The head of Maldanidae polychaetes
of the subfamily Maldaninae

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ABSTRACT

The Maldaninae head and proboscis are described based on dissections of *Asychis amphiglyptus*, *Bathyasychis cristatus*, *Chirimia lobata*, *Maldane sarsi*, *Metasychis disparidentatus*, *Sabaco elongatus*, and *Sonatsa meridionalis*. Consistent features among these species include a well-developed cephalic plate with the rim divided by lateral notches, a wide and muscular palpode, a tri-lobed mouth, and an asymmetrical proboscis. It is suggested that the feeding structure is an axially-modified ventral proboscis. Variable features include the development of the cephalic rim, nuchal organs, palpode, mid-dorsal keel, and proboscis muscles.

RÉSUMÉ

La tête des polychètes Madanidae de la sous-famille des Maldaninae

La description de la tête et du proboscis de *Asychis amphiglyptus*, *Bathyasychis cristatus*, *Chirimia lobata*, *Maldane sarsi*, *Metasychis disparidentatus*, *Sabaco elongatus* et *Sonatsa meridionalis* a été effectuée à partir de dissections. Les principales caractéristiques chez ces espèces sont la présence d'une plaque céphalique bien développée avec un limbe divisé par des échancrures latérales, un palpode large et musculaire, une bouche trilobée, et un proboscis asymétrique. Il est suggéré que cette structure pour l'alimentation provient d'un proboscis ventral axial modifié. Des caractéristiques variables ont été observées sur le développement du limbe céphalique, les organes nucaux, le palpode, la carène médio-dorsale et les muscles du proboscis.

INTRODUCTION

The head is a key feature in the taxonomy of Maldanidae polychaetes. The subfamily Maldaninae (ARWIDSSON, 1907; LIGHT, 1991) is characterized as having a cephalic plate, which refers to the dorsal surface of the head being edged by a raised rim. The cephalic rim is divided by lateral notches into a single posterior border and paired lateral borders. The prostomial palpode is anterior to the plate. Paired nuchal organs occur on the dorsal surface of the plate immediately behind the palpode. A keel (= carina, internuchal ridge, median ridge) refers to a medially raised area between the nuchal organs that may or may not extend into the posterior cephalic border.

Historically, the height and length of the keel was used in keys to separate the Maldaninae genera *Asychis* and *Maldane* (e.g., ARWIDSSON, 1907; FAUCHALD, 1977). However, interpretation of whether the keel is short and

low, or long and high may be difficult (FAUCHALD, 1972: note, keel referred to as palpode). In his revision of the Maldaninae, LIGHT (1991) considered other head features to be of generic importance; i.e., palpode shape, nuchal organ shape, and the development and shape of the lateral borders of the cephalic rim (= lobes, margins) including the degree offusion or separation of them from the palpode.

In contrast to the above features, the mouth and proboscis have received little attention. ARWIDSSON (1907) characterized the maldanin proboscis as being fairly uniform in width, but with a short plate-like bladder at the base, and lacking papillae. ORRHAGE (1973) histologically examined the foregut of *Asychis biceps* and characterized it as a cuticularized ventral sac (with an underlying muscle bulb) beneath a ciliated esophagus. He considered these features to be consistent with DALES (1962) ventral proboscis category.

Muscles concerned with the operation of the maldanin proboscis have not been described. The only available information concerns the maldanid subfamily Euclymeninae (PILGRIM, 1966; KUDENOV, 1977), which have an axial proboscis (ULLMAN & BOOKHOUT, 1949; DALES, 1962; PILGRIM, 1966; ORRHAGE, 1973; KUDENOV, 1977; TZETLIN, 1991). In euclymenins, two paired groups of muscles function as proboscis retractors. The largest set includes the retractor sheath, which inserts on the cuticularized buccal area; and the gular membrane, which inserts on the ciliated esophageal area (sometimes referred to as pharynx). The retractor sheath and gular membrane are considered derivatives of a single septum; their origin on the ventrum marks the boundary between the head and thorax (PILGRIM, 1966). The smallest set of muscles, termed the accessory buccal retractors, insert on the anterior portion of the buccal region (KUDENOV, 1977; PILGRIM, 1966).

The purpose of this paper is to provide additional information about the maldanin head and to describe the foregut and its musculature. Consistency and variability of head features within the subfamily are addressed by examination of representatives of Maldaninae genera recognized by GREEN (1987) and LIGHT (1991): *Asychis*, *Chirimia*, *Maldane*, *Metasychis*, *Sabaco*, and *Sonatsa*.

MATERIALS AND METHODS

Non-type specimens were examined from the Allan Hancock Foundation (AHF) in cooperation with the Los Angeles County Museum of Natural History, and from the author's collection. Material included: *Asychis amphiglyptus*, Antarctica, Hope Bay, 3.5-7.5 m, Staten Island station 46-63 (original label as *Maldane sarsi*) (AHF); *Bathyasychis cristatus*, South America, Peru-Chile Trench, 8°43'S, 80°40'W, 3,939 m, Anton Bruun station AB11-168 (original label as *Sonatsa meridionalis*) (AHF); *Chirimia lobata*: Southern California, San Diego Trough, 32°25'-26°0'N, 117°26.8'-117°28.1'W, 1208-1244 m, trawl, Rokop station 71-45 (original label as *Asychis lobata*) (AHF); *Maldane sarsi*, Arctic Alaska, 71°09.8'N, 151°09.3'W, 45 m (donated by H. JONES); *Maldane* cf. *sarsi*, southern California, Santa Monica Bay, 184 m (donated by L. HARRIS); *Metasychis disparidentatus*, southern California, Newport Beach, 100 m (donated by L. LOVELL); *Sabaco elongatus*, northern California, San Francisco Bay (donated by M. WICKSTEN); *Sonatsa meridionalis*, South America, Peru-Chile Trench, 8°38'S, 80°40'W, 3,590-3,479 m, trawl, Anton Bruun station AB11-165 (AHF). Representatives of all examined species are retained in the AHF.

Terminology used by PILGRIM (1966) and KUDENOV (1977) to describe heads of euclymenins is largely adopted. However, their use of the term pharynx for the ciliated portion of the proboscis is not followed. This is because the term pharynx has been variously defined as a muscular portion of the proboscis (DALES, 1962) or as the entire stomodeal region involved in the uptake of food (PURSCHKE, 1988). Here, the proboscis is considered the protrusile part of the gut; I refer to the cuticularized portion as the buccal mass, and the ciliated portion as the esophagus.

Nuchal organ shape is described with reference to stems and tips. The stem is the end most posterior on the head; the tip is anterior. In the case of recurved nuchal organs, the stem is alongside the internuchal area, and the tip curves away.

Internal features were studied through dissections; a sagittal cut was made through the head and at least the first setiger. Drawings were made using a drawing tube fitted to a dissecting microscope. The surface of the foregut was characterized as cuticularized (i.e., same appearance as the external integument) or ciliated (i.e., finely textured or granular appearance). The presence or absence of cilia was confirmed by examining slide preparations of each type of surface using a compound microscope.

Features identified in the figures are abbreviated, as follows:

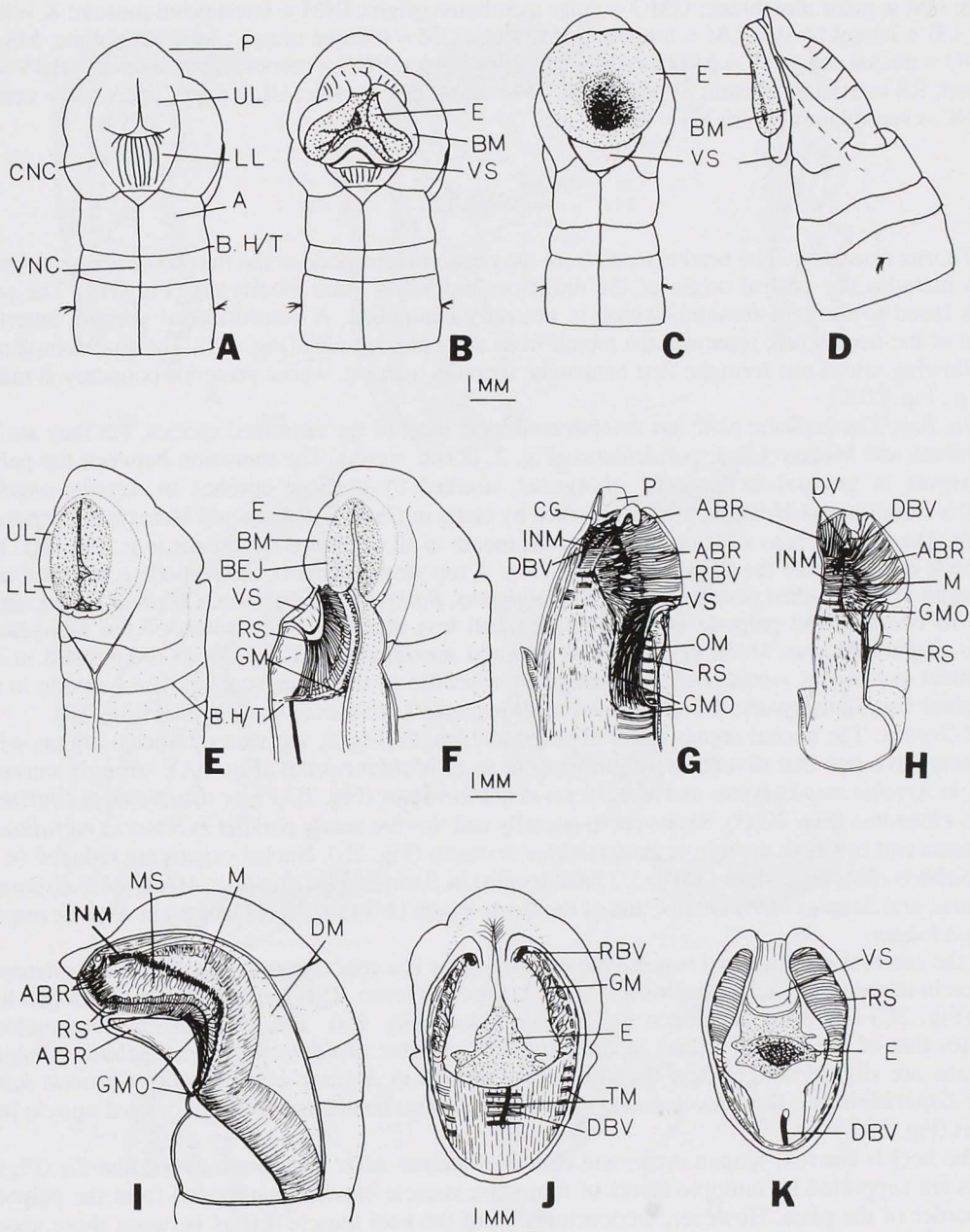A = aboral annulus; ABR = accessory buccal retractors; BM = buccal mass; B.H/T = boundary of head and

FIG. 1. — *Maldane* cf. *sarsi*: A, ventral view of head and first thoracic segment; B, ventral view, proboscis partially retracted; C, ventral view, proboscis everted; D, lateral view, proboscis everted. *Asychis amphiglyptus*: E, ventro-lateral view, proboscis partially everted; F, same view as in E, but with mid-ventral cut and right side folded back; G, internal ventro-lateral view with esophageal portion of proboscis removed; H, ventral view of G. *Maldane sarsi*: I, lateral view with foregut and musculature exposed; J, ventral view of transverse cut made dorsal to retractor sheath; K, dorsal view of head exposed from transverse cut in J. Note: not all blood vessels are shown. See Materials and Methods for definition of letter abbreviations.

thorax; BEJ = bucco-esophageal junction; CG = cerebral ganglion; CM = circular muscle; CNC = circumesophageal nerve connective; DBV = dorsal blood vessel; DM = dorsal mesentery; DV = dorsal valve; E = esophagus; GM = gular membrane; GMO = gular membrane origin; INM = internuchal muscle; K = keel; LL = lower lip; LB = lateral border; LM = longitudinal muscle; OM = oblique muscle; M = membrane; MS = muscle strands; NO = nuchal organs; P = palpode; PB = posterior border; POC = paroesophageal cavity; RBV = retractor blood vessel; RS = retractor sheath; SP = septum; TM = transverse muscle; UL = upper lip; VBV = ventral blood vessel; VNC = ventral nerve cord; VS = ventral sac.

RESULTS

Head/Thorax Boundary. The head extends from the prostomial palpode to the first complete annulus (Fig. 1A-D), which includes the ventral origin of the retractor sheath and gular membrane (Fig. 1E). The prostomial palpode is fused to the peristomium, which is ventrally biannulate. A ventro-lateral groove, anterior to the bifurcation of the nerve cord, separates the mouth from an aboral annulus (Fig. 1A). The first complete annulus and the following setous one form the first biannulate thoracic segment, whose posterior boundary is marked by a septum (e.g., Fig. 2B).

Cephalic Rim. The cephalic plate has smooth borders in most of the examined species, but they are serrate in Chirimia lobata and Metasychis disparidentatus (Fig. 2, dorsal views). The transition between the palpode and lateral margins is gradual in *Sonatsa elongatus*, marked by shallow notches in *Asychis amphiglyptus*, *Bathyasychis cristatus* and *Maldane sarsi*, or marked by clefts in *Chirimia lobata* and *Metasychis disparidentatus*.

Palpode. The palpode is as wide or wider than the mouth in all examined specimens (e.g., Fig 1A). The shape of the palpode complements the shape of the plate (Fig. 2, top views). That is, the palpode is rounded and nearly the same width of the rounded plate in *Asychis amphiglyptus*, *Bathyasychis cristatus*, *Chirimia lobata*, and *Sabaco elongatus*. In contrast, the palpode is spade-shaped and less than 75 % the width of the elongate plate in *Metasychis disparidentatus*, *Maldane sarsi*, and *Sonatsa meridionalis*. The palpode is upturned in *Chirimia lobata*, conical in *Sonatsa meridionalis*, and angular in profile in the other species. The palpode is muscular (Fig. 2, sagittal views); transverse muscle development is greatest in *Sonatsa meridionalis* (Fig. 2B).

Nuchal Organs. The nuchal organs differ in shape and length (Fig. 2, top views). Nuchal organs with nearly parallel stems have tips that diverge or slightly curve as in *Maldane sarsi* (Fig. 2A), strongly curve or bend laterally as in *Asychis amphiglyptus* and *Metasychis disparidentatus* (Fig. 2D,F), or recurve as in *Chirimia lobata* and *Sabaco elongatus* (Fig. 2C,G). Stems curve laterally and tips are nearly parallel in *Sonatsa meridionalis* (Fig. 2B). The stems and tips both diverge in *Bathyasychis cristatus* (Fig. 2E). Nuchal organs are reduced (< 1/6 head length) in *Sabaco elongatus*; short (1/6 to 1/3 head length) in *Bathyasychis cristatus*, *Metasychis disparidentatus*, *Maldane sarsi*, and *Sonatsa meridionalis*; and of moderate length (1/3 to 1/2 head length) in *Asychis amphiglyptus* and *Chirimia lobata*.

Behind the cerebral ganglion and beneath the nuchal organs is a concentration of transversely oriented muscle bundles, herein termed the internuchal muscle (Fig. 2, sagittal views). This muscle is least developed in *Sabaco elongatus* (Fig. 2C) and most developed in *Chirimia lobata* (Fig. 2G). The length of the internuchal muscle approximates that of the nuchal organs in *Bathyasychis cristatus*, *Maldane sarsi*, and *Sabaco elongatus*; the nuchal organs are slightly longer than the internuchal muscle in *Asychis amphiglyptus*, *Chirimia lobata*, and *Metasychis disparidentatus*. Keel development obscures the dorsal boundary of the internuchal muscle in Sonatsa meridionalis (Fig. 2B).

Keel. The keel is convex, long, narrow, and firm in *Maldane sarsi* and *Sonatsa meridionalis* (Figs. 2A,B). These keels are supported by multiple layers of transverse muscle bundles that extend from the palpode to the posterior border of the plate. However, thedevelopment of the keel muscle differs between these species. The transverse muscle bundles are interspersed within a dense layer of longitudinal muscle in *Maldane sarsi*. In contrast, dense aggregations of transverse muscle occur below a layer of longitudinal muscle in *Sonatsa meridionalis*.

Most of the other species have slightly convex (*Metasychis disparidentatus* and *Sabaco elongatus*) to flat (*Asychis amphiglyptus* and *Chirimia lobata*) keels that are marked by a single layer of transverse muscle bundles, the extent of which corresponds to keel length. These keel are relatively narrow and compressible (loses shape when pressed). The keel is relatively wide and firm in *Bathyasychis cristatus* (Fig. 2E). The firmness probably reflects a bulging of the proboscis; there is little space between the esophagus and the inner wall of the head.

Mouth. All examined specimens have a transverse opening and a medially incised upper lip; the lower lip has
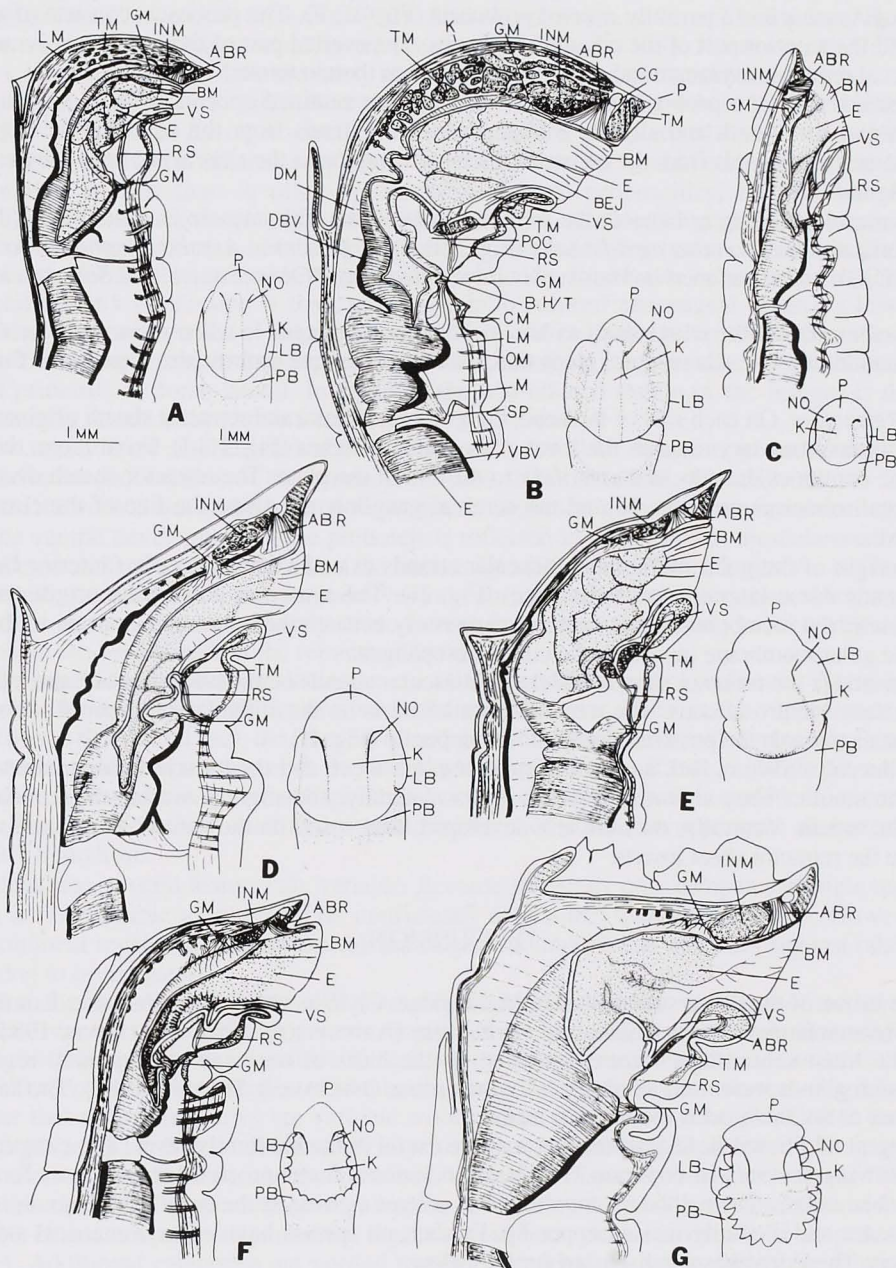
FIG. 2. — Sagittal and dorsal views of heads: A, *Maldane sarsi*; B, *Sonatsa meridionalis*; C, *Sabaco elongatus*; D, *Asychis amphiglyptus*; E, *Bathyasychis cristatus*; F, *Metasychis disparidentatus*; G, *Chirimia lobata*. Notes: All sagittal and dorsal views, respectively, drawn at same scale; scale for each view shown in Fig. 2A. Equivalent features in all sagittal views have same shading pattern, see Fig. 2B for detailed labeling. Not all blood vessels and oblique muscles are shown. See Materials and Methods for definition of letter abbreviations.

several longitudinal folds (e.g., Fig. 1A).

Proboscis. Of the examined material, one specimen of *Maldane* has a fully everted proboscis (Fig. 1C-D), and one specimen of *Asychis* has a partially everted proboscis (Fig. 1E-F). The proboscis consists of a cuticularized buccal mass and the anterior part of the ciliated esophagus. The everted part of the esophagus is cushion-shaped; the everted buccal region is asymmetrical with abasal extension (herein termed ventral sac).

In the retracted state, the proboscis is similar among the examined species (Fig. 2, sagittal views). The cuticularized region is smooth and slightly folded. Part of it extends from the edges of the upper lips to the esophagus. Another part infolds from the corner of the mouth and forms the ventral sac below the esophagus (Fig. 1J-K; Fig. 2, sagittal views).

Transverse muscle may occur beneath the retracted ventral sac. This muscle is relatively well-developed in *Bathyasychis cristatus* and *Sonatsa meridionalis* (Figs. 2B,E), is present in *Asychis amphiglyptus* and *Chirimia lobata* (Figs. 2D,G), and is reduced in *Metasychis disparidentatus*, *Maldane sarsi*, and *Sabaco elongatus* (Figs. 2A,C,F).

The proboscides also differ with regard to how folded the esophagus is when retracted. The folds are taken here as an indication of proboscis volume; given this, the largest volume proboscides were noted for *Bathyasychis* and *Sonatsa*.

Proboscis Retractors. On each side of the head, the gular membrane and retractor sheath originate along a path from the head/thorax boundary towards the level of the lateral notches (Fig. 1G-I). From there, the origin of the gular membrane continues dorsally and anteriorly to the end of the plate. The retractor sheath divergesventrally. Accessory buccal retractors originate behind the cerebral ganglion and along the line of the circumesophageal nerve connectives.

Along the origin of the gular membrane, muscular strands extend ventro-laterally (anterior face) and a thin membrane extends dorso-laterally (posterior face) (Fig. 1I). The muscular part of the origin ends behind the internuchal muscle; the membranous part continues anteriorly beneath the internuchal muscle to the dorsal valve (Fig. 1H-I). The gular membrane inserts on the ciliated esophagus.

This is reversed for the retractor sheath, which has muscular strands on the posterior face and a thin membrane on the anterior face (ventro-lateral). The retractor sheath inserts on the cuticularized ventral sac and the line of insertion continues towards the posterior corner of the upper lip (Fig. 1I).

Accessory buccal retractors lack an obvious membranous sheet, and the muscle strands insert on the buccal mass nearest the mouth. They are most developed dorso-laterally, and slightly overlap the retractor sheath near the corner of the mouth. Ventrally, they are less developed; they insert on the ventral buccal mass, but were not observed where the retractor sheet inserts.

DISCUSSION

Maldaninae is one of the seven subfamilies of Maldanidae: Clymenurinae, Euclymeninae, Lumbriclymeninae, Maldaninae, Nicomachinae, Notoproctinae, and Rhodininae (ARWIDSSON, 1907; DETINOVA, 1985a; IMAJIMA & SHIRAKI, 1982). Most subfamilies were established on the basis of the head and pygidial regions and setal structure, although glands were used to establish Clymenurinae (IMAJIMA & SHIRAKI, 1982). The key head feature has been whether or not the head is modified as a plate.

Results suggest additional head features that may be useful at the subfamily level. The examined specimens shared the following features in common. The head includes a fused prostomium and peristomium, and the peristomium is biannulate. The palpode is muscular and at least as wide as the mouth. The mouth is trilobed with a transverse fissure and medially incised upper lip. Further, all species have an asymmetrical axially-modified ventral proboscis. These features are discussed further below.

The composition of the maldanid head has been controversial, but it is agreed that the prostomium and peristomium are fused (PILGRIM, 1966; LIGHT, 1991). PILGRIM (1966) considered the peristomium of some euclymenins to include an additional fused segment based on the ventral accessory buccal retractors' origin, which she associated with an aboral groove on the ventrum. In maldanins, the ventral origin of these muscles is associated with the nerve connectives rather than the aboral groove. Further, the line oforigin is interrupted by the retractor sheath, and the accessory retractors lack an obvious membrane. For these reasons, I interpret the aboral groove as indicative of a biannulate peristomium rather than a septum.

Palpode development and mouth shape need further assessment in maldanids. Instead of a wide muscular palpode, as in maldanins, some euclymenins have a muscular palpode that is narrower than the mouth (PILGRIM,

1966). However, information about the extent and musculature of the prostomial palpode is lacking for most maldanids. Narrow palpodes are common in clymenurins and euclymenins, and indistinct palpodes are common in the other subfamilies (IMAJIMA & SHIRAKI, 1982). A tri-lobed mouth, as in maldanins, may be unique. Other maldanids have a transverse or longitudinal fissure (IMAJIMA & SHIRAKI, 1982; KUDENOV, 1977; PILGRIM, 1966; TZETLIN, 1991); however, since mouths are rarely mentioned, this feature needs additional study.

Maldanin proboscides appear to differ from the few available reports for other maldanids. ORRHAGE (1973) characterized *Asychis biceps* as having a ventral proboscis because a cuticularized ventral sac (with an underlying muscle bulb) occurs below the ciliated esophagus. He stated that the ventral sac and muscle bulb were less voluminous in this species than in other species with ventral proboscides; i.e., *Nicomache lumbricalis* (Nicomachinae) and *Rhodine gracilior* (Rhodininae), but further detail was not given.Results indicate that the ventral sac is common in maldanins, but the development of the underlying transverse muscle (bulb) is variable. Based on TZETLIN's (1991) illustrations of *Nicomache lumbricalis*, *Nicomache minor*, and *Praxillura longissima* (Lumbriclymeninae), my impression is that the muscle bulb (ventral pharyngeal organ) is less developed in maldanins. Further the configuration of the maldanin proboscis differs from the ventral proboscides of *Nicomache minor* and *Praxillura longissima*. In those species, the non-ciliated region primarily is a ventral structure and the ciliated region primarily is dorso-lateral. In contrast, the non-ciliated region of the foregut is developed both dorsally and ventrally in maldanins, but it forms a narrow sac ventrally.

Because the non-ciliated and ciliated regions evert as a tube-like structure in maldanins, there is some similarity to the axial proboscides of euclymenins (DALES, 1962; PILGRIM, 1966; KUDENOV, 1977; TZETLIN, 1991). However, the ventral sac at the base of the maldanin proboscis gives it an asymmetrical appearance. This difference in the ventral development of the proboscis is reflected in the proboscis musculature. In euclymenins, the gular membrane and retractor sheath share the same origin (PILGRIM, 1966; KUDENOV, 1977). In maldanins, the retractor sheath diverges and follows a more ventral course. Further, accessory buccal retractors, which are well-developed in euclymenins, are mainly dorso-lateral in maldanins and only weakly developed ventrally (presumably due to the ventral path of the retractor sheath).

Accordingly, results suggest that maldanins have a axially-modified ventral proboscis. The axial modification refers to the tube-like appearance of the everted proboscis. However, because the appearance of the tube is asymmetrical (due to the ventral sac), the retractor sheath is ventrally oriented, and a muscle bulb may be present, I consider the structure more consistent with the ventral proboscis category. TZETLIN (1991) provides a hypothesis of proboscideal evolution within the order Capitellida in which the ventral state is considered more primitive than the axial state. Perhaps the axially-modified ventral proboscis of maldanins represents an intermediate state in TZETLIN's (1991) hypothesis.

Within Maldaninae, several features are variable. Because this study only compares a single representative of each genus, it is not possible to comment on consistency of features within each genus. However, results do permit some comment regarding features considered of generic importance, and does suggest other features that may be promising to investigate.

With regard to the cephalic rim, LIGHT (1991) considered the development and shape of the lateral borders and their separation from the palpode as a generic feature. An additional characteristic that may contribute to descriptions of this feature is the development of the notch or cleft that may separate the borders and palpode.

LIGHT (1991) recognized three shapes of Maldaninae palpode; spade-like, mushroom-shaped, and indistinct. Results indicate that shape categories are variable within some genera. For example, LIGHT characterized the palpode of *Asychis* as spade-like, and that of *Metasychis* as mushroom-shaped; however, the examined *Asychis amphiglyptus* has a rounded palpode, and the examined *Metasychis disparidentatus* has a spade-like palpode. It is suggested that descriptions of shape may be improved by considering the profile and thickness of the palpode.

LIGHT (1991) characterized maldanin nuchal organs as four basic shapes (J-shaped, U-shaped, slightly curved, and crescentic). Additional categories are needed to describe nuchal organs in which the stems diverge (as in *Sonatsa*) and in which both stems and tips diverge (as in *Bathyasychis*). It is suggested that descriptions of nuchal organs include reference to stem and tip shape and length. The internuchal muscle appears to relate to characteristics of the nuchal organs (e.g., shape and length), and additional study of this muscle is warranted. The internuchal muscle, which may be prominent in maldanins, has not been investigated for other maldanids.

A cephalic keel, though not considered a generic character by LIGHT (1991), was considered so in the past. Results indicate that the usefulness of the keel as a taxonomic character may be improved by taking into consideration compressibility and width when evaluating the more traditional height and length characters. Examinations of muscle development provides a means to cross check keel designations.

Features of the proboscis vary among the examined species. *Bathyasychis* and *Sonatsa* are similar in having the densest concentrations of transverse muscles beneath the ventral sac, and the largest volume proboscides of the examined species. It is not known whether these similarities are due to feeding in a similar environment (both co-occur at abyssal depths in trenches) or close phylogenetic relationship. Because both taxa have nuchal organs with diverging stems (the tips also diverge in *Bathyasychis*), another feature suggests relationship.

In the past it was questioned whether *Sonatsa* was distinct from *Maldane* since they are morphologically similar (ARWIDSSON, 1922; DETINOVA, 1985b). GREEN (1987) argued for recognition of *Sonatsa* based on nuchal organ shape and the presence of an enlarged ventral glandular pad on setiger 5. The similarities in proboscis development and nuchal organs between *Bathyasychis* and *Sonatsa* support *Sonatsa*'s generic status. So do the differences between *Sonatsa meridionalis* and *Maldane sarsi* in the muscle development of the proboscis, keel, and palpode.

Other species provide an additional example where similarity in external morphology does not correspond with proboscis musculature. For example, *Chirimia lobata* and *Metasychis disparidentatus* have serrate cephalic borders; however, the development of the muscles beneath the ventral sac differ. Proboscis muscles are more similar between *Chirimia lobata* and *Asychis amphiglyptus*; these species also are similar in having well-developed internuchal muscles. Conversely, the appearance of the plaque differs among *Metasychis disparidentatus*, *Maldane sarsi*, and *Sabaco elongatus*, but they are similar in having reduced ventral sac muscles. The internuchal muscle is similar between *Metasychis disparidentatus* and *Maldane sarsi*, but is unique in *Sabaco elongatus*.

Although it is not known at this time which features are more reflective of convergence or relationship, this study supports the status of the genera. It also supports the view that important features include the development of the cephalic rim and nuchal organs. I suggest that proboscis musculature, keel development, and palpode shape may be important, but need further study.

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