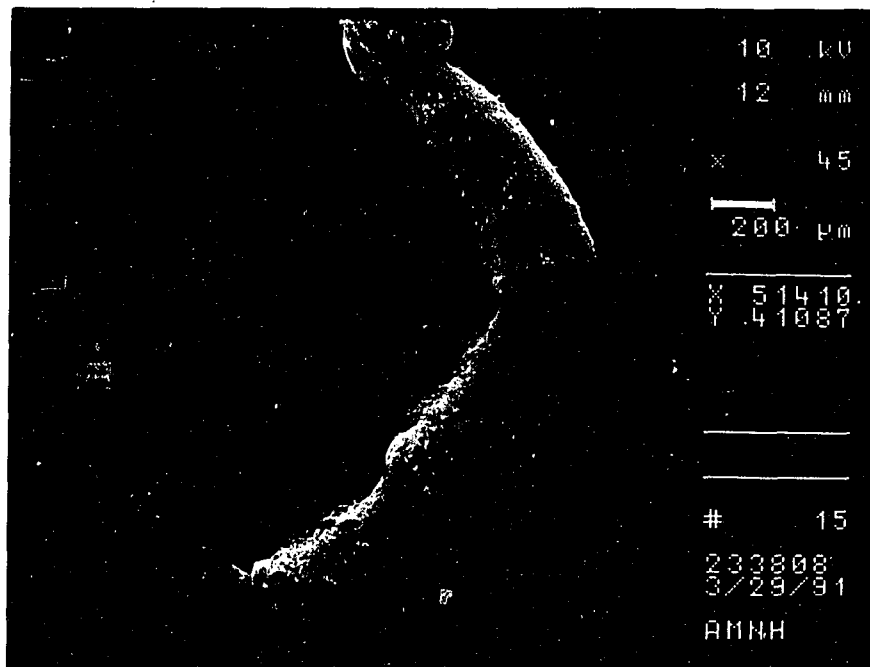
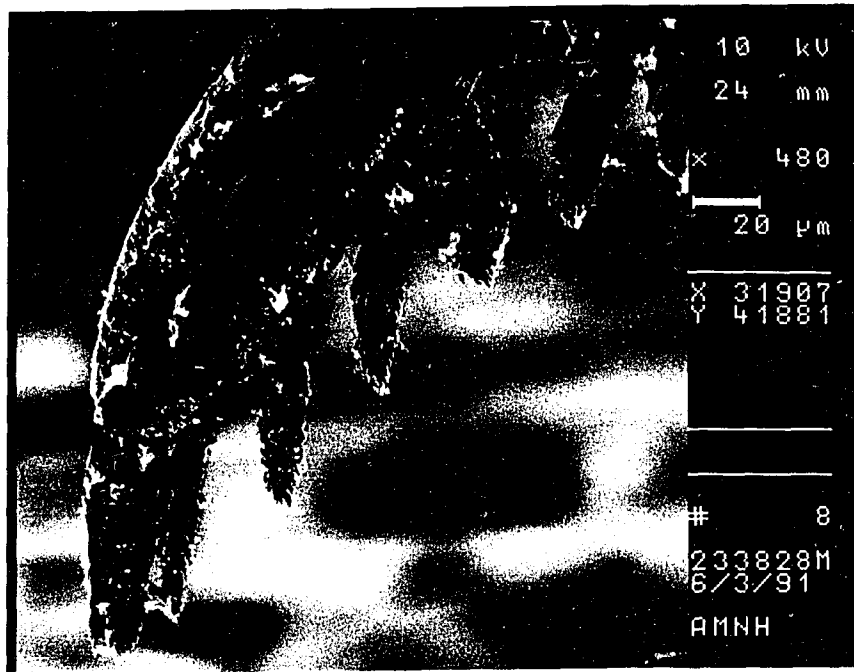


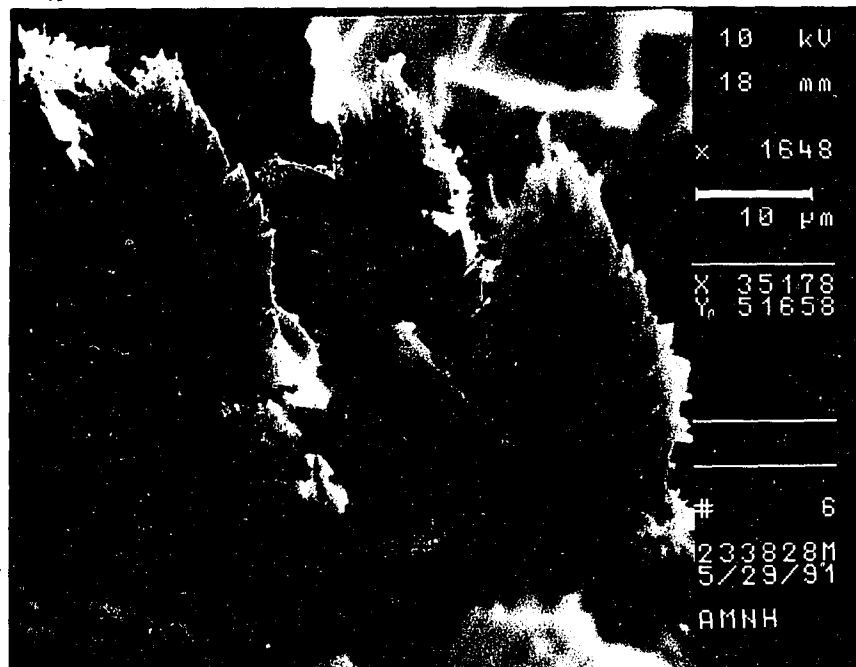
FIGURE 24

Tarapallene cristata, strigilis.

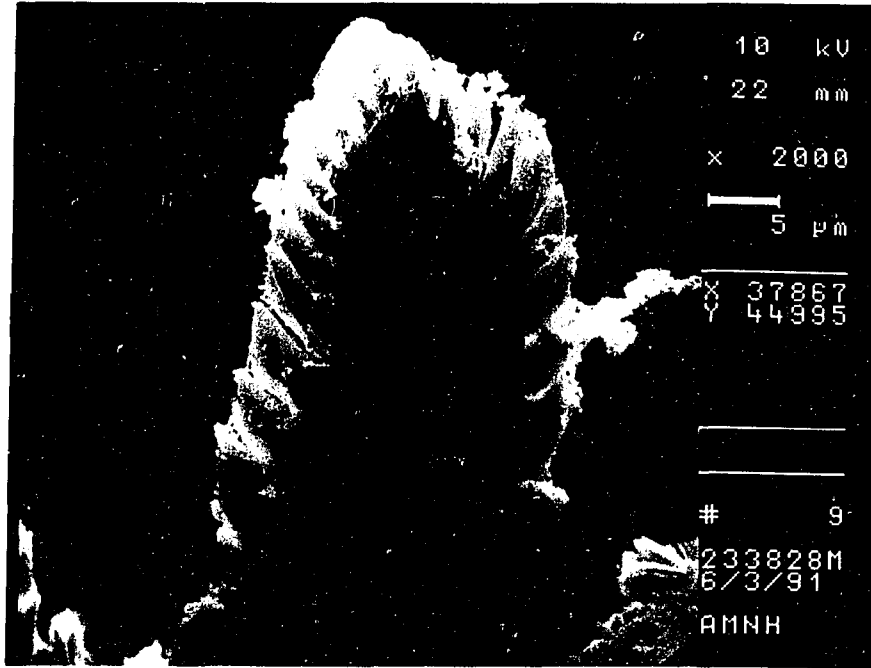
25a



25b



25c



chiro na Tt. 9

FIGURE 25

Austropallene brachyura, 25a. Distal end of segment 10; 25b. Compound spines on segment 10; 25c. Close-up of one spine in 25b.

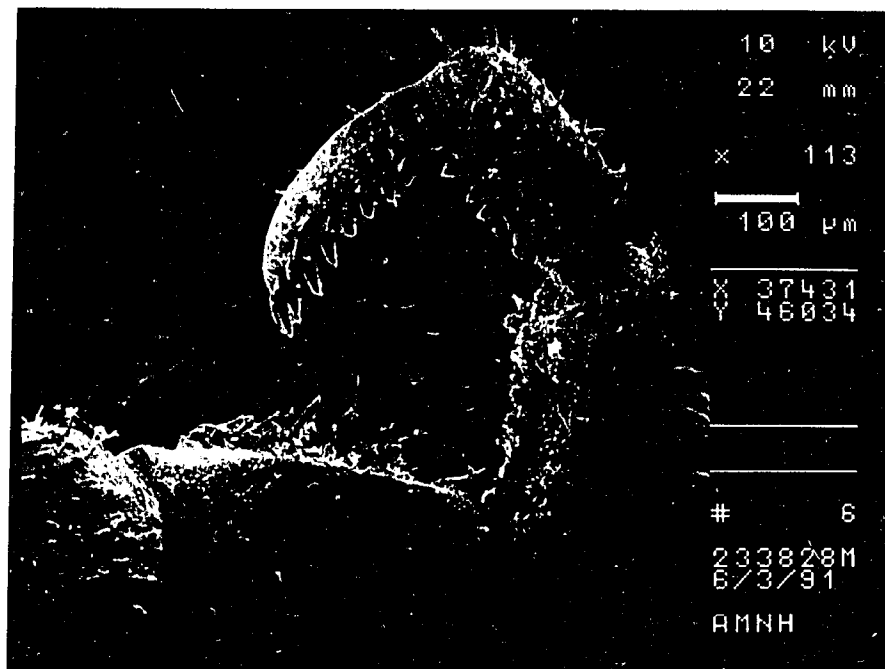


FIGURE 26

Austropallene brachyura, strigilis.

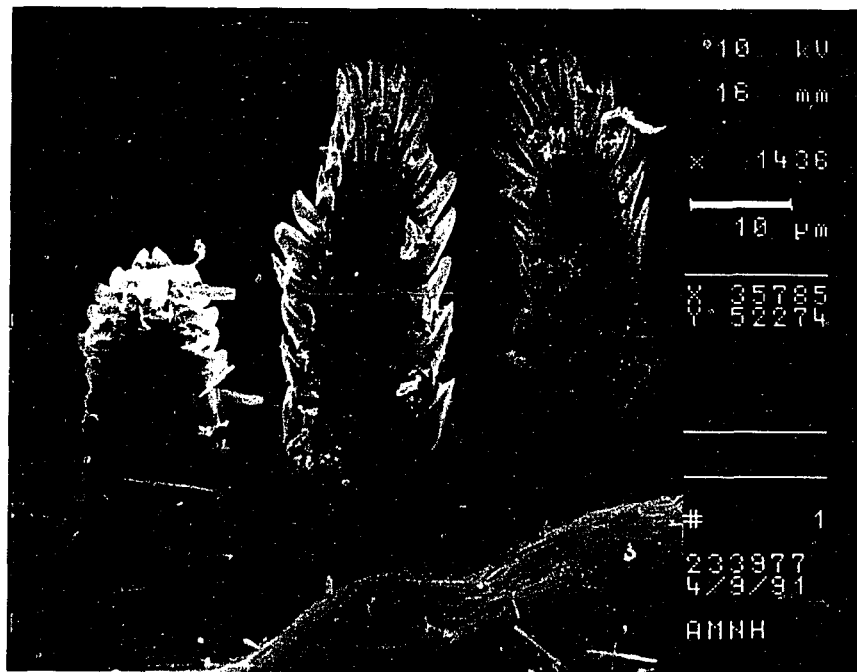


FIGURE 27

Austropallene calmani, compound spines.

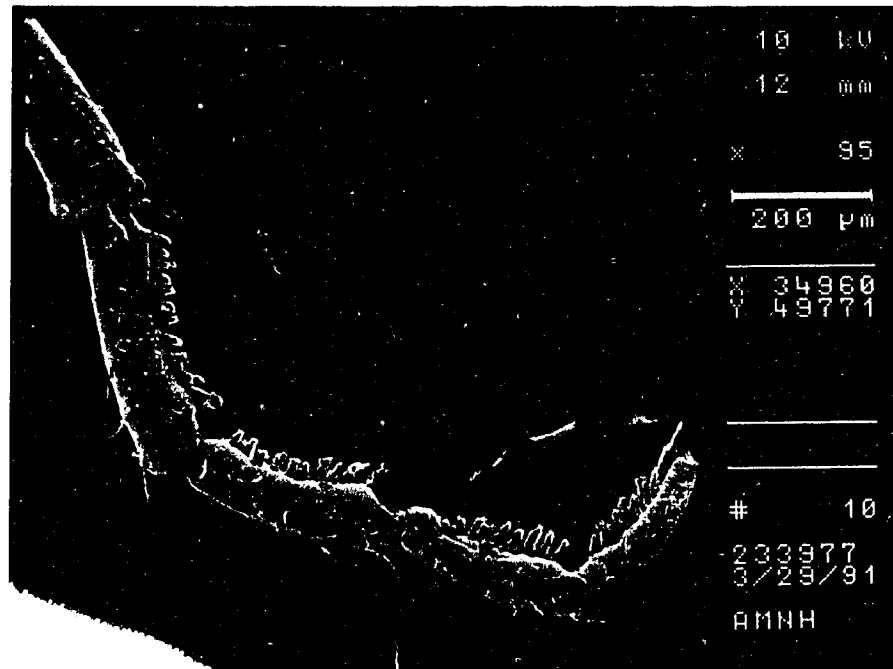


FIGURE 28

Austropallene calmani, strigilis.



FIGURE 29

Austropallene gracilipes, compound spines, ♀.

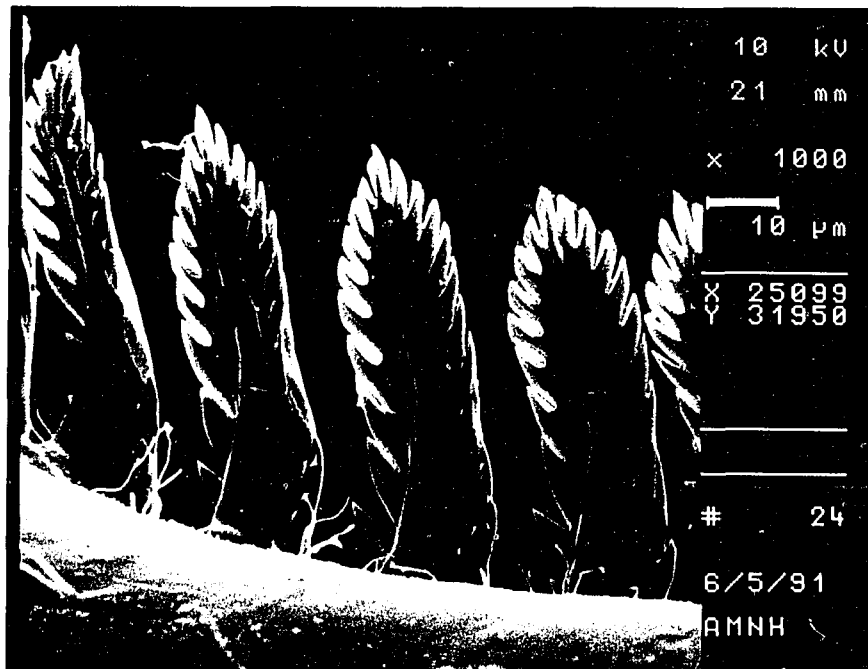


FIGURE 30

Austropallene gracilipes, compound spines, ♂.

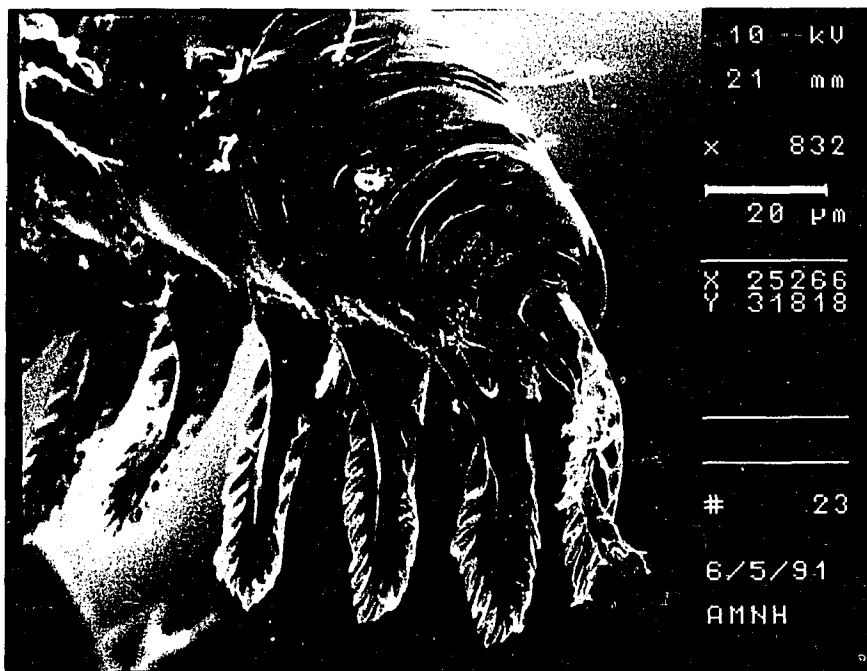


FIGURE 31

Austropallene gracilipes, distal end of strigilis, ♂.

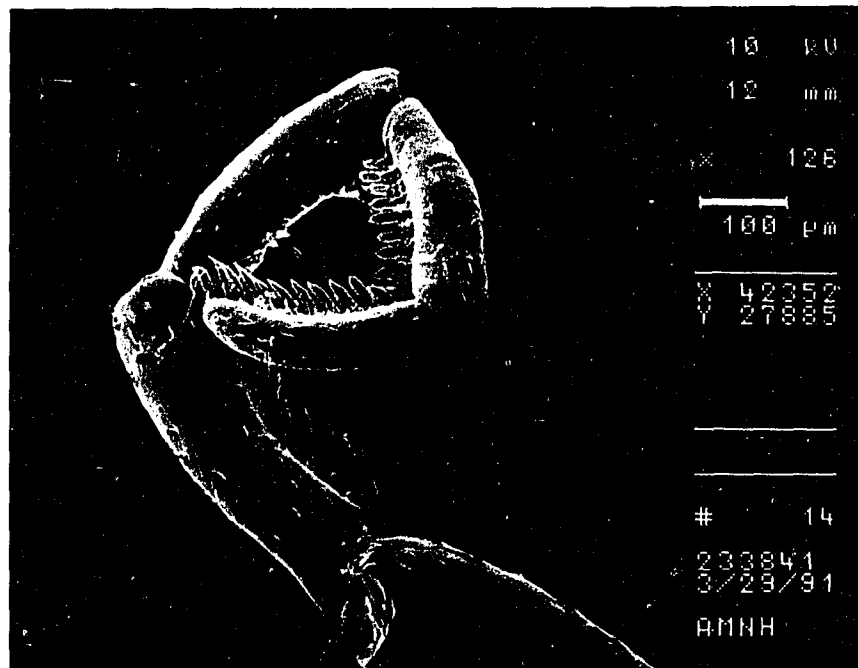
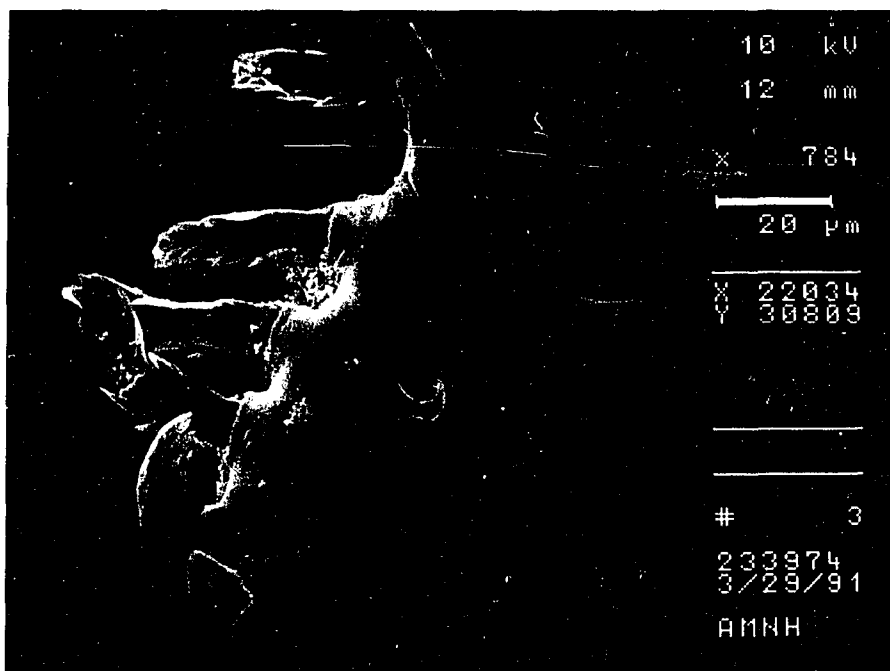


FIGURE 32

Austropallene gracilipes, strigilis.

33a



33b

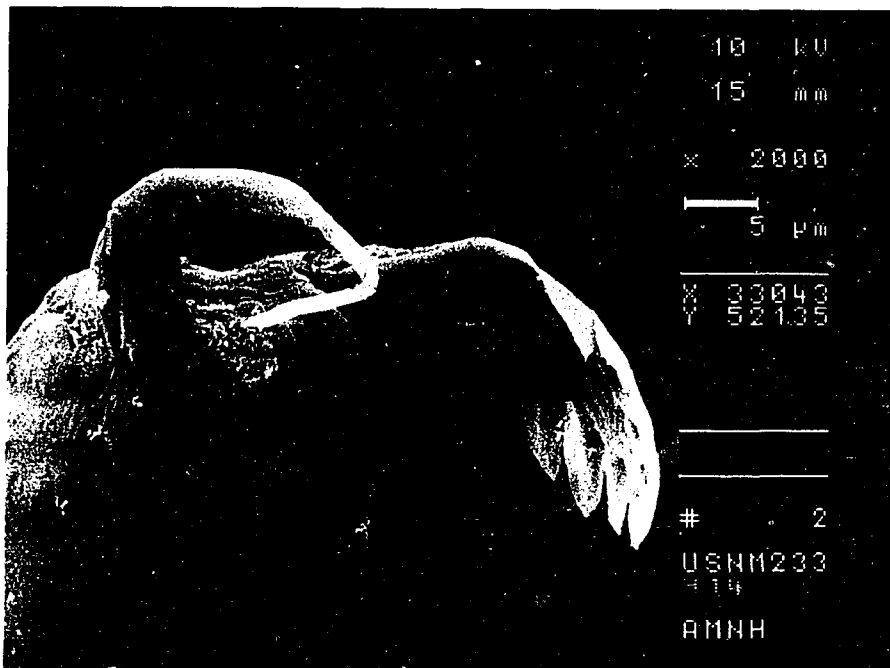
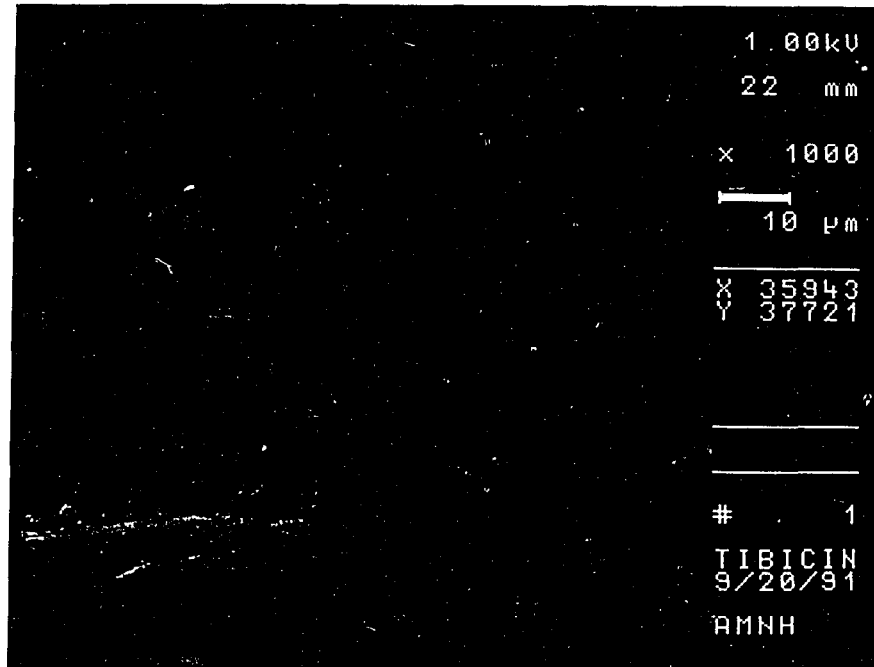


FIGURE 33

Austropallene tcherniai, 33a. Distal end of segment 10;
33b. Close-up of end spines shown in 33a.

34a



34b

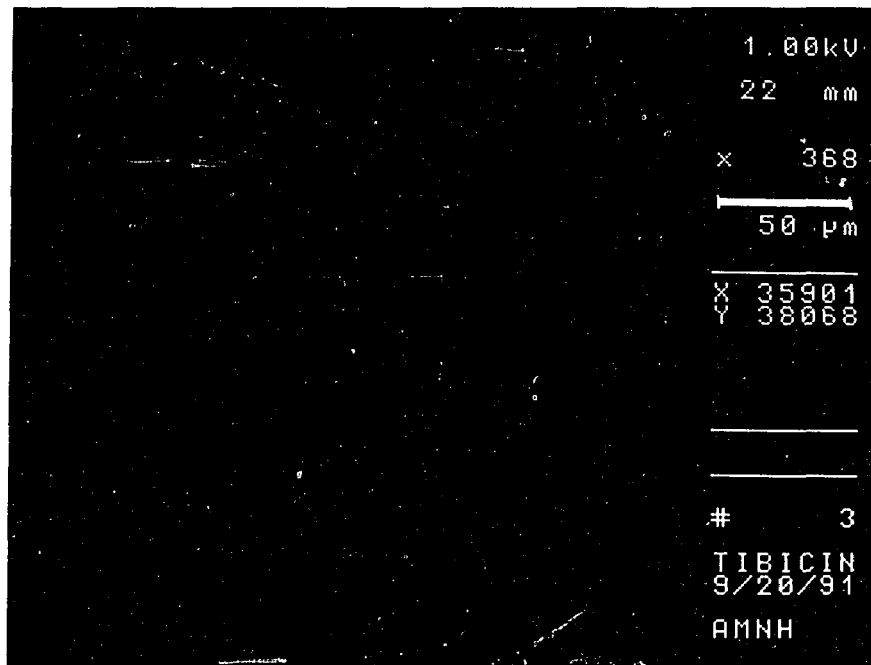


FIGURE 34

Austropallene tibicina, 34a. compound spines, segment 8;
34b. entire segment 10.

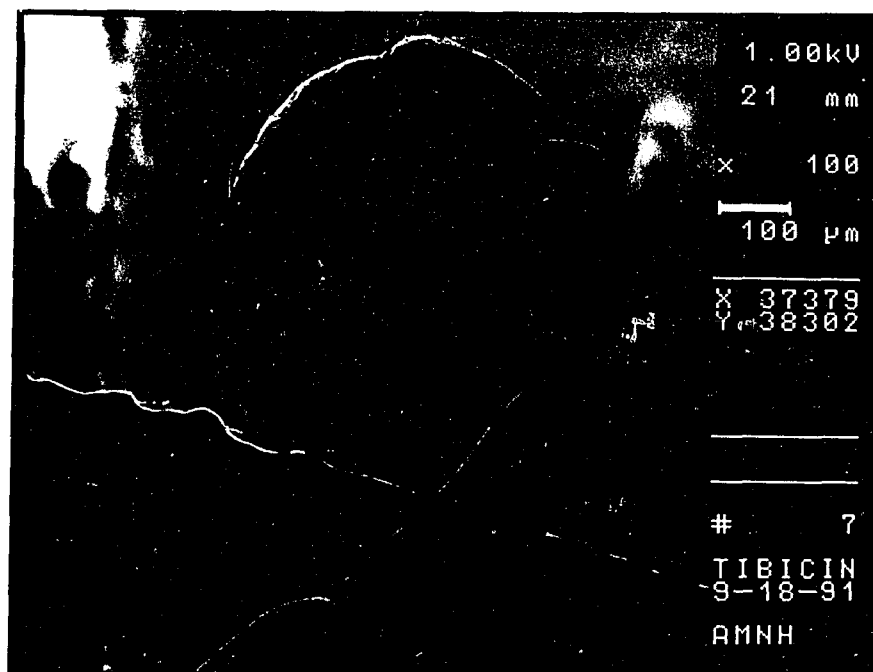
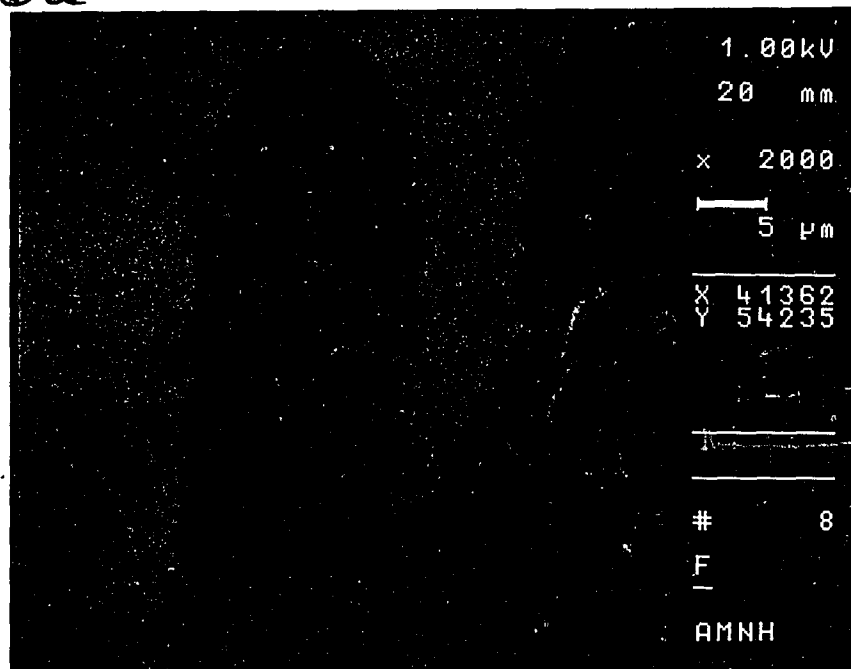
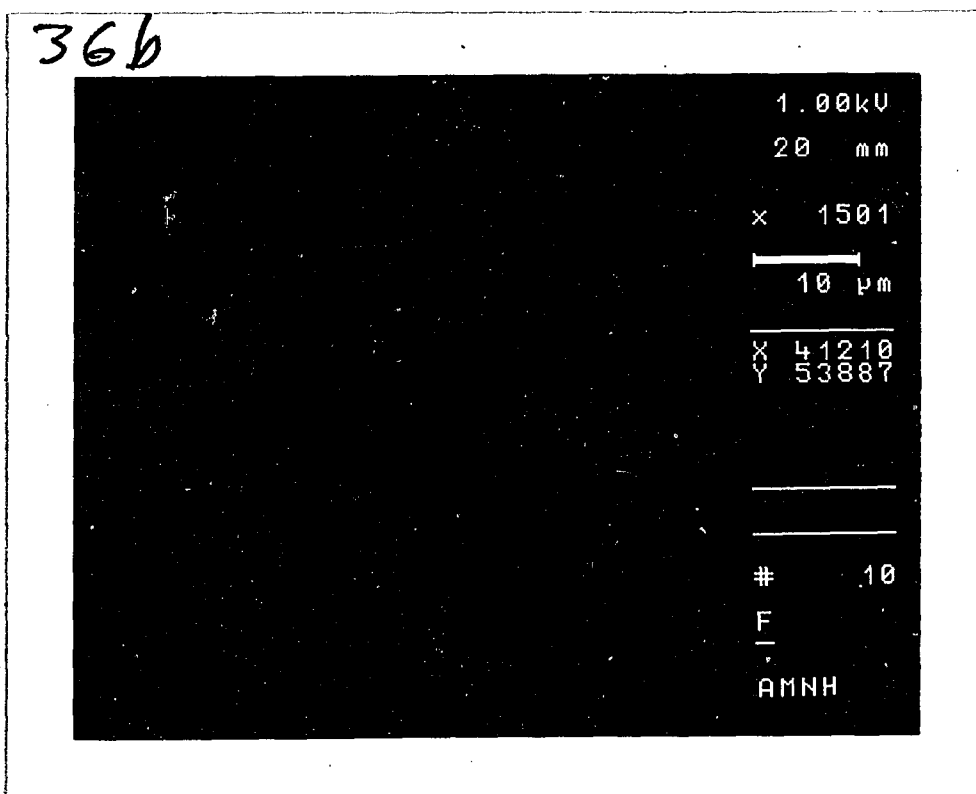


FIGURE 35

Austropallene tibicina, strigilis.

36a





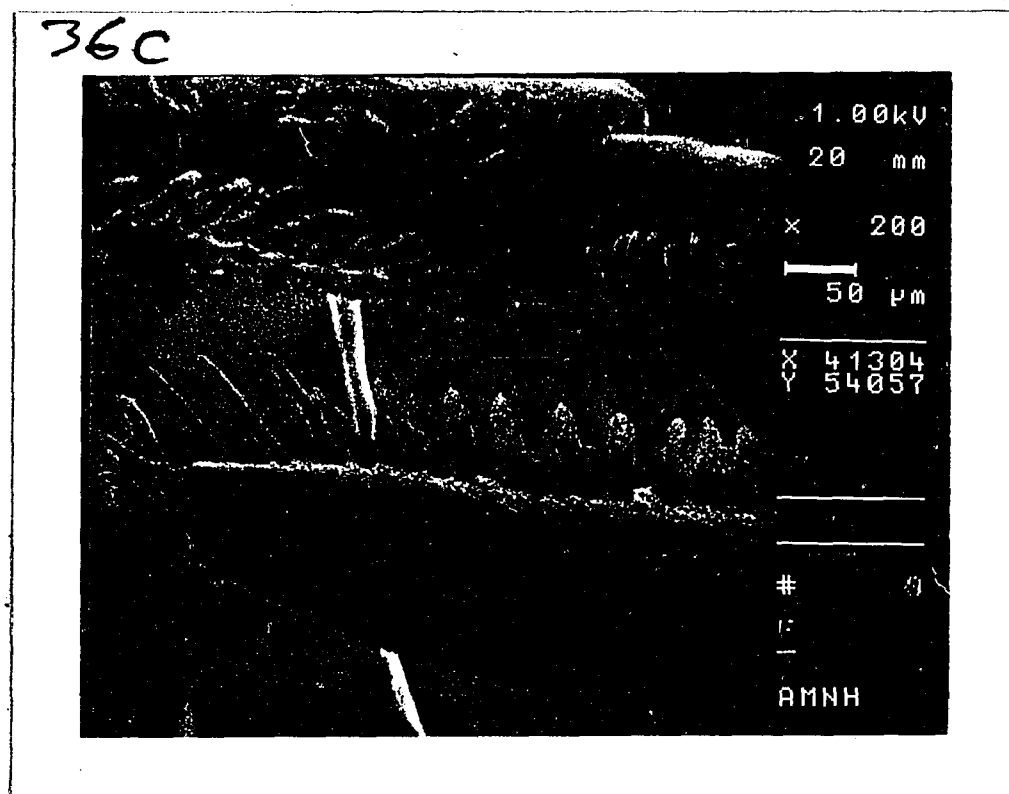
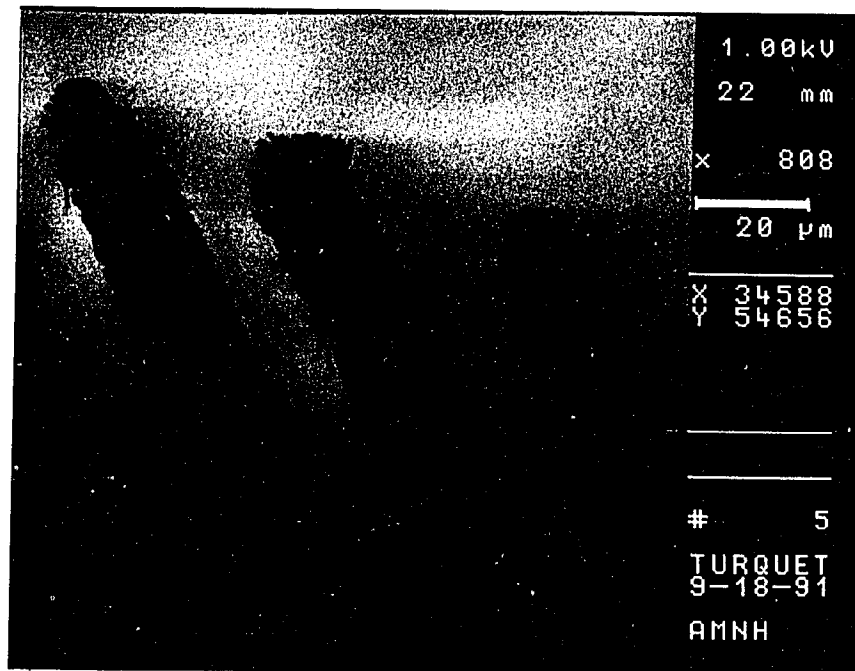


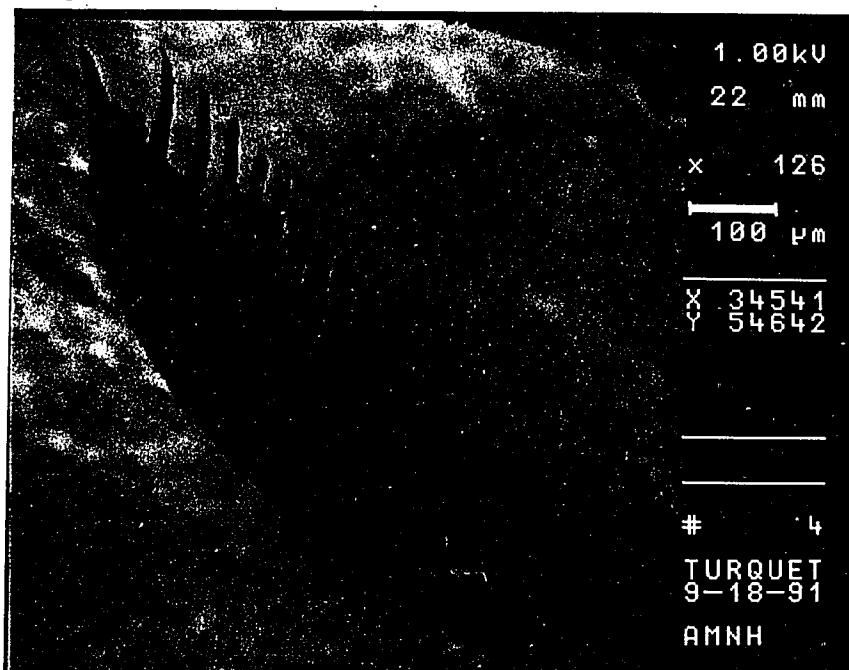
FIGURE 36

Austropallene australis, 36a. Compound spines, segment 10 (middle of segment); 36b. Long compound spine, segment 10 (near end of segment); 36c. Segment 10, entire.

37a



37b



37c

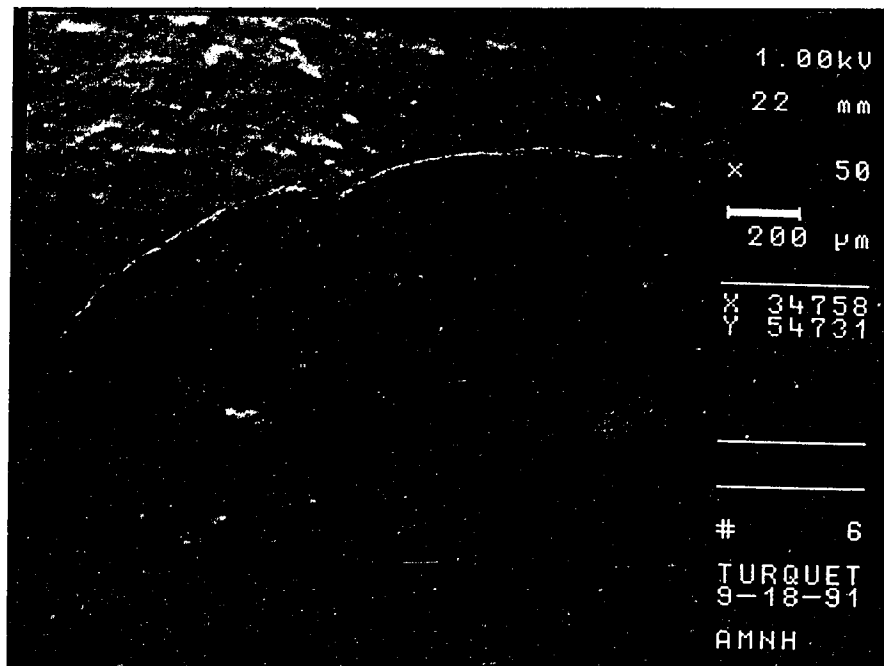
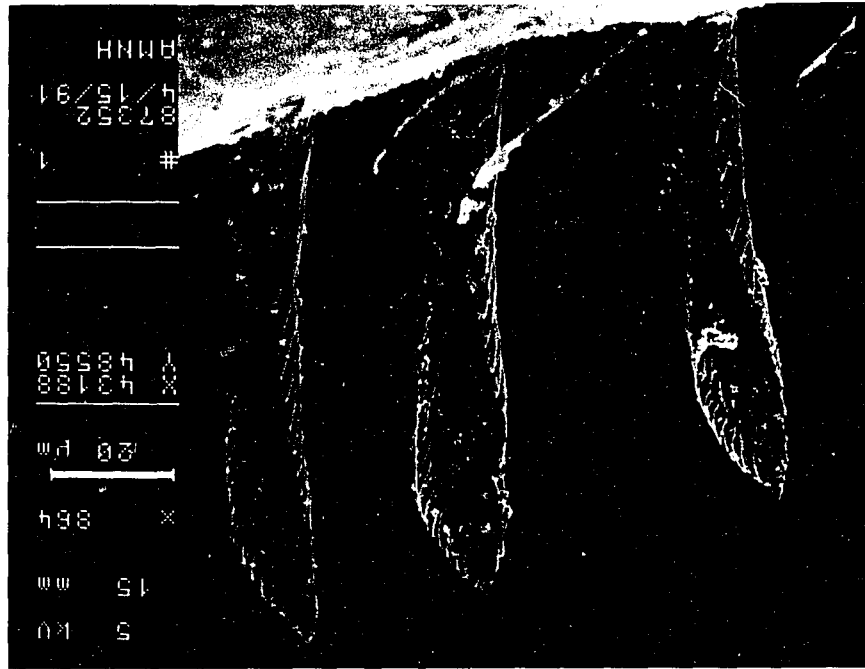
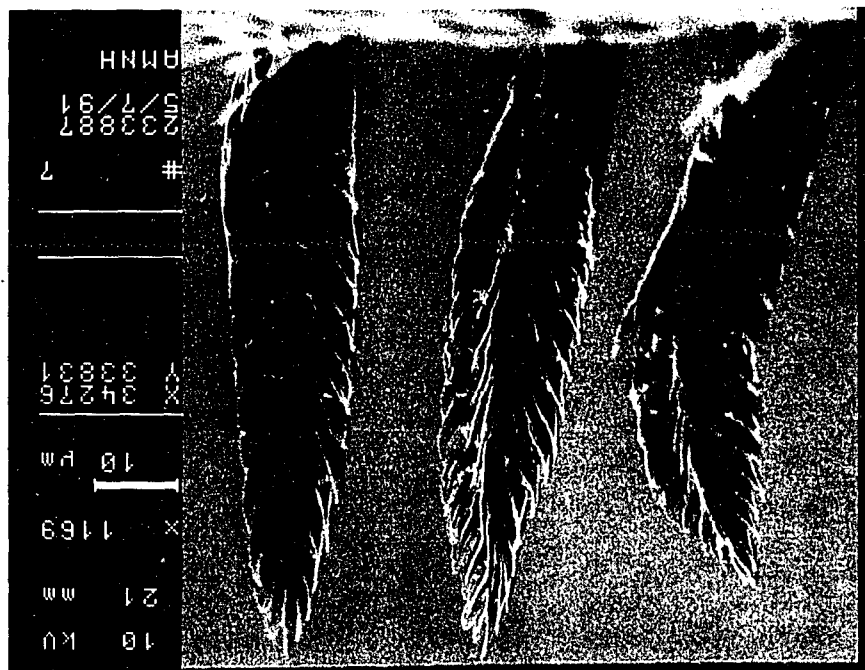


FIGURE 37

Austropallene turqueti, 37a. Compound spines, segment 10;
37b. Segment 10, entire; 37c. Strigilis.



38b



38a

38c

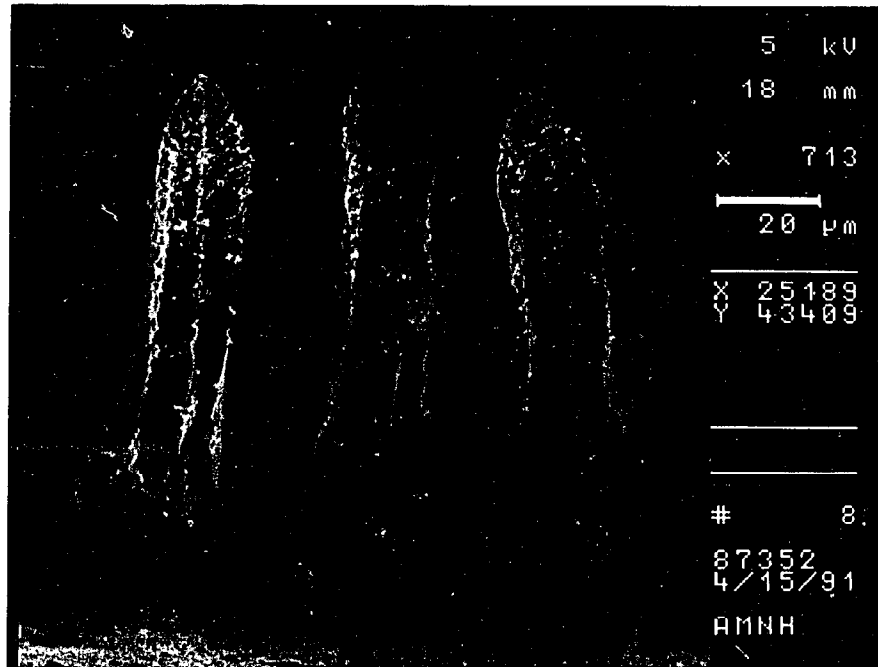


FIGURE 38

Austropallene wolfgangi, 38a. Compound spines, segment 10 (USNM 233887, ♂); 38b. Compound spines, segment 10 (USNM 87352, ♂); 38c. Compound spines, segment 7 (USNM 87352, ♂).

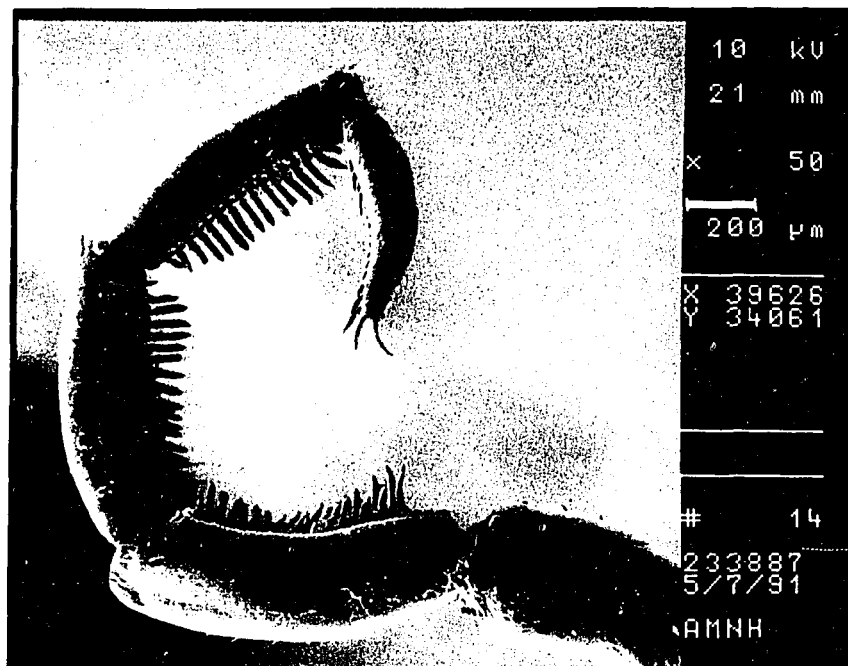
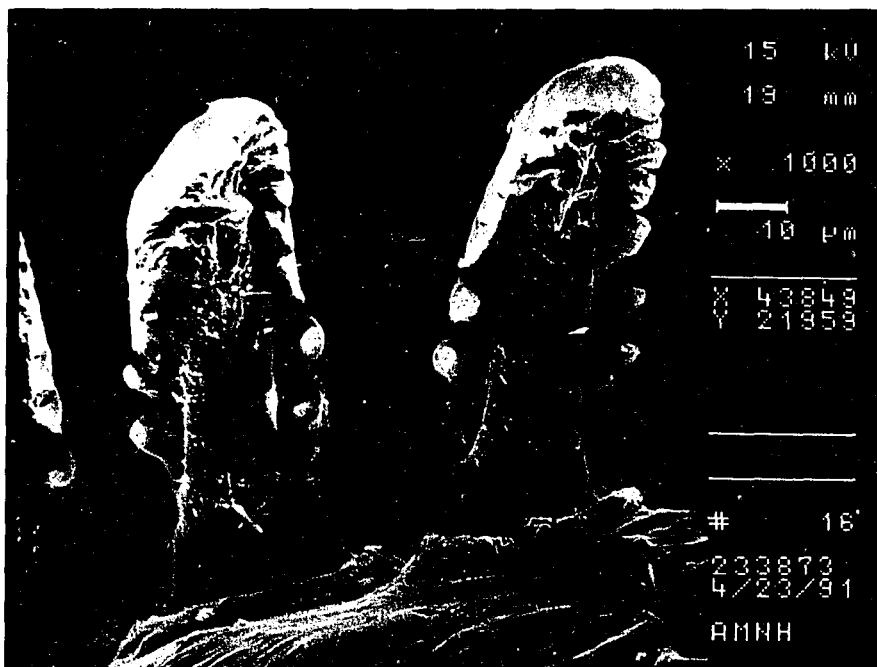


FIGURE 39

Austropallene wolfgangi, strigilis.

40a



40b



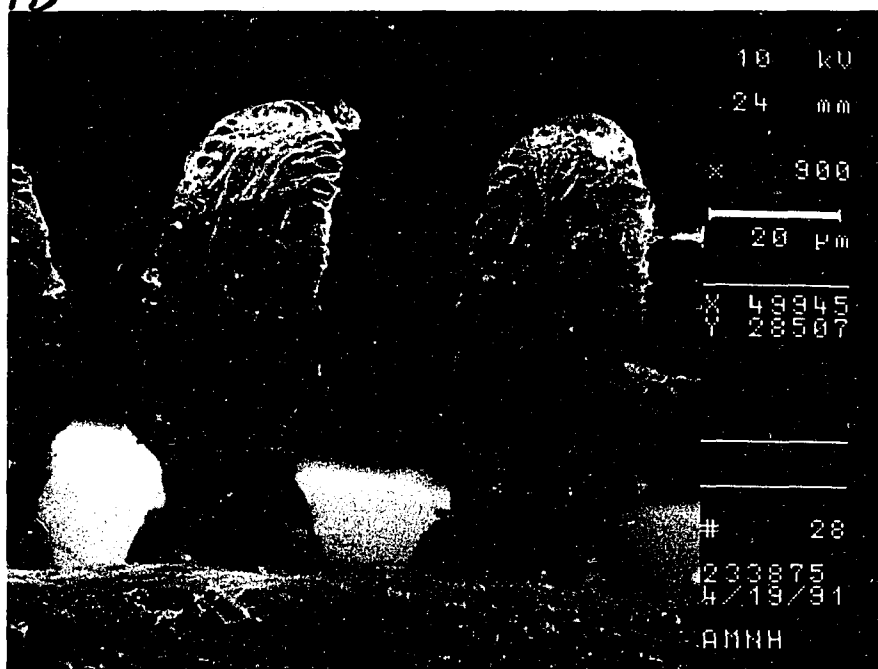
FIGURE 40

Austropallene maryae, 40a. Compound spines, segment 9; 40b. Distal end of segment 10.

41a



41b



41c

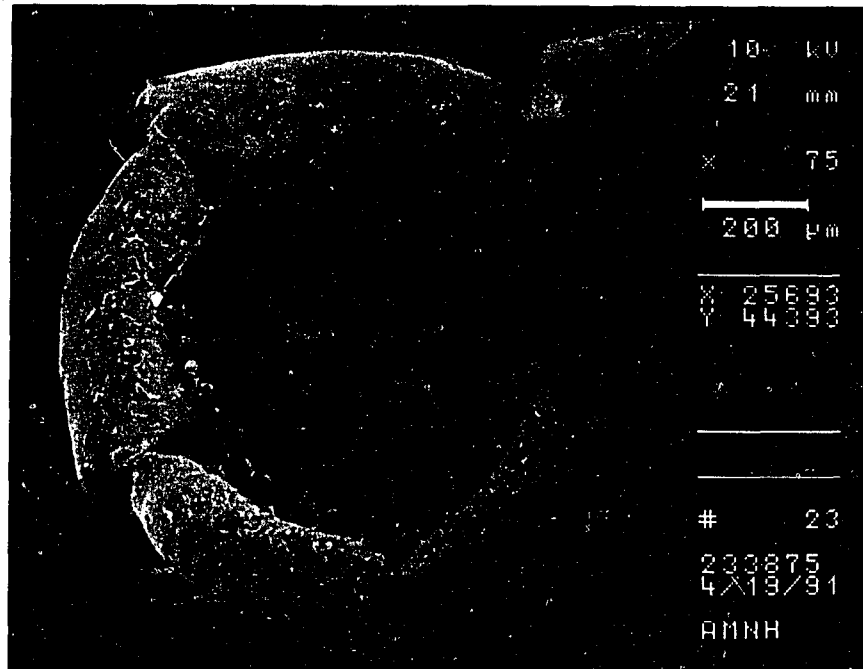
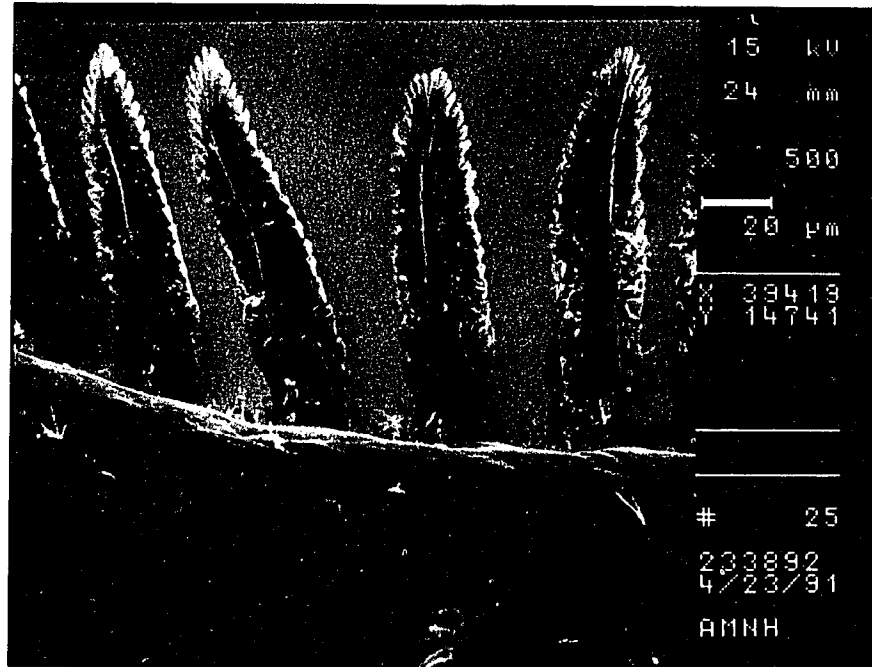


FIGURE 41

Austropallene jamesi, 41a. Compound spines, segment 9; 41b. Compound spines, segment 7; 41c. Strigilis.

42a



42b



FIGURE 42

Austropallene lanceoli, 42a. Compound spines, segment 9;
42b. Compound spines, segment 7.

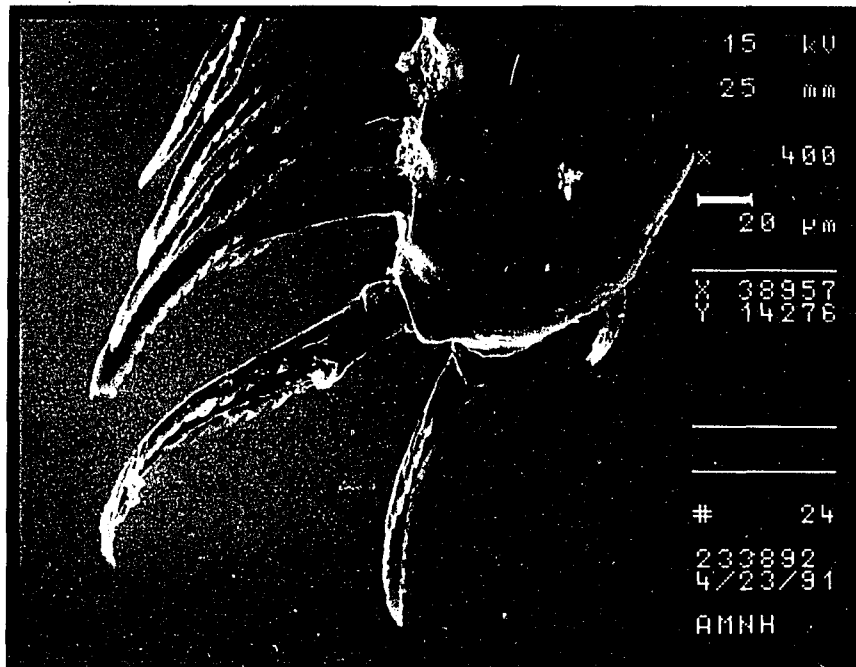


FIGURE 43

Austropallene lanceoli, distal end of segment 10.

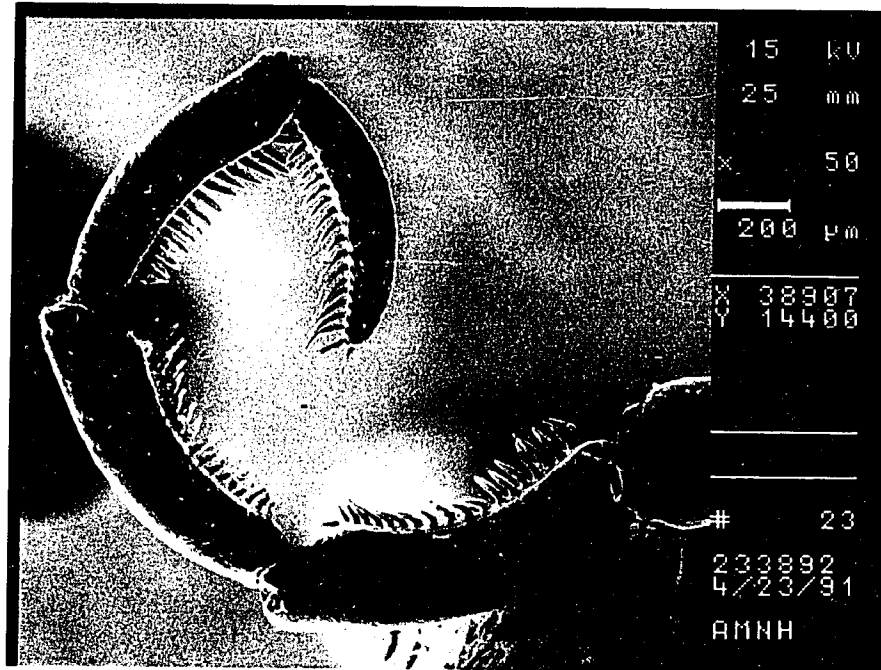
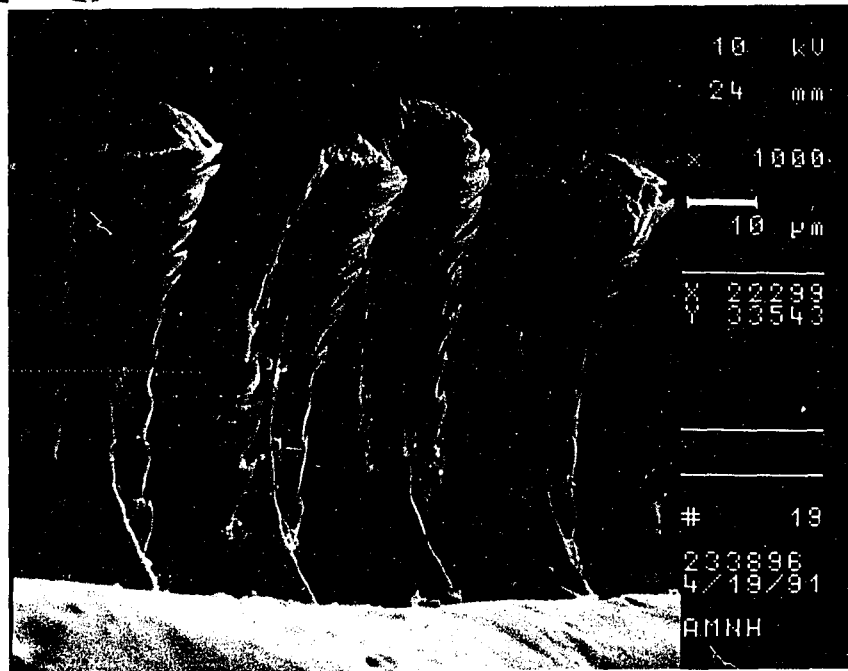


FIGURE 44

Austropallene lanceoli, strigilis.

45a



45b

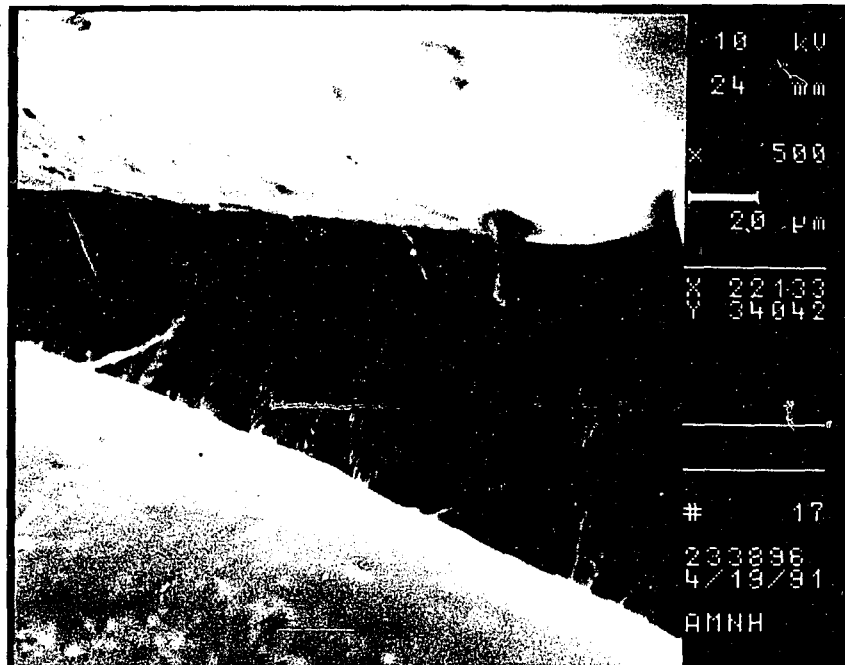
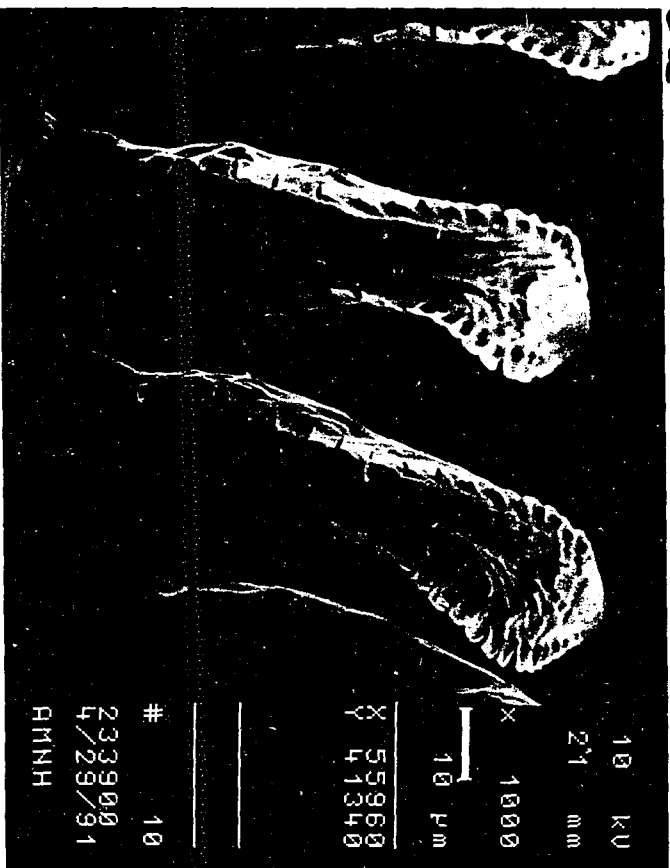


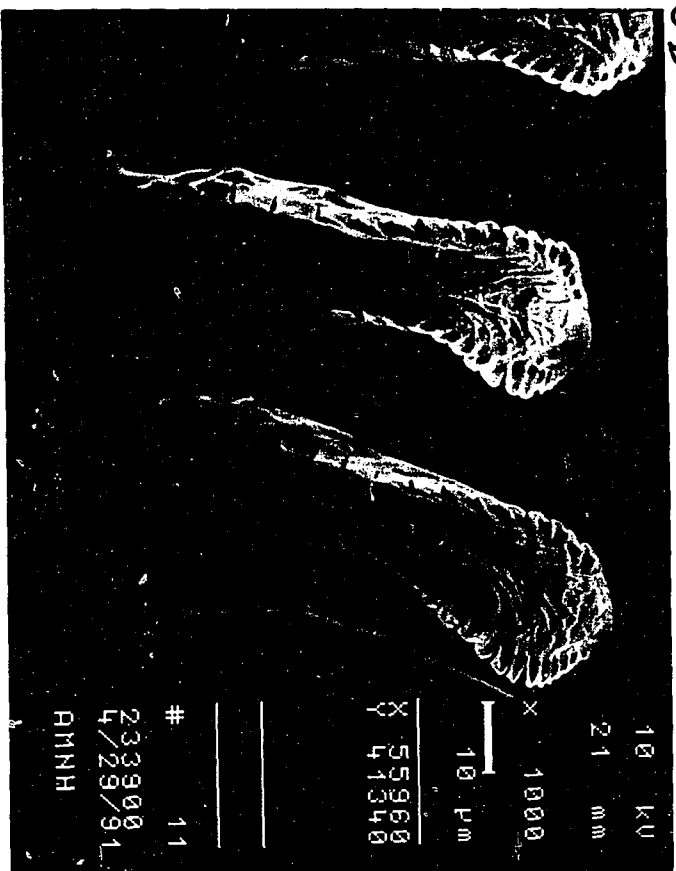
FIGURE 45

Austropallene edwardi, 45a. Compound spines, segment 10;
45b. Compound spines, segment 7.

46a



46b



46c



46d

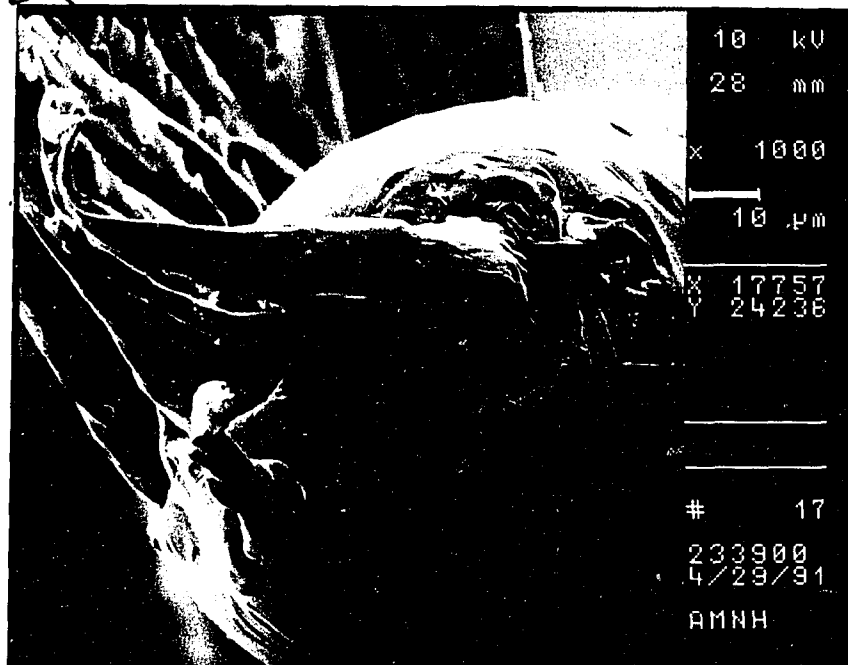


FIGURE 46

Austropallene brandti, 46a. Compound spines, segment 10; 46b. Compound spines, segment 10; 46c. Distal end, segment 10; 46d. Close-up of end spine on segment 10.

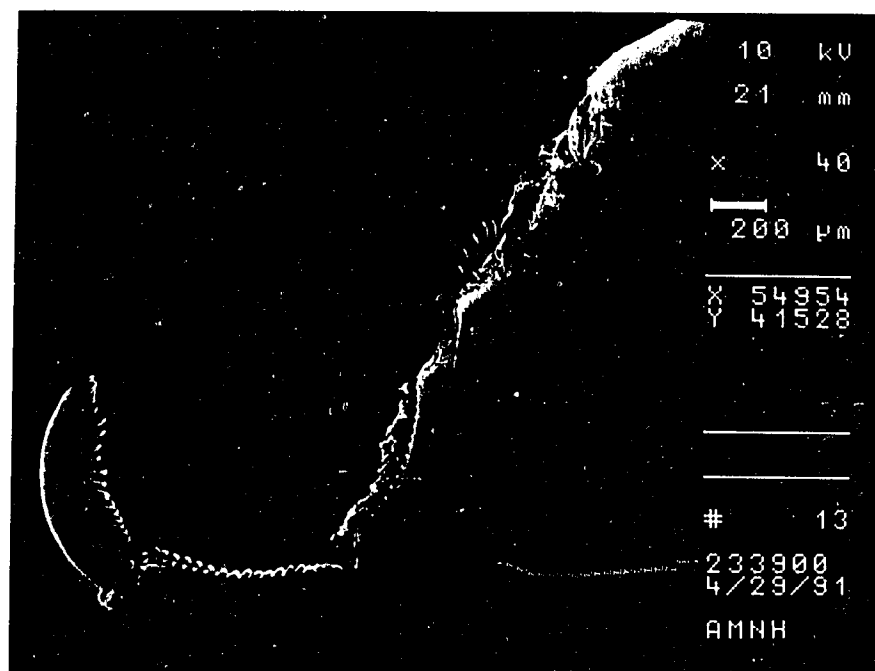
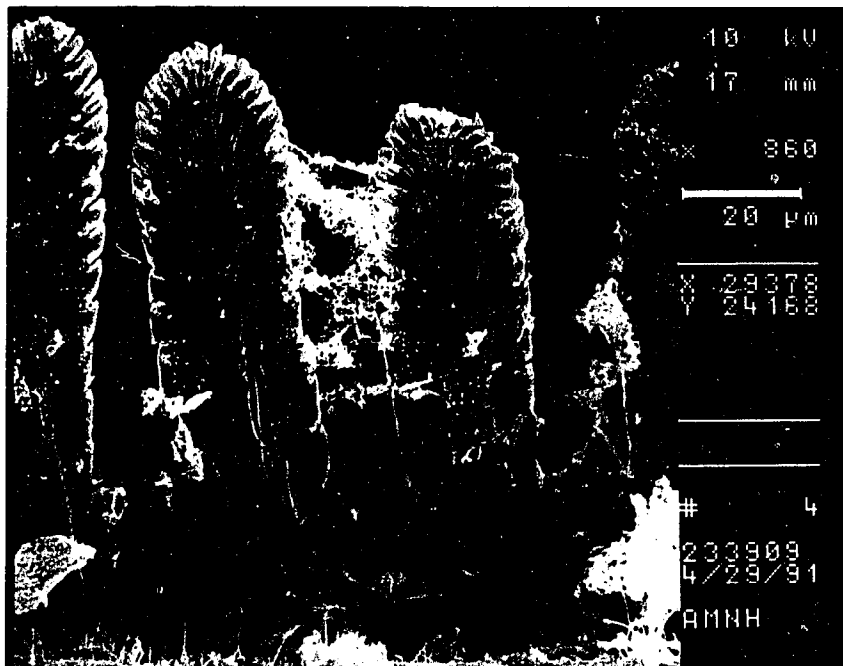


FIGURE 47

Austropallene brandti, strigilis.

48a



48b

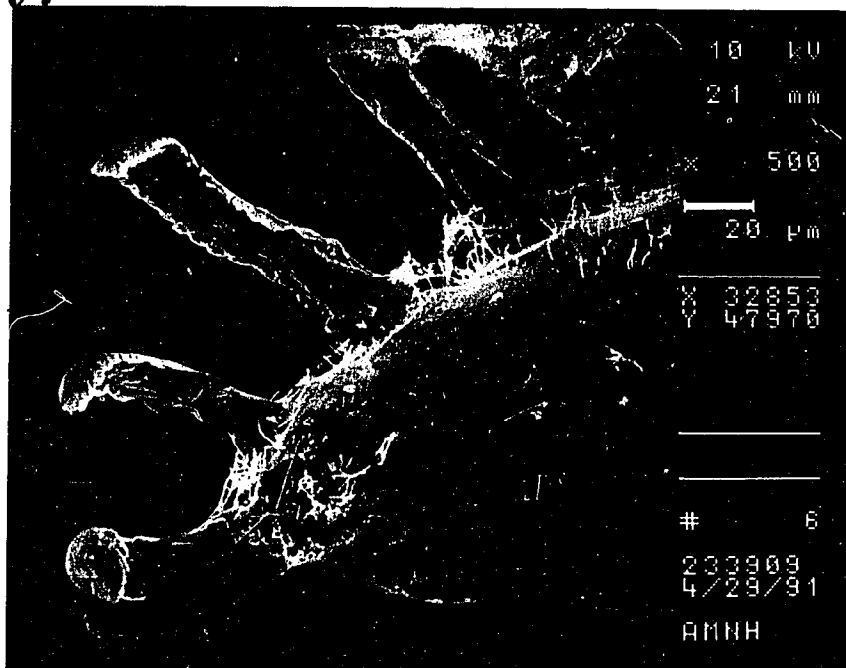


FIGURE 48

Austropallene hermani, 48a. Compound spines, segment 9;
48b. Distal end of segment 10.

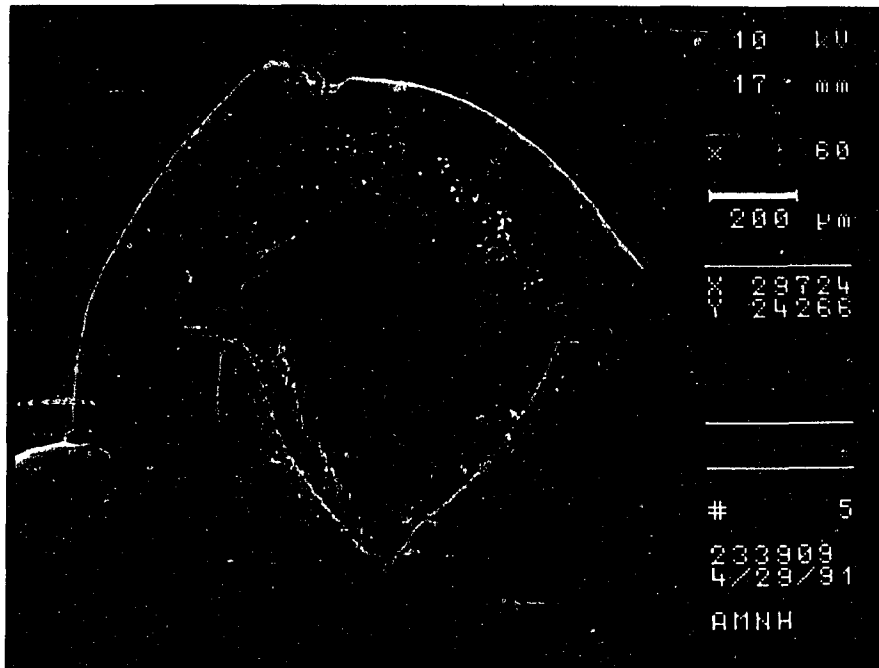


FIGURE 49

Austropallene hermani, strigilis.

Appendix V

xread

'Austropallene (Nymphon outgroup)'

14 8

Nymphon

00010 0000 00000

Brachyura

00010 0101 10111

Calmani

11100 0101 11111

Cristata

11001 0100 00110

Gracilipes

01100 0111 11111

Tibicina

00100 0111 11111

Tcherniai

00010 0111 11111

Cornigera

00110 1010 01111

;

proc / ;

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