The Bulletin of the Bingham Oceanographic Collection, established by Harry Payne Bingham (Yale 1910) in 1927, published scientific articles and monographs on marine and freshwater organisms and oceanography for the Bingham Oceanographic Collection at Yale University.

The series ceased independent publication after Volume 19, Article 2, and was merged into the Bulletin of the Peabody Museum of Natural History monograph series after 1967.

See also the Bingham Oceanographic Collection Archives, Invertebrate Zoology, Yale Peabody Museum, in the Archives at Yale:
https://archives.yale.edu/repositories/15/resources/11140

This work is licensed under a Creative Commons Attribution-NonCommercial-ShareAlike 4.0 International License.
https://creativecommons.org/licenses/by-nc-sa/4.0/
BULLETIN
OF
THE BINGHAM OCEANOGRAPHIC COLLECTION
Peabody Museum of Natural History
Yale University

Volume X, Articles 3 and 4

3. A SYSTEMATIC AND ECOLOGICAL STUDY OF THE HALACARIDAE OF EASTERN NORTH AMERICA

By Irwin M. Newell
Osborn Zoological Laboratory
Yale University

4. STUDIES ON THE MORPHOLOGY AND SYSTEMATICS OF THE FAMILY HALARACHNIDAE Oudemans 1906 (ACARI, PARASITOIDEA)

By Irwin M. Newell
Woods Hole Oceanographic Institution
Woods Hole, Massachusetts

Issued June, 1947
New Haven, Conn., U. S. A.
PUBLISHED BY
THE BINGHAM OCEANOGRAPHIC LABORATORY
"Founded for the Purpose
of Oceanographic Research"

Daniel Merriman
Director
E. F. Thompson
Curator
G. E. Pickford
Research Associate
Y. H. Olsen
Managing Editor
G. A. Riley
Research Associate
Louva Henn
Secretary
Honorary Associates
C. M. Breder, Jr.
American Museum
of Natural History
A. E. Parr
American Museum
of Natural History
Scientific Consultants
Werner Bergmann
Sterling Chemistry Laboratory,
Yale University
G. E. Hutchinson
Osborn Zoological Laboratory,
Yale University
R. F. Nigrelli
N. Y. Zoological Society
A SYSTEMATIC AND ECOLOGICAL STUDY OF THE HALACARIDAE OF EASTERN NORTH AMERICA

By

Irwin M. Newell

VOLUME X, ARTICLE 3

BULLETIN
OF
THE BINGHAM OCEANOGRAPHIC COLLECTION
Peabody Museum of Natural History
Yale University

Issued June, 1947
New Haven, Conn., U. S. A.
A SYSTEMATIC AND ECOLOGICAL STUDY OF THE HALACARIDAE OF EASTERN NORTH AMERICA

By Irwin M. Newell

Osborn Zoological Laboratory
Yale University

TABLE OF CONTENTS

ABSTRACT .......................................................... 2
ACKNOWLEDGMENTS .................................................... 3
INTRODUCTION .......................................................... 4
    HISTORY OF THE NORTH AMERICAN FAUNA ..................... 4
    EQUIPMENT AND METHODS ..................................... 5
    NOTES ON FIGURES, DESCRIPTIONS AND CONVENTIONS .......... 14
GENERAL SYSTEMATICS ............................................... 17
    DIAGNOSIS OF THE FAMILY HALACARIDAE MURRAY 1876 .......... 17
    KEY TO THE SUBFAMILIES OF HALACARIDAE ..................... 18
    KEY TO THE GENERA AND SUBGENERA ........................... 20
    SYSTEMATIC AND NOMENCLATORIAL NOTES ON THE SUBFAMILIES AND GENERA 25
    SUMMARY OF HALACARIDAE MURRAY 1876 ........................ 38
THE NORTH AMERICAN MARINE HALACARIDAE ........................ 39
    SUBFAMILY RHOMBOGNATHINAE Viets 1927 ....................... 39
        Genus Rhombognathus Trouessart 1888 .................... 39
        Genus Rhombognathides Viets 1927, emended ............... 47
        Genus Metarhombognathus, new genus ....................... 60
        Genus Isobactrus, new genus ............................... 68
    SUBFAMILY HALACARINAe VIETS 1927 ........................... 81
        Genus Halacarus Gosse 1855 ............................... 81
        Subgenus Thalassarachna Packard 1871 .................... 100
        Genus Copidognathus Trouessart 1888 ..................... 129
        Subgenus Arhodeoporus, new subgenus ...................... 173
        Genus Agaue Lohmann 1889 ................................. 183
        Genus Agauopsis Viets 1927 ............................... 184

1 A dissertation submitted to fulfill in part the requirements for the degree of Doctor of Philosophy in Yale University.
2 Now in the Department of Biology, University of Oregon, Eugene, Oregon.
This study is based upon collections of Halacaridae from New Brunswick, Canada, Long Island Sound, Chesapeake Bay, North Carolina and southern Florida. Improved methods for making permanent preparations of mites were developed and are presented in detail.

The morphology of several structures, including the tarsus, ambulacrum, lateral claws, rosette pores and genito-anal area is discussed and their taxonomic significance is pointed out. Keys to all subfamilies, genera and subgenera are given and two genera and one subgenus are newly described. The subfamily Rhombognathinae and the genus Copidognathus are revised along natural lines and the nomenclatorial status of several genera and species is clarified. The general and detailed anatomy of the species is illustrated by 330 figures. A glossary of terms is given, and all important structures, including the newly named ones, are labelled in at least one figure.

The number of species, subspecies and varieties from eastern North America is increased from 4 to 41, of which 14 are new. Only two of the four forms known from previous works were rediscovered. Keys to the North American species are given.

The halacarid fauna of Florida is the richest on our eastern coast, that of New England is the second richest, and intermediate regions are the poorest. There is no correlation between the New England-New Brunswick fauna and that of Florida. The fauna of southern Florida is tropical in character and is closely related to that of the Dutch West Indies and Bermuda. Nearly 70 per cent of the forms in the American Boreal Atlantic are identical with, or closely related to, forms in the European Boreal Atlantic. The transitional nature of the fauna between the
ACKNOWLEDGMENTS

The author is especially indebted to G. Evelyn Hutchinson, who suggested the problem and aided in its execution in ways far too numerous to mention; to Alexander Petrunkevitch for valuable counsel on many points regarding mites in general; to Daniel Merriman of the Bingham Oceanographic Laboratory; and to A. W. H. Needler of the Atlantic Biological Station, St. Andrews, New Brunswick, Canada, who obtained material of extreme value and interest from that locality. Other members of the Bingham Laboratory generously assisted in the collecting of material from the deeper waters of Long Island Sound. Stanley C. Ball and the Peabody Museum made it possible for the writer to collect at Solomon's Island, Maryland, and at Beaufort, North Carolina, in October of 1944. The expenses of this trip were met entirely by a grant from the Peabody Museum. S. C. Ball also gave the writer permission to collect mites from jars of preserved marine material in the Peabody Museum collection.

R. V. Truitt, director of the Chesapeake Biological Laboratory, and his staff extended every favor to the writer during his stay at Solomon's Island. H. F. Prytherch, Aquatic Biologist in charge of the United States Fishery Biological Laboratory at Beaufort, North Carolina, and his staff were equally generous in providing laboratory facilities and transportation during the time the writer was at Beaufort.

American Boreal and Tropical regions is shown to consist more of a dropping out of some Boreal genera than of an overlapping of Boreal and Tropical species. The distribution of certain species or species groups in the Caribbean, Mediterranean and southwest Pacific regions suggests a Tethyian halacarid fauna parallel to that of other groups of animals.

The fauna of the subtidal zone is more uniform than that of the intertidal zone, especially from a qualitative standpoint. Limited collections near the eastern end of Long Island Sound suggest a transition from a eulittoral to a sublittoral fauna. Observations on the absence of certain Rhombognathinae from special nontidal habitats indicate that some species require periodic exposure to air, thus accounting for their absence from the subtidal zone.

A well developed sand fauna consisting of three psammobiont and one psammophile species is found in Long Island Sound. The fauna is very similar to that of Europe. Of the faunae developed upon molluscs, those on Modiolus and Ostrea are most complex. The encrustation of Modiolus by Balanus greatly increases the ability of this substrate to support an halacarid fauna.

The algicolous faunae are dominated by the Rhombognathinae; none of the Halacarinae are typically algicolous. Estuarine habitats, because of their low salinity, are characterized by halacarid faunae containing a small number of species.
H. J. Lutz of the School of Forestry loaned equipment to the writer throughout the course of the investigations. W. D. Hartman provided the writer with deep-water material from Long Island Sound, and H. W. Baird of Opa-Locka, Florida, made extremely valuable collections in the region of Biscayne Bay, Florida. The Osborn Zoological Laboratory generously provided nearly all of the equipment used, and met a considerable share of the expenses involved in carrying out the study.

The writer is greatly indebted to his wife for her invaluable aid in the preparation of the manuscripts and plates. It is impossible, of course, to express appreciation here to all those who have made lesser, but nevertheless important, contributions to the completion of this work.

INTRODUCTION

HISTORY OF THE NORTH AMERICAN FAUNA

The history of our knowledge of the Halacaridae of eastern North America is brief and unimpressive. The first record of the occurrence of members of this family on western Atlantic shores was in 1871, when Packard (1871a) described Halacarus (Thalassarachna) basteri (Johnston) 1836 from Eastport, Maine, under the name of Thalassarachna verrilli. Packard did not recognize the affinities of this mite with the few European Halacaridae which had been described and properly named at that time; in fact, he attempted to ally it with the fresh-water mites. Trouessart (1893d: 259–261) described Copidognathus (s. str.) poucheti from Spitzbergen and stated that it also had been found on calcareous algae (Lithothamnion) from Labrador. Kramer (1897a: 83) listed two species from the west coast of Greenland (Sermilik Fjord). One of these he identified as Rhombognathus notops (Gosse) 1855, but the other species was represented by a single larva and was listed simply as a species of Halacarus. Trägårdh (1905a: 63) misidentified a specimen of Halacarus (Thalassarachna) basteri from Greenland as Agauopsis hirsuta (Trouessart). He did not know the precise locality. Gimbel (1919a: 124–128) described Copidognathus (s. str.) punctatissimus from Newport, North America (presumably Newport, Rhode Island) and this species is redescribed in this work from numerous specimens taken by the writer. Finally, the present writer (Newell, 1945a) has recently shown that Thalassarachna verrilli Packard 1871 is none other than the well known Halacarus basteri of Europe.
Therefore, up to the present time five species of Halacaridae have been listed from the shores of Greenland and eastern North America, and one of these (Halacarus sp. Kramer 1897) is not recognizable because it was not described. The North American species have never been treated from an ecological or zoogeographic standpoint. The purpose of this work is to describe as great a portion as possible of this virtually unknown segment of our marine fauna, to determine in so far as possible what factors affect the ranges and habitats of the various species, and to study the relationship between the fauna of our shores and that of other parts of the Atlantic region. In addition, a number of contributions to the systematics and morphology of the family as a whole have been made in the course of the study, and these are presented in detail.

**Equiptment and Methods**

*Collecting and sorting.* At each locality as great a variety of substrates as possible was sampled and the material was taken to the laboratory for study. In most cases 500 ml. samples were found to be as large as could be examined in a reasonable length of time. Paraffined “Sealright” containers, used for packing dairy products, were found most convenient because of their lightness. Sand samples were washed in a battery jar with a fine, strong jet of tap water, and the water was decanted quickly into a second jar. The washing was repeated until the sand was thoroughly cleaned. Large materials such as algae, molluscs, sponges, etc., were placed in a sieve with 2 mm. apertures while being washed. The washings were freed of all silt and other fine material by washing over a sieve with apertures of 0.1 mm. The residue was then washed through a series of sieves with apertures of 1.0, 0.5, 0.25, and 0.1 mm., except in the case of samples with a small amount of detritus in the 0.5-0.1 mm. fraction, where the 0.25 mm. sieve was omitted. The time required in washing the residue through this series of sieves was more than regained in sorting the mites from the residue, for the specimens could be seen easily and removed quickly as they crawled about on particles of their own size. If too much water accumulated in the various containers during the process of sieving, the jars were set aside for three or four minutes and then decanted through the 0.1 mm. sieve to catch any specimens which might adhere to the surface of the water. The fractions were placed in 100 ml. beakers, after which concentrated (4 times) sea water was added to give an approximately natural solution.
The residue was examined under the binoculars in convenient quantities in a square dish with a ridged bottom. Specimens were transferred to a small dish by means of a fine pipette. In population studies, the more easily recognized species or stages were simply recorded and not removed unless wanted for special purposes. The others were removed and subsequently placed on a ruled slide, crushed under a heavy cover slip and counted under the compound microscope. Any forms intended for preservation were removed from the slide and mounted as described below.

**Preparation of mites prior to killing.** As a rule the mites collected from marine habitats have a variable amount of detritus clinging to them. The simplest way to eliminate this is to place the live mites in a small dish of clean sea water with a very thin layer (3–4 grains deep) of clean white sand of uniform texture (i.e., with all of the coarser and finer fractions sieved out). After a few hours of crawling about, most of the mites become quite clean and exceptionally dirty specimens can be transferred to a second sand dish. When clean the mites are transferred to tap water in deep depression slides (capacity ca. 1 ml.), at which time the species or stages are segregated. Mites which are obtained from samples which have been washed through sieves in the manner described previously usually require no further cleaning.

**Killing.** With a sharp needle the mites are pierced ventrally, and with a second (dull) needle the greater part of the gut contents is forced out, this latter procedure being absolutely essential in the case of the more heavily pigmented forms (Rhombognathinae). The specimens are then syringed to free them of as much as possible of the extruded material. This leaves the weakly armored mites somewhat crushed, but these regain their form in the process of digestion in trypsin. An alternate method of evisceration is as follows. The mites are placed in a small drop of water on a clean slide, a cover slip is then dropped on them and pressure is applied with a fine needle. The cover slip is removed, the mites are washed into a depression slide and transferred to the trypsin tubes. This method is especially convenient in faunistic studies, for identification can be made on the slide and specimens which are not needed for preservation can be discarded. However, the large species often remain flattened by such treatment, thus being permanently distorted. These are best treated by making a fairly deep incision in the side of the mite with the broken corner of a
razor blade and gently forcing out most of the gut contents. By this method less compression is required to clean the specimens and distortion is less frequent than when the specimens are pierced or crushed.

**Preparation of digestion tubes.** Convenient trypsin tubes can be prepared as follows. A vial with an inside diameter of 12 mm. is scored with the sharpened end of a three-cornered file 2 cm. from the bottom of the vial. The vial is rotated in the corner of the lid of a microscope slide box, with the sharpened corner of the file held against it. The vial is then rotated in a microflame (3 mm. long) with the flame touching the scratch on the vial, thus producing a very smooth cut. The upper edge is levelled by rubbing it on a wet carborundum. Covers are made from vials just large enough to slip over the 12 mm. vial, these being cut in the same manner as outlined above but only 10 mm. long. Small vials with an inside diameter of 4–5 mm. are then cut 15 mm. long. The trypsin digestion solution is placed in the small inner vial, the toluene in the outer one.

**Digestion.** Halacaridae cannot be treated with even dilute solutions of alkali, as these dissolve the outer layer of the cuticle, thus rendering the plates practically invisible and destroying the characteristic sculpturing on them. The digestion solution is prepared by dissolving 0.2 g. of powdered trypsin in 10.0 ml. of 0.5 per cent Na₂CO₃ and filtering after the solution has been allowed to stand several hours, during which time it must be protected by storage in an atmosphere saturated with toluene. It should be filtered at least twice with the same filter paper. This solution can be stored in a refrigerator, but the writer has obtained the best results by using a screw-cap storage bottle patterned after the digestion tubes, that is, with an inner well having a capacity of 10 ml., surrounded by cotton or paper towel (to reduce the likelihood of spilling) saturated with toluene. Trypsin has been kept as long as a month in this way, whereas refrigerated trypsin without toluene cannot be kept clear for more than a few days. Mites are left in this solution 24–72 hours in a humidor at 40° C. After the body contents have been adequately digested the specimens are washed in distilled water and transferred to the dehydration dishes.

**Dehydration.** Small stender dishes (30 mm. inside) are fitted with a square piece of microscope slide which is cut small enough to lie in contact with the bottom of the dish. The mites are transferred to a drop of water on this plate and the legs are pulled into proper position by using a very fine needle and by taking advantage of surface tension
to hold the specimens. A small circular cover slip is carefully dropped onto the flat drop of water containing the specimens. Excess water which may hold the slip far above the mites is removed so that the mites are held quite firmly but without crushing. Absolute alcohol is pipetted onto the cover slip until the dish is filled to a level just above the cover slip. The alcohol gradually diffuses under the cover slip and dehydration is completed within an hour or so.

*Infiltration with alpha-chloronaphthalene (acn).* The specimens are transferred from alcohol to small tubes with an inside diameter of about 4 mm. If it is suspected that an appreciable quantity of water is still present it is necessary to add fresh absolute alcohol. All but the bottom 2 mm. or so are pipetted off after a half hour, and acn is carefully added by flowing it down the side of the tube rather than by dropping it directly into the alcohol. The acn sinks to the bottom, thus forcing the alcohol and mites to rise above it. Because of the small diameter of the tube, infiltration is slow and distortion is avoided. The alcohol is driven off in an oven at 40° C.

*Mounting in Hyrax.* When evaporation of the alcohol is complete, the mites are transferred by means of a flattened, bent dissecting needle, first to clean acn and then to "Hyrax" dissolved in acn. Round cover slips 10 mm. in diameter are fastened to a glass slide by means of a very small quantity of glycerine (not mineral oil, which causes Hyrax to become heavily clouded). A thick film of the Hyrax-acn mixture is spread over the cover slips, the mites are transferred from acn directly to this film, and these preparations are then placed in an oven at 40-50° C. for three or four days. Because of the low volatility of acn, infiltration with Hyrax is slow and distortion is reduced to a minimum. The dry Hyrax preparations (which should be hard when cooled to room temperature) are inverted on clean slides and gently warmed on the bottom of the warming oven. Pressure is applied with a small lead weight placed on the cover slip.

Specimens of even such weakly armored forms as *Metarhombognathus armatus americanus*, n. subsp., showed less than five per cent decrease in length when mounted by the above method. A series of 12 specimens of *Copidognathus arenarius* n. sp., averaged 315.1μ before dehydration and 317.2μ in the finished mounts. The discrepancy is well within the limits of error, since the measurements were made at low magnification. Eleven specimens of *C. punctatissimus* averaged 314.4μ before dehydration and 308.2μ after the mounts were com-
completed, showing an average reduction of only 2.2 per cent in length. Such forms mounted in balsam, etc., by the usual methods would shrink about 10 per cent. But the principal benefit from this method is the high degree of optical contrast obtained. When completely dry, Hyrax has a refractive index of 1.72 or more, and since that of the cuticle of the mites varies around 1.5, even the most minute cuticular structures are usually clearly defined. Berlese fluid, glycerine jelly, balsam and other standard mountants are entirely unsatisfactory for Halacaridae; and the first two, because of their lack of permanence, should never be used for more than cursory examination of any mite.

Although the technique outlined above was not completely developed until about 1943, the writer has specimens which were mounted in Hyrax in July of 1940 by less satisfactory methods. Six years later the only noticeable change is a slight darkening around the edges of the mounts, and this is not as great as in balsam mounts prepared at the same time. Hyrax is evidently as stable as balsam, and its optical properties make it incomparably superior to the latter as a mounting medium. Mites of many groups can be satisfactorily mounted in Hyrax by the above method. These include most Parasitoidea, small Trombidoidea, Acaroidea, all but the darkest Oribatoidea and isolated skeletal portions of all groups. In a few cases the soft parts can be safely hydrolyzed in five per cent KOH at room temperature, but wherever possible trypsin should be used, for specimens treated with alkali are usually brittle when dehydrated and the setae are especially liable to be broken off due to a general weakening of the cuticle.

Mounting in Clarite. Large and deeply pigmented mites can often be mounted in Clarite, with or without previous hydrolysis of the soft parts. They are killed by pouring hot (60-80° C.) 90 per cent insect saline or 60 per cent alcohol over them. These solutions are slightly hypotonic and the osmotic pressure built up inside the specimens extends the legs, but hot water alone should not be used as this is too hypotonic and usually causes distortion or rupture of the specimens. The mites are dehydrated in small vials or in dehydrating dishes by the same procedures outlined above, but methyl salicylate is substituted for acn in the next step. It is pipetted very carefully down the side of the tube as was the acn and the mites and alcohol lie above it. The alcohol is driven off at 40° C. and the mites are then mounted directly in Clarite. Because dry Clarite is so brittle it is advisable to mix 77 parts of dry Clarite with 23 parts of mineral oil (by weight)
before dissolving it in toluene. If the specimens show a tendency to become evacuated (i.e., to become opaque because of the removal of methyl salicylate before infiltration with Clarite can take place) it may be necessary to pierce the specimens to allow more rapid entry of the mountant. Evacuation occurs commonly when mites are transferred from toluene or xylene to resinous media, but only rarely if the less volatile methyl salicylate is used. Valuable specimens in which this occurs can be recovered by running back to methyl salicylate (or to alcohol if too brittle), piercing and remounting. Careful comparative tests show that mineral oil is less satisfactory than methyl salicylate as an infiltrating medium prior to mounting in Clarite because it causes greater distortion.

**Permanent glycerine mounts.** During the course of this study the writer has developed a method for making glycerine mounts which show promise of being relatively permanent, at least as permanent as Berlese fluid or glycerine jelly preparations and with far better optical properties. Furthermore, it is more adaptable, since the most delicate organisms can be infiltrated with glycerine with little or no serious distortion, whereas gum or gelatinous media are often useless for these. The technique may appear involved and tedious at first glance, but large numbers of slides can be produced with a small output of time per slide when the materials are assembled and the routine is properly organized. Essentially the technique involves mounting the objects between a small and large cover slip, flooding the preparation with a thermoplastic sealing compound, drying, and attaching the cover slip preparation to a slide with the aid of heat. The procedure is outlined in the accompanying diagram, in which the letters correspond with the letters in the following descriptive account.

For convenience in handling the cover slip preparations during the initial steps a special slide is used which consists of a 3 x 1 inch glass slide to which two half inch squares of glass are cemented by means of Clarite (Text-Fig. 1 A). These slides can be used indefinitely, of course, and need be prepared only once. A very small drop of glycerine is placed on the glass square (B), and a clean 22 mm. cover slip is placed on it (C), where it is held firmly by the glycerine. A drop of anhydrous glycerine is then placed on the upper surface of the cover

---

*The use of mineral oil to reduce the brittleness of Clarite was suggested to the writer by Alexander Petrunkevitch. Further details on the preparation of Clarite-mineral oil mixtures are given on page 12.*
The tendency to removal of a gelatinous sheath placed in rapid entry of the quadrate process are transient rarely if the gels in which salicylate (or equivalent compound) is dissolved is without the cover glass because it

This study the mounts which permanent is better optical microscopy of most details or no serious emphasis for these. are lost glance, but the output of time is properly placing the object under observation with a the cover slip picture is outlined correspond with

Sections during the 5 x 1 inch glass of by means of indefinitely, of a drop of glycerin, cover slip picture. A drop of the cover suggested to the

Text-Figure 1
slip (D), the amount depending upon the size of the objects to be mounted. The specimens are transferred to the glycerine (E), along with glass supports if these are necessary (shown as glass rods in cross-section in the text-figure). A 12 mm. cover slip is placed over the glycerine containing the specimens (F), and the preparation is flooded with a solution of Clarite and mineral oil dissolved in toluene (G). Complete details for making the Clarite mixture are given at the completion of this account. Some experience will be necessary to judge the quantity of sealing mixture required to produce the best mount, but complete failure even on the first slides would be difficult.

The preparation is now placed in an oven set at 40° C. for one or two days, and finally it is left on the bottom of the oven near the heating element for another day, or until the sealing mixture is hard when cooled to room temperature (H). The cover slip preparations are removed from the temporary carriers, inverted, and placed upon a clean slide, either singly or doubly (I, L). The slide is then placed upon a sand bath or hot plate at a temperature of 170–175° C. until the Clarite spreads beyond the edge of the cover slip (K, N). The preparation is likely to slip off the edge of the slide during this step, but this can be avoided by using a tripod consisting of three fine pins or needles set in a thin piece of wood (J, I). A similar device containing five pins is used when two preparations are to be mounted on the same slide (L, M).

Clarite 77%, mineral oil 23% by weight, thinned with toluene to a workable consistency, is the formula of the sealing mixture used by the writer, with the materials available to him. The proportions of Clarite and mineral oil are not matters of personal choice, but must be exact in order to obtain a sealing mixture of proper consistency. On the one hand, a very slight excess (0.5%) of mineral oil will result in a mixture that will allow slow movement of the cover slips, especially in warm weather. On the other hand, as much mineral oil as permissible should be added in order to reduce the brittleness of the Clarite and improve its otherwise poor adherence. Since significant differences may be found in different lots of Clarite and especially of mineral oil, it is desirable to set aside a considerable quantity of each for just this purpose and to make up four or five small trial solutions containing different proportions (e.g., 20: 80, 22: 78, 24: 76, 26: 74, by weight), using an analytical balance. These mixtures are dissolved completely in toluene and drops of each solution are placed on a slide and allowed
to dry for at least a day on the bottom of an oven set at 40° C. Those mixtures which are too soft or too brittle can be detected readily by pushing a dissecting needle through the dried samples. A second series of test solutions in the critical range may be advisable before selecting the most satisfactory formula. Further tests are unnecessary unless a new lot of either mineral oil or Clarite is used.

It is essential that anhydrous glycerine be used. In wet climates or during wet seasons of the year, special precautions are necessary to keep the glycerine free of water, which may be done by storing it in the warming oven near the heating unit. In damp weather initial steps of the mounting should be completed as quickly as possible, for glycerine is markedly hygroscopic. Under such circumstances it is advisable to place the preparations in the drying oven for two or three hours prior to adding the small cover slip and flooding with Clarite, that is, between steps E and F.

This technique has been found useful for dissected parts of Halacaridae, and also for certain small mites such as tarsonemids, hypopi and many of the small Trombidoidea which are difficult to handle by other means. It is also very satisfactory for Nematoda, Tardigrada, many small insects and Crustacea. However, whole animals must be gradually infiltrated with glycerine if distortion is to be avoided. The specimens are transferred alive or dead to a small dish containing a solution of 28 parts of water, 68 parts of 95% alcohol, 3 parts of glycerine and 1 part of glacial acetic acid (omit acid if CaCO₃ is present), by volume. The solution is then allowed to concentrate slowly by evaporation over a period of from one to several days, depending upon the resistance of the animals to deformation. The specimens are mounted in fresh glycerine as outlined above. Some animals, when placed in the infiltration solution, become temporarily shrunken, but eventually they regain their normal form.

Trypsin treatment of mites or other arthropods prior to dissection or mounting is advisable. If appreciable quantities of colloidal substances or oils are present following digestion these should be precipitated or dissolved in absolute alcohol to prevent their detracting from the serviceability of the mount. The writer regards dissections of legs, mouthparts and special structures as indispensable to a thorough study of mites, for even in a large series of specimens of a species not all parts can be examined satisfactorily on whole mounts. Tarsal structure cannot be determined in a satisfactory manner from dorsal
or ventral sides alone, and the best way to assure serviceable preparations is to make at least one dissection, but preferably three or four, of each species. By the above method these can be made an invaluable and permanent part of the collection, not merely temporary mounts which must be discarded eventually because of the lack of a satisfactory method of preserving them. Because the mouthparts are so much smaller than the rest of the mite, these are mounted on a separate cover slip, and both preparations are then attached to the same slide (L, M). The legs are usually removed from both sides of the body, and all are oriented in the same manner (e.g., claws to the right, extensor surface uppermost) so that both lateral and medial aspects of each pair of legs are presented.

NOTES ON FIGURES, DESCRIPTIONS AND CONVENTIONS

In preparing the following descriptions and figures as many specimens as feasible have been examined, and the descriptions are believed to approximate closely the true conditions. The most obvious variations have been noted in the text. However, the writer has attempted to make an exhaustive survey of the external anatomy of each species in the belief that close attention to such details as number, form and arrangement of setae on the body and appendages may eventually provide morphological criteria for the recognition of natural groups within subfamilies or genera. With so many details being checked closely it has been impossible to explore the limits of variability in any of them. As a further consequence of this it is probable that some minute details were actually obtained from atypical specimens; but such cases, if present, are extremely rare. As a rule at least two specimens were examined (from different localities if possible); if exact correspondence was noted no further study was made, but additional specimens were studied if differences were found, and the possibilities of local variation and unilateral variation upon individuals were explored.

The tables showing the arrangement of the setae on the legs should be used with the consideration that it is not possible, in practice, to divide a leg segment into perfect dorsal, ventral, lateral and medial sectors; also, setae which are dorso-lateral in position may be grouped with the dorsal or the lateral setae (etc.), according to the material examined. Furthermore, it is sometimes convenient to give the number of setae which constitute a characteristic group of setae under a
single column, despite the fact that one of their number may have
gone somewhat astray (e. g., in the case of the triangle setae on seg-
ments three and five of the legs). However, the total number of setae
is that which the writer believed to be typical for that segment. Also
the bacillum, prebacillum and parambulacral setae are not included in
the tables but are discussed separately in the text accompanying the
tables. The tables showing dimensions of the segments must be used
with reasonable caution, for although the figures presented are accu-
rate for the specimen measured, variations certainly occur from speci-
men to specimen. With the typical adult halacarid having 24 leg
segments on each side, it is obviously impossible to analyze the varia-
tions found in each. Ratios are always more reliable than absolute
lengths. With the ocular micrometer used, and at the magnifications
employed, a single micrometer unit had the following values: 6.93μ
at 100, 1.66μ at 430, and 0.75μ at 970. Measurements were made to
the nearest half unit, so that the measurements are accurate to about
1.7, 0.4 or 0.2μ at the magnifications employed. Most of the species
are small enough so that leg segments could be measured under oil
immersion, thus reducing the error to ± 0.2μ. Errors due to limita-
tions of the optical equipment would therefore be insignificant, with
one or two possible exceptions.

The original drawings were made with a camera lucida at linear
magnifications ranging from 160 to 2200, and occasionally at 4000.
Scales are provided with most figures and these can be used with con-
siderable confidence to obtain measurements not given in the text,
except in certain cases in which structures are drawn in oblique view.
These are usually quite obvious, either from the drawings themselves,
from notations in the text or from the legends. Not all the drawings
for even one of the sexes of any species are from the same individual,
of course, except in cases in which a single specimen was available.

The lengths of the leg segments are given in micra, the measurements
being the maximum dorsal length measured in a straight line from the
base to the end of the segment. Overlapping of segments is usually
insignificant. The height of a segment is its maximum height perpen-
dicular to the longitudinal axis of the segment. The length of the
tarsus is the measurement to the base of the carpite in the Rhom-
bognathinae, and to the base of the median claw in the other groups,
since this point was more easily seen than the true disti-dorsal end of
the tarsus. The length of the ambulacrum, then, is the maximum
straight line distance from the base of the carpite, or the median claw, to the outermost surface of the claw.

The loosely used terms “swollen” and “not swollen” as applied to leg segments in the Halacaridae are augmented by actual ratios. Those segments with a ratio of length to height (L/H) of 2.0 or more are “not swollen”; those in which L/H is less than 2.0 are “slightly swollen,” “swollen,” etc. This system does not eliminate border-line cases, but it should reduce the amount of overlapping which results from purely descriptive terms.

Where scales have been provided for the drawings, each division on the scale equals 10 μ. A scale with only one division represents 10 μ, a scale with three divisions represents 30 μ, etc. In the scales which are 10 divisions long, a slightly longer mark has been made at the 50 μ point. There are no exceptions.

The following abbreviations of frequently recurring terms have been employed:

- **AD** antero-dorsal plate.
- **AE** anterior epimeral plate.
- **AD-PD** distance between antero-dorsal plate and postero-dorsal plate.
- **Ambul.** ambulacrum.
- **av.** average.
- **ca.** circa.
- **d.** dorsal (in tables on chaetotaxy of legs).
- **GA** genito-anal plate.
- **l.** lateral (in tables of chaetotaxy of legs).
- **L/H** the ratio of length to height (of a segment).
- **L/W** the ratio of length to width (of the body, or a plate, etc.).
- **m.** medial (in tables of chaetotaxy of legs).
- **OC** ocular plates.
- **OC-OC** the distance between the most medial points on the right and left ocular plates.
- **P-1** palpal segment one.
- **P-3** palpal segment three.
- **PD** postero-dorsal plate.
- **PE** posterior epimeral plate (or plates).
- **T/BL** total length of leg divided by the body length.
- **v.** ventral (in tables of chaetotaxy of legs).
GENERAL SYSTEMATICS

DIAGNOSIS OF THE FAMILY HALACARIDAE MURRAY 1876

Trombidoidea with body typically flattened or, more rarely, circular in cross-section; elliptical in outline. Mouthparts forming a distinct capitulum nearly always projecting well beyond anterior margin of body, but in a few forms completely hidden in dorsal view. Palpi with 3 or 4 segments, attached laterally, dorso-laterally or dorsally to base of capitulum. Maxillary portions of palpi completely fused. Chelicerae retractile, lying in a dorsal groove in rostrum; ventral digit large, movable; dorsal digit reduced to a pointed membrane. Tracheal system very rudimentary and quite certainly not functional in respiration. Cuticle of body wall usually reinforced with 4 plates dorsally (predorsal, postdorsal, and right and left ocular plates) and 4 plates ventrally and laterally (anterior epimeral, right and left posterior epimeral, genito-anal plates), these plates showing varying degrees of subdivision or fusion in different genera, in different species of a single genus, or rarely in the two sexes of a single species. Legs attached laterally, pairs I and II borne on anterior epimeral plate (or plates) and projecting anteriorly; pairs III and IV borne on right and left posterior epimeral plates and projecting posteriorly. Legs with 6 segments in adult. Larvae with only 3 pairs of 5-segmented legs, protonymph with leg IV 5-segmented also, but legs I, II and III 6-segmented. Deutonymph with all legs 6-segmented. Tarsus always with 2 lateral claws; median claw present or absent. Salivary glands well developed. Midgut not opening by way of anus. Anus present, but functioning entirely as an opening for the single, dorso-median excretory tubule. Sexes separate; sexual dimorphism marked in genito-anal plate and genitalia; other structures usually (but not always) identical in form in both sexes. Three eye spots apparently always present; corneae 2, 4 or 6 in number, or absent. Median eye without cornea.

Principally marine, but with numerous fresh-water forms (“Porohalacaridae” of Viets). Not capable of swimming. Predominantly predaceous or herbivorous, but three parasitic genera are known.
Remarks. The assumption that the posterior opening in the Halacaridae is not the anus is not adhered to by the present writer. The fact that there is no connection between this opening and the midgut is unimportant from a morphological standpoint. Unless it be shown (and it would be impossible to do so) that the opening is morphologically and phylogenetically a separate opening from the anus, it is proper and preferable that this opening be called the anus. At the same time its excretory function must not be overlooked. This is in keeping with the principle that homologous structures may, with propriety, be designated by the same name, despite differing physiological adaptations.

The coxae are incorporated into the body wall, forming the epimeral plates. Since the epimeral plates are composite sclerites, which in most forms consist of the modified coxae, plus additional sclerotized portions of the body wall, the term epimeral plate is to be preferred to the terms coxa or coxal plate. The free segments of the legs are, then: (1) trochanter, (2) basifemur, (3) femur, (4) patella, (5) tibia, (6) tarsus. In the larvae, and in leg IV of protonymphs, the basifemur and the femur are undivided and the legs are then composed of five free segments.

**Key to the Subfamilies of Halacaridae**

1a. Middle piece of claw articulating with carpite, which in turn articulates with (Figs. 25, 48), or is fused with (Fig. 68), end of tarsus. Palpi always very small, sometimes 3-segmented and always closely appressed to sides of rostrum. Gut caeca always green or greenish black. Predominantly marine and intertidal (rarely found in fresh water?) and never living under conditions which preclude algal growth.

2a. Palpi 3- or 4-segmented, attached laterally. All dorsal plates present and occasionally fused to form a single dorsal plate, in which case corneae are present. Female genital opening terminal or ventral. Principally intertidal (rarely in fresh water?). RHOMBOGNATHINAE Viets 1927; p. 20. Cosmopolitan.


1b. Middle piece of claw articulating directly with end of tarsus; carpite absent (Figs. 212, 311). Palpi usually distinctly 4-segmented but usually not closely appressed to sides of rostrum; however, in the few parasitic forms the palpi may be greatly reduced. Predaceous or parasitic (a few may be scavengers) on marine or fresh-water animals. Gut caeca nearly always gray, brown, red, orange, yellow or lavender. Fresh water or marine; intertidal to abyssal.
3a. Palpi attached to capitulum dorsally, separated by an interval no greater than width of base of P-1 (Fig. 329); bases of palpi not clearly visible in ventral view.

4a. Rostrum about as long as palpi (in uncompressed specimens), relatively uniform in width or even expanded distally; opposed to downwardly turned elongate palpi. Rostrum at least three times as long as high. Marine or fresh water......LOHMANNELLINAE Viets 1927; p. 23. Probably cosmopolitan.

4b. Rostrum much shorter than palpi, less than twice as long as high.


3b. Palpi attached to capitulum laterally; bases of palpi separated by an interval considerably greater than width of P-1, and clearly visible in ventral view (Fig. 313).

6a. Palpi extremely small, 3-segmented.

7a. Parasitic in gut of echinoderms, at least in larval and nymphal instars. ENTEROHALACARINAE Viets 1938; p. 25. Western Pacific Ocean.

7b. Predaceous......SIMOGNATHINAE Viets 1927, in part; p. 23. Bay of Biscay; western Indian Ocean.

6b. Palpi 4-segmented, although P-3 and P-4 may be very small or fused; in the latter case the demarcation between P-3 and P-4 is still evident.

8a. P-3 and P-4 greatly reduced, their combined length less than ½ that of P-2. Parasitic.

9a. Rostrum and palpi as long as, or longer than, base of capitulum. Rostrum barbed distally, the barbs pointing posteriorly. Ventral digit of chelicerae with coarse teeth. Parasitic, at least as nymphs, on gills of Amphineura......HALIXODINAE Viets 1927; p. 24. New Zealand.

9b. Rostrum and palpi much shorter than base of capitulum. Rostrum not barbed distally. Ventral digit of chelicerae with coarse teeth. Parasitic, at least as nymphs, on gills of fresh-water decapod Crustacea. ASTACOPSIPHAGINAE Viets 1931; p. 25. Australia.

8b. Combined length of P-3 and P-4 greater than ½ the length of P-2. Predaceous.


Although these characters are undesirable from a morphological standpoint, there are no reliable ones available upon which to base a separation here, owing to inadequate and probably inaccurate descriptions.
Subfamily Rhombognathinae Viets 1927

1a. Genital opening of female terminal, guarded by a pair of large, cusp-like opercula (Fig. 13). Armor usually heavy. Claws smooth or pectinate; 2 claws on all tarsi, or 3 claws on all tarsi, or 3 claws on I and II and 2 on III and IV. Tarsi I and II with only the bacillum, which is more than five times as long as thick and usually 10 to 15 times as long as thick. Carpite not fused to end of tarsus (Fig. 25). End of tarsi I and II with ventral seta (Fig. 23). Nymphs with genital and anal plates fused. ...... Rhombognathides Viets 1927; p. 47. French Mediterranean coast, and Connecticut coast of North America northward. Tierra del Fuego, Pacific-Antarctic Ocean (Macquarie Islands); apparently not tropical.

lb. Genital opening of female not terminal, nor guarded by a pair of large cusp-like opercula, but situated in ventral body wall and guarded by a pair of elongate, band-like sclerites at the most (Figs. 5, 55). Either 2 or 3 claws on all tarsi. Tarsus I with bacillum and prebacillum or with only the bacillum (in which case the latter is less than five times as long as thick). Carpite either fused to end of tarsus or free. End of tarsi I and II with or without ventral seta. Nymphs with genital and anal plates fused or separate.

2a. Three claws (in all forms known at present) on all tarsi, with the median claw nearly as heavy as lateral claws. Deutonymphs more heavily armored than adults. Both bacillum and prebacillum on I-6 short, no more than five times as long as thick (Fig. 47). Carpite free. End of tarsi I and II with ventral seta (usually difficult to see). Nymphs with genital and anal plates fused. ...... Metarhombognathus, new genus; p. 60. North Sea, and North Carolina coast of North America northward into Arctic Ocean; apparently not tropical.

2b. Two claws (in all forms known at present) on all tarsi. Adults more heavily armored than nymphs, frequently with all dorsal or all ventral plates fused. Only the bacillum present, or with a very rudimentary bacillum and a long, slender prebacillum. Carpite apparently free or visibly fused to tarsus. End of tarsi I and II without ventral seta. Nymphs with genital and anal plates separate.

3a. Tarsi I and II each with a single, short, club-like seta (the bacillum) in front of lateral disti-dorsal seta (Fig. 71). Coxal plates II on right and left sides absent, or, if present, not fused (Fig. 80). Ventral armor re-
duced and not forming a solid plate. Femur I less than 1.5 times as long as high (greatly swollen). Carpite fused to end of tarsus and with a moniliform, flexible shaft (Fig. 64)......*Isobactrus*, new genus; p. 68. European and American Boreal; Kerguelen.

3b. Tarsi I and II with a stub-like bacillum and a long, slender prebacillum (Fig. 9). Coxal plates II on right and left sides fused (Fig. 3). Ventral armor usually extensive in adult, often forming a solid plate which almost completely encloses genital opening. Femur I usually more than 1.5 times as long as high. Carpite not fused to end of tarsus and with a straight, nonflexible, nonmoniliform shaft (Fig. 1).


Subfamily Actacarinae Viet 1939

Represented by a single genus. See characters in key, p. 18. Arenicolous.


Subfamily Halacarinae Viet 1927

1a. Palpi apparently 3-segmented, with segments 2 and 3 (or 3 and 4?) fused. Littoral to abyssal.......

1b. Palpi distinctly 4-segmented (Figs. 110, 202, 319).

2a. P-2 with a medial spinoform seta. P-3 without such a seta. Attenuate distal portion of P-4 shorter than the cylindrical basal portion. Littoral.

*Pontacarus* Lohmann 1901. Brazil.

2b. P-2 without a medial spiniform seta, although one may be present on P-3. Attenuate distal portion of P-4 longer than the cylindrical basal portion.

3a. Palpi nearly always relatively straight (Fig. 89). (A line drawn along the ventral surface of P-2 in an undistorted palp forms an angle of less than 30° [usually less than 20°] with a line drawn from the tip of P-4 to the bottom of P-3. Exception: *H. anomalus* Trouessart, easily distinguished by cylindrical body and the division of PD into right and left halves [Figs. 131-137]. This species goes to group 3b.) Rostrum usually parallel-sided, or very nearly so. P-3 plus P-4 shorter than P-2 in probably all species.

4a. Rostrum usually tapering at least very slightly throughout its length and never broader distally than near the base. Capitulum relatively short, never reaching to end of I-3. P-3 often with heavy medial setae. Body and legs never with elaborate lamellae. Leg I often with heavy, rod-shaped setae medially and ventrally......*Agauopsis* Viet 1927; p. 184. Cosmopolitan.

4b. Rostrum nearly always relatively straight (Fig. 87). (A line drawn along the ventral surface of P-2 in an undistorted palp forms an angle of less than 30° [usually less than 20°] with a line drawn from the tip of P-4 to the bottom of P-3. Exception: *H. anomalus* Trouessart, easily distinguished by cylindrical body and the division of PD into right and left halves [Figs. 131-137]. This species goes to group 3b.) Rostrum usually parallel-sided, or very nearly so. P-3 plus P-4 shorter than P-2 in probably all species.

Generally, palpi which have been removed from specimens treated with trypsin, or from specimens preserved in 50–60% alcohol (no higher), or in Viet's glycerine-acetic acid-water mixture, will have palpi which are in a natural state of extension, provided there is no distortion from the cover slip.
4b. Rostrum usually distinctly parallel-sided and often slightly broader near the distal end than near the middle. Capitulum often reaching to, or very nearly to, end of I-3. P-3 never with a thick medial seta. Leg I without heavy, rod-shaped setae medially and ventrally. Body and legs often with elaborate lamellae. \textit{Agae} Lohmann 1889; p. 183. Cosmopolitan.

3b. Palpi nearly always distinctly geniculate (Fig. 145). (Lines drawn as above usually form an angle of more than 30° [ca. 20° in \textit{H. anomalus}].) P-3 plus P-4 usually longer than P-2. Sides of rostrum in most (but not all) species distinctly convergent.

5a. P-3 with a medial seta which is usually spiniform, but which is rarely very slender (\textit{Halacarus} s. lat.).

6a. I-4 very nearly as long as, or slightly longer than, either I-3 or I-5 (Fig. 124). \textit{Halacarus} s. str. Gosse 1855; p. 81. Cosmopolitan.

6b. I-4 distinctly shorter than either I-3 or I-5 (Fig. 171).

5b. P-3 without setae (\textit{Copidognathus} s. lat.).


7b. I-1 with 2 pairs of ventral setae in deutonymphs and adults (Fig. 312). Rosette pores absent. Marine or brackish water. \textit{Arhodeoporus}, new subgenus; p. 173. Apparently not tropical.

Subfamily Porohalacarinae Viets 1933

1a. I-4 as long as, or nearly as long as, I-3 and I-5. \textit{Lobohalacarus} Viets 1939. Europe, South America.

1b. I-4 appreciably shorter than I-3 and I-5.

2a. Medial member of the ring of 3 setae on base of P-4 short, spine-like. \textit{Troglohalacarus} Viets 1937 Spain.

2b. All 3 setae at base of P-4 long, slender.


\textsuperscript{6} First record.
Subfamily LOHMANNELLINAE Viets 1927


1b. Internal genital suckers only. Marine or brackish water.

2a. Capitulum sometimes very long, but only 1/6 to 3/4 as wide as body. Rostrum of uniform width beyond middle, rounded terminally, not broadened (dorsal view). Marine or brackish water.
    Lohmannella Trouessart 1901; p. 190. Possibly cosmopolitan, but not yet recorded from tropical waters.

2b. Capitulum grotesquely enlarged; base of capitulum nearly, or more than half, as broad as body. End of rostrum considerably broadened, wider than middle portion of rostrum (dorsal view). Marine.
    Scaptoognathus Trouessart 1889. Ireland, English Channel, France.

Subfamily SIMOGNATHINAE Viets 1927

1a. I-6 reduced to a short clawless stump. Basal portion of I-5 more slender than distal end, widening abruptly a little beyond basal end (i.e., I-5 pedunculate). Highest portion of I-5 proximal to middle of that segment. I-5 with only slender setae. Ocular plates absent. Palpi contiguous basally. (Known from only two specimens of the genotype.)
    Acaromantis Trouessart et Neumann 1893. French Atlantic coast.

1b. I-6 with 2 heavy claws. I-5 pedunculate or not, but with highest portion of segment at, or beyond, middle. I-5 also with a heavy ventral seta at level of maximum height. Ocular plates present or absent.

2a. I-5 highest at middle of segment, so that the ventral seta does not reach as far as the claws on I-6 but would contact this segment at a point proximal to the base of claws. I-6 (including claws) slightly longer than I-5. (Known from a single female.) Profundal (1410 meters) ....
    Atelopsalis Trouessart 1896. Bay of Biscay.

2b. I-5 highest at distal end, so that the heavy ventral seta is displaced distally and is opposable to the claws on I-6 when the latter is flexed. I-6 (including claws) slightly shorter than I-5.

3a. Epimera III and IV contiguous (as seen in ventral view).

3b. Epimera III and IV separated by a thin band of striate cuticle,
    Ischyrognathus Trouessart 1900. Western Indian Ocean.

First record.
Subfamily LIMNOHALACARINAE Viets 1927*

1a. Claws on I-6 with a distal mushroom-like expansion which bears peripherally about 8 to 10 teeth directed parallel to stalk of claw (i.e., the teeth curve back sharply toward the base of the claw).... (Soldanellonyx s. lat. Walter 1917.)

2a. P-I attached proximally to P-2 in the normal manner; axis of palp not forming a right angle between P-1 and P-2. Rostrum (as seen from above) slender, conical, pointed. Palpal insertions not elevated dorsally above base of capitulum. Chelicera distinctly 2-segmented, the movable digit distinct from base of claw. I-3, I-4 and I-5 of essentially the same dorso-ventral height. Fresh water. ............... Soldanellonyx s. str. Walter 1917. Europe, North America, Java.

2b. P-1 attached basi-ventrally to P-2, so that axis of palp forms somewhat of a right angle between these two segments. Rostrum (as seen from above) wide at base and broadly triangular. Palpal insertions on tubercles which are elevated well above dorsal surface of base of the capitulum. Chelicerae dagger-like, the movable digit not distinct from the basal portion. I-3 and I-5 greatly swollen, much higher than I-4.


1b. Claws on I-6 without such a mushroom-like expansion. Claws more or less pectinate, but the pecten is a straight comb.


3b. P-3 with heavy seta disti-ventrally. Claws distinctly pectinate. (Limnohalacarus s. lat. Walter 1917.)


4b. I-5 to IV-5 each with a pair of disti-ventral, flattened, coarsely-toothed setae. P-1 as high as P-2 and oriented along the same axis (not at right angles). P-2 with a short seta disti-dorsally as well as basally.


Subfamily HALIXODINAE Viets 1927


* This is a close translation of Viets' key (1934a: 138).
* First record.
Subfamily ENTEROHALACARINAE Viets 1938

Subfamily ASTACOPSIPHAGINAE Viets 1931

SYSTEMATIC AND NOMENCLATORIAL NOTES
ON THE SUBFAMILIES AND GENERA

Porohalacarinae Viets 1933. The family Porohalacaridae of Viets has been combined with the Halacaridae, since this is a more natural arrangement than that heretofore employed. It is obvious that Porolohmannella should never be allied with Porohalacarus and at the same time separated from its direct relative, Lohmannella, for these two genera are so close that the writer does not believe the presence of external genital suckers is sufficient grounds for even a subfamilial distinction. It seems more important from a systematic standpoint to express the fundamental morphological likeness of these two genera than to point out special ecological adaptations. Accordingly, the subfamily Porolohmannellinae Viets 1933 is made a synonym of Lohmannellinae Viets 1927. Viets' distinction between Halacaridae and Porohalacaridae is, in the final analysis, strictly ecological (see Viets 1940g: 114), without regard to natural lines, and the Porohalacaridae should therefore be abandoned as a taxonomic group.

Both the subfamilies Porohalacarinae and Limnohalacarinae will require further internal reorganization as the relationships between the various genera are more clearly established and the relationships to other groups in the Halacaridae are determined. However, at present this is not possible owing to our limited knowledge of most of the genera.

Rhombognathinae Viets 1927. The revision of the Rhombognathinae is also made with a view to expressing fundamental relationships between groups of species which underlie superficial specific differences. Viets (1927a: 97–115) divided Rhombognathus Trouessart 1888 into three subgenera on the basis of claw characters: Rhombognathus s. str. Trouessart 1888 (two claws on all tarsi; type, R. notops

For several years it has been apparent that this grouping may lead to difficulty in the case of *Rhombognathus pascens* (Lohmann) 1889. *R. pascens* (= *Aletes pascens*) was described as having a median claw on only legs I and II, and it was so considered until 1935. Schulz (1935a: 86) noted in Helgoland material two specimens which had a median claw on all legs, which according to Viets’ characterization would make this a *Rhombognathopsis*. However, since the other characters indicated that these were *R. pascens*, Schulz considered them simply a variety of this species (no name was given). However, Schulz did not discuss the significance of the occupation of two subgenera by the type of *Rhombognathides*. Viets (1939c: 534) considered that Schulz actually had specimens of *Rhombognathus mucronatus*, but there seems to be no way of proving this, unless Schulz still has his specimens. Viets stated more positively (1940g: 110, footnote) “Abzustreichen ist *Rhombognathides pascens* var. Schulz 1935; es hat sich herausgestellt, dass darin *Rhombognathopsis mucronatus* Viets vorliegt.” But Viets again did not substantiate this statement in any way. However, even if it were true the other grounds for the revision of *Rhombognathides* are adequate.

The extremely close similarity between *pascens* and *seahami* is further evidence that the subdivision of *Rhombognathus* s. lat. on the basis of claw characters alone is unnatural. It is inconceivable that such similarity could have arisen by convergence of two naturally distinct groups, and it is also inconceivable that *R. seahami* could be more closely related to *Rhombognathus* (s. lat.) *armatus* than to *R. pascens*, as its present nomenclatorial position does indicate.

Finally, the present writer has found a species on the North American coast which is represented by two distinct varieties, distinguishable only on the basis of claw characters. One of these (*R. merrimani merrimani*, n. sp., n. var.) would go in *Rhombognathus* s. str.; the other (*R. m. needleri*, n. sp., n. var.) would go in *Rhombognathides* as these are now defined by Viets. This, of course, is an illogical situation.

*Rhombognathides*, as defined by Viets (1927–1940), therefore overlaps both *Rhombognathopsis* and *Rhombognathus* s. str. Even if this were not the case the subgeneric separation of certain species (including the types) of these two nomenclatorial groups is unnatural.
However, natural groups do exist within the *Rhombognathinae*. *R. pascens*, *seahami*, *trionyx*, *merrimani*, n. sp., and *mucronatus* are quite different from other species in certain respects (e.g., *notops* [Gosse], *longirostris* Trouessart and *pellatus* Viets). One fundamental difference between these two groups is the form and position of the female genital opening. In *R. pascens* this opening is terminal and ventral to the anus and is covered by a pair of heavy, cusp-like opercula. In other species the genital opening of the female is anatomically, as well as morphologically, anterior to the anus and is guarded by a pair of simple, band-like sclerites at the most. *Rhombognathus* (s. lat.) *armatus armatus*, *armatus americanus* and *nudus* differ in several respects from species of both *Rhombognathus* and *Rhombognathides*, and merit generic distinction. The species *setosus*, *levis* and *hutchinsoni*, n. sp., form a natural group which may also include *magnus*. For these reasons it is necessary and desirable to revise the *Rhombognathinae*.

This case somewhat resembles that found in a number of the Oribatoidea in which mono-, di- and tridactyle forms are found within a single species, as for example *Scheloribates praeincisus* Berlese 1910 (see Willmann 1931b: 271–272). It has long been recognized by workers in the Oribatoidea that the number of claws is completely unreliable as a generic character and that in many cases it does not have even specific value.

It appears likely that positive identification of larvae can be made on the basis of the bacillum and prebacillum, since these structures have been found constant throughout the development of the few species for which all stages are available. Observations on the condition of the genital and anal plates will probably reveal that nymphs also can be easily segregated into their proper genera. Because of the fact that all larvae and nymphs will probably be shown to be distinguishable generically, and since the various differential characters are quite fundamental, the subfamily will hereafter be considered as containing four distinct genera.

*Rhombognathus* Trouessart 1888. In this genus are retained those forms which are congeneric with the type, *R. notops*, and provisionally those which cannot yet be placed in the other genera because of inadequate descriptions. The ventral armor of the adults is completely or almost completely fused, the genital opening of the female is ventral,
and although the band-like sclerites may be relatively broad, they are not cusp-like. The deutonymph has the genital and anal plates separated. In the forms seen by the writer the carpite was (apparently) not fused to the end of the tarsus and the shaft was straight and without a moniliform structure. The end of the tarsus is without a ventral seta. The bacillum is very rudimentary on I-6 and absent on II-6; the prebacillum is very long and slender. The parambulacral setae on I-6 and II-6 are divaricate. The genital and anal plates of the nymphs are separate.

Type. *R. notops* (Gosse) 1855.

With the removal of four species to the new genus *Isobactrus*, *Rhombognathus* is now left with the following:

1. *notops* (Gosse), 1855 (genotype).
2. *magnirostris magnirostris* Trouessart 1889.
4. *magnirostris lionyx* Trouessart 1900.
5. *magnirostris praegracilis* Viets 1939.
11. *intermedius* Schulz 1933.

That the first ten of these are congeneric is certain, although the distinctions between them have not been adequate in some cases. These ten must be restudied thoroughly to determine the relative importance of the characters on which the species and subspecies are based and the degree of variability that occurs in these characters. It is most probable that some of the species are really no more than varieties of *R. magnirostris*, or that some of the latter should be considered as distinct species. The writer has seen only two of this group and cannot make any contribution to their revision.

*R. spinipes* certainly is not congeneric with the first ten. It shows characters that ally it to *Rhombognathiades* or possibly *Metarhombognathus*, but the description (based only on the deutonymph) does not
allow positive disposition of the species. It is not related to *Isobactrus levis*, nor to any other *Isobactrus*, despite the smooth claws! Viets (1933d: fig. 9a, b) showed a bacillum and a prebacillum on I-6 and a bacillum on II-6, which are relatively long.

*R. uniscutatus* shows very significant differences from the first ten. Its closest relatives lie in *Isobactrus* or *Metarhomibognathus*, but its true position is not ascertainable at present. It is not a *Rhomibognathus*.

The description of *R. intermedius* is not adequate to permit certain placing of the species. It is not clear from either the description or the figures given by Schulz just what the true structure of the ventral surface is, but Viets (1939d: 530–531) placed this species in the group with all ventral plates fused (i.e., *Rhomibognathus*). This appears logical to the present writer in view of the number and arrangement of the setae around the genital opening, which is similar to that found in species of *Rhomibognathus* and quite unlike that found in the other genera.

*Rhomibognathus magnipalpus* Viets (1928a: 13) is a lapsus calami for *magnirostris*, and hence it is a synonym of *R. magnirostris magnirostris*.

*Aletes gracilis* Lohmann 1893 is a synonym of *Rhomibognathus notops* (Gosse). The name was a provisional one to be applied in the event the Baltic form should eventually be shown to be distinct from the British form. Subsequent workers have considered them identical.

*Rhomibognathides* Viets 1927, emended. In this genus the genital opening of the female is terminal and is guarded by a pair of large, cusp-like opercula. The armor is usually heavy. The claws are angularly bent and pectinate, or scythe-shaped, and with or without accessory tooth. Two claws are present on all tarsi, or three on I and II and two on III and IV, or three claws on all tarsi. I-6 and II-6 have only the bacillum, which is long and rod-shaped and more than five times as long as thick in the forms known to the writer. In the nymphs the genital and anal plates are completely fused.

Synonym. *Rhomibognathopsis* Viets 1927 (genotypes congeneric, and *Rhomibognathides* has line precedence [Viets 1927a: 88, line 5] over *Rhomibognathopsis* [Viets 1927a: 88, line 6]).

Type. *Rhomibognathides pascens* (Lohmann) 1889, by original designation.

Eight species, one of which is represented by two varieties, can be assigned to *Rhomibognathides*. Of these *Rhomibognathides pascens*,
seahami, mucronatus, trionyx and merrimani, n. sp., are well known and adequately described. Rhombognathides exoplus has not been well described, although apparently it is a valid species; but Rhombognathides nigrescens and minutus are open to considerable question. The latter two are almost certainly not distinct species, and the recorded habitat of R. nigrescens (Crag Lake, Northumberland, England) is probably erroneous. The key given here includes the two apparently nominal species as well as the six which are valid. A separate key to the North American species is given on page 47.

1a. Lateral claws pectinate.
   2a. Fresh water. (Median claw on all legs.) Length 700μ.  
      nigrescens (Brady) 1877. England (Northumberland, Crag Lake?).

2b. Marine.
   3a. Ocular plates with 2 corneae. Minute median claw on all legs.  
      exoplus Trouessart 1901. English Channel (France).

3b. Ocular plates with 1 cornea.
   4a. Median claw on all legs, ¾ as long as lateral claws. Setae surrounding genital area of male reaching to or beyond middle of GA. A pair of setae in the membranous area between AD and PD.  

4b. Median claw on all legs, or only on I and II; only ½ as long as lateral claws. Setae surrounding genital area of male not reaching to middle of GA. All dorsal setae included within the plates.
   5a. Median claw on only legs I and II (except Schulz 1935?). Body 300–360μ long.  

5b. Median claw on all legs. Body 360–420μ long (but usually distinctly longer than pascens)  

1b. Lateral claws not pectinate; accessory tooth present or absent.
   6a. Lateral claws with accessory tooth. Known only as larva.  
      minutus (Hodge) 1863. England (Seaham Harbor).

6b. Lateral claws without accessory tooth.
Newell: The Halacaridae of Eastern North America

7a. Two cornae present. .................. *trionyx* Trouessart 1900. Tierra del Fuego; French Atlantic coast.


8a. All legs lacking median claw.

*merrimani merrimani*, new species, new variety; p. 56.

8b. Legs I and II with median claw; III and IV with only the lateral claws.

*merrimani needleri*, new species, new variety; p. 59.

*Rhomognathides minutus* (Hodge) 1863. Viets (1940g: 535) stated in his key, “5 (4). Larve! Seitenkrallen ohne Nebenzinke, sichel-förmig, ohne Kamm . . . minutus (Hodge) 1863.” But elsewhere (1927a: 107) he said, “Krallen einfach sichelförmig, ohne Kamm, mit Nebenzinke” which is correct. Hodge (1863: 11) clearly showed an accessory tooth. This species is very inadequately described, but clearly it is neither a *Metarhombognathus* nor a *Rhombognathus*, and since its claw characters do not exclude it from *Rhomognathides* it is placed in that genus.

*Rhomognathides nigrescens* (Brady) 1877. Although this has never been adequately described it apparently belongs in this genus. There is a median claw on the tarsi and the lateral claws are angularly bent and pectinate, as in *Rhomognathides pascens*, *seahami* and *mucronatus*; it is completely unlike any of the species in *Metarhombognathus*. Its true status is no clearer today than it was in 1877.

*Rhomognathides exoplus* (Trouessart) 1901. André’s redescription (1939c: 312) of this species is apparently based on a male, although his drawing leaves some doubt about this. The general facies is that of a *Rhomognathides* species, however, and it is placed in that genus. It is not related to any of the *Metarhombognathus* species.

*Rhomognathides seahami* (Hodge) 1860. Since all workers after 1889 have recognized *R. seahami* of the British Isles as identical with that of the Baltic, *Aletes triunguiculatus* Lohmann 1889 (p. 326) is a synonym of *Rhomognathides seahami*. The name was a provisional one, advanced by Lohmann to be applied to the Baltic form in the event it should prove distinct from the British form.

*Metarhombognathus*, new genus. In this genus there are three very heavy, scythe-shaped claws (in forms known at present) on all tarsi, and the median claw is nearly as heavy as the lateral claws. The
deutonymphs are more heavily armored than the adults. The genital opening of the female is subterminal and not guarded by cusp-like opercula. The epimeral plates are greatly reduced in the adult but normal in the deutonymphs. I-6 has both a bacillum and a prebacillum, but II-6 has only the bacillum; these are short and club-shaped and less than five times as long as thick. Genital and anal plates of the protonymph and deutonymph are undivided, but those of the adult are separated by a band of striate cuticle.

Type. Metarhombognathus armatus (Lohmann) 1893.

The known species of Metarhombognathus can be distinguished by the following key.

1a. Lateral claws bifurcate or trifurcate at end. Fourth pair of setae in dorsal series just in front of PD of deutonymph. . . . . . nudus (Viets) 1928; p. 62. Arctic Ocean (Kola Fjord).

1b. All claws simple and hook-like. Fourth pair of setae in dorsal series included in PD [armatus (Lohmann) 1893].

2a. PD in deutonymph extending only to level of dorso-lateral setae of PE. Seta lateral to corneae lying in the membranous area. OC separated by a space greater than width of AD . . . armatus armatus (Lohmann) 1893; p. 60. North Sea.

2b. PD in deutonymph extending beyond level of dorso-lateral setae of PE. Seta lateral to corneae lying in OC. OC separated by a space less than width of AD . . . . . . . . . . . . . . . . . . . . . armatus americanus, new subspecies; p. 60. North America.

Metarhombognathus armatus armatus (Lohmann) 1893. Rhombognathopsis mollis Viets 1927 is a synonym (see p. 60).

Metarhombognathus nudus (Viets) 1928. Rhombognathopsis conctectus Viets 1928 is a synonym (see p. 62).

Isobactrus new genus. In this genus the genital opening of the female is ventral in position, not guarded by a pair of large, cusp-like opercula, and surrounded by only three pairs of setae. The adults are more heavily armored than the nymphs, but all dorsal and ventral plates are separate; the ventral plates are greatly reduced and do not form a solid plate. Femur I is greatly swollen and is less than 1.5 times as long as high. Tarsi I and II each have a single club-like seta in front of lateral disti-dorsal seta. (The generic name indicates the contrast between this condition and that in which there are two such setae—the bacillum and prebacillum—on I, but only the bacillum on II. Of course this is not the sole character on which the genus is
The known species of Isobactrus can be distinguished by the key given below. A key to the North American species is given on page 69.

1a. Claws with a well developed comb which projects medially from the shaft of claw. (Note. When the claw is lying on its side, or somewhat obliquely, it may appear to have only an accessory tooth or even to be completely smooth.)

   setosus (Lohmann) 1889; p. 69.
   Connecticut, British Isles, French Atlantic coast, North Sea, Baltic.

1b. Claws completely smooth, or with a tooth on concave margin of claw near base (not to be confused with an "accessory tooth," which is absent).

2a. Claws with basal tooth as above. magnus (Lohmann) 1907; p. 33.
   Kerguelen.

2b. Claws completely smooth.

3a. Tarsus with a single long seta dorsally near middle of segment. Panelling very pronounced; PD with costae. hutchinsoni, new species; p. 77.
   Connecticut.

3b. Tarsus with 2 long setae dorsally near middle of segment. Panelling present but rather feebly developed; costae absent from PD.

   levis (Viets) 1927; p. 74.
   Baltic; Connecticut.

Isobactrus magnus is placed in this genus provisionally, since it appears, on the basis of Lohmann's descriptions, to agree more closely with this genus than with any of the others. It appears to be somewhat different from the other species of Isobactrus, however, although the significance of the differences cannot be evaluated at present. Lohmann's drawings clearly showed a moniliform carpite.

R. cryptorhynchus Trouessart is a synonym of R. setosus (Lohmann), according to André. See discussion, page 71.

Agae Lohmann 1889. The redefinition of Agae Lohmann 1889 by Viets (1927a: 90–95) has been reviewed several times by Viets, André, and Womersley, and therefore it need not be discussed again here, except to say that the change was fully warranted on morphological and taxonomic grounds and is accepted in the present paper.
Copidognathus Trouessart 1888. Viets (1927a: 87, 91, 144) divided Copidognathus Trouessart into two subgenera on the basis of the form of the ocular plates. Those with elongate ocular plates, often with the posterior portion caudiform, were placed in the subgenus Copidognathopsis, while the others were left in Copidognathus s. str. As is often the case with purely relative diagnostic characters of this type, it might be supposed that as more and more species became known the distinction between the two subgenera would become more and more difficult, until eventually cases would arise in which closely related species were placed in different subgenera along with forms to which they were only remotely related. Such a discrepancy appears to exist in the case of C. extensus Viets 1940 (g: 37–39) and C. pachypus, n. sp. Although these species differ in many details, they also appear to be more closely related to each other than to any other species. According to Viets’ most recent characterization of Copidognathopsis, C. pachypus seems to be more of a Copidognathopsis than a Copidognathus s. str., and yet its closest relative appears to be C. extensus. It is certain that such ambiguities will only increase in the future if the present systematic arrangement is retained. In short, the form of the ocular plates may be a useful key character, but its use as a subgeneric character is more of an impediment than an aid in the taxonomy of the group. There is no doubt that the present arrangement serves to obscure fundamental characters on which to base a division of Copidognathus. The present writer regards Copidognathopsis Viets 1927 as a synonym of Copidognathus Trouessart 1888, because the characters upon which the genotypes have been separated are inadequate.

On the other hand, there is a group of species which formerly were placed in the subgenus Copidognathopsis, but which are distinct from all other species of Copidognathus in the number of ventral setae on tibia I. The other species of Copidognathus are remarkable for the apparently absolute constancy of the number (three) and arrangement (two ventro-medial; one ventral or ventro-lateral) of the ventral setae on the first and second tibiae. But in C. arenarius, n. sp., C. submarinus, n. sp., C. gracilipes gracilipes (Trouessart) 1889, C. gracilipes quadricostatus (Trouessart) 1894 and C. gracilipes largiforatus (Trouessart) 1899 there are two pairs of ventral setae on 1-5 in both the deutonymph and the adult. These five forms are clearly more closely
related to each other than to any other species in the genus and therefore form a distinct and natural species group. All have a short, blunt rostrum which extends only a little beyond the middle of P-2, and apparently all lack rosette pores on any of the plates. The above five forms are removed to Arhodeoporus, n. subg. The name indicates the absence of rosette pores, but this is not the most important character on which the subgenus is based. Furthermore, not all "arhodeoporose" species belong here.

Werthella Lohmann 1907 is herein synonymized with Copidognathus s. str. because its type is a Copidognathus s. str. The species that have been described in the genus are also Copidognathus species. Lohmann (1907a: 390), in his diagnosis of the genus, stated (translation),

Especially characteristic of Werthella are the short maxillary palpi which are widely separated at the base by a broad epistome, but which come together over the chelicerae so that the distal ends of the thick second segments nearly, or almost nearly, touch. The body is flat and broad, the legs graceful and short. Leg I is somewhat heavier than the others, but in other respects is no different. The capitulum consists of a short, compact basal portion and a triangular, basally broadened rostrum. Palpi distinctly four-segmented, short, and heavy. Segment 2 is especially thick, but the terminal segment is nearly cylindrical, with a short, stylus-like point. Chelicerae two-segmented with a typical 'claw'. Tarsal claws attached to legs only by a 'Krallenmittelestückes'. A claw fossa is well developed.

Since the genus is obviously closest to Copidognathus it is necessary to compare it only with that genus. All but the first sentence in the above translation could be applied to any typical Copidognathus species. An examination of Lohmann's plate 31, fig. 9, shows that the chaetotaxy of I-5 is identical with that of all Copidognathus s. lat. species with the exception of C. gracilipes, arenarius and submarinus (which certainly deserve subgeneric distinction). In all species except these three, I-5 has three heavy setae on the ventral and medial surfaces, as is the case in Lohmann's species.

Turning to the characters in the first sentence of the translation, then, it is apparent that these are also inadequate to merit even subgeneric distinction for Werthella. The approximation of the palpi dorsally is shown exceptionally well (even more strikingly than in Werthella parvirostris!) in Lohmann's plate 41, fig. 1 (Copidognathus [s. str.] simonis). This condition shows up occasionally in individuals

That is, without a carpite.
of many species of Copidognathus, for example, C. (s. str.) bairdi, n. sp., and C. (s. str.) punctatissimus (Gimbel), etc. Therefore this character has no generic value, since it cannot be applied in practice even as a specific character. That leaves only the shortness of the palpi, which is quite probably as much apparent as real and in any event is only a specific character, since there are no structural changes associated with it. It is due in part to the sharply dorsad course of P-2, although the palpi apparently are really smaller than usual. However, the size of the palpi is not even a critical subgeneric character, for reduction in size could occur, and undoubtedly has occurred, at several points within the genus Copidognathus. Hence, Werthella parvirostris (Trouessart) is only a Copidognathus s. str. with relatively short palpi, and Werthella is therefore made a synonym of Copidognathus s. str.

Trouessart (1914a: 6–8) described a second species, Werthella bouvieri, in which the convergence of the palpi is completely lacking, the palpi being shown as parallel. The palpi are relatively short, but it is also apparent that the rostrum is of unusual length, it being appreciably longer than the base of the capitulum. But there are no morphological differences whatever between the capitulum of this species and that of other species of the genus Copidognathus. Therefore, Werthella bouvieri Trouessart 1914 is a synonym of Copidognathus bouvieri (Trouessart) 1914. Either Trouessart’s drawing or his measurements are inaccurate. The total length of his fig. 3 is 60 mm. (to tip of rostrum) and the width is 35 mm. (L/W = 1.71). But Trouessart’s measurements (700/350) give a ratio of 2.0—a significant difference. Other errors in the drawings are indicated by Trouessart on page 16 of his paper.

Copidognathus (s. str.) curassaviensis Viets 1936 is also a form in which the palpi are relatively small. P-3 and P-4 combined scarcely equal the length of P-2, and the rostrum extends beyond P-3. But this form is a typical Copidognathus species and there are no valid morphological grounds on which it could be removed from that genus. Viets was correct in placing it in Copidognathus.

For the same reasons outlined above, Werthella johnstoni Womersley 1937 is a synonym of Copidognathus johnstoni (Womersley) 1937. The elimination of Werthella is dictated on morphological grounds, but its elimination is also advisable for purely practical reasons, for it would be impossible to define the point which made a particular species either a Copidognathus or a Werthella. Post-mortem differ-
Simognathinae Viets 1927. As Viets has already pointed out (1927a: 95–96), the subfamily Simognathinae Viets 1927 contains four genera of uncertain relationship. This uncertainty is principally due to the rareness of their representatives. Trouessart is the only one who has done any completely original work on the genera Acaromantis, Atelopsalis and Ischyrognathus, and his descriptions are inadequate in several fundamental details, although they would permit recognition of the forms. Each of these three genera is represented by a single species and apparently by no more than two specimens of each at most. André's (1938b: 170–172) restudy of Trouessart's type specimen of Ischyrognathus coutieri still leaves much to be desired. Obviously new material is necessary. There seems to be no reason for separating it from Simognathus, either generically or subgenerically. The genus Simognathus is well known through the work of Viets (1936d, 1940g). The genus Atelopsalis, known from only a single female, is too superficially described to properly evaluate its systematic position. Trouessart's figures (drawn by Neumann), although relatively good, show considerable evidence of having been drawn from a compressed specimen. Thus the position of the attachment of the palpi may have been altered. Also, the position of the palpi is not favorable for study, so that it cannot be safely assumed that these are three-segmented, as claimed by Trouessart. Although the genera of Simognathinae appear to have (on the basis of published descriptions) certain differences, they also have several points of similarity, the relative importance of which cannot be evaluated at present. Accordingly, it is best to leave them as they now stand until further work can be done.
SUMMARY OF HALACARIDAE MURRAY 1876

Those genera or subgenera which are marked by an asterisk are known to be present in North America. A double asterisk indicates those which are herein recorded for the first time, but which, being fresh-water genera, will not be treated in detail in this paper (see keys on pages 20–25).

<table>
<thead>
<tr>
<th>Subfamilies</th>
<th>Genera</th>
<th>Subgenera</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhombognathinae</td>
<td>*Rhombognathus</td>
<td>*Halacarus s. str.</td>
</tr>
<tr>
<td></td>
<td>*Rhombognathides</td>
<td>*Thalassarachna</td>
</tr>
<tr>
<td></td>
<td>*Metarhombognathus, n. gen.</td>
<td>*Copidognathus s. str.</td>
</tr>
<tr>
<td>Actacarinae</td>
<td>Actacarus</td>
<td></td>
</tr>
<tr>
<td>Halacarinae</td>
<td>*Halacarus s. lat.</td>
<td>*Halacarus s. str.</td>
</tr>
<tr>
<td></td>
<td>*Copidognathus s. lat.</td>
<td>*Thalassarachna</td>
</tr>
<tr>
<td></td>
<td>*Agae</td>
<td>*Copidognathus s. str.</td>
</tr>
<tr>
<td></td>
<td>*Agauopsis</td>
<td>*Arhodeorhodorus n. subg.</td>
</tr>
<tr>
<td></td>
<td>Coloboceras</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Pontacarus</td>
<td></td>
</tr>
<tr>
<td>Porohalacarinae</td>
<td>**Porohalacarus</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Caspialacarus</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Lobohalacarus</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Troglohalacarus</td>
<td></td>
</tr>
<tr>
<td>Lohmannellinae</td>
<td>*Lohmannella</td>
<td></td>
</tr>
<tr>
<td></td>
<td>**Porohalacarinae</td>
<td></td>
</tr>
<tr>
<td>Simognathinae</td>
<td>Scaptognathus</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Simognathus</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ischyrogathus</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Acaromantis</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Atelopsalis</td>
<td></td>
</tr>
<tr>
<td>Limnohalacarinae</td>
<td>*Soldanellonyx s. lat.</td>
<td>*Soldanellonyx s. lat.</td>
</tr>
<tr>
<td></td>
<td>*Limnohalacarus s. lat.</td>
<td>Parasoldanellonyx</td>
</tr>
<tr>
<td></td>
<td></td>
<td>**Limnohalacarus s. str.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Stygohalacarus</td>
</tr>
<tr>
<td>Halixodinae</td>
<td>*Hamohalacarus</td>
<td></td>
</tr>
<tr>
<td>Enterohalacarinae</td>
<td>Halixodes</td>
<td></td>
</tr>
<tr>
<td>Astacopsiphaginiae</td>
<td>Enterohalacarus</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Astacopsiphagus</td>
<td></td>
</tr>
</tbody>
</table>

*Soldanellonyx* and *Hamohalacarus* were first recorded from North America (Indiana) by Walter, 1931a.
THE NORTH AMERICAN MARINE HALACARIDAE

Included here are descriptions of the genera, species, subspecies and varieties of the North American marine Halacaridae which have been taken by the writer. In some cases in which previous descriptions of the species have been adequate only the records of capture and miscellaneous notes on the anatomy are given. Keys to the North American species of the genera are provided except where only one or two are known. For definitions of the morphological terms employed, or references to labelled figures, see pages 222 to 226. The bibliographical lists contain references to only those papers which have an important bearing on the nomenclature or systematics of the genus or species involved, or in which good figures or descriptions are available, but all known synonyms of the genus or species are included.

SUBFAMILY RHOMBOGNATHINAE VIETS 1927

Diagnosis. Middle piece of claw articulating with carpite, which in turn articulates with, or is fused with, end of tarsus. Palpi very small, 4 or 3-segmented, closely appressed to sides of rostrum. All dorsal plates present and occasionally fused to form a single dorsal plate, in which case corneae are present. Predominantly marine and intertidal. Never surviving under conditions which preclude algal growth, and rarely, if ever, in fresh water. Cosmopolitan.

Genus Rhombognathus Trouessart 1888


Diagnosis. Genital opening of female ventral, not terminal, and guarded by a pair of band-like genital sclerites which may be broad but which are not cusp-like. Ventral armor of adults completely or almost completely fused. Deutonymph and protonymph with genital and anal plates separated. Carpite apparently not fused to end of tarsus (Figs. 1, 11), the shaft straight, without moniliform structure. End of tarsus lacking ventral seta. Bacillum very rudimentary on I-6 and absent on II-6; prebacillum very long and slender. Parambularal setae on I-6 and II-6 divaricate.
Type. *Rhombognathus notops* (Gosse) 1855 (= *Pachygnathus notops* Gosse 1855), by original designation.

Remarks. Neither Lohmann nor any subsequent worker designated a type for *Aletes* Lohmann 1889. Although *Aletes* is unavailable for either of the new genera of Rhombognathinae established in this paper,\(^{12}\) it is desirable to designate a type in order that its true status can be established. All writers since 1889 have listed *Aletes* Lohmann as a synonym of *Rhombognathus* Trouessart 1888. Accordingly, the present writer designates *Rhombognathus notops* (Gosse) 1855 (also type of *Rhombognathus*)\(^{13}\) as type of *Aletes* Lohmann 1888. This was the fifth species listed by Lohmann, but to name any other would introduce needless confusion, since it would invalidate all previous statements regarding the synonymic status of *Aletes* Lohmann. *Aletes* Lohmann 1889 is a synonym of *Rhombognathus* Trouessart 1888 because their genotypes are identical, and *Rhombognathus* has priority.

**Key to North American Species (Adults)**

1a. All dorsal plates separate. Base of capitulum readily visible in dorsal view and not concealed by AD. Setae postero-medially from corneae lying in CC and not in the membranous area. Each OC with 2 corneae. Claws completely smooth, without accessory tooth or fan-like lamella bearing a row of teeth along distal margin.*magnirostris* magnirostris Trouessart 1900; p. 45. North Carolina. Also Adriatic, English Channel, North Sea, Spitzbergen, Pacific-Antarctic (Macquarie Islands).

1b. As above, but claw not completely smooth, with at least one accessory tooth.

2a. Claws (ventral or dorsal view) with only one accessory tooth. PD not reaching between OC. *notops* (Gosse) 1855; p. 41. Greenland, Great Britain, Baltic, French Atlantic coast.

2b. Lateral claws (in ventral view) with a fan-shaped lamella along dorsal and inner edge of claw, which bears a row of 5 to 20 teeth along its distal margin.*magnirostris* magnirostris Trouessart 1889; p. 41. Florida; Chesapeake Bay. Also French Mediterranean, Adriatic, Black Sea, English Channel, North Sea.

\(^{12}\) The name *Aletes* was used three times prior to 1888, by F. Chapuis, 1874, Coleoptera, Chrysomelidae; C. Rafinesque, 1815, Lepidoptera, Pyralidae; P. Carpenter, 1856, Gastropoda.

\(^{13}\) According to the international rules of zoological nomenclature, types of other genera are not to be excluded from consideration in establishing the type of a genus. The present case is an example of the value of this provision in avoiding unnecessary nomenclatorial changes.
Rhombognathus notops (Gosse) 1855


Remarks. This species was reported from the west coast of Greenland by Kramer in 1897, the locality being given as Sermilik Fjord. It has not been seen by the present writer.

Rhombognathus magnirostris var. magnirostris Trouessart 1889

Figures 1–11


Specimens obtained from Florida agree more closely with descriptions of this than with the descriptions of any of the other varieties of R. magnirostris. The author has only one intact female, which is 298μ long and 197μ wide. Thus it is identical in length with R. pectinatus Viets 1936 (Caribbean Sea) and shorter than any other recorded specimens of R. magnirostris magnirostris, which range from 380 to 450μ.

Female. AD 101 x 106μ, OC 83 x 56μ, and 85 x 58μ, OC-OC 58μ, AD-PD 30μ. Membranous areas more restricted than in R. pectinatus or R. magnirostris magnirostris (as described by Viets), but less restricted than in R. magnirostris praegracilis Viets 1939. OC with 2 pairs of setae and 3 pairs of lateral pores. Two pairs of perforated
corneae present. PD with a pair of setae antero-laterally. A short and a long seta on AE just behind leg II on each side. Three lateral setae anterior to leg III, the most anterior one ventral, the second and third dorsal, and the third seta shortest. Dorsal plates with a small amount of conchoidal panelling as shown in Fig. 2.

Capitulum (Fig. 4) 79μ long to tip of rostrum and 62μ wide. Rostrum not sharply demarcated from base of capitulum. Two pairs of setae at the swollen middle of rostrum (anterior pair difficult to find). Palpi 4-segmented. Capitulum readily visible from above, the tips of palpi extending to, or a little beyond, middle of I-3 when the latter is extended anteriorly (Fig. 2). (The writer finds it impossible to interpret Viets' [1939c: 532] purely relative character “Stirnrand des Präadorsale das Capitulum fast vollig, kapuzenartig deckend,” which he uses to differentiate R. pectinatus from all other Rhombognathus species.)

Chaetotaxy of legs:

<table>
<thead>
<tr>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
</tr>
</thead>
<tbody>
<tr>
<td>d. v. l. m.</td>
<td>d. v. l. m.</td>
<td>d. v. l. m.</td>
<td>d. v. l. m.</td>
</tr>
<tr>
<td>1.</td>
<td>-</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>2.</td>
<td>1</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>3.</td>
<td>2</td>
<td>2</td>
<td>-</td>
</tr>
<tr>
<td>4.</td>
<td>2</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>5.</td>
<td>3</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>6.</td>
<td>3</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

In a female of unknown body length the following measurements were obtained:

<table>
<thead>
<tr>
<th>I+2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>Ambul.</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>30μ</td>
<td>60/34</td>
<td>26</td>
<td>48/26</td>
<td>51</td>
<td>32</td>
</tr>
<tr>
<td>II</td>
<td>30</td>
<td>63/31</td>
<td>26</td>
<td>48/25</td>
<td>51</td>
<td>32</td>
</tr>
<tr>
<td>III</td>
<td>47</td>
<td>53</td>
<td>26</td>
<td>47</td>
<td>59</td>
<td>42</td>
</tr>
<tr>
<td>IV</td>
<td>48</td>
<td>54</td>
<td>26</td>
<td>47</td>
<td>60</td>
<td>41</td>
</tr>
</tbody>
</table>

I-3 and I-5 1.77 and 1.85 times as long as high (swollen). The chaetography agrees closely with that shown by Viets (1939c: 536). Ventral and medial setae of I-5 pectinate. I-6 with bacillum greatly reduced and appearing as a mere stub; prebacillum very long and slender. Parambulacrular setae divaricate. Ventral setae absent. II-3 and II-5 2.16 and 1.92 times as long as high. II-5 and III-5 with only the medial setae pectinate. II-5 with bacillum absent;
prebacillum very long and slender; parambularcal setae divaricate. III-6 with 4 setae dorsally, rather than the 3 found on all other tarsi (shown also by Viets). The disti-dorsal setae of the tarsi show an irregular tendency to be faintly pectinate. Parambularcal setae reduced to a single rod-shaped seta medially and a spine-like seta laterally. III-5 with ventral and medial setae pectinate, as on I-5. Parambularcal setae represented by a pair of spine-like setae which may or may not be pectinate (more accurate observation not possible due to inadequate material). Claw fossa weakly developed and membranes absent. The distribution of the pectinate setae in the Florida specimens, as well as in European specimens described by Viets (1927a: 101), Trouessart (1889a: 231; “troisième article” should read “5° article”), and in R. pectinatus, is given here in tabular form (S = smooth, P = pectinate, X = no seta found in this position):

<table>
<thead>
<tr>
<th></th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>4 5</td>
<td>4 5</td>
<td>4 5</td>
<td>4 5</td>
</tr>
<tr>
<td>Ventro-lateral</td>
<td>S  P</td>
<td>S  S</td>
<td>S  S</td>
<td>S  P</td>
</tr>
<tr>
<td>Medial</td>
<td>S  P</td>
<td>S  P</td>
<td>X  P</td>
<td>X  P</td>
</tr>
<tr>
<td>Total P, Florida forms</td>
<td>0 2</td>
<td>0 1</td>
<td>0 1</td>
<td>0 2</td>
</tr>
</tbody>
</table>

Viets, 1927

<table>
<thead>
<tr>
<th></th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0 2</td>
<td>0 1</td>
<td>0 1</td>
<td>0 2</td>
</tr>
</tbody>
</table>

Trouessart, 1889

<table>
<thead>
<tr>
<th></th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
</tbody>
</table>

R. pectinatus

<table>
<thead>
<tr>
<th></th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>

Carpite long, slender, shaft not moniliform, not visibly fused to end of tarsus. Median claw absent. Lateral claws with an elaborate, fan-shaped (when seen ventrally or dorsally) expansion which bears a row of about 20 long, slender teeth along its distal margin. A second female has a narrower plate with only 10–15 teeth along the distal margin.

Evidence is shown in Fig. 11 that the carpite is attached to the end of the tarsus (or the carpal membrane), despite the fact it does not appear to be joined. All but the basal portion of the carpal membrane had been torn off, which must have occurred prior to mounting, for the claws could not be found in the glycerine mount. In addition, the writer cannot recall any case in which claws have been broken off mites while the legs were being dissected. Furthermore, two of the other posterior tarsi had been broken off near the ends prior to the
death of the mite, possibly in an encounter with an amphipod or other predator, for they showed complete healing of the injury. But in the one tarsus drawn, only the ambulacrum had been injured, and despite this injury the carpite remained attached to the tarsus. This is probably the condition in all Rhombognathinae, although the fusion of the carpite to the tarsus is apparent only in *Isobactrus*.

**Deutonymph.** Dorsal plates as in adult, but of smaller size. OC with setae nearer edge of plate, especially the anterior seta. Three pores and 2 perforate corneae present. Setae of PD at edge of plate. Epimeral plates separated by weakly striated cuticle. Setae arranged as in adult, except for those around genital opening. Genital plate (Fig. 7) with no clearly defined suckers. Two pairs of large setae and a pair of subgenital setae present. Anal plate completely separate from genital plate. Capitulum projecting to a point slightly beyond middle of I-3. Pectinate setae as in adult, but pectinations less distinct. Claws as in adult.

**Remarks.** Although the size and form of the plates would suggest this form to be identical with *R. pectinatus* Viets 1936, which was taken on Bonaire and Curacao off the Venezuelan coast, Viets' description of that form as having the capitulum almost completely concealed under the anterior end of the body makes it impossible to relate the two. Since the condition pointed out by Viets would be unique in this genus, it would be desirable to have a more exact description of the orientation of the capitulum. This condition is characteristic of *Isobactrus*, but that group is generically distinct from *Rhombognathus*.

Either there has been too little search for fundamental distinguishing characters in some of the closely related forms of this genus, or else there are none, in which case certain names must be abandoned. Probably the only way to obtain a final answer to the question of the validity of the morphological characters in this genus is by rearing isolated females in aquaria under different conditions and analyzing the distribution of these characters in the resulting progeny.

Three females taken at Solomon's Island, Maryland, key out to *R. magnirostris magnirostris* in Viets' key (1939c: 530–534), and agree with the above description in all major details except for the form of the comb on the lateral claws. This is very short in the three specimens and contains only five or six teeth. The arrangement of the pectinate setae on the legs is exactly as given for the Florida specimens. There are no pectinate setae on segment 4 of any of the legs. It
should be noted that considerable variation is found in the degree of development of the comb on the lateral claws of the Florida specimens.

**Distribution.** North America: Florida (Biscayne Bay, on Soldier's Key); Chesapeake Bay (Solomon's Island, Maryland).

French Mediterranean, Adriatic, Black Sea, French Atlantic, English Channel, North Sea (Norway).

**Rhombognathus magnirostris var. lionyx Trouessart 1900**


**Remarks.** This form is known in North America from a single deutonymph from Beaufort, North Carolina. In most features it is very similar to deutonymphs of *R. magnirostris magnirostris*, but the claws are completely smooth. The distribution of pectinate setae on the legs differs slightly from that given by Viets (1927a: 101), but since the validity of this questionable character has never been demonstrated, no new name can be given. The arrangement and form of the setae on segments 4 and 5 is as follows (S = smooth, P = pectinate, X = no seta present in this position):

<table>
<thead>
<tr>
<th></th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ventro-lateral</td>
<td>4</td>
<td>5</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
<td>Medial</td>
<td>P</td>
<td>P</td>
<td>S</td>
<td>S</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>P</td>
<td>X</td>
<td>P</td>
</tr>
<tr>
<td>Total P</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>1</td>
</tr>
</tbody>
</table>

Viets, 1927a

1 2 0 1 0 1 1 2

Viets noted a single pectinate seta on both III-5 and IV-4, but otherwise there is agreement between his specimens from the Baltic and those from Florida.

**Distribution.** North America: Beaufort, North Carolina (Piver's Island).

Southern Pacific (Macquarie Islands), Adriatic, English Channel, North Sea, Baltic, Arctic Ocean (Spitzbergen).
Genus *Rhombognathides* Viets 1927, emended


**Diagnosis.** Genital opening of female terminal and guarded by a pair of large, cusp-like opercula (the modified genital sclerites). Armor usually heavy in adult. Claws angularly bent and pectinate, or scythe-shaped and with or without accessory tooth. Two claws on all tarsi, or 3 on I-II and 2 on III-IV, or 3 claws on all tarsi. I-6 and II-6 with only the bacillum, which is long and rod-shaped and more than five times as long as thick in forms known to the writer. Genital and anal plates completely fused.

**Type.** *Rhombognathides pascens* (Lohmann) 1889 (= *Aletes pascens* Lohmann 1889), by original designation.

**Remarks.** The synonymic status of *Rhombognathopsis* is discussed in detail on pages 26 to 27, and 29.

**Key to North American Species (All Stages)**

1a. Lateral claws completely smooth, with neither accessory tooth nor pecten. Ocular plates with single cornea. ............... *merrimani* new species; p. 56.

2a. All legs lacking median claw; only lateral claws present. *merrimani merrimani* new species, new variety; p. 56.

   North America (New Brunswick).

2b. Legs I–II with median claw and lateral claws; III-IV with lateral claws. *merrimani needleri* new species, new variety; p. 59.

   North America (New Brunswick).

1b. Lateral claws pectinate. Ocular plates with single cornea.

3a. Median claw on all legs ¾ as long as lateral claws. Setae surrounding genital area of male reaching to or beyond middle of GA. A pair of setae in the membranous area between AD and PD. ....... *mucronatus* Viets 1927; p. 54.

   North Sea, North America.

3b. Median claw on all legs or only on I and II; only ½ as long as lateral claws. Setae surrounding genital area of male not reaching to middle of GA. All dorsal setae included within the plates.

**Figures 1–11.** *Rhombognathus magnirostris magnirostris* Trouessart 1889. 1 Female: I-6, ventral view. 2 Female: dorsum. 3 Deutonymph: venter. 4 Deutonymph: venter. 5 Female: venter. 6 Female: genito-anal region. 7 Deutonymph: genito-anal region. 8 Female: IV-6, outer aspect of claw. 9 Female: I-6, lateral view, ambulacrum omitted. 10 Female: II-6, lateral view, ambulacrum omitted (same scale as 9). 11 Female: III-6, ventro-medial view (same scale as 9).


*Rhombognathides pascens* (Lohmann) 1889

Figures 12–19


Female. Body 305–360μ long, 201–235μ wide (av. 326 x 213μ); L/W = 1.45–1.62 (av. 1.53), based on 10 females. AD an elongate, anteriorly rounded pentagon, the panelling usually confined to the median and antero-lateral portions of the plate; 1 pair of setae. OC four-sided, with a single cornea and 3 setae; panelling usually distributed as shown in Fig. 12. PD straight anteriorly, with sloping antero-lateral margins; elliptical posteriorly; 5 pairs of setae; panelling arranged in 3 rows as shown in Fig. 12. Membranous areas greatly reduced, lacking setae; striae distinct, parallel. In a female 325μ long the following measurements were obtained (L/W): AD 105/100; OC 75/63, and 76/63; PD 193/153μ; AD-PD 12μ, OC-OC 65μ. AE (Fig. 13) undivided, with 3 pairs of minute setae. PE with 2 pairs of setae ventrally and 1 pair dorsally. GA undivided. Genital opening


Figure 20. *Rhombognathides seahami* (Hodge) 1860. Male: genito-anal area (body 375μ long).
completely terminal, extending beyond the anal papilla and concealing the latter in ventral view. Three pairs of setae ventrally; 1 pair on anal papilla. Membranous areas greatly restricted, striate.

Capitulum (Fig. 14) rather elongate and panelled dorsally; rostrum somewhat swollen, with 2 pairs of setae ventrally. Palpi with lateral seta on P-4 greatly enlarged, flattened. In a female with a body length of 367 μ the following measurements were obtained: capitulum 72 μ long to tip of rostrum and 59 μ wide; rostrum alone 18 μ long and 12 μ wide. Legs as in R. seahami, except that there is no median claw on III-6 and IV-6.

**Male.** Body 284–340 μ long, 187–229 μ wide (av. 314 x 208 μ); L/W = 1.47–1.55 (av. 1.51); based on 10 specimens. Those from New Haven are slightly smaller than those from Woods Hole. Male somewhat more rounded posteriorly than female as a rule. Form and panelling of dorsal plates on male and female identical.

Genital area (in a specimen 360 μ long) enclosed in an unpanelled, punctate area, about 51 μ wide, in each side of which are found 14 to 17 setae. Genital opening immediately surrounded by a flask-shaped area 56 μ long and 39 μ wide, produced (as in R. seahami) by an internal thickening of the cuticle. In some specimens the “neck” of the “flask” is not distinct. Genital area placed relatively further back than in R. seahami, so that only the tip and the sides of the anal papilla are visible through the V-shaped apical notch. The differences between the genital areas of R. pascens and R. seahami seem to be largely associated with this posteriad displacement. Capitulum as in female.

**Deutonymph.** Easily recognizable by claws. Dorsum and venter as shown in Figs. 17 and 15. PD with anterior 2 pairs of setae lying in the membranous area rather than in PD as in adult. GA undivided; only 2 pairs of setae. Two pairs of genital suckers present; subgenital setae absent. All ventral setae inserted in the plates. Leg IV with 6 segments.

**Protonymph.** Resembling the deutonymph in general appearance but smaller; a single pair of genital suckers and leg IV with 5 segments. Both nymphs vary in appearance with degree of repletion. Plates not increasing in size between the molts, so that in more mature nymphs the membranous areas are relatively more extensive.

**Remarks.** This species not only resembles, but is truly related to, R. seahami (Hodge). The two species are certainly more closely related to each other than to any other species of Rhombognathinae.
It seems most unreasonable, therefore, to separate them on the basis of the median claw on III and IV, as Viets did. Therefore, *Rhombognathides* Viets 1927 is redefined to include both forms, with *R. pascens* as type.

**Distribution.** North America: Woods Hole, Massachusetts; New Haven County, Connecticut (Double Beach; Morgan Point). French Atlantic, English Channel, Ireland, North Sea, Baltic, Black Sea.

*Rhombognathides seahami* (Hodge) 1860

**Figures 20–23**


**Female.** Body 381–416µ long, 212–270µ wide (av. 397 x 260µ); L/W = 1.44–1.62 (av. 1.53); based on 10 females. Noticeably larger than *R. pascens* even macroscopically, but identical in form. Form of dorsal plates, chaetotaxy and sculpturing as in *R. pascens*, so that Fig. 12 (pascens) will also serve for the recognition of this species. Ventral surface also as in *R. pascens*. Capitulum identical with that of *R. pascens*, but larger. In a female with a body length of 395µ the following measurements were obtained: capitulum 76µ long to tip of rostrum and 63µ wide. Rostrum alone 19µ long and 14µ wide. Palpi as in *R. pascens*. Legs rough, panelled; femora I and II swollen, the ratio of dorsal length to maximum height about 1.31 and 1.43 respectively. Femora III and IV swollen, about 1.57 and 1.62 times as long as high respectively. Setae as follows (*d.* = dorsal, *l.* = lateral, *m.* = medial, *v.* = ventral):

<table>
<thead>
<tr>
<th></th>
<th><em>I</em></th>
<th><em>II</em></th>
<th><em>III</em></th>
<th><em>IV</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><em>d.</em></td>
<td><em>v.</em></td>
<td><em>l.</em></td>
<td><em>m.</em></td>
</tr>
<tr>
<td>1.</td>
<td>– – – 1</td>
<td>– – – 1</td>
<td>– – 1</td>
<td>– – –</td>
</tr>
<tr>
<td>2.</td>
<td>1 1 – –</td>
<td>1 2 – –</td>
<td>1 1 –</td>
<td>1 1 –</td>
</tr>
<tr>
<td>3.</td>
<td>3 1 – –</td>
<td>1 1 2 –</td>
<td>2 1 –</td>
<td>2 1 –</td>
</tr>
<tr>
<td>4.</td>
<td>1 1 1 –</td>
<td>1 1 1 –</td>
<td>1 1 –</td>
<td>1 1 –</td>
</tr>
<tr>
<td>5.</td>
<td>3 2 – –</td>
<td>3 2 – –</td>
<td>3 2 –</td>
<td>3 2 –</td>
</tr>
<tr>
<td>6.</td>
<td>3 1 – –</td>
<td>3 1 – –</td>
<td>4 – –</td>
<td>3 – –</td>
</tr>
</tbody>
</table>
I-3 with a finely serrate seta dorsally. I-5 with a pair of broad, very finely pectinate setae ventrally. I-6 like II-6. II-5 with only the medial member of the ventral pair pectinate, the other slender and tapering. II-6 (Fig. 21) with a single dorsal seta near middle and a pair of dorsal setae nearer the end of the segment. Just anterior to the lateral member of this pair is a long bacillum. Parambulacrals setae divaricating. Ventro-medial seta of III-5 and IV-5 rather heavy and usually faintly pectinate. III-6 with dorsal seta near middle of segment duplicated; IV-6 with the usual single seta here. Bacillum lacking. Parambulacral setae of III-6 divaricate medially; ventral member heavy, spine-like and the dorsal member long, slender, rod-like; only a single spine-like seta present laterally. On IV-6 only a pair of heavy, spine-like setae is present. (See also the discussion of the parambulacral setae of *Metarhombognathus armatus americanus*, n. subsp.). Two lateral claws and median claw on all legs (Figs. 21, 22, 23).

In a female with a body length of 416μ the following measurements were obtained:

<table>
<thead>
<tr>
<th></th>
<th>1+2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>Ambul.</th>
<th>Total</th>
<th>T/BL</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>51μ</td>
<td>71</td>
<td>30</td>
<td>55</td>
<td>55</td>
<td>30</td>
<td>292</td>
<td>.70</td>
</tr>
<tr>
<td>II</td>
<td>50</td>
<td>66</td>
<td>30</td>
<td>53</td>
<td>55</td>
<td>33</td>
<td>287</td>
<td>.69</td>
</tr>
<tr>
<td>III</td>
<td>65</td>
<td>55</td>
<td>28</td>
<td>53</td>
<td>58</td>
<td>40</td>
<td>299</td>
<td>.72</td>
</tr>
<tr>
<td>IV</td>
<td>71</td>
<td>56</td>
<td>30</td>
<td>50</td>
<td>61</td>
<td>38</td>
<td>306</td>
<td>.74</td>
</tr>
</tbody>
</table>

Male. Body 360-395μ long, 242-270μ wide (av. 371 x 261μ); L/W = 1.36-1.58 (av. 1.48); based on 10 males. Appreciably larger than male of *R. pascens*. More rounded posteriorly than female.

Genital area as shown in Fig. 20, consisting of an area of punctate cuticle 75μ wide (specimen 375μ long) in which genital opening is found surrounded by 19 to 22 setae on each side. Genital opening immediately surrounded by a flask-shaped area 77μ long and 43μ wide, apparently produced by an internal thickening of the body wall. Genital area distinctly elevated from anal area posteriorly, with a rectangular apical notch, leaving anal papilla almost completely exposed. In the latter two features, *R. seahami* appears to differ quite

---


Figure 27. *Rhombognathides merrimani merrimani* new species, new variety. Male: genito-anal area.

air of broad, I-3 with only slender and middle and a

est anterior to Parambophi

(i rather heavy near middle of rear. Basilarly; ventral

cluded only in IV-6 only in discussion of

tax americanus legs (Figs. 2, 3.

Measurement

Tarsus 7.25
295 70
297 80
299 70
300 70
301 70

I in 261.3), IV is
likely larger than
male

area of peritoni

tinal opening

bental opening

and split with the body wall

tergally, with a

pletely on

to differ spn

s 1. middle

armative; soleral

middle area
consistently from *R. pascens*. One *R. seahami* male was found in which the genital area is displaced far posteriorly as in *R. pascens*, but the apical notch is rectangular (not V-shaped) and it is otherwise clearly recognizable as a male of *R. seahami*.

**Remarks.** A comparison of figs. 22 and 28 in Viets (1927b: 11, 13) would indicate an appreciable difference in the relative extent of the membranous areas and plates in *R. pascens* and *R. seahami*. *R. seahami* (female dorsum) is shown as having relatively wide spaces between the plates, such as one would find in a deutonymph (although it is obvious that Viets’ figure was not drawn from a deutonymph, as indicated by the positions of the dorsal setae), or in an extremely replete female. Lohmann (1889a: figs. 64, 88) showed no such difference in the extent of the membranous areas. Lohmann’s fig. 88 (dorsum of *R. seahami*) was drawn from a male, but Lohmann did not state which sex of *R. pascens* he illustrated by his fig. 64; since he had both males and females of this species, no assumption would be safe. But his figs. 64 and 88 could very well represent the same species, showing that Lohmann’s specimens of *R. pascens* and *R. seahami* were as similar in dorsal view as those seen by the writer in North America. As pointed out above, a drawing of either species in dorsa view could serve for the other as well.

**Distribution.** North America: Woods Hole, Massachusetts. French Atlantic, English Channel, Ireland, North Sea, Shetland Islands, Baltic.

*Rhombognathides mucronatus* (Viets) 1927

Figures 24–26


The writer has taken this species from three localities and has only two males and a few nymphs. It is easily identified, however. Its claws, the weakly developed panelling and the presence of one of the pairs of dorsal setae in the membranous area provide sharply defined diagnostic characters to differentiate it from *R. pascens* and *R. seahami*, to which it is most closely related. Viets (1927a: 114) figured the
female dorsum, the male GA, chelicera, palp, and tarsi I to IV, as well as (1927b: 15) the male dorsum and male and female venters.

**Adult.** Body 430μ long (Viets: 450μ). Dorsal plates somewhat less extensive than in *R. pascens*, with a pair of setae in the membranous area between AD and PD. The homologues in *R. pascens* and *R. seahami* are included in PD. OC each with 3 setae and 2 corneae, the posterior cornea extremely rudimentary and possibly occasionally absent. Dorsal plates with panelling weakly developed as a rule, finely and densely porose. Female with membranous areas more extensive (at least in gravid females) than in male; AD and PD separated by a distance as great as, or greater than, length of OC. Male, and perhaps young females, with AD and PD separated by a distance less than length of OC.

Ventral plates finely and densely porose, but panelling invisible at low magnifications (150x), and only faintly visible along sides of plates at higher powers (645x). In *R. pascens* and *seahami* the panelling is readily visible even at 50x. Female with genital opening terminal, guarded by cusp-like opercula (Viets 1927b: 15). Male GA with flask-shaped area greatly elongate, extending well beyond middle of plate and surrounded by from 30 to 35 slender setae. Apical notch not developed. Three pairs of genital suckers (Fig. 26).

Chaetotaxy of legs as in *R. seahami*. Ventral seta of 1-4 faintly pectinate. Both ventral setae on III-5 may be pectinate rather than just the medial one. Otherwise the pectinate setae are as described for *R. seahami*. Bacillum, prebacillum and parambulacral setae of all legs morphologically identical with those of *R. seahami, pascens* and *merrimani*. Carpite typical for the genus. All legs with a pair of angularly bent, pectinate claws, and with a median scythe-shaped claw at least \( \frac{3}{4} \) as long as lateral claws (Fig. 25).

**Deutonymph.** Easily recognizable by claw characters. OC with 3 setae and 2 corneae as in adult. Two pairs of setae between AD and PD as in nymphs of *R. seahami, pascens* and *merrimani*. All legs with 6 segments. GA undivided, with 2 pairs of genital suckers.

**Protonymph.** Also recognizable by claw characters. OC with 3 setae and a single cornea. Leg IV lacking basifemur. GA undivided, 1 pair of genital suckers. Nymphal plates not showing an increase in size except at time of molt.

**Remarks.** The position and form of the female genital opening, the form of the male genital area, the chaetography of tarsi I and II,
the presence of an undivided GA in both nymphal instars, and the nonisometric growth of the plates in relation to the growth of the body of the nymphs show beyond doubt that *R. pascens, seahami, merrimani*, n. sp., and *mucronatus* form a natural genus. All the characters listed are common to all these species and contrary to those found in *Metarhombognathus*, n. gen. Therefore, *R. mucronatus* and *R. seahami* must not be separated from the other species on the single superficial character of the median claw on all legs; nor can they be allied with such forms as *Metarhombognathus armatus* from which they differ in many fundamental details.


*Rhombognathides merrimani*, new species

Figures 27–35

This species is represented by two distinct varieties differing principally in the number of claws. *R. merrimani* var. *merrimani* has two claws on all legs. *R. merrimani* var. *needleri* has three claws on I and II, but only two on III and IV. In the author's collection, there are more of the 3–3–2–2 variety than of the 2–2–2–2 variety.

*Rhombognathides merrimani*, new species, *merrimani*, new variety

*Female.* Body 319–346μ long, 194–215μ wide; L/W = 1.56–1.70; based on 4 specimens. In a specimen 322μ long the following measurements were obtained (L/W): AD 100/80, OC 75/63 and 76/66, PD 203/136; AD-PD 10μ, OC-OC 58μ.

AD slightly conical anteriorly; capitulum projecting somewhat so that the palpi and a portion of the base are clearly visible from above. AD rounded posteriorly, with a pair of setae just anterior to the middle. OC four-cornered, the margins nearly straight; single cornea present. Three setae and a pore present as shown in Fig. 28. PD extending to middle of OC; anterior margin straight; antero-lateral margins straight or slightly concave; posterior half of PD elliptical, not concealing the anus; 5 pairs of setae. All dorsal plates densely punctate, the panelling feebly developed and distributed as shown in Fig. 28. PD with a central panelled area which is 4 panels wide; lateral areas 2 to 3 panels wide. Membranous areas greatly reduced; striae feebly developed or absent. The inclusion of all the dorsal setae within the dorsal plates
emphasizes the relative extensiveness of the plates. Epimera I and II (Fig. 34) completely fused medially. AE usually (but not always) somewhat more rounded posteriorly than in male; PE with 2 pairs of setae ventrally and 1 pair dorsally. GA nearly straight anteriorly. Genital opening extending to end of body, covered by a pair of opercula, the posterior ends of which are directly ventral to the tip of the anal papilla. GA with 3 pairs of setae. All ventral plates densely porose; panelling feebly developed, and sometimes absent on AE.

**Male.** Body 312–325µ long, 201–211µ wide, L/W = 1.48–1.58; based on 3 specimens. Dorsoventrally described for female. Opposing margins of AE and GA usually straighter (less convex) than in female. GA with 19 to 22 setae on each side as shown in Fig. 27. Cuticle densely porose, panelling indistinct and limited to margin of half the shield as a rule. Genital opening further anterior than in female and guarded by 2 pairs of setae.

Capitulum (in a male 321µ long) 64µ long; rostrum 19.5µ long and 10µ wide, bearing the usual 2 pairs of setae. Base of capitulum 57µ wide, globular in form, strongly sculptured dorsally, heavily punctate ventrally. Palpi extending beyond tip of rostrum. The drawing (Fig. 35) was made from a specimen in which the ventral margin is inclined ventrad at an angle of about 18°. In other specimens the capitulum appears to be somewhat more conical, probably because it is more nearly horizontal.

Legs with setae as follows (d. = dorsal, v. = ventral, l. = lateral, m. = medial):

<table>
<thead>
<tr>
<th></th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
</tr>
</thead>
<tbody>
<tr>
<td>d.</td>
<td>v.</td>
<td>l.</td>
<td>d.</td>
<td>v.</td>
</tr>
<tr>
<td>1.</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>2.</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>3.</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>4.</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>5.</td>
<td>3</td>
<td>2</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>6.</td>
<td>3</td>
<td>1</td>
<td>4</td>
<td>3</td>
</tr>
</tbody>
</table>

I-1 with very fine medial setae; I-5 with ventral setae flattened and pectinate like medial seta on II-5. I-6 with 3 setae dorsally in addition to the long bacillum at base of ambulacrum. Parambularal setae divaricate; a single spine ventral to base of ambulacrum. II-5 with only the medial member of ventral pair pectinate. II-6 resembling I-6. Tarsi I and II with a median claw which is of the same
This respects the following:

- Figure 37: Slightly different in shape.
- Figures 38 and 39: Ventral view shows variations in appearance.
- Figures 40 and 41: Same as above, but from a different angle.
- Figures 42 and 43: Ventral view with a notable feature.

Chaeomolg (P. calmolge) is followed by:

Proto... with on...
form as lateral claws but somewhat smaller; lateral claws completely smooth (Fig. 30). III-5 with medial member of ventral pair pectinate, as on II-5; the other one very minute, simple. III-6 with 2 pairs of setae dorsally. Claws slender, scythe-shaped, without comb or accessory tooth. Lengths of leg segments as given below for R. m. needleri. Parambulacral setae identical morphologically with those of R. seahami, mucronatus and pascens, and also Metarhombognathus armatus americanus.

**Deutonymph.** Easily recognizable by claw characters and sculpturing. Dorsal plates (Fig. 29) less extensive than in adult; PD with only the 3 posterior pairs of setae; the 2 anterior pairs in the membranous area. GA with only 2 pairs of setae and 2 pairs of suckers; subgenital setae absent. Genital and anal portions separated by a delicate transverse line which does not appear to divide the plate. In young deutonymph, all plates are very close together, as in adult.

**Protonymph.** Also easily recognized by claws and plates. Leg IV with only 5 segments.

*Rhombognathides merrimani,* new species, *needleri,* new variety

This variety is identical with *R. m. merrimani,* n. sp., n. var., in all respects except the claws and cuticular characters, so that Figs. 27 to 35 suffice for this variety also. The cuticle of *R. m. merrimani* appears to be slightly darker (perhaps thicker) and the punctations and paneling are slightly more distinct.

Chaetotaxy of legs as described for *R. m. merrimani.* Legs III and IV longer than I and II. In a female with a body length of 332 μ the following leg measurements were obtained (dorsal length in μ).

<table>
<thead>
<tr>
<th></th>
<th>1+2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>Ambul.</th>
<th>Total</th>
<th>T/BL</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>35μ</td>
<td>68</td>
<td>23</td>
<td>51</td>
<td>37</td>
<td>35</td>
<td>249</td>
<td>.75</td>
</tr>
<tr>
<td>II</td>
<td>32</td>
<td>61</td>
<td>23</td>
<td>50</td>
<td>45</td>
<td>33</td>
<td>244</td>
<td>.74</td>
</tr>
<tr>
<td>III</td>
<td>53</td>
<td>50</td>
<td>22</td>
<td>45</td>
<td>56</td>
<td>37</td>
<td>263</td>
<td>.79</td>
</tr>
<tr>
<td>IV</td>
<td>50</td>
<td>51</td>
<td>23</td>
<td>51</td>
<td>56</td>
<td>35</td>
<td>266</td>
<td>.80</td>
</tr>
</tbody>
</table>


Figure 31. *Rhombognathides merrimani needleri* new species, new variety. Male: I-6, ventral view.


Trouessart (1901c: 152) said (author’s translation):

Most noteworthy are (1) the claw structure: middle piece of claw drawn out into a long slender claw nearly like the lateral claws; and (2) the characteristic structure of the dorsal plates: closely spaced, nearly circular panels with somewhat elevated, wall-like margins. Large genito-anal plate present. Capitulum 80 long, body 300 long ventrally; total length 380. Form of body plump, legs very heavy, posterior end broadly rounded.

Trouessart (1901c: 152) said (author’s translation):

Remarks. This species is closely related to Rhombognathides trionyx (Trouessart) as described by André (1939c: 310–312). The principal differences are the possession by R. merrimani of a single cornea instead of two; and the large setae on I-5 of R. trionyx are smooth and not feathered. Certain differences in the chaetotaxy of the ventral plates may also exist, judging from André’s illustration, but this is not certain.

Distribution. Both varieties have the same type locality: St. Andrews, New Brunswick. They have not been taken elsewhere.

Genus Metarhombognathus, new genus

Diagnosis. Three very heavy scythe-shaped claws (in forms known at present) on all tarsi; median claw nearly as heavy as lateral claws. Genital opening of female subterminal and not guarded by cusp-like opercula. I-6 with bacillum and prebacillum; II-6 with bacillum only; these are short and club-shaped and less than five times as long as thick. Deutonymphs more heavily armored than adults. Epimeral plates greatly reduced in adult but normal in deutonymph. Genital and anal plates of protonymph and deutonymph undivided but those of adult separated by band of striate cuticle.

Type. Metarhombognathus armatus (Lohmann) 1893 (= Rhombognathus armatus Lohmann 1893).

Remarks. Only one North American form is known, Metarhombognathus armatus americanus, new subspecies.

Metarhombognathus armatus armatus (Lohmann) 1893

Lohmann (1893a: 18) described this form briefly in a footnote, but the description was incomplete because Lohmann had only deutonymphs (although on page 42 he noted that he found a mature individual in August). A free translation of the principal points in Lohmann’s description is as follows:

Most noteworthy are (1) the claw structure: middle piece of claw drawn out into a long slender claw nearly like the lateral claws; and (2) the characteristic structure of the dorsal plates: closely spaced, nearly circular panels with somewhat elevated, wall-like margins. Large genito-anal plate present. Capitulum 80 long, body 300 long ventrally; total length 380. Form of body plump, legs very heavy, posterior end broadly rounded.
Viets (1927a: 108–111) described carefully the deutonymph of *Rhombognathopsis armatus*, based on material from Helgoland, and also described as new *Rhombognathopsis mollis*, based on males and females taken at the same places where *armatus* was found. The chief differences between *armatus* Lohmann and *mollis* Viets 1927 are in the degree of development of the armor, which in *armatus* is heavy, extensive, and deeply sculptured and in *mollis* greatly reduced and without sculpturing except on the minute post-dorsal plate. The dorsal plates of *mollis* are greatly reduced and the ocular plates are virtually absent. Because of these differences, Viets considered these two forms (one known only from the deutonymph, the other from the adult) as separate species.

However, observations of the author show that *mollis* is identical with *armatus*. These observations have been made on a form which is beyond any doubt a subspecies of *armatus* Lohmann and which is similar to the latter in virtually all respects except the degree of development of the deutonymphal armor. The adults are very weakly armored as in *mollis* Viets. Conclusive evidence of the relationship between these two instars was obtained by dissecting an adult from a quiescent deutonymph (Slide 43-177-75b). Even before this, however, convincing circumstantial evidence of the identity of the two was obtained. Both the deutonymph and adult are very common on the Connecticut coast; these are the only two forms with three heavy, smooth, scythe-shaped claws. Considering the extent of the collections made, it is virtually impossible that two such abundant forms could coexist with one being known only as the deutonymph and the other only as the adult. The two forms displace each other seasonally, the heavily armored nymphs appearing from May to December and the adults from December to June. Viets (1927a: 160) recorded "*mollis*" only in spring collections and *armatus* only in summer collections, which corresponds exactly with the situation in the North American subspecies. Also, many adults are found which have traces of the heavy nymphal panelling on the ocular plates. Although the writer has never seen specimens of the European form, there is no
doubt that the situation in the European subspecies is identical with that in the American subspecies. Therefore: *Metarhombognathus armatus* (Lohmann) 1893 (= *Rhombognathus armatus* Lohmann, = *Rhomognathopsis mollis* Viets 1927).

The only question remaining is, why did Trouessart report the adult of *armatus* Lohmann as being heavily armored, with the plates joining completely? It seems possible that the very weakness of the plates, rendering their limits indistinct, caused Trouessart to consider the dorsal plates as continuous; but there is no three-clawed halacarid yet known in which the latter condition exists. It is also possible, of course, that Trouessart had another species.

As Viets pointed out, a reduction in the armor plates at the molt would be unique in a halacarid; therefore one can appreciate Viets' reluctance to accept the adults of this species as being derived from the heavily armored deutonymphs which Lohmann called *armatus*. It is ironic that the most weakly armored of all Rhombognathinae should be named *armatus*.

**Distribution.** North Sea; French Atlantic (?).

**Remarks.** *M. nudus* (Viets) 1928 and *Rhomognathopsis contectus* Viets 1928 provide a case parallel to that of the above two subspecies. These were taken at the same place (Murmansk coast, Kolafjord, at the north end of Olenij Island, on *Diploderma*, July 19, 1924). Considering the close similarity between the weakly armored *M. nudus* and adults of *M. armatus*, and between the heavily armored *R. contectus* and deutonymphs of *M. armatus*, there is no doubt that *contectus* is a synonym of *nudus* (which was named and described first). Here again, without direct evidence, there is the very strong suggestion from the abundance of the two forms that they are adult and deutonymph of the same species. Viets (1928: 83) described both as "zahlreich." It is highly improbable that two extremely closely related forms (as shown by the unique structure of the lateral claws) could occupy the same habitat, both forms being numerous, and yet one be known only as the adult and the other only as the deutonymph. But the most convincing evidence is the obvious close phylogenetic relationship between *M. nudus* and *M. armatus americanus*, n. subsp., in the latter of which the conspecificity of the adult and deutonymph has been conclusively demonstrated.
Metarhombognathus armatus americanus, new subspecies

Figures 36–53

Male. Body 350–450μ long. Similar to M. armatus armatus Lohmann in most respects, but somewhat smaller. In one male 405μ long and 285μ wide the following measurements were obtained (L/W): AD 100/80, OC 52/45, PD 103/93μ. AD pyriform, with panelling only on small posterior portion; 2 heavy setae present. OC reduced to a small oval area containing 2 corneae and surrounded by a punctate area which may include a few shallow panels. One small seta lateral to corneae and 1 at posterior end of plate. PD faintly panelled except on the 2 longitudinal costae; 3 pairs of setae included in the plate. AE with right and left sides separated by a wide interval as in M. armatus armatus. GA very feebly developed but large, consisting of a broad elliptical area in which striations are lacking; chaetotaxy only slightly different from that of the European form as figured by Viets. Chelicera 93μ long, apparently somewhat more curved than in the European form, and with a more slender claw 22μ long. Palpi and legs as in female.

Female. Somewhat larger than male, at least in spring when the abdomen is filled with eggs; 350–550μ long. Dorsal plates comparable in form and size to those of male. In a specimen 415μ long the following measurements were obtained (L/W): AD 100/75, OC 50/42, PD 98/93μ. Ventral surface as in M. armatus armatus. Distinct plates lacking in genital and anal areas, but striae completely absent from these portions. Genital and anal portions separated by a narrow band in which striae run transversely. The enclosed areas are neither panelled nor punctate. A single pair of setae lies antero-laterally in genital area; 2 pairs in anal area.

Chelicerae as in male. Capitulum 71–75μ long and 75–79μ wide. Rostrum virtually absent, represented only by a short, truncate cone which is excavated at the tip. A pair of small setae at base of cone and a pair of minute, spine-like processes near tip. Pharynx long, narrow; pharyngeal plate without panels. Palpi 45μ long. P-2 30μ long and 16μ high. P-3 and P-4 fused, forming a 3-segmented palp. P-2 with a long dorsal seta slightly beyond middle. Terminal segment with heavy seta projecting ventro-laterally. Terminal structures difficult to interpret except in a favorable terminal view (Fig. 50)
in which a dorso-median seta and 2 heavy lamellar structures can be
discerned as in Rhombognathides (Viets) 1927. The outer lamella
extends very slightly beyond the slender tip of the palp; the inner
lamella does not reach to the tip. Chaetotaxy of legs as follows:

<table>
<thead>
<tr>
<th></th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
</tr>
</thead>
<tbody>
<tr>
<td>d. v. l. m.</td>
<td>d. v. l. m.</td>
<td>d. v. l. m.</td>
<td>d. v. l. m.</td>
<td></td>
</tr>
<tr>
<td>1.</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>2.</td>
<td>1</td>
<td>--</td>
<td>1</td>
<td>--</td>
</tr>
<tr>
<td>3.</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>4.</td>
<td>2</td>
<td>--</td>
<td>1</td>
<td>--</td>
</tr>
<tr>
<td>5.</td>
<td>3</td>
<td>2</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>6.</td>
<td>3</td>
<td>--</td>
<td>1</td>
<td>--</td>
</tr>
</tbody>
</table>

In one female (of unknown body length) the following measure-
ments were obtained:

<table>
<thead>
<tr>
<th></th>
<th>I+2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>Ambul.</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>61μ</td>
<td>69/71</td>
<td>39</td>
<td>54</td>
<td>71</td>
<td>50</td>
<td>344</td>
</tr>
<tr>
<td>II</td>
<td>62</td>
<td>69/65</td>
<td>41</td>
<td>53</td>
<td>75</td>
<td>53</td>
<td>353</td>
</tr>
<tr>
<td>III</td>
<td>89</td>
<td>62/53</td>
<td>36</td>
<td>55</td>
<td>81</td>
<td>59</td>
<td>382</td>
</tr>
<tr>
<td>IV</td>
<td>94</td>
<td>66/55</td>
<td>38</td>
<td>57</td>
<td>83</td>
<td>63</td>
<td>401</td>
</tr>
</tbody>
</table>

Trochanter and femur of all legs hirsute, especially dorsally; femur
greatly swollen. Femora I-IV 0.97 (higher than long), 1.06, 1.17 and
1.20 times as long as high. All tibiae with 3 setae dorsally, one of
which is very slender, and with a very heavy seta ventrally and another
ventro-medially; the latter sometimes faintly pectinate (oil immersion).
Ventral setae of III-5 and IV-5 completely ventral, not as heavy as
those on I-5 and II-5 and apparently always smooth. I-6 and II-6
with 3 setae dorsally and a heavy ventral seta closely applied to disti-
ventral margin of tarsus. Tarsi with claw fossa. Claws scythe-
shaped and without accessory tooth. Under oil immersion a rough-
ened ridge can be seen along the outer side of the lateral claws near the
convex margin; this appears to represent a crude comb. Median claw
scythe-shaped, nearly as large as lateral claws and completely smooth.
At the base of the median claw is a thin keel (Figs. 45, 46), which is
somewhat larger on leg IV than on leg I.

Deutonymph. 320μ long just after emergence from protonymphal
exuvium, but attaining a length of 440μ or slightly greater. Adults
upon emergence noticeably smaller than deutonymphs. The general
appearance of the nymph does not change during this instar despite
the considerable increase in length, for growth of the various parts of
the body, at least the legs and plates, is isometric. Dorsal plates very
extensive, heavily panelled and thick; panels not angular, but consist­
ing of deep circular pits. AD roughly hexagonal, distinctly concave
posteriorly and bearing the usual pair of setae. OC five-sided; 2
corneae on each plate. The usual setae are present, but whereas in
the protonymph (and occasionally in the adult) the post-ocular seta
is in the membranous area just behind OC, in the deutonymph it is
near the center of the plate. PD with 4 heavy longitudinal ridges in
which panelling is lacking. Four pairs of setae included in plate, the
2 anterior pairs of which are found in the membranous area in both
protonymph and adult. Posterior end of plate distinctly excavated
and flattened, projecting beyond end of the body in such a way as
to conceal the setae which are readily visible at end of abdomen in
adult. Dorsal membranous areas greatly reduced and heavily striate,
even in old deutonymphs. Owing to encroachment of the dorsal
plates, only 2 pairs of setae are found here. In a specimen with a body
415µ long and 275µ wide the following measurements were obtained
(L/W): AD 113/108, OC 118/93, and 108/85, PD 290/235, AE 98, GA
148/86µ.

Ventral surface also with plates more extensive than in M. armatus
armatus. AE with right and left halves fused, not divided as in proto­
nymph and adult. Lateral portions of PD visible ventrally. GA
well developed and undivided, with 2 internal suckers present. Setae
as in M. armatus armatus; subgenital setae absent. Panelling usually
limited to lateral portions of PE and GA. Legs heavy, as in adult,
but claws shorter, relatively heavier, the median claw lacking small
keel at base. Chaetography of legs identical with adult in all respects
except that IV-2 lacks the dorsal seta and IV-3 lacks the ventral seta.
Parambulacral seta of III-6 divaricate laterally but reduced to a single
member medially.

*Protonymph.* Body 270–320µ long; about 0.8 as broad as long.
Dorsal plates greatly reduced as in adult. OC variable in shape, usu­
ally rounded; single cornea present. Dorsal setae as in adult. Ventral
plates greatly reduced; AE divided into right and left halves; a single
pair of genital suckers. Panelling developed only on dorsal plates,
of same type found in adult. Tarsi with 3 simple claws. Chaetog­
raphy of tarsi identical with that in adult.
Bacillum and Prebacillum

The diagram shows various anatomical features of Bacillum and Prebacillum. The illustrations include views of the head, eyes, and other parts of the organism. The labels indicate specific parts and features, such as eyes (labeled as 40, 41, 42), head (labeled as 43, 44, 45, 46), and other anatomical structures.

The diagram is likely from a scientific publication, possibly related to the Bingham Oceanographic Collection, as indicated by the text "Bulletin of the Bingham Oceanographic Collection."
Remarks. This subspecies differs from *M. armatus armatus* Lohmann chiefly in the extent of the plates. The plates of the deutonymph are considerably more extensive than is the case in *M. armatus armatus*. In the latter, PD extends just to the level of the dorsal seta of PE, whereas in *M. armatus americanus* PD extends appreciably beyond this point. According to Viets' fig. 28 (1927a: 109), the seta lateral to the corneae lies outside OC, whereas in *M. armatus americanus* it has been found invariably within OC. The medial margin of OC in *M. armatus armatus* is nearly straight, not quite reaching to the line which could be drawn between the anterior seta of the membranous area and the anterior seta of PD; in the new subspecies, OC always exceeds this line and is convex medially. This difference is not associated with the degree of repletion of the nymph, as is the case in all *Rhombognathides* and *Rhombognathus* species, for as pointed out above, the growth of the plates is isometric with respect to the body as a whole. Therefore, young deutonymphs are not relatively more heavily armored than deutonymphs which are quiescent just prior to the final molt. This is unique in the Halacaridae.

The chaetotaxy of the tarsus of this subspecies is of great interest in the morphology of the tarsus of Halacaridae. On I-6 (Fig. 47), just anterior to the lateral member of the disti-dorsal pair of setae, are two setae of slightly different form. The more proximal one (bacillum) is 4.0 to 4.5μ long and has a stalk about half as long as the swollen outer portion of the seta. This is certainly homologous with the bacilliform seta which occupies a corresponding position in other Halacaridae [e. g., *Rhombognathides seahami* (Fig. 22) and *Copidognathus* (s. str.) *punctatissimus* (Fig. 207)]. Anterior to the bacillum is a seta with a relatively shorter stalk, 6.0 to 6.5μ long (prebacillum). The prebacillum is lacking on II-6 and both setae are absent from III and IV. This subspecies also provides convincing evidence of the true homology existing between the parambulacral setae of all the legs. On legs I and II these are divaricate; that is, they consist of a dorsal and a ventral member arising from a single opening in the wall of the

Genus *Isobactrus*, new genus

**Diagnosis.** Genital opening of female ventral in position, not guarded by a pair of large, cusp-like opercula and surrounded by only 3 pairs of setae. Adults more heavily armored than nymphs; all dorsal and ventral plates separate. Ventral plates greatly reduced and not forming a solid shield. Femur I greatly swollen, less than 1.5 times as long as high. Tarsi I and II each with a single club-like seta in front of lateral disti-dorsal seta. Two claws on all tarsi of known forms.

**Type.** *Isobactrus setosus* (Lohmann) 1889 ( = *Aletes setosus* Lohmann 1889).
KEY TO NORTH AMERICAN SPECIES (ADULTS)

1a. Claws with a well developed comb which projects medially from shaft of claw.  
(Note. When the claw is lying on its side, or somewhat obliquely, it may appear to be completely smooth or to have only an accessory tooth.)

I sobactrus setosus (Lohmann) 1889; p. 69.  
Connecticut, British Isles, French Atlantic coast, North Sea, Baltic.

1b. Claws completely smooth, lacking even an accessory tooth.

2a. Tarsus with single long seta dorsally near middle of segment. Panelling very pronounced (in Hyrax or glycerine); PD with costae.

hutchinsoni new species; p. 77.  
Connecticut.

2b. Tarsus with 2 long setae dorsally near middle of segment. Panelling present, but rather feebly developed; costae absent from PD.

levis (Viets) 1927; p. 74.  
Baltic; Connecticut.

I sobactrus setosus (Lohmann) 1889

Figures 54–70


Female. Body 294–395 \( \mu \) long, 208–284 \( \mu \) wide, L/W = 1.32–1.49 (av. of 11 specimens, 344 x 242 \( \mu \), L/W = 1.42). In a female 395 \( \mu \) long (longest measured) the following measurements were obtained: AD 138 x 173 \( \mu \), OC both 66 \( \mu \) long (true width not discernible because of lateral position), PD 201 x 193 \( \mu \), AD–PD 95 \( \mu \), OC–OC 188 \( \mu \). In a female 294 \( \mu \) long (shortest measured) the following were obtained: AD 108 x 133 \( \mu \), OC 50 and 46 \( \mu \) long, PD 166 x 166 \( \mu \), OC–OC 139 \( \mu \). As the specimen is somewhat distorted, AD–PD can not be measured.

The dorsal plates appear to be somewhat more extensive in the North American form than in the European forms, but they are also quite variable. The general appearance of the mite can be greatly influenced by the amount of compression it undergoes while being mounted, and by the degree of repletion (compare Fig. 54 with 57).
Dorsal plates faintly panelled. PD only rarely showing a faint interruption of the panels in the region occupied by the costae of other species; true costae are never developed. Epimera I and II of opposite sides completely separated by the striated membranous area. Plates I and II on each side are fused along their adjoining surfaces, but I is divided into a broader anterior portion (bearing the first seta) and a narrower posterior portion which is fused with II along its entire posterior margin. Epimeral plates III and IV separated by a narrow band of striate cuticle. Anal plate extremely small, pyriform, sub-terminal. Setae anterior to first genital sucker apparently internal rather than external. Only 2 pairs of internal suckers are in such a position as to be evident in ventral view, as a rule, since the third pair is usually obscured by the posterior pair of internal spines (but see Figs. 59, 60).

Capitulum completely concealed in dorsal view (Fig. 63). Palpi clearly four-segmented, but all segments very short. Capitulum 64 μ long (when seen horizontally) and 70 μ wide. Rostrum alone 30 μ long and 14 μ wide; swollen at middle and bearing 2 pairs of setae. Pharyngeal plate without panels, but with 7 to 9 tendon-like apodemes inserted on each side of mid-line.

Chaetotaxy of legs as follows:

<table>
<thead>
<tr>
<th></th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>d. v. l. m.</td>
<td>d. v. l. m.</td>
<td>d. v. l. m.</td>
<td>d. v. l. m.</td>
</tr>
<tr>
<td>1</td>
<td>— — 1</td>
<td>— — 1</td>
<td>— 1 —</td>
<td>— — —</td>
</tr>
<tr>
<td>2</td>
<td>1 1 —</td>
<td>1 1 —</td>
<td>1 1 —</td>
<td>1 1 —</td>
</tr>
<tr>
<td>3</td>
<td>2 1 1 —</td>
<td>2 1 1 —</td>
<td>2 1 —</td>
<td>2 1 —</td>
</tr>
<tr>
<td>4</td>
<td>1 1 1 —</td>
<td>1 1 1 —</td>
<td>1 1 1 —</td>
<td>2 1 —</td>
</tr>
<tr>
<td>5</td>
<td>1 1 2 1</td>
<td>1 1 2 1</td>
<td>2 1 1 1</td>
<td>2 1 1 1</td>
</tr>
<tr>
<td>6</td>
<td>3 — — —</td>
<td>3 — — —</td>
<td>3 — — —</td>
<td>3 — — —</td>
</tr>
</tbody>
</table>

In a female of unknown body length the following measurements were obtained (for I-3, I-5, II-3 and II-5 the height is also given):

<table>
<thead>
<tr>
<th></th>
<th>I+2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>Ambul.</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>41 μ</td>
<td>62/50</td>
<td>32</td>
<td>41/41</td>
<td>60</td>
<td>37</td>
<td>273</td>
</tr>
<tr>
<td>II</td>
<td>41</td>
<td>62/47</td>
<td>32</td>
<td>43/37</td>
<td>63</td>
<td>38</td>
<td>279</td>
</tr>
<tr>
<td>III</td>
<td>49</td>
<td>50</td>
<td>30</td>
<td>41</td>
<td>60</td>
<td>41</td>
<td>271</td>
</tr>
<tr>
<td>IV</td>
<td>50</td>
<td>53</td>
<td>30</td>
<td>42</td>
<td>66</td>
<td>38</td>
<td>279</td>
</tr>
</tbody>
</table>

Legs I and II very similar in size and chaetography, but ventral seta of I-2 shorter and more slender than that of II-2 (Figs. 67, 69). I-3
and II-3 only 1.20 and 1.32 times as long as high (swollen). Medial seta of I-5 and II-5 flattened, pectinate. I-6 and II-6 with bacillum and divaricate parambulacral setae, but without prebacillum. Median claw absent from all legs. Lateral claws with comb which projects medially from shaft and which is oriented in the same plane of curvature as outer edge of claw, so that in lateral view the claw may appear to be smooth or to have an accessory tooth but no comb (compare Fig. 58 with 67). III-5 and IV-5 with ventro-medial seta very long, slender, smooth. Parambulacral seta of III-6 reduced to a divaricate seta medially and a pectinate spine-like seta laterally. These are further reduced on IV-6, the medial member being represented by a single rod-shaped seta; outer member heavy and serrate or pectinate as on III-6. Lateral parambulacral seta in some specimens apparently coarsely pectinate, but in others the processes occupy only one side of the seta. In all cases the pectinations or serrations are visible only in favorably oriented tarsi, and in lateral view the appearance is that of a smooth, spine-like seta. All tarsi lack a claw fossa.

**Male.** Of the more than 50 adults in the author’s collection, all are females. These have been collected at different seasons of the year in various localities around New Haven. Many other specimens also have been examined in an unsuccessful search for males, and it is quite possible that males do not exist in this part of the range. Lohmann (1889a: 326–328) made no mention of males, nor did Viets (1927a: 102–106, etc.). But André (1939c: 308–310), in a restudy of the type of *Rhomognathus cryptorrhynchus* Trouessart 1901, concluded that his single specimen (a male) was simply a specimen of *R. setosus*. At least André showed that claws III and IV had a comb such as that on I and II. The absence of this comb was the character that Trouessart (1901c: 151–152) used to distinguish his “new species” from *setosus*. André’s figures show epimeral plates III and IV as contiguous, which is not the case in females of *setosus*, but in other characters André’s figures agree quite well with *setosus*, and the present writer can see no reason for rejecting André’s conclusion. There are cases known, for example among the Ostracoda, in which certain species reproduce only parthenogenetically in one part of their range but bisexually in other parts. It is not impossible that such is the case in *Isobactrus setosus* also.

**Nymphs and larvae.** These can be easily distinguished on the basis of the claw characters alone, at least in the northeastern United States.
An unexplained situation is found in the nymphal genital areas. The protonymphs (leg IV with five segments) have a single pair of anteriorly-inclined genital suckers (Fig. 62). Two other types of nymphal genital areas have been found also. In nymphs about 230μ long (leg IV with six segments) there are two pairs of genital suckers (Fig. 61), of which the anterior pair lacks the terminal disc; the posterior pair slopes posteriorly and these have terminal discs. In larger nymphs (ca. 300μ long) there is a third pair of suckers added posteriorly, and the form and position of the four anterior suckers is markedly changed (compare Fig. 60 with 61). This has been verified in several nymphs of each type, and the number, form and orientation of the suckers is constant. In the larger nymphs there is a pair of setae projecting from the genital groove. These can be seen in all specimens. Only one of the smaller nymphs was in a favorable position, and very careful examination showed that there were no setae in the genital groove. No setae could be found here in the poorly oriented specimens either, although they could be seen in the older nymphs almost regardless of orientation. The possibility of a third nymphal stage is suggested but by no means proved by these facts. Although the third pair of internal suckers could be added during the active deutonymphal stage, the addition of a pair of setae appears most improbable.

Remarks. Schulz (1933: 96) expressed doubt that R. setosus of Viets 1927 is really that of Lohmann, but he gave no reason for his doubt, and the present writer can see no reason for any. The species is highly variable in the appearance of the dorsal plates (see above), but the ventral armor is very characteristic, and Lohmann’s and Viets’ descriptions and figures are in close agreement on the details of this. A peculiar type of carpal structure is found in I. setosus, levis and hutchinsoni, n. sp. Whereas in the other Rhombognathinae the carpite is a distinctly separate sclerite lying between the tip of the tarsus and the middle piece of the claw, the carpite in these three species is fused

Figures 54–63. Isobactrus setosus (Lohmann) 1889. 54 Female: dorsum. 55 Female: venter. 56 Female: capitulum, ventral view (drawn from a slightly compressed specimen in which the capitulum is completely horizontal). 57 Female: dorsum (rotated). 58 Female: claw, ventral view. 59 Female: genito-anal area. 60 Deutonymph: genito-anal area (drawn from a specimen with a body length of 299μ, leg IV with 6 segments). 61 Deutonymph: genito-anal area (drawn from a specimen with a body length of 229μ, leg IV with 6 segments). 62 Protonymph: genital area. 63 Female: sagittal section (the line is vertical to the horizontal plane of the mite).
to the end of the tarsus. It is a thin long plate, folded longitudinally down the middle and enlarged distally where it articulates with the middle piece (Figs. 68, 70). The moniliform structure of the basal half would appear to provide greater flexibility of the shaft and to distribute the stress over a greater length of the carpite, insofar as one can judge the value of this arrangement by the examination of mounted specimens. The beads do not represent separate sclerites, but merely local structural differences in a continuous sclerite. This type of carpite probably represents a valid generic character for Isobactrus, since it has been found in the three species of Isobactrus seen by the writer and is very different from that seen in Rhombognathides, Metarhombognathus, and also in Rhombognathus. The shape of the carpite is approximately the same in the latter as in Isobactrus, but the separation from the tarsus is complete. The type of carpite appearing in Isobactrus has also been seen by the writer in Scirus Hermann 1804, and Cyta von Heyden 1826 (Bdellidae). In these genera the moniliform portion of the carpite is longer than in Isobactrus. There is, however, no direct relationship between Isobactrus and the other two genera.


French Atlantic, Ireland, North Sea, Baltic.

*Isobactrus levis* (Viets) 1927

**Figures 71–73**


This species was taken on only one occasion, when four females were obtained. Although very similar to *R. setosus* in general appearance when observed alive and at low magnifications, it attracted attention when first seen because of its movements and the long setae of the tarsi which aided in its recognition under the binoculars. With little material available a full description is not possible but the distinguishing characters of the species will be pointed out. Viets (1927a: 103–106) gave four figures and a detailed comparison with *I. setosus*.

**Female.** Body 325–353μ long. The specimens were slightly compressed and unusually broad, but the one which appeared most normal
was 353 x 229μ (L/W = 1.55) prior to mounting. In this mite the following measurements were obtained: AD 130 x 100μ, OC 48μ long (width not measurable because of lateral position), PD 163 x 149μ. All plates distinctly panelled. Epimeral plates divided as in I. setosus, but much more reduced in extent, with all ventral setae lying in the membranous area. Capitulum of same form as in I. setosus, completely hidden in dorsal view. In a female with a body 325μ long, the following measurements were obtained: capitulum 53μ long to tip of rostrum and 64μ wide at base; rostrum alone 26μ long and 11μ wide, swollen at middle and bearing 2 pairs of setae just as in I. setosus. Palpi 4-segmented.

Chaetotaxy of legs:

<table>
<thead>
<tr>
<th></th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
</tr>
</thead>
<tbody>
<tr>
<td>d.</td>
<td>v.</td>
<td>l.</td>
<td>m.</td>
<td>d.</td>
</tr>
<tr>
<td>1.</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>2.</td>
<td>1</td>
<td>1</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>3.</td>
<td>3</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>4.</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>5.</td>
<td>3</td>
<td>2</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>6.</td>
<td>4</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

Since the legs could be studied only on firmly fixed specimens, it is possible, but not very likely, that some of the setae were overlooked. The complete absence of the dorsal setae on III-2 and IV-2, and the duplication of the long basi-dorsal setae on all tarsi are unusual characters. The latter is especially unusual. These setae appear to be longer than on Viets' specimens, but this is not a significant difference. Medial member of ventral pair of setae on I-5 broad and pectinate, but corresponding seta on II-5 slender and smooth. No setae ventrally on I-6 and II-6. Both I-6 and II-6 with a clavate bacillum, but prebacillum absent from both. Parambuberal setae divaricate and of same form on both I-6 and II-6 (Fig. 71). III-5 and IV-5 without pectinate seta. III-6 and IV-6 with medial parambuberal seta very slender, single; lateral seta also single, but very broad, scale-like and notched. Claw fossa on all tarsi, but best developed on I and II. Lateral membranes absent. Lateral claws scythe-shaped, with neither pecten nor accessory tooth. Median claw absent.

Remarks. This species is distinguishable from I. setosus in all stages on the basis of the claw characters alone. It can be distinguished from I. hutchinsoni, n. sp., by the less distinct panelling and the
absence of the costae, which are well developed in *hutchinsoni*. The duplication of the basi-dorsal seta on all tarsi is a unique character. The coxal areas are much less extensive than in *I. hutchinsoni* also, and the setae do not show any marked tendency toward pectination. Other differences will be apparent from the figures and descriptions.

**Distribution.** North America: New Haven County, Connecticut (Morris Cove).

North Sea.

*Isobactrus hutchinsoni*, new species

Figures 74–82

**Male.** Body (7 specimens) 340–375μ long, 215–250μ wide (av. 359 x 237μ); L/W = 1.44–1.58 (av. 1.51).

AD produced over capitulum so that no more than tips of palpi and chelicerae can be seen from above; rounded anteriorly, nearly straight posteriorly. OC somewhat irregular and variable in form, with single round cornea antero-laterally. PD rounded anteriorly, projecting between OC, usually distinctly narrowed behind middle. Setae absent, or so small as to be overlooked easily, even under oil immersion. In a male 353μ long the following measurements were obtained (L/W): AD 126/130; OC 65/61 and 69/58; PD 215/151; AD-PD 23; OC-OC 63μ.

All dorsal plates clearly panelled and finely punctate; numerous pores present (Fig. 78). AD with 7 groups of panels, or only 5 when anterior and lateral groups are coalesced. Panels limited to center of OC and a small area at anterior end. PD with 2 parallel ridges which are finely punctate but not panelled. Membranous areas with parallel striae and very numerous minute hairs (Fig. 82) which can be most easily observed on the margins of the body. The hairs arise from the crests of the striae. A single pair of setae lies in the dorsal membranous area.

Venter as described below for female, except for genital area. A feebly developed genital plate is present on which a small amount of panelling is faintly discernible. In a specimen 370μ long the genital...
plate was 93μ long and 70μ wide, with 30 to 32 pairs of setae present (Fig. 76). Anus as in female; not terminal.

Capitulum as described for female. Legs characterized by presence of serrate setae, the long unpaired seta on the tarsi and the slender claws which lack comb and accessory tooth. I-1 with very fine seta medially; I-2 with a dorsal and a ventral smooth seta; I-3 with 4 setae (Fig. 75), all but the dorso-lateral one serrate; I-4 with 3 setae, the lateral one smooth; I-5 with 1 serrate ventral seta, 3 smooth setae and the very conspicuous feather seta. I-6 with a slender, hooked dorsal seta at middle, a pair of serrate setae more distally, a pair of divaricate parambacular setae and a single minute bacillum at the base of the ambulacrum. Claws smooth as in I. levis (Viets) 1927. Leg II identical with I in arrangement of all setae. III-3 and IV-3 with only 3 setae. III-6 and IV-6 with parambacular setae spiniform, bacillum absent; otherwise III and IV identical with I and II chaetographically. Feather seta on III-5 and IV-5 much longer and more slender than on I and II, but distinctly pectinate. Subterminal dorsal setae on IV-6 often very elaborate. In a male with a body length of 360μ the following measurements were obtained:

<table>
<thead>
<tr>
<th></th>
<th>1+2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>Ambul.</th>
<th>Total</th>
<th>T/BL</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>38μ</td>
<td>53</td>
<td>30</td>
<td>43</td>
<td>55</td>
<td>42</td>
<td>261</td>
<td>.73</td>
</tr>
<tr>
<td>II</td>
<td>40</td>
<td>51</td>
<td>30</td>
<td>42</td>
<td>55</td>
<td>43</td>
<td>261</td>
<td>.73</td>
</tr>
<tr>
<td>III</td>
<td>50</td>
<td>46</td>
<td>30</td>
<td>42</td>
<td>60</td>
<td>45</td>
<td>273</td>
<td>.76</td>
</tr>
<tr>
<td>IV</td>
<td>48</td>
<td>48</td>
<td>30</td>
<td>45</td>
<td>70</td>
<td>45</td>
<td>286</td>
<td>.79</td>
</tr>
</tbody>
</table>

Chaetotaxy of legs:

<table>
<thead>
<tr>
<th></th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
</tr>
</thead>
<tbody>
<tr>
<td>d.</td>
<td>v. l. m.</td>
<td>d. v. l. m.</td>
<td>d. v. l. m.</td>
<td>d. v. l. m.</td>
</tr>
<tr>
<td>1</td>
<td>- - 1</td>
<td>- - 1</td>
<td>- - 1</td>
<td>- - 1</td>
</tr>
<tr>
<td>2</td>
<td>1 1 -</td>
<td>1 1 -</td>
<td>1 1 -</td>
<td>1 -</td>
</tr>
<tr>
<td>3</td>
<td>3 - 1</td>
<td>3 - 1</td>
<td>2 1 -</td>
<td>2 1 -</td>
</tr>
<tr>
<td>4</td>
<td>2 - 1</td>
<td>1 1 1</td>
<td>1 1 1</td>
<td>1 1 1</td>
</tr>
<tr>
<td>5</td>
<td>3 1 -</td>
<td>3 1 -</td>
<td>3 2 -</td>
<td>3 2 -</td>
</tr>
<tr>
<td>6</td>
<td>3 - -</td>
<td>3 - -</td>
<td>3 - -</td>
<td>3 - -</td>
</tr>
</tbody>
</table>

Female. Body (5 specimens) 346–385μ long; 220–256μ wide (av. 364 x 238μ); L/W 1.50–1.54 (av. 1.53); virtually same size as male. Dorsal and ventral surfaces as in male except for genital area (Fig. 80).

Venter with epimera I and II of each side fused but completely separated medially from those of opposite side; I not quite divided by the striate membranous area; III and IV also fused completely. Epimera only faintly panelled, the marginal portions of epimera punctate but not panelled and each with a single pair of setae (epimera II in the female drawn showed a duplication of the seta of the left side). Genital area surrounded by 3 pairs of setae. Postero-lateral margins of PD visible ventrally. Anal area separated from genital area by a space only 5–6μ wide. Anus separated from end of body by an interval 0.5 the length of the anal area. Striae well developed, sparsely pilose.

Capitulum 65μ long to tip of rostrum and 75μ at widest part of base; rostrum 26μ long and 14μ wide, bearing 2 pairs of setae. Capitulum very similar to that of I. setosus, but base relatively heavier and rostrum relatively shorter. Most of the differences between the figures of the capitula of the two species are more apparent than real, however, and are due in part to the angle from which the structures are drawn. Legs as in male.

**Deutonymph.** Plates and sculpturing as in adult. Genital area as shown in Fig. 81.

**Protonymph.** Resembling deutonymph in nearly all respects and easily recognizable by characters of plates and legs. Genital area as in deutonymph but with single pair of suckers. In the one specimen which could be studied there are no setae anterior to the genital area, but the lateral setae are present.

**Remarks.** This species shows a superficial similarity to *Isobactrus levis* (Viets) 1927, but differs in several important respects. AD is relatively broader and more rounded anteriorly; the paneling on all dorsal plates is much more distinct than in I. levis. PD extends anteriorly between OC; the longitudinal ridges are completely devoid of paneling, whereas in I. levis the panels cover the entire plate uniformly. In *I. hutchinsoni* the tarsi are apparently more slender, and there is a single long dorsal seta instead of the two setae in I. levis. I-3 and II-3 have a large ventral seta which is absent in I. levis. The epimera are more extensive than in I. levis, I being fused with II, and III with IV; in I. levis, I is virtually absent and III and IV are completely separated. The epimeral setae are included in the plates, whereas in I. levis they lie in the membranous area.

**Distribution.** North America: New Haven County, Connecticut (Lighthouse Point, in tidal creek [type locality]).
SUBFAMILY HALACARINAE VIETS 1927

Diagnosis. Middle piece of claw articulating directly with end of tarsus; carpite absent. Palpi 4-segmented, although P-3 and P-4 may be very small or fused, in which case the demarcation between the segments is still visible. Palpi attached to capitulum laterally, so that bases of palpi are separated by an interval considerably greater than width of P-1 and are clearly visible in ventral view. Combined length of P-3 and P-4 greater than \( \frac{1}{2} \) the length of P-2. Principally marine; rarely fresh water; intertidal to abyssal. Predaceous. Cosmopolitan.

Genus Halacarus Gosse 1855


Diagnosis. Palpi 4-segmented; P-3 with a seta on medial surface which is usually spine-like or rod-like. Palpi rather distinctly geniculate (a line drawn along ventral surface of P-2 in an undistorted palp forms an angle of at least 20°, and usually more than 30°, with a line drawn along ventral side of P-3 and P-4. Sides of rostrum rarely parallel except for a short distance. I-4 and II-4 nearly as long as, or slightly longer than, either segments 3 or 5. Median claw present, carpite absent. Dorsal plates sometimes greatly reduced. Four or 5 pairs of dorsal pores\(^{14}\) surrounded by a prominent chitinous ring. Typically, one of these is found on AD, one on OC, one between AE and PE near sides of body, and 2 on PD, but when the plates are greatly reduced or absent the pores lie in the membranous area. Cosmopolitan. Marine.

Type. H. ctenopus Gosse 1855 (subsequent designation by Viets, 1927a).

\(^{14}\) Not spiracles, as intimated by Trouessart (1894b: 175).
Key to North American Species (Adults)

1a. Body cylindrical, flexible, the height equal to width. OC and corneae absent; PD divided into a right and a left platelet; AE also divided medially (Fig. 131).
   Arenicolous. ........................................... anomalus Trouessart 1894; p. 97. Connecticut to North Carolina. Also English Channel, North Sea, Baltic.

1b. Body of usual form, broader than high, not flexible. OC present or absent, with corneae present but greatly modified. PD, when present, not divided medially; AE not divided medially (Figs. 83, 84). Not arenicolous.

2a. PD present, bearing the last 2 pairs of dorsal pores. OC well developed, bearing a large pore and with a seta in the indistinct antero-median angle (Fig. 84). ........................................... ctenopus Gosse 1855; p. 82. Florida. Also Ireland, England (North Sea and English Channel), France, Shetland Islands, Bermuda.

2b. PD absent, pores lying in the membranous area. Cornea present; OC entirely or almost entirely absent, the seta and pore lying in the membranous area.

3a. Anterior pair of dorsal pores at, or slightly behind, middle of AD and posterior to the setae of AD. Genital plate of female with pigmented portion continuous in front of opening, not divided into a right and a left crescentic area. Two pairs of setae at sides of opening and a single pair anterior to GA. ...................... actenos Trouessart 1889; p. 87. Florida. Also Ireland, English Channel, Bay of Biscay, Cape Verde, Kerguelen.

3b. Anterior pair of dorsal pores very near end of frontal spine and far anterior to the setae of AD. The latter lie outside AD in the adult but in the sides of AD in the larva. Genital plate of female divided into a right and a left crescentic area by a reticulate area which contains 4 or 5 pairs of setae (Fig. 129). Seven to 10 setae lie at sides of genital opening. Below tide zone. ...................... frontiporus, new species; p. 91. Long Island Sound.

Halacarus (s. str.) ctenopus Gosse 1855

Figures 83–93

Male. The two intact specimens in the author's collection measure 471 x 242\mu and 450 x 250\mu (L/W = 1.80–1.92). In the smaller specimen the following measurements were obtained: AD 158 x 100\mu, OC 81 x 42\mu and 80 x 37\mu, PD 214 x 100\mu. Portion of plate anterior to pores only a little more than half as long as the posterior portion; frontal spine not quite reaching to end of I-1 (Fig. 84). Pores situated just behind insertions of leg I on a pair of rather prominent tubercles. Posterior portion of AD faintly panelled, gently rounded, extending to a point just slightly anterior to the large pores on OC. All but central part of plate posterior to pores striate, the striae continuous with those of the membranous area. However, the striae of the plates differ from those of the membranous area in that rows of very minute pores lie in the grooves (Fig. 88). Setae of AD posterior to pores. Ocular plates with single large cornea\textsuperscript{15} which is perforated by a minute canal. Cuticle not panelled, but striate like that of AD. A large pore behind middle of plate and a small seta just mediad of cornea. PD reaching to, or nearly to, insertion of leg III; long, ovate in outline, with a pair of large pores and a pair of setae just behind insertions of IV; another pair of pores and setae at end of plate. Central and postero-lateral portions of plate depressed, faintly panelled, most of plate striate like AD. Two pairs of setae in the membranous area between AD and PD. Membranous area faintly striate, the striae very numerous and parallel.

Venter as in female, except for the characters of GA. GA 225\mu long and 105\mu wide. There appears to be a separation between the genital and anal portions of GA (Fig. 86), but this is probably due to the vertical course of the wall of the plate behind the genital opening. It is doubtful that there is an actual separation. Anterior, lateral and posterior portions of GA striate and porose; remainder of plate (surrounding genital opening) sparsely porose and smooth. Genital opening surrounded by a single row of about 30 small setae (14 to 16 on each side). In addition there is a row of longer setae nearer the margins of the plates. Opening guarded by a pair of slender sclerites.

Capitulum as in female. Palpi (Fig. 89) with P-2 very long and bearing a medial seta at middle of segment in addition to that at the end. P-3 with medial seta rod-shaped and not tapering as shown by

\textsuperscript{15} Viets in his key (1939c: 550) stated: "16 (11) Okularia ± deutlich mit 2 Hornhäuten," which is incorrect, for this would exclude \textit{H. ctenopus}. It should have read "mit 1 oder 2 Hornhäuten."
Lohmann (1893a: pl. 9, fig. 5, male). Although favorably mounted material is not available for study of the legs, the following features were noted. All legs with circularly-arranged striae. Femora I and II with a prominent porose area basi-dorsally. I-3 with a heavy, tapering seta ventrally; I-4 with 2, and I-5 with 4, such setae, all of which are smooth. I-6 identical with that of H. frontiporus in that the 2 disti-ventral setae are rod-shaped and rounded terminally. In both species the homologues of these setae on II-6 are tapering. Bacillum and prebacillum both present on I-6, but only the bacillum on II-6. Parambulacral setae on I and II like those of H. frontiporus, except that those on II appear to be somewhat shorter than those on I, rather than of approximately equal length. As in H. frontiporus, homologues of the heavy ventral setae of I-3, I-4 and I-5 are replaced on II by more slender setae, except for the medial member of the distiventral pair on II-5, which is very prominently pectinate. III-2 and IV-2 with a heavy pectinate seta dorsally (Fig. 87, oil immersion). III-6 with 4 setae dorsally, IV-6 with 3. Parambulacral setae in unfavorable position for study, but those on IV-6 of the male definitely pectinate, as in male of H. frontiporus. All tarsi with pectinate lateral claws and a median claw. Lateral claws pectinate on legs II, III and IV, but those on I seemingly smooth. However, under oil immersion it can be seen that what is apparently a simple accessory tooth on all the claws is, in reality, the distal end of the comb. Even on I-6, the “accessory tooth” contains from 3 to 5 minute teeth. A similar relationship between comb and accessory tooth is seen in H. basteri (q. v.) in which the “accessory tooth” is only the distal portion of the comb, which gives the false impression of being a single large tooth, when seen in side view.

16 Viets (1939c: 550; 1940g: 1) used the form of this seta in distinguishing between H. ctenopus, and H. oblongus and subtilis.

17 Lohmann (1893a: 83) said of H. oblongus: “An beiden Hinterbeinen trägt ferner das 2. Glied am Innenrande einen kräftigen Dorn, der schwach gefiedert ist.” There is no seta on the inner surface of III-2 or IV-2 in any halacarid yet studied by the writer (it would be an impediment to the movement of the leg) and there is no doubt that Lohmann meant the dorsal seta (which is never more than slightly dorso-median). Because of Lohmann’s statement, Viets (1940g: 6) may have overlooked pectinations on this seta in H. subtilis. At any rate, the absence of pectination on this seta in H. subtilis and H. oblongus must be considered an uncertain key character in distinguishing between H. subtilis and H. oblongus, for Viets apparently accepted Lohmann’s statement without question.
Female. The only female in the author's collection is 547μ long to the tip of the frontal spine and 305μ wide (L/W = 1.79). All dorsal plates approximately same length as those in male, but OC and AD slightly narrower, hence PD relatively (but not actually) shorter. In the male the distance from the anterior end of PD to the fourth pair of dorsal pores (counting the lateral pores) is almost as great (0.94) as the distance from the fourth to the fifth pair of pores. In the female the former distance is only about two-thirds as great (0.63) as the latter. AE undivided, bearing 3 pairs of setae. GA (Fig. 83) containing two roughly crescentic, heavily sclerotized areas at the sides of the genital opening. Anterior portion of plate only faintly demarcated from membranous areas, and bearing a pair of setae. A second pair of setae lies at sides of genital opening.

Capitulum (Fig. 93) 176μ long and 72μ wide; rostrum alone about 100μ long. Base of capitulum only slightly longer than broad. Pharyngeal plate very weakly panelled. Rostrum reaching a little beyond end of P-3, bearing 2 pairs of setae and a pair of minute spines at tips.

Deutonymph. Genital plate completely separated from anal plate, with anterior portion indistinct as in adult. Two pairs of internal suckers, 2 pairs of large setae and a pair of small subgenital setae present (Fig. 92).

Remarks. H. ctenopus, subtilis Viets 1940 and oblongus Lohmann 1893 form a group of closely related species within Halacarus s. str. The distinctions between these species have not been clearly established owing to errors or to the fact that homologous structures have not received equal attention in the published descriptions of the several species (a very common defect of many descriptions of closely related species). For example, Lohmann's figure of the ventral surface of the female of H. oblongus (1893a: pl. 9, fig. 3) shows the homologues of the anterior setae of GA in H. subtilis and H. ctenopus to lie free in the membranous area, the plate consisting solely of the crescentic areas. But since these three species are so closely related, and since two of the three are known to have a very weakly developed antero-median portion which includes these setae, the writer hesitates to accept Lohmann's figure as accurate. Similarly, the position of the setae at the anterior end of OC in Lohmann's pl. 9, fig. 1, is questionable. At first glance these setae in H. ctenopus appear to lie outside OC, but closer study shows that they lie in the very indistinct antero-median angle of the plate. Lohmann did not even show these setae.
in his drawing of *H. ctenopus*, so that a comparison is impossible, but in *H. subtilis* they lie in the corner of the plate just as in *H. ctenopus*. These are critical points and are also points in which errors are easily made. It is essential in such cases that homologous structures be compared point for point, at the highest magnifications practicable, and in media of low or high refraction. There is little doubt that these three species differ significantly from each other, but it is equally certain that the differences which are most apparent from the published descriptions and figures cannot be accepted without question. For the present the distinctions can be made principally on the basis of the form of AD and PD of the adult, the published figures of which are probably reliable. Sexual differences must be considered, of course, since they do exist in *H. ctenopus* and *H. subtilis*, and probably in *H. oblongus* (male not yet known).

**Distribution.** North America: Florida (Biscayne Bay, on Soldier's Key).

North Sea (England), English Channel, Ireland, Bermudas.

*Halacarus (s. str.) actenos actenos* Trouessart 1889

Figures 94-102


This species is also poorly represented in the author’s collection, there being only a single male and female and three nymphs. Of these, one of the nymphs has all eight legs, but every one of the legs of the four other mites has been broken off between basifemur and femur, indicating some structural weakness of this joint in this species. These mites were probably dead at the time the material was collected.

**Male.** The single male is 422μ long to the tip of the frontal spine and 235μ wide (apparently somewhat flattened). AD very indistinct, extending to a point slightly posterior to cornea, bearing a pair of pores and a pair of setae antero-medial to the pores. Portion of AD

---

anterior to pores longer than posterior portion, the spine reaching well beyond dorsal seta of I-2. OC greatly reduced, almost invisible even in Hyrax, the corneae very irregular and indistinct. In the male shown in Fig. 97 the plate is simply a small irregular portion of the cuticle which is not striate. There is not even a trace of a post-dorsal plate. All dorsal setae and pores behind AD lie in the membranous area, except for dorsal seta of PE.

Ventral surface as in female, except for characters of GA. GA (Fig. 95) pyriform. Genital opening circular, surrounded by 55 or 60 setae (28 + 31 in the specimen drawn) in a single to double row and guarded by a pair of sclerites bearing 5 pairs of setae as shown; 3 pairs of genital suckers present. A pair of setae in the membranous area anterior to plate.

Capitulum (Fig. 94) 134µ long to tip of rostrum and 66µ wide; rostrum alone about 79µ long, extending beyond end of P-2, bearing 2 pairs of setae. Base of capitulum slightly broader than long. Pharyngeal plate not panelled. Palpi typical of the subgenus. Medial seta of P-2 somewhat beyond middle, but variable in position; medial seta of P-3 rod-shaped, blunt distally, less than 10µ long. In the female the latter seta is tapering throughout, pointed at the end and more than 10µ long (compare Fig. 99 with 100). The difference in size probably represents a true sexual difference, but the difference in form is not very clear-cut. Fig. 100 shows that a considerable difference in form of the spine on the two palpi of an individual can

18 Lohmann (1893: pl. 10, fig. 1) showed only the corneae and stated that the ocular plates were completely absent (as in the female described here by the present writer). Viets (1939c: 549, 550) indicated that Lohmann's figures and statements disagree on the structure of the ocular plate. But an examination of the figures and descriptions of the three species in which Viets claimed this discrepancy to occur shows that there is no discrepancy in Lohmann's statements. Since in all three cases only corneae are present, it is obvious that "Okularplatten" meant, to Lohmann, that part of the plate outside the cornea. It is simply a question of terms, and Viets' keys to the species of Halacarus s. str. suffer from his failure to make this point clear. Lohmann's description was based on a female, in which there are sunken, rudimentary corneae, but no trace of a plate.
Newell: The Halacaridae of Eastern North America

A fine reaching almost invisible in the male portion of the face of a post.

The difference between 59 and 60 is visible.

The difference between 59 and 60 is visible.

The difference between 59 and 60 is visible.
occur. Slight differences in such characters as this must not be assigned any taxonomic importance, as has been done by some workers, without very close study. Natural variations do occur, and, more important, in the past such structures have been drawn at such low magnifications that an error no greater than the width of a line could cause significant differences in the appearance of the structure.

A recheck on the medial seta of P-3 of *H. ctenopus* and *H. frontiporus* shows that in these species also the seta in the male is appreciably smaller than in the female (Figs. 90, 91, 113, 114), but in all three species P-3 is proportionately smaller in the male than in the female so that there is no special correlation between sex and size of seta, but only the general correlation of body size difference, the male being smaller in these three species.

**Female.** The single female measured 519μ long to the tip of the frontal spine and 263μ wide (L/W = 1.97). AD as in male, but reaching only to level of anterior margin of corneae. OC completely absent, except for cornea, the latter completely surrounded by striate cuticle. Under oil immersion the cuticle just over the submerged cornea is seen to be reticulate, rather than striate, and the reticulate area is divided by a line which runs diagonally over the cornea. This agrees with Lohmann's description and shows that there is a sexual difference in the degree of development of OC in *H. actenos* just as in *H. ctenopus*. PD completely absent. Setae and pores as in male.

Ventral surface as shown in Figs. 98 and 102. AE undivided. PE with 3 pairs of setae ventrally and 1 pair dorsally. GA without antero-median striate area and with the single pair of setae lying free in the membranous area in front of plate. Heavily sclerotized, pigmented area not divided anteriorly, but continuous. Two pairs of setae at sides of genital opening. Lohmann (1893a: pl. 10, fig. 2) showed one pair here, but since the anterior pair is very slender it may have been overlooked. Trouessart (1894b: pl. 10, fig. 2) showed two pairs. Genital opening guarded by a pair of sclerites bearing 5 pairs of setae. Also, 4 or 5 pairs of long setae (5 according to Trouessart, 1894b) protrude from the opening. Capitulum essentially as in male, q. v. Since the legs were broken off they cannot be described.

**Deutonymph.** Recognizable by very long, slender frontal spine and complete absence of PD. AD as in adult but slightly smaller. Corneae present, but OC completely absent, the striae passing over deep-lying, atrophied cornea without interruption or change in structure.
Halacarus (s. str.) frontiporus new species

(Fig. 103–129). Genital and anal plates completely separate, the genital plate very small; 2 pairs of genital suckers and a pair of minute subgenital setae present (oil immersion). A pair of larger setae lies in the lateral angles of the plate and a second pair lies far anterior to the plate.

The one deutonymph which had not lost its legs was in an unfavorable position for study, but the following features were noted. I-3 and I-4 have a pair of heavy, tapering setae ventrally and I-5 has 2 pairs, all of which are smooth. The medial member of the distal pair of ventral setae of II-5 is pectinate, as in H. ctenopus. Dorsal seta of basifemur of all legs smooth. Cuticle of legs not striate, but with a reticular structure similar to, but not so heavily developed as, that on H. frontiporus. Median claw extremely small, lateral claws without comb along side of shaft, but under oil immersion it can be seen that the accessory tooth is really not a single tooth but a remnant of the comb containing a few small teeth (as in H. ctenopus).

Distribution. North America: Florida (Biscayne Bay, on Soldier’s Key).

French Atlantic, English Channel, Cape Verde, Kerguelen.

Halacarus (s. str.) frontiporus new species

Figures 103–129

Female. Body 581–665μ long to tip of frontal spine and 346–402μ wide, L/W = 1.68 and 1.65 (2 specimens only). PD and OC absent, except for modified cornea; AD greatly reduced, detectable only by a difference in cuticular markings (Fig. 108). The area enclosed by the dotted lines in Fig. 105 is reticulate and is surrounded by an area about 50μ wide in which the cuticle is irregularly striate. The striae are not of the type usually found in other Halacaridae and they merge almost imperceptibly into the irregular reticulae of the area occupied by AD, and also into the reticulae which cover the rest of the dorsum. Anterior margin drawn out into a sharp frontal spine which projects antero-ventrally (Fig. 103). A pair of anteriorly projecting pores at sides of spine. A single pair of very thick, columellar corneae present (Fig. 125) in dorsal cuticle, but no trace of OC. Three pairs of pores lie posterior to the corneae, the most posterior pair being nearly terminal. Six pairs of very minute setae in membranous area, including that pair which in the larva lies within or at margin of AD.
A large urocyst could be seen inside the body of every specimen examined. In the living mite this is median in position, occupying the excretory duct, but this is usually shifted during preparation of the mite.

AE distinct, undivided medially, with 3 pairs of setae. Epimeral pore absent. PE with 3 ventral setae and 1 lateral seta on each side. AE and PE with very characteristic, irregular panelling (Fig. 123). Membranous area like that of dorsal surface; not with parallel striae. GA (Fig. 129) undivided, broadly pyriform, with the narrower end posteriorly. On each side of genital opening is a large crescentic sclerotized area occupying the greater part of plate. At first glance these sclerotized areas appear to represent the entire genital plate, especially since they are pale brown in color, in sharp contrast with the remainder of GA which is nearly colorless. But closer study shows that the entire pyriform area shown in Fig. 129 is the plate, of which the prominent brown crescentic areas are only a part. Anterior to the opening is a T-shaped reticulate area bearing 8-10 setae; a similar area posteriorly includes the very simple slit-like anus. These two areas are joined by a narrow strip of reticulate cuticle which extends around each side of the genital opening and which bears 7-10 setae on each side. The brown crescentic areas are neither panelled nor porose, but have a characteristic fibrous structure. Remainder of GA reticulate like AD, the membranous area surrounding plate marked in same way as that surrounding AD. A pair of slender, reticulate sclerites guarding opening, each sclerite bearing a seta at each end, with 3 pairs of genital suckers readily visible. Ovipositor with 2 pairs of very long setae which protrude through opening and extend beyond anus.

Capitulum elongate, basal portion rectangular (Fig. 110). In a female with a body length of \(658\mu\) the following measurements were obtained: capitulum \(157\mu\) long and \(81\mu\) wide, the rostrum alone \(66\mu\) long and \(46\mu\) wide at base. Rostrum very broad at tip, not constricted basally or swollen at middle, extending to or nearly to level of
spine on P-3; 2 pairs of setae as shown in Fig. 110 and a pair of very minute spines at tip. Base of capitulum not swollen, the widest part at base of palpi. Pharyngeal plate with a few degenerate panels. Cuticle sculptured like that on epimera; rostrum smooth. Since the capitulum inclines antero-ventrally it normally appears much shorter than shown in Fig. 110, which is drawn from a female in which the capitulum is horizontal.

Chaetotaxy of legs:

<table>
<thead>
<tr>
<th></th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>d. v. l. m.</td>
<td>d. v. l. m.</td>
<td>d. v. l. m.</td>
<td>d. v. l. m.</td>
</tr>
<tr>
<td>1.</td>
<td>- - - 1</td>
<td>- - - 1</td>
<td>- - - 1</td>
<td>- - - 1</td>
</tr>
<tr>
<td>2.</td>
<td>1 1 - -</td>
<td>1 1 1 -</td>
<td>1 1 - -</td>
<td>1 1 - -</td>
</tr>
<tr>
<td>3.</td>
<td>3 1 1 1</td>
<td>3 1 1 1</td>
<td>3 1 - -</td>
<td>1 1 - -</td>
</tr>
<tr>
<td>4.</td>
<td>5 1 - -</td>
<td>3 1 1 1</td>
<td>3 2 1 -</td>
<td>3 2 1 -</td>
</tr>
<tr>
<td>5.</td>
<td>6 4 1 1</td>
<td>4 4 2 -</td>
<td>2 4 1 -</td>
<td>2 4 1 -</td>
</tr>
<tr>
<td>6.</td>
<td>5 4 - -</td>
<td>4 4 1 -</td>
<td>3 2 - -</td>
<td>3 2 - -</td>
</tr>
</tbody>
</table>

Dorsal seta of I-2 short, spine-like; I-3 with spine-like seta ventromedially and a ventral seta which is thick basally but which tapers quickly to a slender, sharp point. Ventral and medial setae of I-4 and ventral seta of I-5 also tapering rapidly to a sharp point. I-6 with 2 pairs of setae ventrally and 5 setae dorsally, in addition to the parambualcral setae, the bacillum and the prebacillum. Parambualcral setae of usual form; divaricate, rounded terminally. Bacillum and prebacillum lateral in position and well formed, except that the latter lacks an alveolus (Fig. 116). Claw fossa absent. Each lateral claw with an accessory tooth and a greatly reduced comb which occupies only the middle third of the inner side of claw and does not reach to the concave margin of the claw. Median claw bidentate, dorsal tooth small. Heavy setae found on I replaced on II by longer, gradually tapering setae, as a rule, with exception of dorsal seta on II-2, which is spine-like. Prebacillum absent, bacillum medial in position, parambualcral setae divaricate (Fig. 117). Comb on lateral claws a little longer than on I; teeth of comb much longer and extending beyond concave margin of claw. Setae of III and IV long and slender except for most basal seta of segment 4, which is short and blunt. III-6 and IV-6 without bacillum or prebacillum. III-6 with medial parambualcral seta divaricate; lateral seta single. Ventral member of medial seta sometimes slender and tapering rather than as shown in Fig. 118. In two of the four females examined the ventral member was rod-
shaped on both third legs; but in one specimen the same seta was rod-shaped on one leg, tapering on the other, and in the fourth specimen it was tapering on both legs. Claws as on II. IV-6 (Fig. 119) with parambulacral seta reduced to a single tapering seta on each side (compare with male). Lateral claws smooth; dorsal tooth of median claw weakly developed. Claw fossa absent. All legs with epicuticle greatly thickened, reticulate, the reticulations of the same form as those on AD. Femora I and II 1.84 and 1.95 times as long as high (moderately swollen).

In a female of unknown body length the following measurements were obtained:

<table>
<thead>
<tr>
<th>Segment</th>
<th>Ambul.</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>1+2</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>I</td>
<td>88μ</td>
<td>138/75</td>
</tr>
<tr>
<td>II</td>
<td>73</td>
<td>103/53</td>
</tr>
<tr>
<td>III</td>
<td>101</td>
<td>90</td>
</tr>
<tr>
<td>IV</td>
<td>116</td>
<td>110</td>
</tr>
</tbody>
</table>

Segment 4 of all legs approximately of same length as segments 3 and 5, or only slightly shorter or longer.

**Male.** Resembling female in most respects except in characters of GA and of tarsus IV. The only male available for measurement is 520μ long and 319μ wide (L/W = 1.63); probably somewhat smaller than female as a rule. Parambulacral seta of IV-6 elaborately pectinate (2 specimens) as shown in Fig. 120, not simple as in female. A similar condition is found in *C. punctatissimus* (Fig. 209). GA (Fig. 128) pyriform as in female, cuticle reticulate, with a single pair of setae within the ring-like reticular area. Inside the latter is another ring-like area bearing from 29 to 35 setae on each side. Cuticle in this part of plate punctate, but not reticulate. Opening guarded by 6 spine-like setae; 3 pairs of internal suckers at posterior end of opening.

**Deutonymph.** Resembling adult in most respects except in size and genitalia. AD more distinct than in adult and relatively larger, since the setae lie closer to the margins of the plate and are subterminal rather than terminal in position (with reference to the plate). Genital plate (Fig. 115) completely separated from anus by an interval about as long as plate itself (probably varies with age). Outline of genital plate very irregular, cuticle minutely reticulate; a pair of setae at lateral corners of plate (these may be outside the plate) and a second pair in the membranous area antero-laterally from plate. No sub-genital setae were found.
Larva. AD long, narrow, distinct, relatively longer than in adult (since it includes the setae which in the adult lie well outside AD). Cuticle with incomplete reticulae represented by minute papillate elevations which are usually joined by narrow ridges to form short chains. Membranous area marked with maze-like striae (Fig. 121); only at the margins of the body do parallel striae appear. Five pairs of setae lie in the membranous area. OC completely absent, except for the highly modified cornea; PD absent. AE not divided medially, with only 2 pairs of setae. PE with a single pair of setae ventrally and no lateral setae. Sculpturing on AE and PE identical with that of AD. As shown in Fig. 125, part of the venter is marked with parallel striae, but the central and posterior portions are marked with maze-like striae such as are found on the dorsum (Fig. 121). Two pairs of pores and a pair of refractile bodies (behind leg III) are present. Legs with 5 segments. Claws II and III with an accessory tooth and a very weak comb (oil immersion); I apparently smooth but not in a good position for study.

Distribution. North America: Rhode Island (three miles north of Block Island, at 34 meters).

_Halacarus_ (s. str.) anomalus Trouessart 1894

Figures 130–142


**Female.** Body 290–353μ long to base of capitulum and 422–465μ long to tip of rostrum. In a female 312μ long the body is 138μ wide (L/W = 2.26). In a female 318μ long the body is 129μ high (L/H = 2.42). Body cylindrical and very flexible. Plates greatly reduced. AD (Fig. 132) with a pair of minute pores and a pair of setae. PD (Fig. 133) divided into a right and a left half, each platelet bearing a pore at each end and a seta at the posterior end. The panel-like structures seen in the figure are not panels but are areas of muscle insertion.

Distribution. North America: Rhode Island (three miles north of Block Island, at 34 meters).
OC and cornaeae absent. AE (Fig. 131) divided medially, with the usual 3 pairs of setae; epimeral pore large. PE (Fig. 135) with only the 3 ventral setae. Genital plate separate from anal plate, completely divided into right and left halves, each bearing 2 setae on posterior half. A separate sclerite (folded in figure) between genital opening and anal papilla. All plates of body minutely porose.

Capitulum (Fig. 137) 130-140\(\mu\) long to tip of rostrum. Rostrum alone about 70\(\mu\) long, not reaching to end of P-2 (i.e., the disti-dorsal end). P-1 to P-4, in a female with a body length of 353\(\mu\), as follows (L/H): 13/13, 64/11, 6/7, 24/5\(\mu\). P-2 not as high as P-1 and nearly six times as long as high; without setae. (Trouessart [1894b: pl. 10] showed a dorsal seta, but this is probably erroneous. The present writer has examined several specimens closely, and all lacked both the dorsal and the medial seta.) P-3 with a heavy, spine-like seta medi­ally, P-4 with 3 basal setae. Combined length of P-3 and P-4 approximately half that of P-2.

I-1 and II-1 apparently without medial seta. Ventro-medial seta of basal half of I-5 and I-6 spiniform. I-6 (Figs. 140, 141) with bacillum and prebacillum on inner surface of the large lateral membrane of the claw fossa and difficult to distinguish because they are closely applied to each other and to the edge of the membrane. Parambulacral setae double laterally, single medially. Lateral claws with accessory tooth, not pectinate. Median claw unidentate. Leg II without spiniform setae but with a heavy pectinate seta ventro-medially on II-5. Claw fossa very pronounced, the height of the tarsus decreasing sharply beyond the disti-dorsal setae, the membranes only feebly developed. Bacillum lateral, very large, strongly arched and not lying in contact with the membrane; prebacillum absent (Fig. 142). Parambulacral setae single on both sides of tarsus. Lateral claws as on I but considerably longer. III-4 with 1 pectinate seta disti-ventrally; III-5 with a pair of these (Fig. 139). III-6 with claw fossa less pronounced than on II-6; membranes absent. Parambulacral setae single and tapering on each side of tarsus. Pectinate setae and parambulacral setae of IV just as on III.

Figure 129. Halacarus (s. str.) frontiporus (continued). Female: genito-anal plate. Figures 130–137. Halacarus (s. str.) anomalus Trouessart 1894. 130 Female: genito-anal area. 131 Female: ventro-lateral view. 132 Female: antero-dorsal plate. 133 Female: PD of right side. 134 Female: AE of right side, ventral view (same scale as 135). 135 Female: PE of right side, ventral view. 136 Female: palp, lateral view. 137 Female: capitulum, ventro-lateral view.

...with the long, slender setae on the fore legs, conspicuous in the males. The setae are arranged in two series: one on the ventral side of the leg, and one on the dorsal side. The setae on the ventral side are longer and more numerous than those on the dorsal side. The legs are covered with fine hairs, which are especially dense on the tarsi.

In the male, the genital opening is situated on the first coxae, and is covered with a pair of setae. The setae are club-shaped and have a long, slender process at the base. The process is distinctly curved and is inserted into the coxal cavity. The setae are arranged in two rows, one on each side of the genital opening.

The female differs from the male in having a pair of short, stout setae on each coxa. These setae are not as long as those on the male.

The diagram illustrates the structure of the legs and the position of the setae on the male and female. The setae are indicated by arrows, and their arrangement is clearly shown.

Additional details on the anatomy of these setae and their function in the life cycle of these animals are provided in the text.
Male. No males are in the author's collection, although several have been seen. They are distinguishable from the female by the numerous setae around the genital opening. Trouessart (1894b: pl. 7) gave a figure of the genital area of the male.

Distribution. North America: St. Andrews, New Brunswick; New Haven County, Connecticut (Pine Orchard, Morris Cove, South End); Solomon's Island, Maryland; Beaufort, North Carolina (Piver's Island).

France (English Channel), North Sea, Baltic.

Subgenus Thalassarachna Packard 1871


Diagnosis. Characters as in Halacarus (s. str.) Gosse 1855 with the following exceptions. Medial seta of P-3 spiniform in nearly all species, but may be reduced to a minute hair-like seta. I-4 and II-4 very noticeably shorter than segments 3 and 5. Dorsal plates never as greatly reduced as in Halacarus s. str. and dorsal pores not surrounded by prominent chitinous rings.

Type. Halacarus (Thalassarachna) basteri (Johnston) 1836 (=Acarus basteri Johnston 1836).

Remarks. All of the "groups," genera and subgenera given in the above list are synonyms of Thalassarachna Packard 1871 because the species which are "typical" of them, or their types, are consubgeneric with Halacarus (Thal.) basteri basteri, the type of Thalassarachna. The correct status of Thalassarachna has been discussed in detail by the present writer (Newell 1945a: 58–62). It was shown that Thalassarachna verrilli Packard 1871 is actually Halacarus basteri (Johnston) 1836, and since H. basteri is consubgeneric with H. balticus, which
Viets designated as type of his subgenus *Halacarellus* (1927a: 91), then *Thalassarachna* and *Halacarellus* are identical. The former has priority and must replace the latter.

The position of *Leptopsalis* Trouessart 1888 and *Leptospathis* Trouessart 1894 has been confused ever since 1894. *Leptopsalis* was established for *Leptopsalis longipes*, which is now properly placed in the subgenus *Thalassarachna*. The genus was monotypic at the time of its erection. In 1894 Trouessart proposed the new name *Leptospathis* to replace *Leptopsalis* Trouessart 1888, which was preoccupied by *Leptopsalis* Thorell 1882. Meanwhile *Leptopsalis chevreuxi* Trouessart 1889 (now *Agaue chevreuxi*) had been acquired by the genus *Leptopsalis* Trouessart. In the course of the change to the name *Leptospathis*, as a consequence of several taxonomic errors by Trouessart, *Leptopsalis* “lost” its genotype¹º and was left with only *Leptopsalis chevreuxi*. Trouessart identified his new name *Leptospathis* with Lohmann’s “Chevreuxi-Gruppe,” which must be considered a synonym of *Agaue*, since the “typical” species of the “Chevreuxi-Gruppe,” *Agaue chevreuxi*, is congeneric with the genotype of *Agaue* (*A. parva*). All subsequent workers appear to have started with this completely erratic procedure of Trouessart’s in evaluating the position of *Leptopsalis* Trouessart and *Leptospathis* Trouessart, for all have synonymized these two names with *Agaue* Lohmann.

The situation is simple. *Leptopsalis* Trouessart 1888a is a synonym of *Thalassarachna* Packard, because its type was *L. longipes* which is consubgeneric with the type of *Thalassarachna*. *Leptospathis* Trouessart was only a new name advanced to replace the preoccupied name *Leptopsalis*; hence it must retain the genotype *Leptopsalis* and the two names must therefore receive identical taxonomic treatment.

**KEY TO NORTH AMERICAN SPECIES (ADULTS AND NYMPHS)**

1a. AD in all instars drawn out into a prominent frontal spine (Fig. 143). Adults with 4 pairs of setae ventrally on 1-5, of which the basal 3 pairs are spiniform. Dorsal plates panelled................. *basteri basteri* (Johnston) 1836; p. 102. Connecticut, Maine, New Brunswick. Also Greenland, Ireland, European Arctic Ocean, North Sea, French Atlantic coast, Baltic, Black Sea.

¹º Trouessart (1894a: 170) declared longipes Trouessart 1888 a synonym of *Halacarus murrayi* Lohmann 1889. This is erroneous, since longipes has priority, regardless of its unsatisfactory original description.
1b. AD not drawn out into a prominent frontal spine; with a broad and short triangular projection at most (Figs. 157, 180).

2a. Adults and nymphs with 3 pairs of small sclerites, each bearing a seta in the membranous area posterior, medial, and anterior to OC (Fig. 180). Arenicolous............................ *capuzinus* Lohmann 1893; p. 118.
Connecticut; New Brunswick.
Also Baltic.

2b. Without such sclerites, or at most with a single elongate sclerite behind OC; this sclerite does not bear a seta.

3a. With an elongate sclerite in membranous area behind OC, between levels of legs III and IV (Fig. 169). Cornea absent. I-3 of adult with 3 long, spiniform setae ventrally (deutonymph with 2 and protonymph with 1 here). Arenicolous............................ *subterreanus* (Schulz) 1933; p. 112.
Connecticut; New Brunswick.
Also Baltic.

3b. Without such a sclerite behind OC. Cornea present. I-3 of adult without 3 long, spinelike setae ventrally. Not typically arenicolous.

4a. Anal papilla distinctly forcipate in appearance (Fig. 196). Posterior pair of maxillary setae borne on base of capitulum. Nymphal genital plate completely separated from anus. Typically subtidal.

*longipes* (Trouessart) 1888; p. 126.
Long Island Sound. Also French Atlantic coast, North Sea, Baltic.

4b. Anal papilla not forcipate, scarcely projecting beyond end of body (Fig. 158). Both pairs of rostral setae borne on rostrum. Nymphal GA undivided. Typically intertidal...... *balticus* Lohmann 1889; p. 106.
Connecticut; New Brunswick.
Also French Atlantic coast, North Sea, Baltic.

**Halacarus (Thalassarachna) basteri basteri** (Johnston) 1836

Figures 143–154

Newell: The Halacaridae of Eastern North America


**Adult.** No satisfactory specimens are available for illustrating the entire animal. A good figure of the female was given by André (1927f, after Lohmann 1893a). André also reproduced Johnston's original figures. The appearance of the adult is essentially like that of the deutonymph (Fig. 143).

Palpi (Fig. 145) 4-segmented. P-2 1.54 times as long as P-4. Disti-dorsal seta of P-2 very long, extending well beyond tip of P-3. Spine on P-3 long, thick, more than half as long as P-3.

**Chaetotaxy of legs:**

<table>
<thead>
<tr>
<th></th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>d. v.</td>
<td>l. m.</td>
<td>d. v.</td>
<td>l. m.</td>
</tr>
<tr>
<td>1.</td>
<td>-</td>
<td>-1</td>
<td>-1</td>
<td>-</td>
</tr>
<tr>
<td>2.</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>3.</td>
<td>4</td>
<td>2</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>4.</td>
<td>4</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>5.</td>
<td>6</td>
<td>4</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>6.</td>
<td>6</td>
<td>8</td>
<td>2</td>
<td>1</td>
</tr>
</tbody>
</table>

I-3 with the ventral setae and the medial seta spine-like. I-4 with the medial seta spine-like as in deutonymph, but with the ventral seta slender and tapering. I-5 with 3 pairs of heavy setae and 1 pair of slender setae ventrally and medially. In the specimen from which Fig. 150 is drawn the distal member of the lateral row (which is usually ventro-lateral in position) had moved ventrally so that it arose very close to the insertion of the distal member of the ventral series. On I-6, in addition to the setae shown in the table, there is a single bacillum just distal to the insertion of the lateral member of the disti-dorsal pair, as in the deutonymph. Parambulacral setae very small, scarcely reaching to end of tarsus. There is probably some variation in the number of setae of the ventral surface, as is the case in the deutonymph. Claws of leg I shorter than those of other tarsi, but with same structure.

The setae of leg II are generally more slender than those of I, although their number and arrangement correspond closely. The
principal differences are apparent from the tables and the figures. Bacillum on medial membrane rather than on lateral membrane of claw fossa. Parambularcal setae divaricate. The principal chaetographic feature of III and IV is in the disti-ventral pair of setae of segment 5. The medial member of this pair is heavier and shorter than the inner member of the pair. There is a single parambularcal seta on each side of tarsi III and IV.

**Deutonymph.** Dorsum as shown in Fig. 143. AD with prominent frontal process. Genital and anal plates separated by considerable distance (1.5 times length of genital plate in older nymphs). Genital plate wider posteriorly than anteriorly, with 1 seta at each corner and 2 pairs of subgenital setae; 2 pairs of internal suckers present. Palpi and chelicerae as in adult but smaller.

Median and ventral setae on I-3 and I-4 spine-like (Fig. 152), but ventral seta of I-4 more tapering than the others. I-5 with 2 spiniform setae and a long seta ventrally and medially, the medial member of each pair being smaller. Bacillum and parambularcal setae as in adult. Carpus very short, carpite absent. Median claw bidentate. Lateral claws short, heavy, with distinct comb and an apparent accessory tooth.\(^{20}\) Claw fossa well developed; membrane equally well developed on each side of fossa and bearing the disti-dorsal setae of I-6. Bacillum curved ventrad so that it lies close against the lateral membrane of the claw fossa (difficult to find). Chaetography of II nearly

\(^{20}\) Lohmann (1889a: 344) interpreted the comb as a double comb, which would lead one to believe there was a separate comb on each side of the claw. Actually, there is a single J-shaped comb, the long arm of which extends down that side of the lateral claw which is nearer the median claw, bends smoothly around the end of the claw, and extends up the other side for about one-third the length of the claw. This is shown in Fig. 147, which is an oblique view from below, and Fig. 148, which is a direct ventral view of the claw. From these it is apparent that the accessory tooth in this species is an illusion, it being simply the most distal teeth at the end of the canopy-like comb. In other forms, of course, this is not true, since there is usually a distinct accessory tooth which is developed as the enlarged terminal tooth of the comb, or as an isolated tooth when the comb is absent.

---

**Figures 138–142.** *Halacarus* (s. str.) *anomalus* (continued). 138 Female: leg I, lateral view. 139 Female: III-5 and III-6, lateral view. 140 Female: I-6, disti-lateral view. 141 Female: I-6, medial view (bacillum and prebacillum omitted). 142 Female: II-5 and II-6, medial view (bacillum is lateral in position).

Halacarus (Thalassarachna) balticus Lohmann 1889

Figures 155-167


identical with that of I, but the spiniform setae of I are here reduced to long, stiff, tapering setae (Fig. 153). The proximal ventral seta of II-5 is unpaired and the distal pair of setae is longer and heavier than the proximal, whereas on I-5 the distal pair is the smallest. III-6 with 5 setae dorsally, in addition to the bacillum, which is on the medial membrane of the claw fossa rather than the lateral, and is more erect than that on I-6. The ventral setae show considerable variation, there being from 3 to 5 setae here, judging from the material available (1 unpaired plus 1 paired, 1 unpaired plus 1 paired plus 1 unpaired, or 1 unpaired plus 2 paired, the basal member always being unpaired, with 1, 1½, or 2 pairs of setae distally). In addition there are the divaricate parambicular setae. There are no special chaetographic features on III and IV. The parambicular setae are simple, there being a single seta on each side of the tarsus. A prominent claw fossa is found on all tarsi, and membranes are also present.

Remarks. This was the first halacarid to be described from our shores, having been described by Packard in 1871 under the name of Thalassarachna verrilli. The present writer has elsewhere (1945a) established the identity of Packard’s mite and has discussed the taxonomic significance of its rediscovery. This subspecies can be separated from the other subspecies by means of Viets’ key (1940g: 10). Thor (1931e: 61) erroneously listed this species as being synonymous with Molgus (Molgus) littoralis (L.) 1745.


Halacarus (Thalassarachna) balticus Lohmann 1889

Figures 155–167

Female and male of same size, 595–700μ long (av. 665μ) and 380–465μ wide (av. 430μ); body 1.45–1.70 times as long as broad (av. 1.50); based on 8 males and 8 females.

Male. (650μ long.) AD 167μ long and 165μ wide at level of leg I. Anterior margin convex, not produced; lateral margins converging posteriorly, the postero-lateral margin rounded and the posterior margin concave. Conchoidal sculpturing present anteriorly, laterally and posteriorly; remainder of surface only punctate. A single pair of setae near middle of plate.

OC 91 and 100μ long, 75 and 78μ wide; not quite reaching to level of AD anteriorly nor PD posteriorly. Lateral angle a rounded protuberance extending beyond margin of body and visible in ventral view. A pore opens on this protuberance and a second pore is at the posterior end of OC. Single cornea present near anterior margin. Conchoidal sculpturing especially well developed along medial margin but variably developed laterally. PD 346μ long and 256μ wide (1.35 times as long as broad), with a pair of prominent longitudinal ridges. Portions between, and lateral to, ridges depressed and with prominent conchoidal sculpturing. A pair of setae in lateral depressed areas near middle of plate; posterior margin bluntly produced, concealing anal protuberance below. GA and PD completely fused posteriorly, as verified in sectioned material. Dorsal membranous area with 3 pairs of setae. On either side the striations between the two anterior setae and those between the posterior setae and OC are very irregular (even in gravid females). Ocular plates 215μ apart; AD and PD 120μ apart. AE 190μ long, extending to level of seta anterior to III. Cuticle minutely punctate, but neither sculptured nor panelled. Margins of body with slight constriction between AE and PE at level of lateral protuberances of OC.

PE with only 2 pairs of setae ventrally and 1 pair dorsally; panelling present laterally and dorsally, but ventral surface only punctate (as in AE). GA 300μ long and 255μ wide, extending to or slightly beyond level of posterior setae of PE; oval in form. Genital opening 115μ long, surrounded by 125–140 long, slender setae. Genital opening on a raised portion of GA. Most of cuticle punctate, with panelling developed only along lateral margin and posterior to genital area. Opening guarded by 5 pairs of external setae (external position verified in sections). Membranous areas of ventral surface deeply striate except for the spindle-shaped muscle attachment areas between...
AE and PE. Striations very irregular near the medial angle of each PE.

Capitulum (Fig. 159) 200μ long and 118μ wide; rostrum 85μ long and 48μ wide at base. (A second male, 680μ long, has a capitulum 218μ long and 125μ wide at the widest part of the base. The rostrum alone was 81μ long and 48μ wide.) Cuticle of base punctate but not panelled. Rostrum smooth, conical, reaching to a point about 1/2 length of P-2 from end of that segment, with a pair of long setae at or slightly beyond level of distal end of P-1, a second pair about 1/2 length of rostrum from end, and a pair of very minute setae at tip. Because of their oblique course, the latter setae appear to be only 3μ long, whereas actually they are 7μ or 8μ long and 1μ thick. Base of rostrum very slightly constricted. Pharyngeal plate bearing 16 to 18 closed cells in an irregular double row which is bordered on each side by a row of 8 to 9 cells which lack distinct outer walls. Chelicerae and palpi as in female.

I-3 with 2 setae ventrally. I-5 with 4 pairs of ventral setae, the basal pair and the outer member of the second pair spine-like.

In one specimen the first three setae on the outer side, as well as the first seta on the inner side, are spine-like. Lohmann (1889: 342) showed considerable variation in these setae. I-6 with an unpaired ventro-median spine. II-5 with 2½ or 3 pairs of setae ventrally. III and IV lacking any special chaetographic features. All tarsi with prominent claw fossa, all claws pectinate and with accessory tooth. A very minute middle claw can be seen on tarsi I and II of some specimens, but this is weakly developed and variable, sometimes being found on only one or two tarsi of an individual. Color in life highly variable, ranging from yellow and orange in young adults and nymphs to brown, gray or nearly black in adults.

Female. Virtually identical with male except in characters of GA. In a female 670μ long, GA measured 263μ long and 263μ wide. Antero-lateral margin at least flattened and usually slightly concave; anterior margin straight or nearly so. Two pairs of setae on genital portion of plate, and a third pair of strongly incurved setae dorsal and


Figures 155–156. *Halacarus (Thalassarachna) balticus* Lohmann 1889. 155 Female: leg I, lateral view. 156 Female: palp, median view.
Newell: The Halacaridae of Eastern North America

The rostrum is about 1/2 as long as the cephalothorax. The rostrum is punctate but not smooth. There is a row of long setae at or near the tip. The rostrum is about 1/2 as long as the cephalothorax. The rostrum is punctate but not smooth. There is a row of long setae at or near the tip.

The rostrum is about 1/2 as long as the cephalothorax. The rostrum is punctate but not smooth. There is a row of long setae at or near the tip. The rostrum is about 1/2 as long as the cephalothorax. The rostrum is punctate but not smooth. There is a row of long setae at or near the tip.

The rostrum is about 1/2 as long as the cephalothorax. The rostrum is punctate but not smooth. There is a row of long setae at or near the tip. The rostrum is about 1/2 as long as the cephalothorax. The rostrum is punctate but not smooth. There is a row of long setae at or near the tip.

The rostrum is about 1/2 as long as the cephalothorax. The rostrum is punctate but not smooth. There is a row of long setae at or near the tip. The rostrum is about 1/2 as long as the cephalothorax. The rostrum is punctate but not smooth. There is a row of long setae at or near the tip.

The rostrum is about 1/2 as long as the cephalothorax. The rostrum is punctate but not smooth. There is a row of long setae at or near the tip. The rostrum is about 1/2 as long as the cephalothorax. The rostrum is punctate but not smooth. There is a row of long setae at or near the tip.

The rostrum is about 1/2 as long as the cephalothorax. The rostrum is punctate but not smooth. There is a row of long setae at or near the tip. The rostrum is about 1/2 as long as the cephalothorax. The rostrum is punctate but not smooth. There is a row of long setae at or near the tip.

The rostrum is about 1/2 as long as the cephalothorax. The rostrum is punctate but not smooth. There is a row of long setae at or near the tip. The rostrum is about 1/2 as long as the cephalothorax. The rostrum is punctate but not smooth. There is a row of long setae at or near the tip.
lateral to anus in region where GA and PD are continuous. Similar setae in male. Oval genital area 141μ long and 106μ wide. GA in younger adult females extending anteriorly beyond IV, but in old gravid females not quite reaching to IV owing to the stretching of the membranous area (cf. Viets 1927a: 122, in which the cephalad extent of GA is used as one diagnostic character).

Palpi, chelicerae and legs as in male. The following measurements and notes are based on a female about 700μ long. Palpi as in most other species of the subgenus. One long seta dorsally on P-2, 3 on basal portion of P-4, and an extremely small seta near tip of P-4. P-4 with 2 small setae closely appressed to sides of tip of segment. P-3 with heavy spine. L/H of P-1 to P-4: 25/31, 83/36, 27/22, 51/10μ. Chelicera 4.9 times as long as high. Leg I with L/H of principal segments as follows:

<table>
<thead>
<tr>
<th></th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>Claw</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>135/55</td>
<td>73/45</td>
<td>131/47</td>
<td>55/28</td>
<td>37/15</td>
</tr>
<tr>
<td>II</td>
<td>120/50</td>
<td>63/42</td>
<td>118/38</td>
<td>108/17</td>
<td>48/32</td>
</tr>
<tr>
<td>III</td>
<td>116/41</td>
<td>75/37</td>
<td>125/33</td>
<td>128/27</td>
<td>42/32</td>
</tr>
<tr>
<td>IV</td>
<td>131/48</td>
<td>75/40</td>
<td>131/35</td>
<td>131/27</td>
<td>43/30</td>
</tr>
</tbody>
</table>

*Deutonymph.* 425–570μ long. The drawings are made from a specimen 465 x 300μ. Dorsal plates very similar to those of adults. OC projecting beyond lateral margins as in adult; cornea present. GA undivided; 2 pairs of genital suckers present, 2 pairs of setae ventral to anterior suckers.

*Protonymph.* 310–430μ long. Dorsal plates very similar to those of deutonymph and adult except in size. OC projecting beyond lateral margin, cornea present. GA undivided; a single pair of genital suckers present.

I-3 with only the triangle setae. I-5 ventrally with 2 pairs of setae of which the basal pair is spine-like. Tarsi and claws as in adult. In Figs. 163 and 164, two protonymphs are drawn to the same scale, and from these drawings it is clear that nymphal growth within any
Newell: The Halacaridae of Eastern North America

Continuous. Similar to A. laevigata. GA in IV, but in old beets stretching of the cephalad extent of wing measurements.

Palpi as in most species on P-3. 3 on tibia near tip of P-4. Base of tip of segment, 5.8, 7.5, 8.0, 8.75, 9.0, 9.5.

Ch. 1/2 of principal

are made from 1 to those of adults, with 2 pairs of setae very similar to those projecting beyond single pair of gnath.

with 2 pairs of setae claws as in adult to the same scale growth within say

118

157

158

159

160

161

162

163

164

165

166

167

168

SUBGENITAL SETAE

Halacarus (Thalassarachna) subterraneus (Schulz) 1933

Figures 168-178

Female. Body 450–568μ long, 256–332μ wide, L/W = 1.60–1.84 (average of 10 specimens 490 x 286μ. L/W = 1.71).

Anterior and posterior margins of AD nearly straight as a rule, but posterior margin occasionally distinctly convex, or there may be short postero-lateral margins forming a six-sided plate; lateral margins converging only slightly (Fig. 169); a single pair of setae anterior to the middle of AD. Widest portion of OC about ⅓ length of OC from its anterior end; plates tapering to a rounded point posteriorly; corneae absent, but 2 pairs of pores lie along sides of plates. PD straight anteriorly, with sides converging only slightly and with 3 pairs of setae present. Anus projecting beyond end of plate. Dorsal plates finely punctate; delicate panelling covering most of surface. Membranous areas greatly restricted, with very delicate parallel striae, with a pair of setae anterior to OC, and with a second pair near the antero-lateral angles of PD. A pair of slender platelets between PD and PE which are punctate and occasionally have a few small panels but which bear neither setae nor pores.

AE with right and left halves fused; posterior margin straight; 3 pairs of setae present. PE with 3 pairs of setae ventrally and 1 pair dorsally. GA undivided; 2 pairs of setae outside the oval area. Genital opening about ⅓ length of GA, guarded by a pair of strap-like sclerites extending longitudinally, each bearing 2 minute setae (or 1 seta) at anterior end and a heavier seta behind middle of sclerite. Three pairs of suckers internally, 2 pairs at middle of opening and 1 pair near posterior end; 2 pairs of heavy internal setae between posterior suckers (Fig. 173). These latter setae are on the ovipositor itself and are certainly the posterior 2 pairs of setae which Schulz (1933: 101) associated with the pair near the middle of the band. However, the former are external whereas the latter are internal. Membranous areas restricted and containing 2 (or 3) pairs of sclerites. The largest pairs (the “längliche lichtbrechende Flecken” of Schulz, 1933: 101) are always present and lie between AE and PE and between PE and GA. In addition, there is usually a pair of very minute sclerites at the inner angles of PE. The 2 large pairs serve as muscle attachments. In a female with a body length of 488μ and a width of 291μ, the following measurements were obtained: AD 138μ long, 164μ wide; OC 125 x 58μ, and 126 x 65μ; PD 332 x 201μ; AE 166μ long; GA 256 x 194μ; genital area 97 x 76μ.

Capitulum as in male and palpi of usual form. In one female
(AE 126µ long and 141µ wide) these measurements of P-1 to P-4 were obtained (dorsal L/H): 15/23, 56/37, 22/15, 29/7.5µ (ratios of L/H = 0.65, 1.51, 1.47, 3.87). Chelicerae 153µ long and 40µ high. Base of chelicera relatively short and quite uniformly thick.

Legs very characteristic; chaetotaxy as follows:

<table>
<thead>
<tr>
<th></th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
</tr>
</thead>
<tbody>
<tr>
<td>d.</td>
<td>v. l.</td>
<td>m.</td>
<td>d.</td>
<td>v. l.</td>
</tr>
<tr>
<td>1.</td>
<td>-</td>
<td>-</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>2.</td>
<td>1</td>
<td>1</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>3.</td>
<td>2</td>
<td>3</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>4.</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>5.</td>
<td>4</td>
<td>4</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td>6.</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
</tr>
</tbody>
</table>

I-3 with 2 stiff, blunt setae dorsally and 3 very long, heavy spine-like setae ventrally. Medial seta of I-4 flattened, pectinate. I-5 with a row of 4 setae ventrally, the basal 3 spine-like, the fourth slender and tapering; a similar row of setae found medially. Three of 20 specimens have only 2½ pairs of spine-like setae on one leg (1½ pairs of slender setae), but the other leg has the normal three pairs. It must be expected, therefore, that an occasional individual will be found which has 2½ pairs of spines on each side, but this would have no taxonomic significance whatever if it were found only in isolated instances. The six “dorsal” setae in the above table are not strictly dorsal, but are so designated to avoid confusion with the others. Chaetography of I-6 virtually identical with that of H. capuzinus, differing only in relative sizes of the various setae (compare Fig. 171 with 187). Prebacillum not so perfectly formed and appearing to be a flattened expansion of the membrane rather than a distinct seta; although partly hollow, it does not appear to have an external opening. Median claw bidentate, lateral claws completely smooth.

II-3 with only 1 slender seta ventrally. Medial seta of I-4 often faintly pectinate, but not always so. II-5 has only 3 pairs of heavy setae, none of which are as heavy as those on I-5; the medial 3 are pectinate. II-6 with the bacillum but without prebacillum; parambulacral setae well formed. The bacillum is on the medial claw.

long, heavy spined, pectinate. In the fourth slightly. Three of B in one leg (1 1/2 pain and three pairs. It will be found this would have oed only in isolated e are not strictly in with the other of H, cf. op. (compare Fig. 11 appearing to be an a distinct set s external opening ooth.

sets of L-4 six 3 pairs of heavy the medial 3 are bacillum; para-
the medial clas
membrane rather than on the lateral membrane. Median claw not bidentate; lateral claws with comb and a fine accessory tooth.

III-3 and IV-3 with 2 stiff, usually blunt setae dorsally; III-5 and IV-5 with the 3 ventro-medial setae heavy, pectinate, the ventro-lateral seta slender, smooth. III-6 and IV-6 without bacillum.

**Male.** Somewhat smaller than female. Body 422–506 μ long, 242–298 μ wide, L/W = 1.65–1.74 (average of 10 specimens: 469 x 276 μ, L/W = 1.70). Dorsum and venter as in female, except for GA. Schulz (1933: 101) indicated that the posterior platelets between GA and PE are absent in the male, but this was probably due to an oversight. Occasionally in prepared specimens they are turned on edge or pushed under the edge of GA so that they are difficult to see.

GA with 22 to 26 slender setae on each side of the plate. There is also a group of 12 to 15 small refractile spots on each side of the opening which are either pores or large puncta; they are quite irregular in shape and size and usually are disposed in a somewhat radial manner. Genital opening guarded by 5 pairs of heavy setae (Fig. 176). **Fig. 178, at a much higher magnification, shows the form and arrangement of the setae more accurately, and shows also the three genital suckers of the right side. Since these face the mid-line they appear as block-like structures rather than circles (compare with *H. capuzinus*). It is difficult to determine whether the setae are external, but they most likely are (see *H. balticus*).

Capitulum (in a male with a body length of 464 μ) 139 μ long and 95 μ wide; rostrum alone 61 μ long and 38 μ wide just distal to the slightly constricted base (Fig. 177). Tip of rostrum sharp, reaching to, or nearly to, end of P-2. Sides of rostrum converging uniformly toward tip; 2 pairs of setae present and a pair of short, heavy spines at end of rostrum. Pharyngeal plate with about 15 closed cells and 6 to 8 open cells. Palpi as in female. Legs also as in female but with a tendency toward slightly heavier spines and more distinct pectinations.

---

**Figures 176–178. Halacarus (Thalassarachna) subterraneus** (continued). **176** Male: genito-anal plate. **177** Male: capitulum, ventral view. **178** Male: genital opening (internal suckers on one side, setae on other).

**Figures 179–184. Halacarus (Thalassarachna) capuzinus** Lohmann 1893. **179** Female: cheliceræ. **180** Female: dorsum. **181** Female: venter. **182** Deutonymph: genito-anal plate. **183** Female: leg IV, ventro-medial view. **184** Male: genito-anal plate (same scale as 182).
Newell: The Halacaridae of Eastern North America

1947

Figure 176: Median claw not very tooth.

Figure 177: III-3 and 4 acute, the ventral cuticularium.

Figure 178: 2-506a long, 241-nenos: 406-276.

Figure 179: A, except for Gp. electa between Gp. clypeus due to an over-lapping or edginess difficult to see.

Figure 180: A plate. There is a side of the opening of the irregular in shape at radial manner (Fig. 178). Fig. a and arrangement of the apical plates appear as block-like in H. abdominalis, but they are distinct perinotum.

Figure 181: 130a b long at the just distal to the um, sharply, reaching the lamina uniformly short, heavy spines.

Figure 182: 5 closed cells and in male but with a distinct perinautal plate (accessorial).
**Deutonymph.** Body 360 x 200 μ (varying, of course, with age of nymph), closely resembling adult in general appearance. PD rather sharply rounded anteriorly but not truncate as in adult; a pair of platelets between PD and PE as in adult. I-3 with only 2 spines ventrally and with only a single seta dorsally behind the triangle setae. I-4 with single pair of spines ventrally and the triangle setae dorsally. I-5 usually with 3 pairs of setae ventrally and medially, only 2 pairs of which are spine-like. This segment is variable as in the adult. III-5 and IV-5 with 2 small pectinate setae ventro-medially. In one individual a single one is present on III-5 of one side, and 2 on the opposite leg. Platelets between AE and PE and between PE and GA present as in adult. GA undivided; 2 pairs of setae away from genital area and 2 pairs of smaller subgenital setae near the suckers, arranged as shown in Fig. 168.

**Protonymph.** Easily recognized on plate characters. I-3 with a single ventral spine; I-4 with a very heavy spine-like seta ventrally, which is not only relatively, but actually, longer than in deutonymph or adult (Fig. 174). GA as in deutonymph but with only 2 suckers.

**Larva.** Most easily recognized by heavy ventral seta on I-4 and the ventral platelets between AE and PE. The dorsal platelets and the ventral platelet between GA and PE are lacking. Legs 5 segmented, segments 2 and 3 fused.

**Remarks.** There can be little question that this is identical in all significant respects with the European form, although this is not apparent when the present description is compared with the original one of Schulz. The fact that Schulz completely overlooked the very striking platelets behind OC indicates that any discrepancies in the two descriptions probably do not represent real differences. Viets (1936f: 548) showed these platelets to be present in the European form.

**Distribution.** North America: New Haven County, Connecticut (Morris Cove).

Baltic Sea.

**Halacarus (Thalassarachna) capuzinus** Lohmann 1893

Figures 179–191

Newell: The Halacaridae of Eastern North America

119


Female. Body 290–367µ long, 145–196µ wide; 1.8 to 2.0 times as long as broad. AD 75–80µ long, 80–85µ wide; usually with short, broad antero-median projection. Panelling weakly developed except at margins. Posterior margin nearly straight, the postero-lateral angles rounded. A single pair of setae at about middle of plate. OC 40–50µ long, 25–30µ wide; rather variable in proportions. Anterior margins sloping outward, the sides parallel for a considerable distance or converging posteriorly throughout. Cuticle usually with several conchoidal panels. Anterior end of plates anterior to hind margin of AD. Corneae absent; 1 pore at posterior end. PD 190–210µ long, 110–120µ wide, separated from AD by a distance of about 12µ, rather ovoid, with truncate, slightly convex anterior margin, the widest portion about ⅔ length of plate from anterior end. Conchoidal panelling covering usually only the postero-lateral margins, but occasionally more extensive. A pair of setae at widest portion of plate and a second pair at the posterior end dorsal to the projecting anus. In the striated membranous areas of the dorsal side are 3 pairs of platelets, each bearing a seta.

AE 100µ long, convex posteriorly, with 3 pairs of setae; panelling absent. GA 142µ long, 91µ wide, oval in outline, with a deep furrow between genital and anal portions. Genital opening 55µ long and 35µ wide. A few conchoidal panels at margin of plate opposite genital opening; remainder of plate smooth, with 2 pairs of setae present. PE with a long seta dorsally, anterior to III; 2 pairs of small setae ventrally. Panels few in number, conchoidal in form and irregularly disposed. Dorsal margin of PE often very irregular between III and IV.

Capitulum 83µ long and 58µ wide; cuticle punctate but not panelled. Rostrum alone 38µ long, usually reaching to a point about ¼ length of P-2 from distal end of that segment (in one specimen it extended slightly beyond the tip of P-2); base swollen but not constricted. A series of five specimens had rostra 35 to 45µ long and 1.62 to 1.76 times as long as broad. Pharyngeal plate with 10 or 12 cells in a double row, sometimes irregular in arrangement and with open lateral cells. Palpi with P-2 somewhat swollen; P-4 much shorter than P-2; all segments faintly punctate. One long seta dorsally on P-2, 3
on basal portion of P-4 and an extremely small seta near tip of P-4. At least 1 and probably 2 setae lie closely appressed to end of P-4, but exact structure of tip of palp difficult to determine. Dorsal lengths of P-1 to P-4/vertical height: 9/27, 41/21, 14/13, 24/6μ. The spine on P-3 is very heavy and is about 8μ long and 4μ wide at base.

Chaetotaxy of legs:

<table>
<thead>
<tr>
<th></th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
</tr>
</thead>
<tbody>
<tr>
<td>d. v. l. m.</td>
<td>d. v. l. m.</td>
<td>d. v. l. m.</td>
<td>d. v. l. m.</td>
<td></td>
</tr>
<tr>
<td>1.</td>
<td>- - - 1</td>
<td>- - - 1</td>
<td>- - - 1</td>
<td>- - - -</td>
</tr>
<tr>
<td>2.</td>
<td>1 1 - -</td>
<td>1 1 - -</td>
<td>1 - - 1</td>
<td>1 1 - -</td>
</tr>
<tr>
<td>3.</td>
<td>3 1 - -</td>
<td>3 1 - -</td>
<td>2 - - 2</td>
<td>2 - - -</td>
</tr>
<tr>
<td>4.</td>
<td>3 2 - -</td>
<td>3 2 - -</td>
<td>2 - 1 -</td>
<td>2 1 - -</td>
</tr>
<tr>
<td>5.</td>
<td>5 6 - -</td>
<td>4 2 - -</td>
<td>3 3 - -</td>
<td>3 3 - -</td>
</tr>
<tr>
<td>6.</td>
<td>3 2 - 1</td>
<td>3 - - -</td>
<td>3 - - -</td>
<td>3 - - -</td>
</tr>
</tbody>
</table>

Typically there are three setae dorsally on I-3, but frequently there are only two, the basal seta usually being the one to drop out, although at least one case was observed in which the medial member of the distal pair is absent. Medial member of ventral pair of setae on I-4 often pectinate (oil immersion); lateral member smooth. I-5 with basal pair of setae spiniform but others slender. One specimen has II-5 of both sides with two pairs of spines and two pairs of setae, but this is probably an individual variation which would be found to intergrade with the normal condition if a large enough series were available for study. In all other respects this mite is similar to the others. Outer members of 2 distal pairs of setae somewhat heavier than inner members. In addition to the setae noted in the table, I-6 bears a bacillum, a degenerate prebacillum and the divaricate parambulacral setae. Bacillum on inner surface of lateral membrane of claw fossa, and somewhat thicker distally than basally. Just anterior to the base of the bacillum is the prebacillum. In Fig. 185 the medial membrane of the claw fossa partly conceals the prebacillum and the base of the bacillum. The lateral parambulacral setae are larger than the medial setae. The abnormally erect position of the medial parambulacral setae, and also the dorsal setae in Fig. 185 is due to distortion during preparation. Medial seta of I-6 spine-like. Claws with accessory tooth but without comb. Claw fossa well developed. Median claw bidentate.

Leg II differing from I in several respects. Medial member of ventral pair of setae on II-4 extremely fine but not pectinate. II-5
with only 2 setae ventrally, the lateral one pectinate; one specimen
from New Brunswick had 2 pectinate setae and 1 smooth seta ventrally
on II-5 of the left side, but the right leg was normal. II-6 with no
ventral setae; in addition to the dorsal setae there is a bacillum but no
prebacillum, and the parambculacral seta is reduced to a single member
on each side. However, there is no doubt that this represents the
double seta on I-5. The bacillum is on the medial membrane rather
than the lateral and is larger than that on I-6. Claws with accessory
tooth and a comb, the proximal teeth usually very heavy (Fig. 183).
Median claw not bidentate.

Ventral-medial setae on III-5 and IV-5 prominently pectinate, the
ventro-lateral seta slender, smooth. III-6 and IV-6 with 3 dorsal
setae and in addition, 2 setae near base of ambulacrum which are
homologous with the divaricate setae on I-6 and their single-membered
homologues on II-6. However, these setae have undergone further
modification, for although the medial member is rod-like as on I and
II, the lateral member is very slender and tapering. Claws on III
and IV identical in form with those of II; median claw with a single
tooth. In a female with a body length of 346\(\mu\) the following measure-
ments were obtained (dorsal length in \(\mu\)/maximum height):

\[
\begin{array}{ccccccc}
1+2 & 3 & 4 & 5 & 6 & \text{Ambul. Total} & T/BL \\
I & 35 & 78/28 & 46/27 & 78/23 & 56/13 & 16 & 309 & .89 \\
II & 32 & 55/23 & 32/20 & 55/20 & 53/13 & 20 & 247 & .72 \\
III & 58 & 50/20 & 35/18 & 66/17 & 70/13 & 22 & 301 & .87 \\
IV & 60 & 61/18 & 37/18 & 66/18 & 65/13 & 20 & 309 & .89 \\
\end{array}
\]

The color of the mid-gut is highly variable. Brown is common, but
yellow and red also occur.

**Male.** The bodies of three males measure 291–298\(\mu\) long and 148–
152\(\mu\) wide, L/W = 1.91–1.97. Virtually identical with female in all
respects except in characteristics of GA. In a male with a body length
of 291\(\mu\), GA was 150 × 107\(\mu\); the genital opening was 48 × 30\(\mu\).
Genital portion of plate separated from anal portion by a deep furrow,
bearing 35 to 38 setae on each side of opening. Genital opening
-guarded by 5 pairs of setae as shown in Fig. 184, with 3 pairs of in-
ternal genital suckers present at posterior end of opening. Panelling
absent on anterior half of GA but faintly developed in raised posterior
half in which genital opening is located.
Deutonymph. 250–260μ long, 130–140μ wide, resembling adult and protonymph in most major features (Fig. 190). I-5 with 2 pairs of setae ventrally and 4 setae dorsally. GA undivided; 2 pairs of suckers present (Fig. 182). In addition to the 2 pairs of large setae there are 2 pairs of very minute setae just anterior to the genital suckers (oil immersion).

Protonymph. The specimen from which the figure is drawn is 200μ long and 110μ wide. Closely resembling adult and deutonymph in the presence of the antero-median projection of AD, the six dorsal platelets lying in the striated membranous area and in chaetotaxy of plates. The platelets are as large as in the adult and consequently they are relatively more conspicuous. Plates prominently sculptured. PD with a pair of longitudinal costae. GA undivided, with one pair of genital suckers. I-5 with single pair of setae ventrally and the triangle setae dorsally.


Baltic Sea.

Halacarus (Thalassarachna) capuzinus Lohmann and H. (Th.) procerus Viets 1927

These have the following characteristics in common (among others): Male and female with 3 pairs of platelets within dorsal membranous area, one between OC and AD, one between OC and OC and one between OC and PD. Each platelet bears a seta. OC without corneae.

The European forms have been separated on the following characters by Viets (1927a: 127–128).

H. capuzinus Lohmann: I-5 with 3 pairs of setae ventrally, 5 of the 6 being spiniform. AD with frontal process. Ocular plates distinctly less than twice as long as broad. Body 280–300μ long.

H. procerus Viets: I-5 with 4 pairs of ventral setae, of which the proximal pair is spine-like, the remainder setiform. OC more than twice as long as broad (67 x 30μ). Membrane between dorsal plates
essentially broader than in _capuzinus_. Body 475μ long and 240μ wide. I-5 with 2 setae behind triangle setae. Rostrum 65 x 35μ (L/W = 1.86), reaching to end of P-2. AD lacking frontal process. P-2 (_not_ nearly 4) 3 times as long as P-3. Membranous areas more extensive than in _H. capuzinus_. I-4 (_not_) relatively longer than in _H. capuzinus_. The parentheses have been inserted by the present writer to show where Viets' statements are refuted by his measurements or figures.

Further study of _H. capuzinus_ by Schulz and by the present writer indicate that the actual differences between that species and _H. procerus_ are not so great as would appear from the published descriptions, and that at least _H. capuzinus_ is highly variable. Schulz (1933: 98–99) recorded a form from the Baltic which he identified as _H. capuzinus_, although it differed from Lohmann's description in a few respects. In Schulz's form I-5 had three pairs of setae ventrally, of which the basal pair was spine-like and the others setiform. This is the condition found in New Brunswick and Connecticut specimens and is probably typical of the species. That this character can be extremely variable is shown by the specimen noted by the writer in which there are four pairs of setae on I-5, of which the two basal pairs are spine-like. Another specimen shows this condition on one side of I-5 of one leg, but the other side of this segment is normal, and I-5 of the opposite leg is also normal. Another specimen has two setae dorsally and one pair of setae ventrally (Slide 43-123-62) on I-5 of the left side, but the right side is normal. It seems very probable that much of this variation is brought about by injury of the trichogens in the nymphal stages. The fact that _H. (Th.) subterraneus_ shows similar variability suggests that arenicolous mites in general, especially the larger ones, may be subject to marked variations in the setae of the legs, possibly owing to the rather precarious nature of the habitat of those individuals living in the top few centimeters of the beach. In Schulz's specimens there were five setae dorsally on I-5 (as in the North American forms), whereas Lohmann noted only three.

Schulz also noted that OC is not always rhombic but may be longer, approaching those of _H. procerus_ in proportions. The writer has found that in the North American forms OC may be 2.0 times as long as broad (51 x 25μ), although as a rule they are relatively shorter. The greater extent of the membranous area, the dorsal body length (475μ) and the relatively greater extent of the rostrum in _H. procerus_ may be
significant characters, but the differences in form between the rostrum of *H. procerus* and that of *H. capuzinus* is probably not as clear-cut as one would expect from the descriptions. In *procerus*, the rostrum is 1.86 times as long as broad (1 specimen apparently), while in the five North American specimens measured by the writer the rostrum is 1.62 to 1.76 times as long as broad. Thus, the range in these five specimens is greater than the difference between the most slender rostrum in the series and Viets' single record.

Viets (1927a: 128) gave the dorsal lengths of P-1 to P-4 as 15, 65, 22, and 37μ, which agreed with his figure and scale on p. 127. But he also said (in comparing *H. capuzinus* and *H. procerus*), "Das P. II ist, mit dem des *H. capuzinus* verglichen, erheblich schlanker (fast viermal so lang wie P. III, dort wenig mehr als dreimal so lang)." This statement does not agree in any way with his measurements and is incorrect as given. According to his measurements P-2 is 2.95 times as long as P-3. In the *capuzinus* specimen measured by the writer P-2 is 2.93 times as long as P-3; that is, it is identical with Viets' *procerus* specimen. Viets' distinction based on the presumed relatively greater length of I-4 in *H. procerus* also breaks down. Using Viets' measurements for *procerus* and the writer's measurements for *capuzinus*, I-4 is 0.59 times as long as I-3 in both cases; in *H. capuzinus* I-4 is also 0.59 times as long as I-5, whereas Viets' figures of 68μ and 112μ give a ratio of 0.61, an insignificant difference. Further, two *capuzinus* specimens have been found by the writer in which the frontal process is absent, and another in which the process is so broad as to make AD appear gently rounded along the anterior margin.

Therefore, the only distinctions between *H. procerus* and *H. capuzinus* which have not been found to intergrade are the size, the extent of the membranous areas, and the proportions of OC and of the rostrum. Since Viets' description of *procerus* appears to have been based on limited material (perhaps a single specimen), it is very probable that further study will show the differences to be even less significant. Those which now exist may be attributable to the difference in size alone. Unless further work does show *procerus* and *capuzinus* to be distinct, it would be advisable to consider *procerus* a synonym of *capuzinus*. For the present, however, it seems advisable to leave the nomenclature as little disturbed as possible.
Halacarus (Thalassarachna) longipes (Trouessart) 1888
Figures 192–196


Male. Only one adult male was taken, so that a satisfactory description of the species is not possible. It was very soft-bodied and apparently young. Body 410µ long to tips of anal papilla and 305µ wide. AD 101µ long, 102µ wide, OC 55µ long, PD 174 x 115µ. Panelling very feebly developed on PD and AD. AD and OC with a few coarse pores as shown in Fig. 196; 2 feebly developed corneae present, the posterior one much smaller than the anterior; PD with a single pair of setae. Several prominent apodemes at posterior end of AD.

AE with several delicate multi-pronged apodemes (internal); 3 pairs of setae present. PE with only 2 pairs of setae, the middle pair lying free in the membranous area on a minute sclerite. GA (Fig. 194) with an outer and an inner area in which the structure of the cuticle is slightly different. Outer portion with a structure very similar to that of the other ventral plates (thin, colorless, smooth), the inner portion faintly pigmented and thicker, bearing 90–100 (49 + 48 in the male studied) setae, the posterior setae very long. Genital opening immediately surrounded by a thick, chitinous band of unusual form and guarded by 4 pairs of spine-like setae, which are apparently internal. Two pairs of pores lie lateral to anal papilla. The anal...
a satisfactory
was very soft-bodied
of anal papillae
long, PD 174 vs. 115
AD and OC with a
developed cornae
anter. PD with
theses at posterior and

cements (internal); 1
stages, the middle pair
A (Fig. 194)
portion of the cuticle
very similar to
smooth), the inner
00 (49 - 48 in the
Genital opening
of unusual form
are apparently
spills. The anal
opercula, which are usually cusp-like in this genus, are greatly reduced, are not pointed at the end and reach only halfway to the end of the papilla. At the same time the side portions are relatively larger than usual, producing the forcipate appearance of the anal papilla which is so characteristic of this species. Membranous areas striate, with 2 pairs of apodeme-bearing platelets and a pair of minute, ring-like refractile bodies near the lateral margin between AE and PE, these probably being pores.

Capitulum (Fig. 192) 144μ long to tip of rostrum and 73μ wide; rostrum alone 71μ long and 28μ wide at base. Base of capitulum only slightly swollen. Rostrum nearly parallel-sided, the sides converging at an angle of less than 10° at the middle (therefore not strictly parallel). Tip of rostrum reaching to middle of P-3. Base of rostrum slightly swollen and bearing a pair of setae; base of capitulum bearing the second pair. Pharyngeal plate with 4 rows of closed cells.

On I-5 of the single male specimen available there are only 3 of the long setae ventrally but 4 medially (3½ pairs). In addition there are only 7 other setae on I-5 whereas Viets (1927a: fig. 49) showed 4 pairs of ventral setae plus 9 additional setae. In the specimen in the writer's collection there are 4 setae dorsally on I-3, whereas Viets showed 5. However, this is not sufficient grounds for a subspecific distinction on the basis of our present knowledge. Viets' specimen was a female, in which I-3 and I-5 measured 160 and 156μ respectively. In the author's single male I-3 and I-5 measure 121 and 119μ. The smaller number of setae in the latter may be directly correlated with this appreciable difference in size. Viets (1927b: 37) gave three additional figures of I-5. These agree with his previous figure (4 pairs of ventral setae plus 9 others). A large number of specimens from several localities would have to be examined in order to evaluate the significance of the differences pointed out above. Since, on other characters, the specimens in the author's collection are clearly H. longipes, it is advisable not to propose a new name.

Protonymph. This is the stage commonly taken in summer collections (from which the adults are absent). In life, they can be easily distinguished by their thick, leathery cuticle and bluish tint, as well as by the forcipate anal papilla. I-5 with 2 pairs of setae ventrally. Two pairs of corneae present on OC, the posterior one not so well developed. AD and PD small, but each contains a pair of setae (in addition to the ones just above the anal papilla).
Distribution. North America: Casco Bay, Maine; Connecticut (Stratford Point, and two unidentified stations in Long Island Sound, all below the intertidal zone).

English Channel, North Sea, Baltic, Mediterranean (?).

Genus *Copidognathus* Trouessart 1888


All the "groups," genera and subgenera listed above are synonyms of *Copidognathus* s. str. because the species that are "typical" of them, or their types, are consubgeneric with *Copidognathus* (s. str.) *glyptoderma* Trouessart 1888.

Diagnosis. Palpi attached to capitulum laterally; bases of palpi separated by a distance considerably greater than width of P-1, and clearly visible in ventral view. Palpi distinctly 4-segmented. P-4 usually longer than P-2, slender, tapering; attenuate distal portion longer than basal portion. P-2 with a single, usually long dorsal seta. P-3 without setae; P-4 with 3 setae on the thick basal portion. Palpi distinctly geniculate (see key). Genital suckers internal. Predaceous, usually marine; rarely fresh water. Cosmopolitan.

Type. *C. glyptoderma* Trouessart 1888.
**Key to North American Species (Males and Females)**

1a. Costae of PD with porose panels (Figs. 286, 292); not with rosette pores or modifications of these.

2a. OC drawn out into a caudiform appendage which reaches beyond insertion of leg III (Fig. 291). Female (and male?) with all ventral plates fused. With 2 pairs of maxillary setae. *bonairensis* (Viets) 1936; p. 172. Florida; Bonaire.

2b. OC rounded or angular posteriorly, not reaching to insertion of leg III. All ventral plates separate. With 3 pairs of maxillary setae.

3a. Ocular plates less than twice as long as broad. Posterior and anterior groups of porose panels of AD not confluent (Fig. 280). Portions of dorsal plates outside porose areas very distinctly panelled. When naturally extended, leg I is at least 0.7 as long as body. *pulcher* (Lohmann) 1893; p. 167. Florida; Bermudas, Ascension Island, Australia.

3b. Ocular plates more than twice as long as broad. Posterior and anterior groups of porose panels confluent (Fig. 284). Portions of dorsal plates outside porose areas very faintly panelled, appearing almost smooth at low magnification. Legs very short, leg I less than 0.6 as long as body. *pachypus*, new species; p. 170. Florida.

1b. Costae of PD with rosette pores (Figs. 234, 240, 248). If the rosette pores are modified, the modification consists of a reduction or loss of the canaliculi so that only a single to double row of coarse ostia or alveoli may be visible (*Copidognathus bairdi*, Fig. 234), but these never form porose panels.

4a. PD with rosette pores only on the costae (Fig. 263).

5a. Setae of AD behind posterior group (or groups) of rosette pores (Fig. 268).

6a. Costae of PD very narrow, only 1 rosette pore wide (Fig. 266). Cuticle between costae panelled, the panels not subdivided. III-6 and IV-6 with 4 setae dorsally. Leg I very nearly as long as, or as long, as body. *hummelincki* (Viets) 1936; p. 162. Florida; Bonaire; Aruba.

6b. Costae of PD 1 to 2 rosette pores wide (Fig. 268). Cuticle between costae panelled, the panels subdivided. III-6 with 4 setae dorsally, IV-6 with only 3. Leg I only about 0.8 as long as body when naturally extended. *caudatus*, new species; p. 164. Florida.

5b. Setae of AD in front of posterior group (or groups) of rosette pores (Fig. 253).

7a. AD with only 2 groups of rosette pores, the posterior group rectangular in form. Ocular plates with a sharp antero-lateral process. Cornea

**Note:** This key cannot be used safely to identify specimens mounted in balsam, damar, Clarite, glycerine jelly, or Berlese mixtures, because the structure of the rosette pores and certain other minute features cannot be resolved with ordinary optics when these media are employed. Hyrax, glycerine, water, and alcohol are satisfactory.
either absent, or directed forward in such a manner that they are not easily seen in dorsal view. AE with a few rosette pores behind the epimeral pores (Fig. 254).

7b. AD with 3 groups of rosette pores. Ocular plates without sharp anterolateral process. Cornea in usual position, clearly visible in dorsal view. AE without rosette pores behind the epimeral pore (Fig. 247).

8a. OC rounded posteriorly, extending only to level of leg III, not attenuate (Fig. 245). Rostrum reaching to end of P-2. Legs I and II with well developed lamellae on segments 3, 4 and 5 (degree of variability not yet known). Costae of PD not joined posteriorly by a transverse band of rosette pores... _anguistus floridensis_, new subspecies; p. 155.

Florida.

8b. OC attenuate posteriorly, extending well beyond level of leg III (Fig. 253). Legs I and II (also III and IV) with only small, usually pointed lamellae on segments 3, 4 and 5. Costae of PD usually joined posteriorly by a transverse band of rosette pores.

9a. Costae with a pronounced lateral swelling just behind level of leg IV, where the costae are about twice their normal width (Fig. 228). Rosette pores lacking canaliculi, appearing as coarse, simple pores. Female with ventral plate separate, male with ventral plates fused... _bairdi_, new species; p. 145.

Florida.

9b. Costae of relatively uniform width throughout, although sometimes slightly swollen at posterior extremities. Canaliculi present.

10a. Second pair of dorsal setae lying in the membranous area between AD and OC (Fig. 237). OC attenuate posteriorly, reaching beyond level of leg III. Posterior porose areas of AD about three times as long as broad, and lying on a W-shaped elevated portion of the plate. I-5 and II-5 with 2 sharp ventral processes (not setae).

11a. I-5 and II-5 with a pair of sharp ventral processes (not setae) as shown in Fig. 208. Lateral claws with a well developed comb, readily visible at magnifications of 400–500 x. Accessory tooth well developed. III-6 with 4 setae dorsally; IV-6 with 3.
11b. I-5 and II-5 without a pair of sharp ventral processes. Comb very weakly developed or absent, or, if present, then visible only at highest magnifications (900–1500 x). Accessory tooth present or absent. III-6 and IV-6 each with 4 setae dorsally.

12a. Rosette pores of typical form (Figs. 205, 206), with alveolus and ostium well developed. Porose panels of AE with pores uniformly distributed over surface of panel (Fig. 223). Anterior margin of PD somewhat pointed. Rostrum not reaching to end of P-2. acutus, new species; p. 140. North Carolina.

12b. Rosette pores consisting essentially of depressed porose panels in which the canaliculi are restricted to the periphery of the panel; ostium of same diameter as alveolus, so that a discrete alveolus is lacking. Porose panels of AE also with pores restricted to periphery (Fig. 235). Anterior margin of PD broadly rounded or truncate. Rostrum reaching to or beyond end of P-3. curassaviensis Viets 1936; p. 150. Florida; Curacao.

Trouessart’s descriptions (1893d: 259–262; 1895a: 193–197, 199) of H. poucheti do not allow precise disposition of that species in the above key. Assuming his figures to be essentially correct, and also making certain assumptions concerning the characters of Trouessart’s species which seem to be warranted by its general facies, it would fall under group 8 in the above key. It differs from C. angustus floridensis in its range (Spitzbergen; Labrador) and the confluent bands of rosette pores, and from C. septentrionalis in the possession of ocular plates which are rounded posteriorly. However, its position is by no means certain.

Copidognathus (s. str.) punctatissimus (Gimbel) 1919

Figures 197–211


Male. Body 318–346μ long to tip of frontal process of AD, 208–229μ wide, L/W = 1.42–1.61 (average of 5 specimens 331.0 × 217.5μ, L/W = 1.52).

Figures 197–201. Copidognathus (s. str.) punctatissimus (Gimbel) 1919. 197 Male: dorsum (rectangle shows area drawn in 200). 198 Female: venter. 199 Female: portion of AE including the epimeral pore and a number of porose panels. 200 Female: panelling of PD (area drawn is shown by rectangle in 197; same scale as 199). 201 Male: palp, lateral view.
PECTINATE SETA

POSTERIOR MAXILLARY SETA

BASE OF CAPITULUM

PHARYNGEAL PLATE

ROSTRUM

OSTIUM

ALVEOLUS

CANALICULI

CLAW FOSSA

BACILLUM

ACCESSORY TOOTH

COMB

LATERAL CLAW

PARAMBULACRAL SETA (DIVARICATE)

MEDIAN CLAW

PENDIS

AD with a small, rounded projection just above base of capitulum; postero-lateral margins broadly rounded; posterior margin slightly concave. Panelling very well developed; 3 areas of elaborate rosette pores, with the rosettes larger and more perfectly formed than those in PD. A single pair of setae present. OC with anterior half rectangular, posterior half triangular; longitudinal axes converging anteriorly. Two corneae present, with a small area of rosette pores between them. Corneae sometimes joined by a bridge consisting of a narrow polished area at lateral ends of corneae. Posterior end of OC extending very slightly beyond insertion of leg III and tapering to a sharp point; a pair of setae at anterior end of plate. PD oval in outline, somewhat truncate anteriorly. Panelling well developed; 4 rows of rosette pores present, with the rosettes most perfectly developed in posterior half of each band. As can be seen in Fig. 200, the cuticular canals are greatly reduced in size and number as compared with those on the ventral plates (Fig. 199). The panelling effect on the dorsal plates is due entirely to the presence of depressed areas, whereas that on the ventral plates is due to a great extent to the localization of the coarse cuticular canals in roughly pentagonal or hexagonal areas, as well as to the existence of depressed areas. PD with 3 pairs of setae. Dorsal membranous areas moderately restricted; a thin band of striate cuticle visible between PD and anus. Membranous areas pilose, the hairs extremely fine and ranging up to 8μ in length.

Venter as in female, except for characters of GA. Genital opening extending to middle of GA, surrounded by 16 to 20 setae on each side. A group of 5 to 8 puncta on each side of opening. Opening guarded by 2 narrow sclerites bearing 4 pairs of setae. Anus projecting beyond end of body. Cuticle distinctly panelled. Capitulum and legs as in female. Palp (Fig. 201) in a male with PD 224μ long with P-1 to P-4 having following lengths: 19, 38, 10, 40μ.

Female. Body 325–360μ long to tip of frontal process, 208–249μ wide (L/W = 1.43–1.56) (average of 10 specimens, 343.5 x 226.5μ, L/W = 1.52); slightly larger than male. Dorsal and ventral surfaces as in male, except for GA. AE with 3 pairs of setae and pores as...
shown in Fig. 198. PE with 1 pair of setae dorsally and 3 pairs ventrally, the most anterior of the ventral setae being almost completely lateral. GA with 3 pairs of setae, the genital opening guarded by a pair of slender sclerites which bear a pair of setae anteriorly. One pair of suckers is readily seen, but the others are not, although they probably are present. Anus terminal.

Capitulum (Fig. 202), in a female 356μ long, 111μ long to tip of rostrum; rostrum alone 51μ long, usually reaching to middle of P-3. Tip of rostrum very sharp; sides of rostrum converging uniformly throughout, except at very tip, and not constricted at base. Base of capitulum 73μ wide, heavily punctate except for the smooth area just ventral to pharynx; panelling not as distinct as on ventral plates. Pharyngeal plate with 5 pairs of median closed cells, and 2 pairs of lateral cells, one or both of which may be closed. Some specimens have a third pair of lateral cells anterior to those shown in Fig. 202. Palp as in male.

Chaetotaxy of legs:

<table>
<thead>
<tr>
<th></th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
</tr>
</thead>
<tbody>
<tr>
<td>d. v. l. m.</td>
<td>d. v. l. m.</td>
<td>d. v. l. m.</td>
<td>d. v. l. m.</td>
<td></td>
</tr>
<tr>
<td>1.</td>
<td>--</td>
<td>--</td>
<td>1</td>
<td>--</td>
</tr>
<tr>
<td>2.</td>
<td>1</td>
<td>1</td>
<td>--</td>
<td>1</td>
</tr>
<tr>
<td>3.</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>--</td>
</tr>
<tr>
<td>4.</td>
<td>2</td>
<td>2</td>
<td>--</td>
<td>1</td>
</tr>
<tr>
<td>5.</td>
<td>3</td>
<td>1</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>6.</td>
<td>3</td>
<td>3</td>
<td>--</td>
<td>--</td>
</tr>
</tbody>
</table>

In a male with a body length of 304μ the following measurements were obtained:

<table>
<thead>
<tr>
<th></th>
<th>1+2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>Ambul.</th>
<th>Total</th>
<th>T/BL</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>42μ</td>
<td>65*</td>
<td>23</td>
<td>65</td>
<td>49</td>
<td>23</td>
<td>267</td>
<td>.78</td>
</tr>
<tr>
<td>II</td>
<td>44</td>
<td>58**</td>
<td>23</td>
<td>56</td>
<td>53</td>
<td>27</td>
<td>261</td>
<td>.77</td>
</tr>
<tr>
<td>III</td>
<td>60</td>
<td>48</td>
<td>25</td>
<td>60</td>
<td>65</td>
<td>28</td>
<td>286</td>
<td>.84</td>
</tr>
<tr>
<td>IV</td>
<td>65</td>
<td>58</td>
<td>28</td>
<td>60</td>
<td>63</td>
<td>28</td>
<td>302</td>
<td>.89</td>
</tr>
</tbody>
</table>

* Dorsal height = 38μ. ** Dorsal height = 30μ.

Legs rough-looking, thick-walled. All femora panelled, the paneling on I and II especially prominent. Basal segments, especially trochanter, pilose, the pilosity appearing principally at disti-dorsal end of segment. I-3 1.7 times as long as high (swollen) and with prominent punctate area ventrally. I-5 with 2 pectinate setae ventro-medially
and a single smooth seta ventrally. Ventral margin with 2 very sharp, thin processes directed distally. I-6 with 3 large setae dorsally and 3 small setae ventrally, the latter being difficult to find except with oil immersion. There is also a bacillum on the lateral membrane of the claw fossa and a pair of divaricate parambucral setae. The prebacillum is very rudimentary or absent, but one can usually find a minute, closed canal extending from the lumen of the tarsus toward the point where it is ordinarily found. Claw fossa very deep but almost completely open medially because of small size of medial membrane. Lateral claws weakly pectinate, with accessory tooth; median claw bidentate.

Leg II remarkably similar to I. II-3 1.90 times as long as high; II-5 identical with I-5, medial setae pectinate. II-6 identical with I-6 except for absence of the 3 ventral setae; bacillum lateral. Medial membrane of claw fossa as on I-6. Lateral and median claws as on I-6, but pecten more strongly developed. III-5 (Fig. 204) with a heavy pectinate seta medially. III-6 (Fig. 211) with 4 setae dorsally and a pair of setae at base of ambulacrum, the homologues of the divaricate setae on I and II. Medial seta of this pair rod-shaped and rounded terminally; lateral member moderately heavy, tapering and serrate. IV without the heavy pectinate setae found on III-5, but with an ordinary seta in its place (Fig. 210). IV-6 with only 3 setae dorsally and the pair at the base of the ambulacrum, both of the latter tapering and serrate (Fig. 209). In the female these are of the same form, but the serration is very feebly developed or absent. III-6 and IV-6 with a shallow fossa; membranes very low. Claw IV like III, but slightly longer.

Remarks. This is unquestionably C. punctatissimus (Gimbel) 1919 (pp. 124-128), but there are certain differences between the description above and that given by Gimbel (based on two males and a third specimen whose sex could not be determined). The writer has had the advantage of examining many specimens from several localities. Gimbel stated that the rostrum is rounded anteriorly and reaches to the end of P-3, but in the specimens examined by the writer the tip of the rostrum is very sharply pointed, although it widens rapidly just behind the tip, and it almost invariably reaches only to the middle of P-3. Gimbel's specimens were probably somewhat compressed in preparation, as he gave L/W = 1.35, which is broader than any of the fifteen mites measured by the writer. Gimbel noted only a single pair
of setae on AE, whereas there are the usual three pairs. Gimbel’s "zwei Schuppen" are probably apodemes. The writer found leg IV to be distinctly longer than I, and leg II is not appreciably shorter than I. The two heavy setae which Gimbel noted only on II-5 are found also on I-5 and are distinctly pectinate on both legs (oil immersion). As careful study shows that the setae on legs I and II are identical except for the absence of the three very minute ventral setae on II-5, it may be assumed that Gimbel referred to these setae when he said: "Tast­borsten befinden sich nur an den Vorderbeinen." However, Gimbel did not figure the ventral setae of I-6 in his fig. 22a. Gimbel’s specimens were slightly smaller than those observed by the writer. The type locality was given simply as Newport (North America), which was probably Newport, Rhode Island, rather than Newport News, Virginia, although the known range includes both localities. Because the rostrum is not as long as reported by Gimbel, and because I-5 and II-5 have pectinate setae, this species cannot be identified through the use of Viets’ keys (1927a: 134–139; 1940g: 17–27).

Examination of specimens from Beaufort shows that the species is very constant throughout its known range. A close study of the following characters show the Beaufort mites to agree completely with the above description. Panels of PD with a few scattered puncta, and with coarser pores between the depressions (as in Fig. 200); membranous areas pilose. Setae on sclerites guarding genital opening identical in form and position with those of the northern forms. I-5 and II-5 with pectinate medial setae, and with 2 sharp processes ventrally. III-6 with 4 setae dorsally; IV-6 with only 3 setae here. Homologues of parambulacral setae as described above. Size as given above for the northern forms. All these minute characters, then, have a high degree of validity for recognition of this species throughout its known range.

**Distribution.** North America: Rhode Island (Newport; and 3 miles north of Block Island, at 34 meters); New Haven County, Connecticut (Morris Cove; South End; Double Beach); Beaufort, North Carolina (Piver’s Island; Town Marsh; Harker’s Island).

Newell: The Halacaridae of Eastern North America

139

... and J.-I. Connell, North Carolina...
Copidognathus (s. str.) acutus, new species

Figures 212–223

Male. Body 291–318 μ long, 187–211 μ wide, 1.48–1.59 times as long as wide; average of 8 specimens 305.5 x 200.1 μ, L/W = 1.55. Superficially similar to C. punctatissimus (Gimbel), with which it occurred at Beaufort, North Carolina, but differing from it in many details.

In a male 305 x 198 μ the following measurements were obtained: AD 91 μ long, 97 μ wide; each OC 91 x 56 μ; PD 214 x 144 μ. AD broader than long, with a frontal process of variable sharpness, with 3 prominent elevated porose areas and a pair of setae. Posterior margin broad, convex. OC broad, the antero-median margin about ¾ as long as postero-median margin. Corneae usually joined by a bridge of refractile cuticle, the seta mediad of anterior cornea. Three areas of rosette pores present, the posterior one of which contains from 1 to 15 pores (highly variable), and has never been found absent. Posterior end of OC sharply rounded, or slightly angular, extending only to level of leg III. PD with sides nearly parallel for a considerable distance; antero-lateral margins converging rapidly (forming an angle of about 90°) to a usually sharply rounded point (hence the specific name, acutus). Costae prominent, with rosette pores, the posterior end turned outward; a second row of rosette pores along each side of plate, nearly continuous with the more medial row at posterior end of plate. Three pairs of setae present as shown, the anterior pair always at edge of plate, the posterior pair well behind insertions of leg IV. Dorsal plates only faintly panelled in most specimens; panels subdivided so that a faintly reticulate pattern is imposed upon the panel pattern (Fig. 222). A minute pore is visible under each subdivision of the panels, but the pores do not reach the surface in all cases. Rosette pores of AD (Fig. 218) much larger than those of PD; those on OC of the same type as found on PD, but sometimes slightly larger. In addition to the rosette pores there is a pair of large pores on AD (antero-laterally from posterior rosette areas), OC (lateral to posterior corneae), and PD (at ends of costae). However, the pore found between setae 2 and 3 in PD of C. bairdi, n. sp., has no homologue in C. acutus, n. sp. Membranous areas moderately restricted.

Ventral armor as in female except for characters of GA. In a male with a body length of 305 μ the following measurements were obtained:
Since the legs of this specimen are not much longer than those of the male (only 3 to 4%), it is probable that if the exact length of this

Newell: The Halacaridae of Eastern North America 141

GA 166 x 130μ, genital opening 53 x 39μ, 71μ from anterior end of plate. Anal papilla prominent. Cuticle panelled and punctate as on AE, except around the opening where the cuticle is smooth with a few scattered minute pores. Genital opening guarded by a pair of heavy sclerites bearing 4 pairs of setae, the anterior end of each plate sculptured. An area of 7 to 10 puncta present on each side of posterior half of genital opening.

Capitulum (Fig. 220), in a male 305μ long, 86μ long to tip of rostrum, and 63μ wide; rostrum alone 41μ long and 29μ wide at base, not reaching to end of P-2. Sides of rostrum converging uniformly except at tip; not constricted at base. Base of capitulum densely porose. Palpi (in a male with a body 291μ long) with P-1 to P-4 as follows: 16, 37, 8, 44μ long; P-4 longer than P-2 (Fig. 215).

Chaetotaxy of legs:

<table>
<thead>
<tr>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
</tr>
</thead>
<tbody>
<tr>
<td>d.</td>
<td>v.</td>
<td>l.</td>
<td>m.</td>
</tr>
<tr>
<td>1.</td>
<td>-</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>2.</td>
<td>1</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>3.</td>
<td>3</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>4.</td>
<td>2</td>
<td>2</td>
<td>-</td>
</tr>
<tr>
<td>5.</td>
<td>3</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>6.</td>
<td>3</td>
<td>3</td>
<td>-</td>
</tr>
</tbody>
</table>

In a small male with a body length of 291μ, the following measurements were obtained (for I-3, I-5, II-3 and II-5 the height is also given):

<table>
<thead>
<tr>
<th>I+2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>Ambul.</th>
<th>Total</th>
<th>T/BL</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>38μ</td>
<td>66/30</td>
<td>23</td>
<td>65/18</td>
<td>44</td>
<td>20</td>
<td>256</td>
</tr>
<tr>
<td>II</td>
<td>35</td>
<td>59/25</td>
<td>21</td>
<td>53/20</td>
<td>48</td>
<td>23</td>
<td>239</td>
</tr>
<tr>
<td>III</td>
<td>54</td>
<td>47</td>
<td>22</td>
<td>56</td>
<td>56</td>
<td>28</td>
<td>263</td>
</tr>
<tr>
<td>rt. IV</td>
<td>56</td>
<td>56</td>
<td>26</td>
<td>58</td>
<td>60</td>
<td>30</td>
<td>286</td>
</tr>
<tr>
<td>lt. IV</td>
<td>59</td>
<td>55</td>
<td>26</td>
<td>59</td>
<td>61</td>
<td>29</td>
<td>289</td>
</tr>
</tbody>
</table>

In an appreciably larger female (exact length unknown) legs III and IV had the following measurements:

<table>
<thead>
<tr>
<th>I+2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>Ambul.</th>
<th>Total</th>
<th>T/BL</th>
</tr>
</thead>
<tbody>
<tr>
<td>III</td>
<td>56μ</td>
<td>49</td>
<td>23</td>
<td>58</td>
<td>59</td>
<td>27</td>
<td>272</td>
</tr>
<tr>
<td>IV</td>
<td>61</td>
<td>59</td>
<td>25</td>
<td>62</td>
<td>62</td>
<td>29</td>
<td>298</td>
</tr>
</tbody>
</table>

Since the legs of this specimen are not much longer than those of the male (only 3 to 4%), it is probable that if the exact length of this
specimen were known, legs IV would not be 0.98 to 0.99 times as long as the body, but somewhat shorter.

I-3 (Fig. 219) 2.20 times as long as high (not swollen); dorsal setae relatively short, erect. Medial setae of I-5 pectinate (oil immersion), the distal seta larger than the proximal one. I-6 with the bacillum and parambulacral setae in addition to those noted in table; prebacillum absent. The 2 disti-ventral setae are rounded terminally like the parambulacral setae, but the basi-ventral member of this group is tapering. In one male, at a magnification of 1500 diameters, a very reduced comb is found along the inner side of claws I, III and IV (Fig. 221); but on another specimen (female) no trace of a comb is found. This presumably is not a sexual difference, but simply an individual variation. The comb never extends to the concave inner margin of the claw and would be visible only under the most favorable conditions even when present. In some specimens an extremely fine, hairlike, accessory tooth is present, but in others it is represented only by a slight break in the outline of the convex side of the claw, and in others the outer side of the claw is completely smooth. Under low magnifications the lateral claws of all specimens appear smooth, with neither accessory tooth nor comb. Median claw coarsely bidentate (Fig. 217). Claw fossa shallow, completely open medially. I-1 hirsute dorsally and lateral half of I-3 also hirsute, the hairs being longest disti-ventrally. Lateral surface of I-3 also faintly panelled; medial surface neither hirsute nor panelled.

In II-3 the dorso-lateral seta has shifted to a completely lateral position, while the homologue of the lateral seta of I-3 has become ventral. II-3 2.36 times as long as high. Medial setae of II-5 pectinate, the distal one very long, extending nearly to level of basi-dorsal seta of II-6. II-6 like I-6 except that the bacillum is twice as far from disti-dorsal seta as from base of claw, and the ventral setae are lacking. II-1 and II-3 hirsute as on leg I.

III-3 with 2 very slender setae dorsally, but none ventrally; IV-3 with 2 setae dorsally and one ventrally. III-5 with disti-ventral seta

Figures 219–223. Copidognathus (s. str.) acutus (continued). 219 Male: leg I, median view (the median seta was drawn in from the opposite leg). 220 Male: capitulum, ventral view. 221 Male: III-5 and III-6, median view. 222 Female: P D, at level of second seta. 223 Male: porose panels of AE.

Newell: The Halacaridae of Eastern North America

143

E.99 times as long
(211
(212
(213
(214
(215
(216
(217
(218
(219
(220
(221
(222
(223
(224
(225
(226
(227
(139
(140
(141
(142
(143
(144
(145
(146
(147
(148
(149
(150
(151
(152
(153
(154
(155
(156
(157
(158
(159
(160
(161
(162
(163
(164
(165
(166
(167
(168
(169
(170
(171
(172
(173
(174
(175
(176
(177
(178
(179
(180
(181
(182
(183
(184
(185
(186
(187
(188
(189
(190
(191
(192
(193
(194
(195
(196
(197
(198
(199
(200
(201
(202
(203
(204
(205
(206
(207
(208
(209
(210
(211
(212
(213
(214
(215
(216
(217
(218
(219
(220
(221
(222
(223
(224
(225
(226
(227
(228
(229
(230
(231
(232
(233
(234
(235
(236
(237
(238
(239
(240
(241
(242
(243
(244
(245
(246
(247
(248
(249
(250
(251
(252
(253
(254
(255
(256
(257
(258
(259
(260
(261
(262
(263
(264
(265
(266
(267
(268
(269
(270
(271
(272
(273
(274
(275
(276
(277
(278
(279
(280
(281
(282
(283
(284
(285
(286
(287
(288
(289
(290
(291
(292
(293
(294
(295
(296
(297
(298
(299
(300
(301
(302
(303
(304
(305
(306
(307
(308
(309
(310
(311
(312
(313
(314
(315
(316
(317
(318
(319
(320
(321
(322
(323
(324
(325
(326
(327
(328
(329
(330
(331
(332
(333
(334
(335
(336
(337
(338
(339
(340
(341
(342
(343
(344
(345
(346
(347
(348
(349
(350
(351
(352
(353
(354
(355
(356
(357
(358
(359
(360
(361
(362
(363
(364
(365
(366
(367
(368
(369
(370
(371
(372
(373
(374
(375
(376
(377
(378
(379
(380
(381
(382
(383
(384
(385
(386
(387
(388
(389
(390
(391
(392
(393
(394
(395
(396
(397
(398
(399
(400
(401
(402
(403
(404
(405
(406
(407
(408
(409
(410
(411
(412
(413
(414
(415
(416
(417
(418
(419
(420
(421
(422
(423
(424
(425
(426
(427
(428
(429
(430
(431
(432
(433
(434
(435
(436
(437
(438
(439
(440
(441
(442
(443
(444
(445
(446
(447
(448
(449
(450
(451
(452
(453
(454
(455
(456
(457
(458
(459
(460
(461
(462
(463
(464
(465
(466
(467
(468
(469
(470
(471
(472
(473
(474
(475
(476
(477
(478
(479
(480
(481
(482
(483
(484
(485
(486
(487
(488
(489
(490
(491
(492
(493
(494
(495
(496
(497
(498
(499
(500
(501
(502)

...
heavy, pectinate; homologous seta on IV-5 slender, tapering. III-6 and IV-6 each with 4 setae dorsally, the basi-dorsal one on IV-6 characteristically short, blunt. On III-6 the homologues of the parambulaeal setae consist of a rod-shaped seta medially and a spine-like seta laterally (Fig. 221); on IV-6 they are both spine-like (only the medial one is shown in Fig. 221). Tarsi III and IV slightly flattened disti-dorsally but without true fossa. Median claw with the 2 teeth much more slender than on I and II.

Female. Six females measure 284–319 μ long, 180–211 μ wide, $L/W = 1.48–1.58$ (average 306.8 x 201.5, $L/W = 1.53$); dimensions as in male. Differing from male only in characters of GA. Ventral plates prominently panelled and porose. GA with 3 pairs of setae, the genital opening very close to anus, considerably more than its own length from anterior end of GA, guarded by a pair of finely sculptured sclerites, each bearing a seta at the anterior end. In a female 315 μ long, GA was 161 μ long and 120 μ wide; the opening was 61 x 38 μ and was 76 μ from anterior end of GA.

Remarks. This species goes to $C.$ (s. str.) latus Viets 1927 in Viets' key (1927a: 134–139) and is more closely related to that species than to any other yet described. The species differ in the following respects.

$C.$ acutus: Body 284–319 μ long. Rostrum shorter than base of capitulum, not reaching to end of P-2. P-4 longer than P-2. PD including the anterior pair of setae. Posterior ends of costae diverging. Lateral rows of rosette pores extending an equal distance each way from the insertions of leg IV. OC with a group of rosette pores on the posterior half of the plate. Dorsal and ventral membranous areas relatively reduced. Female genital opening 0.38–0.39 as long as GA, but removed from anterior margin of GA by a distance 1.25 times as long as opening. PE with 3 pairs of setae ventrally. Lateral claws with feebly developed comb and accessory tooth which may often be absent. Medial setae of I-5 and II-5 pectinate. III-6 and IV-6 each with 4 setae dorsally.

$C.$ latus: Body 505 μ long. Rostrum longer than basal part of capitulum, reaching somewhat beyond end of P-2. P-4 shorter than P-2. Homologues of anterior setae of PD lying in the membranous area. Posterior ends of costae converging. Viets did not mention the lateral rows of rosette pores on PD, although he did figure them (Viets 1927a: fig. 74). However, it is not certain from Viets’ drawing that he showed the full posterior extent of the lateral rows. If he did, then they are
much shorter than those in *C. acutus*, for they are only half as long and end at the level of IV. OC without posterior porose area. Dorsal and ventral membranous areas relatively extensive. Female genital opening 0.40 as long as GA, but removed from anterior margin of GA by a distance only 0.75 the length of the opening. Viets showed PE as having only two pairs of setae ventrally, which is a significant character if correct. Lateral claws with a distinct comb and tooth. According to Viets the medial setae on I-5 are not pectinate, but those on II-5 are. Viets (1927a: fig. 76c) showed only three setae dorsally on III-6.

**Distribution.** North America: Beaufort, North Carolina (Piver's Island [type locality]; Newport River, at 2.5 meters; Harker's Island; off Beaufort Entrance, at 10 meters).

*Copidognathus* (s. str.) *bairdi*, new species

Figures 224–234

**Male.** Body 270–284\(\mu\) long, 159–180\(\mu\) wide, L/W = 1.57–1.69 (av. 277.0 x 142.7\(\mu\), L/W = 1.61), based on 5 males. Somewhat shorter than female and appreciably narrower. AD produced anteriorly, the posterior half sharply elevated above anterior half just anterior to middle of plate; 3 large areas of coarse pores and a pair of minute setae present; a few large pores at posterior margin. OC tapering to a sharp point just behind leg III. Two corneae, 2 porose areas, and 1 seta present on each plate. Lateral porose areas forming a prominent lateral projection. PD usually rounded anteriorly, slightly truncate or somewhat concave, the shape of this part of the margin being greatly influenced by the degree of development of costae. The latter are sharply elevated and bear a row of coarse simple pores, 1 or 2 pores wide. Behind leg IV the costae are greatly swollen laterally and bear a pair of large pores. Posterior ends of bands also slightly swollen. A single row of simple pores along each side of plate between levels of legs III and IV. Three pairs of setae present at positions shown in Fig. 228. All dorsal plates distinctly panelled, the walls of the panels usually tuberose, and the panels subdivided by smaller ridges (Fig. 234). Under oil immersion it can be seen that the ostia in the 12 porose areas of the dorsal plates open into alveoli of greater diameter, which in turn appear to continue through the cuticle. Canaliculi absent. In Fig. 228 the circles representing the pores actually represent the deeper portions of these rather than
the minute external openings. Membranous areas greatly reduced. In the specimens in the writer's collection, AD overlaps OC, and sometimes PD also, which is probably due to shrinkage.

Venter (Figs. 225, 229) with plates almost completely fused. AE fused with PE, or separated from it by only a suture; fused with GA. Membranous areas completely absent. GA fused with PE. The plates carry the setae characteristic of the genus. Panelling absent except for a pair of small areas on GA at each side of posterior half of genital opening. PE with a dorso-lateral notch anterior to III and IV. GA coarsely porose, the pores of the same type as those found on PD (Fig. 234). AE with a Y-shaped porose area. In the central portion of this the pores are small and single, but at the ends of the arms and the stem of the Y the pores are larger and tend to clump together and even to coalesce (Fig. 233). A patch of single pores is also found at the anterior end of GA, and six other patches of clumped or coalesced pores as shown in Fig. 225. In all these areas the pores are of the same type as those on PD, but usually smaller. Genital opening with 10 or 11 very slender setae on each side, but without punctate areas such as are found in *C. (s. str.) punctatissimus*. Opening guarded by a pair of sclerites bearing 4 pairs of setae. In a male with a body length of 277μ the opening was 48 x 38μ (L/W = 1.26).

Capitulum (in a male with a body length of 277μ) 75μ to tip of rostrum and 56μ wide at base. Rostrum alone 34μ long and 22μ wide at base, not reaching to end of P-2. Setae as in Fig. 231. Base of rostrum with pores like those on PD. Dorsal wall of pharynx faintly panelled, the lateral walls of panels sometimes indistinct. Palpi and legs as in female.

**Female.** Body 291–305μ long, 191–201μ wide, L/W = 1.45–1.53 (av. 293.6 x 198.1μ, L/W = 1.48), based on 5 specimens, somewhat longer and appreciably wider than male. Dorsal plates as in male, but PD broader. In a female with a body length of 298μ, PD was 201 x 139μ (L/W = 1.44); whereas in the male in Fig. 228 L/W = 1.54. Ventral plates characteristic for the genus, not fused as in male; membranous areas well developed, striate. Distribution and form of pores as in male. GA nearly parallel-sided, slightly convex anteriorly (Fig. 224), with 3 pairs of setae. Genital opening guarded by a pair of sclerites bearing a single pair of setae near anterior end; a single pair of genital suckers visible. In a female with a body length of 298μ the following measurements were obtained: GA 156 x 111μ; genital opening 60 x 35μ, 63μ from anterior end of GA.
Palpi (Fig. 230) in a female with PD $205\mu$ long, with P-1 to P-4 13.5, 36, 7.5, 41$\mu$ long. P-4 longer than P-2.

Chaetotaxy of legs:

<table>
<thead>
<tr>
<th></th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>d. v. l. m.</td>
<td>d. v. l. m.</td>
<td>d. v. l. m.</td>
<td>d. v. l. m.</td>
</tr>
<tr>
<td>1</td>
<td>1 - - 1</td>
<td>1 - - 1</td>
<td>1 - - 1</td>
<td>1 - - 1</td>
</tr>
<tr>
<td>2</td>
<td>1 1 - -</td>
<td>1 1 - -</td>
<td>1 1 - -</td>
<td>1 1 - -</td>
</tr>
<tr>
<td>3</td>
<td>3 1 1 -</td>
<td>3 1 1 -</td>
<td>2 - - -</td>
<td>2 - - -</td>
</tr>
<tr>
<td>4</td>
<td>2 2 - -</td>
<td>1 1 1 1</td>
<td>1 1 1 -</td>
<td>2 1 1 -</td>
</tr>
<tr>
<td>5</td>
<td>4 1 - 2</td>
<td>3 1 1 2</td>
<td>2 1 1 1</td>
<td>2 1 1 1</td>
</tr>
<tr>
<td>6</td>
<td>3 3 - -</td>
<td>3 - - -</td>
<td>4 - - -</td>
<td>4 - - -</td>
</tr>
</tbody>
</table>

In a female with a body length of $305\mu$ the following measurements were obtained (for I-3, I-5, II-3 and II-5 the height is also given):

<table>
<thead>
<tr>
<th></th>
<th>I+2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>Ambul.</th>
<th>Total T/BL.</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>34$\mu$</td>
<td>65/33</td>
<td>22</td>
<td>68/25</td>
<td>44</td>
<td>19</td>
<td>249</td>
</tr>
<tr>
<td>II</td>
<td>31</td>
<td>50/26</td>
<td>19</td>
<td>53/23</td>
<td>48</td>
<td>22</td>
<td>223</td>
</tr>
<tr>
<td>III</td>
<td>47</td>
<td>47</td>
<td>17</td>
<td>53</td>
<td>58</td>
<td>26</td>
<td>248</td>
</tr>
<tr>
<td>IV</td>
<td>49</td>
<td>52</td>
<td>18</td>
<td>53</td>
<td>59</td>
<td>25</td>
<td>256</td>
</tr>
</tbody>
</table>

I-3 and II-3 1.98 and 1.92 times as long as high (only slightly swollen). All femora with ventrally projecting carinae which make the ventral side of the segment somewhat concave (Fig. 227). Paneling feebly developed on I-3, the rest of the legs only punctate. All claws pectinate, median claw bidentate.

Leg I without ventral process on femur; 3 heavy setae ventrally and medially on I-5. In one specimen the medial setae appear pectinate, but the pectinations are so fine that they would show up only in specimens favorably oriented. I-6 almost identical with I-6 of C. punctatissimus, except that the bacillum is somewhat more distally placed (about halfway between disti-dorsal seta and base of claw) and is more tapering. Medial membrane of claw fossa completely lacking. Prebacillum absent. II-5 with medial setae somewhat more distinctly pectinate; II-6 identical with I-6 except for absence of 3 ventral setae. Bacillum lateral, about halfway between disti-dorsal seta and base of claw, the medial membrane absent. III-3 and IV-3 without ventral seta. III-4 with 1 seta dorsally, IV-4 with 2. III-5 as in C. punctatissimus (Fig. 204), with a long, smooth ventral seta and a long pectinate seta; IV-5 with pectinate seta replaced by a slender seta. III-6 and IV-6 each with 4 setae dorsally (compare with C. punctatissimus).
In IV-6 the most proximal of the dorsal setae is retained, whereas in *C. punctatissimus* it does not develop. At the base of the ambulacrum of III-6, on the medial side, is a rod-like seta as in *C. punctatissimus*; but it is paired with a short spine-like seta, the form of which is difficult to discern because of its close apposition to the tarsus. IV-6 with both members of this terminal pair short and spine-like. III-6 and IV-6 with shallow claw fossa, but with no distinct membranes.

**Remarks.** This species is very closely related to *C.* (s. str.) *gibberipes* Viets 1936 (Bonaire, Dutch West Indies). The pores at the posterior end of AD are much fewer in number (4–8) than in *C. gibberipes* (ca. 20), and the cuticle between and anterior to the posterior porose areas of AD is distinctly panelled. The lateral swellings of the costae of PD are more prominent than in *C. gibberipes*, and there is a single row of pores along each side of PD which Viets did not figure or mention in his *C. gibberipes*. Pores are entirely lacking from the remainder of PD, whereas in *C. gibberipes* there are large pores between the costae. Viets showed no lateral expansion of OC in the region of the lateral porose areas of these plates, but in *C. bairdi* this expansion is considerable. Capitulum appreciably shorter, rostrum not reaching to end of P-2; in *C. gibberipes* the rostrum reaches beyond P-3. The base of the capitulum is coarsely porose. The posterior pair of setae is borne on the base of the capitulum; but in *C. gibberipes* these are on the rostrum itself. I-3 with ventral carinae (“leicht lamellösen Beugeseitenerweiterung” of Viets 1936d: 404) but without a tubercle.

Viets’ statement on page 405 “Alle Krallen haben eine kleine Aussenzinke, aber keinen Kamm” is obviously unintentional, for his figures show all claws pectinate. This error is repeated elsewhere (Viets 1940g: 26). Viets was uncertain of the sex of his mite, saying simply that it was “vermutlich ein Männchen.” However, ratios calculated from Viets’ measurements of PD and the genital opening are intermediate to the ratios obtained for the males and females of *C. bairdi* and are therefore inconclusive. Calculating the position of the morphological “anterior margin” of GA of the male of *C. bairdi*
Newell: The Halacaridae of Eastern North America

149

The pores at the 3–8 than in C. prior to the posterior lateral swellings of the rips, and there is a lacking from the large pores between OC in the region of rudi this expansion a strum not reaching beyond P3. The nter pair of setae pipheres these an height lamellae without a tubercle on each side external, for two the exuviae of the mite, sayi

However, that the genital opening es and females d the position of male of C. nor

---

Male: dorso. 22
222 Male capsule. 222 Male posterior. 222 Female: dorso.
(using the anterior setae of GA, the posterior setae of AE and the middle pair of setae of PE as reference points), the anterior margin of the plate would lie 142\(\mu\) from the tip of the anal papilla. The male genital opening is 46\(\mu\) long in this specimen (Fig. 225). The corresponding measurements in the female are 156\(\mu\) and 60\(\mu\) (see text above). Therefore, in the male of \textit{C. bairdi} the ratio of length of GA to the length of the genital opening is 3.09; in the female it is 2.60. Viets' figures of 128\(\mu\) and 54\(\mu\) give a ratio of 2.37, which suggests a female rather than a male. The fact that these two species are very closely related (despite the numerous minor differences pointed out above) also suggests that Viets' mite was a female, for one would be justified in expecting that the ventral plates in the two species would correspond, and therefore that the male of \textit{C. gibberipes} Viets 1936 would have fused ventral plates and the female separate ventral plates. Since Viets was able to measure GA and did not note any fusion (such as he noted in \textit{C. bonairensis} [Viets 1936: 416], it seems very probable that Viets' description of \textit{C. gibberipes} was based on a female and not on a male.

\textbf{Distribution.} \textit{North America: Florida} (Biscayne Bay, on Soldier's Key).

\textit{Copidognathus (s. str.) curassaviensis} Viets 1936

\textit{Figures 235–236}


Viets (1936d: 399–402) gave a good account of this species, and the specimens in the writer's collection agree well with his description and figures. However, a very small comb is found on claws II and IV, so that one must overlook the first dichotomy in using Viets' key (1940g: 17). The presence or absence of combs on the claws of \textit{Copidognathus} species is an undesirable primary key character, for although there are many species with clearly pectinate claws, and some which have completely smooth claws (but usually with an accessory tooth), there are many in which the comb is present but difficult to observe, even with oil immersion. In this latter group of species which are apparently in the process of losing the pecten, there are unquestionably some species which show individual variation (e. g., \textit{C. acutus}, n. sp.), some specimens having smooth claws, and others having faintly pectinate claws.
Only the usual three setae were found on GA rather than four as noted by Viets. The Florida specimens agreed with Viets' specimens in the following specific characters: the minute patch of pores on the posterior end of AD, the arrangement of the pores on OC, the short row of pores on the sides of PD, the rough structure of the striae between AD and PD, the one slender and two spiniform setae ventrally on I-5, the absence of membranes beside the claw fossa and the presence of four setae dorsally on both III-6 and IV-6. Two females (the only adults taken) measured 374μ long (Viets, 380-412μ).

As was shown by Viets, the palpi are short, and P-3 plus P-4 are shorter than P-2. In Fig. 236 it can be seen that the rostrum extends beyond the ring of basal setae on P-4. The ventral plates are coarsely porose; and the pores form roughly pentagonal or hexagonal areas which are very prominent (Fig. 235).

**Distribution.** North America: Florida (Biscayne Bay, on Soldier's Key).

**Curaçao.**

*Copidognathus* (s. str.) *biscayenus*, new species

Figures 237-244

This species is represented by a single female which lacks a capitulum. It keys out to *Copidognathus manubriatus* in Viets' key (1940g: 55). That species is also inadequately described because of insufficient material. Nevertheless, the present form is not *C. manubriatus*, judging from the form of the legs and the structure of OC, and appears to occupy an isolated position.

**Female.** Body 346 x 204μ (L/W = 1.70). AD 106 x 77μ, nearly parallel-sided, with a rounded frontal protuberance. Three porose areas present, the anterior one containing coarse pores of irregular arrangement, the 2 posterior ones elongate and containing pores of an unusual structure (Fig. 237). The canaliculi are in groups of 6 to 12, and these open neither individually nor all through a single large pore as in the true rosette pores, but through 3, 4 or 5 irregularly arranged pores, each one of which is connected with 1, 2 or 3 canaliculi (Fig. 240, oil immersion). The three groups of canaliculi drawn are typical of the pores found in this specimen, but many of the pores are of more irregular arrangement. Often a single canaliculus opens directly to the surface. Posterior porose areas borne on a W-shaped prominence, a coarse pore and a seta at anterior end of each arm of the W. Ten
to 12 deep pits at posterior end of W mark positions of internal apodemem. OC 110 x 32 μ and 104 x 35 μ; posterior end drawn out into a short, sharp tail extending beyond III. Corneae borne on a prominent elevation on anterior half of plate (Fig. 244). The usual 2 corneae elongate and indistinct. Posterior to these is a very distinct, solid, highly refractile body which has the appearance of, and may actually function as, a cornea. However, it appears to be homologous with the pore found in this position in most species of *Copidognathus*, and there is no such pore here or anywhere else on the plate. The usual minute pores are present, and although the majority of the canaliculi appear to open singly, some open in groups of two or three by means of a common pore, as is the rule on AD. A pair of setae between OC and AD. Posterior portion of OC faintly panelled, the panels subdivided so that the plate appears as much reticulate as panelled.

PD 222 x 133 μ (not including anal papilla), oval in outline. Costae with a double row of pore panels, the pores being of the same type as those on AD and OC. The canaliculi often open individually, but two or three sometimes open by a common pore. Although the canaliculi are coarse, the pores are much smaller than those on AD and OC. The canaliculi often open individually, but two or three sometimes open by a common pore. Although the canaliculi are coarse, the pores are much smaller than those on AD and OC. The usual minute pores are present, and although the majority of the canaliculi appear to open singly, some open in groups of two or three by means of a common pore, as is the rule on AD. A pair of setae between OC and AD. Posterior portion of OC faintly panelled, the panels subdivided so that the plate appears as much reticulate as panelled.

Ventral surface as shown in Fig. 241. AE and GA each with 3 pairs of setae. PE with 3 pairs of setae ventrally and 1 pair dorsally. One ventral and 1 dorsal seta are completely absent, even including the alveolus. GA 166 x 116 μ; genital opening 71 μ long, 66 μ from anterior margin of plate. All ventral plates distinctly panelled and porose.
Newell: The Halacaridae of Eastern North America

1947

As of internal spiracles drawn out into pouches. The usual two pairs are very distinct, and may be arranged in such a way as to be homologous with those of Copidosoma, and others. The majority of the species of two or three pairs are not so arranged. A pair of setae at the base of each segment is faintly pencilled, the most reticulate is...
Leg I (Fig. 242) with lamellae weakly developed on segments 3, 4 and 5. Chaetotaxy identical with that of \textit{C. (s. str.) punctatissimus} (Gimbel). I-5 also with 2 sharp ventral spines as in that species, and with medial setae faintly pectinate. I-6 with bacillum and divaricate parambularcal setae but prebacillum absent; claw fossa present, the membranes greatly reduced; 3 ventral setae present. I-3, I-4 and I-5 with weakly developed lamellae. Lateral claws without a longitudinal comb, but accessory tooth containing 4 or 5 very small teeth (oil immersion). Median claw faintly bidentate and apparently worn.

Leg II (Fig. 243) also identical with that of \textit{C. punctatissimus} in number and position of setae. I-3 and II-3 less than twice as long as high (swollen). II-5 also with 2 ventral spines, medial setae pectinate. II-6 without ventral setae, but with bacillum and divaricate parambularcal setae. II-3, II-4 and II-5 with lamellae, those on II-5 being best developed. Lateral claws with longitudinal comb and accessory “tooth” which contains 4 or 5 minute teeth as on claws of tarsus I. Median claw faintly bidentate; apparently worn. Claw fossa present, but not pronounced; membrane absent. III-1 and IV-1 greatly swollen dorsally. Segments 3, 4 and 5 of III and IV with lamellae (Figs. 238, 239). III-5 with medial member of disti-ventral pair of setae pectinate; its homologue on IV-5 smooth, slender. III-6 with 4 setae dorsally; only 3 are observed here on IV-6, but the segment is in poor position for study. A refractile spot on each tarsus suggests an alveolus from which the seta has been removed, but this cannot be ascertained. Tarsi III and IV tapering, but claw fossa and membranes absent. Medial parambularcal seta of III-6 rod-shaped, slender; lateral seta spiniform or scale-like (not in favorable position for study). One of the lateral claws on IV-6 of the left side is seen in direct ventral view, and it is identical in form with the claw of \textit{Halacarus (Th.) basteri basteri} (Figs. 147, 148). In the present species, therefore, there is no true accessory “tooth,” but only an apparent one [see the discussion under \textit{Halacarus (Th.) basteri basteri}]. As pointed out previously, even the accessory “tooth” on I-6 is only a fragment of a comb.

\textit{Distribution.} North America: Florida (Biscayne Bay, on Soldier’s Key).
This keys out, with certain difficulties,\(^{22}\) to *C. angustus* Viets 1936 in Viets' key (1940g: 15–27), and agrees closely with the original description of that species (Viets 1936d: 393–396). The slight differences that exist between the Florida and the Curacao forms are greatly outweighed by the fundamental similarities, and accordingly they are considered to be related subspecifically.

*Male.* One of the males is 291 x 187µ (L/W = 1.56) and the other is 301µ long. Dorsal plates as in female of *C. angustus angustus* in most respects. According to Viets the panelling on AD of *C. angustus angustus* is not very distinct. That on AD of *C. angustus floridensis* is very distinct, nearly as distinct as that between the costae of PD. Although the membranous areas are greatly reduced, the closeness of the plates is exaggerated in Fig. 245, owing to the shrinkage of the delicate cuticle between the plates. Panelling of all dorsal plates very distinct (Fig. 248). All the coarse pores shown in the dorsal plates are rosette pores. Canaliculi of rosette pores minute and often irregular in arrangement, occasionally opening directly onto surface. Costae not reaching to anterior margin of PD, but reaching to a point slightly beyond anterior pair of setae; setae difficult to find because of roughness of plates. Venter as in female, except for characters of GA. Pores of anterior half of GA arranged in more definite polygonal areas than in female, but still not as definite as those on AE. Genital sclerites with 4 pairs of setae. Ten or 11 pairs of setae on each side of plate, the most anterior ones lying at a point halfway between anterior margin of opening and anterior margin of plate. Several rosette-pores lie along the postero-lateral margins of the plate, each opening into a panel-like depression in the cuticle.

Capitulum as in female (Fig. 246). Legs as in *C. angustus angustus* and *C. lamellosus*. All legs with lamellae on segments 3, 4 and 5, those on III and IV being smaller and simpler than those on I and II. Lateral lamellae of segments 3 and 4 of legs I and II larger than those

\(^{22}\) Viets stated in his key (1940g: 20): “26 (25) Rostrum nicht bis Ende des P. III reichend . . . ” This leads eventually to “36 (37) Okularia hinten gerundet. Rostrum fast doppelt so lang wie breit, bis Ende des P. III reichend . . . angustus Viets 1936.” The latter agrees with the original description and figures; the former is incorrect.
on 5. I-3 (Fig. 252) only 1.75 times as long as high (swollen); wall thick, panelled, margin finely serrate. Medial setae of I-5 pectinate. I-6 with deep claw fossa and prominent membranes, bacillum on lateral membrane, prebacillum absent, parambucral setae divaricate. Claws faintly pectinate (oil immersion) and with accessory tooth, the median claw bidentate. II-3 also swollen (L/H = 1.42). Medial setae of II-5 serrate (oil immersion). Bacillum on lateral membrane of claw fossa. Parambucral setae unfavorable for study, but if divaricate, one member distinctly shorter than other. Medial member of disti-ventral pair of setae of III-5 pectinate; its homologue on IV-5 slender, smooth. Lamellae on legs III and IV simple, rounded, or with slightly angular projections at the distal ends of segments 3, 4 and 5.

Remarks. C. lamellosus (Lohmann) 1893, C. angustus angustus Viets 1936 and C. angustus floridensis, n. subsp., form a natural group within Copidognathus s. str. This is evidenced, not by the mere possession of lamellae on the legs, but by the virtually identical structure of the lamellae in the three forms, and this identity is paralleled by very close similarity or identity in nearly all other structural details. Certain of the minor differences which appear to exist on the basis of the published descriptions should be re-examined to see if they are real and consistent. The three forms are separable as follows.

C. lamellosus: OC pointed posteriorly, but not tail-like. Polygonal porose areas of AE not covering entire plate but restricted to a transverse band of porose areas anterior to the epimeral pores, and a slightly wider band posterior to the epimeral pores. The anterior and posterior transverse bands may be joined by a narrow longitudinal band only as wide as two or three porose areas (sexual difference?). Genital opening of female separated from anterior margin of GA by a distance as great as length of opening. Rostrum extending to end of P-2. (Posterior cornea subdivided? Legs without pectinate setae? Claws not pectinate? These may prove to be rather tenuous characters, if not inaccurate.) Bermuda, Brazil, Australia (Sydney), Mediterranean, English Channel.


Figure 253. Copidognathus (s. str.) septentrionalis (Halbert) 1915. Female: dorsum.
Newell: The Halacaridae of Eastern North America

1947
Copidognathus (s. str.) septentrionalis (Halbert) 1915

Halbert 1915, 125: Halacarus (Copidognathus) lamellosus var. septentrionalis, new variety. Viets 1940g, 27, 104: Copidognathus s. str. lamellosus septentrionalis Halbert 1915.

A form living in Long Island Sound agrees well with the characters of C. lamellosus septentrionalis that have been pointed out in the literature. However, it differs from specimens of C. angustus floridensis in a number of respects. As pointed out above, the latter is very closely related to C. lamellosus. Accordingly, Halbert's variety is herein made a separate species, which is, nevertheless, closely related to C. lamellosus.
Female. The female is shown in Fig. 253. Five specimens measure 277–305µ to the tip of the frontal process. Halbert gave the length as 396–410µ. AD with 3 prominences bearing rosette pores, but in one specimen the 2 posterior areas of rosette pores are coalesced with each other. One to 3 simple pores usually found on each corner of posterior margin. OC variable in form, attenuate posteriorly and sometimes distinctly caudiform, the inner angle sometimes produced mediad, forming a sharp point; 2 groups of rosette pores present as shown. The single pore near the level of the dorsal seta of PE is often rosette-like. Costae of PD not prominent, joined posteriorly by a transverse band of rosette pores (an unusual feature indicated also in Halbert’s fig. 40a). Anal papilla sometimes largely covered by PD. Rosette pores of dorsal plates usually not well developed, the canaliculi small and few in number. In one specimen there are virtually no canaliculi whatever. Ventral surface very similar to that of C. angustus floridensis (Fig. 247).

Rostrum shorter than in latter form, not reaching to end of P-2, the sides converging more sharply. In a female with a body length of 307µ the following measurements were obtained:

<table>
<thead>
<tr>
<th></th>
<th>Length</th>
<th>Height</th>
<th>L/H</th>
</tr>
</thead>
<tbody>
<tr>
<td>I-3</td>
<td>65µ</td>
<td>34</td>
<td>1.91</td>
</tr>
<tr>
<td>I-5</td>
<td>71</td>
<td>28</td>
<td>2.54</td>
</tr>
<tr>
<td>II-3</td>
<td>51</td>
<td>31</td>
<td>1.65</td>
</tr>
<tr>
<td>II-5</td>
<td>55</td>
<td>23</td>
<td>2.83</td>
</tr>
</tbody>
</table>

Segments 3 and 5 somewhat less swollen than in C. angustus floridensis. Segments 3, 4 and 5 of all legs with pointed or rounded lamellae distiventrally, the lateral lamellae being best developed; lamellae on legs I and II no more elaborately developed than those on III and IV. III-5 and IV-5 each with medial member of disti-ventral pair of setae heavier and shorter than lateral member, but medial seta smooth, or at most very faintly pectinate, and always setiform and not scale-like. Tarsi III and IV each with 4 dorsal setae. All tarsi with claw fossa and membranes. Lateral claws I to IV with accessory tooth and very small comb (oil immersion).

Remarks. This species provides another point in favor of the elimination of Copidognathopsis Viets 1927. Although its closest relatives are to be found in C. lamellosus and related species, some specimens have remarkably attenuate ocular plates and would there-
fore be placed in *Copidognathopsis*. When first seen by the writer it was thought that these might be specimens of *C. oculatus*, but the form of the legs removes this possibility completely.

*Distribution.* North America: Rhode Island (three miles north of Block Island); New Haven County, Connecticut (Double Beach). Ireland.

*Copidognathus* (s. str.) *poucheti* (Trouessart) 1893


The original description and figures of this species were published twice. It was described from material from Spitzbergen, and Trouessart stated that he had also seen specimens which were collected on *Lithothamnion* from Labrador. The present writer has not seen any mites answering the description of this species. It has not been recorded from any other region.

*Copidognathus* (s. str.) *gracilis* (Viets) 1936

Figures 254–256

Viets 1936d, 390–391, 409–411: *Copidognathopsis* *gracilis*, new species. Viets 1940g, 56: *Copidognathopsis* *gracilis* Viets 1936.

This species was described well by Viets (1936d: 409–411). The writer obtained a single female from Florida which keys out with little difficulty in Viets’ key (1940g: 56). The following notes are added. Setae of AD minute, anterior to the single posterior rectangular group of rosette pores. Cornea or corneae scarcely discernible in dorsal view because of their anteriad orientation. OC with a seta mediad of the corneae. Costae of PD with rosette pores, PD panelled, each panel enclosing 8 to 10 pores, each in a slightly depressed area so that the

---

*Figures 254–256.* *Copidognathus* (s. str.) *gracilis* (Viets) 1936. 254 Female: venter. 255 Female: portion of PD at level of second seta. 256 Female: left epimeral pore, and surrounding rosette pores and porose panels.

*Figures 257–267.* *Copidognathus* (s. str.) *hummelinki* (Viets) 1936. 257 Female: PD at level of second seta, including a portion of the left costa. 258–265 Corneae of OC (258–259 are drawn from the same mite, but all the others are from different mites. All at same magnification). 266 Male: dorsum. 267 Female: venter.
panels appear subdivided (Fig. 255). A ventral view of the female is given in Fig. 254. The distribution of the rosette pores is unusual, especially in the presence of true rosette pores on the posterior half of AE. These are not always truly rosette-like in structure, for on the other side of the plate many of the canaliculi open directly onto the surface of AE. In fact one can find a complete series from the polygonal areas of simple, minute pores to true rosette pores. Fig. 256 shows the left epimeral pore and a small portion of AE to the left of, and anterior to, that pore. Six rosette pores can be seen anterior to the epimeral pore. The two posterior rosette pores are smaller than the others. Just to the left of these two is a group of coarse, prominent pores which under the proper circumstances of growth almost certainly would have formed a rosette pore. Such intermediate types in the transition from the ordinary type of pores to the rosette pore can be found with little difficulty.

The single female measured 298 x 159 \mu (L/W = 1.86). Viets gave 285 x 145 \mu for the dimensions of the male (L/W = 1.97).

**Distribution.** North America: Florida (Biscayne Bay, on Soldier’s Key).

Curaçao.

*Copidognathus (s. str.) hummelincki* (Viets) 1936

Figures 257–267


Viets (1936d: 411–415) gave a good account of this species, so that a full description is unnecessary here. However, the material from Florida gives an opportunity to demonstrate the variability in this species, which makes it impossible to key out certain individuals with the use of Viets’ key (1940g: 52–56).

Ten females measure 284–325 \mu long (av. 306.1 \mu); five males measure 284–319 \mu (av. 296.4) (Viets 1936d gave the length as 278–297 \mu). The more significant diagnostic features are as follows. AD with only 2 small groups of rosette pores, one directly behind the other (Fig. 266). Setae of AD behind posterior group and well behind middle of plate. A pair of pores lateral to posterior group of rosette pores. OC with a seta near middle of anterior margin; usually 1 to 4 rosette pores between anterior and posterior corneae. Corneae highly variable, rang-
ing from those in which the posterior cornea is only faintly constricted (Fig. 265) to those in which it is divided into two discrete corneae (Figs. 260, 264). The number of rosette pores medial to the corneae range from 1 to 3 in this series, and in one (Fig. 264) all the canaliculi open directly to the surface rather than into an alveolus. All dorsal plates clearly panelled, the panels sharply delimited (Fig. 257). AE and GA delicately panelled and uniformly porose, except for a very minute circular area slightly behind the margin of GA. PE with only 2 pairs of setae ventrally.

I-5 with the usual 3 ventral setae, but these are very long, slender and smooth, whereas on II-5 the 2 medial setae are faintly pectinate. III-5 with medial disti-ventral seta pectinate; its homologue on IV-5 smooth, slender. I-6 with 3 dorsal and 3 ventral setae, in addition to the bacillum and the divericate parambulacral setae. III-6 and IV-6 each with 4 setae dorsally. Claws I to IV pectinate (oil immersion). Median claw bidentate.

Remarks. Viets (1940g: 56–58) has pointed out the similarity between C. (s. str.) adriatica and C. (s. str.) tricorneata Lohmann 1938 (Viets 1938e: 127–132). There is no doubt that C. adriatica is at least equally closely related to C. hummelincki, and probably more so. The three are separable as follows.

C. hummelincki: AD with 2 small but prominent areas of rosette pores. OC with seta near middle of anterior margin. Costae of PD reaching beyond level of first pair of setae. Panels of dorsal plates distinct, not subdivided; all dorsal setae slender. AE and GA uniformly porose. Ovipositor not reaching to anterior end of GA. PE with only 2 pairs of setae ventrally. III-6 and IV-6 with 4 setae dorsally. Florida. Also Bonaire and Aruba.

C. adriatica: AD apparently lacking rosette pores. Homologue of anterior seta of OC of C. hummelincki lying in the membranous area mediad from OC. Costae of PD not reaching to level of first pair of setae. Panels of dorsal plates not subdivided; all dorsal setae slender. AE with pores restricted to a V-shaped area; GA with pores restricted to a U-shaped area in the anterior half of the plate. Ovipositor not reaching to anterior margin of GA. PE with the usual three pairs of ventral setae. III-6 with 4, IV-6 with 3 setae dorsally. Adriatic Sea.

C. tricorneata: AD lacking rosette pores. Homologue of anterior seta of OC of C. hummelincki lying in the membranous area. Costae of PD reaching to or beyond level of anterior pair of setae. Panels of
dorsal plates subdivided; setae between OC and PD, and the first and second pairs of setae of PD, short, broad and nearly scale-like. PE apparently with only 2 pairs of setae ventrally (Lohmann’s sketches showed 2 on one side and 1 on the other). Ovipositor reaching beyond margin of GA. Australia (Sydney).

As shown above, the corneae are completely unreliable as a specific character in C. hummelincki, and it must be suspected, for the present, that the same may be true in the other two species as well.

There is no direct relationship between this species and C. (Arhodeo­porus) gracilipes (Trouessart), despite the smooth legs (compare with Viets 1936d: 414).

**Distribution.** North America: Florida (Biscayne Bay, on Soldier’s Key).

Bonaire; Aruba.

*Copidognathus* (s. str.) *caudatus*, new species

Figures 268–276

The description of this species is based on a single male and female. It keys out to *C. (s. str.) hummelincki* in Viets’ key (1940g: 53), but there appears to be no direct relationship.

**Female.** Body 312 x 180μ (L/W = 1.73). AD (Fig. 268) 86 x 81μ, pyriform, slightly concave posteriorly, 2 raised groups of rosette pores present, the anterior one projecting slightly beyond the anterior margin of plate and containing only 4 or 5 poorly defined rosettes; the posterior group in the form of an inverted V and containing 20 to 25 well defined, coarse, closely-packed rosette pores. The canaliculi of these pores open not only into the sides but also into the bottom of the alveolus. The setae lie behind the posterior group of rosette pores. OC 100 x 44μ and 103 x 38μ, the attenuate posterior cornea with margins slightly less distinct than in anterior cornea. A group of rosette pores between the corneae and a seta mediad from the anterior cornea. The
and the first and third scale-like PE of Hermann's sketches are reaching beyond.

...is a specific, for the present, as well.

...as C. (Archidolus) legs (compare with

...Bay, on Soldier's

...male and female

...Fig. 286, 286 x 81,

...up of rosette pores

...the anterior margin

...setae; the posterior

...to 15 well-defined,

...all of these pores

...n of the alveolus

...pores. OC 100 x

...with margins slight-

...rosette pores be-

...or cornes. The

...Female, dorsal.

...Male: ventral. 172

...Anal plate. 271

...of A.E. near posterior

...of penis and anterior

...Male: posterior.

...Female:
usual pore lies laterad from the posterior cornea. PD 219 x 130μ. Costae prominent, bearing a single to double row of rosette pores. PD and OC distinctly panelled outside the elevated portions (Fig. 274), the panels less distinct than on PD.

Venter as in male, except for characters of GA. GA (Fig. 273) 167 x 106μ; distorted by an injury during the life of the mite (there is no trace of recent mechanical injury). On the right side of the plate there are the usual three setae, but on the abnormal left side the posterior seta is duplicated. The ovipositor is displaced far to the right.

Capitulum as in male. Legs not in favorable position for study, but the following features were observed. Legs relatively slender; leg I, when naturally extended, about 0.78 as long as body. I-3 and II-3 more than twice as long as high. I-5 and II-5 with medial setae pectinate (oil immersion). III-5 with medial member of ventral pair of setae pectinate; its homologue on IV-5 long, slender, but also faintly pectinate, at least in some cases. Legs without lamellae; I, II and III with shallow claw fossa, IV with neither fossa nor membranes. Claw I without longitudinal comb, but the accessory tooth appears to consist of three or four minute teeth. Claws II, III and IV with comb and accessory tooth; all median claws slender, bidentate.

Male. Capitulum (Fig. 269) 92μ long to tip of rostrum and 56μ wide. Rostrum alone 46μ long and 19μ wide near base. Sides of rostrum parallel for a short distance near base and then tapering to a sharp point. Rostrum not reaching to end of P-2, P-2 reaching to or very nearly to end of I-3 when the latter is extended. Base of capitulum panelled, densely porose, pharyngeal plate with 7 closed cells. PE (Fig. 271) with 3 pairs of setae ventrally and 1 pair dorsally; AE and GA panelled and porose. In the postero-median portion of AE the pores are smaller, fewer in number and more widely spaced than on the rest of the plate (Figs. 272, 275). The median portion of GA from the anterior margin to the genital opening is also sparsely porose (Fig. 276), whereas the lateral portions of the plates are like the anterior and lateral portions of AE. GA (Fig. 270) 171 x 112μ. Genital opening surrounded by 35 (19 + 16) very slender setae, the most anterior of which extend to a point 0.40 the length of the plate from the anterior margin. Genital opening 43 x 35μ, removed from anterior margin of plate by a distance about 2.5 times as great as length of opening. Genital sclerites bearing 4 pairs of setae.
margins of GA with rosette pores. Anal papilla protruding slightly beyond PD. The single male had a body 319 x 180 μ (L/W = 1.77).

**Distribution.** North America: Florida (Biscayne Bay, on Soldier’s Key).

*Copidognathus* (s. str.) *pulcher* (Lohmann) 1893

Figures 277–281

Lohmann 1893a, 22–23, 75–79: *Halacarus pulcher*, new species. Lohmann 1901a, 279, 296, 300: *Halacarus (Copidognathus) pulcher* Lohm. Viets 1927a, 139: *Copidognathus* (s. str.) *pulcher* (Lohm.). Viets 1940g, 19, 104, 106: *Copidognathus* (s. str.) *pulcher* (Lohm.).

This species was very beautifully figured in Lohmann’s original description (1893a: pl. 5) and it can be keyed out easily in Viets’ key (1940g: 19). The material in the writer’s collection (2 females and 1 male) are not satisfactory for drawing, but some notes on variation and morphology are given here.

One of the unusual features is the absence of rosette pores. These are replaced by porose panels, the pores of which are rather coarse and open directly to the surface. On AD of one of the females, and in the male, there are two separate areas of porose panels in the position occupied by the posterior groups of rosette pores of other species (as shown in Lohmann’s pl. 5, fig. 8). But in the other female these two groups are joined. The pores in the anterior group of AD of the male are rudimentary, but in the two females these are prominent (see Figs. 277, 280). These are apparently individual variations and not sexual differences. Considerable variation is seen in OC also, even in the few specimens in the writer’s collection, for in the male (Fig. 278) the two posterior corneae are very rudimentary and conceivably could be absent from some individuals. In the two females all three corneae were distinct. It is clear from their size and orientation that the two posterior corneae represent the single posterior cornea of most *Copidognathus* species. In outline the posterior end of the plates ranges from rounded to angular (Figs. 278, 281). The structure of the costae of PD is precisely as shown by Lohmann, the rosette pores being replaced by porose panels which extend to within 2 or 3 panels of the anterior margin of PD. Costae 1 to 2 porose panels wide.

An unusual feature of this species is the addition of a third pair of maxillary setae at about the middle of the base of the capitulum. This seta was shown by Lohmann and is also present in the specimens seen
by the writer. Lohmann did not mention pectinate setae on legs I and II, nor were they shown in his figures. Viets' (1940g: 18) statement that they are absent must be considered as entirely original, since he gave no indication of any knowledge of the species outside of Lohmann's description. Actually, both ventro-medial setae on II-5 are pectinate. On I-5 the distal member of this group appears smooth, but the proximal member is pectinate. Both III-5 and IV-5 have the medial member of the disti-ventral pair of setae scale-like and pectinate, as was noted by Lohmann.

Lengths: Male 284μ; female 312–319μ (Lohmann gave the size as 253–290μ).

Remarks: This species is closely related to *C. triops* Viets (1936d: 405–408), from Aruba, as can be seen from the similar size, form of the plates and the possession of three cornae. The distal member of the ventro-medial setae on I-5 is slender in both species, but in each the posterior member is pectinate. In both species III-5 and IV-5 have the medial member of the disti-ventral pair of setae scale-like and pectinate. The most significant differential characters are the following.

*C. pulcher*: Three pairs of ventral maxillary setae, the additional pair lying near middle of base of capitulum. Rostrum not reaching to end of P-2.

*C. triops*: With only the usual 2 pairs of maxillary setae present, one near the base of the rostrum and the other somewhat beyond the middle of the rostrum. Rostrum extending beyond P-3. Aruba, Dutch West Indies.

The characters given above to indicate the relationship between *C. pulcher* and *triops* also indicate a direct relationship between these two species and *C. magnipalpus magnipalpus* (Police) 1909 (Mediterranean, Bay of Naples) and *C. magnipalpus serratisetus* Viets 1940 (northern Adriatic). However, the relationship of these four forms to *C. magnipalpus ponticus* Viets (1936b: 199) of the Black Sea is not so clear.

---

Figures 280–281. *Copidognathus* (s. str.) *pulcher* (continued). 280 Female: antero-dorsal plate (same scale as 277–279). 281 Female: right OC of mite from which 280 is drawn (same scale as 277–279).

More accurate figures on the type of panelling and pores would be of value here.

**Distribution.** North America: Florida (Biscayne Bay, on Soldier's Key).
Bermudas, Ascension, Australia (Sydney).

*Copidognathus* (s. str.) *pachypus* new species

Figures 282–290

This species is represented by a single female which lacks all the legs of one side. Body 294 x 150μ (L/W = 1.96), nearly twice as long as broad. AD 93 x 73μ, anterior margin nearly straight, posterior margin concave, sides constricted at level of leg II; widest portion of plate anterior to the constriction. A pair of setae and a pair of pores in widest portion of plate, several deep pits near posterior margin, marking positions of internal apodemes. OC 61 x 24μ and 58 x 23μ (L/W = 2.54 and 2.52). A seta between OC and AD. Cornea prominent, the posterior one divided to form 2 small corneaæ. Posterior half of OC attenuate. Under low power OC of the right side appears to have a blunt end, but under high power it can be seen that the portion of the plate not covered by striate cuticle is actually attenuate (Fig. 282), just like OC of the left side. PD 183 x 91μ (exclusive of anal papilla), with costae weakly developed except posteriorly, 3 pairs of setae present as shown. All dorsal plates lacking rosette pores but possessing porose panels. The surface of the plates outside these areas very faintly panelled, the paneling more distinct at low than at high magnifications. Each panel enclosing 5 or 6 very minute pores (shown only in Fig. 282). Panelling on OC scarcely discernible. Coarse pores lying over posterior corneaæ apparently incomplete, penetrating only a short way into cuticle.

AE (Fig. 285) with 3 pairs of setae, posterior margin concave. PE with 4 pairs of setae. GA 128 x 81μ; with 3 pairs of setae. Genital opening 56μ long, 46μ from anterior margin of plate. Genital sclerites projecting only slightly beyond posterior margin of opening, with a single pair of setae. AE with prominent porose panels (Fig. 283) covering plate uniformly; GA and PE also porose like AE, but paneling less distinct.

Capitulum (Figs. 289, 290) 98μ long to tip of rostrum, the base of capitulum longer than broad (63 x 56μ), densely porose (Fig. 290).
Rostrum alone 32 µ long, not reaching to end of P-2 but reaching nearly to end of I-3. Three pairs of maxillary setae rather than the usual 2 pairs. Minute setae at tip of rostrum relatively long and slender. Pharyngeal plate with 7 or 8 closed panels.

Leg I (Fig. 287) very heavy, short, only 166 µ long (0.57 as long as body) when in a naturally extended position. In *C. biscayneus*, n. sp., which also has relatively short legs and in which I-3 and II-3 are swollen, leg I is 0.64 as long as the body. In *C. hummelincki* leg I, when normally extended, is fully as long as the body. I-3 very short, thick, less than 1.5 times as long as high, the ventral half of segment with coarse pores as shown; lateral seta very faintly pectinate. I-4 with medial seta pectinate (oil immersion). I-5 with proximal ventro-medial seta broad and coarsely pectinate; the distal one smooth. Distal end of tarsus nearly as high as base, the claw fossa nearly vertical; lateral membrane produced distally; medial membrane smaller. The lateral claws are withdrawn into the fossa so that the presence or absence of a comb and accessory tooth cannot be ascertained. Disti-dorsal setae and bacillum not in favorable position for study, 3 ventral setae present. The parambularacral setae are present laterally, but the medial ones are apparently broken off, since only an alveolus is present. Tarsus I is in an unfavorable position for study. Unfortunately, leg I of the other side is broken off, so that it is impossible to determine whether or not the rather unusual structure of the tarsus is normal.

Leg II with femur even shorter than that of leg I, less than 1.25 times as long as high. Medial seta of II-4 smooth, pectinate. Both ventro-medial setae of II-5 heavy, pectinate. II-6 with claw fossa less vertical than that of I-6 and with membranes not so well developed; 3 dorsal setae present, ventral setae absent. Bacillum and divaricate parambularacral setae present. Lateral claws with accessory tooth and with a very minute comb which does not project beyond the concave margin of the claw (oil immersion). Median claw bidentate. Femora III and IV also with a small porose area ventrally. Medial member of disti-ventral pair of setae of III-5 and IV-5 pectinate, the lateral member smooth. Tarsi III and IV with prominent claw fossa and lateral membranes. Claws as on II-6; comb discernible only with difficulty.

Remarks. As pointed out in the introduction to *Copidognathus* s. str., this species appears to be more closely related to *C.* (s. str.)
**Copidognathus** (s. str.) *bonairensis* Viets 1936

Figures 291-292


This species was well described by Viets, so that a redescription here is unnecessary. Figs. 291 and 292 will enable one to recognize this very unique form, the most important diagnostic features of which are as follows. AD with an elevated area in the shape of an inverted goblet, the setae lying on the anterior margin of the large posterior
Subgenus *Arhodeoporus*, new subgenus

**Diagnosis.** *Copidognathus* s. lat. species in which tibia I has 2 pairs of setae ventrally rather than 3 unpaired setae as in *Copidognathus* s. str. Rostrum broad at base (nearly as broad as long) with tip of rostrum scarcely extending beyond middle of P-2. Rosette pores absent (excluding the 2 epimeral pores which may be rosette-like).
Ocular plate drawn out into a long, posterior, caudiform projection in the species known at present.

Type. *Copidognathus (Arhodeoporus) arenarius*, n. sp.

**Key to North American Species (Adult)**

1a. Medial margin of OC convex, projecting between AD and PD. Genital opening of male removed from tip of anal papilla by a distance greater than length of opening. Body 300–340μ long. Arenicolous, or in shallow water.

*arenarius*, new species; p. 175. Massachusetts to North Carolina.


*submarinus*, new species; p. 178. Long Island Sound.

**Copidognathus (Arhodeoporus) arenarius**, new species

Figures 293–304

*Female.* Body 300–340μ long; 180μ wide. AD 110μ long, 110μ wide, bearing a pair of pores on 2 antero-lateral prominences. In some individuals (including the type) a third prominence is developed antero-medially, but this shows various degrees of reduction. Cuticle densely covered with coarse pores; panelling feebly developed or lacking and usually restricted to posterior part of plate. Posterior margin straight. OC similar in form to that of *Copidognathus gracilipes gracilipes* (Trouessart), but larger, and extending only to a point 2/3 distance between legs III and IV; caudiform process variable in width. Cornea at anterior end feebly developed, sometimes apparently lacking. A large pore at lateral angle, and posterior to this a fine pore. Cuticle irregularly porose but panelling only feebly developed. PD 200–235μ long, 150μ wide; surface porose, panelling well developed except on the 2 longitudinal ridges and around the large pores at level of leg IV. Another pair of large pores at ends of ridges. Posterior half of plate elliptical; antero-lateral margins straight, converging anteriorly; anterior margin straight or only slightly convex.


AE extending to or slightly beyond level of leg III, posterior margins slightly concave, lateral margins concave. Panelling well developed and similar to that on PD. PE with 3 pairs of setae ventrally and 1 pair dorsally. GA 150–160μ long, 115–125μ wide; anterior margin straight, lateral margins nearly parallel and postero-lateral margins rounded or gently sinuate; cuticle panelled; 3 pairs of setae present. Genital opening central, 66μ long and 40μ wide. Anus terminal, projecting slightly; 33μ from genital opening. Membranous areas considerably restricted, striate; plates nearly contiguous. OC-OC 100–115μ.

Capitulum 80μ long and 66μ wide; cuticle punctate but not panelled. Rostrum conical, smooth, 36μ long, reaching to a point about ¼ length of P-2 from end of that segment. Base of rostrum slightly constricted. Pharyngeal plate bearing 10 or 12 cells in a double row; lateral cells absent. Palpi (based on male) with P-2 as long as, or only slightly longer than, P-4; P-1 and P-2 sparsely and uniformly punctate; one dorsal seta on P-2, 3 on basal portion of P-4 and an extremely small seta medially near tip of P-4. Lengths of P-1 to P-4, 14, 36, 9, 32μ. Chelicerae 80μ long and 24μ high; cheliceral membrane more than ½ as long as edge of movable digit; the latter finely toothed.

Dimensions of principal leg segments as follows (given as dorsal length in μ/maximum height):

<table>
<thead>
<tr>
<th></th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>Claw</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>75/33μ</td>
<td>28/23</td>
<td>73/25</td>
<td>40/12</td>
<td>17</td>
</tr>
<tr>
<td>II</td>
<td>60/25</td>
<td>25/20</td>
<td>56/18</td>
<td>48/12</td>
<td>23</td>
</tr>
<tr>
<td>III</td>
<td>50/17</td>
<td>25/15</td>
<td>58/15</td>
<td>54/12</td>
<td>25</td>
</tr>
<tr>
<td>IV</td>
<td>58/20</td>
<td>28/17</td>
<td>63/16</td>
<td>54/11</td>
<td>26</td>
</tr>
</tbody>
</table>

I-3 and II-3 2.3–2.4 times as long as high (not swollen); I-5 and II-5 2.0–3.1 times as long as high (above measurements from male with body length of 327μ; female essentially identical). I-3 and II-3 flattened ventrally, with 1 prominent and 1 or 2 less prominent longitudinal ridges. I-5 ventrally with a pair of slender setae distally, and another pair of setae near the middle, the medial member of which is flattened and faintly pectinate; II-5 with 2 very large, flat, pectinate setae medially and a smaller seta ventro-laterally. Both III-5 and IV-5 with a pair of setae disti-ventrally, the medial member of which is enlarged, flattened and pectinate. I-3 with 1 dorsal seta behind triangle setae, and 1 ventral seta near middle of segment. I-6 and
II-6 with very shallow claw-fossa (best developed on I-6), and each
with a curved bacillum behind claw (not easily seen on leg I, but very
distinct on II). Claw fossa on III and IV very faint and without
membrane; bacillum lacking. Each tarsus with 2 strongly curved,
nonpectinate claws, each of which has a prominent accessory tooth
dorsally. All legs uniformly punctate; not panelled.

Color in life. The midgut is usually a delicate brownish-orange.
As many as four pairs of elongate white spots may be seen dorsally.
Under high magnification each of the dorsal white spots is seen to con­
sist of a sac, densely packed with long filaments. The sac opens at
the pore with which it is associated and the contents can be ejected by
compression with a needle.

Male. The male resembles the female in most details, including
size. The only discernible differences are in the form of GA, which is
165 μ long and 125 μ wide. Anterior edge straight, the sides nearly
parallel; surface irregularly covered with coarse pores, not panelled,
and with 30–35 long, slender setae. Genital opening 50 μ long and
37 μ wide, guarded by 8 small setae arranged in 2 groups of 4 setae.
Anus terminal, projecting slightly.

Deutonymph. As in most halacarids, the nymphs vary greatly in
appearance depending on the stage of development. The following
description is based on a deutonymph 270 μ long and 180 μ wide.
Dorsal plates smaller and more rounded than in adult. AD 83 μ long,
81 μ wide. OC rounded posteriorly, extending only to level of leg III;
a single rudimentary cornea anteriorly. PD 146 μ long, 108 μ wide;
oval in outline except at posterior end. Ventral plates also less exten­
sive than in adult. Anal and genital plates separate. Genital plate
61 μ long, 68 μ wide, rounded anteriorly and square posteriorly. Anal
plate 34 μ long and 60 μ wide. All plates faintly but distinctly panelled.
The species is compared with C. submarinus, n. sp., in the section on
that species (p. 181).

Distribution. North America: Woods Hole, Massachusetts; New
Haven County, Connecticut (Double Beach; Morris Cove [type
locality]); Beaufort, North Carolina (Newport River at 3 meters,
Piver's Island, Town Marsh, Harker's Island).
Copidognathus (Arhodeoporus) submarinus, new species

Figures 305–314

Female. Body 340–416μ long, 222–256μ wide, L/W = 1.53–1.66 (av. of 6 specimens 370 x 231μ, L/W = 1.61).

AD with broadest portion usually very near straight posterior margin, with a pair of pores and 1 pair of setae. OC with 1 well developed cornea and a pore, and often with a less well developed cornea behind the first. Medial margin straight or gently convex, but with no prominent medial angle. Tail of OC rather thick, extending to a point about halfway between III and IV.

One or two very minute fragments of sclerotized cuticle often found in membranous area behind end of tail, but these never form a continuous sclerite reaching beyond IV. PD elliptical, truncate anteriorly, with 3 pairs of setae and 2 pairs of pores. Dorsal plates faintly panelled and with very minute cuticular pores except for a few areas in which the pores are very coarse. Usually 3 such areas on AD, 2 on each OC, and broad longitudinal bands on PD. The longitudinal bands on PD are not markedly elevated and owe their prominence principally to the coarseness of the pores found there. In a female with a body length of 353μ the following measurements were obtained: AD 83μ long, 125μ wide; OC 145 x 35μ, and 142 x 35μ; PD 263 x 166μ; OC–OC 130μ.

AE undivided; the posterior pair of setae at the same level as the anterior ventral pair on PE. A pair of large, simple pores between I and II. Internal apodemes prominent. GA undivided, sides parallel. Genital opening large, displaced posteriorly; anterior margin of opening often less than length of opening from anterior margin of GA. Anal papilla projecting only slightly, or not at all, beyond end of PD. Three pairs of setae present, the most anterior pair at the same level as posterior setae on PE. In the above female (353μ) GA is 169 x 123μ, the genital opening 81 x 43μ, and the anterior end of the opening 68μ from the anterior margin of GA. Ventral plates faintly and uniformly panelled, without coarse cuticular pores.

Capitulum (Fig. 313) identical in form with that of C. arenarius, n. 


Newell: The Halacaridae of Eastern North America

L/W = 1.33-1.86

Right posterior mala
g with 1 well de
dveloped corn

convex, but with no
tick, extending to a

cuticle often found
ever form a con

tural, truncate ante
dorsal plates fairly

left for a few area

areas on AD 2 a

The longitudinal
te their prominence

e. In a female with

the same level as the

euple pores between 1

tided, sides pubes

er margin of opes

er margin of Ga

beyond end of FI

at the same level as

Ga is 169 x 130,

do the oenopid

is faintly and un

C. armarius, n.

301 302 303

304 305 306

307
In a female with a body length of 367μ, these measurements were obtained: capitulum 90μ long to tip of rostrum and 73μ wide; rostrum alone 37μ long and 32μ wide at base, not constricted, reaching slightly beyond middle of P-2. Pharyngeal plate with 10 to 12 closed cells; lateral cells absent. Base of capitulum punctate and faintly panelled; rostrum smooth. P-1 to P-4 16, 46, 11, 49μ long respectively (body length 395μ). Chaetography of all legs identical with that of C. arenarius, n. sp., but setae somewhat heavier and the bacilliform setae on I and II more nearly alike than in arenarius.

<table>
<thead>
<tr>
<th></th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
</tr>
</thead>
<tbody>
<tr>
<td>d.</td>
<td>v.</td>
<td>l.</td>
<td>m.</td>
<td>d.</td>
</tr>
<tr>
<td>1.</td>
<td>-</td>
<td>-</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>2.</td>
<td>1</td>
<td>1</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>3.</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>4.</td>
<td>2</td>
<td>2</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>5.</td>
<td>4</td>
<td>4</td>
<td>-</td>
<td>3</td>
</tr>
<tr>
<td>6.</td>
<td>3</td>
<td>3</td>
<td>-</td>
<td>3</td>
</tr>
</tbody>
</table>

* One female has two dorsal setae on IV-4 of one side.

In a female with a body length of 395μ, the following measurements were obtained:

<table>
<thead>
<tr>
<th></th>
<th>1+2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>Ambul.</th>
<th>Total</th>
<th>T/BL</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>42μ</td>
<td>83/38</td>
<td>32</td>
<td>83</td>
<td>56</td>
<td>22</td>
<td>318</td>
<td>0.80</td>
</tr>
<tr>
<td>II</td>
<td>38</td>
<td>65/28</td>
<td>27</td>
<td>61</td>
<td>55</td>
<td>27</td>
<td>273</td>
<td>0.69</td>
</tr>
<tr>
<td>III</td>
<td>50</td>
<td>51</td>
<td>32</td>
<td>60</td>
<td>61</td>
<td>28</td>
<td>282</td>
<td>0.72</td>
</tr>
<tr>
<td>IV</td>
<td>53</td>
<td>59</td>
<td>35</td>
<td>61</td>
<td>65</td>
<td>30</td>
<td>303</td>
<td>0.77</td>
</tr>
</tbody>
</table>

I-3 2.18 times as long as high (not swollen). Medial member of proximal pair of ventral setae on I-5 faintly pectinate. The proximal ventral seta on I-6 is often difficult to find as it is very closely applied to the ventral surface of the segment. I-6 with 3 setae dorsally and 3 ventrally in addition to bacillum and parambulacral setae. Bacillum long, only slightly curved, relatively erect, and inserted on the lateral side. Parambulacral setae not joined at base, although arising from a common area. Lateral claws not pectinate, but with a very long accessory tooth; median claw bidentate. Claw fossa represented by only a very shallow depression; membranes absent. Leg II as in C. arenarius, n. sp., but femur more smooth ventrally. II-5 with 2 pectinate setae medially. II-6 (Fig. 310) with bacillum on lateral side, but without prebacillum; parambulacral setae replaced by a single
Newell: The Halacaridae of Eastern North America

 blunt seta on each side. Claws not pectinate, the median claw bidentate. III-5 and IV-5 with a pair of disti-ventral setae, the medial member of which is flattened and pectinate, the other slender, very long and smooth. III-6 and IV-6 with 3 setae dorsally, and with a seta and a very heavy spine at base of the ambulacrum which are homologous with the parambulacral setae on I and II. Claws III and IV as on I and II.

Male. Comparable to female in size and form. Three males measure 360–374μ long and 218–225μ wide (L/W = 1.65–1.66). The only differences in the plates lie in GA. GA parallel-sided as in female, the genital opening relatively near anus but not so close to anus as in female. Opening surrounded by 13 to 16 very slender setae on each side, and with a cluster of 8 to 10 coarse puncta on each side. In a male with a body length of 360μ GA is 174 x 141μ; the genital opening is 50 x 38μ and 93μ from the anterior margin of GA (i. e., nearly twice the length of the genital opening).

Remarks. This species is highly variable in form. A number of specimens were found in which the entire body is much narrower than in the specimens on which the above description is based. But the characters of these intergrade with the characters of the common form to such an extent, even with the relatively few adults available for study, that these forms cannot be considered as constituting a distinct variety. The narrowest specimen, a female, measures 374 x 208μ (L/W = 1.80). Considerable variation is also found in the cornea (as in C. arenarius, n. sp.). As a rule there is a single well developed cornea, behind which sometimes lies an irregular patch of polished, refractile cuticle. The latter is often absent, however, and occasionally even the anterior cornea is not very distinct.

C. (A.) submarinus, n. sp., arenarius, n. sp., and gracilipes gracilipes (Trouessart) are quite similar in most respects. Using Viets' descriptions and figures (1927a: 145–148; 1940g: 59–60) as a basis of comparison, the three species can be differentiated as follows.

C. submarinus: Medial margin of OC not projecting between AD and OC, but relatively straight. Second dorsal seta lying in anterior angle of OC, the third dorsal setae in PD. OC not extending to level of insertion of leg IV. Costae of PD usually not projecting prominently. Posterior setae of AE about 4 times as far from hind margin of plate as the most posterior apodemes. Porose panels uniformly developed over entire surface of plate. PE with 4 pairs of setae.
Genital opening of female removed from anterior margin of GA a distance nearly as great as length of opening. Genital opening of male separated from end of anal papilla by a distance less than length of opening.

*C. arenarius*: As above, except for the following features. Medial margin of OC distinctly convex, projecting between AD and PD. Genital opening of male removed from tip of anal papilla by a distance greater than length of the opening.

*C. gracilipes gracilipes*: Medial margin of OC projecting between AD and PD, distinctly convex. Second and third dorsal setae lying in the membranous area. OC extending beyond insertion of IV. Costae of PD projecting prominently. Posterior setae of AE near edge of plate, at same level as the most posterior apodemes. Coxal areas I and II of each side with an area of prominent porose panels. PE with 5 pairs of setae. Genital opening of female removed from anterior margin of GA by a distance much greater than (1.5 times) the length of the opening.

*Distribution.* North America: Rhode Island (3 miles north of Block Island, at 34 meters).

Genus *Agaue* Lohmann 1889


*Diagnosis.* Body and legs often with elaborate lamellae. Capitulum often reaching to or very nearly to end of I-3. Palpi relatively straight (see key to genera), distinctly 4-segmented, attached to capitulum laterally, so that bases of palpi are clearly visible in ventral view and are separated from each other by a distance greater than width of P-1. Combined length of P-3 and P-4 less than length of P-2, but greater than one-third length of P-2. P-3 never with a thick medial seta. Rostrum usually distinctly parallel-sided, or even slightly

broader near distal end than near middle. Leg I without heavy, rod-shaped setae medially and ventrally. Middle piece of ambulacrum articulating directly with end of tarsus; carpite absent.

*Type. Agaue parva* (Chilton) 1883; by monotypy.

*Remarks.* A single species is known from North America.

*Agaue nationalis* (Lohmann) 1893

Figure 315


This is one of the most beautiful of all mites, owing to the elaborate development of lamellae on the body and legs (Fig. 315). These develop as extensions of the walls of panels, so that the cavity of the panel, instead of being a shallow depression, is a long, tubular chamber, tapering gradually toward the edge of the lamella, where it often opens through a small circular pore. The species can be differentiated from other species of the genus by the greatly swollen ends of the tibiae of all the legs, the complete absence of setae from P-3, and the very elaborate development of the lamellae. The rostrum reaches to or slightly beyond the middle of P-4, and the tips of the palpi extend beyond the end of I-3.

*Distribution.* North America: Florida (Biscayne Bay, on Soldier's Key). Bermudas.

Northeastern Brazil.

**Genus Agauopsis Viets 1927**


*Diagnosis.* Middle piece of claw articulating directly with tip of tarsus, carpite absent. Palpi distinctly 4-segmented; P-3 plus P-4 shorter than P-2 in probably all species. Palpi attached laterally,
Newell: The Halacaridae of Eastern North America

1947

185

Newell: The Halacaridae of Eastern North America

1947

185

Newell: The Halacaridae of Eastern North America

1947

185

Newell: The Halacaridae of Eastern North America

1947

185

Newell: The Halacaridae of Eastern North America

1947

185

Newell: The Halacaridae of Eastern North America

1947

185

Newell: The Halacaridae of Eastern North America

1947

185

Newell: The Halacaridae of Eastern North America
Agauopsis borealis, new species

Figures 317-326

Female. The only intact females in the author's collection measure 471 x 322 (L/W = 1.46) and 500 x 346 (L/W = 1.44), the length measured to the minutely rounded tip of AD. In the shorter specimen the following measurements were obtained: AD 183 x 158, OC 108 x 88 and 110 x 96, PD 215 x 215, the latter not including the anal papilla.

Type. Agauopsis brevipalpus (Trouessart) 1889 (by original designation).

Remarks: Only two forms, A. brevipalpus brevipalpus and A. borealis, n. sp., are known from North America. These are compared in the description of A. borealis, in lieu of a formal key.

Agauopsis brevipalpus brevipalpus (Trouessart) 1889

Figure 316


Agauopsis brevipalpus brevipalpus and A. b. pontica (Chichkoff) 1907 have been treated so extensively by previous workers (most critically by Viets, 1928c: 60–64; 1940g: 74, 76, 78–81, etc.; also by Lohmann 1893a: 22, 23, 85, 87) that no further treatment is necessary here.

One of the Florida specimens is drawn in dorsal view (Fig. 316) to aid in distinguishing it from A. borealis, n. sp., with which it is compared below. Three females measure 409–422 long (to the tip of AD), whereas six males measure 325–367.

Distribution. North America: Florida (Biscayne Bay, on Soldier's Key).

Brazil (northeastern), Bermudas, Azores, Canary Islands, French Atlantic, Ireland, Mediterranean, northern Adriatic, Black Sea, Australia (Sydney).

Agauopsis borealis, new species

Figures 317–326

Female. The only intact females in the author's collection measure 471 x 322 (L/W = 1.46) and 500 x 346 (L/W = 1.44), the length measured to the minutely rounded tip of AD. In the shorter specimen the following measurements were obtained: AD 183 x 158, OC 108 x 88 and 110 x 96, PD 215 x 215, the latter not including the anal papilla.
AD depressed around margins in such a way as to form an H-shaped elevated area. Depressed areas panelled and porose. OC with portion on which the 2 corneae are found are porose only; rest of plate both porose and panelled. PD with costae nearly or completely parallel, not diverging anteriorly. Costae porose and only moderately prominent; rest of plate panelled and porose. In the specimen drawn in Fig. 318, the membranous area is considerably contracted. The plates do not overlap.

AE (to posterior margin of camerostome) as long as GA. PE with 3 pairs of setae ventrally and 1 pair dorsally. GA with 3 pairs of setae, the posterior pair very slender. Internal suckers as shown in Fig. 324. Ventral plates uniformly porose (Fig. 325), very faintly panelled.

Capitulum 171 μ long to tip of rostrum (body length 500 μ) and about 89 μ wide. Rostrum alone 88 μ long and 26 μ wide near base, reaching very nearly to tip of palp. In Fig. 319 the palp is slightly flexed. The specimen was dissected in glycerine without treatment of any kind. Two specimens treated with trypsin show that the palpi extend about 5 or 6 μ beyond the rostrum. This is, therefore, a very tenuous diagnostic character. Posterior pair of rostral setae 2 or 3 times the dorsal length of P-1 behind insertion of palp. P-1 to P-4 7, 68, 9, 19 μ long; P-2 16 μ high (body length of specimen unknown). Medial seta of P-3 very heavy, much longer than P-3 itself, and about 1/3 as high. P-4 with only 2 basal setae.

Chaetography of leg I (Fig. 322) identical with that of A. brevipalpus brevipalpus as figured by Viets (1940g: 79). I-3 not swollen (L/H = 2.2). I-6 (Fig. 323) with bacillum but without a prebacillum, unless the large process anterior to the bacillum represents a greatly modified prebacillum [as in Halacarus (Th.) subterraneus; Fig. 175]. Parambular setae divaricate. Lateral claws not pectinate, accessory tooth present. Median claw bidentate. Chaetography of leg II also identical with that of H. brevipalpus brevipalpus (see Viets 1940g: 79). Heavy ventral setae of II-5 faintly pectinate. II-6 without medial or ventral setae. Lateral parambular seta divaricate, with ventral member less than half as long as dorsal member (Fig. 326). Although no bacillum can be seen on II-6, there is such a well developed cuticular canal anterior to the medial disti-dorsal seta that it seems most likely that a bacillum had been present but was broken off. A sharply-bent, minute bacillum is found in this position in A. brevipalpus.
brevipalpus. Lateral claws pectinate and with accessory tooth, median claw absent. III-5 and IV-5 with a pair of heavy, faintly pectinate setae disti-ventrally. III-6 and IV-6 with only the lateral paramembilacral setae present, spiniform. Claws III and IV pectinate, median claw absent. Claw fossa on I-6 very small, other tarsi only tapering.

Remarks. This species appears to resemble A. brevipalpus brevipalpus (Trouessart) more closely than any other, although it differs in several respects. The most apparent diagnostic features are as follows.

A. borealis: AD with H-shaped area distinct but not sharply elevated above the plate, well removed from sides of plate. PD with costae parallel. Palpi slightly longer than rostrum. Spiniform setae of leg I relatively small.

A. brevipalpus brevipalpus: AD with posterior arms of H-shaped area very prominent, their outer edges sharply elevated above the surface of the plate and forming a virtual keel. PD with costae distinctly divergent anteriorly. Palpi slightly shorter than rostrum. Spiniform setae of leg I relatively large.

Viet (1928c: 60–65) gave a detailed comparison of A. brevipalpus brevipalpus with A. brevipalpus pontica. A. borealis is more closely allied to the former.

Distribution. North America: New Haven County, Connecticut (Morris Cove, type locality); Solomon's Island, Maryland; Beaufort, North Carolina (Newport River at 2.5 meters; Town Marsh; Harker's Island).

Subfamily LOHMANNELLINAe VIETS 1927

Diagnosis. Middle piece of claw articulating directly with end of tarsus; carpite absent. Palpi attached to capitulum dorsally, separated by an interval not greater than width of base of P-1, distinctly 4-segmented. Rostrum about as long as palpi in uncompressed specimens, relatively uniform in width, opposed to downwardly turned elongate palpi. Rostrum at least three times as long as high. Marine or fresh water. Predaceous. Probably cosmopolitan.

Figures 322–326. Aqauopsis borealis (continued). 322 Female: leg I, median view. 323 Female: I-6, lateral view. 324 Female: genital opening. 325 Female: portion of cuticle from center of AE. 326 Female: II-6, ventro-lateral view.

Genus *Lohmannella* Trouessart 1901


*Diagnosis.* Capitulum sometimes very long, about 1/6 to 1/3 as wide as body. Rostrum about as long as palpi and uniform in width beyond middle; rounded terminally, not broadened, opposed to downwardly turned palpi. Palpi distinctly 4-segmented, attached to base of capitulum dorsally, separated basally by an interval no greater than width of P-1. Genital suckers external.

*Type.* *Lohmannella falcata* (Hodge); by monotypy.

*Lohmannella falcata* (Hodge) 1863

Figures 327–330


The male shown in Fig. 330 has a body 374 x 291 μ (L/W = 1.28); length to tips of palpi 585 μ. AD pentagonal, bearing a pair of long, slender setae. OC broadly rounded laterally, with 2 reduced corneae anteriorly and a slit-like pore just behind middle of lateral margin. Corneae distinctly smaller than those of deutonymph and sometimes almost lacking. PD ovate, distinctly broader anteriorly than poste-
ECOLOGY

INTERRELATIONSHIPS OF THE FAUNAE OF THE EASTERN COAST OF NORTH AMERICA

The most intensively studied areas on the eastern coast of North America are: New Brunswick (St. Andrews), Long Island Sound (Connecticut and Rhode Island), Chesapeake Bay (Solomon’s Island, Maryland), North Carolina (Beaufort) and southern Florida (Biscayne Bay). Miscellaneous records from Massachusetts (Woods Hole), and Maine (Casco Bay and Eastport) are also included, as are the records of previous workers.

A total of 41 species, subspecies and varieties of Halacaridae are now recorded from eastern North America and Greenland, as compared with the four which were known previously (Table I). Of the latter, two [Halacarus (Thalassarachna) basteri basteri and Copidognathus (s. str.) punctatissimus] were rediscovered in the course of the present work, whereas the other two [Rhombognathus notops and Copidognathus (s. str.) poucheti] were not. Of the 41 forms, 27 were known from previous works and 14 are newly described. The number of North American genera and subgenera has been increased from three to eleven. Of these, three are newly described herein, but each of these contains representatives which were previously known from Europe.
Table I. Distribution of the Marine Halacaridae of Eastern

Genera, Subgenera, Species, Subspecies, and Varieties

<table>
<thead>
<tr>
<th>Rhombognathus</th>
<th>+</th>
<th>+</th>
<th>+</th>
<th>+</th>
<th>+</th>
</tr>
</thead>
<tbody>
<tr>
<td>magnirostris magnirostris</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>magnirostris lionyx</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>notops</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rhombognathides</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>pascens</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>seahami</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>mucronatus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Merrimani Merrimani</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Merrimani Needleri</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Metarhombognathus</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>armatus americanus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Isobactrus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>setosus</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>levis</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>hutchinsoni</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Halacarus s. str.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ctenopus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>actenos</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>frontiporus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>anomalus</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>H. (Thalassarachna)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>basteri basteri</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>longipes</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>balicus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>capuzinus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>subterraneus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The entire number of forms from each region must be considered in the light of the effort expended in collecting. Thus, the 19 forms known from Long Island Sound were collected over a period of nearly three years, during which time scores of samples were examined, from both intertidal and subtidal habitats. On the other hand, 15 forms were taken in one small collection from Soldier's Key, Biscayne Bay, Florida, and all but one of these (Copidognathus pulcher) were found
on two small bunches of *Halimeda*, a calcareous green alga. Had collections been made in Florida on the same scale as those in Long Island Sound, two or three times the number of species probably would have been found. Six days of intensive collecting at Beaufort, North Carolina, during which 26 samples were taken from a wide variety of habitats, yielded only seven species. Only three species were taken at Solomon's Island, Maryland, in three days. Equivalent

---

<table>
<thead>
<tr>
<th>Genera, Subgenera, Species, Subspecies, and Varieties</th>
<th>Agaue</th>
<th>C. (Arhodeoporus)</th>
<th>Agauopsis</th>
<th>Lohmannella</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>nationalis</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>COpidognathus s. str.</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>punctatissimus</strong></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>acutus</strong></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>bairdi</strong></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>curassaviensis</strong></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>bicaynneus</strong></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>angustus floridensis</strong></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>septentrionalis</strong></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>poucheti</strong></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>gracilis</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>hummelincki</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>caudatus</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>pulcher</strong></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>pachypus</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>bonaitensis</strong></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>arenarius</strong></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>submarinus</strong></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>brevipalpus brevipalpus</strong></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>borealis</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>falcata</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Totals:**

<table>
<thead>
<tr>
<th>North Carolina</th>
<th>Chesapeake Bay</th>
<th>Conn.-Rhode Island</th>
<th>Massachusetts</th>
<th>Maine</th>
<th>New Brunswick</th>
<th>Labrador</th>
<th>Greenland</th>
</tr>
</thead>
<tbody>
<tr>
<td>15</td>
<td>7</td>
<td>3</td>
<td>19</td>
<td>3</td>
<td>2</td>
<td>8</td>
<td>1</td>
</tr>
</tbody>
</table>

---

North America. See Text, p. 191
collecting in habitats in the vicinity of New Haven probably would have yielded 12 to 15 species. To be sure, the fauna at Solomon's Island (salinity 10-12%/o) is not to be compared directly with that at the mouth of Chesapeake Bay, but it seems likely that even on the open coast the fauna would not be as rich as that to the north. Twelve samples from the intertidal zone at St. Andrews, New Brunswick, contained eight species, indicating that the fauna there is probably about as rich as that around New Haven. Therefore, the Florida fauna is certainly the richest on our eastern coast, that of the New England coast is the second richest, and intermediate regions are the poorest.

The most striking feature noticeable in Table I is the complete lack of correlation between the faunae of Florida and the New England-New Brunswick coast, there being not one species common to both regions. In fact, only three of the 11 genera are found in both regions. The following genera or subgenera of the New England-New Brunswick coast are lacking in southern Florida: Rhombognathides, Meta-rhombognathus, Isobactrus, Halacarus (Thalassarachna), Copidognathus (Arhodeoporus) and Lohmannella. The genera Agaue and Rhombognathus are lacking in the north.

The fauna at Beaufort is much more closely related to the northern fauna than to that of Florida, for of the seven forms taken at Beaufort, five are northern species, one is endemic and only one is subspecifically related to a Florida species. The genus Rhombognathus is found there, whereas it has not been found by the writer north of Chesapeake Bay. The paucity of the fauna at Beaufort is due to a dropping out of entire genera or subgenera. Thus, Halacarus (Thalassarachna), Rhombognathides, Isobactrus and Lohmannella are completely lacking there, whereas these four groups contribute a total of 14 forms to the fauna of the New England-New Brunswick region. At the same time, Beaufort does not have the extreme development of Copidognathus (s. str.) which is seen in southern Florida.

The structure of the North Carolina coast is very complicated, the main coast being separated from the open Atlantic by an almost continuous series of offshore bars. The intervening sounds communicate with the Atlantic through a few narrow inlets, numerous rivers open into the sounds, and therefore the water in these sounds is less saline than that outside the bars. McDougall (1943: 330) stated that the salinity at Piver’s Island is normally about 30%/o, with the extremes
at 8 and 38°/0. In the open ocean the salinity is usually 35 to 36°/00 and with a smaller range of variation. Water temperatures are also influenced by the structural features of the coast. At Cape Lookout Lighthouse the surface water temperature ranges from 25–27° C. in July and August down to 10° C. in January, whereas at Beaufort, only 10 miles west of Cape Lookout but inside the bar, the temperatures in December and January of 1930 were below 7° C. (Parr 1933: 57–58). In July of 1941 the water temperature ranged as high as 30° C., and the mean for the month was 28° C. The mean temperature in February 1942 was 5.5°, with temperatures as low as 2° being recorded (McDougall 1943: 331). Thus, the offshore bar serves to increase the annual temperature range in the sounds. Winter temperatures are lower than outside the bar because the effects of local cooling are not nullified by free mixing with the water in the open Atlantic. Parr (1933: 50, 53) placed the inner margin of the Gulf Stream between 20 and 25 land miles from the Cape Lookout Lighthouse, and mixing along the margins of the stream has a marked influence on the water along the coast south of Cape Hatteras. It is conceivable that the latitudinal range of certain of the Boreal species is extended further southward because of the protecting bars along the Carolina coast, but unfortunately it was not possible to reach favorable collecting sites on the outer edge of the bar to determine whether or not the halacarid fauna differs from that found inside. It is possible that Long Island likewise permits a southward extension of the ranges of one or two species in Long Island Sound, for the mean temperature in the Sound is lower than that outside. However, the North Carolina coast is a much more critical point in the range of the northern fauna, and the influence of the offshore bar should be more marked than that of Long Island.

The extremely small number of species found at Solomon's Island, Maryland, can be attributed largely to the low salinity which is normally 10–12 %/0 and is occasionally much less at such times when the Patuxent River is bringing in large quantities of fresh water. Further studies would undoubtedly reveal a greater number of species toward the entrance of Chesapeake Bay and on the Atlantic coast of Delaware, but even there the fauna probably would not be as rich as that in Long Island Sound, since it is unlikely that the southward decline of the Halacaridae occurs at any one point along the coast (Cape Hatteras).

The fauna north of Connecticut appears to be relatively uniform as
far as New Brunswick, since the total number of species taken in New Brunswick is not appreciably less than would be found in an equal number of samples from Long Island Sound. One species, *Rhombo­gnathides merrimani*, with its two varieties, is found only in New Brunswick. *Rhombo­gnathides pascens* and *seahami*, which appear together at Woods Hole, Massachusetts, are not found in the St. Andrews collections; and of these, only *R. pascens* is found in Long Island Sound. It is significant that there are as many species in 12 intertidal samples from St. Andrews as in the 26 carefully selected samples from intertidal and subtidal habitats in Beaufort. *Rhombo­gnathides*, *Isobactrus*, *Thalassarachna* and *Arhodeoporus* reach their maximum development in the region between Connecticut and New Brunswick. *Copidogna­thus* s. str., on the other hand, is represented by only two species, as contrasted with the 10 which were found on two small bunches of *Halimeda* from Florida.

The small number of species known from Greenland and Labrador does not permit any comparison with the regions further to the south.

**RELATIONSHIP OF THE NORTH AMERICAN FAUNA TO THE WORLD FAUNA**

As is true in so many animal groups, the zoogeography of the Halacaridae is obscured by two important facts. In the first place earlier writers failed to note the relationship between closely related species from the various zoogeographic regions of the earth, and in the second place species have been compared with only remotely related species on superficial characters (e. g., the common possession of heavy armor, or distinct panelling, or the absence of pectens on the claws) while fundamental and irreconcilable differences have been overlooked. Consequently, published descriptions of even closely related species (since the descriptions were usually incomplete) have often directed attention to entirely different characters so that it has been impossible for subsequent workers to make direct comparisons or contrasts between species. The most satisfactory work on the Halacaridae has been done by Lohmann and Viets, their descriptions and figures having been sufficiently detailed and accurate in most cases to permit other workers to recognize their species easily, but most important is the fact that their descriptions usually permit one to draw accurate conclusions as to the relationship or lack of relationship between species from different parts of the world.
The Halacaridae are an extremely important family from an ecological and zoogeographic standpoint, for there are few groups of microscopic animals which possess such a fortunate variety and number of morphological characters. Accordingly, it is usually possible to distinguish between fundamental and superficial differences and therefore to detect natural species groups within genera. The ease with which most of the Halacaridae can be transported from one place to another on floating seaweed, wood, etc., makes it possible to mark the limits of the ranges of the various species with considerable certainty, for if a particular species is absent from a region it is usually because that species cannot live there, or because it cannot tolerate the conditions in the regions through which it would have to pass to get there. Hence the littoral Halacaridae should be of considerable value in establishing natural zoogeographic boundary zones when more extensive faunistic studies are available from parts of the world other than those which have now been studied. At the present time our knowledge of the Halacaridae of the world is rather meager, for only the North Atlantic, Caribbean, Mediterranean and Antarctic areas have been very extensively studied, while the Pacific Ocean has hardly been touched.

In Table II the fauna of North America has been compared with that of other parts of the earth, the comparison having been based not simply upon species common to the various regions, but also upon closely related species. Those species which, in the opinion of the writer, are immediately related to North American species, but which have not been found on this continent, are placed directly under their North American relatives and are indented. These include only the cases where direct relationship is virtually indisputable, all questionable relatives having been omitted.

Preliminary to a discussion of the relationship of the North American halacarid fauna to those faunae of other parts of the world, let us consider briefly the general aspects of distribution of marine littoral faunae. Ekman (1935) divided the littoral into a number of zoogeographic regions, the limits of which are marked by significant, but rarely abrupt, changes in the fauna. Fig. 331 shows those regions which are of greatest importance in the present discussion. The extent of the various regions is conditioned primarily by surface water temperature and therefore is influenced greatly by currents. Widely separated littoral regions, even if they have virtually identical thermal charac-
|                         | Ascension I | NE, S. America | Caribbean Sea | S. Florida | Bermuda | Cape Verde | Azores | Mediterranean Sea | N. Adriatic Sea | Black Sea | SE, Australia | Macquarie Is. | Kerguelen I. | Antarctic Ocean | North Carolina | Chesapeake Bay | Conn.-Rhode Island | Massachusetts | Maine | New Brunswick | Labrador | Greenland | French Atlantic | British Isles | North Sea | Baltic Sea | Arctic Ocean |
|-------------------------|-------------|----------------|---------------|------------|---------|------------|--------|------------------|----------------|-----------|--------------|----------------|---------------|----------------|----------------|----------------|-------------------|----------------|--------|--------------|----------|----------|----------------|-----------|-----------|-------------|------------|---------|-----------|-----------|
| **Rhombognathus**       |             |                |               |            |         |            |        |                  |                |           |              |                |               |                |                |                |                  |                |         |              |          |          |                |           |           |              |           |         |            |            |
| magnirostris            |             |                |               |            |         |            |        |                  |                |           |              |                |               |                |                |                |                  |                |         |              |          |          |                |           |           |              |           |         |            |            |
| magnirostris lioni     |             |                |               |            |         |            |        |                  |                |           |              |                |               |                |                |                |                  |                |         |              |          |          |                |           |           |              |           |         |            |            |
| notops                 |             |                |               |            |         |            |        |                  |                |           |              |                |               |                |                |                |                  |                |         |              |          |          |                |           |           |              |           |         |            |            |
| **Rhombognathides**    |             |                |               |            |         |            |        |                  |                |           |              |                |               |                |                |                |                  |                |         |              |          |          |                |           |           |              |           |         |            |            |
| pascens                |             |                |               |            |         |            |        |                  |                |           |              |                |               |                |                |                |                  |                |         |              |          |          |                |           |           |              |           |         |            |            |
| seahami               |             |                |               |            |         |            |        |                  |                |           |              |                |               |                |                |                |                  |                |         |              |          |          |                |           |           |              |           |         |            |            |
| mucronatus             |             |                |               |            |         |            |        |                  |                |           |              |                |               |                |                |                |                  |                |         |              |          |          |                |           |           |              |           |         |            |            |
| merrimani              |             |                |               |            |         |            |        |                  |                |           |              |                |               |                |                |                |                  |                |         |              |          |          |                |           |           |              |           |         |            |            |
| merrimani needleri    |             |                |               |            |         |            |        |                  |                |           |              |                |               |                |                |                |                  |                |         |              |          |          |                |           |           |              |           |         |            |            |
| **Metarhombognathus**   |             |                |               |            |         |            |        |                  |                |           |              |                |               |                |                |                |                  |                |         |              |          |          |                |           |           |              |           |         |            |            |
| armatus americanus     |             |                |               |            |         |            |        |                  |                |           |              |                |               |                |                |                |                  |                |         |              |          |          |                |           |           |              |           |         |            |            |
| armatus arnatus        |             |                |               |            |         |            |        |                  |                |           |              |                |               |                |                |                |                  |                |         |              |          |          |                |           |           |              |           |         |            |            |
| **Isobactrus**         |             |                |               |            |         |            |        |                  |                |           |              |                |               |                |                |                |                  |                |         |              |          |          |                |           |           |              |           |         |            |            |
| setosus                |             |                |               |            |         |            |        |                  |                |           |              |                |               |                |                |                |                  |                |         |              |          |          |                |           |           |              |           |         |            |            |
| levis                  |             |                |               |            |         |            |        |                  |                |           |              |                |               |                |                |                |                  |                |         |              |          |          |                |           |           |              |           |         |            |            |
| hutchinsoni            |             |                |               |            |         |            |        |                  |                |           |              |                |               |                |                |                |                  |                |         |              |          |          |                |           |           |              |           |         |            |            |
| **Halacarbus s. str.** |             |                |               |            |         |            |        |                  |                |           |              |                |               |                |                |                |                  |                |         |              |          |          |                |           |           |              |           |         |            |            |
| cenopod                |             |                |               |            |         |            |        |                  |                |           |              |                |               |                |                |                |                  |                |         |              |          |          |                |           |           |              |           |         |            |            |
| subtus                 |             |                |               |            |         |            |        |                  |                |           |              |                |               |                |                |                |                  |                |         |              |          |          |                |           |           |              |           |         |            |            |
| oblongus               |             |                |               |            |         |            |        |                  |                |           |              |                |               |                |                |                |                  |                |         |              |          |          |                |           |           |              |           |         |            |            |
| actenos                |             |                |               |            |         |            |        |                  |                |           |              |                |               |                |                |                |                  |                |         |              |          |          |                |           |           |              |           |         |            |            |
| actenos robusta        |             |                |               |            |         |            |        |                  |                |           |              |                |               |                |                |                |                  |                |         |              |          |          |                |           |           |              |           |         |            |            |
| frontiporus            |             |                |               |            |         |            |        |                  |                |           |              |                |               |                |                |                |                  |                |         |              |          |          |                |           |           |              |           |         |            |            |
| anomalus               |             |                |               |            |         |            |        |                  |                |           |              |                |               |                |                |                |                  |                |         |              |          |          |                |           |           |              |           |         |            |            |
Table II. Relationship of the North American Fauna to the World Fauna. See Text, p. 196 (cont.)

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>basteri basteri</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>b. septentrionalis</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>b. affinis</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>longipes</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>balticus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>capucinus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>procerus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>subterraneus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Agaue</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>nationalis</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>adriatica</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Copidognathus s. str. punctatissimus</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>acutus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>latus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>bairds</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>gibberipes</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>curassaeensis</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>biscaynus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>angustus floridenis</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>angustus angustus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>lamellosus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>septentrionalis</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>poucheti</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>gracilis</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table II. Relationship of the North American Fauna to the World Fauna. See Text, p. 196 (cont.)

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>hummelincki</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>adriatica</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>tricorneata</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>caudatus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>pulcher</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>triclops</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>magnipalpus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>magnipalpus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>magnipalpus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ponticus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>pachypus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>extensus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>bonaitensis</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. (Arthrodeoporus)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>arenarius</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>gracilipes s. lat.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>submarinus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Agauopsis</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>breipalpus breipalpus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>breipalpus pontica</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>borealis</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lohmannella</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>falcata</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Newell: The Halacaridae of Eastern North America

Figure 331. Ekman’s zoogeographic regions, based on Ekman (1935) and on Sverdrup, Johnson and Fleming (1942: 804). The principal points of study in the western hemisphere are also included. The Bermuda fauna is known through the work of Lohmann (1893a); that of Aruba, Bonaire and Curaçao through the work of Viets (1936d). The dotted lines indicate the mean annual position of the 25°, 20°, 10° and 0° C. isotherms according to Schott (1926) and Sverdrup, Johnson and Fleming (1942).
teristics, usually differ faunistically because of land, abyssal or temperature barriers, or because oceanic currents may be such as to prevent the free dispersal of the members of the faunae. Historical factors are also of prime importance in the development of similarities or differences between faunae. The Atlantic coast of North America lies within three faunistic regions: the Arctic region extending approximately to northern Newfoundland, the Boreal Atlantic region extending approximately to Cape Hatteras, and the American Tropical Atlantic region which includes southern Florida, Bermuda, the Caribbean Sea, and reaches to the southeastern coast of Brazil.

**American Boreal Atlantic Fauna.** The fauna of the American Boreal Atlantic has a close affinity with that of the European Boreal region. Of the 25 American Boreal forms listed in Table II, 15 (60%) are found in the European Boreal region, two (8%) are closely related to European forms but not identical, and eight (32%) are endemic. Therefore, nearly 70 per cent of the American forms are identical with, or closely related to, European Halacaridae. Schulz (1935a: 87) listed a total of 41 forms from the North Sea and Baltic combined. Of these, 36 forms are known from the North Sea, but five are of questionable validity, leaving a total of 31 forms known from the North Sea as compared with 25 from the American Boreal Atlantic. But in addition, Schulz listed 24 forms from the Baltic, five of which are not known from the North Sea, making a total of 36 forms from the Baltic and North Sea. These combined make up the present known halacarid fauna from the European Boreal Atlantic. If one assumes the fauna of the American coast to be as extensive as that of Europe, then only about 70 per cent of our fauna has been discovered.

The American Boreal fauna shows very little affinity with the Tropical faunae, for only one species, the definitely eurythermal *Rhombognathus magnirostris*, with its two varieties, has been found in Tropical as well as in Boreal regions. On the European coast this species extends at least as far north as Bergen, Norway (about 60° 30' N. latitude), whereas its northernmost limit on our coast is approximately between 38° and 41° N. latitude, judging from our present knowledge.

23 Schulz 1935a, 87: "... 8. Rhombognathides pascens nov. var., ... 10. Rhombognathopsis minutus, ... 24. Halacarellus capucinus, ... 27. Halacarellus floridearum nov. var., ... 36. Copidognathus spec. ..." The latter is evidently *Halacarus* sp.? (Larve) Lohmann 1893.
A slightly greater affinity is seen between the American Boreal and the Mediterranean-Atlantic. Five of the 25 American forms are either identical (two varieties of *R. magnirostris*; *Lohmannella falcata*) with Mediterranean forms, or have close relatives there (*Halacarus (Thalassarachna) basteri basteri*, *Copidognathus (Arhodeoporus) arenarius*). This is not surprising in view of the fact that many Mediterranean animals extend far into the European Boreal, and some even reach into the Arctic.

**Transition Zone.** Ekman designated the region between Cape Hatteras and southern Florida as a transition zone. As pointed out on page 194, its transitional nature consists not so much of an overlapping of Tropical and Boreal faunae as it does of the dropping out of certain of the Boreal genera or subgenera. The one endemic species found at Beaufort has its closest relative in *C. latus*, a North Sea form, so that it can be considered a Boreal rather than a Tropical species. The short distance separating the American Boreal from the American Tropical region contrasts sharply with the great distance between the European Boreal and the Tropical West African. It seems unlikely that there is room enough for the development of an endemic fauna in the transitional zone from Cape Hatteras to Florida, and therefore it is probable that future work will show that this portion of the coast is occupied by a fauna comprising largely the most eurythermal species of the Tropical and Boreal faunae. The great annual latitudinal shifts of the isotherms in this region would wipe out any species with restricted temperature requirements, and for this reason the Mediterranean Atlantic fauna has no real counterpart on the eastern coast of North America. This is due to the convergence of the isotherms on the North American coast in contrast with their divergence on the European-African coast, which in turn is due to the influence of the North Atlantic and Labrador Currents.

**American Tropical Atlantic Fauna.** The Florida fauna is clearly tropical in character. It has been pointed out (see p. 194) that there is no correlation between the Florida and the American Boreal faunae, except through the eurythermal *Rhombognathus magnirostris*; but there is a close affinity between the faunae of the Dutch West Indies, southern Florida and Bermuda, all of which lie within Ekman’s American Tropical Atlantic region. Of the 15 forms known from Florida, four are also found in the Dutch West Indies, and at least three others are
clearly related to Dutch West Indies species. Thus, seven (32%) of the 22 species known from both the Dutch West Indies and Florida are either common to the two or are represented by closely related forms, and it is most likely that further collection from the Caribbean Sea and Florida will show even greater homogeneity in this region. Lohmann (1893a) listed seven species from Bermuda, five of which are represented in the Florida fauna, four being identical and another closely related to a Florida species.

The Halacaridae of the Tropical West African fauna are unknown, hence a comparison with the American Tropical Atlantic cannot be made at this time. But the work of Viets (1939c, 1940g), who listed a total of 54 forms from the Mediterranean, Adriatic and Black Seas, makes possible a comparison with the Mediterranean fauna. Viets listed 28 forms from the Mediterranean, two of which are identical with and two closely related (total 14%) to forms from the American Tropical Atlantic. Viets also listed 34 forms from the northern Adriatic, and eleven (32%) of these are either identical with (3), or closely related to (8), American Tropical Atlantic forms. Sixteen forms are known from the Black Sea, of which five (31%) are near (3), or identical with (2), Tropical American forms.

**Tethyan fauna.** Note that five of the 15 Florida species are either identical with species from both the Mediterranean and from southeastern Australia, or are members of species groups which occupy this wide range. This is of particular interest in connection with the Tethys Sea which was in existence throughout the Mesozoic and the early Cenozoic. Although this sea varied considerably in extent and form during this period, it maintained a virtually uninterrupted marine connection between the western Pacific and what is now the Caribbean. The mild climates which prevailed were at least partly due to the disposition of the land masses, which more or less restricted the interchange of water between the Tropical and Arctic seas, and as a consequence the entire Tethys Sea was tropical, supporting one of the richest marine faunae of all time. This fauna was relatively uniform throughout its entire extent until the extensive mountain-building and general continental emergence of the Tertiary broke up the Tethys Sea into a number of isolated basins, namely the Caribbean, Mediterranean, Black and Caspian Seas, and the Indo-West Pacific Ocean. The fate of the Tethys fauna with which the present day remnants of this
ancient sea were once uniformly endowed has depended upon the subsequent history of the remnants. The Caribbean and Indo-West Pacific regions have remained tropical in character and have maintained their Tethyan fauna most successfully. The Mediterranean, Black and Caspian Seas, because of interrelated geographical and climatological changes, have lost their tropical fauna to a lesser or greater degree. Of these the Mediterranean fauna most closely approaches that of the Tropical seas, whereas the Caspian fauna shows the greatest change. When the Halacaridae of the Pacific and Indian Oceans have been more extensively studied it is likely that they will augment the picture which has been created from a study of other animal groups.

**Distribution of the Genera and Subgenera**

Table II shows that the absence of *Rhombognathides*, *Metarhombognathus*, *Isobactrus*, *Thalassarachna*, *Arhodeoporus* and *Lohmannella* from the Florida collections was no artifact, for representatives of these have never been recorded from Tropical regions. *Lohmannella* and *Arhodeoporus* are known from the Mediterranean, Adriatic and Black Seas; but *Rhombognathides*, *Metarhombognathus* and *Isobactrus* are characteristically Boreal or Arctic in their ranges. *Rhombognathides* is found in the Black Sea, which, despite its Tethyan ancestry, has a fauna containing a number of species of Arctic or Boreal origin.

The other genera or subgenera are less restricted in their ranges. *Rhombognathus*, *Halacarus* s. str., *Agaue*, *Copidognathus* s. str. and *Agauopsis* have been reported from both Antarctic and Tropical regions. The distribution of *Agauopsis* in the North Atlantic is of interest. Only two forms (*Agauopsis brevipalpus brevipalpus* and *A. microrhyncha minor*) are known from the European Atlantic Coast, but these have not been found north of Ireland or the English Channel. On the American coast *A. borealis* is found at least as far north as Long Island Sound, which is equivalent, zoogeographically, to Norwegian latitudes.

One of the most significant features of the Tropical fauna is the predominance of *Copidognathus* s. str. Ten of the 15 species (67%) taken in the Florida collections belong to this group. Of the 11 species which Viets (1936d) listed from the Dutch West Indies, nine (82%)

---

24 Trouessart (1900a; 1901c) listed *Rhombognathides trionyz* (Trt.) 1900 from Tierra del Fuego, and also from St. Guenole on the French coast. This is the only record of *Rhombognathides* outside the northern hemisphere.
were *Copidognathus* s. str. species. In the Mediterranean-Black Sea region the predominance is less marked. Only 24 of the 54 species (45%) listed from there (Viets, 1940g) belong to the subgenus. Of the 36 certain species from the European Boreal Atlantic (Schulz, 1935a), only six (16%) are *Copidognathus* s. str. species, and in the American Boreal Atlantic, the proportion is of the same order of magnitude \(\frac{3}{25} = 12\%\). Four of the 23 species (17%) of Halacaridae now known from the Antarctic region are *Copidognathus* s. str. species (Viets, 1931f: 8).

**The Structure of Local Faunae**

As pointed out in the previous two sections, the subdivisions of the halacarid fauna of our coast follow in general the zoogeographic subdivisions outlined by Ekman (1935), and these in turn are determined largely by temperature; but in any one locality temperature appears to be of little direct significance in determining the structure of the fauna within the numerous special habitats. Exceptions to this generalization are probably numerous, but most of them would be of an extremely local nature and would not affect an appreciable portion of the population. Significant exceptions may be demonstrable along the North Carolina coast and in similar situations where offshore bars result in markedly different temperatures within small areas, but under usual conditions such factors as tides, substrate and salinity play the major roles in determining the structure of the fauna of any given locality.

**The Subtidal Fauna**

The collections which have been made from subtidal habitats in Long Island Sound indicate a relatively uniform halacarid fauna as compared with that of the intertidal zone. Although differences in abundance do occur in the former the sharp qualitative differences which are seen between the various intertidal habitats do not appear in the subtidal zone, due to the more uniform distribution of food, which consists principally of copepods and ostracods in the case of most of the subtidal Halacaridae. The Rhombognathinae are restricted to algal food, but as will be seen later, many of these are excluded from the subtidal zone by factors other than food.

Tables III and VII show that the dominant species are *Copidognathus* (*Arhodeoporus*) *arenarius* and *C.* (s. str.) *septentrionalis*. The predominance of the first of these is probably more marked than the
<table>
<thead>
<tr>
<th>Sample No.</th>
<th>Locality</th>
<th>Depth (m.)</th>
<th>Substrate</th>
<th>Date</th>
<th>Species</th>
<th>Total Halacaridae</th>
</tr>
</thead>
<tbody>
<tr>
<td>44-71</td>
<td>Off Stratford Point, Conn.</td>
<td>16</td>
<td><em>Ostrea</em>; 7; av. length 8.2 cm.</td>
<td>July 14, 1944</td>
<td><em>Rhomobothridae pascens</em></td>
<td>21710</td>
</tr>
<tr>
<td>44-72</td>
<td>About 2 mi. s. of Momaugun, Conn.</td>
<td>10</td>
<td><em>Ostrea</em>; 1; 18 em. long</td>
<td>July 14, 1944</td>
<td>Halocarcus (s. str.) fronticulus</td>
<td>60</td>
</tr>
<tr>
<td>44-73</td>
<td>About 2 mi. s. of Momaugun, Conn.</td>
<td>10</td>
<td><em>Suberites</em>; ca. 9 cm. in diameter</td>
<td>July 14, 1944</td>
<td>Halocarcus (s. str.) anomatus</td>
<td>21</td>
</tr>
<tr>
<td>44-74</td>
<td>Off Mansfield Point, Conn.</td>
<td>3.5</td>
<td><em>Laminaria</em>; 50 g.</td>
<td>Aug. 4, 1944</td>
<td><em>H. (Thalassarachna) basteri bacteri</em></td>
<td>0</td>
</tr>
<tr>
<td>44-75</td>
<td>Off Mansfield Point, Conn.</td>
<td>3.5</td>
<td><em>Laminaria</em> overgrown with <em>Sertularia</em>; 52 g.</td>
<td>Aug. 4, 1944</td>
<td><em>H. (Thalassarachna) basteri bacteric</em></td>
<td>34</td>
</tr>
<tr>
<td>44-76</td>
<td>Off Mansfield Point, Conn.</td>
<td>3.5</td>
<td>Filamentous red algae; 5.8 g.</td>
<td>Aug. 4, 1944</td>
<td>Copidoccephalus (s. str.) prouti</td>
<td>18</td>
</tr>
<tr>
<td>44-77</td>
<td>Off Mansfield Point, Conn.</td>
<td>3.5</td>
<td>Filamentous green algae; 2.5 g.</td>
<td>Aug. 4, 1944</td>
<td>Copidoccephalus (s. str.) prouti</td>
<td>20</td>
</tr>
<tr>
<td>44-80</td>
<td>Off Mansfield Point, Conn.</td>
<td>3.5</td>
<td><em>Detached Fucus</em>; 14.7 g.</td>
<td>Aug. 4, 1944</td>
<td><em>C. (Archaedoporus) arenarius</em></td>
<td>11</td>
</tr>
<tr>
<td>44-81</td>
<td>New Haven Harbor, between Lighthouse Point and Morris Cove</td>
<td>3 to 4</td>
<td>Empty <em>Ostrea</em> valves extensively pitted by <em>Cliona</em>; 5; av. length 9.5 cm.</td>
<td>Aug. 4, 1944</td>
<td><em>C. (Archaedoporus) arenarius</em></td>
<td>514</td>
</tr>
<tr>
<td>45-1</td>
<td>New Haven Harbor, on west side of channel</td>
<td>3 to 6</td>
<td>Broken <em>Ostrea</em> valves</td>
<td>Jan. 4, 1945</td>
<td>Laminaria overgrown with <em>Sertularia</em></td>
<td>920</td>
</tr>
<tr>
<td>44-82</td>
<td>About 3 mi. ne. of Block Island, Rhode Island</td>
<td>41</td>
<td><em>Laminaria</em> overgrown with <em>Sertularia</em></td>
<td>Aug. 13, 1944</td>
<td>Laminaria overgrown with <em>Sertularia</em></td>
<td>43359</td>
</tr>
</tbody>
</table>

**TABLE III. NUMBERS OF HALACARIDAE OBTAINED FROM VARIOUS MATERIALS DREDGED FROM LONG ISLAND SOUND**
totals in Table VII indicate, for most of the specimens of *C. septentrionalis* were obtained in a single sample, but *C. arenarius* appeared more frequently and usually in greater numbers. *C. arenarius* extends into the intertidal area as well, where it becomes an arenicolous form, but *C. septentrionalis* does not, only one individual having been taken there.

*C. (s. str.) punctatissimus* is the third most abundant species in the subtidal zone. Like *C. arenarius* it also ranges into the intertidal zone, but unlike the latter it is not a very successful arenicolous species, possibly owing to its unfavorable form. Although both species are of approximately the same length, the body of *C. punctatissimus* is 0.66 as broad as long, whereas that of *C. arenarius* is only about 0.56 as broad as long. In the other arenicolous forms most individuals have a body less than 0.60 as broad as long, and in *Halacarus (s. str.) anomalus* the ratio of width to length is about 0.45.

*Halacarus (Thalassarachna) longipes* and *Lohmannella falcata* are typically subtidal, but they are much less abundant than the other forms. *Halacarus (Thalassarachna) basteri basteri* appears both above and below the low tide zone. Although *Halacarus (s. str.) anomalus* has been taken in one subtidal collection, it is a typical arenicolous form. The presence of *Rhombognathides pascens* below the intertidal is seemingly a natural occurrence, for it has been taken on at least three occasions, living specimens having been found each time. Viets (1927a: 166) also showed both *Rhombognathides pascens* and *seahami* to be present in most samples which he took below the tide zone in the North Sea. The complete absence of *Metarhombognathus* and *Iso­bactrus* from subtidal collections is significant, for Viets (1927a: 160–161, 166) showed a similar distribution of these two intertidal genera in his North Sea collections. (For further discussion, see p. 216).

*Halacarus (Thalassarachna) balticus, capuzinus* and *subterraneus* are absent from the subtidal zone and are typically intertidal forms. Limited collections somewhat beyond the eastern end of Long Island Sound indicate the development of a rather different fauna at depths of 40 meters, suggesting a transition from a eulittoral to a sublittoral fauna. Two new species appear here, *Halacarus (s. str.) frontiporus*, and *Copidognathus (Arhodeoporus) submarinus*. The former is clearly a sublittoral type, being weakly armored and having a soft cuticle; the dorsal plates are not recognizable as distinct sclerites and the corneae are highly modified. *Copidognathus (Arhodeoporus) submarinus* replaces *arenarius* which is found in shallower water. *Rhombognathides pascens* is also found here.
The Intertidal Fauna

In contrast with the relatively uniform halacarid fauna in the subtidal zone, the intertidal zone of Long Island Sound is characterized by a number of distinct faunae showing a close correlation with the substrate upon which they are developed. In this area there are numerous sandy beaches and usually there is sand of sufficient particle size to permit the development of a typical arenicolous fauna. Exposed rocks provide attachment places for Fucus, Chondrus, Ascosiphylhum and other algae, as well as for Mytilus, Modiolus and Ostrea. Patches of salt grass and mud flats often support algae which may be used as food by the Rhombognathinae, or these may support populations of other microscopic animals which are preyed upon by the Halacarinae and other predaceous groups. Because of the diversity of the faunae of the intertidal zone, the principal ones will be considered separately, these being the faunae of the sand, molluscs and algae.

**Intertidal Sand Fauna.** The intertidal sand fauna contains three species which are rarely found in other habitats, and in addition Copidognathus (Arhodeoporus) arenarius, which is typically a subtidal form, appears consistently and often in appreciable numbers in the intertidal, especially in the low tide zone. As can be seen in Table IV, Copidognathus arenarius is found at considerable depths in the beach, and therefore it can be considered a truly arenicolous species rather than a psammoxene form whose frequent appearance in the intertidal is due simply to its abundance in the subtidal zone.

The species which are most characteristically arenicolous are: Halacarus (s. str.) anomalus, Halacarus (Thalassarachna) capuzinus and Halacarus (Thalassarachna) subterraneus. Halacarus anomalus is well adapted to its arenicolous environment, its body being cylindrical in form, more than twice as long as broad, and flexible, the last being a unique character among the Halacaridae. The long slender legs, the third and fourth pairs of which are displaced far posteriorly, enable the mite to move through sand with considerable ease either forward or backward, whereas on a glass surface it is the most helpless and awkward of the Halacaridae seen by the writer. The two other species show less striking modifications, but both are unique in the possession of additional platelets in the membranous areas. Halacarus capuzinus has an unusually slender body for this subgenus (L/W = 1.8-2.0), whereas Halacarus subterraneus is not especially narrowed, although
it is noticeably flatter than most species. Generally, the appearance of Rhombognathinae in sand samples is fortuitous, the mites probably having been dislodged from their normal substrate. The finding of more specimens of *Rhombognathides mucronatus* in sand than on other substrates is almost certainly an artifact, for *Rhombognathides* is an algicolous genus, and these were taken in clean sand. *Isobactrus setosus*, because of its small size, may be able to live at limited depths in the sand, but most individuals found there probably are to be considered as psammoxene forms. In the latter category are also *Halacarus (Thalassarachna) basteri basteri* and *Copidognathus (s. str.) septentrionalis*. In locations where sand has been overgrown with salt grass, which effectively reduces the impact of the water upon the sand, there may develop an atypical sand fauna which includes Rhombognathinae and other forms generally found in association with *Balanus* due to the growth of filamentous green algae over the surface of the sand. *Metrarhombognathus armatus americanus* is often found in considerable numbers in such situations, as is shown in Table XI (sample 44–85). The same situation is common in Long Island Sound.

The Halacaridae found in sand may be classified as follows:

**Psammobiont.**

*Halacarus* (s. str.) *anomalus.*

*Halacarus (Thalassarachna) capuzinus.*

*Halacarus (Thalassarachna) subterraneus.*

**Psammophile.**

*Copidognathus (Arhodeoporus) arenarius.*

**Psammoxene.**

Rhombognathinae.

*Halacarus (Thalassarachna) basteri basteri.*

*Copidognathus (s. str.) punctatissimus.*

*Copidognathus (s. str.) septentrionalis.*

There is a close similarity between the sand fauna of the American Boreal Atlantic and that of the European Boreal, since all three of the above psammobiont species are common to the two regions. Schulz (1933, 1935a) has listed them as members of the coastal ground-water fauna. However, *Copidognathus (Arhodeoporus) gracilipes* has not been shown to occupy a position homologous with that of *Copido-
TABLE IV. NUMBERS OF HALACARIDAE OBTAINED FROM INTERTIDAL SAND SAMPLES, LONG ISLAND SOUND, NEW HAVEN COUNTY, CONNECTICUT; ALL 500 cc. SAMPLES

<table>
<thead>
<tr>
<th>Locality and Date</th>
<th>Sample No.</th>
<th>Tide Zone</th>
<th>Depth (cm.)</th>
<th>Rhomobothrius macrorhachis</th>
<th>Metaphothonotus armatus armatus</th>
<th>Isotbacus setosus</th>
<th>Helocaratus (s.str.) anomalous</th>
<th>H. (Thalassarachna) batesi</th>
<th>H. (Thalassarachna) capulinus</th>
<th>H. (Thalassarachna) subterraneus</th>
<th>Cylindrobothrius (s.str.) punctatissimus</th>
<th>C. (Achthocephorus) armarius</th>
<th>Total Halacaridae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Morris Cove, March 22-29, 1944</td>
<td>44-1</td>
<td>Low</td>
<td>0 to 1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>44-15</td>
<td>Low</td>
<td>0 to 1</td>
<td>0</td>
<td>1</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>44-16</td>
<td>Mid</td>
<td>0 to 1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>44-3</td>
<td>Mid</td>
<td>10</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>44-37</td>
<td>High</td>
<td>0 to 1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>44-9</td>
<td>High</td>
<td>30</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>44-10</td>
<td>High</td>
<td>50</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>South End, April 7, 1944</td>
<td>44-22</td>
<td>Low</td>
<td>0 to 1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>44-23</td>
<td>Low</td>
<td>5</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>44-24</td>
<td>Low</td>
<td>0 to 4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>44-25</td>
<td>Low</td>
<td>5 to 10</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>44-26</td>
<td>Mid</td>
<td>0 to 4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>44-27</td>
<td>Mid</td>
<td>30 to 35</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>44-28</td>
<td>High</td>
<td>0 to 5</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>44-29</td>
<td>High</td>
<td>55 to 60</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Double Beach, Oct. 13, 1943</td>
<td>43-43</td>
<td>Low</td>
<td>0 to 5</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>43-51</td>
<td>Low</td>
<td>0 to 10</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>43-44</td>
<td>Mid</td>
<td>0 to 1</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>43-50</td>
<td>High</td>
<td>16</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Totals:</td>
<td></td>
<td></td>
<td></td>
<td>30</td>
<td>4</td>
<td>280</td>
<td>3</td>
<td>33</td>
<td>74</td>
<td>11</td>
<td>1</td>
<td>208</td>
<td>677</td>
</tr>
</tbody>
</table>
gnathus (Arhodeoporus) arenarius, and if it does not, this may be in part attributable to its greater size.

**Intertidal Molluscan Fauna.** Three molluscs in particular provide a substrate for the development of halacarid faunae, namely Mytilus, Modiolus and Ostrea, of which the Mytilus fauna is the simplest. Because the byssal threads often provide attachment for filamentous green algae, the fauna is probably a self-sustaining one and not dependent upon repeated introductions from surrounding habitats. Note in Table V that the dominant forms are also the principal psammosxene species. Since the matted byssal threads usually contain sand, it is not surprising that certain psammobiont or psammophile species occasionally appear.

The ribbed surface of Modiolus is somewhat more suitable for the development of a typical fauna than the relatively smooth surface of Mytilus, but more important, it provides an excellent attachment place for Balanus. The resulting surface contains many crevices in which Isobactrus setosus and Metarhomgbognathus armatus americanus can find secure footing and a certain amount of protection from Amphipoda and other enemies. Balanus-encrusted surfaces usually support a moderately heavy growth of unicellular or filamentous algae. The fact that the dominant species are algicolous demonstrates that the algae are really the most important part of this association so far as the Halacaridae are concerned.

The significance of the encrustation of Modiolus by Balanus can be seen by comparing sample 44-4 (unencrusted) with 44-5, 43-28 and 43-30 (Table V). Three samples of encrusted molluscs contain only 2.5 times as many Modiolus as sample 44-4, but 27 times as many mites. Halacarus (Thalassarachna) balticus is a characteristic species of this fauna, for its large size prohibits its living in the sand, and although it seemingly is not restricted to intertidal habitats, it is not common below the low tide zone (Table VII of this paper; also Viets 1927a: 161, 166). The two species of Rhombognathinae with which it lives probably form a principal part of its diet, for the writer has seen it feeding upon these species on numerous occasions in laboratory cultures. The halacarid fauna developed upon Ostrea in the intertidal zone is essentially like that of Modiolus and Balanus.

**Algicolous Fauna.** The halacarid faunae developed on intertidal algae are dominated by the Rhombognathinae. Of the 309 mites
<table>
<thead>
<tr>
<th>Sample No.</th>
<th>Locality, Date</th>
<th>Substrate</th>
<th>Number</th>
<th>Av. Length (cm.)</th>
<th>Species</th>
<th>Total Halacaridae</th>
</tr>
</thead>
<tbody>
<tr>
<td>44-7</td>
<td>Morris Cove, March 29, 1944</td>
<td>Mytilus</td>
<td>10</td>
<td>5.1</td>
<td>Rhombopinax mucronatus</td>
<td>10</td>
</tr>
<tr>
<td>44-6</td>
<td>Morris Cove, March 29, 1944</td>
<td>Mytilus</td>
<td>11</td>
<td>4.8</td>
<td>Metarhombopinax armatus</td>
<td>17</td>
</tr>
<tr>
<td>44-32</td>
<td>Lighthouse Point, April 19, 1944</td>
<td>Mytilus</td>
<td>4</td>
<td>5.5</td>
<td>Isobaculites setosus</td>
<td>1</td>
</tr>
<tr>
<td>43-28</td>
<td>Morris Cove, June 11, 1943</td>
<td>Modiolus encrusted with Balanus</td>
<td>10</td>
<td>?</td>
<td>Halacarus (Thalassarhaeana)</td>
<td>1</td>
</tr>
<tr>
<td>43-30</td>
<td>Morris Cove, June 25, 1943</td>
<td>Modiolus encrusted with Balanus</td>
<td>6</td>
<td>?</td>
<td>Halacarus (Thalassarhaeana)</td>
<td>2</td>
</tr>
<tr>
<td>44-5</td>
<td>Morris Cove, March 29, 1944</td>
<td>Modiolus encrusted with Balanus</td>
<td>8</td>
<td>6.6</td>
<td>Cephalopinax (A. terebrata)</td>
<td>1</td>
</tr>
<tr>
<td>44-4</td>
<td>Morris Cove, March 29, 1944</td>
<td>Modiolus, unencrusted</td>
<td>10</td>
<td>5.6</td>
<td>Cephalopinax (A. terebrata)</td>
<td>2</td>
</tr>
<tr>
<td>44-70</td>
<td>Fort Hale Park, June 3, 1944</td>
<td>Modiolus growing in non-tidal pool, Salinity 25.4%</td>
<td>3</td>
<td>7.5</td>
<td>-</td>
<td>2</td>
</tr>
</tbody>
</table>
### Table VI. Numbers of Halacaridae Obtained from Intertidal Algae in Long Island Sound; All From New Haven County, Connecticut

<table>
<thead>
<tr>
<th>Sample No.</th>
<th>Locality, Date</th>
<th>Substrate</th>
<th>Weight (g.)</th>
<th>Tide Zone</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>43-26</td>
<td>Morris Cove, June 11, 1943</td>
<td>Enteromorpha, mostly dead</td>
<td>50</td>
<td>High</td>
<td>Rhombomathides pascorn</td>
</tr>
<tr>
<td>43-37</td>
<td>Morris Cove, Oct. 9, 1943</td>
<td>Enteromorpha</td>
<td>40</td>
<td>Low</td>
<td>Miterothonathus armatus</td>
</tr>
<tr>
<td>44-20</td>
<td>South End, Apr. 7, 1944</td>
<td>Chondrus</td>
<td>74</td>
<td>Low</td>
<td>Isobatrachus arenatus</td>
</tr>
<tr>
<td>44-21</td>
<td>South End, Apr. 7, 1944</td>
<td>Ascophyllum</td>
<td>153</td>
<td>Low</td>
<td>Halacarus (Thallassarachna)</td>
</tr>
<tr>
<td>44-30</td>
<td>South End, Apr. 7, 1944</td>
<td>Enteromorpha</td>
<td>42</td>
<td>Mid</td>
<td>Halacarus (Thallassarachna)</td>
</tr>
<tr>
<td>43-38</td>
<td>Double Beach, Oct. 13, 1943</td>
<td>Ascophyllum</td>
<td>70</td>
<td>Low</td>
<td>Halacarus (Thallassarachna)</td>
</tr>
<tr>
<td>43-39</td>
<td>Double Beach, Oct. 13, 1943</td>
<td>Polysiphonia</td>
<td>17</td>
<td>Low</td>
<td>Halacarus (Thallassarachna)</td>
</tr>
<tr>
<td>43-40</td>
<td>Double Beach, Oct. 13, 1943</td>
<td>Chondrus</td>
<td>50</td>
<td>Low</td>
<td>Halacarus (Thallassarachna)</td>
</tr>
<tr>
<td>43-41</td>
<td>Double Beach, Oct. 13, 1943</td>
<td>Chondrus</td>
<td>60</td>
<td>Low</td>
<td>Halacarus (Thallassarachna)</td>
</tr>
<tr>
<td>43-42</td>
<td>Double Beach, Oct. 13, 1943</td>
<td>Ulva</td>
<td>125</td>
<td>Low</td>
<td>Halacarus (Thallassarachna)</td>
</tr>
</tbody>
</table>

**Total Halacaridae**

- 158
- 104
- 10
- 2
- 2
- 5
- 21
- 7
- 6
- 1
- 5
recorded in Table VI, all but nine, or about 97 per cent, are Rhombo-
ognathinae. None of the Halacarinae can be considered typical
algicolous forms. One of the most interesting aspects of the local dis-
tribution of the Rhombognathinae is the absence of Rhombognathides
pascens from collections made inside New Haven Harbor, although
this species is found at South End, which is just a mile southeast of
Morris Cove, but on the Sound. The reasons for this distribution are
not clear, but it is probably related to the slightly lower salinities or
the higher temperatures found inside the harbor. The dropping out
of Rhombognathides seahami between Woods Hole and New Haven,
and the total absence of Rhombognathides from the North Carolina
collections, suggest that Long Island Sound may be near the southern
limit of the range of the genus, in which case local distribution of the
species may be considerably affected by slight local variations in tem-
peratures. Rhombognathides merrimani is not known from Connecticut
and may disappear even between New Brunswick and Cape Cod.

It was indicated above that the Modiolus-Balanus fauna is essen-
tially an algicolous one, since the dominant species depend upon En-
teromorpha and filamentous green algae growing on the Balanus. The
addition of Halacarus (Thalassarachna) balticus is a refinement not
found in strictly algicolous faunae, however, and for that reason the
fauna must be considered distinct from those found on algae.

### Table VII. Summary of General Collections in Long Island Sound

<table>
<thead>
<tr>
<th>Subtidal</th>
<th>Intertidal</th>
<th>Totals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sand</td>
<td>Mollusca</td>
<td>Algae</td>
</tr>
<tr>
<td>Rhombognathides pascens</td>
<td>11</td>
<td>30</td>
</tr>
<tr>
<td>Rhombognathides mucronatus</td>
<td>–</td>
<td>9</td>
</tr>
<tr>
<td>Metarhombognathus armatus americanus</td>
<td>–</td>
<td>3</td>
</tr>
<tr>
<td>Isobactrus setosus</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Isobactrus levis</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Isobactrus hutchinsoni</td>
<td>–</td>
<td>4</td>
</tr>
<tr>
<td>Halacarus (s. str.) anomalus</td>
<td>3</td>
<td>280</td>
</tr>
<tr>
<td>Halacarus (s. str.) frontiporus</td>
<td>11</td>
<td>3</td>
</tr>
<tr>
<td>H. (Thalassarachna) basteri basteri</td>
<td>9</td>
<td>3</td>
</tr>
<tr>
<td>H. (Thalassarachna) balticus</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>H. (Thalassarachna) capucinus</td>
<td>–</td>
<td>33</td>
</tr>
<tr>
<td>H. (Thalassarachna) subterraneus</td>
<td>–</td>
<td>74</td>
</tr>
<tr>
<td>H. (Thalassarachna) longipes</td>
<td>6</td>
<td>–</td>
</tr>
<tr>
<td>Copidognathus (s. str.) punctatissimus</td>
<td>61</td>
<td>11</td>
</tr>
<tr>
<td>Copidognathus (s. str.) septentrionalis</td>
<td>105</td>
<td>1</td>
</tr>
<tr>
<td>C. (Arhodeoporus) arenarius</td>
<td>1739</td>
<td>208</td>
</tr>
<tr>
<td>C. (Arhodeoporus) submarinus</td>
<td>26</td>
<td>–</td>
</tr>
<tr>
<td>Aquopsis borealis</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Lohmannella falcata</td>
<td>4</td>
<td>–</td>
</tr>
</tbody>
</table>

Total | 5121 |
The Fauna of Nontidal Habitats in the Intertidal Zone

The writer has had the opportunity of studying two examples of a special type of habitat which reveal important facts in the ecology of certain Halacaridae. The first of these habitats is the old moat around Fort Hale in what is now Fort Hale Park, New Haven, Connecticut. This moat is triangular in shape with a perimeter of about 375 meters and is probably no more than two meters deep at its deepest point. The only communication with New Haven Harbor is through a floodgate which is kept closed, so that there is only a limited exchange between the water in the moat and the harbor at high tide. The salinity in the moat (25.4%\text{oe} on June 3, 1944) was insignificantly lower than that in the harbor (26.0%\text{oe}), but the temperature was somewhat higher (27.0 compared with 23.8° C.). Several species of marine algae grow here and clumps of \textit{Modiolus} are found around the margin of the water; and in other respects this is a typical marine environment, except that, despite its intertidal position, it is nontidal. Only \textit{Copidognathus} (s. str.) \textit{punctatissimus} and \textit{Copidognathus} (\textit{Arhodeoporus}) \textit{arenarius} have been found here, and both of these are characteristically found below the intertidal zone, so their appearance in the moat is not surprising. More significant is the absence of \textit{Metarhombognathus armatus americanus} and \textit{Isobactrus setosus}, which are abundant in the harbor outside the moat. It is unlikely that this can be explained solely on the basis of high temperature, for \textit{Copidognathus} (s. str.) \textit{punctatissimus}, \textit{Copidognathus} (\textit{Arhodeoporus}) \textit{arenarius} and \textit{Metarhombognathus armatus americanus} are all known from Beaufort, where summer temperatures are little if any lower than in the Fort Hale moat.

The second example of this type of habitat is found at Beaufort, North Carolina, at the edge of Town Marsh, only 300 to 400 feet from the southern end of Piver's Island. Here a sand bar has blocked off a pool little more than three meters in diameter. At high tide this pool is in direct communication with freely circulating water in the channel between Town Marsh and Piver's Island. Because of the small size of the pool, the interchange of water between the pool and the channel at high tide must be significant, so that the temperature and salinity are maintained at the same level as in the channel. Several clumps of \textit{Ostrea} were growing in this pool and were covered with a sparse coating of small but living \textit{Enteromorpha} and filamentous green algae. Four species of Halacaridae were found here, \textit{Rhombognathus}
Table VIII. Data on Collections Made in Fort Hale Moat, New Haven, Conn.

<table>
<thead>
<tr>
<th>Sample No.</th>
<th>Copidognathus (s. str.) punctatissimus</th>
<th>Copidognathus (Arhodeoporus) arenarius</th>
</tr>
</thead>
<tbody>
<tr>
<td>October 9, 1943</td>
<td></td>
<td></td>
</tr>
<tr>
<td>43-35 Polysiphonia; 42 g.</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>43-36 Utea; 30 g.</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>June 3, 1944</td>
<td></td>
<td></td>
</tr>
<tr>
<td>44-65 Utea; 40 g.; 15,000 to 20,000 copepods, and 20,000 to 30,000 nematodes present</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>44-66 Algal scum from surface of water; ca. 10 g. Thousands of copepods and nematodes present</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>44-67 Sand below surface of water; 500 cc.</td>
<td>7</td>
<td>0</td>
</tr>
<tr>
<td>44-68 Sand just above surface of water; 500 cc.</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>44-69 Polysiphonia; 25 g.</td>
<td>25</td>
<td>0</td>
</tr>
<tr>
<td>44-70 Modiolus; imbedded in mud; 3; 7 to 8 cm. long</td>
<td>4</td>
<td>0</td>
</tr>
</tbody>
</table>

magnirostris lionyx, Copidognathus (s. str.) acutus, Copidognathus (Arhodeoporus) arenarius and Agauopsis borealis (Table XII), but Metarhombognathus armatus americanus, which was found in considerable numbers on Ostrea from Piver's Island, was not present.

The absence of Metarhombognathus and Isobactrus from these special non-tidal habitats is significant when it is remembered that these two genera are also absent in subtidal habitats. The latter situation is shown in both the Long Island Sound and Beaufort collections, as well as in Viets' collections in the North Sea (1927a: 161, 166). Species of these two genera probably require periodic exposure to air in order to survive.25 It is interesting to note that Metarhombognathus is present in the North Sea but not in the Baltic which is virtually non-tidal. This absence may be due to the lack of an intertidal zone in the Baltic. If this is correct, then it would be necessary to assume that Isobactrus setosus was able to adapt itself more readily to the narrow wave zone, for this species is present in the Baltic. It is certainly much more agile than Metarhombognathus species, and this may be of value in maintaining the species along the restricted shores of the Baltic Sea.

25 A parallel situation has been observed in Hyadesia sp. (Acaroidea, Hyadesiidae) at Beaufort and in Long Island Sound. This species is abundant in the intertidal zone where it occupies habitats identical with those of Metarhombognathus armatus americanus. It is not found below the tide zone, nor in the two special habitats discussed above. Hyadesia fusca (Lohmann) 1894 is known from the Baltic Sea.


Salinity and Local Distribution of Halacaridae

It is to be expected that habitats having markedly different salinities will differ in the composition of their faunae. Thus the number of species in an estuary decreases toward the upper end of the estuary until eventually the marine Halacaridae drop out entirely. Although the number of species is less than in marine habitats, the number of individuals is often very great.

In Table IX are given the records of samples taken in a tidal creek at Lighthouse Point, New Haven, Conn. Two points of particular interest are shown here. The first is that *I. setosus*, the dominant species of *Isobactrus* in Long Island Sound and Morris Cove, is replaced by *I. hutchinsoni*. It is not known how stable this condition is, so it cannot be stated definitely that *I. hutchinsoni* owes this local superiority to low salinity. However, considering the general abundance of *I. setosus* it is very likely that the predominance of *I. hutchinsoni* is due to the inability of the former species to compete with the latter at the salinities prevailing in this creek. The second point of interest is that the greatest population is developed in the lower one-fifth of the portion of the creek which was studied, where the salinity was around 12°/oo, and that the mites decreased in abundance from this point onward. At a point 1000 meters from the mouth of the creek, where the salinity was less than 1.0°/oo, no mites were found. The absence of the Halacarinae cannot be considered very significant, for like most tidal creeks, this one is very muddy, and generally it provided little opportunity for other than algicolous species to become established.
The poorness of the fauna at Solomon's Island, Maryland, is due in a large part to the low salinity there. One could reasonably assume that the fauna at the lower end of Chesapeake Bay should contain at least as many species as were found at Beaufort, N. C., with the possible exception of *Copidognathus* (s. str.) *acutus*. But only three species were found at Solomon's Island, where the salinity is generally 10–12°/oo.

**The Fauna at Beaufort, North Carolina**

The Beaufort collections are summarized in Tables X, XI and XII, and it will be necessary to point out only how they agree with the above discussion. The subtidal fauna is dominated by *Copidognathus* (*Arhodeoporus*) *arenarius*, just as is that of Long Island Sound. *Copidognathus* (s. str.) *septentrionalis*, however, is replaced by a new

### Table X. Subtidal Collections Made at Beaufort, North Carolina, October 18–24, 1944. Various Substrates

<table>
<thead>
<tr>
<th>Sample No.</th>
<th>Locality and Substrate</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td><em>Rhombothemus magnicostatus</em></td>
</tr>
<tr>
<td>44–87</td>
<td>Newport River, about 1 mile north of railway bridge, at 2.5 m.</td>
<td>3</td>
</tr>
<tr>
<td>44–88</td>
<td>Gracilaria; 110 g.</td>
<td>7</td>
</tr>
<tr>
<td>44–89</td>
<td>Ascidians; 30</td>
<td>7</td>
</tr>
<tr>
<td>44–90</td>
<td>Gracilaria; 83 g.</td>
<td>6</td>
</tr>
<tr>
<td>44–91</td>
<td>Hydroids; various species</td>
<td>39</td>
</tr>
<tr>
<td>44–92</td>
<td>Hydroids and ascidians</td>
<td>31</td>
</tr>
<tr>
<td>44–93</td>
<td>Broken, rough shells, perforated by <em>Cliona</em></td>
<td>52</td>
</tr>
<tr>
<td>44–109</td>
<td>About 1 mile southwest of Beaufort Entrance, at 10 m.</td>
<td></td>
</tr>
<tr>
<td>44–103</td>
<td>Algal fragments; worm tubes</td>
<td>1</td>
</tr>
<tr>
<td>44–104</td>
<td>East end of Harker’s Island, just below low tide zone</td>
<td></td>
</tr>
<tr>
<td>44–105</td>
<td>Brown algae; 150 g.</td>
<td>1</td>
</tr>
<tr>
<td>44–106</td>
<td>Mixed algae; 17 g.</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>Broken shells and fine sand</td>
<td></td>
</tr>
<tr>
<td>44–107</td>
<td>Sponges; 500 cc., loosely packed</td>
<td>8</td>
</tr>
<tr>
<td>44–107</td>
<td>Piver’s Island, on pier at Fisheries Laboratory, just below low tide zone</td>
<td>1</td>
</tr>
</tbody>
</table>
TABLE XII. COLLECTIONS FROM TOWN MARSH, JUST SOUTH OF PIVER’S ISLAND, ON THE SHELTERED SIDE OF THE MARSH; IN THE HIGH TIDE ZONE, BUT IN A POOL FORMED BY THE BLOCKING OF A BTL-FALL INLET BY A SAND BAR AND HENCE FILLED WITH WATER AT ALL TIMES

<table>
<thead>
<tr>
<th>Sample No.</th>
<th>Locality and Substrate</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>44-85</td>
<td>Silty sand in salt grass; mid-tide zone; filamentous green algae present; 200 cc.</td>
<td>Rhombognathus magnirostris; Metarhomphobognathus americanus; Holocerus; Copidognathus punctatissimus; C. acutus.</td>
</tr>
<tr>
<td>44-97</td>
<td>Medium and fine sand; broken shells; 500 cc.</td>
<td>1 135</td>
</tr>
<tr>
<td>44-95</td>
<td>Medium and fine sand; 500 cc.</td>
<td>- - 1 1 - - - 1</td>
</tr>
<tr>
<td>44-96</td>
<td>Very fine sand; 500 cc.</td>
<td>- - - - - - - - 1</td>
</tr>
<tr>
<td>44-98</td>
<td>Ostrea; 25; av. length 6.5 cm. From south end of island where wave action is strongest; filamentous green algae virtually absent</td>
<td>- - - - 1 6 4 11</td>
</tr>
<tr>
<td>44-101</td>
<td>Ostrea; 10; av. length 9 cm. From east side of island (sheltered); filamentous green algae abundant</td>
<td>- 75 - - - - 75</td>
</tr>
</tbody>
</table>

TABLE XII. COLLECTIONS FROM TOWN MARSH, JUST SOUTH OF PIVER’S ISLAND, ON THE SHELTERED SIDE OF THE MARSH; IN THE HIGH TIDE ZONE, BUT IN A POOL FORMED BY THE BLOCKING OF A SMALL INLET BY A SAND BAR AND HENCE FILLED WITH WATER AT ALL TIMES

<table>
<thead>
<tr>
<th>Sample No.</th>
<th>Substrate</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>44-101</td>
<td>Ostrea; 17; av. length 9 cm. Sparse coating of small, but living, Enteromorpha and filamentous green algae present</td>
<td>Rhombognathus magnirostris; Metarhomphobognathus americanus; Holocerus; Copidognathus punctatissimus; C. acutus.</td>
</tr>
<tr>
<td>44-102</td>
<td>Coarse, broken shells; 1000 cc.</td>
<td>1 2 - - - 1 7 1 4 11</td>
</tr>
</tbody>
</table>

species, Copidognathus acutus. C. punctatissimus is the third most common species, as it is in Long Island Sound. The absence of Metarhomphobognathus from subtidal and other nontidal habitats is very noticeable and agrees with what has already been said about the local
distribution of that genus. *Agauopsis borealis* was taken below the tide zone, whereas in Long Island Sound it was found in the intertidal zone. It is probably not restricted to either, but is most abundant just below the low tide zone. An extensive sand fauna is not developed, although occasional specimens of *Halacarus* (s. str.) *anomalous* are found. The fineness of the sand, most of it less than 0.25 mm. in diameter, would itself be a great barrier to the arenicolous species. *Copidognathus* (*Arhodeoporus*) *arenarius* is not arenicolous in the Beaufort region. With respect to the Beaufort fauna, it is a psam-moxene form. This is probably true along a greater part of the coast between New Jersey and North Carolina, where the sand is too fine to provide a habitat for the Halacaridae.

**ECOLOGICAL SUMMARY**

1. A total of 41 species, subspecies and varieties of Halacaridae are recorded from North America and Greenland.

2. The Florida fauna is the richest on our eastern coast, that of New England is the second richest, and intermediate regions are the poorest.

3. There is no correlation between the New England-New Brunswick fauna and that of Florida.

4. The fauna at Beaufort, North Carolina, is more closely related to the northern than to the Florida fauna.

5. Nearly 70 per cent of the forms in the American Boreal Atlantic are identical with or closely related to forms in the European Boreal Atlantic. There is less relationship with the Mediterranean-Atlantic fauna, and virtually none with the Tropical fauna.

6. The transitional character of the fauna between Cape Hatteras and southern Florida is shown to consist more of a dropping out of certain Boreal genera and subgenera than of an overlapping of Boreal and Tropical elements.

7. The fauna of southern Florida is Tropical in character and is closely related to that of the Dutch West Indies and Bermuda.

8. The distribution of certain species or species groups in the Caribbean, Mediterranean and southwest Pacific regions suggests a Tethyan halacarid fauna parallel to that of other groups of animals.

9. *Rhombognathides, Metarhombognathus, Isobactrus, Thalassarachna, Arhodeoporus* and *Lohmannella* are shown to be nontropical, and the first three are characteristically Boreal or Arctic.
10. One of the most characteristic features of the Tropical fauna is the predominance of *Copidognathus* s. str.

11. The fauna of the subtidal zone is more uniform than that of the intertidal zone, especially from a qualitative standpoint.

12. *Copidognathus (Arhodeoporus) arenarius* is the dominant species in the subtidal zone in Long Island Sound and at Beaufort, North Carolina.

13. Limited collections near the eastern end of Long Island Sound suggest a transition from a eulittoral to a sublittoral fauna.

14. A well developed sand fauna consisting of three psammobiont and one psammophile species is found in Long Island Sound. The sand fauna of the American Boreal Atlantic is very similar to that of Europe.

15. Of the faunae developed upon molluscs, those on *Modiolus* and *Ostrea* are the richest and most complex. The encrustation of *Modiolus* by *Balanus* greatly increases the ability of this substrate to support an halacarid fauna.

16. The algicolous faunae are dominated by the Rhombognathinae; none of the Halacarinae are typically algicolous.

17. Observations on the absence of *Isobactrus* and *Metarhombognathus* from special nontidal habitats indicate that species of these genera require periodic exposure to air, thus accounting for their absence from subtidal habitats.

18. Habitats characterized by low salinity are also characterized by halacarid faunae containing a small number of species.

**GLOSSARY OF TERMS**

Some of the terms used in this paper are defined below, but in other cases only a reference to a labelled figure is given. Terms which have been applied to the Halacaridae for the first time are marked with an asterisk. References to species under which certain structures have been discussed more extensively are also given. A list of equivalent terms used by German workers has also been added, but this does not include those whose equivalence is obvious.

Accessory tooth. Fig. 207.

*Alveolus. Fig. 205. See rosette pore.

Ambulacrum. Fig. 211. All the structures lying beyond the tip of the tarsus, including carpus, carpite (if present), lateral claws, middle piece, and median claw (if present).
Anal papilla. Fig. 197.
Anal plate. Figs. 3, 7. The plate bearing the anus in those forms in which the genital and anal plates are separate.
Anterior epimeral plate (AE). Figs. 197, 198.
Antero-dorsal plate (AD). Fig. 197.
Anus. Fig. 198.
Apodemes. Fig. 198. These structures are frequently alluded to in the literature, but few workers seem to realize their true nature. They are muscle insertions and are internal rather than external. They may be accompanied by invaginations of the cuticle (see *Copidognathus* [s. str.] *pachypus*, n. sp., and *C.* [s. str.] *caudatus*, n. sp.).

*Apodemes.* Fig. 198. Any setae which is of nearly uniform diameter throughout and rounded terminally rather than tapering.

*Bacillum.* Figs. 47, 207. A seta of variable form, usually bacilliform, just anterior to either the medial or lateral disti-dorsal seta of I-6 and II-6. The form and position of the bacillum is of taxonomic significance.

Base of capitulum. Fig. 202.
Camerostome. Fig. 198. The opening between AD and AE at which the capitulum is attached.

*Canaliculi.* Fig. 205. See rosette pore.
Capitulum. Fig. 202. This includes the base of the capitulum, rostrum, palpi and chelicerae.

*Carpite.* Fig. 25. A minute sclerite lying between the end of the tarsus and the middle piece of the ambulacrum, found only in the Rhombognathinae (and probably the Actacarinae). Its systematic importance has not been fully realized. See *Rhomobognathus magnirostris magnirostris* and *Isobactrus setosus*.

*Carpus.* Figs. 25, 211. The flexible portion of the leg between the end of the tarsus and the base of the claws. Fundamentally it is a thin-walled cylindrical membrane which is a direct continuation of the wall of the tarsus. The lateral claws and the middle piece of the claw (with or without a median claw) are attached distally. In the Rhombognathinae the carpite extends through the carpus.

---

26 Womersley (1937: 13–14) said of his new species, *Agaue hamiltoni*, "This species appears to be distinct from all other species and can be easily recognized by the "peculiar setae."" The "peculiar setae" referred to are apodemes on the internal surface of AE! Viets (1940g: 66) again referred to these as "Borsten" (Viets' quotation marks).
Chelicera. Fig. 179.
Cheliceral membrane. Fig. 179. The pointed dorsal digit of the chelicera.

Claw fossa. Fig. 207. The inflection of the dorsal margin of the tarsus, distal to the disti-dorsal setae of the tarsus. The tarsi of nearly all species taper gradually, at least, but a fossa is present only if there is a noticeable inflection of the margin. Membranes may be present or absent.

Comb, or Pecten. Fig. 207.

Cornea. Fig. 197.

Costae (of PD). Fig. 197. The two central elevated ridges of the postero-dorsal plate.

Divaricate. Fig. 207. A term applied to the parambularal setae when these are two-pronged. The members may be equal or unequal in size and form.

Epimeral pore. Figs. 198, 199. The large pores lying in AE, in the boundary between coxal areas I and II. This boundary is usually well marked in the lateral portions of AE by an internal ridge or external suture, or both.

Genital opening. Fig. 198. Generally this term has been used to refer to the circular or oval area, rather than to the slit-like opening itself.

Genital plate. Figs. 7, 76. The plate bearing the genital opening (or presumptive genital opening) in those forms in which genital and anal plates are separate.

*Genital sclerites. Fig. 198. Paired elongate sclerites lying within the membranous flaps covering the genital opening. In Rhombognathides and Actacarus they are enlarged and cusp-like.

Genito-anal plate. Fig. 198. The single plate enclosing both genital and anal openings.

Lateral claws. Fig. 207.

*Maxillary setae (rostral setae). Fig. 202. The term maxillary setae is preferable, because one of the two pairs may be on the base of the capitulum rather than on the rostrum. Furthermore, in species in which a third pair is added this pair is always on the base of the capitulum.

Median claw. Figs. 25, 207. A claw-like extension of the middle piece of the ambulacrum. It may be nearly as large as the lateral claws but is usually much smaller, or it may be absent. It may be unidentate or bidentate.
Membrane (of claw fossa). A lamellar distal or disti-dorsal expansion of the wall of the tarsus on one or both sides of the claw fossa.

Membranous area. Fig. 197.

Middle piece. Fig. 25. The chitinous sclerite to which the lateral claws are more or less firmly attached. In most species it is produced distally to form the median claw.

Ocular plate. Fig. 197.

Ostium (of rosette pore). Fig. 205. See rosette pore.

Palpi. Figs. 201, 202.

Panelling. Figs. 199, 200.

*Parambulacral setae. Fig. 207. The setae lying at the base of the ambulacrum on the sides of the tarsus. They are of characteristic form, and those on tarsi I and II are usually divaricate. See *Meta-rhombognathus armatus americanus*, n. subsp., and *Halacarus* (s. str.) *frontiporus*, n. sp.

Pectinate seta. Fig. 204. Any seta which is pectinate along one or two sides of the shaft.

*Pharyngeal plate. Fig. 202. The dorsal wall of the pharynx to which the dilator muscles are attached.

Porose panel. Fig. 199. A panel-like area, depressed or not, containing a number of pores.

Postero-dorsal plate. Fig. 197.

Posterior epimeral plate. Figs. 197, 198.

*Prebacillum. Fig. 47. A usually bacilliform seta lying anterior to the bacillum of tarsus I in certain genera. It has not been found on tarsus II in any species yet seen by the writer. In *Rhombognathus* it is longer than the degenerate bacillum, but probably in all other genera it is shorter. See bacillum. See also *Metarhombognathus armatus americanus*, n. subsp., and *Rhombognathus magnirostris magnirostris* Trouessart.

Rosette pore. Figs. 205, 206. A type of pore found only in *Copidognathus* s. str. (as redefined in this paper). Morphologically it probably represents a sunken porose panel (*q. v.*). Several types are known, but the pores in a given species are generally constant in form. Despite the fact that they are very promising systematic and morphological characters, they have been used very little, probably owing to a lack of understanding of their structure. A full morphological treatment will not be given here, but the typical rosette pore is described. Discussions of variations in structure can be found under the various
species, especially *C. bairdi*, n. sp., *C. angustus floridensis*, n. subsp., *C. hummelincki* (Viets), *C. gracilis* (Viets), and *C. caudatus*, n. sp. The most elaborate type of rosette pore is diagrammed in Fig. 205. It consists of a central chamber, or alveolus, opening to the exterior by an ostium. Several canaliculi open into the alveolus, and these extend to the inner surface of the cuticle. In direct dorsal view the rosette pore appears as shown in Fig. 206. Although the canaliculi are represented in the same manner that one would represent a pore opening directly to the surface, it must be remembered that they open into the alveolus. However, occasionally a canaliculus does open directly to the surface. Variations in the rosette pores occur principally in the diameter of the ostium, the depth and diameter of the alveolus, the number and size of the canaliculi, and the uniformity or degree of perfection in the structure of the pores.

*Rostral setae. See maxillary setae.*

*Rostrum. Fig. 202.*

*Subgenital setae. Fig. 168. Minute setae in or very near the small furrow (presumptive genital opening) just ventral to the genital suckers. They are usually visible only with oil immersion.*

*Triangle setae. Fig. 210. Three setae arranged in a triangular manner on the dorsal side of segments 3 and 5 of the legs. The base of the triangle lies near the distal end of the segment.*

Equivalent Terms Used in German Writings

- Aussenzinke: Accessory tooth.
- Cilienkamm: Comb.
- Excretionsporus: Anus.
- Fiederborste: Pectinate seta.
- Hornhaut: Cornea.
- Kamm: Pecten; comb.
- Krallengruben: Claw fossae.
- Krallengrubenmembran: Membrane of claw fossa.
- Krallenmittelstück: Middle piece (of ambulacrum).
- Krallenzwischenstück: Carpite.
- Längslinien; Längsbandern: Costae (of PD).
- Mandibel: Chelicera.
- Maxillarorgans: Capitulum.
- Mittelkrallen: Median claws.
- Ocularplatten; Okularia: Ocular plates (OC).
- Palpengruben: Palpal insertions.
Postdorsalplatte  | Postero-dorsal plate (PD).
Prädorsalplatte | Antero-dorsal plate (AD).
Rücken haut    | Dorsal membranous area.
Schnabel       | Rostrum.
Seitenkrallen  | Lateral claws.
Tasthaare (Lohmann 1889a: figs. 51, 55, 57).

**DISPOSITION OF SPECIMENS**

Specimens of all species seen in the course of this work have been retained in the writer's collection, but where duplicates are available they will be distributed as indicated below. A = author's collection, B = British Museum, London; P = Peabody Museum, Yale University; U = United States National Museum, Washington, D. C. The figures indicate the number of slides.

*Rhomognathus magnirostris magnirostris*, 2A, 1P; magnirostris lionyx, 1A.

*Rhombognathides pascens*, 8A, 1B, 1P, 1U; seahami, 7A, 1B, 1P, 1U; mucronatus, 3A, 1P, 1U; merrimani merrimani, 1A; merrimani needleri, 1A, 1P.

*Metarhombognathus armatus americanus*, 54A, 1B, 2P, 2U.

*Isobactrus setosus*, 16A, 1B, 2P, 1U; levis, 1A; hutchinsoni, 1A, 1P.

*Halacarus (s. str.) ctenopus*, 2A; actenos, 2A, 1B, 1P, 1U; frontiporus, 8A, 1B, 1P (holotype), 1U; anomalus, 1A.

*Halacarus (Thalassarachna) basteri basteri*, 5A, 1B, 1P, 1U; longipes, 2A; balticus, 24A, 2B, 2P, 2U; subterraneus, 7A, 1B, 1U; capuzinus, 7A, 1B, 1P, 1U.

*Copidognathus (s. str.) punctatissimus*, 12A, 1B, 2P, 1U; acutus, 16A, 1B (paratype), 2P (paratypes), 1U (paratype); Bairdi, 4A, 1B (paratype), 1P (paratype), 1U (paratype); curassaviensis, 3A; biscoyneus, 1A; angustus floridensis, 1A; septentrionalis, 3A, 1B, 1P, 1U; gracilis, 1A; hummelincki, 4A, 1B, 1P, 1U; caudatus, 1A; pulcher, 2A; pachypus, 1A; bonairensis 1A.

*Copidognathus (Arhodeoporus) arenarius*, 21A, 1B, 2P, 1U; submarinus, 5A, 1P, 1U.

*Agaue nationalis*, 1A.

*Aguopsis brevipalpus brevipalpus*, 5A, 1B, 1P, 1U; borealis, 3A, 1P, 1U.

*Lohmannella falcata*, 2A.
LITERATURE CITED

André, Marc

Banks, Nathan

Berlese, Antonio

Brady, G. S.

Brucker, E. A. and E. L. Trouessart

Canestrini, Giovanni

Chilton, Charles

Ekman, Sven

Giard, Alfred

Gimbel, O.

Gosse, P. H.

Halbert, J. N.
Hodge, George


Johnston, George

King, L. A. L.

Kramer, P.

1893b. Bemerkungen zu den auf der Holsatia-Fahrt 1887 gesammelten Halacarinen. 6th Bericht Komm. deutsche Meere, III (Schluss-) Heft: 199–204.


McDougall, K. D.

Murray, Andrew

Newell, I. M.

Oudemans, A. C.

Packard, A. S.

Parr, A. E.
POLICE, GESUALDO  

SCHOTT, GERHARD  

SCHULZ, ERICH  

SVERDRUP, H. U., M. W. JOHNSON, AND R. H. FLEMING  

THOR, SIG  

TRÅGÅRDH, IVAR  

TROUSSART E. L.  


TROUSSAERT, E. L. AND L. G. NEUMANN

1893e. Description d'un nouveau genre et d'une nouvelle espèce de la famille des Halacaridae ou acariens marins. Naturaliste, 7° Année, 2° Ser.: 207–208.

VIETS, KARL


1938a. Eine merkwürdige, neue, in tiefsee-echiniden schmarotzende Halacariden­
1938e. Über eine neue Art von Meeresmilben, Copidognathus tricorneata
1939c. Meeresmilben aus der Adria. (Halacaridae und Hydrachnellae, Acari).
1940g. Meeresmilben aus der Adria. (Halacaridae und Hydrachnellae, Acari).

WALTER, C. H.
1917c. Schweizerische Süßwasserformen der Halacariden. Rev. suisse Zool.,
1931a. Campagne spéologique de C. Bolivar et R. Jeannel dans l’Amérique du
(Biospeologica. LVI): 375–381.

WILLMANN, CARL
1931b. Oribatei (Acari), gesammelt von der Deutschen Limnologischen Sunda-

WOMERSLEY, HERBERT
(6): 1–24, pls. 1–11.