

A REVISION OF THE GENUS *THEMISTE* (SIPUNCULA)

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Abstract.—The 31 putative species of the sipunculan genus *Themiste* and the morphological characters used to differentiate them are critically reviewed. The monograph of Stephen & Edmonds (1972) is used as a starting point and all changes made in the intervening years are reiterated. All available type material was studied and new collections of Hawaiian and Californian material are used to analyze within-deme variation. Four characters are determined to be useful at the species level and three at the subgeneric level. A key to and a discussion of each of the 10 remaining species (plus one reduced to subspecies) with the newly designated synonyms are presented. A brief statement of the known distribution and an overall summary of the zoogeography of the two subgenera (largely non-overlapping) are given.

This is a continuation of our series in which we reevaluate the species of sipunculan worms (e.g., Cutler & Cutler 1985a, b, 1986, 1987). With this work we complete our survey of the genera in the Class Sipunculida. The monograph of Stephen & Edmonds (1972) is the starting place for this work (25 species names). In that same work there were three names listed as species inquirendae or incertae sedis that subsequently were considered members of this genus and are addressed herein. The one species and the subgenera erected and the two species transferred into this genus since that time are also included (Table 1).

The genus *Themiste* was erected by Gray in 1828, but this name dropped from sight for over a century. The name *Dendrostomum* (Grube & Oersted, 1858) took its place until 1964 when Stephen resurrected Gray's name. The genus has been placed in its own family, Themistidae of the order Golfingiiformes by Cutler & Gibbs (1985).

While no formal subgenera exist in Stephen & Edmonds (1972), there were six groups that Edmonds later (1980) converted into three subgenera. These subgenera were considered in Gibbs & Cutler (1987), and the one with four retractors (*Stephensonum*)

was determined to be a junior synonym of the genus name *Golfingia*. One of its two species (*Themiste pinnifolia* Keferstein, 1865) was regarded as nomen dubium and the other (*T. stephensoni* Stephen, 1942) was a mixture of *Golfingia capensis* and *T. lageniformis* (see below). The remaining two subgenera (based on differences in contractile vessel villi or tubules) are used here. We do question the presumed homologous nature of these tubular extensions. They are very different in size, distribution, and number. It seems likely that these elaborations resulted from two different evolutionary events (homoplasy).

The type (10 mm trunk), and only specimen of *Themiste spinifera*, Sluiter, 1902 is not in the museum collections (ZMUA) with the other *Siboga* material. Certain aspects of the figures and description make us doubt the generic affinity, and, with no way to verify this, we reduce its status to that of incertae sedis.

Whenever possible we have obtained type material to verify the original descriptions. In several cases we have made detailed observations on series of recently collected individuals to better evaluate the traditionally used morphological characters. Collecting

Table 1.—Species considered and proposed taxonomic changes.

Present name	Proposed name
Subgenus <i>Themiste</i>	
<i>Themiste alutacea</i> (Grube & Oersted, 1858)	no change
<i>Themiste blanda</i> (Selenka et al, 1883)	no change
<i>Themiste dyscrita</i> (Fisher, 1952)	no change
<i>Themiste hennahi</i> Gray, 1828	no change
<i>Themiste hexadactyla</i> (Sato, 1930)	<i>Themiste pyroides</i>
<i>Themiste lissa</i> (Fisher, 1952)	<i>Themiste hennahi</i>
<i>Themiste orbiniensis</i> (de Quatrefages, 1865)	<i>Themiste alutacea</i>
<i>Themiste perimeces</i> (Fisher, 1928)	<i>Themiste hennahi</i>
<i>Themiste petricola</i> (Amor, 1964)	<i>Themiste alutacea</i>
<i>Themiste pyroides</i> (Chamberlin, 1920)	no change
<i>Dendrostomum ramosum</i> Quatrefages, 1865	<i>Themiste hennahi</i>
<i>Sipunculus rapa</i> Quatrefages, 1865	<i>Themiste hennahi</i>
<i>Themiste rosacea</i> (Amor, 1964)	<i>Themiste alutacea</i>
<i>Themiste schmitti</i> (Fisher, 1952)	<i>Themiste hennahi</i>
<i>Themiste spinifera</i> (Sluiter, 1902)	incertae sedis
<i>Themiste zostericola</i> (Chamberlin, 1920)	<i>Themiste hennahi</i>
Subgenus <i>Lagenopsis</i>	
<i>Themiste cymodoceae</i> (Edmonds, 1956)	no change
<i>Themiste dehamata</i> (Kesteven, 1903)	no change
<i>Themiste elliptica</i> (Sato, 1934)	<i>Themiste dehamata</i>
<i>Themiste fisheri</i> (Amor, 1964)	<i>Themiste dehamata</i>
<i>Themiste fusca</i> (Edmonds, 1960)	<i>Themiste minor minor</i>
<i>Themiste glauca</i> (Lanchester, 1905)	<i>Themiste lageniformis</i>
<i>Themiste huttoni</i> (Benham, 1904)	<i>Themiste minor huttoni</i>
<i>Themiste lageniformis</i> (Baird, 1868)	no change
<i>Themiste minor</i> (Ikeda, 1904)	<i>Themiste minor minor</i>
<i>Themiste pyriformis</i> (Lanchester, 1905)	<i>Themiste lageniformis</i>
<i>Themiste robertsoni</i> (Stephen & Robertson, 1952)	<i>Themiste lageniformis</i>
<i>Themiste tropica</i> (Sato, 1935)	<i>Themiste lageniformis</i>
<i>Themiste variospinosa</i> Edmonds, 1980	no change
Subgenus <i>stephensonum</i> (now void)	
<i>Themiste pinnifolia</i> (Keferstein, 1865)	nomen dubium
<i>Themiste stephensoni</i> (Stephen, 1942)	<i>Golfingia capensis</i>

trips to Hawaii and California have greatly facilitated this effort. The opportunity to see the differences in the habitat of these animals and to observe living material is invaluable.

We first discuss the morphological characters in light of our recent analyses. Next a key to all the species we consider valid and a section where each of these species is discussed; this includes a synonymy, a discussion of newly added junior synonyms, and a summary of their distribution. Within

each subgenus the species are grouped according to whether or not hooks are present. A short zoogeographical summary is also presented.

The following abbreviations are used in this text for the museums from which we borrowed material: Bernice P. Bishop Museum, Honolulu (BPBM); British Museum (Natural History) (BMNH); Museum of Comparative Zoology, Harvard (MCZH); Museum für Naturkunde der Humboldt-Universität zu Berlin (MNHU); Royal Scot-

tish Museum, Edinburgh (RSME); Santa Barbara Museum of Natural History (SBNH); University Zoological Museum, Cambridge (UZMC); National Museum of Natural History, Washington, D.C. (USNM); Zoologisk Museum, Copenhagen (UZMK); Zoological Institute, Tohoku University, Sendai (ZITU); Zoological Museum, Hamburg (ZMUH); Zoology Museum, University of Tokyo (ZMUT).

Morphological Characters

Historically the following characters have been used to differentiate *Themiste* species. Earlier descriptions were not always based on a good understanding of possible variation within a population (species). In this section we evaluate these characters in light of our experience with large sample sizes. It must be emphasized that if the specimens are not relaxed prior to fixation the measurements of diverse parts can be misleadingly different. For instance, in the Hawaiian *T. lageniformis* population we had access to one collection with completely retracted introverts and another which was preserved with introverts extended. The length of the introverts did vary considerably (Fig. 1), but this is partly an artifact of preservation technique. Introverts of retracted specimens were measured by dissecting the body wall and determining the distance from the nephridiopores to the base of the tentacles.

We have observed other differences that are not of the classical type but worth mentioning. The niche concept is particularly applicable in the Californian species; we found one (*T. hennahi*) lives in unconsolidated sediments (various mixtures of silt/sand/gravel), and a second (*T. dyscrita*) lives in discrete holes made by other animals in shales or sandstones. These also have different sporozoan parasites in their intestine (F. Hochberg, pers. comm.) and respond very differently to anesthesia (*T. hennahi* is much more likely to extend its introvert in response to refrigeration or menthol). The

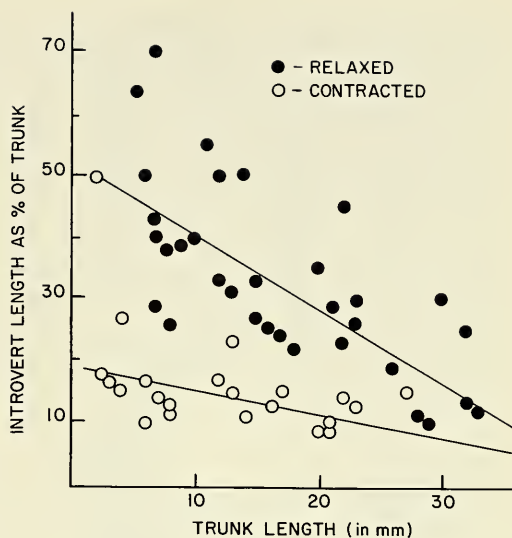


Fig. 1. Introvert length of *T. lageniformis* to show how such measurements can differ between relaxed and contracted worms. As in other genera, the relative length of this body part becomes shorter with age (in linear regression $b = -1.2$ and -0.27).

third species (*T. pyroides*) lives in fissures/crevices in granitic rock, is much more eurybathyal, and does not relax easily. A similar case (ill-defined but different niches) seems to exist for the Australian complex (S. J. Edmonds, pers. comm.).

Karyology may be an attribute that biologists can use to differentiate species. A more detailed statement will be published separately, but, based on a preliminary analysis of three species, it appears that the members of this genus have ten pairs of chromosomes. The apparent similarities preclude using this as a diagnostic character at the species level. Information about developmental pathways and parasites might be useful, but at this time the data base is far from complete.

1. *Contractile vessel villi*.—In sipunculans a closed, fluid filled, tubular system extends into the tentacles from one or two vessels running along the esophagus functioning as a circulatory system helping in the exchange of gases between the external and internal

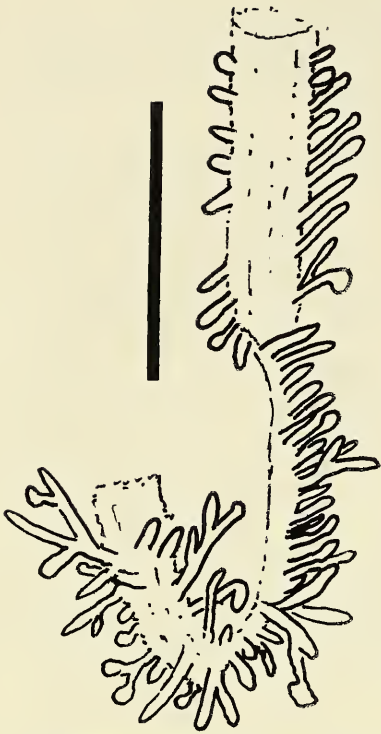


Fig. 2. Contractile vessel villi from a 5 mm *T. lageniformis* showing bifurcations in a small specimen and the increasing frequency of bifurcations toward the posterior end (bottom of figure). Scale line is 1 mm.

environments. It may also be a turgor pressure system not unlike the polian vessels in echinoderms aiding in the expansion of the tentacular crown. In five genera, digitiform villi along this vessel increase the volume and the surface area for internal gas exchange. In this genus are two rather different configurations, and this character is used to separate the two subgenera (Edmonds 1980). The more common pattern (found in other genera) of many (more than 100) short villi is found in *T. (Lagenopsis)*. In *T. (Themiste)* a unique design exists: few (usually 8–14) long threadlike extensions off the posterior quarter of the vessel, often with a corkscrew or beads-on-a-string shape.

A question that has been raised about the shorter villi is whether or not the individual units bifurcate; a few species have been al-

leged to lack any bifurcating villi. Our examination of recently collected Hawaiian *T. lageniformis*, ranging in size from 2–33 mm, shows that while more bifurcation exists in larger worms, all those over 3 mm show at least some evidence of bifurcation (Fig. 2). One must look carefully in smaller worms. In addition to an ontogenetic change, we have observed an anterior/posterior gradient. The branching complexity (and size of villi) increase towards the posterior end—sometimes more than three terminal branches can be seen.

In the subgenus *T. (Themiste)* none of the tubular extensions (villi seems inappropriate here) bifurcates in the same manner. In some larger specimens a complex branching occurs near the base (see Fisher 1952 pl. 30, fig. 3). The variable, occasionally used in species descriptions, is the number, e.g., more than 10 vs. 10 or less. The exact number of tubules is difficult to determine, and our data suggest that smaller worms (under 30 mm) have less than 10 while larger worms (same population) usually have more than 10 tubules. To use this difference as a species specific character is unwise.

Only a few references to anastomosing “networks” of the vessel around the esophagus exist, but our examination shows this feature to be age dependent, thus rarely developed in smaller worms (see *T. pyroides* section for more detail). Therefore, its use as a taxonomic character is limited.

2. *Introvert hooks*.—In both subgenera some species carry dark, horny, chitinous hooks scattered on the introvert. In some genera hooks appear to be deciduous, but that does not seem to be the case here. However, we know very little about the ontogeny of those species lacking hooks as adults. The one such species we do have information on is *T. lageniformis*. Awati & Pradhan (1935) reported hooks on early stages and Pilger (1987) reported hooks in a five day specimen. Also, Williams (1977:38) observed that 13 day old Hawaiian specimens

(about 0.5 mm) have “. . . several rows of hooks.” We saw no hooks on our 2–3 mm worms from Hawaii.

One record suggests the reverse pattern exists in one species that has hooks as adults: Fisher's (1952) discussion of *T. pyroides* includes the observation that smaller worms have fewer hooks (no hooks in those less than 18 mm, 4–18 hooks in two 18 mm worms, 50 hooks in a 24 mm worm). One must remember that Fisher's measurements include both the trunk and the introvert, the later being about $\frac{1}{3}$ the total. Our recent collections from the same area (Carmel and Monterey) included only a few small worms and all of these have hooks (30–80 hooks in worms with a total length of 15–21 mm; trunks from 10–14 mm). In the *T. blanda* we collected in Japan only one with a 2 mm trunk has no hooks; those 3 mm and larger carried them.

These data suggest that all *Themiste* species, as early juveniles, have hooks which are soon lost. While some species never replace these, other species do so in later stages of ontogeny. This hypothesis needs more testing, but Rice (1967) did observe one row of hooks in one month old specimens of *T. pyroides*, the same species Fisher was referring to above. She has also recorded (Rice 1975b) the presence of a row of hooks at one month in *T. alutacea*. Nevertheless, a presence/absence dichotomy in adult worms exists and therefore, this character can be helpful to the systematist. If these early juvenile hooks are real and are arranged in rings, we may have reason to reverse our earlier assumptions about the polarity of this character in our cladistic analyses, i.e., this may be the plesiomorphic not the apomorphic state.

The adult hooks are often large, sparse, and arrayed over a wide band on the proximal part ($\frac{1}{3}$ – $\frac{2}{3}$) of the introvert (Fig. 3). Descriptions sometimes include comments on their number, size, and arrangement. As shown above, the number changes with trunk size. We originally thought that the

amount of introvert covered by hooks (most animals have less than 45% covered, but in others the hooked region seems to cover more than 50% of the introvert) as genetically determined. Observations from our field work in California strongly suggest that those animals living in areas of high energy (open rocky intertidal) have fewer hooks covering a smaller area with many more broken hooks than other members of the same species at more protected or subtidal depths (e.g., *T. pyroides*). It now seems clear that, within limits, this trait is partly an environmentally determined feature. The arrangement is not constant within a species or species specific, generally being scattered and oriented posteriorly (one exception is *T. variospinosa*). Hook size also changes with trunk size: In the Japanese *T. blanda* population we analyzed, a 5 mm worm had hooks about 50 μm tall, an 8 mm worm had 75 μm hooks, and an 11 mm worm had hooks about 100 μm tall. The upper limit in this genus is about 450 μm in large adults.

3. *Tentacular crown*. — The diverse interpretations of this feature have been one of the most troublesome aspects of *Themiste*. The dendritic branching pattern is unique within Sipuncula and makes the identification of these worms to the generic level easy (if the tentacles are extended). However, the question of how many tentacular “stems” exist has led to some unfortunate confusion. Perhaps the classic (but not only) case is the holotype of *T. hennahi*. Gray (1828) saw five main stems; Stephen (1964) reported only four main branches; but, when Rice and Stephen (1970) reexamined the same worm, they reported six tentacular stems.

The lack of consistency in language describing these tentacles has compounded the confusion. We are defining the terms as follows: The four structures arising from the oral disc are the stems; these stems divide into branches (primary, secondary, etc.); the final subdivisions or terminal units are tentacles. Finally, one tentacle is the entire

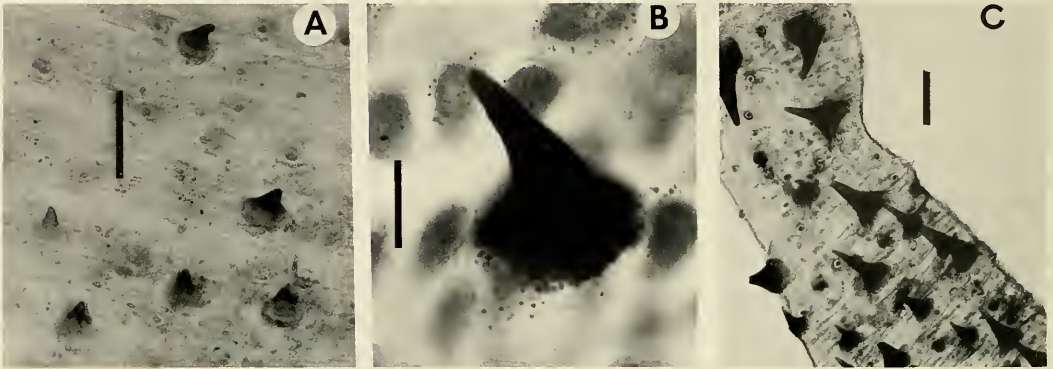


Fig. 3. Introvert hooks showing different sizes and orientation among species: A. *T. minor minor*; B. *T. pyroides*; C. *T. variospinosa*. Scale lines all equal 200 μm .

array of subunits beginning with one stem. While this is somewhat arbitrary, it is consistent with several earlier authors (Fisher 1952, Edmonds 1980).

The basic plan in this genus is four stems, but most of the problems arise when the first dichotomy appears close to the base of a stem. During the ontogeny of these worms different species exhibit different patterns vis-a-vis the timing of the "splitting." Two adult patterns result—either 4 or 6 (occasionally 5) putative stems. Those animals with 5 or 6 may have a developmental pathway that involves an early post-larval subdivision of the dorsal pair. At times the dorsal stems will be longer/larger than the ventrals. Our work with the Hawaiian and Californian populations supports the hypothesis that as these worms increase in size a corresponding increase in the complexity of the tentacular crown occurs, more branches and more tentacles (Fig. 4). Therefore, the number of apparent tentacular stems varies and should not be considered species specific.

A separate issue relates to the branching pattern that has been asserted to be either dendritic, pinnate, or palmate by different authors, sometimes for the same species. These adjectives have been used with minimal precision and suggest differences that

do not exist. In the subgenus *Lagenopsis* the four stems divide into smaller branches relatively few times (1–3), depending on their age/size (Fig. 4). On all of these branches as well as the main stems, terminal tentacles are given off along the entire length from near the branch points to the tip. The length of these tentacles exhibits some consistency within a species. We measured the longest ones in *T. lageniformis*, 2–4 mm; shorter in *T. cymodoceae*, 1–2 mm; and shortest in *T. dehamata*, 0.5–1 mm). The trunk lengths of the measured specimens, in order, are 10–30 mm, 79–85 mm, and 45–68 mm.

In the subgenus *Themiste* each stem branches dichotomously several times with discrete internodes. In small individuals (less than 15 mm) the dendritic crown exists but with fewer branches and shorter internodes (see Fig. 4 and Fisher 1952 for more detail). The terminal tentacles are present as clusters near the tips of the terminal branches. Tentacles are widely spaced (what Fisher (1952) illustrated and called processes) along the branches. In small worms the relative size of the parts gives the crown a more *Lagenopsis*-like appearance. In general, the complexities and variations in the branching patterns mitigate against using it for taxonomic purposes at the species level. The exception (helpful in particular species com-

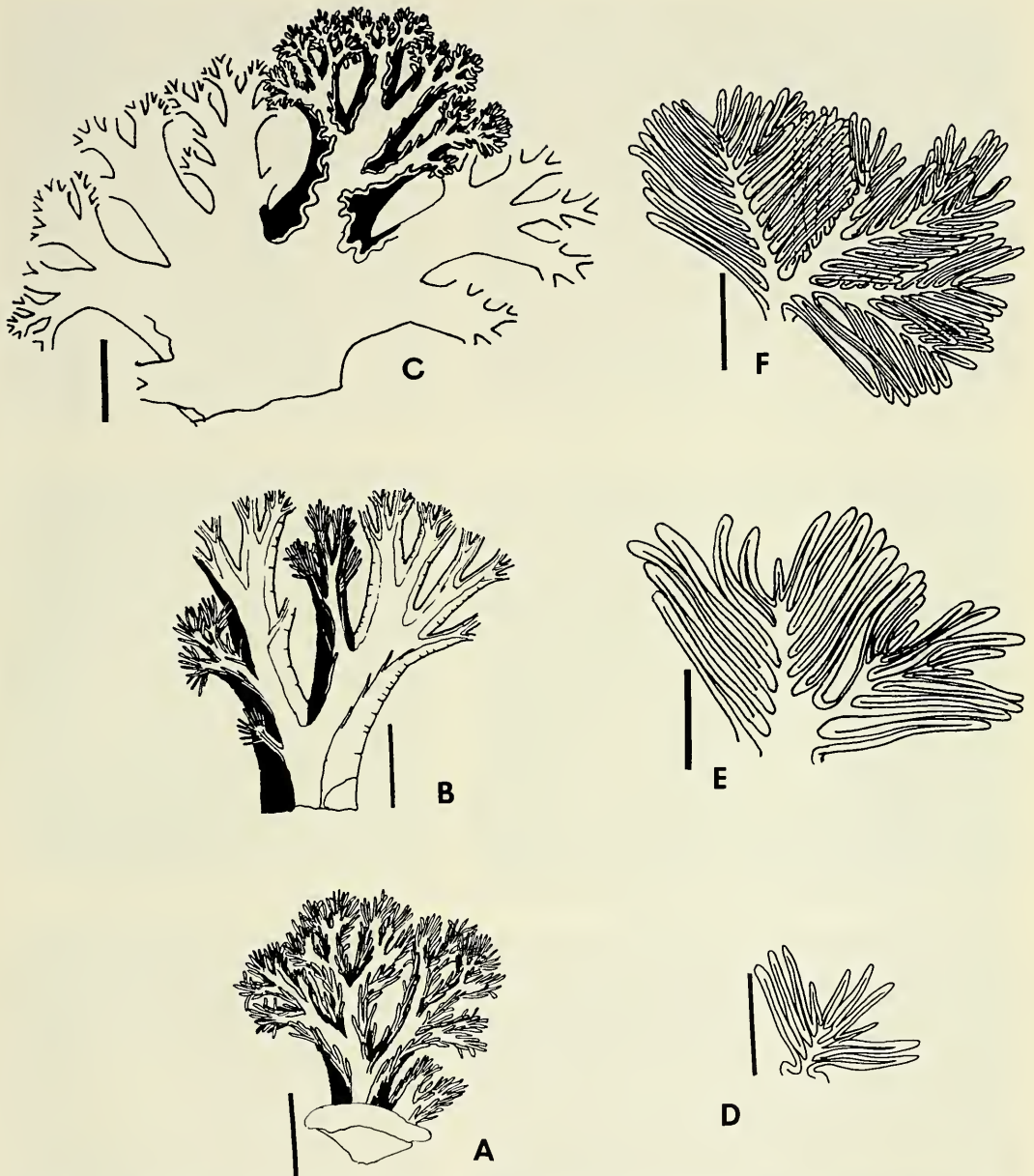


Fig. 4. Left dorsal tentacle from two *Themiste* species showing size-related changes in branching pattern in the two subgenera: A–C are *T. (Themiste) hennahi* trunk lengths are 25, 80 and 140 mm. D–F are *T. (Lagenopsis) lageniformis*; trunk lengths are 6, 16 and 30 mm. Scale line is 1 mm.

plexes), is unequal length of dorsal vs. ventral stems and whether or not the ventral stems split at the same time as dorsals.

4. *Anus-nephridia relationship*.—As in

other genera the relative anterior/posterior relationship of these openings has been reported and sometimes used to differentiate species. The language is often general; these

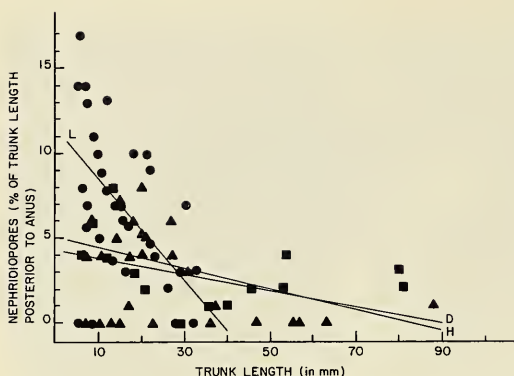


Fig. 5. Distance nephridiopores are posterior to anus as percentage of trunk length. Circles are *T. lageniformis*, squares are *T. dyscrita*, triangles are *T. hennahi*. This distance decreases with size but with much overlap among species.

are at the same level, nearly the same level, or the nephridiopores open posterior to the anus. In our study of the Hawaiian *T. lageniformis* population, the nephridia are almost always posterior to the anus, commonly at a distance equal to 3–7% of the trunk length, occasionally up to 12–15%, but a few at the same level (Fig. 5). In one Californian population of *T. hennahi* this distance is usually only 0–1% but in a few small worms it is 5%. In a population of *T. dyscrita* this distance is 1–4%. Fisher (1952) weighted this heavily in the California complex to distinguish his *T. lissa* from its neighbors, but our measurements of Fisher's material show that only in the holotype is this distance 10% while in four of the paratypes this value ranged from 4–6%.

Our conclusion is that since this distance is small, not easy to measure precisely, and, most importantly, since there can be much variation within demes, it has very little taxonomic significance and should not be used.

5. *Trunk size and shape.*—While this kind of information is often reported imprecisely (large vs. small or slender vs. stout), it may have some meaning. Based on our observations there do appear to be two size classes for adult worms. Those that generally in-

habit soft substrata commonly have trunks exceeding 60 mm (some over 200 mm) while those living in rock or coral rarely exceed 30 mm. However, the north Pacific *T. pyroides* may reach 150 mm. Most of the smaller worms have a similar pyriform shape. Shape of preserved material is partly dependent on the animal's unique set of circumstances prior to fixation (physical microhabitat and anesthesia, if any). However, worms living in unconsolidated sediments are cylindrical and elongate while those from rock/fissures/coral have stouter and more pyriform bodies. When these occupy holes made by boring bivalves the body is shaped by the mold chosen by the juvenile worm (Fig. 6). This shape is difficult to quantify and therefore difficult to communicate without ambiguity. Our observations on living, freshly-collected material lead us to conclude that trunk shape is partly environmentally determined. Nevertheless, this character (especially as an indicator of niche) can be used by the taxonomist.

6. *Fixing muscle attachments.*—Small threadlike muscles connect some part of the digestive tract to the body wall. The general pattern in *Themiste* is three muscles labeled F1, F2, F3. In the subgenus *Themiste*, F1 anchors the esophagus in the area of the long contractile vessel villi to the body wall of the mid-trunk, while in *Lagenopsis* it anchors the esophagus near the posterior part of the trunk where the esophagus turns forward and may take the form of several threads or a membrane. F2 is generally on the posterior esophagus or first gut coil while F3 is more often on the last intestinal coil or the rectum. The precise insertion of these muscles has been asserted to be constant and taxonomically meaningful (Fisher 1952 compares *T. hexadactyla* to *T. pyroides* or *T. dyscrita* to *T. zostericola*). However, Fisher did illustrate variations and Foster (1974:856) working with several hundred *T. dyscrita* from one deme commented on the novel and abnormal arrangement of the F2, other than that described by Fisher. Our

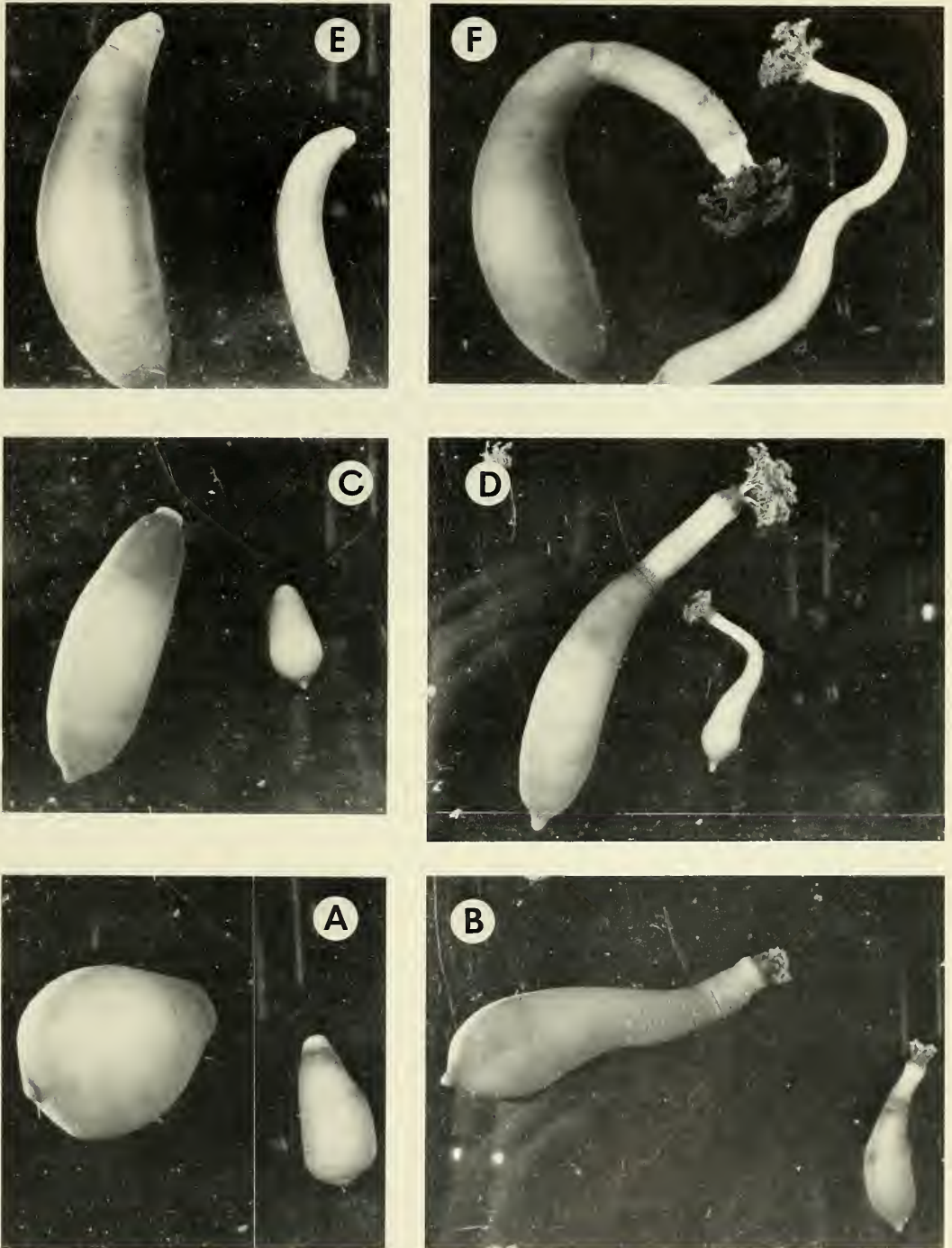


Fig. 6. Comparison of fully contracted (A, C, and E) with extended (B, D, and F) body shape in three pairs of living worms from different Californian microhabitats: A-B. *T. dyscrita* from boring mollusc (pholid) holes in shale at Santa Barbara; C-D. Same species from burrows in sandstone at Santa Cruz; E-F. *T. hennahi* from coarse sand at Santa Barbara.

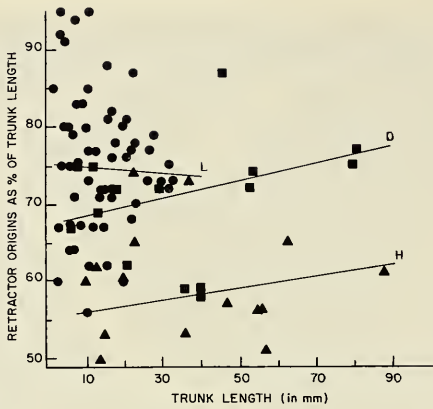


Fig. 7. Introvert retractor muscle origins on body wall as percentage of trunk length towards the posterior end in three species. Circles are *T. lageniformis*, squares are *T. dyscrita*, triangles are *T. hennahi*. This is not a size related character (all values for b (linear regression) are less than 0.1).

own analysis shows variation within populations (some lacking the full complement or the insertion of F2 being at different points and sometimes branched with several points of attachment). Therefore, as this variation also overlaps among species, it can only be used in a general manner.

7. *Retractor muscle origins.*—In adults one pair of muscles functions to retract the introvert into the trunk. These muscles have their origins on the body wall on either side of the ventral nerve cord and insert in the cephalic region. The anterior/posterior location of these origins has sometimes been used by systematists to describe a species using phrases like “in the middle third” or “in the last quarter.” One must also determine whether the author is talking about the whole body (including the introvert) or just the trunk when giving measurements. In order to standardize these data we record it as a percentage of the trunk length using the nephridiopores to mark the anterior border of the trunk. Our analysis shows that the vast majority of individuals have their retractor origins from 60–80% of the distance towards the posterior end. In two California populations that we examined (*T. dyscrita* and *T. hennahi*), there is a smaller

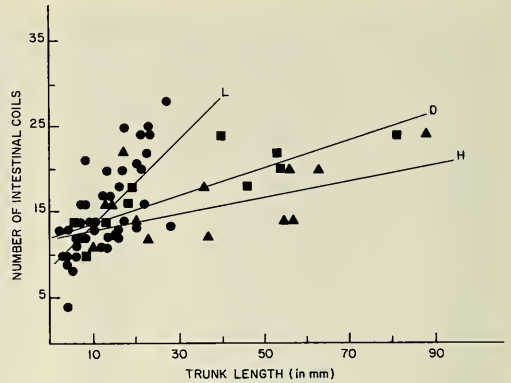


Fig. 8. Number of intestinal coils showing varying increases in number with increase in size for the same species as Fig. 7. The positive slopes (b in the linear regression) are 0.5, 0.16 and 0.09.

size related shift in the point of origin than that noted in other genera (Fig. 7). As this figure shows *T. dyscrita* is generally more anterior than *T. hennahi*, which is more anterior than *T. lageniformis*. The linear regression is a very poor fit because of much overlap, especially in smaller worms, and so much scatter of the data points.

8. *Number of intestinal coils.*—As in other genera the number of coils is directly correlated with the size of the worm: commonly 12 to 24 coils (Fig. 8). One apparent exception to this is: some larger individuals (over 200 mm) in the California population of *T. hennahi* may have more than 80 coils. Four species seem to have irregular, loosely wound gut coils; however, since we find much within-deme variation and overlap among species, this is not a useful character.

9. *Pigmentation on tentacles and introvert.*—Some species have dark bluish pigment in a collar-like band around the introvert and others have dark purple/blue pigmented patches on the tentacles (Fig. 9). The presence or absence of the dark collar on the introvert is consistent. Pigment on the branches is inconsistent, but its presence or absence on the tentacles of certain species is reliable and helpful to the systematist.

10. *Papillae size and shape.*—As with



Fig. 9. Distal introverts of two species; *T. dyscrita* on left with pigmented collar region and pale tentacles; *T. hennahi* on the right with unpigmented collar and dark tentacles.

other genera, these worms have glandular secretory papillae on the introvert and trunk. These are more numerous and larger near both ends of the trunk. While some authors have used the size and/or shape of these bodies to distinguish species we do not concur. The morphology of these papillae is simply too variable to be useful.

11. *Spindle muscle*.—As in other sipunculans, a thread-like muscle runs through the center of the gut coil, connected along its length to help anchor the intestinal coils. It originates anteriorly in all genera but does not insert on the body wall posteriorly in this genus. Some authors have described it as terminating on the rectum in certain species. After carefully analyzing this character, we conclude that all *Themiste* species are similar: after originating from the body wall anterior to the anus it appears to become part of the rectal wall, is difficult to trace but can be seen posteriorly attached to the caecum before entering the gut coil.

Summary.—Of these characters, the type

of contractile vessel villi, branching pattern of the tentacular crown, and the origin and insertion of F1 are useful at the subgeneric level only. The presence or absence of hooks, trunk size and shape, pigmented collar on the introvert, and tentacule pigmentation can be useful at the species level. The remaining characters exhibit too much within-deme variation or among species overlap to have value for the systematist.

Key to *Themiste* Species

- 1. Contractile vessel with numerous (more than 40) short digitiform villi (subgenus *Lagenopsis*) 2
- Contractile vessel with few (less than 20) long thread-like tubular extensions (subgenus *Themiste*) 6
- 2. Introvert without hooks 3
- Introvert bearing dark scattered hooks 5
- 3. Small (trunk <35 mm); introvert with purple “collar”; lives in hard substrates *T. lageniformis*

other animals, commonly pholid bivalves, in intertidal shales or sandstones. It does not appear to coexist with the hooked *T. pyroides*, which may live in the same bay but occupies a different niche. The body color ranges from pale cream in small worms to dark brown in larger ones.

Distribution.—The U.S. west coast from Oregon to southern California at intertidal depths (one record at 18 m).

Themiste hennahi Gray, 1828

Themiste hennahi Gray, 1828:8, pl. 6, figs. 4, 4a.—Baird, 1868:98.—Stephen, 1964:458; 1967:92–94.—Rice & Stephen, 1970:53–56.—Amor, 1970:495–504; 1975:21–23.—Stephen & Edmonds, 1972:201–203.—Tarifeno, 1975:251–266; 1976:29–37.—Tarifeno & Rojas, 1978:118–119.

Dendrostomum lissum Fisher, 1952:419–422, pl. 35.

Themiste lissa.—Stephen & Edmonds, 1972:206.—(Not Cutler & Cutler, 1979a:966–967).

Dendrostoma mythecha Chamberlin, 1920:30.

Dendrostoma perimeces Fisher, 1928:196–198, pl. 6, figs. 3, 3a, pl. 7, fig. 1, pl. 8, figs. 2, 2a; 1952:415–417.—MacGinitie, 1935:631–682.

Themiste perimeces.—Stephen & Edmonds, 1972:207–209.

Dendrostoma peruvianum Collin, 1892:179–180.—Fischer, 1914b:12–13.

Dendrostomum peruvianum.—Wesenberg-Lund, 1955:12–13.

Dendrostomum ramosum Quatrefages, 1865:629.—Leroy, 1936:425.

Themiste ramosa.—Baird, 1868:98.—Stephen & Edmonds, 1972:340 (in list of incertae sedis, etc.).—Saiz Salinas, 1984:184–185.

Sipunculus (Aedematosomum) rapa Quatrefages, 1865:627.—Saiz Salinas, 1984:172–173.

Phascolosoma rapa.—Baird, 1868:86.

Dendrostomum schmitti Fisher, 1952:422, fig. 87F.

Themiste schmitti.—Amor, 1970:499.—Stephen & Edmonds, 1972:212.

Dendrostoma zostericum Chamberlin, 1920:30.—Peebles & Fox, 1933:201.

Dendrostomum zostericum.—Fisher, 1952:411–415, pl. 30, fig. 1, text-fig. 87A, pls. 31–32.—Gross, 1954:403–423.

Themiste zostericola.—Stephen & Edmonds, 1972:213–214.—Rice, 1980:493.

Material examined.—BMNH, paralectotype (1965.16.2/5); RSME, two Peru specimens identified by Stephen (1965.27.2); our own 1987 Santa Barbara and Monterey Bay, California material. *T. lissa*: USNM, Fisher's holotype (21222) and (27671). *T. perimeces*: USNM, Holotype (19615), paratype (21547), and other California material (26446, 27612); SBNH (42493, 42494, 47660); specimens at Moss Landing Marine Lab. *D. peruvianum*: MNHU, Collin's syntypes (Nr. 2087); ZMUH, Fischer's from Chile (V6184). *D. ramosum* and *D. rapa*: MNHN, Quatrefages' types (V25). *T. schmitti*: USNM, Fisher's holotype (21216), paratypes (21217). *T. zostericola*: MCZH, type (2181; this is a dried up bag of skin and of no value); SBNH (47662); USNM, Fisher's Baja material; many Californian specimens collected for us by Pacific Bio-Marine.

Discussion.—*Themiste hennahi* is an eastern Pacific taxon inhabiting intertidal gravely to silty sand (including mud flats, eel grass beds and between and under turnable boulders). Trunks are commonly 25–100 mm long (occasionally up to 200 mm, rarely larger) with a slender pyriform to cylindrical shape sometimes with a nipple-like posterior end. The introvert retractors commonly originate at 50–60% of the trunk length (Fig. 7) and the introvert is without a pigmented collar. The careful redescription by Rice and Stephen (1970) is well illustrated. Tarifeno (1975) gives detailed ecological and behavioral information. The tentacular crown is asymmetrical, with the dorsal pair being longer and splitting sooner than the ventral pair giving the appearance

of six stems. The nephridiopores open 0–10% of the trunk length posterior to the anus, in larger worms this distance is usually less than 2%.

The 18 syntypes of Collins' *T. peruvianum* (reduced to junior synonym by Stephen 1964) all had pyriform trunks with the posterior end coming to a blunt point. The spindle muscle is very strong, and in a few this seems to be contracted along the rectum giving the latter an accordion pleated look. This population allegedly has protuberances on the esophagus. However, we see only a few bumps, which easily rub off and appear to be agglutinated gametes adhering to the esophageal wall.

Quatrefages' (1865) two species (*T. rapa* and *T. ramosum*) were considered incertae sedis until the reconsideration by Saiz-Salinas (1984) wherein he determined them to be synonyms of this species.

When Rice & Stephen (1970:56) redescribed this species, they made the following statement: "*Themiste hennahi* also shows many similarities to the species described as *Dendrostomum zostericum* Chamberlin 1919 and *Dendrostomum schmitti* Fisher 1952. The possibility that these may all represent a single species remains to be determined by future studies." We are unable to find any truly meaningful characters that would serve to differentiate these species. Therefore, we reluctantly agree with their suggestion and place the familiar *T. zostericola* in synonymy. The apparent gap in distribution (Peru to Baja California) may be an artifact of undercollection in Central America, but we discarded the possibility of subspecific rank. The small ones look different from the large ones, but, when one fills the gap with middle sized worms, the continuum becomes clear.

Fisher's *T. perimeces* was originally differentiated from *T. zostericola* by having more gut coils, fixing muscles usually absent, papillae of two or three sizes, and fewer contractile vessel villi. Our examination of Fisher's material (some not previously dis-

sected) and other California specimens demonstrated that this dichotomy is artificial. At least one fixing muscle is present in almost every worm. There are usually 8–14 contractile vessel tubules, but one 9 mm worm has only four, so this, as well as both papillae size and number of gut coils, is somewhat age dependent. Variation exists and the worms bearing this name are simply large *T. hennahi*. Rice (1980) in the most recent general treatment of the California fauna did not include *T. perimeces*.

Themiste lissa is not well known (our total sample size is 19) and the putative differences from *T. hennahi* are subtle. Fisher (1952:422) comments on the close relationship between this taxon and his new *T. schmitti* (now considered a synonym of *T. hennahi*): "... possibly they represent the extremes of geographic variation of one species." We concur. In his key Fisher used the location of the gonads "on the surface of the retractors" vs. "on body wall just back of origins" to separate these two taxa. In our analysis of the *T. hennahi/peruvianum* and *T. lissa* material, we found the gonads to be located on the body wall, on the retractors, and on combinations of this in different worms but showing significant within-deme variation.

When Fisher asserted that *T. lissa* differed from the other Californian species (he did not mention *T. hennahi*, which had not been "rediscovered" at that time), he put considerable weight on the distance between the anus and the nephridiopores—he gave no measurements but stated that the distance was "conspicuous." In the holotype (with a 20 mm trunk) the distance is 10% of the trunk length, but in six of Fisher's paratypes (7–11 mm trunks) it varies from 4–7% (in one worm these are at the same level). In two recently collected specimens the distance was 12% in an 8 mm worm and 5% in an 11 mm worm. As noted in the introduction, this is not a species specific character.

Our present construct includes worms of

very different sizes from what may appear to be rather different habitats. The probability exists that some live in more optimal niches than others and that these can achieve a larger size. If a trend exists, it seems to be that the higher latitudes are better suited to this genotype. The smallest worms come from the Gulf of California, and this population may be isolated with restricted gene flow.

A reexamination of the two *T. lissa* from Durban (Cutler & Cutler, 1979a) showed them to be *Antillesoma antillarum*.

Distribution.—Chile and Peru, Gulf of California and California; unconsolidated intertidal or shallow subtidal sediments. Quatrefages' *T. ramosa* specimens are labeled, "Qf. du Bresil M. Pissis," but we are hesitant to accept this as a valid location as there have been no 20th century confirmations outside the eastern Pacific.

Those with hooks:

Themiste alutacea (Grube & Oersted, 1858)

Dendrostomum alutaceum Grube & Oersted, 1858:118.—Quatrefages, 1865:630.—Diesing, 1859:765.—Keferstejn, 1865:438.—Selenka et al., 1883:84–85.—Fischer, 1895:18; 1922:18.—Gerould, 1913:417–418.—Leroy, 1936:425.

Themiste alutacea.—Baird, 1868:98.—Stephen & Edmonds, 1972: 196–197.—Cutler, 1973:162–164.—Cutler & Cutler, 1979b:105–106.—Rice, 1975a:37–47, 1975b:147.

Sipunculus (Phymosomum) orbiniensis de Quatrefages, 1865:622.

Phascolosoma orbiniense.—Baird, 1868: 93.—Stephen & Edmonds, 1972:339 (in list of incertae sedis etc.).

Themiste (Themiste) orbiniensis.—Saiz-Salinas, 1984:124–132.

Themiste blandum [sic].—Murina, 1968: 423.

Dendrostomum petricolum Amor, 1964: 463–467, pl. 3, 5 figs.

Themiste petricola.—Stephen & Edmonds, 1972:209.—Amor, 1975:185–192.

Dendrostomum rosaceum Amor, 1964:459, pls. 1, 2 and 3.

Themiste rosacea.—Stephen & Edmonds, 1972:211–212.

Material examined.—MNHU, Grube's type (1033) plus some of Selenka's from Brazil; other material from North Carolina (Cutler, 1973) and M. Rice's Florida material. *T. orbiniensis*: MNHN, Quatrefages' material (V25). *T. rosacea* and *T. petricola*: USNM, paratypes (30995, 30996). *T. blanda*: ZIAS, Murina's Gulf of Mexico specimens.

Discussion.—This warm water, western Atlantic species inhabits hard substrates (spaces in coral, oyster beds or soft rock), is small (trunk rarely over 25 mm, commonly less than 15), and exhibits indirect development. As an early juvenile it has a single ring of introvert hooks, but these are soon lost and replaced by scattered adult hooks. We have sufficient data on this species (Rice 1975b) to assert that early in a worm's life four tentacular stems exist; two of these often subdivide near the base to give the appearance of six (sometimes five) in many adult worms. This is different than the four dividing into eight seen in *T. blanda*. The subsequent branching of these primary units is limited in the smaller worms, and the thin tentacles (with pigment spots) are located all along each branch. The hooks in this species can be numerous (over 100 in one 5 mm worm) but not as large as in other members of this subgenus (75–150 μ m). This species has lecithotrophic pelagic larvae, i.e., indirect development (Rice 1975b).

Themiste rosacea and *T. petricola* were described from Argentina, and, while we have not been able to obtain additional material, our examination of the literature and the paratypes convinces us that these three putative taxa are not biologically distinct. The presumed differences are in the number of tentacles, the number of hooks, the size,

shape and color of the trunk, and the position of the fixing muscles. As noted in the Introduction, these characters are too variable to be meaningful. While gene flow may be restricted and subspecific status might be appropriate, we cannot discern consistent and meaningful morphological differences.

Our examination of Murina's Gulf of Mexico worms convinced us that they belong to this taxon. The hooks in this population are larger, measuring up to 300 μm . Saiz-Salinas (1984) presented a detailed re-description of Quatrefages' *T. orbiniensis* and a comparison to others in this group. Towards the end of his discussion, he noted that a future comparative study of specimens may result in the synonymizing of Quatrefages' name. When Amor examined this material in 1969, she left a note in the bottle that she thought it was *T. alutacea*, and our analysis of all available information brings us to the same conclusion.

Distribution.—Western Atlantic Ocean from North Carolina (34°N) to Argentina (42°S) at depths less than 30 m.

Themiste blanda (Selenka, deMan, & Bulow 1883)

Dendrostomum blandum Selenka et al., 1883:85–86, pl. 1, fig. 9, pl. 11, figs. 159–162.—Selenka, 1885:14.—Ikeda, 1904:53–55; 1924:30–31.—Ostroumov, 1909:319–324.—(Not Fischer, 1922:18–19)—Sato, 1930:24–28; 1937:162; 1939:412.—Fisher, 1952:405.

Themiste blanda.—(Not Murina, 1968:423)—Stephen & Edmonds, 1972:197.—Cutler, Cutler & Nishikawa, 1984:285.

Material examined.—MNHU, type and paratype (962, 1034); Our 1979 Japanese material.

Discussion.—In Cutler et al. (1984:285) we noted “. . . what has been called *T. blanda* may be simply small *T. hexadactyla*.” Our current studies cast some doubt on that hypothesis and we now consider *T. hexadactyla* to be a junior synonym of *T. pyroides*. While acknowledging the very sim-

ilar nature of this taxon and the other two hooked members of this subgenus, we retain *T. blanda* as a distinct species for the present. It differs from *T. pyroides* in two ways: 1. Tentacular crown—this array is simpler with four tentacular stems, each dividing only once, and it has longer tentacles along each branch giving each branch a somewhat pinnate appearance. 2. The upper limit of trunk size seems to be about 25 mm (vs. 200 mm). The similarities are marked and some of the alleged differences referred to by earlier authors (such as fixing muscle arrangements) are not constant enough to be meaningful. The similarities to *T. alutacea* are also marked, but it differs by having four stems dividing symmetrically into eight, lacking pigment spots on its stouter tentacles, and by living in cool northern Pacific water vs. warmer western Atlantic water.

Distribution.—Intertidal in Honshu and Hokkaido, Japan.

Themiste pyroides (Chamberlin, 1920)

Dendrostoma pyroides Chamberlin, 1920:31.—Fisher, 1952:406–409.

Themistse pyroides.—Stephen & Edmonds, 1972:210.—Rice, 1967:143–171; 1980:492–493.—Frank, 1983:22.

Dendrostoma blandum.—Fischer, 1922:18–19.

Dendrostoma petraeum Fisher, 1928:195–196.

Dendrostoma hexadactylum Sato, 1930:28–33, pl. 4, figs. 20–24, text-figs. 13–15; 1937:162–163; 1939:412.—Okuda, 1946:224.

Dendrostomum hexadactylum.—Fisher, 1952:410–411, pl. 30, fig. 2.

Themiste hexadactyla.—Stephen & Edmonds, 1972:203–204.—Cutler & Cutler, 1981:75.—Cutler, Cutler & Nishikawa, 1984:285–286.

Material examined.—MCZH, Chamberlin's type (2.182) and paratype (2.183); USNM, several of Fisher's California specimens (21503, 21548), a few from Vancouver, B.C. identified by M. Rice (96094); our

1987 Carmel and Monterey, California specimens. *T. hexadactyla*: ZITU, type (G26) plus other Sato material (1-4, 1-5, 4-11, 5-11, 5-15; one now at USNM, 59994); USNM, Fisher's California specimens (21504, 27672).

Discussion.—This taxon is similar to the two previous species but does have a pyriform shape with a bluntly pointed posterior end regardless of size (Fig. 10). The morphological distinction we now affirm is; four primary tentacular stems divide close to their base into 2, 3, or 4 branches, each then subdividing, as the worm grows, into smaller branches giving off unpigmented tentacles mostly at the distal ends. In specimens the same size as a given *T. blanda* or *T. alutacea*, the crown of *T. pyroides* is much more voluminous with shorter terminal tentacles. Whereas many specimens from central California have trunks 20–40 mm long, some worms from the more northern latitudes (British Columbia and Hokkaido) may exceed 100 mm. The fixing muscle placement is not as constant as Fisher (1952) implies nor is the anastomosing network of contractile vessel branches as clearcut or consistent. In 12–14 mm worms only 8 or 10 long tubules are at the terminal end of the vessel, while in a 23 mm worm one sees branches off the main vessel adhering to the sides of the esophagus. In a 40 mm worm these branches are more elaborate and surround the esophagus. This network becomes much more complex in an 80 mm worm, much like that shown in Fisher's (1952) plate 29, fig. 3.

Distribution.—Honshu and Hokkaido, Japan and west coast of North America from southern Alaska to Baja California at intertidal depths.

Subgenus *Themiste* (*Lagenopsis*)
Edmonds, 1980

Diagnosis.—Contractile vessel villi many (more than 100), short and digitiform.

Two subsets exist in this taxon, those species with and without introvert hooks. Within the hookless triad is one common



Fig. 10. *Themiste pyroides* of different sizes showing typical pointed pyriform trunks, hooks on introverts and voluminous tentacular crowns.

circum-subtropical inhabitant of hard substrates, *T. lageniformis*, which has a long list of junior synonyms. The other two species seem to be endemic to Australia living in soft substrates. The hooked subset also has two taxa endemic to Australia and one more widely spread subtropical taxon.

Those without hooks:

Themiste cymodoceae (Edmonds, 1956)

Dendrostomum cymodoceae Edmonds, 1956:299–301, pl. 2, fig. 1, text-figs. 15–16; 1957:55–63.—Åkesson, 1958:147–151.

Themiste cymodoceae.—Stephen & Edmonds, 1972:197–198.—Edmonds, 1980:38–40.

Material examined.—Three specimens (79–85 mm trunks) from the type locality from collections of S. J. Edmonds.

Discussion.—This species is similar to *T. dehamata* in many ways (e.g., pigmented

tentacles but unpigmented collar), and we have reservations about its distinct status. However, S. J. Edmonds (pers. comm.) has collected and observed these in the living state and feels strongly that they are different species. The differences we can agree on are not sharp or easily quantified. The trunk in *T. cymodoceae* is flask shaped or pyriform (length 50–90 mm but less than five times the width) whereas *T. dehamata* is slender and elongate (length at least 10 times width). The second morphological difference has to do with the tentacular crown. In *T. cymodoceae* the tentacular stems are shorter (2.5–4% of trunk length) and are of equal size (giving it a bushy appearance). In *T. dehamata* the stems are longer overall (4.5–7% of trunk length) and in each worm the dorsal stems are longer than the ventrals by 25–67% (Edmonds describes this as plumose). The niches of these two species may differ; however, they have both been collected from among the roots in intertidal eel grass beds (Edmonds, 1980).

Distribution.—South Australia; intertidal unconsolidated sediments.

Themiste dehamata (Kesteven, 1903)

Dendrostoma dehamatum Kesteven, 1903: 69–73, pl. 7, fig. 7.

Dendrostomum dehamatum.—Edmonds, 1956:296.

Themiste dehamata.—Stephen & Edmonds, 1972:198–199.—Edmonds, 1980: 34–36.

Dendrostoma ellipticum Sato, 1934:20–22, pl. 1, fig. 10, text-figs. 22–25; 1939:411.

Themiste elliptica.—Stephen & Edmonds, 1972:199–200.—Cutler & Cutler, 1981: 74–75; Cutler, Cutler & Nishikawa, 1984: 283.

Dendrostomum fisheri Amor, 1964:467–469, pl. 3 and 4.

Themiste fisheri.—Stephen & Edmonds, 1972:200.

Material examined.—Four specimens from near the type locality from the collections of S. J. Edmonds.

Discussion.—This taxon was recently re-described by Edmonds (1980). Whereas the written description resembles *T. lageniformis* (see preceding section for comparison to *T. cymodoceae*), it is distinct in several ways. *Themiste dehamata* is more cylindrical, elongate, larger (commonly over 40 and up to 170 mm), and lives in sand or mud habitats.

Sato's (1934) *D. ellipticum* was based on a single 64 mm worm, which cannot now be located. Although Sato did not comment on the contractile vessel villi branching (and his drawing is not sufficiently detailed), Fisher (1952) asserted that they were unbranched, and, therefore, it was distinct from similar species. Sato differentiated it from others with short villi on the basis of papillae shape (elongate elliptical in this and roundish in others including *T. dehamata*). In Stephen & Edmonds' key (1972) they were unable to differentiate these two species. As suggested in Cutler & Cutler (1981) there now seems no justification for retaining this species name.

Edmonds (1980:35) first suggested that *T. fisheri* is very similar to this species. The only "significant" difference, according to him, is the absence of a rectal caecum in *T. fisheri*; however, Amor stressed the different number of tentacular stems. Amor's species rests on a single 100 mm specimen, which we have tried unsuccessfully to obtain for examination. Having only this one worm with only these minor differences, we hereby reduce it to a junior synonym.

Distribution.—New South Wales and South Australia; intertidal unconsolidated sediments. Because of our synonymies, one record is from Japan and one from Argentina. Since these latter specimens cannot be examined, we would caution against including them in zoogeographical analyses.

Themiste lageniformis Baird, 1868

Themiste lageniformis Baird, 1868:98–99, pl. 10, fig. 3.—Rice & Stephen, 1970:66–67.—Stephen & Edmonds, 1972:205–

- 206.—Cutler, 1977a:147.—Williams, 1977:1–206.—Cutler & Cutler, 1979a: 966.—Edmonds, 1980:41–42.—Pilger, 1982:143–156.—Cutler, Cutler, & Nishikawa, 1984:283–284.
- Dendrostoma signifer* Selenka et al., 1883: 86–87 (part).—Sluiter, 1886:515; 1891: 115; 1902:19.—Fischer, 1895:17; 1914a: 72–74; 1914b:10–11 (part); 1919:282–283 (part); 1922:19 (part); 1923:22.—Augener, 1903:300–301.—Ikeda, 1904:56–57.—Hammerstein, 1915:2–3.—Graveley, 1927:87.—Awati & Pradhan, 1935: 102–113; 1936:114–131.—Leroy, 1942: 41–43.
- Dendrostomum signifer*.—Edmonds, 1956: 297.—Wesenberg-Lund, 1959a:198–199; (Not 1959b:213; 1963:129–130).
- Dendrostoma minor*.—Chin, 1947:100.
- Dendrostoma robertsoni* Stephen & Robertson, 1952:438–439, pl. 1, figs. 3–4.
- Dendrostomum robertsoni*.—Wesenberg-Lund, 1963:130.
- Themiste robertsoni*.—Stephen & Edmonds, 1972:210–211.—Stephen & Cutler, 1969:116.—Cutler & Cutler, 1979a: 967–968.
- Dendrostoma stephensoni* Stephen, 1942: 252–253 (part).
- NOT *Themiste stephensoni*.—Cutler, 1977b: 154.
- Dendrostoma tropicum* Sato, 1935:313–315, pl. 4, fig. 15, text-fig. 11; 1939:411.
- Dendrostomum tropicum*.—Wesenberg-Lund, 1963:131–132.
- Themiste tropica*.—Stephen & Edmonds, 1972:213.—Cutler, 1977b:154.—Cutler & Cutler, 1981:76–77.—Murina, 1981:16.
- Phascolosoma glaucum* Lanchester, 1905a: 32, pl.1, fig. 3.
- Golfingia (Thysanocardia) glauca*.—Stephen & Edmonds, 1972:123.—Cutler, 1977b:152.
- Themiste glauca*.—Gibbs, Cutler, & Cutler, 1983:302.
- Phascolosoma pyriformis* Lanchester, 1905b:39, pl. 2, fig. 5.—Sato, 1939:404–406.
- Golfingia pyriformis*.—Murina, 1964:261; 1967:43.
- Golfingia (Thysanocardia) lanchesteri* pro *Phascolosoma pyriformis* Lanchester, 1905b (pre-occupied by *Phascolosoma pyriforme* Danielssen in Théel 1875): Stephen & Edmonds, 1972:124.
- Themiste pyriformis*.—Gibbs, Cutler, & Cutler, 1983:302.

Material examined.—BMNH, syntypes (165.25.9/10); BPBM, Hawaiian collections (N101, 1973.205); Naval Oceans Systems Center, Kailua (at BPBM) and our 1984 Hawaiian worms plus Sta. 87 from Ft. Pierce, FL in the collections of M. Rice. *D. signifer*: ZMUH, Type (V2052); MNHU (384, 982). *T. robertsoni*: RSME, type (1958.23.74); UZMK, Wesenberg-Lund's; our own from Indian Ocean. *D. stephensoni*: RSME, type (1958.23.34) plus (1958.23.35, 37, 38; 1966.1.10). *T. tropicum*: Galathea Sta. 256 in our collections; the type cannot be located. *G. glauca*: UZMC, type; UZMK, Galathea Sta. 630, 631; *G. pyriformis*: UZMC, type material; ZITU, Sato's from Formosa (3–13).

Discussion.—This is the most common, most studied, and most widely distributed species in the genus. Baird's original description (1868) of this species was overlooked by Selenka and others for almost a century. Williams (1972, 1977) and Williams & Margolis (1974) have contributed to an understanding of its burrowing habits and its development (indirect with pelagic larvae). Pilger (1987) has demonstrated that this species may also be parthenogenic. The nature of this species has been fairly clear over the years with two exceptions. Several authors confused the issue by including some animals with introvert hooks. These are now considered to be *T. minor huttoni*, a taxon remarkably similar to this one except bearing hooks. Wesenberg-Lund (1963) reported the presence of two or three rows of hooks in two worms from Tristan de Cunha. We have not been able to locate these specimens and are reluctant to assign them to this ge-

nus because of the hook arrangement and her lack of comment on the tentacular crown. The alleged number of tentacular stems: 4, 5, 6 or 8 has also added to the confusion (see Morphological Characters).

When Stephen & Robertson (1952) described *T. robertsoni*, they differentiated it from this species on the basis of number of tentacular stems plus a few other points such as number of fixing muscles, length of retractors, number of contractile vessel villi, etc. That model was followed by a few other authors, but, as pointed out by Cutler & Cutler (1979a), the differences are subjective. Our current reexamination of this material indicates that these particular characters are within the range found in one *T. lageniformis* population.

While the holotype and some of Stephen's (1942) material of *T. stephensoni* are *Golfingia capensis* (Gibbs & Cutler 1987, Cutler & Cutler 1987), four specimens are *T. lageniformis*.

The original foundation for *T. tropica* was one 14 mm worm (Sato 1935). He did not compare it to this species since he incorrectly said it (*D. signifer* at that time) had long contractile vessel villi. Wesenberg-Lund (1959b) reported two worms from 90–110 m in the northern Gulf of Guinea. We could not find these in any museum collections, and, since these are the only records from this part of the Atlantic, we are skeptical. A careful reading of her description suggests that these are more probably two *Thysanocardia catharinae*. She later (1963) recorded three small (5–10 mm) worms from Capetown. There were a few puzzling aspects to her paper including rings of hooks and an apparent contradiction (key vs. text) about whether or not the villi were branched, a matter now known to be size dependent, not species specific. Without access to these worms we cannot reassign them with confidence, but they are in the *T. minor* group. Cutler's (1977b) and Murina's (1981) worms were all less than 20 mm long, and nothing

would exclude them from our present concept of *T. lageniformis* (i.e., some unbranched contractile vessel villi in small specimens). Now it is clear that *T. tropica* should be considered a junior synonym.

The confusion created by Lanchester's (1905a,b) two species (*Phascolosoma glauca* and *P. pyriformis*) has been addressed in Gibbs et al. (1983) when they revised the golfingiid subgenus now genus) *Thysanocardia*. At that time it was recognized that these two taxa belong in *Themiste*, but they were not assigned to any different species in anticipation of the present work. All of Lanchester's specimens and some of Sato's (1939) *T. pyriformis* were highly contracted so that the anus and nephridiopores were withdrawn (both said "on the introvert"—a feature also noted by Murina (1964)). In some of our strongly retracted recently collected Hawaii material, the anus and nephridiopores were withdrawn, giving the false impression of being on the introvert (see section on Morphological Characters). Since we now find no significant differences, we submerge both names under *T. lageniformis*.

Themiste lageniformis is one of the smaller species (rarely more than 35 mm) which lacks hooks (after early juvenile stages), usually lives in soft rock, old coral or mussel beds, has a bluish band or collar on the introvert (sometimes very pale), and long tentacles.

Distribution.—Well established in the western Pacific (from Japan to Australia and Hawaii) and throughout the Indian Ocean. It has been recorded from South and South-west Africa, Cuba, and Florida.

Species with hooks:

Themiste minor minor (Ikeda, 1904)

Dendrostoma minor Ikeda, 1904:57–59, text-figs. 16, 92–95.—Sato, 1939:411.—Stephen, 1942:252.—(Not Chin, 1947:100).

Dendrostomum minor.—Wesenberg-Lund, 1963:128–129.

Themiste minor.—Stephen & Cutler, 1969: 116.—Stephen & Edmonds, 1972:207.—Cutler, 1977a:147.—Cutler & Cutler, 1979a:967; 1980:206; 1981:75–76.—Cutler, Cutler, & Nishikawa, 1984:284–285.

Dendrostoma signifer.—Fischer, 1914b:10–11 (part); 1919:282–283 (part); 1922:19 (part).

Dendrostomum fuscum Edmonds, 1960: 165–167, pl. 3, figs. 7–9.

Themiste fusca.—Stephen & Edmonds, 1972:200–201.—Edmonds, 1980:40–41.

Golfingia coriacea.—Murina, 1972:298.

Material examined.—ZMUT, Ikeda's type material was located but is completely dried out; RSME, Stephen and Cutler's South African worms (1966.1.9); our 1979 Japanese material from near the type locality (neotype named in Cutler and Cutler, 1981; part deposited at USNM). *T. fuscum*: two Australian worms from the collections of S. J. Edmonds.

Discussion.—Except for the presence of introvert hooks (generally 50–200 μ m tall) and a more loosely wound gut coil, this taxon is ecologically and morphologically similar to *T. lageniformis*. The animals are small, i.e., trunk length usually less than 20 mm and we have seen 4 mm worms which are sexually mature.

Edmonds' (1960) differentiated *T. fusca* from *T. minor* on the basis of presumed but vague differences in hook and papillae structure, attachment of esophagus and the arrangement of the contractile vessel villi. In 1980 Edmonds did say that it was hard to distinguish it from some Japanese *T. minor* but that the contractile vessel and fixing muscles in the Japanese worms seem simpler. From our analysis of the literature and the animals, we conclude that the differences Edmonds reported probably result from Ikeda's narrowly constructed descrip-

tion but are not biologically meaningful, i.e., this amount of variation does exist within demes (see section on Morphological Characters above).

Murina's 1972 record of a single 7 mm worm which she named *Golfingia coriacea* was attributed to this species by Edmonds (1980:29), and we concur. Chin's 1947 record includes the statement that there were no hooks on his material; we herein move Chin's record to *T. lageniformis*.

Distribution.—Japan, China, South Australia, southern Africa, and one record from southern Argentina. The latter record (Cutler and Cutler, 1980) is a 4 mm worm of uncertain affinity. It seems clear that this is a cool temperate, intertidal, and shallow subtidal species. The few deep water records are based on few, very small specimens and may represent either anomalies or confusion in station data. The Cutler (1977a) record at 4510 m should, therefore, be ignored in zoogeographical analyses.

Themiste minor huttoni (Benham, 1904)

Phascolosoma huttoni Benham, 1903:177–184.

Dendrostoma huttoni Benham, 1904:306–307.

Dendrostomum huttoni.—Edmonds, 1960: 164–165.

Themiste huttoni.—Stephen & Edmonds, 1972:204.—Cutler, 1977a:146.—Edmonds, 1980:36–38.

Dendrostoma signifer Selenka et al., 1883: 86–87 (part).—Augener, 1903:337.—Fischer, 1919:282–283 (part); 1926:206.

Material Examined.—RSME, 1958.23. 124; two from the collections of S. J. Edmonds.

Discussion.—In the years 1903–1904 Benham published one faunal index and two publications in which the name "*huttoni*" appears. The formal new species description was in the 1904 paper. This name is pre-

sented in a confusing context along with *Siphunculus aeneus* Baird, 1868 and *S. lutulentus* Hutton, 1879. The former has been synonymized under *Siphonosoma australe* (Edmonds 1961; Rice and Stephen 1970) and the latter placed on the list of incertae sedis (Stephen & Edmonds 1972).

Themiste minor huttoni is here considered a subspecies of a more cosmopolitan taxon with restricted gene flow between the two populations. The similarities to the nominate form are substantial. The differences we can identify are: Larger (trunk length may reach 55 mm), more hooks, and the hook bearing region extends over more (55–75 vs. 25–35%) of the introvert. These are not clear distinctions and may represent only a more optimal set of conditions and less wave action, inducing or permitting a different expression of the genotype (e.g., larger size and more hooks produced or fewer rubbed off, like the situation seen in the Californian/Japanese *T. pyroides*). This hypothesis needs testing.

Distribution.—Australia, New Zealand and Chatham Is.; intertidal, hard substrates.

Themiste variospinosa Edmonds, 1980

Themiste variospinosa Edmonds, 1980:42–43, figs. 62, 68, 69.

Material examined.—A specimen from the collections of S. J. Edmonds from the type locality.

Discussion.—The six worms upon which this species is based have many ecological and morphological similarities to *T. minor huttoni*. The principal difference lies in the nature of the introvert hooks (Fig. 3). They exhibit much greater variation in size on any given worm (30–400 μm tall) and are pointing in all directions, not just posteriorly. While this may be only a localized variation of the surrounding population of *T. minor huttoni*, we propose no change in its status at this time. We hope that additional material will be collected to more firmly test the validity of this taxon.

Distribution.—Queensland, Australia, intertidal coral.

Zoogeographical Summary

The most striking feature is how non-overlapping the two subgenera are. The five *Themiste* (*Themiste*) species live in the western Atlantic, eastern Pacific and Japanese waters. Three of the five *T. (Lagenopsis)* are endemic to Australia/New Zealand, the fourth lives in the western Pacific Ocean and South Africa while the fifth is circum-tropical/subtropical (but absent in the eastern Pacific). Overlap of subgenera exists on Honshu (central Japan) where *T. (T.) blanda* and *T. (T.) pyroides* are found along with *T. (L.) minor*. Another case is the Caribbean (and east coast of Florida) where *T. (L.) lageniformis* and *T. (T.) alutacea* coexist. Southern Argentina may be a third such place, but at this time the data base is not large enough to use with confidence.

Secondly, like in many other genera, there is one very widespread species (the circum-tropical *T. lageniformis*) while most others have rather restricted distributions. Finally, this genus is absent from the North Atlantic above Cape Hatteras on one side and West Africa on the other.

Acknowledgments

The encouragement and shared frustrations as well as the exchange of ideas and specimens with S. J. Edmonds, Adelaide, have contributed greatly to the completion of this work. Our work in Hawaii was accomplished with the assistance of B. Burch, Bishop Museum and M. Hadfield, Kewalo Marine Laboratory, University of Hawaii. The field work in California was dependant on the generous cooperation of F. Hochberg, Santa Barbara, J. Nybakken, Moss Landing, and M. Saffo, Santa Cruz. L. Cutler, Palo Alto, assisted in the lab and field work in Hawaii and California while J. Silverstein, Seattle, provided valuable assis-

tance in California and was responsible for obtaining the karyotypes. J. Swartwout, Utica; G. McDonald, Santa Cruz; and Anne Darling, Clinton, assisted with the artwork. Financial support was provided by the National Science Foundation (grant BSR 83-14301 and BSR 86-15315).

The cooperation of the following persons and institutions in the loan of reference material and/or providing access to their collections was essential to the completion of this project and greatly appreciated: R. Sims (BMNH); H. Levi (MCZH); J. Renaud-Mornant (MNHN); G. Hartwich (MNHU); S. Chambers (RSME); M. Rice (USNM); J. Kirkegaard (UZMK); Zoological Institute Tohoku University, Sendai; M. Dzwillo (ZMUH); Zoological Museum University of Tokyo.

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