# Revision of *Styraconyx* (Tardigrada: Halechiniscidae), with Descriptions of Two New Species from Disko Bay, West Greenland

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and

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SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 391

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SMITHSONIAN INSTITUTION PRESS
City of Washington
1984

# ABSTRACT

Kristensen, Reinhardt Møbjerg, and Robert P. Higgins. Revision of *Styraconyx* (Tardigrada: Halechiniscidae), with Descriptions of Two New Species from Disko Bay, West Greenland. *Smithsonian Contributions to Zoology*, number 391, 40 pages, 51 figures, 1 map, 5 tables, 1984.—Systematic characters separating *Styraconyx* Thulin, 1942, from the closely related genera *Bathyechiniscus* Steiner, 1926, and *Pleocola* Cantacuzène, 1951, are presented. Descriptions of *Styraconyx haploceros* Thulin, 1942, *S. sargassi* Thulin, 1942, *S. hallasi* Kristensen, 1977, and *S. craticulus* (Pollock, 1983), new combination (formerly *Bathyechiniscus craticulus*), are emended based on a reexamination of type material. New records of *S. craticulus* and *S. kristenseni* Renaud-Mornant, 1981(b) from Al-Ghardaqa (Red Sea), the East Coast of Australia, the Coral Sea, and New Zealand indicate that these species are sympatric sibling species. *Styraconyx paulae* Robotti, 1971, is removed from synonomy with *Bathyechiniscus tetronyx*. Two new species, *Styraconyx nanoqsunguak* and *S. qivitoq*, are described from Disko Bay, West Greenland. Seminal receptacles, segmental glands, and secondary clavae are described for the first time in this genus. Postembryonic development in the two new species indicate that there are at least four instars before female maturation. The presence of both a neotenic dwarf male and a normal-size male, especially in *S. qivitoq* but also in *S. nanoqsunguak*, suggests that this species-group has a life cycle similar to that recently found in *Tetrakentron*. Evaluation of the variability of morphological features used as taxonomic characters is given, in addition to general comments on the distribution, ecology, and phylogeny of the members of this genus.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year*. SERIES COVER DESIGN: The coral *Montastrea cavernosa* (Linnaeus).

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Library of Congress Cataloging in Publication Data
Kristensen, Reinhardt Møbjerg.
Revision of Styraconyx (Tardigrada, Halechiniscidae)
(Smithsonian contributions to zoology ; no 391)
Bibliography: p.
Supt. of Docs. no.: SI 1.27:391
1. Styraconyx—Classification. 2. Tardigrada—Classification. 3. Tardigrada—Greenland—Disko Bay. I. Higgins, Robert P. II. Title. III. Series.
QL1.S54 no. 391 591s [595.1'87] 83-600255 [QL447.5]

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# Revision of *Styraconyx* (Tardigrada: Halechiniscidae), with Descriptions of Two New Species from Disko Bay, West Greenland

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## Introduction

In the last ten years there have been many discoveries of new genera of Heterotardigrada, which, on a generic level, is predominantly a marine class of the phylum Tardigrada. Some of the genera such as *Echiniscoides* Plate, 1889, previously considered to be both cosmopolitan and monotypic (Pollock, 1975), have been studied more intensively (Renaud-Mornant, 1976; Kristensen and Hallas, 1980; Bellido and Bertrand, 1981; Hallas and Kristensen, 1982). In the latter instance, the genus now consists of five species with six subspecies, none of which are cosmopolitan. Sterrer (1973) and Higgins (1983) have reached the same general conclusion that meiofaunal species may not be as cosmopolitan as formerly believed. In this publication we attempt to clarify the status of those species that comprise the genus *Styraconyx* and to discuss their relationships with two closely related genera, *Pleocola* Cantacuzène, 1951, and *Bathyechiniscus* Steiner, 1926.

HISTORICAL REVIEW.—The genus *Styraconyx* was established by Thulin (1942) with the description of *S. haploceros* (type-species) from St. Malo, France, and *S. sargassi* from the Azores. The latter species originally was recorded and illustrated by Marcus (1936), and later by Mathews (1938) as *Bathyechiniscus tetronyx* Steiner, 1926. *Bathyechiniscus* had been described originally from a single specimen found in Antarctic mud at 385 m depth. Thulin (1942) indicated that the *B. tetronyx* specimens of Marcus were more similar to his material of *Styraconyx*, especially regarding the claws. Marcus subsequently agreed with Thulin's assessment as indicated by his relabeling of his microslides as *Styraconyx sargassi*. Later, Eveline du Bois-Reymond Marcus (1952, 1960), published illustrations of the feet and claws from the type material of *S. sargassi* and noted similarities of head structures between *S. sargassi* and *S. haploceros*. The unnumbered illustration of Mathews (1938) is sufficient to identify the specimens he collected from algae (*Dictyota*) found in coastal California, USA, as conspecific with those of Marcus (1936).

Chitwood (1951, 1954) reported tardigrades with transverse plates (= dorsal ridges?) from sediment at Aransas Bay, Texas, and algae (*Sargassum*) from Cedar Bayou, Texas, USA. Appar-

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ently ignoring the work of Thulin, 1942, Chitwood identified his specimens as *Bathyechiniscus tetronyx*. Careful inspection of his illustrations indicates that he may have had two different species, a possibility that is supported further by the fact that the specimens came from two different substrates. Since Chitwood's material no longer exists, one can only suggest that he found one (*S. sargassi*?) and possibly two species of *Styraconyx*.

Rodriguez-Roda (1947, 1952) collected a species of *Styraconyx* from several localities along the Spanish coast of the Mediterranean Sea; he identified them as *B. tetronyx*. Based on Rodriguez-Roda's photomicrographs, however, du Bois-Reymond Marcus (1952) suggested that they were *S. sargassi*.

In 1971, Robotti described a new species, *S. paulae* from Stromboli, Italy. His species is closely related to *S. sargassi*.

Renaud-Mornant, after studying collections of *Styraconyx* from the Pacific Ocean (Renaud-Mornant, 1967, 1976) and the Indian Ocean (Renaud-Mornant, 1979), noted geographic variation in the shape of the primary clavae within different Pacific Ocean populations. Based on these observations Renaud-Mornant (1981b) established two subspecies, *S. kristenseni kristenseni* and *S. kristenseni neocaledoniensis*.

Recently, Pollock (1983) described a new species of Styraconyxinae from algae naming it *Bathyechiniscus craticulus*. Additionally, he synonymized *Styraconyx sargassi*, *S. paulae*, and *S. kristenseni* with *Bathyechiniscus tetronyx*, perhaps being unaware of Renaud-Mornant's (1981b) reexamination of her own material. Another species, *Styraconyx hallasi*, Kristensen, 1977, was changed to *Bathyechiniscus hallasi* by Pollock (1983) thereby leaving *S. haploceros*, the type-species, as the only member of the genus. Pollock's investigation was the first of its kind to be based on many specimens, but the type material of other species of Styraconyxinae was not studied by him.

The first arctic species of *Styraconyx*, *S. hallasi*, was found in a homothermal spring on Disko Island, West Greenland (Kristensen, 1977). In 1981, we discovered two new species of *Styraconyx* during our stay at the Danish Arctic Station on Disko Island. In addition to the type material of *S. haploceros*, *S. sargassi*, *S. hallasi*, and *Bathyechiniscus craticulus*, we have examined new material of *S. kristenseni* and *B. craticulus* found in coralline sand and algae from the Red Sea, the East Coast of Australia, several islands of the Coral Sea Islands Territory (Australia), the Chesterfield Reefs (Coral Sea), and New Zealand. Study of the above material has led us to the conclusion that the genus *Styraconyx* requires revision, which is the primary purpose of this paper. Since Kristensen (1977) indicated that *Styraconyx* is a sister group to *Pleocola* Cantacuzène, 1951, van der Land (1975) and Kristensen (1980) have demonstrated strong similarities between *Styraconyx* and *Tetrakentron* Cuénot, 1892. We also discuss the phylogenetic relationships between the genera of the subfamily Styraconyxinae.

METHODS.—The descriptions of the two new species of *Styraconyx* are based on material collected with a Higgins Meiobenthic Dredge, which, while intended for soft sediment in Disko Bay, encountered a shell-gravel and rocky rubble substrate at 70 m depth near a group of small rock outcrops known as Kronprinsens Ejland, south of Disko Island, 15 September 1981. On 27 July 1982, Kristensen used a special rock dredge with a strong canvas bag to collect more of the same kind of substrate, this time near Udkiggen, Godhavn, Disko Island at 110 m depth. In both instances, the substrate was a mixture of bryozoan colonies on small pieces of rock mixed with shell-gravel. The first sample (about 250 ml volume) contained more than 50 specimens. The second sample (about 50 kg) produced more than 100 specimens. The first sample was fixed immediately after its collection in 4% buffered formalin; the second sample was immersed in fresh water for a few seconds in order osmotically to shock the tardigrades, thereby causing their release from the substrate, and to allow easy extraction by decantation of the detritus through a 62 μm mesh net. Some of these specimens were fixed in 4% buffered formalin, others in Bouin's. The latter fixative allows better examination of internal glandular structures. Some specimens were observed alive on the bryozoan colonies.

Photomicrographs were made with a Zeiss interference contrast microscope of fixed specimens stained either with methyl green in water or osmium tetroxide vapor. Formalin-fixed material was used to prepare specimens for examination by scanning electron microscopy (SEM). The animals had a sticky mucous coat to which detritus adhered; therefore, they were immersed in an ultrasonic cleaning device before being transferred through an ethynol dehydration series culminating in absolute ethynol. Specimens were dried in a critical point depression apparatus using carbon dioxide. They were then mounted on thin glass coverslips coated on one side with Elmer's glue, fixed to aluminum SEM stubs, and coated with carbon and gold-platinum. Scanning electron microscope examinations were made with a Cambridge Stereoscan 250 Mk 2.

The type material of the two new species was mounted in glycerin. Holotypes (female) and allotypes (male) were illustrated with the aid of a camera lucida and SEM photographs. The types of *Styraconyx haploceros* (four specimens) had been mounted in glycerin-jelly by Thulin (1942). That of *S. sargassi* had been mounted originally by Marcus in formalin, which had dried. Specimens were rehydrated and transferred through glycerin-alcohol to glycerin. One specimen was mounted in glycerin, and three in a modified Hoyer's medium (Higgins, 1983). The types of *S. hallasi* (three specimens) were mounted in polyvinyl-lactophenol after being stained with osmium tetroxide. The type material of *Bathyechiniscus craticulus* was mounted by Pollock (1983) in glycerin. All other specimens mentioned in this publication were mounted in either glycerin or polyvinyl-lactophenol.

Specimens of new species have been deposited in the Zoological Museum of Copenhagen, Denmark; in the Muséum National d'Histoire Naturelle (MNHN), Paris, France; and in the National Museum of Natural History, Smithsonian Institution, under the catalog numbers of the former United States National Museum (USNM).

ACKNOWLEDGMENTS.—We gratefully acknowledge the assistance and encouragement of the Board of Directors of the Danish Arctic Station of the University of Copenhagen for allowing us to use their research facilities. We are also grateful to Jacob Broberg of the R/V *Porsild*, who made it possible to make collections under the most strenuous of conditions. N. Svennevig was responsible for the collections of sediment from the East Coast of Australia, Coral Sea, and New Zealand. H. Ramløv provided us with sediment samples from Al-Ghardaqa, Egypt. Susann Braden and Heide Wolf of the Smithsonian's SEM facility generously provided us with technical assistance; Carolyn Gast of the Department of Invertebrate Zoology prepared the illustrations of the new species; Marie Wallace of the Department of Invertebrate Zoology and Gerda Kristensen were of considerable help in the preparation of this manuscript; our colleague, Horton H. Hobbs, Jr., critically reviewed this manuscript and made many valuable suggestions. We are especially grateful to Leland W. Pollock, Drew University, Madison, New Jersey, USA, and Jeanne Renaud-Mornant, Muséum National d'Histoire Naturelle, Paris, France, for their invaluable consultation.

This research was supported financially by the Danish Natural Science Research Council (Grant No. 11-2189 and No. 11-3558), a NATO Science Fellowship and Smithsonian Postdoctoral Fellowship to the senior author, and a grant from the Sumner Gerard Foundation and the Fluid Research Fund of the Smithsonian Institution to the junior author. We deeply appreciate this generous support.

## Order HETEROTARDIGRADA Marcus, 1927

## Suborder ARTHROTARDIGRADA Marcus, 1927

### Family HALECHINISCIDAE Thulin, 1928

DIAGNOSIS.—Arthrotardigrades without strongly sclerotized dorsal segmental plates. Cephalic appendages complete; secondary clavae sometimes club-shaped, transformed into an indistinct dome, or may be totally lacking. Each leg of adult with four digits bearing claws.

COMPOSITION.—The family Halechiniscidae

has been divided recently into four subfamilies. The first, Halechiniscinae Thulin, 1928, is a paraphyletic ancestral group containing four genera: *Microlyda* Hay, 1906 (=*Lydella* Dujardin, 1851); *Halechiniscus* Richters, 1908; *Echinursellus* Iharos, 1968, and *Euclavarctus* Renaud-Mornant, 1975. The second subfamily, Tanarctinae Renaud-Mornant, 1980, is a monophyletic group consisting of two genera: *Actinarctus* Schultz, 1935, and *Tanarctus* Renaud-Debyser, 1959. The third subfamily, Floraractinae Renaud-Mornant, 1982(b), is a monophyletic group consisting of two genera: *Florarctus* Delamare Deboutteville and Renaud-Mornant, 1965; and *Ligiarctus* Renaud-Mornant, 1982(b). The fourth subfamily Styraconyxinae Kristensen and Renaud-Mornant, 1983, is also a monophyletic group consisting of nine genera: *Tetrakentron* Cuénot, 1892; *Bathyechiniscus* Steiner, 1926; *Styraconyx* Thulin, 1942; *Pleocola* Cantacuzène, 1951; *Angursa* Pollock, 1979(b); *Raiarctus* Renaud-Mornant, 1981(a); *Tholoarctus* Kristensen and Renaud-Mornant, 1983; *Lepoarctus* Kristensen and Renaud-Mornant, 1983; and *Rhomboarctus* Renaud-Mornant, 1983.

## Subfamily STYRACONYXINAE
## Kristensen and Renaud-Mornant, 1983

DIAGNOSIS.—Halechiniscidae with two or four peduncles on four digits. Either internal peduncles absent or heart-shaped proximal pad present. Three to four hooks present on each claw, sometimes secondarily reduced to only one or two hooks. Claws retractable into membranous sheath. Secondary clavae normally reduced or lacking. Cirrus A and cirrus E similar; primary clavae and sense organs of the fourth leg also similar. The cuticle is variable, but dorsal cuticular plates are never present.

REMARKS.—The subfamily Styraconyxinae is a monophyletic group that demonstrates some convergence with other groups of Arthrotardigrada, for example *Raiarctus* (Styraconyxinae) and *Actinarctus* (Tanarctininae), both of which have developed long thin pillars in the epicuticle.

The ancestral Styraconyxinae are assumed to have had 3-pointed claws with peduncles (Figures 45, 46) on all four digits. Styraconyxids with simple claws and only external peduncles (Figures 23, 47–50) are postulated to be the most advanced members of the subfamily. An evolutionary trend within the genus *Styraconyx* indicates that such a postulated reduction is highly plausible. Simple claws, or claws with vestigeal secondary hooks, must have developed several times with convergence in *Pleocola* and *Lepoarctus*, as well as in *Rhomboarctus*, Renaud-Mornant, 1983, a genus closely related to *Raiarctus*. The special type of peduncle found on all four digits in members of this subfamily is unique. Note that in the original description of *Bathyechiniscus*, peduncles are not mentioned, but their presence is likely.

A very special hook-shaped peduncle is found in the subfamily Florarctinae. The reduction from four to two peduncles in the Styraconyxinae perhaps has happened only once in the group, as has the development of the two posteriorly situated heart-shaped pads on the internal digits. These heart-shaped pads (Figure 47) are present in *Pleocola*, *Angursa*, *Raiarctus*, *Tholoarctus*, *Lepoarctus*, and in most of the species of *Styraconyx*. This character must be considered as an autapomorphy within the subfamily. Dome-shaped secondary clavae (Figure 32), sense organs on all legs, the presence of stylet supports (Figure 22), placoids (Figures 13, 22), and a typical halechiniscid cuticle are considered plesiomorphic characters for the subfamily. The absence of a spine on legs 2 and 3 in *Angursa* and *Tholoarctus*, and reduced spines in *Lepoarctus*, are considered to be autapomorphic features. The body wall in all three genera is very slender. *Angursa* can be considered as a sister group to *Tholoarctus* and *Lepoarctus*. The lack of real placoids in *Tetrakentron*, *Tholoarctus*, and *Lepoarctus* has resulted from a convergence, as has the enlargement of the secondary clavae. However, in most characters we have no basis for determining convergence or autapomorphy. The lack of pillars (Kristensen, 1980) in *Tetrakentron* is an apomorphic character, as is the lack of the stylet support and real placoids in this parasitic monotypic genus. The reduction of the sense organs, however, is also found in intertidal taxa. *Styraconyx haploceros*, found in halophilous lichens, exhibits the same reductions, seemingly as a form of special adaptation to a more terrestrial way of life.

## Key to the Genera of Styraconyxinae

1. Cuticle with long thin pillars in the epicuticle of the lateral body wall . 2
   Cuticle without long thin pillars in the epicuticle ...................... 3
2. With 3-pointed claws (primary clavae round or short, secondary clavae reduced, body dorsoventrally flattened) ..................... **Raiarctus**
   With simple claws (with vestigeal secondary hooks) ...... **Rhomboarctus**
3. Pillars absent in enlarged, double cuticle (body flattened, parasitic on *Leptosynapta galliennei*) .................................. **Tetrakentron**
   Pillars small, present in enlarged or not, double or single cuticle ....... 4
4. Claws 4-pointed, peduncles not seen (body slender, primary clavae lanceolate-elongate) ...................................... **Bathyechiniscus**
   Claws 3-pointed or less, peduncles present ............................ 5
5. Claws 3-pointed (males and juveniles with simple claws on external digits) ........................................................... 6
   Claws 1- or 2-pointed ................................................ 7
6. Body robust, spines present on all legs ...................... **Styraconyx**
   Body slender (with enlarged bell-shaped cuticle), spines present on first and fourth legs only [as in couplets 7 and 8] .................. **Tholoarctus**
7. Claws 2-pointed with point divergent, median cirrus abortive (body smooth and slender) ................................................. **Angursa**
   Claws simple, median cirrus long .................................... 8
8. Cuticle not separated into two layers (typical halechiniscid cuticle), primary clavae round or oval ........................................ **Pleocola**
   Cuticle separated into two layers, epicuticle enlarged, primary clavae with cup-shaped cirrophore .................................. **Lepoarctus**

### Genus Styraconyx Thulin, 1942

*Styraconyx* Thulin, 1942:1–9, figs. 1–4 [type-species: *Styraconyx haploceros* Thulin, 1942, by original designation; gender: masculine].

Emended Diagnosis (adult).—Halechiniscidae with four digits. External digits always supported by peduncles; internal digits with proximal pads, peduncles present or absent. Claws, with three exposed points (hooks), may be retracted within claw sheath (Figures 24, 45). Dorsal cuticular plates absent although grid-like pattern of 18–23 folds sometimes present on epicuticle. Complete set of cephalic cirri always present (Figure 1); configuration of primary clavae and lateral cirri variable, arising from distinct lateral extension or directly from head; secondary clavae occurring as indistinct flat sacs or dome-shaped papillae. Stylet supports, stylets, and placoids present. Spines present on legs I–III, clavoid papillae, each with spine, on fourth legs. Paired seminal receptacles with ducts opening posterior to female gonopore present between legs III and IV (Figure 38).

Remarks.—The systematic characters used in this paper are consistent with those employed in recent publications by Renaud-Mornant (1980, 1982b) and Kristensen and Renaud-Mornant (1983); the foot in the Arthrotardigrada is considered a conservative character, while the sense organs, especially the secondary clavae and in some genera also the primary clavae, are considered very flexible characters that can be used only at the specific, not the generic, level.

Thulin (1942) and van der Land (1975) indicated similarities between the claws of *Styraconyx haploceros*, *S. sargassi*, and *Tetrakentron synaptae*. Kristensen and Renaud-Mornant (1983) present good evidence that an evolutionary line exists from tardigrades with complex claws, e.g., *Styraconyx* and *Tetrakentron*, to animals with simple claws, e.g., *Pleocola*. This postulate is based on the type of peduncles in the digits, the sense organs, and other characters (Kristensen, 1977). These authors have used the presence of peduncles in the two aberrant genera, *Angursa* Pollock (1979b) and *Raiarctus* Renaud-Mornant (1981a), as a key character separating these animals from other members of the family Halechiniscidae.

In the *Styraconyx sargassi* group, all three hooks of the claw are large (Figure 45); in *Styraconyx hallasi* (Figure 48) and in both new species from Greenland (Figures 49, 50), the accessory hooks are very thin, visible only when the claws are exposed from the claw sheath. The secondary hooks are also very thin. The claw sheath most likely is present in all styraconyxids, but only strongly developed in those species in which the hooks have been reduced, e.g., *Styraconyx hallasi*, *Lepoarctus*, and *Pleocola*. The presence of peduncles on all four digits is known only in *Styraconyx* and *Tetrakentron*, but the special *Styraconyx*-type of peduncle is not present in *Tetrakentron*. The reduction from four to two peduncles probably has happened only once in the group as has the development of the heart-shaped proximal pads on the internal digit.

The genus *Styraconyx* is problematic as Pollock (1983) implied when he split the genus into two groups. With the exception of the type-species, *Styraconyx haploceros*, he transferred all of the species of this genus to *Bathyechiniscus* Steiner, 1926. The description of this latter genus is based on a single specimen from Gauss Station, Antarctica, *B. tetronyx*, which, as its name implies, has four exposed points or hooks on each claw. None of the species of *Styraconyx* has four exposed points. In our opinion, there is insufficient justification for synonymizing *S. sargassi* with *B. tetronyx*. Despite Steiner's (1926) figures, there is no doubt that these two animals represent different species. After reexamination of Marcus' (1936) four specimens of *S. sargassi*, it is clear that *S. sargassi* has digits with four peduncles as found in *S. haploceros*. The presence or absence of a supporting pedestal for the lateral cirri and clavae are not good generic characters; in closely related species of *Styraconyx*, both long and short pedestals may be found. In some species, the female has a well-defined pedestal, which is lacking in the small male. In *S. sargassi*, the pedestal is very short or even absent while in *Bathyechiniscus* it is very long; but, the latter taxon can be defined by its type of digits and claws, primary clavae, and papillae of the fourth leg, all of which are clearly different; furthermore, there is no indication of peduncles in *Bathyechiniscus*. Even if Steiner (1926) did not illustrate his specimen carefully enough to show such details, the entire body, including the head, is so distinctive that it clearly separates *Bathyechiniscus* from other Styraconyxinae. It is interesting to note, however, that the sense organs of our new species from a shell-gravel habitat in Greenland appear to be of the same type as those described in *B. tetronyx*; especially similar are the papillae on the fourth leg.

## Key to the Species of Styraconyx

1. Four peduncles present on each foot [Figures 45B, 46B], primary clavae dome-shaped or surrounded by an enveloping membrane or narrowly elongate or spine-like .................................................. 2

Two peduncles present on each foot [Figures 47–50], primary clavae round to elongate-oval .................................................. 5

2. All cuticular sense organs reduced except for large, flat secondary clavae .................................... **S. haploceros** Thulin, 1942

   All cuticular sense organs well-developed except for indistinct secondary clavae [Figures 20, 22] .............................................. 3

3. Lateral cirri and primary clavae with common membrane extending almost to tip of primary clava [Figure 46A]; dorsal cuticle with grid-like pattern ............... **S. craticulus** (Pollock, 1983), new combination

   Lateral cirri and primary clavae without common membrane, or, when present, never extending beyond base [Figure 45A); dorsal cuticle smooth ........................................................ 4

4. Primary clavae with an extra membrane, leaving only tip free [Figure 45A]; lateral cirri elongate .................... **S. sargassi** Thulin, 1942

   Primary clavae spine-like with a small vesicle; lateral cirri short ......... ............................................**S. paulae** Robotti, 1971

5. Primary clavae ovoid or irregular [Figures 47A, 48A, 50A]; dorsal cuticle smooth ........................................................ 6

   Primary clavae lanceolate [Figure 49A]; dorsal cuticle with 18-21 ridges [Figures 10, 11] ......................... **S. nanoqsunguak**, new species

6. Claws 3-pointed with well-developed accessory and secondary hooks [Figure 47E]; primary clavae irregular with indented mesial margin [Figure 47A] ............................... **S. kristenseni** Renaud-Mornant, 1981

   Claws 3-pointed with reduced accessory and secondary hooks [Figure 48E]; primary clavae ovoid with even margin [Figure 48A] ........... 7

7. Peduncles attached to base of claw [Figure 50B]; claw sheath covering entire claw [Figure 50E]; cuticle telescopic at trunk divisions ........... .............................................**S. qivitoq**, new species

   Peduncles not attached to base of claw [Figure 48B]; primary hooks not entirely enclosed by claw sheath [Figure 48E]; cuticle smooth, not telescopic at trunk divisions .....................**S. hallasi** Kristensen, 1977

## Styraconyx craticulus (Pollock, 1983), new combination

FIGURE 46

*Bathyechiniscus craticulus* Pollock, 1983:112 [type-locality: St. Croix, U.S. Virgin Islands].

MATERIAL EXAMINED.—*Type Material*: Holotype, female (USNM 68683); 2 paratypes, female (USNM 68684, 68685); paratype, juvenile (USNM 68686); col. L.W. Pollock, 22 Mar 1979, St. Croix, Caribbean Sea.

*Other Material*: 1 female, 1 young male (R.M. Kristensen HU 082881.1, 082881.2), col. H. Ramløv, 28 Aug 1981, 0.5 m depth, algae from coral reef, Ahiaa, Al-Ghardaqa, Egypt.

One male (R.M. Kristensen AU 100379.1), col. N. Svennevig, 3 Oct 1979, lower intertidal zone, from barnacles with algae, Nielsen Park, Sydney Harbor, Australia.

Two females (R.M. Kristensen AU 090879.1-2), col. N. Svennevig, 8 Sep 1979, from intertidal barnacles, Hastings Point, Brisbane, Australia.

One young male (R.M. Kristensen AU 091879.1), col. N. Svennevig, 18 Sep 1979, from intertidal barnacles, Coloundra, Moreton Bay, Brisbane, Australia.

One male (R.M. Kristensen AU 120979.1), col. N. Svennevig, 9 Dec 1979, from intertidal barnacles, Cape Cleveland, Australia.

One female (R.M. Kristensen AU 051079.1), col. N. Svennevig, 10 May 1979, from coralline algae in intertidal coralline sand, North Cay, Long Island, Chesterfield Reefs, Coral Sea.

EMENDED DIAGNOSIS.—*Styraconyx* with subterminal mouth cone. Pigmented "eyespots" present. Long primary clavae and short lateral cirri with common sheath (cirrophore) and pedestal (Figure 46A). Lateral cirrus not segmented, indistinct secondary clava present. Peduncle (Figure 46D) present on all digits (Figure 46B); internal digits with proximal pad. Three-pointed claws crescent-shaped, each with three similar-sized hooks (Figure 46E). Claw sheath not covering tip of claw hooks. Sense organs of fourth leg consisting of asymmetrical papillae covered with tubercles and terminal spines (Figure 46C). Dorsal cuticle with grid-like pattern. Seminal receptacles with straight ducts opening near anus.

DISCUSSION.—The excellent description of *Styraconyx craticulus* indicates that it is a member of the *S. sargassi* group, but the common pedestal supporting the primary clava and lateral cirrus suggests a closer relationship to *S. kristenseni* than to *S. sargassi*. The membrane surrounding both the clava and the lateral cirrus, in our opinion, is merely an extension of the lateral edge of the cirrophore as found in other members of this genus. Therefore, the only difference between *S. sargassi* and *S. craticulus*, relevant to this character, is that in the latter species the cirrophore surrounds both the clava and the lateral cirrus, while in the former species the cirrophore surrounds only the clava since no pedestal is present. *Styraconyx kristenseni* is an intermediate form; it has a small pedestal (Figure 47A), and in some specimens the clava and the lateral cirrus also have a very short common cirrophore.

Our examination of the type material of *S. craticulus* requires only a few additional remarks. The lateral cirrus is unsegmented and short (19.8 μm), the primary clava is relatively long (10 μm) and straight. Indistinct secondary clavae are always present. All other cephalic cirri have two segments, a scapus and flagellum. Peduncles are present on all digits, but the internal peduncles ($pe_2$ and $pe_3$) are very thin and the external peduncles ($pe_1$ and $pe_4$) are hook-shaped. The coxal spine of the first three legs is progressively longer posteriorly (5.9–8.8 μm). The spine of the first leg is segmented (consists of a scapus and flagellum), the next two leg spines are not. The papilla of the fourth leg (6.2 μm) has a spine (5.5 μm) and is asymmetrical. The papilla is less curved on the posterior than on the anterior portion. As indicated by Pollock (1983) the papilla tapers into a spine without a segmentation line. The somatic spine (cirrus E) is relatively short ($\bar{x}$ = 16.5 μm). An indistinct cirrophore is present.

ADDITIONAL DISTRIBUTION RECORDS.—The senior author has collected several thousand tardigrades from different localities in the lower intertidal zone (Table 1, Map 1) by rinsing coral, algae, and barnacles covered with algae. *Styraconyx craticulus* has been present in such samples from the tropics and subtropics. Collections of different algal taxa, including *Udotea* sp. and *Halimeda* sp. (Family Codiaceae), from Al-Ghardaqa on the Egyptian coast of the Red Sea contained two specimens of *S. craticulus*. Six additional specimens were found in algae attached to barnacles collected from several localities along the East Coast of Australia including: Sydney Harbor (Nelson Park), Hastings Point (near Brisbane), Moreton Bay (Brisbane), and Cape Cleveland. A single specimen was collected from coralline algae from the Chesterfield Reefs (Long Island) in the Coral Sea.

All specimens of *S. craticulus* were easily separated from other members of the genus. They all had 23 transverse ridges and 5–7 longitudinal ridges, which give the dorsal cuticle its grid-like appearance; furthermore, all specimens had a common membrane associated with the short lateral cirrus and the straight clavae. One female from Hastings Point had well-developed seminal receptacles with ducts opening on two small papillae (posterior to the gonopore), on either side of the anal plate. The gut of some animals was green to brown in color, indicating the ingestion of algae. The type of stylets and stylet supports (small and thin), narrow buccal canal, and straight, thin placoids of *S. craticulus* are consistent with those of other herbivorous Styraconyxinae.

### Styraconyx hallasi Kristensen, 1977

FIGURE 48

*Styraconyx hallasi* Kristensen, 1977:87–89, figs. 1–3 [type-locality: Godhavn, West Greenland].—Renaud-Mornant, 1981a:520; 1981b:804; 1982a:163–169, figs. 1E, 3E, 5G, 7B.—Kristensen and Renaud-Mornant, 1983.
*Bathyechiniscus hallasi*.—Pollock, 1983:112.

MATERIAL EXAMINED.—*Type Material*: Holotype, young male (R.M. Kristensen GO 102176.1, Zoological Museum Copenhagen) 1 juvenile (on same slide as holotype), col. R.M. Kristensen, 26 Oct 1976, warm spring near Engelskmandens Havn, Godhavn, Greenland.

*Other Material*: 1 young female (R.M. Kristensen TA 120177.3), col. R.M. Kristensen, 1 Dec 1977, warm spring called Tarajungitsok, Diskofjord, Greenland.

EMENDED DIAGNOSIS.—*Styraconyx* with terminal mouth opening. Two pigmented "eyespots" present. Primary clavae short, oval, each with large cirriophore surrounding base (Figure 48A). Lateral cirrus inserted directly on head. All cirri with scapus. Peduncles (Figure 48D) present only on external digits (Figure 48B), never attached to base of claw. Internal digits possess heart-shaped proximal pads. Sense organs of fourth leg consist only of oval papilla with a truncated minute projection (Figure 48C). Accessory hooks (= "accessory spine of claw") and secondary hooks of claws reduced. Claw sheath nearly covering all three hooks (Figure 48E). Dorsal cuticle smooth, without separation. Seminal receptacles with spiral ducts opening behind gonopore of female.

REMARKS.—This rare species has been found only in radioactive warm springs on Disko Island (Table 1, Map 1). The species is known from only six specimens; four were found at the type-locality, Engelskmandens Havn, near Godhavn, and two others were from another warm spring at Tarajungitsok, Diskofjord; other marine meiofauna were found in these same warm springs (Kristensen, 1977).

*Styraconyx hallasi* is closely related to *S. qivitoq*, new species. Both have a terminal mouth without mouth papillae. The same kind of spoon-like peduncles (Figure 48D) and reduced 3-pointed claws (Figure 48E) typical in *S. hallasi* are found also in the genus *Pleocola* (cf. Kristensen, 1977). It is important to note that one immature female of *S. hallasi* has a spiral-shaped duct associated with the seminal receptacle duct that is characteristic of our new species, *S. qivitoq*. The sense organs of the two species, however, differ significantly. In *S. hallasi* only the cup-like primary clava inserts on the small pedestal (Figure 48A); the lateral cirrus inserts directly on the head as in *S. sargassi*; and the secondary clavae are indistinct dome-shaped papillae. The morphometric characteristics of the cephalic cirri are also quite different (Kristensen, 1977, table 1). The papilla of the fourth leg is ovoid as in *Pleocola* (Figure 48C).

*Styraconyx hallasi* was found on a species of blue-green algae, which may be endemic in the warm spring from which it was collected. The tardigrade probably is herbivorous judging from the green-color of the gut. Noteworthy is the occurrence of a representative of an otherwise marine tardigrade genus in a freshwater habitat. The only other such instance is in the case of the intertidal genus *Echiniscoides*, which was found in a soil sample (not in a lake!) near the Rwindi River, about 1000 m elevation, in Zaire (Teunissen, 1938:1, 6).

The *Styraconyx hallasi* group (*S. hallasi* and *S. qivitoq*, new species), as noted by Kristensen (1977), forms a link between the *S. sargassi* group (*S. sargassi*, *S. kristenseni*, *S. paullae*, and *S. craticulus*) and the genus *Pleocola*.

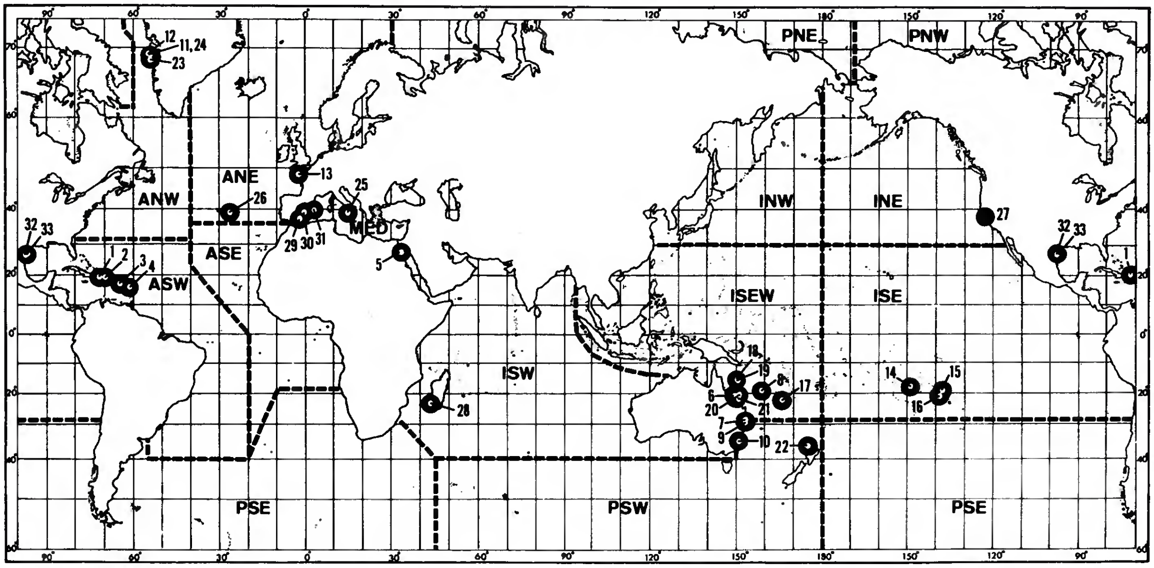
### Styraconyx haploceros Thulin, 1942

*Styraconyx haploceros* Thulin, 1942:1–9, figs. 1–4 [type-locality: St. Malo, France].—Cantacuzène, 1951:1699.—Ramazzotti, 1962:339–344, figs. 139, 140.—Schultz, 1963:4, fig. 9.—Robotti, 1971:1–3, fig. 1A,F,M.—Ramazzotti, 1972: 663–665, figs. 452–453; 1974:162–163, figs. 1A,F,M.—van der Land, 1975:421, figs. 6, 7.—Pollock, 1976:14 [illustrated key].—Kristensen, 1977:89, 90.—Pollock, 1979a: 153.—Renaud-Mornant, 1979:273; 1981b:804; 1982a: 169, fig. 7A.—Kristensen and Renaud-Mornant, 1983.—Pollock, 1983:109.

MATERIAL EXAMINED.—*Type Material*: 4 unnumbered paratypes, Zoological Museum, Co-

TABLE 1.—Distribution of *Styraconyx* (type-localities are in italics, number beside each locality refers to location in Map 1).

| Species | FAO sea area | | Locality | Authority |
|---|---|---|---|---|
| *S. craticulus* | ASW | 1 | Cap Haitien, Republic of Haiti | Pollock, 1983 |
| | ASW | 2 | Puerto Plata, Dominican Republic | Pollock, 1983 |
| | ASW | 3 | *St. Croix*, U.S. Virgin Islands | Pollock, 1983 |
| | ASW | 4 | Guadaloupe | Pollock, 1983 |
| | ISW | 5 | Al-Ghardaqa, Egypt | Kristensen & Higgins, herein |
| | ISEW | 6 | Cape Cleveland, Australia | Kristensen & Higgins, herein |
| | ISEW | 7 | Moreton Bay, Australia | Kristensen & Higgins, herein |
| | ISEW | 8 | Chesterfield Reefs, Coral Sea | Kristensen & Higgins, herein |
| | PSW | 9 | Hastings Point, Australia | Kristensen & Higgins, herein |
| | PSW | 10 | Sydney Harbor, Australia | Kristensen & Higgins, herein |
| *S. hallasi* | ANW | 11 | *Godhavn* (warm spring), W. Greenland | Kristensen, 1977 |
| | ANW | 12 | Diskofjord (warm spring), W. Greenland | Kristensen & Higgins, herein |
| *S. haploceros* | ANE | 13 | *St. Malo*, France | Thulin, 1942 |
| *S. k. kristenseni* | ISE | 14 | *Moorea*, Polynesia | Renaud-Mornant, 1981b |
| | ISE | 15 | Reao, Polynesia | Renaud-Mornant, 1981b |
| | ISE | 16 | Mururoa, Polynesia | Renaud-Mornant, 1981b |
| *S. k. neocaledoniensis* | ISEW | 17 | *Baie Saint-Vincent*, New Caledonia | Renaud-Mornant, 1981b |
| *S. kristenseni*, sensu lato | ISW | 5 | Al-Ghardaqa, Egypt | Kristensen & Higgins, herein |
| | ISEW | 8 | Chesterfield Reef, Coral Sea | Kristensen & Higgins, herein |
| | ISEW | 18 | Willis Island, Coral Sea | Kristensen & Higgins, herein |
| | ISEW | 19 | Magdelaine Reef Cays, Coral Sea | Kristensen & Higgins, herein |
| | ISEW | 20 | Marion Reef, Coral Sea | Kristensen & Higgins, herein |
| | ISEW | 21 | One Tree Island, Australia | Kristensen & Higgins, herein |
| | PSW | 22 | Leigh, North Island, New Zealand | Kristensen & Higgins, herein |
| *S. nanoqsunguak*, new species | ANW | 23 | *Kronprinsens Ejland*, W. Greenland | Kristensen & Higgins, herein |
| | ANW | 24 | Godhavn, W. Greenland | Kristensen & Higgins, herein |
| *S. paulae* | MED | 25 | *Stromboli*, Italy | Robotti, 1971 |
| *S. qivitoq*, new species | ANW | 23 | *Kronprinsens Ejland*, W. Greenland | Kristensen & Higgins, herein |
| | ANW | 24 | Godhavn, W. Greenland | Kristensen & Higgins, herein |
| *S. sargassi* | ANE | 26 | *Azores Islands* | Thulin, 1942 |
| | INE | 27 | California, USA | Mathews, 1938 |
| | ISW | 28 | Tulear, Madagascar | Renaud-Mornant, 1979 |
| | MED | 29 | Alicante, Spain | Rodriguez-Roda, 1952:48 |
| | MED | 30 | Barcelona, Spain | Rodriguez-Roda, 1952:48 |
| | MED | 31 | Mallorca, Spain | Rodriquez-Roda, 1952:48 |
| *S. sargassi*(?) | ASW | 32 | Aransas Bay, Texas, USA | Chitwood, 1951 |
| | ASW | 33 | Cedar Bayou, Texas, USA | Chitwood, 1951 |



MAP 1.—Distribution of *Styraconyx* (see Table 1).

| | | | | | |
|---|---|---|---|---|---|
| ANE | Atlantic Northeast | INW | Indopacific Northwest | ISW | Indopacific Southwest |
| ANW | Atlantic Northwest | ISE | Indopacific Southeast | MED | Mediterranean |
| ASE | Atlantic Southeast | ISEW | Indopacific Southeast-west | PNE | Polar Northeast |
| ASW | Atlantic Southwest | | | PNW | Polar Northwest |
| INE | Indopacific Northeast | | | PSE | Polar Southeast |
| | | | | PSW | Polar Southwest |

penhagen (on two slides marked "5 Jan 1930 Thulin det"), col. G. Thulin, St. Malo, France.

EMENDED DIAGNOSIS.—*Styraconyx* with a nearly terminal mouth cone. Two "eyespots" with brown pigment present. Primary clavae, located near base of short lateral cirri, indistinct. Secondary clavae large, dome-shaped and distinct. Unsegmented cephalic cirri and leg spines reduced. Absence of cirri E doubtful. Peduncle present on all digits. Three-pointed claw with large primary hook, small accessory and secondary hooks. Sense organs of fourth legs consist of ovoid papillae with short spines. Body contour smooth and slender.

REMARKS.—The type material of *S. haploceros* is in a poor state of preservation and only by the use of interference-phase-contrast microscopy could some new characters, characters not reported by Thulin (1942), be seen (Kristensen, 1977). Examination of four of Thulin's specimens revealed well-developed secondary clavae similar to those of *Tetrakentron*, as noted by Thulin (1942): "Sinneskuppen am Vorderkopfe sind nicht vorhanden; aber die Stellen, wo solche bei anderen Tardigraden so finded sind, werden von den anterolateralen Ecken des Kopfes makiert." [Sensory domes of the forehead are not present; but the areas where they are present on other tardigrades are indicated by the anterolateral edges of the head.] Our observation of these structures indicates that they are a pair of dome-shaped secondary clavae, similar to those found in most species of *Styraconyx*.

*Styraconyx haploceros* was found in the supralittoral zone in a lichen (*Lichina pygmaea*) mixed with a red alga (*Catenella opuntia*) (Table 1, Map 1). The intertidal species of other genera of marine tardigrades, such as *Echiniscoides sigismundi* (Schultze, 1865; cf. Hallas and Kristensen, 1982) and *Archechiniscus marci* Schultz, 1953, have reduced sense organs compared with those of subtidal species, such as *Echiniscoides higginsi* Hallas and Kristensen, 1982, and the species of *Archechiniscus* found in coral sand (Renaud-Mornant, 1967). The intertidal *Styraconyx haploceros* has all sense organs reduced except for the secondary clavae.

Thulin's (1942) description of the peduncle ("Stiele") is correct except for his omission of two small lateral processes on the external peduncle. He also observed that the 2-clawed larvae have a different type of peduncle than that of the adults: "sie sind aber nicht winkelig gebogen und setzen sich nicht auf den terminalen Extremitatenabschnitt fort." [However, they are not bent at right angles and do not extend into the terminal portion of the extremities.] Our study of the larvae of six species of *Styraconyx* shows that all have a long, thin peduncle, even in species in which the adult lacks the internal peduncle.

The internal digit has an indistinct proximal pad as in *Styraconyx sargassi*. This was indicated by Thulin (1942:8, fig. 4) when he drew a line across the digit at the termination of the peduncle. The presence of four peduncles on each foot is similar to that of *S. sargassi* and *S. craticulus*, but the 3-pointed claws are much more like those of *S. hallasi* and *S. qivitoq*, new species, described in this paper. Unfortunately, the seminal receptacle of *S. haploceros* could not be seen in the type material.

## Styraconyx kristenseni Renaud-Mornant, 1981

FIGURE 47

*Styraconyx kristenseni* Renaud-Mornant, 1981b:804–807, fig. 2, table 1 [type-locality: Moorea, Polynesia].—Kristensen and Renaud-Mornant, 1983:338.

*Styraconyx kristenseni kristenseni* Renaud-Mornant, 1981b:804–807, fig. 2, table 1 [type-locality: Moorea, Polynesia].

*Styraconyx kristenseni neocaledoniensis* Renaud-Mornant, 1981b:807, 808 [type-locality: Baie Saint-Vincent, New Caledonia].

*Styraconyx sargassi.*—Renaud-Mornant, 1967:111, fig. 3 [Baie Saint Vincent, New Caledonia]; 1971:960; 1976:291.—Pollock, 1976:15 [illustrated key]; 1979a:153. [Not *S. sargassi* Thulin, 1942.]

*Styraconyx sargassi(?).*—Renaud-Mornant, 1982a:156, 169, fig. 7C [Reao and Moorea, Polynesia].

*Bathyechiniscus tetronyx.*—Pollock, 1983:111 [in part].

MATERIAL EXAMINED.—*Type Material*: Holotype, female (MNHN, Paris, AH595), paratypes, 2 females (MNHN, Paris, AH590a, AH610), 1 juvenile (MNHN, Paris, AH597), sediment collected by B. Salvat, coralline sand, 1–2 m, Moorea, Polynesia; specimens extracted and determined by J. Renaud-Mornant; specimens seen but not studied intensively by senior author.

*Other Material:* 4 females, 1 male, 1 juvenile (R.M. Kristensen HU 082881.3–5), col. H. Ramløv, 28 Aug 1981, 0.5 m depth, from coralline sand, Ahiaa, Al-Ghardaqa, Egypt.

One female (R.M. Kristensen AU 103079.1), col. N. Svennevig, 30 Oct 1979, from coralline sand, 2 m depth, Lagoon, One Tree Island, Australia.

One female (R.M.K., AU 042579.1), col. N. Svennevig, 25 Apr 1979, from coralline sand, ~2 m depth, Main Island, Willis Group, Coral Sea.

One juvenile (R.M.K., AU 042679.1), col. N. Svennevig, 26 Apr 1979, from coralline sand, approximately 2 m depth, North Cay, Magdelaine Reef, Coral Sea.

Two females, 6 adults of undetermined sex, 1 two-clawed larva (R.M.K., AU 051279.1-9), col. N. Svennevig, 12 May 1979, from coralline sand, 2 m depth, Cay Sea, Marion Reef, Coral Sea.

One female (R.M.K., AU 050879.1), col. N. Svennevig, 8 May 1979, from intertidal coralline residue, Bennett Island, Chesterfield Reefs, Coral Sea.

Two females (R.M.K., AU 051079.1, 2), col. N. Svennevig, 10 May 1979, from coralline sand-gravel, 2 m depth, Cay North, Long Island, Chesterfield Reefs, Coral Sea.

One juvenile (R.M.K., NZ 011980.1), col. N. Svennevig, 19 Jan 1980, from coralline residue, Leigh, New Zealand.

EMENDED DIAGNOSIS.—*Styraconyx* with nearly terminal mouth opening. Pigmented "eyespots" present in some. Primary clavae short, asymmetrical, inserted together with lateral cirri on pedestals (Figure 47A). Cephalic cirri with scapus and flagellum. Outer contour of secondary clavae not visible. Peduncles (Figure 47D) present only on external digits (Figure 47B). Internal digits with distinct proximal pads. Seminal receptacles with nearly straight ducts. Large folds of cuticle near legs, dorsal cuticle with irregular ridges. Three-pointed claws (Figure 47E) crescent-shaped with posterior point of claw curving outward. Claw sheath covering claw hooks.

REMARKS.—*Styraconyx kristenseni* is strongly stenotopic, found only interstitially in coralline sand. This species exhibits much more geographic variation than other members of this genus. Because of this, Renaud-Mornant (1981b) recognized two subspecies. The nominate subspecies, *S. kristenseni kristenseni* occurs on three different Polynesian atolls, while the second subspecies, *S. kristenseni neocaledoniensis* is from Baie Saint-Vincent, New Caledonia. The body of the nominate subspecies is very slender; that of the New Caledonian subspecies is more robust. Various morphometric characters also distinguish the two subspecies: *Styraconyx kristenseni neocaledoniensis* has long external cirri (25 $\mu$m), reduced internal cirri (8 $\mu$m), and reduced spines (1–2 $\mu$m) on the first three legs; the nominate subspecies has slightly longer internal cirri (12 $\mu$m) than external cirri (10–12 $\mu$m) and the spines on the legs are long (10–11 $\mu$m). The lengths of the lateral cirri and the primary clavae also are different in the two subspecies.

In nearly all other characters, the two subspecies are identical. All cephalic cirri, including the lateral ones, have a scapus. The primary clavae and lateral cirri have a small common pedestal and cirrophore. The primary clavae are strongly asymmetrical and vary from specimen to specimen (Renaud-Mornant, 1982a, fig. 7). The papillae of the fourth leg (Figure 47C) are situated on a well-defined cirrophore; each papilla is ovoid with a distinct spine. Only the internal digits have the hook-shaped peduncle (Fig. 47D); the external digits have relatively long proximal pads. The primary hook of the crescent-shaped claw clearly is longer than both the accessory hook and secondary hook. In both subspecies, the dorsal cuticle has three or four large folds. The buccal apparatus has a nearly terminal mouth opening as in *S. hallasi.* Renaud-Mornant (1981b, fig. 2) indicated that the stylets have their own openings lateral to the mouth opening. Our specimens confirm this unique morphology. The pharyngeal apparatus is large; three curved placoids are present. One specimen from the Reao Atoll has pigmented "eyespots."

NEW RECORDS.—We have found *Styraconyx kristenseni* in 6 of 8 samples of coralline sand taken along a transect from the East Coast of Australia to the Chesterfield Reefs near New Caledonia. These localities (Table 1, Map 1) include: (8) Bennett Island and Long Island, both Chesterfield Reefs, Coral Sea; (18) Main Island, Willis Group, Coral Sea; (19) North Cay, Magdelaine Reef, Coral Sea; (20) Cay Sea, Marion Reef, Coral Sea; (21) One Tree Island (lagoon), Australia. Also, a single specimen of *S. kristenseni* was found in corraline residue collected from (22) Leigh, North Island, New Zealand. In addition to these records, samples of coralline sand from (5) Al-Ghardaqa on the Egyptian Coast of the Red Sea also contained six specimens of *S. kristenseni.* We conclude that this species is widely distributed and likely will be found in many other localities wherever the proper substrate can be found.

As noted already by Renaud-Mornant (1981b), *S. kristenseni* varies morphologically from different geographic areas, but the primary clava, with its asymmetrical structure, appears to remain a constant character. The animals from the Chesterfield Reefs, (Coral Sea) and Al-Ghardaqa (Red Sea) were found together with *S. craticulus* in samples in which algae were present. It would appear that in such a habitat there is some evidence of character displacement. *Styraconyx kristenseni,* in these circumstances, had shorter than normal primary clavae and *S. craticulus* had longer than normal primary clavae. When sympatric with *S. craticulus, S. kirstenseni* had an unsculptured dorsal cuticle. In algae-free coralline sand from the Coral Sea, where *S. craticulus* was not found, *S. kristenseni* had an irregular ridge on the dorsal cuticle; furthermore, a thin common membrane was found at the base of the lateral cirri and the primary clavae. This latter form perhaps could be described as a third subspecies of *S. kristenseni*, but it also could be a form of character displacement caused by competition with its close relative, *S. craticulus*. This relationship requires further investigation.

## Styraconyx nanoqsunguak, new species

FIGURES 1–21, 49

DIAGNOSIS.—*Styraconyx* with subterminal to ventral mouth cone, with 10 mouth papillae (Figures 1, 13). Buccal tube with ventral asymmetric apophysis. Ten to 12 pigment granules (Figure 21) on each side of brain constituting "eyespots." Primary clavae and lateral cirri situated on common pedestal. Secondary clavae sausage-shaped (Figure 6). Cephalic cirri consist of three segments (Figures 2, 3, 6) with exception of 2-segmented lateral cirri (Figure 7). Reduced peduncles (Figure 49D) present only on external digits (Figure 49B). Proximal pad on internal digit heart-shaped. Three-pointed claw (Figures 17, 49E) with reduced accessory and secondary hooks. Tip of the primary hook free of claw sheath. Sense organs of fourth leg each consisting of long, club-shaped papilla with long spine; cirrophore of each sense organ well developed. Female with two large lateral genital papillae (Figures 1, 11, 16) on which ducts of the seminal receptacles open. Dorsal cuticle with 18-20 distinct ridges (Figures 10, 11, 18).

Morphometric data for adult specimens are shown in Tables 2 and 3.

MATERIAL EXAMINED.—*Type Material:* The holotype (Figures 1–9) is an adult female (130 µm long) with well-developed seminal receptacles; it was collected by R.M. Kristensen and R.P. Higgins, 15 Sep 1981, from a shell-gravel substrate

TABLE 2.—Measurements (in µm) of adult females of *Styraconyx nanoqsunguak*

| Character | No. | Range | Mean | SD | CV | Holotype |
|---|---|---|---|---|---|---|
| Total length | 10 | 101–135 | 119.2 | 11.4 | 9.5 | 130 |
| Total width | 10 | 40–50 | 47.1 | 3.4 | 7.2 | 50 |
| Buccal canal | 8 | 13–15 | 14.6 | 0.7 | 5.1 | 15 |
| Pharynx bulb | 9 | 11–13 | 12.0 | 0.9 | 7.2 | 13 |
| Stylet | 8 | 15–16 | 15.5 | 0.5 | 3.5 | 16 |
| Stylet support | 8 | 5–6 | 5.3 | 0.5 | 8.8 | 5 |
| Median cirrus | 9 | 12–13 | 12.4 | 0.5 | 4.2 | 12 |
| Internal cirri | 10 | 14–16 | 15.5 | 0.7 | 4.6 | 16 |
| External cirri | 10 | 13–16 | 14.5 | 0.9 | 5.9 | 15 |
| Lateral cirri | 10 | 27–33 | 29.8 | 2.3 | 7.6 | 28 |
| Primary clavae | 10 | 9–10 | 9.9 | 0.3 | 3.2 | 10 |
| Secondary clavae | 10 | 12–14 | 12.5 | 1.1 | 8.6 | 11 |
| Cirri E | 10 | 30–37 | 33.0 | 2.8 | 8.6 | 29 |
| 4th leg sense organ | 10 | 12–15 | 13.6 | 0.8 | 6.2 | 14 |
| 4th leg papillae | 10 | 9–10 | 9.9 | 0.3 | 3.2 | 10 |
| 4th leg papillae spines | 10 | 3–5 | 3.7 | 0.7 | 18.2 | 4 |
| 3rd leg spines | 10 | 11–16 | 13.6 | 1.7 | 12.1 | 13 |
| 2nd leg spines | 10 | 10–13 | 11.7 | 1.2 | 9.9 | 11 |
| 1st leg spines | 10 | 9–11 | 9.9 | 0.9 | 8.8 | 9 |
| 1st external digits | 10 | 4–6 | 5.0 | 0.5 | 9.4 | 5 |
| 1st internal digits | 10 | 6–8 | 7.1 | 0.6 | 8.0 | 7 |
| 4th external digits | 10 | 7–9 | 8.2 | 0.8 | 9.6 | 9 |
| 4th internal digits | 10 | 10–14 | 12.2 | 1.3 | 10.8 | 14 |
| 4th peduncles | 10 | 4–6 | 5.3 | 0.7 | 12.7 | 6 |

near Kronprinsens Ejland, Disko Bay, West Greenland (69°00′N, 53°17′W), at 70 m depth.

The allotype (Figure 10) is an adult male (125 µm long); other data are the same as for the holotype.

Paratypes include 10 females, 10 males, and 4 juveniles from the type-locality; other data are the same as for the holotype. Additional paratypes, several hundred in number, were collected by R.M. Kristensen, 27 Jul 1982, from a shell-gravel substrate at Udkiggen, Godhavn, Disko Island, West Greenland (69°16′N, 53°35′W), depth 100–110 m.

The specimens from the type-locality were mounted in glycerin and sealed with Murrayite on microslides. The holotype, allotype, and 15 paratypes are deposited at the Zoological Museum, Copenhagen, Denmark. Five paratypes (USNM 81187-81191) are deposited in the invertebrate collection of the National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA. Four paratypes are deposited in the invertebrate collection of the Muséum National d'Histoire Naturelle (MNHN), Paris, France. The remaining paratypes, not used for SEM or TEM purposes, are stored in 4 percent buffered formalin and have been deposited at the Zoological Museum, Copenhagen, Denmark.

ETYMOLOGY.—The name of this species is from the Greenlandic *nanoq* (polar bear) plus *sunguak* (small), pronounced "nan-uk′ sung-wak" and is the Greenlandic name for a mythological animal that cannot be seen.

DISTRIBUTION.—The holotypic female (Figures 1–9) is 130 µm long and has a maximum width of 50 µm. The outer segmentation is indistinct and can be observed only in ventral aspect. Eighteen dorsal ridges begin immediately posterior to the head segment and extend posteriorly to a position slightly beyond the third pair of legs. The dorsal outer cuticle or epicuticle is thin between the ridges and the pillars are evident in

TABLE 3.—Measurements (in µm) of adult males of *Styraconyx nanoqsunguak*

| Character | No. | Range | Mean | SD | CV | Allotype |
|---|---|---|---|---|---|---|
| Total length | 10 | 80–125 | 102.7 | 13.2 | 12.9 | 125 |
| Total width | 10 | 25–40 | 37.5 | 5.0 | 13.4 | 40 |
| Buccal canal | 9 | 12–16 | 14.7 | 1.3 | 9.0 | 16 |
| Pharynx bulb | 10 | 9–11 | 10.4 | 0.9 | 8.4 | 11 |
| Stylet | 8 | 13–17 | 15.4 | 1.2 | 7.7 | 16 |
| Stylet support | 8 | 4–6 | 5.1 | 0.6 | 12.5 | 6 |
| Median cirrus | 10 | 10–14 | 11.7 | 1.5 | 12.8 | 14 |
| Internal cirri | 10 | 12–17 | 14.8 | 1.6 | 10.9 | 17 |
| External cirri | 10 | 10–15 | 12.5 | 1.5 | 12.1 | 15 |
| Lateral cirri | 10 | 21–32 | 27.5 | 2.7 | 9.9 | 32 |
| Primary clavae | 10 | 8–10 | 9.7 | 0.7 | 7.0 | 10 |
| Secondary clavae | 10 | 9–13 | 10.6 | 1.6 | 14.9 | 12 |
| Cirri E | 10 | 25–34 | 30.0 | 3.0 | 9.9 | 31 |
| 4th leg sense organ | 10 | 11–15 | 13.1 | 1.4 | 10.5 | 14 |
| 4th leg papillae | 10 | 8–11 | 9.3 | 1.1 | 11.4 | 10 |
| 4th leg papillae spines | 10 | 3–5 | 3.9 | 0.6 | 14.6 | 4 |
| 3rd leg spines | 10 | 9–13 | 11.5 | 1.2 | 10.3 | 13 |
| 2nd leg spines | 10 | 8–10 | 9.3 | 0.7 | 7.3 | 10 |
| 1st leg spines | 10 | 7–10 | 8.3 | 0.8 | 9.9 | 10 |
| 1st external digits | 9 | 4–7 | 5.6 | 0.9 | 15.9 | 6 |
| 1st internal digits | 9 | 6–9 | 7.7 | 0.9 | 11.3 | 8 |
| 4th external digits | 9 | 5–9 | 7.4 | 1.1 | 15.2 | 9 |
| 4th internal digits | 9 | 8–12 | 11.2 | 1.4 | 12.4 | 12 |
| 4th peduncles | 10 | 3–6 | 5.0 | 0.8 | 16.3 | 6 |

SEM preparations (Figure 18) because of the thin nature of the epicuticle. Each pillar has a large pore canal. The ventral cuticle (Figure 19) is typically halechiniscid with a thick outer, honeycomb layer. The pillars in this region are short and lack the supportive columns; the outer portion of each pillar consists of a round smooth structure well separated from the outer or honeycomb layer.

The buccal canal is narrow (1 μm) and short (15 μm). The stylets are very thin and only 16 μm long. A stylet sheath is present; the stylet supports are small (5 μm) but have a median apophysis for the attachment of a muscle. The mouth opening is subterminal on a distinct mouth cone. The mouth opening is surrounded by 10 sensory mouth papillae, each with a small pore. The pharyngeal bulb is relatively small, 13 μm in diameter, with three, thin placoids. A short esophagus leads to a 6-lobed midgut, the lobes are indistinct and do not continue laterally into the legs. The color of the intestine of living animals was rose to yellow. The anus is located posteriorly between the fourth pair of legs. Two lateral anal plates and a very small posterior anal plate are present.

A complete set of well-developed cephalic sense organs is present (Figure 1). The primary clava (10 μm) and lateral cirrus (28 μm) are inserted on a large pedestal (9 μm). The entire clava is free, without a surrounding membrane (extended margin of cirrophore). Van der Land's body (Figures 7, 49) is seen 1 μm distal from the pedestal base. This diffractive structure, named here, was discovered in *Florarctus* by van der Land (1968). The scapus of the lateral cirrus is 12 μm long and the flagellum (16 μm) is telescopically inserted in the scapus. The secondary clava (11 μm long) is sausage-shaped and surrounds the base of the external cirrus. The outer contour of the secondary clava cannot be seen in SEM, but it is evident under interference-phase-contrast optics as is the prominent innervation. The external cirrus (15 μm long) consists of a very robust scapus (8 μm long) and a 2-part flagellum as in *Florarctus* and *Halechiniscus* (cf. Renaud-Mornant, 1982a), and a large terminal pore (Figure 15, not from holotype) is present; only the external cirri have indistinct cirrophores. The internal cirri (16 μm long) and the single median cirrus (12 μm long) are positioned on the anterior margin of the head; each consists of three parts. The first leg spine (Figure 4) (7 μm long) has a scapus and flagellum as in all cirri. The second leg spine (Figure 5) (8 μm long) and third leg spine (12 μm long) are unsegmented and slightly curved. The sense organs of the fourth leg (Figure 9) have a complex structure; each consists of a papilla (10 μm long) and a spine (4 μm long). The spine has a flexible link to the papilla and a large terminal pore. The papilla is inserted on a bell-shaped structure (8 μm long), which may be homologous with the cirrophore. The base of the papilla is telescopically retractible into the cirrophore. The only somatic sense organ is cirrus E (Figure 8) (29 μm long). The scapus (1 μm long) is indicated by one or two rings.

The nervous system (Figure 1) consists of a very large, 3-lobed brain, a small subpharyngeal ganglion—both located in the head—and a large ventral ganglion in each of the four trunk segments. The brain has 10–12 pigment granules ("eyespots") on each lateral surface. Nerves from the 3-lobed brain innervate the cephalic sense organs. The large dorsal lobe (protocerebrum) innervates the primary clavae and lateral cirri, the smaller dorsal lobe (deuterocerebrum) innervates the internal cirri, the lateral lobe (tritocerebrum) innervates the secondary clavae and external cirri. The median cirrus is innervated by a small ganglion near the center of the brain. The subpharyngeal ganglion innervates the mouth papillae. A very large circumpharyngeal nerve, extending from the posterior part of the protocerebrum, connects the brain with the first trunk ganglion. Each trunk ganglion innervates the sense organs of the legs by way of a smaller sensory ganglion in each leg.

The reproductive system (Figure 1) of the holotypic female consists of two very large ova in a single ovary. Very few nurse cells are present between the two ova. Each ovum is surrounded by a very thin membrane. The gonopore system is similar to that found in all females of the

Halechiniscidae, consisting of six rosette cells, each with an S-shaped cuticular fold. The two seminal receptacles are complex (Figure 12). Two large genital papillae are present laterally; each has a small opening to the exterior. The genital duct within each papilla is straight but changes to a spiral configuration near the seminal receptacle. The seminal receptacle itself consists of a small vesicle surrounded by glandular epidermal cells.

Each leg consists of a coxa, femur, tibia, and tarsus of the styraconyxid type. The coxa bears the sense organs and the tarsus with four digits. The digits of the first three legs are short; the first internal digit is 5 μm long, the first external digit is 7 μm long. The digits of the fourth leg are long; the internal digits are 9 μm long and the external digits are 14 μm long. Only the reduced (6 μm long) external peduncles are present on the fourth digits. The internal digits have proximal pads. The claw has both a reduced accessory hook (= spine) and secondary hook. The accessory hook is situated on the large primary hook. The claw sheath is moderately well developed and the tip of the primary hook is free, even when the claw is retracted.

There are indications that well-developed gonads are found within at least two additional female instars whose maturity is further indicated by the presence of clearly defined rosette-shaped gonopores. An instar (101–125 μm long) smaller than that represented by the holotype was observed with medium-sized oocytes and very large lateral genital openings (Figure 16). A larger instar (122–135 μm long) had two large oocytes and a very large papilla. In this latter instar, the ducts to the seminal receptacle were coiled and the small receptacle itself was filled with sperm. In the smallest instar noted above, the duct to the receptacle was short, straight, and the receptacle empty.

Considering only the seminal receptacle, one might easily assume that two separate species were represented, especially since the larger instar showed some reduction in the alimentary system, i.e., the absence of the large apophysis on the buccal canal (Figures 1, 10, 11), the presence of thinner stylets and straight stylet supports. Observation of females in the process of molting indicated that the smaller female molts after copulation and grows to form the larger instar. Eggs mature in the larger instar, which we suspect may not feed during this part of the life cycle since nothing could be seen in the normally full gut. Once this female oviposits her two very large eggs (45 μm × 35 μm, about one-third the size of the entire animal), a molt cycle ensues, resulting in a smaller individual as in tardigrades that have molted after starvation or after encystment (Marcus, 1929). It seems reasonable to assume that the female can produce several broods of eggs; otherwise, the population would not continue to exist.

The allotype (Figure 10) is an adult male, 125 μm long and 50 μm wide. No secondary sexual dimorphism is present in *S. nanoqsunguak*, and the male is only slightly smaller than the female. The testes and two seminal vesicles are large and contain small, round-headed sperm. The male gonopore is located caudally, near the anus, and consists of a small oval structure with a crescent-shaped opening. Two small accessory openings are present.

The first instar, about 67 μm long, has only two digits each with 3-pointed claws on each leg; this is the so-called "2-clawed stage." These claws are the internal claws and each has a long, straight peduncle (6 μm); internal claw peduncles are absent in all subsequent instars.

The second instar, about 70–80 μm long, has four digits each with claws on each leg. Very small (3 μm) peduncles of the external digits are present and the external claws are simple, without accessory hooks or secondary hooks. The internal claw is 3-pointed. At least one more instar (85–87 μm long), the third, is present and perhaps a fourth instar exists before the gonopore opening is established. The third and fourth instars are similar to the adult but lack mature gonads.

REMARKS.—*Styraconyx nanoqsunguak* has a dorsal cuticle with sculpture similar to but not identical with that of *S. craticulus*. The ventral cuticle is a typical halechiniscid cuticle with a thick outer honeycomb layer, but the pillars are short and lack the supportive columns found in *Halechiniscus* (cf. Greven, 1975), *Batillipes* (cf. Kristensen, 1976) and *Echiniscus* (cf. Schuster et al., 1975). Pollock (1983, fig. 3D) has reported the same kind of pillar in *S. craticulus*. The sense organs of the new species are similar to those of *Bathyechiniscus tetronyx*, especially the long, lanceolate primary clavae and the sense organs of the fourth leg. However, we are convinced that these similarities are insignificant; the long, lanceolate primary clavae, in particular, is a plesiomorphic character found in *Raiarctus* as well. *Styraconyx nanoqsunguak* is a very aberrant member of the subfamily Styraconyxinae. The peduncles and the claw are the same kind as found in *Raiarctus* Renaud-Mornant, 1981; the buccal tube and apophyses of the two taxa are similar also. The two accessory openings of the male gonopore are similar to those of *Echiniscoides* (cf. Kristensen and Hallas, 1980). One very small male (80 μm long), found among the 20 males investigated, had simple external claws while the internal claws were normal. This same kind of male also has been noted in *S. qivitoq*, new species, and *Tholoarctus natans* Kristensen and Renaud-Mornant, 1983.

### Styraconyx paulae Robotti, 1971

*Styraconyx paulae* Robotti, 1971:1–3, fig. 1C,E,H,O,S [type-locality: Stromboli, Italy].—Ramazzotti, 1974:161–163, fig. 80C,E,H,L,O.—Pollock, 1976:14 [illustrated key].—Kristensen, 1977:90.—Pollock, 1979a:153.—Renaud-Mornant, 1981b:804; 1982a:169, fig. 7A.—Kristensen and Renaud-Mornant, 1983:338.

*Bathyechiniscus tetronyx*.—Pollock, 1983:111 [in part].

MATERIAL EXAMINED.—None.

EMENDED DIAGNOSIS.—*Styraconyx* with subterminal mouth. Pigmented "eyespots" present. Long spine-shaped primary clavae with small terminal vesicles. Common pedestal of the lateral cirri and primary clavae absent. Sense organs of fourth leg consist of ovoid papillae, each with long spine.

REMARKS.—This species appears closely related to *Styraconyx sargassi*, but the primary clavae (9 μm long) and lateral cirri (13 μm long) are shorter. Additionally, the shape of the primary clavae differ by being spinose with a terminal vesicle. There is no common pedestal or cirrophore present. The 3-pointed claw is similar to that of *S. sargassi* but Robotti (1971) did not illustrate a peduncle. The papilla of each fourth leg (12 μm long) is club-shaped with a long spine, differing from those of other members of the *S. sargassi* group. Renaud-Mornant (1981b, 1982a) recently demonstrated that the morphology of the primary clavae (length and shape) is an important taxonomic character in nearly all marine tardigrades, especially in a polytypic genus such as *Styraconyx*. Despite the fact that *S. paulae* is based on a single specimen, we choose to recognize it as a sibling species of *S. sargassi*. *Styraconyx paulae* was found epizoic on the coral *Coenocyathus dohrni* at 2 m depth at (25) Stromboli, Italy (Table 1, Map 1). The gut contained what appeared to be green chlorophyll-like matter suggesting that the tardigrade did not feed on the coral itself, but on the unicellular algae on the coral.

### Styraconyx qivitoq, new species

FIGURES 22–44, 50

DIAGNOSIS.—*Styraconyx* with a terminal mouth opening (Figures 30, 40), no papillae. When extruded, stylets cross one another (Figure 41). Pigmented "eyespots" not present. Ovoid primary clavae and lateral cirri (Figures 37, 41, 50A) situated on small common pedestal in female or inserted directly on head in male (Figure 29). Cephalic cirri consist of two parts (Figures 33, 34). External digits (Figures 23, 50B) with a spoon-shaped peduncle (Figures 43, 50D). Three-pointed claw (Figure 50E) with a very thin accessory spine (= very thin hook) and secondary hook. Claw can be totally retracted inside the claw sheath (Figure 43). Sense organs of fourth leg (Figure 50C) consist of ovoid papillae with spines. Epicuticle separated from pillar layer (Figures 26, 29). Three to four telescopic folds present in cuticle. Female rosette-shaped gonopore with extra membrane. Genital duct (Figure 38) of seminal receptacle spiral (Figure 24), opening on each side of anus. Segmental glands present in head (Figure 30) and trunk in both sexes (Figures 26, 29).

Morphometric data for adult specimens are shown in Tables 4 and 5.

MATERIAL EXAMINED.—*Type Material:* The holotype is an adult female (172 μm long) with well-developed seminal receptacles; it was collected by R.M. Kristensen and R.P. Higgins 15 Sep 1981 from a bryozoan colony near Kronprinsens Ejland, Disko Bay, West Greenland (69°00′N, 53°17′W); depth 70 m.

The allotype is an adult male (115 μm long); other data are the same as for the holotype.

Paratypes include 24 females, 5 males, and one larval stage from the type-locality; other data are the same as for the holotype. Several hundred additional paratypes are collected by R.M. Kristensen, 27 Jul 1982, from a shell-gravel substrate at Udkiggen, Godhavn, Disko Island, West Greenland (69°16′N, 53°35′W), depth 90 m.

The specimens from the type-locality (23) (Table 1, Map 1) were mounted in glycerin on microslides and sealed with Murrayite. The holotype, allotype, and 10 paratypes are deposited in the Zoological Museum, Copenhagen, Denmark. Ten paratypes (USNM 81192-81196) are deposited in the invertebrate collection of the National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA. Four paratypes are deposited in the invertebrate collection of the Muséum National d'Histoire Naturelle (MNHN), Paris, France. The remaining paratypes, not used for SEM or TEM purposes, are stored in 4 percent buffered formalin and have been deposited at the Zoological Museum, Copenhagen, Denmark.

ETYMOLOGY.—The name of this species refers to the Greenlandic name for the ghost of a banished member of a village and is pronounced

TABLE 4.—Measurements (in μm) of adult females of *Styraconyx qivitoq*

| Character | No. | Range | Mean | SD | CV | Holotype |
|---|---|---|---|---|---|---|
| Total length | 25 | 145-200 | 172.1 | 14.4 | 8.4 | 172 |
| Total width | 25 | 48-78 | 57.0 | 7.6 | 13.4 | 54 |
| Buccal canal | 20 | 21-25 | 23.5 | 1.6 | 6.7 | 25 |
| Pharynx bulb | 25 | 18-24 | 20.1 | 1.4 | 6.9 | 20 |
| Stylet | 20 | 23-30 | 26.3 | 1.7 | 6.5 | 28 |
| Stylet support | 20 | 8-11 | 9.0 | 0.9 | 10.2 | 11 |
| Median cirrus | 25 | 4-7 | 5.6 | 0.7 | 12.8 | 6 |
| Internal cirri | 24 | 9-12 | 10.3 | 10.0 | 9.3 | 12 |
| External cirri | 24 | 12-15 | 12.7 | 0.9 | 6.8 | 13 |
| Lateral cirri | 25 | 21-29 | 25.0 | 1.8 | 7.1 | 25 |
| Primary clavae | 25 | 8-10 | 9.2 | 0.8 | 8.3 | 9 |
| Secondary clavae | 25 | 10-15 | 12.3 | 1.2 | 9.9 | 12 |
| Cirri E | 22 | 40-55 | 45.7 | 4.5 | 9.9 | 43 |
| 4th leg sense organ | 24 | 8-12 | 9.2 | 1.1 | 11.5 | 9 |
| 4th leg papillae | 24 | 6-8 | 6.3 | 1.5 | 24.1 | 6 |
| 4th leg papillae spines | 24 | 2-4 | 2.7 | 0.6 | 23.9 | 3 |
| 3rd leg spines | 22 | 13-18 | 15.0 | 1.6 | 10.8 | 16 |
| 2nd leg spines | 22 | 10-15 | 12.6 | 1.3 | 10.3 | 14 |
| 1st leg spines | 22 | 8-12 | 9.6 | 1.1 | 11.8 | 11 |
| 1st external digits | 25 | 7-10 | 8.4 | 0.9 | 10.3 | 8 |
| 1st internal digits | 25 | 10-13 | 11.7 | 0.9 | 7.7 | 11 |
| 4th external digits | 25 | 8-13 | 11.2 | 1.2 | 11.0 | 12 |
| 4th internal digits | 25 | 13-18 | 16.1 | 1.4 | 8.6 | 16 |
| 4th peduncles | 25 | 7-10 | 8.3 | 0.7 | 8.3 | 9 |

TABLE 5.—Measurements (in μm) of adult males of *Styraconyx qivitoq*

| Character | No. | Range | Mean | SD | CV | Allotype |
|---|---|---|---|---|---|---|
| Total length | 6 | 95–120 | 106.8 | 9.8 | 9.2 | 115 |
| Total width | 6 | 22–35 | 28.7 | 5.3 | 18.4 | 28 |
| Buccal canal | 6 | 16–21 | 18.8 | 2.2 | 11.8 | 20 |
| Pharynx bulb | 6 | 13–15 | 13.7 | 0.8 | 6.0 | 13 |
| Stylet | 5 | 21–27 | 23.6 | 2.7 | 11.5 | 27 |
| Stylet support | 5 | 6–8 | 6.8 | 0.8 | 12.3 | 8 |
| Median cirrus | 5 | 4–5 | 4.2 | 0.5 | 10.7 | 4 |
| Internal cirri | 5 | 7–8 | 7.4 | 0.6 | 7.4 | 8 |
| External cirri | 5 | 10–12 | 11.2 | 0.8 | 7.5 | 12 |
| Lateral cirri | 6 | 15–20 | 17.2 | 1.9 | 11.3 | 17 |
| Primary clavae | 6 | 7–8 | 7.7 | 0.5 | 6.7 | 8 |
| Secondary clavae | 6 | 9–12 | 10.8 | 1.3 | 12.3 | 12 |
| Cirri E | 5 | 27–37 | 30.8 | 4.0 | 12.9 | 32 |
| 4th leg sense organ | 6 | 7–8 | 7.7 | 0.5 | 6.7 | 8 |
| 4th leg papillae | 6 | 5–6 | 5.5 | 0.6 | 10.0 | 6 |
| 4th leg papillae spines | 6 | 2–3 | 2.2 | 0.4 | 18.8 | 2 |
| 3rd leg spines | 5 | 8–10 | 9.0 | 1.0 | 11.1 | 10 |
| 2nd leg spines | 5 | 6–9 | 7.6 | 1.1 | 15.0 | 9 |
| 1st leg spines | 5 | 6–7 | 6.4 | 0.6 | 8.6 | 7 |
| 1st external digits | 6 | 5–7 | 5.8 | 0.8 | 12.9 | 6 |
| 1st internal digits | 6 | 7–9 | 8.0 | 0.9 | 11.2 | 8 |
| 4th external digits | 6 | 6–10 | 7.8 | 1.6 | 20.5 | 8 |
| 4th internal digits | 6 | 10–13 | 12.0 | 1.6 | 12.9 | 13 |
| 4th peduncles | 6 | 5–7 | 6.2 | 0.8 | 12.2 | 6 |

"krevi′ dok"; a ghostly appearance is suggested by the double cuticle of this species.

DESCRIPTION.—The holotypic female (Figures 26–28, 31–37) is 172 μm long and has a maximum width of 54 μm. Both the ventral and dorsal epicuticles are very thin and lack any connection with the pillar layer. The outer epicuticle of fixed specimens has three to four large folds. Two large cuticular head pores (Figure 42, not from holotype) are situated on either side of the median cirrus.

The buccal canal (Figure 26) is broad (4 μm) and long (25 μm). The stylets are very large (28 μm long). The stylets cross slightly before they protrude from the terminal mouth opening. Large stylet sheaths and supports are present. The mouth opening can be telescopically retracted within the head. The pharyngeal bulb is large, about 20 μm in diameter, and has three distinct placoids. A short esophagus leads to the midgut, which contains a white, amorphous substance, perhaps from the bryozoan host. The anus is situated posteriorly so that part of it is visible from the dorsal aspect. The two lateral anal plates are large and the terminal plate very small. The anal opening (Figure 44) is closed with an undulant cuticular fold (Figures 25, 38).

A complete set of cephalic sense organs (Figures 26) is present but the median cirrus (Figure 31) is reduced (6 μm long). The primary clava (Figure 37) (9 μm long) and the lateral cirrus (25 μm long) are inserted together on a small pedestal (4 μm); both the primary clava and lateral cirrus are surrounded basally by the thin membrane of the cirrophore. Van der Land's body is found on the same level as the cirrophore. The scapus of the lateral cirrus is 11 μm long. The long (14 μm) flagellum is not telescopically inserted in the scapus. The secondary clava (Figure 32) (12 μm long) is a large, dome-shaped structure easily overlooked unless phase optics are employed. The external cirrus (Figure 34) (13 μm) has a cirrophore (4 μm) and a very robust scapus (9 μm) with a smaller flagellum (5 μm). The internal cirrus (Figure 33) (12 μm) lacks a cirrophore and has a short scapus (5 μm) and robust flagellum (7 μm). All cirri have a large terminal pore. The first leg spine (Figure 35) (11 μm) has a scapus and flagellum; the second leg spine (14 μm) is slightly curved; the third leg spine (Figure 36) (16 μm long) has a spiral scapus. Each sense organ of the fourth leg (Figure 28) has a clavoid papilla (6 μm long) and a small spine. Each cirrus E (Figure 27) is long (32 μm) and has a bell-shaped cirrophore (10 μm), a spiral scapus (5 μm), and a long flagellum (17 μm), which is thread-like distally. The cirrophore is retracted within the specimen and was not measured.

The nervous system (Figure 26) consists of the same elements as described for *Styraconyx nanoqsunguak*, but the protocerebrum is much larger. The innervation is also the same. *Styraconyx qivitoq* has four pairs of segmental glands; one pair is situated dorsally in the head, three additional pairs of glands are in the trunk. The trunk glands consist of a ventral cell and a dorsal cell. They are strongly osmiophilic with ducts opening on the coxae of the first three legs.

The digits of the first three pairs of legs are short. The internal digits of the first legs are 6 μm long and the external digits are 8 μm long. The digits of the fourth leg are long; the internal digits are 13 μm long and the external digits are 8 μm long. The external peduncles are spoon-shaped, very large (9 μm long), and attached to the base of the claw; the claw has both reduced accessory and secondary hooks. The claw sheath is very large and covers all of the hooks of the claw.

Other females (Figures 30, 39), regardless of size, were very similar. The smallest female was 145 μm long; the largest female, 220 μm long, is the largest recorded for this genus.

The allotype (Figure 29) is an adult male 125 μm long and 28 μm wide, much smaller than the female. The considerable difference in size between the sexes is the only form of secondary sexual dimorphism noted. The primary clavae and lateral cirri have no pedestals. The secondary clavae, relative to body length, are much larger (12 μm) in the male than in the female. The testes are small and the sperm within the two lateral seminal vesicles have carrot-shaped heads.

Two variants were noted among the other males: one 98–120 μm long with 3-pointed claws on all digits, the other 92–98 μm long with simple claws on the external digits. The latter form is considered a dwarf male.

LARVAE AND JUVENILES.—The smallest 2-clawed larva, 93 μm long, was larger than the dwarf male. Both the first and second instar females are 2-clawed, followed by 4-clawed juvenile (115 μm long) with simple external claws and a fourth instar with 3-pointed claws, but lacking a gonopore. The fifth instar is an adult. The male can mature after the second instar (dwarf male) or after the fourth instar, which is more usual. The sense organ of the first leg of all juveniles and males is not segmented.

REMARKS.—*Styraconyx qivitoq* appears to feed on its bryozoan host in a manner similar to that of another parasitic Styraconyxinae, *Tetrakentron leptosynaptae*, which feeds on a holothurian host, *Leptosynapta galliennei*. This is indicated by the very large, extended stylets that can be extruded about one-third the length of the mouth and by the apparent contents of the gut. Both parasitic tardigrades have the aberrant double cuticle, but *Tetrakentron* lacks the pillar layer, which is well developed in *S. qivitoq*. Both species have dwarf males, but only *S. qivitoq* has external digits with simple claws; the latter condition is considered neotenic. We assume that these similarities are convergences, adaptations to parasitism. The species most closely related to *S. qivitoq* appears to be the herbivorous *S. hallasi*. Both have terminal mouth openings, spiraled genital tubes, and the same kinds of peduncles and claws.

### Styraconyx sargassi Thulin, 1942

FIGURE 45

*Styraconyx sargassi* Thulin, 1942:10 [type-locality: Azores Islands].—du Bois-Reymond Marcus, 1952:195, 196, pl. 4; 1960:52–54, figs. 23, 24.—Ramazzotti, 1962:484, 485, figs. 269, 270.—Schulz, 1963:4, 9.—Robotti, 1971:1–3, fig. 1B,D,G,I,N.—Ramazzotti, 1972:665, 666, figs. 8, 454, 455.—Sterrer, 1973:203, fig 2.—Ramazzotti, 1974:162, 163, fig.

80B,D,G,I,N.—van der Land, 1975:421, fig. 8.—Kristensen, 1977:87, 90.—Renaud-Mornant, 1979:273, 274; 1981b: 804–808; 1982a:169, fig. 7A.—Kristensen and Renaud-Mornant, 1983:338.

*Bathyechiniscus tetronyx.*—Marcus, 1936:23, 24, fig. 35 [Azores Islands].—Mathews, 1938:624, unnumbered fig.—Rodriguez-Roda, 1947:103, fig. 1, plate photo 1 ["East Coast of Spain" defined by Rodriguez-Roda in 1952 as Alicante, Barcelona, Mallorca, Spain].—Chitwood, 1951:111, fig. 1 [Texas, USA].—Rodriguez-Roda, 1952:48, 49, fig. 10, plate photo 2 [Spain].—Chitwood, 1954:325.—Pollock, 1983:111 [in part]. [Not *Bathyechiniscus tetronyx* Steiner, 1926.]

Not *Styraconyx sargassi.*—Renaud-Mornant, 1967:111, fig. 3 [= *Styraconyx kristenseni neocaledoniensis*]; 1971:960; 1976: 291, fig. 1 [= *Styraconyx kristenseni kristenseni*].—Pollock, 1976:15; 1979a:153 [= *Styraconyx kristenseni*].

Not *Styraconyx sargassi(?).*—Renaud-Mornant, 1982a:156, 169, fig. 7C [= *Styraconyx kristenseni kristenseni*].

MATERIAL EXAMINED.—*Type Material:* 4 paratypes from Marcus collection on two slides (USNM 81197, 1 specimen; USNM 81198, 3 specimens), col. P. Hummelick-Utrecht, 21 Dec 1930 from *Sargassum* near Azores.

EMENDED DIAGNOSIS.—*Styraconyx* with subterminal mouth cone. Pigmented "eyespots" not visible. Primary clavae (Figure 45A) long, with extended membrane of cirrophore leaving only terminal end free. Common pedestal for lateral cirri and primary clavae not visible. Large dome-shaped secondary clava present. Peduncle (Figure 45D) present on all digits (Figure 45B). Proximal pad of internal digits indistinct. Three-pointed claws (Figure 45E) with hooks, nearly equal size. Claw sheath not covering tip of claw hooks. Sense organs of fourth leg (Figure 45C) consist of symmetrical papillae with long spines. Cirrus E with cirrophore. Dorsal cuticle smooth.

REMARKS.—The only two records of *Styraconyx sargassi* that appear to be reliable are those represented by the type material from the Azores Islands and those of Mathews (1938) from the coast of California, USA (Table 1, Map 1). Although it is possible that Rodriguez-Roda's records (1947, 1952) of *Bathyechiniscus tetronyx* from the Mediterranean Sea could be *Styraconyx sargassi*, Chitwood's (1951) records of styraconyxines from the Gulf of Mexico surely are not based on members of this species. The transverse plates (ridges) noted by Chitwood could be the grid-like patterns Pollock (1983) described in *S. craticulus* or possibly the kind of ridges we have described in *S. nanoqsunguak*. The specimen Chitwood (1951, fig. 1) referred to as a young one does not belong to the same species as his adult specimen. The primary clavae are different and so is the position of the mouth opening.

Our study of the four specimens of Marcus (1936), which are the type specimens of *S. sargassi* Thulin (1942), and the same specimens referred to by du Bois-Reymond Marcus (1952, 1960), are the basis for the several observations that follow.

The long primary clavae (10–12.5 μm) are slightly S-shaped and surrounded by an extra membrane, which we assume is the extended portion of the cirrophore. The round distal part of each clava is free. Near the base of the primary clavae is van der Land's body. The lateral cirri and primary clavae have no common pedestal and the lateral cirri are directly inserted on the head near the base of the clavae. The lateral cirri are not segmented; only a very thin line indicates the separation between the scapus and flagellum. This same condition seems to be present in the other cephalic cirri; furthermore, the cirri are not divided by a median constriction as in *S. hallasi* Kristensen (1977).

The sense organs of the first three legs are long, thin, straight spines. That of each fourth leg (Figure 45C) consists of a symmetrical papilla with a relatively long spine. The 3-pointed claws (Figure 45E) have a very thin claw-sheath only at the base of the hooks. The hooks are nearly the same size although the accessory and secondary hooks can be larger than the primary hook. The claw is not crescent-shaped as in *Styraconyx kristenseni* and *S. craticulus*, but attached to the peduncle at nearly a right angle (Figure 45B) as indicated by du Bois-Reymond Marcus (1952). The posteriormost tip of the claw, attached to the peduncle, should not be interpreted as a fourth "point" as suggested by Pollock (1983). Chitwood's (1951, fig. 1) illustration of a crescent-shaped claw suggests that his animal was not *S. sargassi*. The claw has a very thin apodeme (Figure 45E) to which a thin cuticular fiber attaches; in turn, this fiber is joined to a muscle as indicated by Kristensen (1977). When the muscle retracts, the claw is moved forward, clear of the claw sheath. In Figures 45–50, we have shown the claw condition both when the muscle is relaxed hence the claw extended (Figure 45B), and contracted so that the claw is partially or entirely within the sheath (Figure 45E). The external peduncle is very thin and terminates nearly one-third the distance from the base of the digit where a relatively long, indistinct pad is situated. Cirrus E has a cirrophore one-fourth the distance from the base as indicated by Mathews (1938:624).

*Styraconyx sargassi* was found on drifting algae (*Sargassum*) in the region of the Azores Islands (43°4′N, 31°W). Mathews' specimens were found on *Dictyota* along the coast of California, USA. As we will discuss later (p. 24), *S. sargassi* may be restricted to an algal association and when reported from any other substrate, the accuracy of the identification should be carefully checked.

## Notes on Some Morphological Features

The terminology used in this publication follows some of the ideas used by van der Land (1975), Kristensen (1977), and Renaud-Mornant (1980). The segments of the legs are called the coxa, femur, tibia, and tarsus. The segments of the cirri are called the cirriphore, scapus, and flagellum. However, since the flagellum can consist of two parts, four segments may exist, as in the external cirri of *S. nanoqsunguak* (Figure 6). One of the segments, the cirrophore, can be missing as in the median cirrus and internal cirri of *S. nanoqsunguak* (Figures 2, 3), but the scapus can be reduced as in cirri E of the latter species (Figure 8). Occasionally, problems in interpretation occur when two different sense organs are mounted on a common pedestal (= socket, Pollock, 1983; Renaud-Mornant, 1981b) as in the primary clavae and the lateral cirri of four of the *Styraconyx* species. The pedestal, in some instances, cannot be separated from the cirrophore (Figure 7). In *S. qivitoq* (Figure 37) the cirrophore projects from a reduced pedestal. In species in which two sense organs arise separately as in *S. sargassi*, *S. paulae*, and *S. hallasi*, two independent enveloping membranes, extensions of the cirrophore, can be present (Figure 48A) or there may be a single such membrane, homologous to the cirrophore of the primary clavae (Figure 45A). The sense organs of the leg also can be segmented, the first spine, for example can have the same appearance as a cirrus (Figure 4). The sense organs of the fourth leg usually are clavoid, and using the same terminology employed for the cirri can be difficult (Figures 9, 28). The segment below van der Land's body surely is homologous with the cirrophore; the papilla is homologous with the scapus, and the spine is homologous with the flagellum.

The claw terminology used in this paper is the same as that of Kristensen (1977), Renaud-Mornant (1981b), and Pollock (1983). The middle hook is the primary hook, even if all three hooks are the same size (Figure 45B); this concept is based on ontogenetic information and our current concept of the evolutionary history of the group. This hook is the only one present on the external claws of juveniles and in the reduced internal and external claws of the adults of *Pleocola*. The accessory hook (as) (first hook, Figure 45B) can be reduced to only a spine-like structure in the *S. hallasi* group (Figures 48B and 50B); the secondary hook may also be reduced significantly; the essential trend of reduction leads to a single-hooked claw as in *Pleocola*.

The terms used to describe the nervous system also parallel those used for arthropods, as in the case of the legs and sense organs. A more comprehensive publication, under preparation by the senior author (Kristensen, in prep.), on the subject of the cerebrum and subpharyngeal ganglion, will provide details not appropriate for inclusion here. Regardless of their superficial appearance, there is no evidence that the 2 to 12 pigment granules found on the brain function as "eye-spots" as indicated by Robotti (1971) and by Kristensen (1977). On the contrary, these granulae appear to be homologous with the organs described by Grell (1937), which have been identified as photosynthetic products ("Stoffwechselprodukte") in the coelomocytes of *Actinarctus*.

Measurements of the different taxonomic characters, such as the sense organs, buccal apparatus, total length, and total width, normally are used in the species descriptions of the genus *Styraconyx* (Kristensen, 1977; Renaud-Mornant, 1981b; and Pollock, 1983). In Tables 2–5, morphometric data are given for the two new species *S. nanoqsunguak* and *S. qivitoq*. Twenty-four different characters were measured; data for females and males are separated and no juveniles are included. Despite this, it is surprising to find that the coefficient of variability often is relatively high in most. Such measurements appear even less useful in the morphometric comparison of six of the eight species of *Styraconyx* (Figures 45–50), e.g., the primary clavae have nearly the same length in five of the six species, even if the shape is totally different. The same is true in the case of the lateral cirri and fourth leg papillae. The numerical length of a morphological feature does not necessarily show the real variation in a character from one species to another; therefore, we have illustrated (Figures 45–50) the characters we consider of greatest taxonomic (and phylogenetic) value. The types of peduncles and claws, when linked with another character, such as the type of sense organs, often indicate a close relationship between two species (e.g., *S. hallasi* and *S. qivitoq*) despite the fact that morphometric data suggest significant differences. The use of internal structures, such as the presence of "eyespots," buccal apparatus, and especially the seminal receptacle, also has a much higher taxonomic value than morphometric data appear to have. Unfortunately, descriptions of internal structures have not been included in all prior descriptions of *Styraconyx* species.

## Distribution and Ecology

The genus *Styraconyx* is found from the Arctic to the tropics as indicated in Table 1 and Map 1. There are now 33 locality records for the genus, but we suspect that it is represented in all marine waters. Three species, *S. hallasi, S. nanoqsunguak,* and *S. qivitoq*, have been found only in Greenland. *Styraconyx haploceros* and *S. paulae* each have been collected only once in Europe, while *S. craticulus* and *S. kristenseni* appear to be common in subtropical and tropical marine environments. *Styraconyx sargassi*, which until recently (Sterrer, 1973) was considered to be a cosmopolitan species, may have a more restricted distribution; the record of this species on Madagascar should be confirmed. We suspect that *S. sargassi* may have a subtropical to temperate distribution.

The species of *Styraconyx* are very selective in their choice of substrate or microhabitat. Therefore, it is unlikely that the same species (*Bathyechiniscus tetronyx*) found in Antarctic mud, a common microhabitat of marine tardigrades, is the same as one (*S. sargassi*) found epiphytic on the alga *Sargassum* as reported by previous authors (Marcus, 1936; Pollock, 1983).

One species, *S. hallasi*, has been found, together with other relict marine invertebrates, only in radioactive warm springs on Disko Island, West Greenland (Kristensen, 1977). This species is associated with a blue-green alga that may be endemic to these springs. The springs have a 500–1000 times higher gamma radiation than the background, and high levels of double fluoride salts are present. Another member of the *S. hallasi* group, *S. qivitoq*, has been found feeding on bryozoan colonies in the Arctic. Recently, however, we have found an undescribed, closely related species off the coast of Florida, USA. *Styraconyx nanoqsunguak*, although collected with *S. qivitoq*, clearly was associated with the shell-gravel portion of the dredge haul. Other tardigrades found in the same shell-gravel along with *S. nanoqsunguak* include several undescribed species of *Batillipes* and *Tanarctus.*

*Styraconyx kristenseni* is a stenotopic species, until now found only in coralline sand, where it is very common. About 80 percent of the samples from the Coral Sea contained this species. *Styraconyx craticulus* occurs on intertidal algae, barnacles covered with algae, and coralline sand mixed with algae. This same microhabitat in the Coral Sea is shared with *Echiniscoides sigismundi polynesiensis* Renaud-Mornant, 1976, and *Archechiniscus marci.*

*Styraconyx paulae*, from the Mediterranean Sea, has been reported only once. It was present on a coral, but was feeding on unicellular algae living on the coral. Another species associated with algae is *S. sargassi*, as mentioned previously. Further studies are necessary before we can be certain that reports of this latter species living on other substrates are based upon accurate identifications.

*Styraconyx haploceros* may not be a marine species in the strict sense. It was collected one time only on lichens growing above the high tide level. Attempts by the senior author to re-collect this species from its type-locality, St. Malo (Thulin, 1942), were unsuccessful.

## Phylogenetic Relationships

As indicated by Renaud-Mornant (1981b), an evolutionary trend exists from Styraconyxinae with long sense organs to those with very short sense organs. In particular, the primary and secondary clavae have undergone reduction several times within the Arthrotardigrada. An example of this can be found in the closely related subfamily Tanarctinae. Here, the primary and secondary clavae may be present or absent (Renaud-Mornant, 1980). In *Styraconyx* the reduction of primary clava from a long, lanceolate structure on a pedestal to a small, indistinct dome, establishes an evolutionary trend in the sequence *S. paulae—sargassi—kristenseni—hallasi—haploceros*. Because of this, we contend that *Styraconyx haploceros* should not be separated from the other members of this genus as Pollock (1983) has done, although we agree with him that Thulin's definition was faulty. The Styraconyxinae may have a pedestal for both the lateral cirrus and the primary clavae (Renaud-Mornant, 1981b) or the pedestal may be absent.

Renaud-Mornant (1980, 1982b) has used leg, digit, and claw morphology to indicate the close relationship of *Tanarctus* to *Actinarctus* and *Ligiarctus* to *Florarctus*. In this paper we also have given these same features (Figures 45–50) greater emphasis than the morphology of the sense organs in the separation of *Styraconyx* from the other genera within the subfamily. However, in defining the species, we have used both sense organ and seminal receptacle morphology, insofar as such information is available.

The genus *Styraconyx* probably is paraphyletic, consisting of an ancestral group, the *S. sargassi* group (*S. sargassi, S. paulae, S. kristenseni*, and *S. craticulus*), and two different evolutionary lines, one which includes *S. nanoqsunguak*, a species closely related to members of *Raiarctus*, and the other embracing the *S. hallasi* group (*S. hallasi* and *S. qivitoq*), which is closely related to *Pleocola*. The type-species, *S. haploceros*, seems to have many apomorphic characters which, with the exception of the *S. sargassi*-like claws, are not shared with other species. Representatives of three undescribed species of *Styraconyx*, which were collected during the preparation of this paper, fit well within the generic concept we have proposed here. Two of these three species share certain characters with *S. qivitoq* and *S. nanoqsunguak*, whereas the third seems to link the latter with *S. craticulus*.

It is still possible to postulate that the genus *Pleocola* had a common origin with the *S. hallasi* group, and that the genus *Raiarctus* developed from *S. nanoqsunguak*. Along with the previously noted undescribed species of *Styraconyx*, we have collected two undescribed species of *Raiarctus*, both of which have the same kind of large genital papillae and seminal receptacles as found in *S. nanoqsunguak*. Furthermore, in *Raiarctus* the peduncles (Figure 49D), as well as a buccal tube with apophyses, are like those in *S. nanoqsunguak*, thereby complicating the problem of placing this latter species in a phylogenetic scheme (Figure 51). The reduction of claws in *S. nanoqsunguak* indicates that it is most closely related to *S. hallasi* and *S. qivitoq*. In other characters, such as the well-developed cirrophore of the fourth leg sense organs and the dorsal sculpture, alternatively it could be considered to be more closely related to *S. kristenseni* and *S. craticulus*.

Another evolutionary line is suggested by the sequence: *S. hallasi—S. qivitoq—Tholoarctus natans—Lepoarctus coniferus* (= *Pleocola conifera*)—*Pleocola*. The genus *Pleocola* and the closely related, deep-sea tardigrade *Lepoarctus coniferus* both have simple claws; but as noted earlier, the juveniles of *Styraconyx* also have simple claws on the external digits. There is almost a total reduction of the accessory and secondary hooks in *S. qivitoq* and a step further in this direction would result in a simple claw as found in *Pleocola*. The type of peduncle found in *Pleocola* is the same as that in *S. qivitoq*; however, in this latter species, the cuticle forms only three or four telescopic trunk folds whereas in *Tholoarctus natans* the outer epicuticle assumes the shape of a large bell, which helps maintain its suspension in the water column (Kristensen and Renaud-Mornant, 1983).

The evolutionary lines that we postulate for the genus *Styraconyx* are shown in Figure 51. The numbers on the various branches of the cladogram indicate the apomorphic characters for each branch beginning with "1," which represents the autapomorphic characters for *Styraconyx* relevant to other genera in the subfamily Styraconyxinae. In respect to the species that constitute the genus, however, this same number represents the greatest number of plesiomorphic characters. Other numbers (2–14) relate to the apomorphic characters for the different branches of the cladogram, the greatest number being the most apomorphic. The numbered character states are as follows:

1. Dome-shaped secondary clavae; cirri divided into two or three segments; 3-pointed claws; peduncles on all digits; subterminal mouth opening.
2. Large secondary clavae; other sense organs reduced; no seminal receptacles noted; two large pigmented "eyespots" present.
3. Hooks of 3-pointed claws nearly equal in size; claw membrane does not cover tip of claw hooks; external peduncle hook-shaped.
4. Primary clavae and lateral cirrus lacking common cirrophore; cuticle smooth; no seminal receptacles noted.
5. Primary clavae and lateral cirri with common base and common cirrophore; dorsal cuticle sculptured or with folds; seminal receptacles simple, with straight ducts.
6. Primary clavae with extra membrane (= cirrophore?), which leaves only the terminal ends free; no pigmented "eyespots" present.
7. Primary clavae spine-like with small round to ovoid structure at terminal ends; two pigmented "eyespots" present.
8. Primary clavae and nonsegmented lateral cirri bound together with a sheath (cirrophore?); dorsal cuticle with grid-like pattern.
9. Primary clavae short to ovoid, not bound together with the segmented lateral cirri; dorsal epicuticle with large folds near each pair of legs; internal peduncles reduced.
10. Peduncles on internal digits absent; accessory hooks of claw reduced; dwarf male present.
11. Primary clavae lanceolate and secondary clavae sausage-shaped; cirri with well-defined scapus and flagellum; dorsal cuticle with 21–23 folds; external openings of seminal receptacles on large lateral papillae; external peduncles reduced.
12. Primary clavae ovoid, seminal receptacles spiral-shaped; claws completely covered by claw membranes; spoon-shaped peduncles; mouth terminal.
13. One-third of each primary clava covered by sheath (cirrophore); secondary clavae reduced to indistinct dome; fourth leg spine papillae reduced; cuticle smooth.
14. Primary clavae not covered by sheath; secondary clavae with large ovoid structure; outer epicuticle separated from remaining cuticle.

It is our conclusion that the genus *Styraconyx* is relatively unspecialized and has, on several occasions, given rise to more highly specialized genera, such as *Raiarctus* with its long pillars and *Tholoarctus* with its bell-like cuticle. *Bathyechiniscus* is closely related to *Styraconyx*. Steiner's (1926, fig. 2) illustration of *B. tetronyx* might be interpreted as indicating a double cuticle as in *S. qivitoq*; otherwise, *Bathyechiniscus* has some distinctive apomorphic characters that include the claws and digits. The claws of the latter genus are 4-pointed and could have developed from the crescent-shaped 3-pointed claws as suggested by Pollock (1983). Internal digits of different lengths (i.e., when one of the two mesial digits of the four digit group is significantly smaller than the other) normally are not found in the subfamily Styraconyxinae, but they are characteristic of the subfamily Halechiniscinae. Similarly, Steiner (1926, fig. 3) suggests the existence of two additional characters of Halechinscinae: the transverse line posterior to the claw and the three additional transverse lines near the base of the digits, which result from the contraction of the claw and subsequent wrinkling of the cuticle. The presence of the peduncle in a digit (e.g., *Styraconyx*) provides rigidity and, therefore, such stress lines are not formed.

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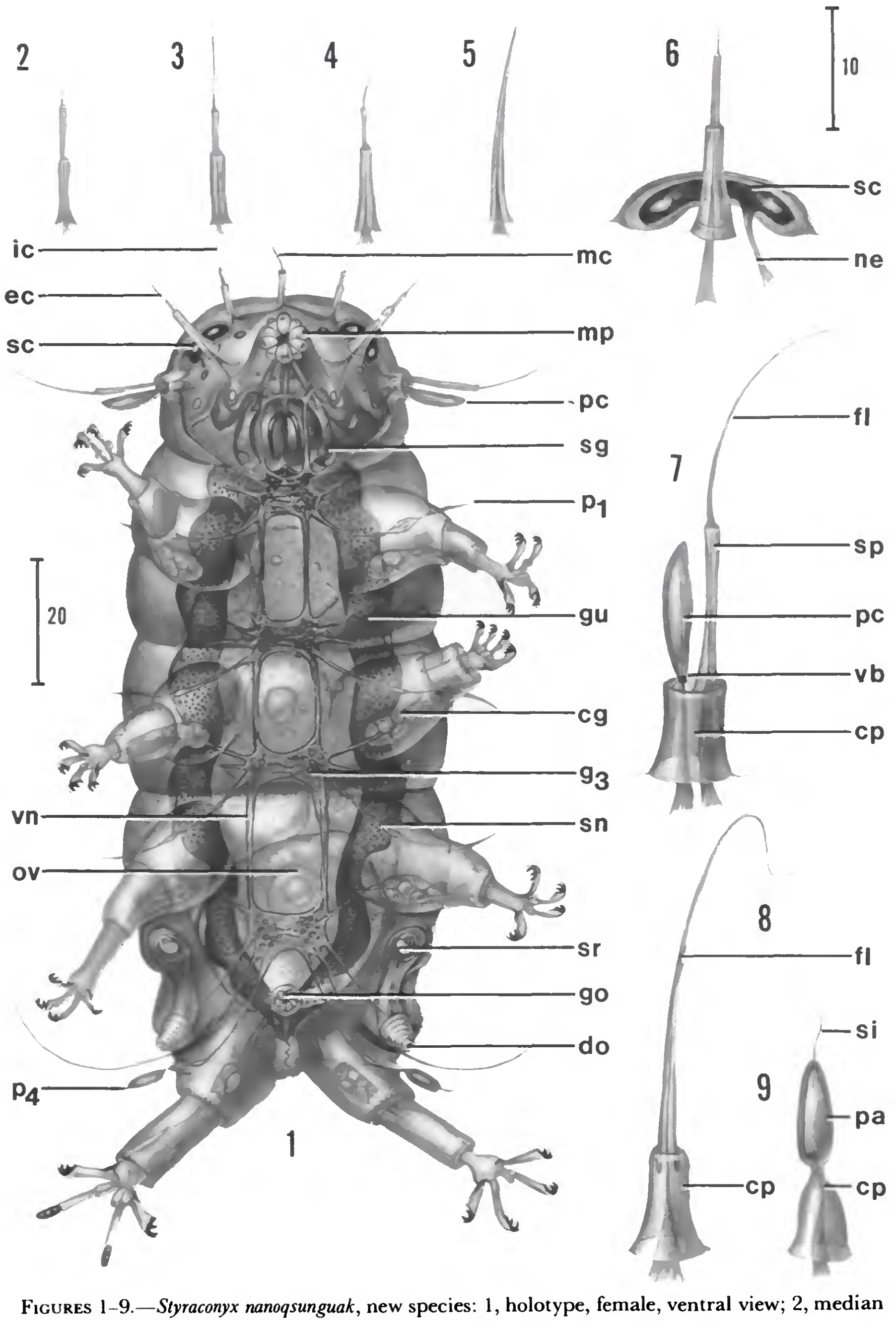
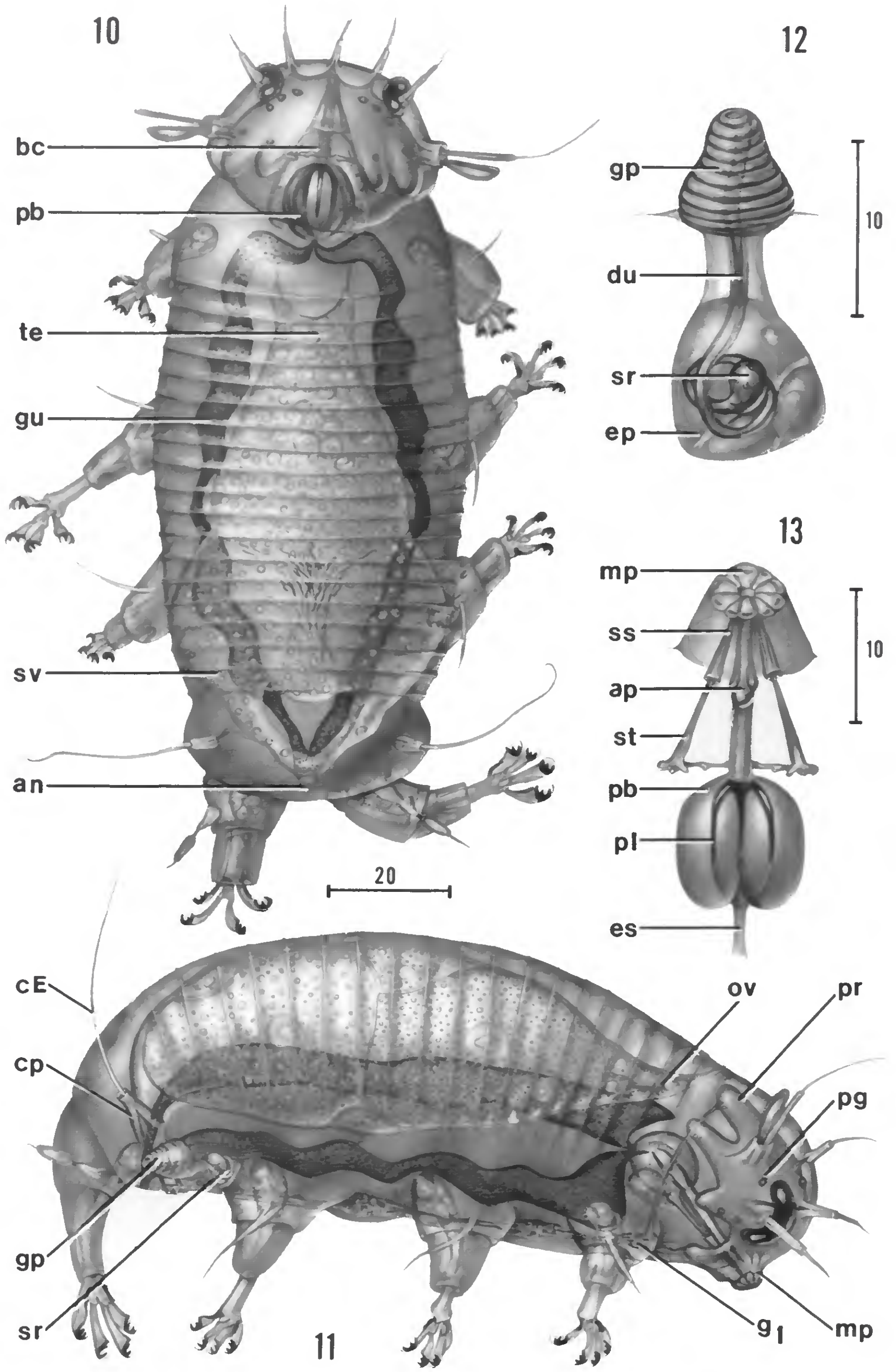
# Abbreviations

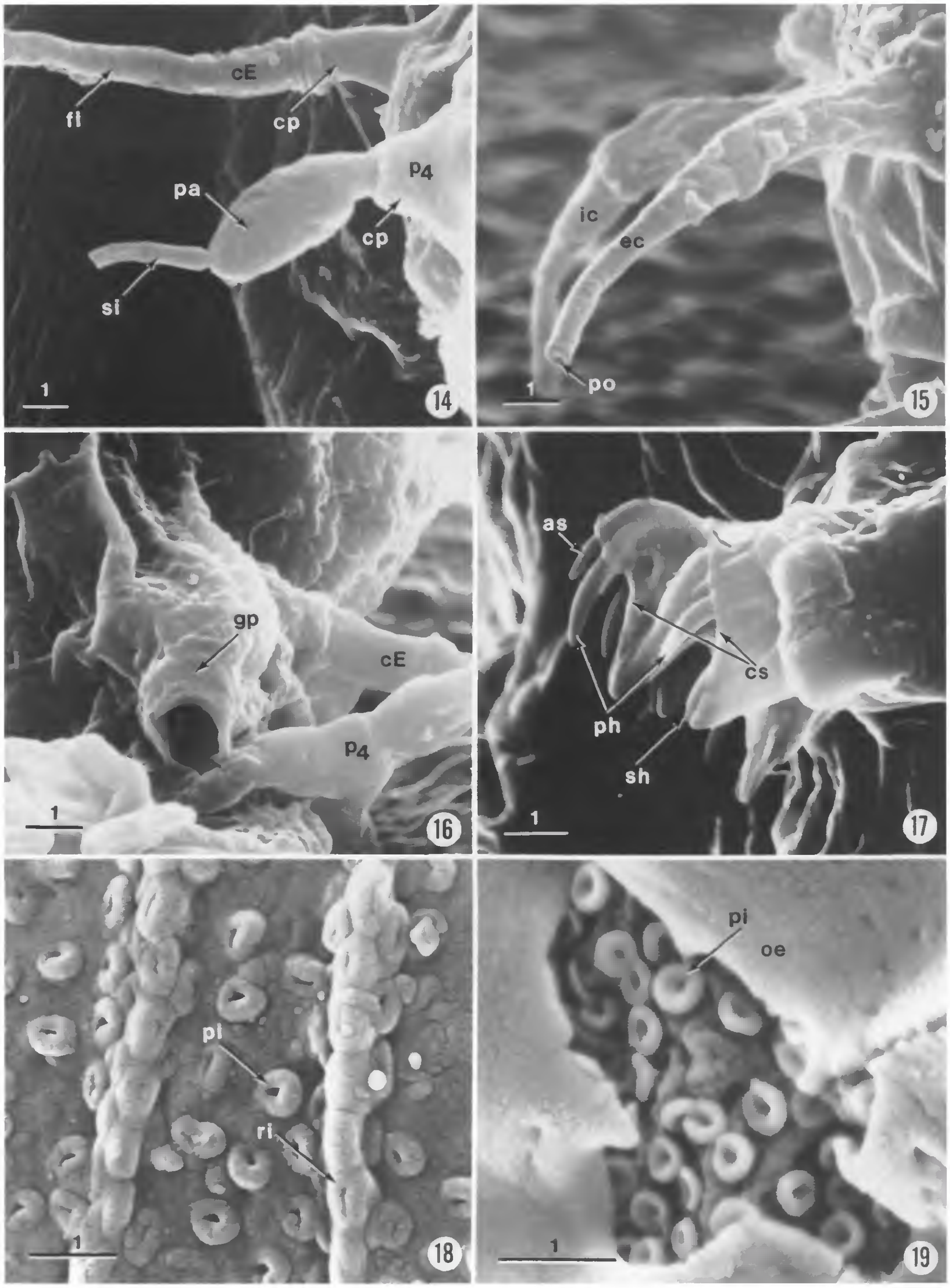
| | |
|---|---|
| an | anus |
| ap | apophysis on buccal canal |
| as | accessory hook of claw |
| bc | buccal canal |
| ca | claw apodeme |
| cc | coelomocyte |
| cE | cirrus E |
| cg | claw gland |
| cn | circumpharyngeal nerve |
| co | coxa |
| cp | cirrophore |
| cs | claw sheath |
| de | deuterocerebrum |
| do | opening of genital duct |
| du | genital duct |
| ec | external cirrus |
| ed | external digit |
| ep | epidermal cell |
| es | esophagus |
| fe | femur |
| fl | flagellum |
| $g_{1-4}$ | ventral ganglia |
| gm | gonopore membrane |
| go | gonopore |
| gp | genital papilla |
| gu | gut |
| hg | head gland |
| hp | head pore |
| ic | internal cirrus |
| id | internal digit |
| ie | inner cuticle |
| lc | lateral cirrus |
| mc | median cirrus |
| mp | mouth papilla |
| ne | nerve to secondary clava |
| oe | outer cuticle |
| ov | ovum |
| $p_{1-4}$ | sense organs of legs |
| pa | papilla of 4th leg sense organ |
| pb | pharyngeal bulb |
| pc | primary clava |
| $pe_{1-4}$ | peduncles |
| pg | pigment granule |
| ph | primary hook |
| pi | pillar in epicuticle |
| pl | placoid |
| po | pore on external cirrus |
| pp | proximal pad on digit |
| pr | protocerebrum |
| ri | ridge of dorsal epicuticle |
| sc | secondary clava |
| se | sensillum |
| sg | stylet gland |
| sh | secondary hook |
| si | spine of 4th leg papilla |
| sn | sensory nerve |
| so | subpharyngeal ganglion |
| sp | scapus |
| sr | seminal receptacle |
| ss | stylet sheath |
| st | stylet |
| su | stylet support |
| sv | seminal vesicle |
| te | testis |
| tg | trunk gland |
| th | thread-like portion of flagellum |
| ti | tibia |
| tr | tritocerebrum |
| vb | van der Land's body |
| vn | ventral nerve |



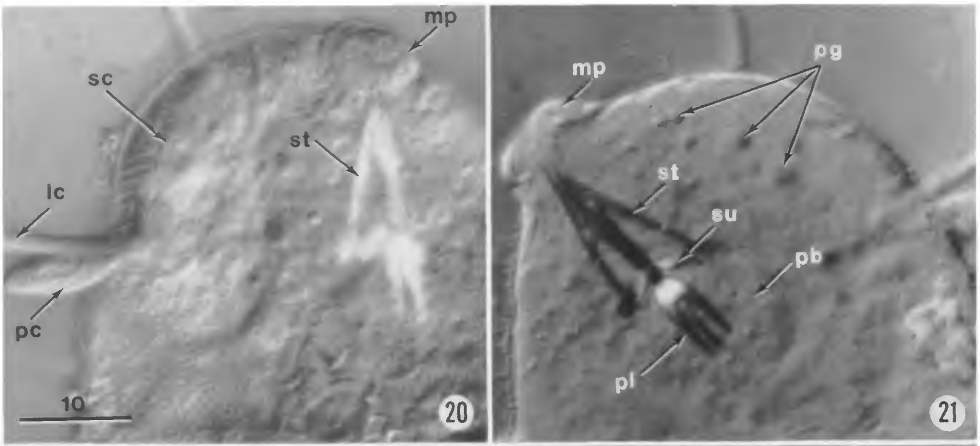
Figures 1–9.—*Styraconyx nanoqsunguak*, new species: 1, holotype, female, ventral view; 2, median cirrus; 3, internal cirrus; 4, first leg spine; 5, third leg spine; 6, external cirrus and secondary clava; 7, lateral cirrus and primary clava; 8, cirrus E; 9, fourth leg papilla. (Scales in µm.)

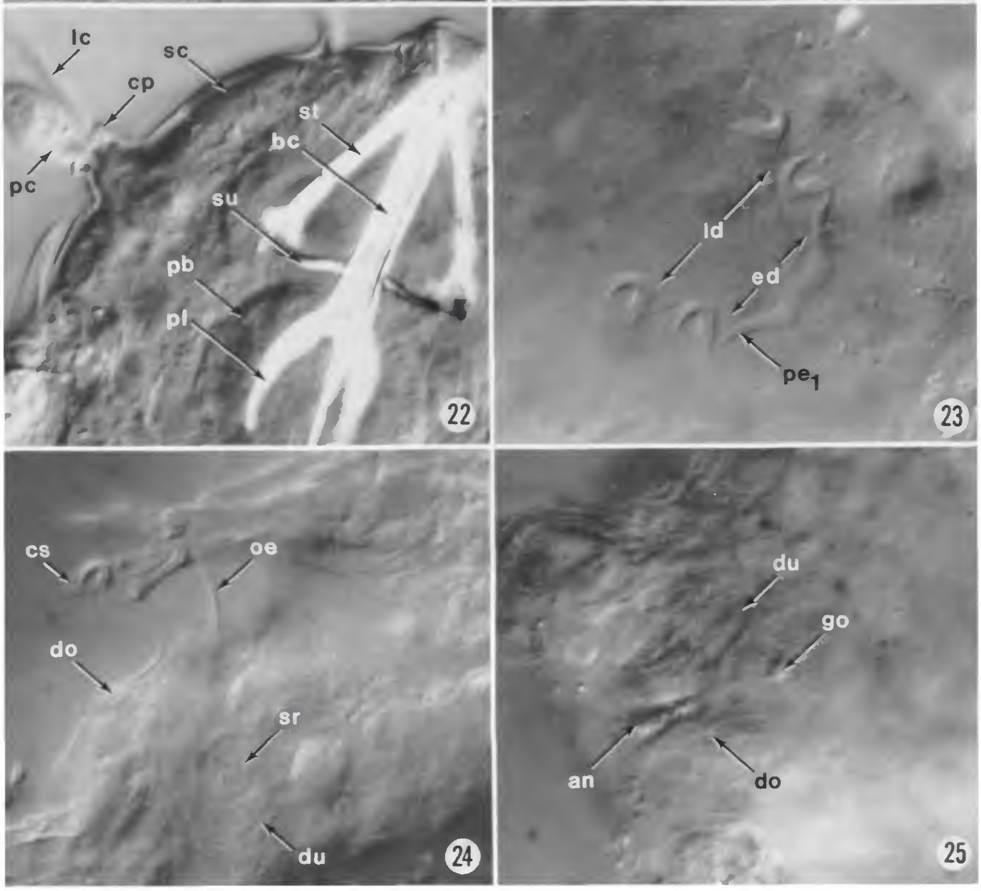


FIGURES 10–13.—*Styraconyx nanoqsunguak*, new species: 10, allotypic male, dorsal view; 11, paratypic female, lateral view; 12, seminal receptacle with genital papilla; 13, mouth cone and pharyngeal apparatus of a paratypic juvenile. (Scales in μm.)



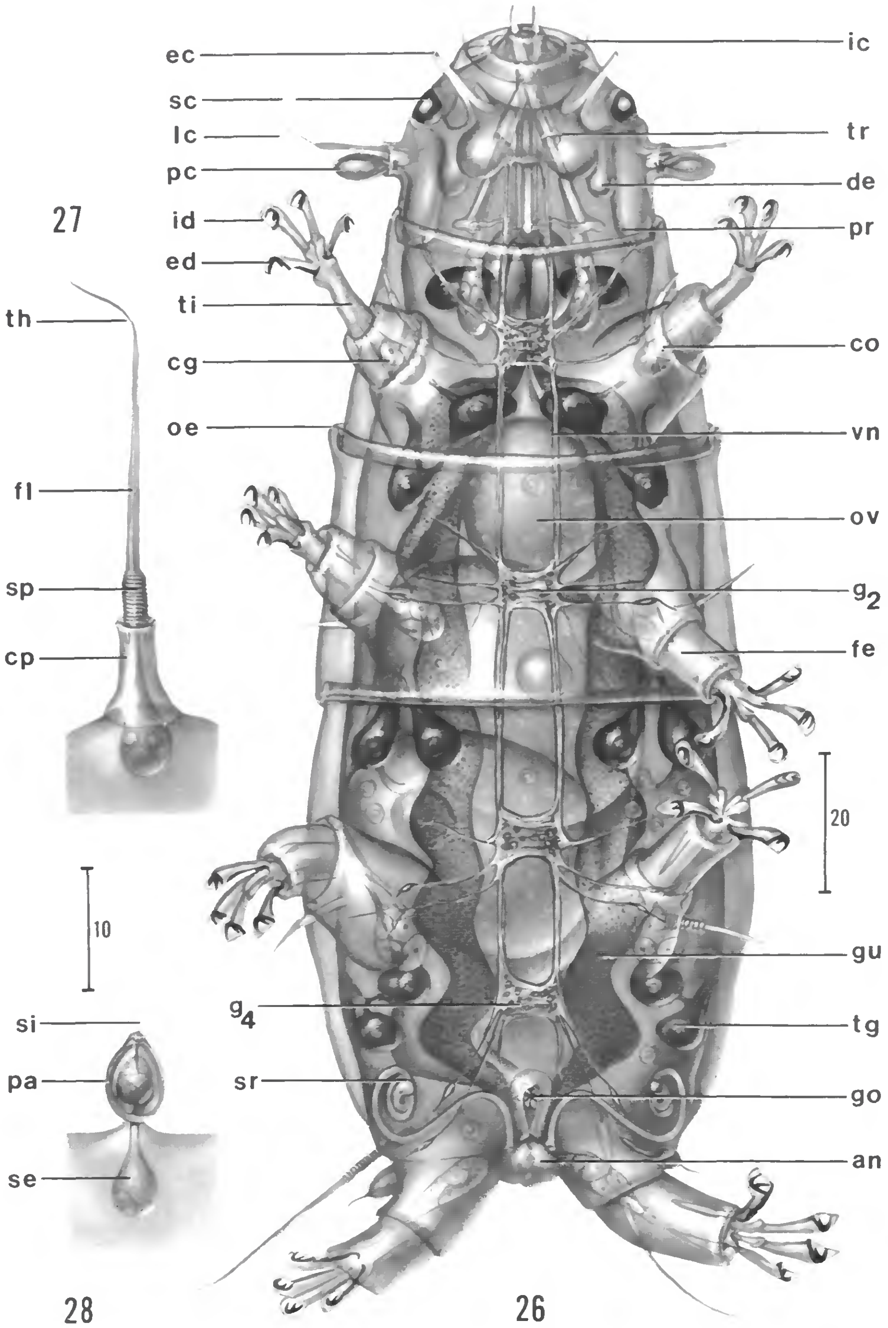
FIGURES 14–19.—*Styraconyx nanoqsunguak*, new species: 14, fourth leg papilla and cirrus E; 15, external cirrus (showing terminal pore) and internal cirrus (background); 16, opening to seminal receptacle in a young female paratype; 17, claws of second leg (note claw sheath); 18, dorsal cuticle showing two ridges of the epicuticle (the thin honeycomb layer reveals the outline of the underlying pillars); 19, ventral cuticle at a ruptured area showing the honeycomb layer and pillars. (SEM photographs; scales in μm.)



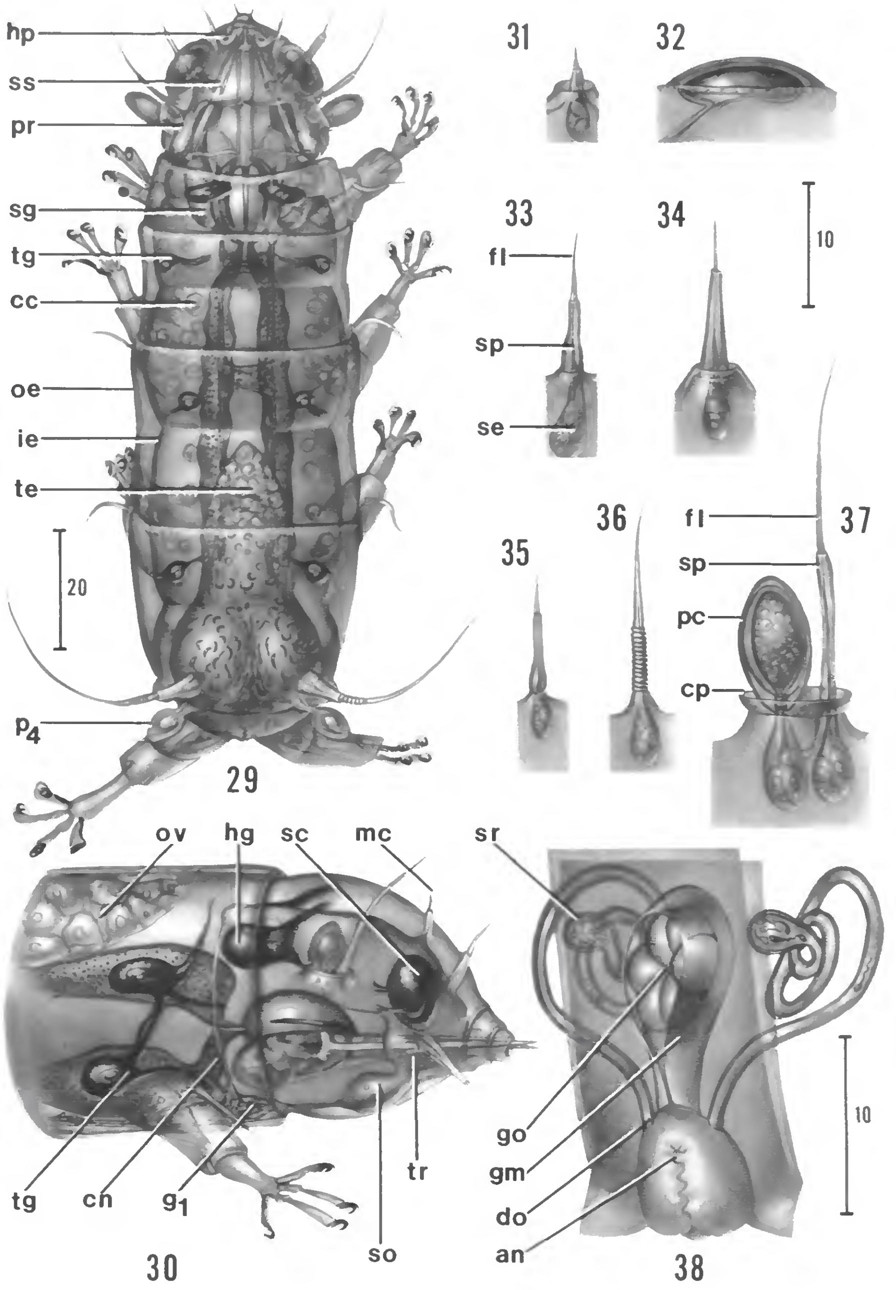


FIGURES 20–21.—*Styraconyx nanoqsunguak*, new species; 20, left side of head, dorsal view (note punctiform epicuticle resulting from underlying pillars); 21, lateral view, different specimen.

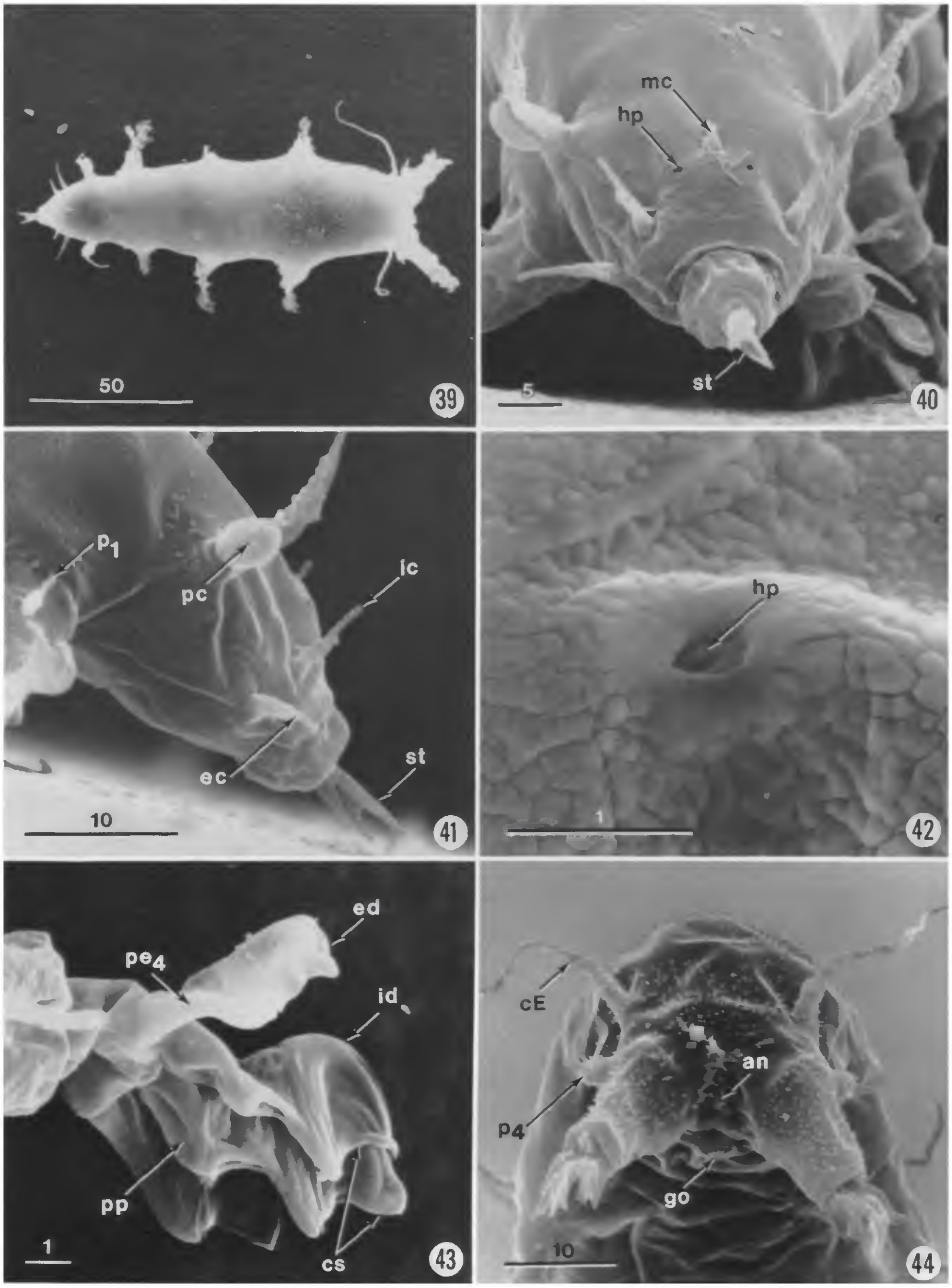
FIGURES 22–25.—*Styraconyx qivitoq*, new species: 22, head, ventral view; 23, claws of second leg; 24, area posterior to third leg showing duct of seminal receptacle; 25, area between fourth legs, ventral view showing female gonopore, seminal receptacle ducts and anus. (Interference contrast photographs with same scale, in μm, as shown in Figure 20.)



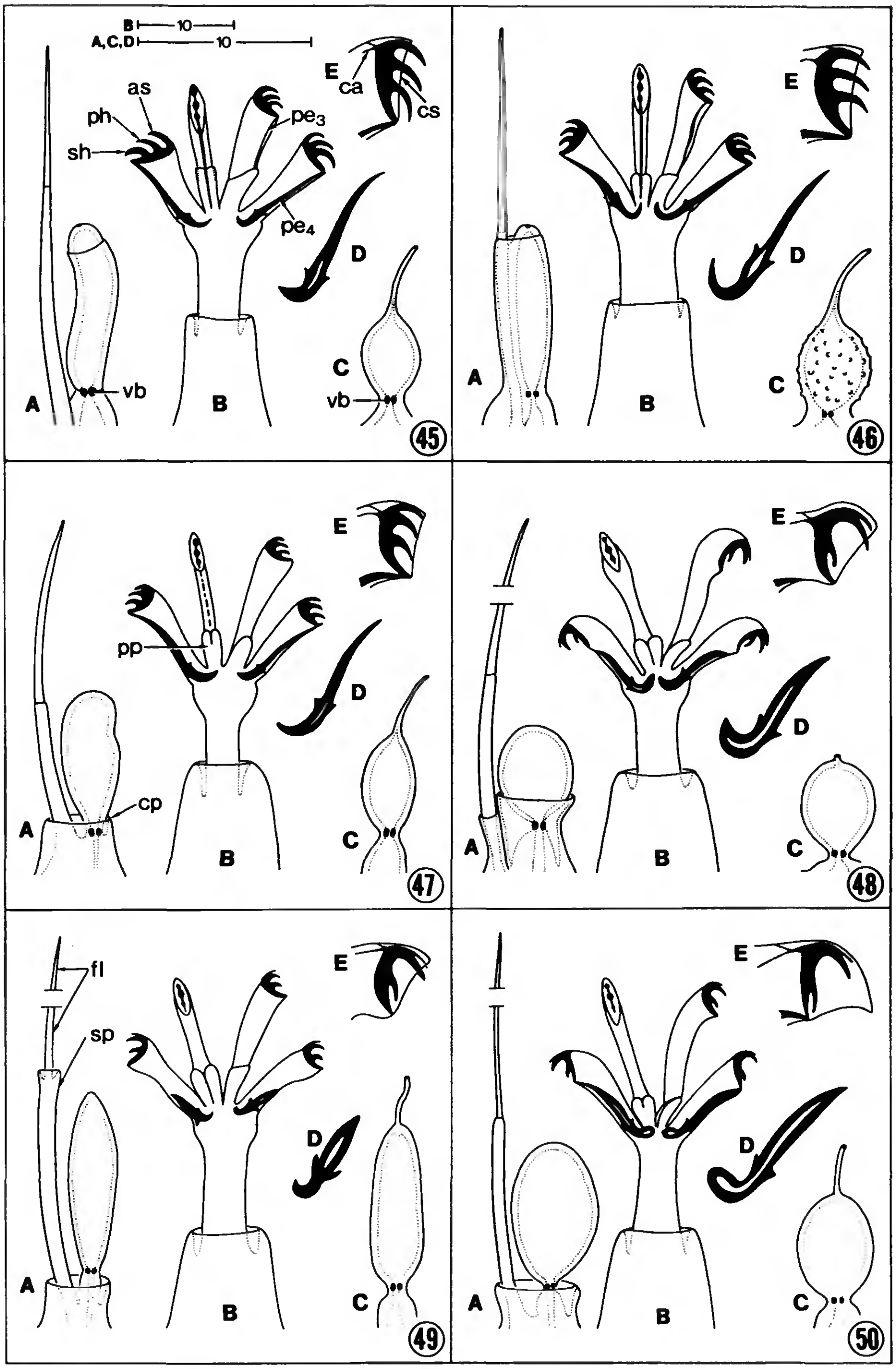
FIGURES 26–28.—*Styraconyx qivitoq*, new species, holotype female, 26, ventral view; 27, cirrus E; 28, fourth leg papilla. (Scales in μm.)



FIGURES 29-38.—*Styraconyx qivitoq*, new species: 29, allotypic male, dorsal view; 30, paratypic juvenile, head and first trunk segment. Holotype, female: 31, median cirrus; 32, secondary clava; 33, internal cirrus; 34, external cirrus; 35, first leg spine; 36, third leg spine; 37, lateral cirrus and lateral claws. 38, Female gonopore, associated ducts, seminal receptacle and anus; note the double cuticle. (Scales in μm.)



FIGURES 39–44.—*Styraconyx qivitoq*, new species, female: 39, dorsal view; 40, frontal view showing protruded stylets; 41, head, lateral view; 42, head pore; 43, first leg claws (covered by sheath); 44, caudal view of trunk. (SEM photographs; scales in μm.)



FIGURES 45–50.—Systematic characters of *Styraconyx*: 45, *S. sargassi* (Azores Islands); 46, *S. craticulus* (Moreton Bay); 47, *S. kristenseni* (Chesterfield Reefs); 48, *S. hallasi* (Disko Island); 49, *S. nanoqsunguak*, new species (Disko Bay); 50, *S. qivitoq*, new species (Disko Bay) (A, lateral cirrus and primary clava; B, fourth leg (claws extended); C, fourth leg papilla; D, peduncle of external digit; E, external claw retracted into sheath; scales in μm.)

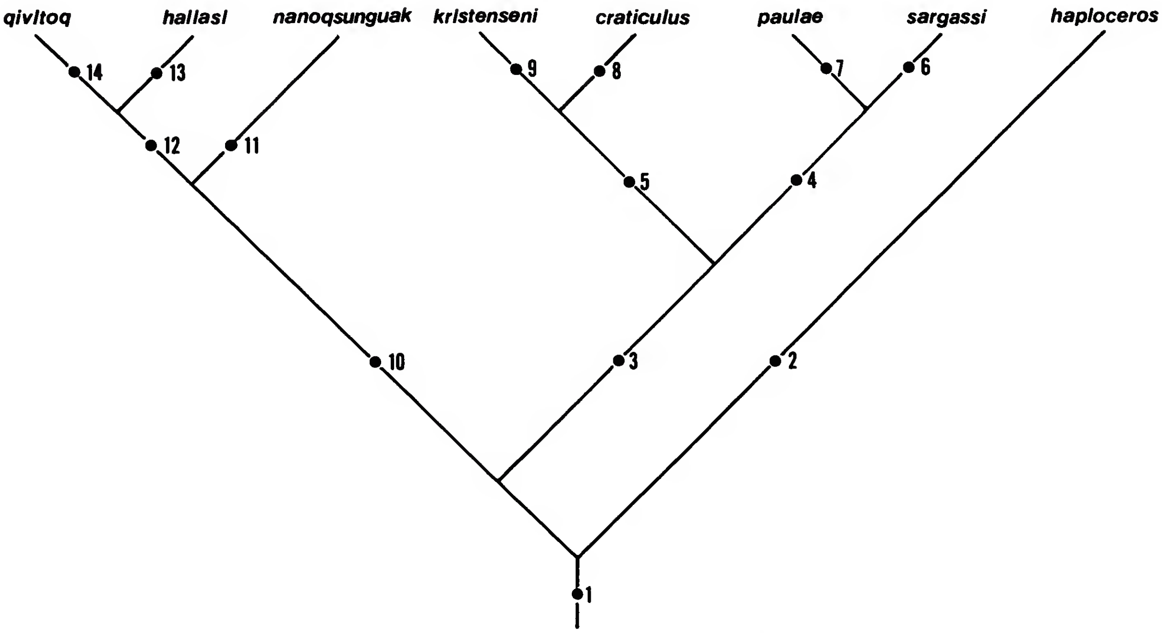


FIGURE 51.—Cladogram of *Styraconyx* (numbers refer to apomorphic characters discussed in text).

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