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COMPARATIVE STOMATOGENESIS OF TWO ENDOCOMMENSAL SCUTICOCILIATES, *PENICULISTOMA MYTILI* AND *MYTILOPHILUS PACIFICAE* FROM MARINE MYTILID MUSSELS (1)

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SUMMARY

A comparison of stomatogenic sequences of *Peniculistoma mytili* and *Mytilophilus pacificae,* endocommensal ciliates of *Mytilus* mussels, is based on silver-stained specimens. Four characteristics of scuticociliate stomatogenesis are used to construct a hierarchy of stomatogenic similarity. Placement of *P. mytili* and *M. pacificae* within the hierarchy indicates that the species are closely related to *Pleuronema,* but the pair are most closely related to one another. The ciliates, found in different mytilid species, are similar in gross morphology (size, shape, ciliature, and nuclear configuration) but exhibit major differences in adult buccal structure. Despite the disparity in buccal structures, close correspondence in stomatogenesis, gross morphology and habitat indicate a very close phylogenetic relationship.

Key words : *Peniculistoma mytili, Mytilophilus pacificae,* stomatogenesis, mytilid endocommensals, ciliate phylogeny, systematics.

RÉSUMÉ

Comparaison entre les séquences stomatogénétiques de *Peniculistoma mytili* et *Mytilophilus pacificae,* ciliés endocommensaux de la moule, d'après des spécimens imprégnés à l'argent. Quatre caractères ont permis d'établir une hiérarchie des similitudes stomatogénétiques. La position de *P. mytili* et de *M. pacificae* au sein de cette hiérarchie indique que ces deux espèces sont étroitement apparentées au genre *Pleuronema* mais qu'elles sont encore plus proches l'une de l'autre que de tout autre scuticocilié. Ces ciliés, trouvés chez différentes espèces de Mytilides, ont une morphologie générale semblable (dimensions, forme, ciliature et configuration nucléaire) mais diffèrent toutefois très nettement à l'état adulte par leur structure buccale. En dépit des différences constatées, les analogies présentées par la stomatogenèse, la morphologie générale et l'habitat, sont le signe d'une étroite parenté phylogénétique.

Mots-clés : *Peniculistoma mytili, Mytilophilus pacificae,* stomatogenèse, endocommensaux de Mytilides, phylogénie des ciliés, systématique.

INTRODUCTION

In the present study the stomatogenesis of two host-specific *Mytilus* mussel endocommensal ciliates (*Peniculistoma mytili* DE MORGAN, 1925 and *Mytilophilus pacificae* ANTIPA and DOLAN, 1985), is investigated. A number of characteristics links members of the order Scuticociliatida (DE PUYTORAC *et al.,* 1984; SMALL and LYNN, 1985), however, scuticociliates are considered to be united primarily on the basis of their stomatogenic patterns (CORLISS, 1979; SMALL, 1967). The two stomatogenic

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sequences presented here are analyzed within the framework of known scuticociliate patterns in order to verify the taxonomic placement of the species within the Scuticociliatida and to investigate the relationship between the two species. *P. mytili* and *M. pacificae* share a close correspondence in gross morphology yet differ considerably in adult buccal structure.

P. mytili found in *Mytilus edulis* L. (BEERS, 1959; DE MORGAN, 1925; FENCHEL, 1965; KIDDER, 1933; JANKOWSKI, 1964; RAABE, 1949) and *M. pacificae* found in *Mytilus californianus* CONRAD (ANTIPA and DOLAN, 1985) are both kidney-shaped, approximately 100 μm in length, densely ciliated, and have a large ovoid macronucleus and 2-4 micronuclei. The buccal structure of *P. mytili* is reminiscent of that described for *Pleuronema* (GROLIÈRE and DETCHEVA, 1974; SMALL, 1967) with a long, sweeping paroral membrane (pm), bipartite membranelle 2, part as a large buccal structure (m2a) and part as a small hairpin-shaped organelle (m2b) adjacent to membranelle 3 (m3). In contrast to *P. mytili* and other pleuronematine scuticociliates (SMALL and LYNN, 1985), the buccal structure of *M. pacificae* is dominated by m3. A long sweeping pm is present, and m1, m2a and m2b are less developed in comparison to their counterparts in *P. mytili.*

On the basis of gross morphology and habitat, *P. mytili* was originally placed in the genus *Conchophthirus* (DE MORGAN, 1925). Subsequently, the species was removed and given its own genus on the basis of oral structure (KAHL, 1934; RAABE, 1934). JANKOWSKI'S (1964) appellation *Peniculistoma* has been accepted as the first non-homonymic name proposed (CORLISS, 1979; FENCHEL, 1965) despite the objections of CANELLA (1970). Jankowski placed *P. mytili* within the Pleuronematina *(sensu lato)* (JANKOWSKI in FENCHEL, 1965), and when Fenchel re-described *P. mytili,* he gave the species its own family, Peniculistomatidae, and placed it within the order Thigmotrichida *(sensu lato)* (FENCHEL, 1965). SMALL (1967) placed *P. mytili* within the suborder Pleuronematina of the order Scuticociliatida on the basis of an incomplete stomatogenic sequence. *M. pacificae* has been provisionally placed in the family Peniculistomatidae on the basis of gross morphology and habitat (ANTIPA and DOLAN, 1985). We resolve, here, stomatogenesis-related questions of the taxonomic placement for both *Peniculistoma* and *Mytilophilus.* A preliminary report of this investigation has appeared (DOLAN and ANTIPA, 1982).

MATERIALS AND METHODS

Host collection, maintenance and examination

Peniculistoma mytili were isolated from the mantle cavities of *Mytilus edulis* L. collected either during low tides in rocky areas of San Francisco Bay or from floating docks at marinas around the bay. *Mytilophilus pacificae* were isolated from the mantle cavities of *Mytilus californianus* Conrad collected during low tides from several locations on the Pacific coast between Moss Beach and Pigeon Point, California. Host mussels were held in separate aquaria of appropriate salinity and examined as soon as possible after collection.

The following procedure was used to remove ciliates from the host mussels. Mussel valves were pried open, without cutting adductor muscles. Filtered sea water was vigorously squirted across the mantle cavity, and the resulting rinse fluid was collected in a syracuse dish. Ciliates were individually removed from the syracuse dish with a micropipette and placed into the appropriate fixative for subsequent staining. The procedure was repeated three to ten times for each mussel.

Cytological techniques

Two methods of silver-staining were used, the silver nitrate method of CHATTON and LWOFF (CORLISS, 1953) and the silver protein protargol method of BODIAN (KIRBY, 1950). Dr. T. FENCHEL kindly provided slides of stained *P. mytili* collected from Scandinavian *M. edulis.*

Ciliates undergoing binary fission, and therefore stomatogenesis, were identified by their characteristic cell shape, nuclear morphology and pattern of somatic ciliation. Observations of stomatogenic events were made almost exclusively from protargol-stained cells. Approximately 100 dividing specimens of *P. mytili* and 150 specimens of *M. pacificae* were examined for construction of the stomatogenic sequences. Stomatogenic stages were arranged by matching them with the serial changes in cell shape, nuclear morphology and somatic ciliation which characterize cell division and have been shown to be tightly coupled with stomatogenic events (ANTIPA and HATZIDIMITRIOU, 1981). Drawings were based on camera lucida sketches.

In the case of *M. pacificae,* the location of membranelles often required observation of the oral area from an indirect perspective. Hence, drawings are of specimens oriented at slight but significant differences in angle. This sometimes yields an impression of a major change in the shape or location of primordia. Such is not the case unless specifically mentioned in the text.

RESULTS

Peniculistoma mytili

A description of this organism appears elsewhere (FENCHEL, 1965). Buccal organelles consist of a paroral membrane (pm) and three membranelles (m1, m2, m3) (Fig. 1). The pm lies along the right margin of the oral area. M1 lies along the left margin of the oral area and circles its posterior margin. M2a is found between m1 and the pm, and parallels m1. M2b appears as a double row of

kinetosomes in a hairpin formation to the right of the posterior quadrant of m2a. M3 is a curved field of kinetosomes posterior to m2b and perpendicular to m2a.

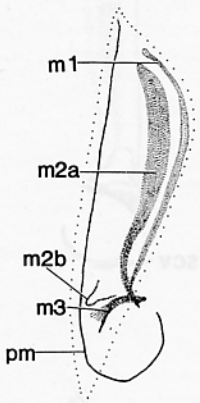


FIG. 1. — Buccal structure of *Peniculistoma mytili* based on protargol-stained specimens. m1, m2a, m2b, m3: adoral organelles; pm: paroral membrane. See Results section for explanation.

Early stomatogenic stages of *P. mytili*

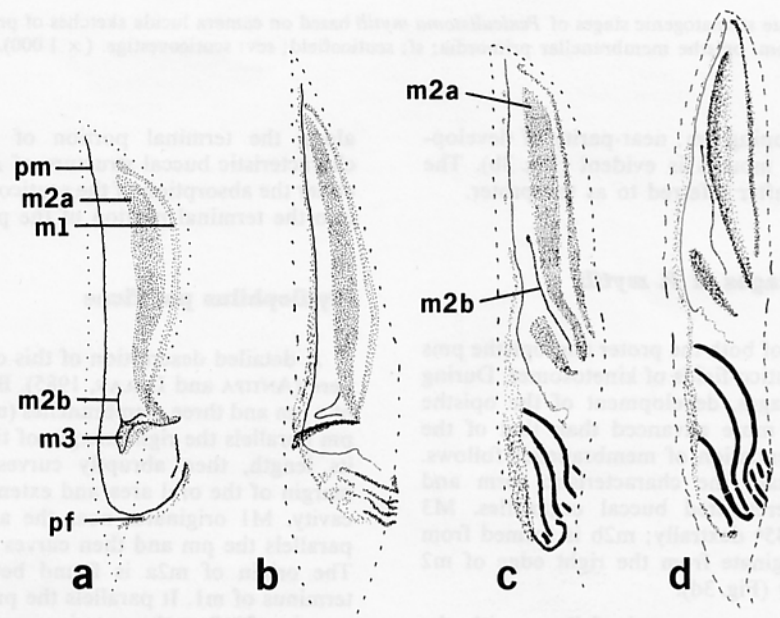
Stomatogenesis begins with the formation of a small field of ciliated kinetosomes, the primordial field (pf), along the terminal portion of the pm (Fig. 2a). Subsequently, parental buccal dedifferentiation begins. M1 and m2a become centered in the anterior half of the enlarged oral area while the primordial field develops in the posterior third of the oral area with the contribution of kinetosomes which originate along the length of the pm (Fig. 2b).

Parental buccal dedifferentiation proceeds with the unfolding and anterior migration of m2b. The kinetosomes of m1, m2a, and m3 all appear less regularly arranged. At this stage, the primordial field begins to become organized into distinct membranellar primordia as dense groups of kinetosomes form (Fig. 2c).

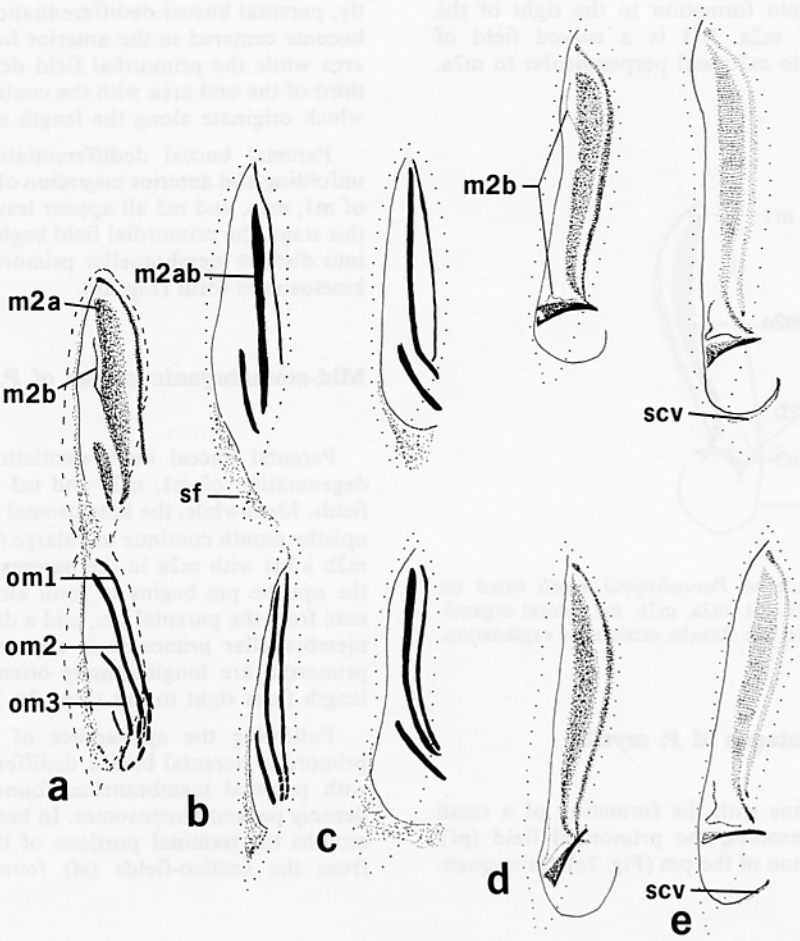
Mid-stomatogenic stages of *P. mytili*

Parental buccal dedifferentiation continues with the degeneration of m1, m2a and m3 into loosely organized fields. Meanwhile, the kinetosomal units of the developing opisthe mouth continue to enlarge (Fig. 2d). Subsequently, m2b joins with m2a in the parental mouth. At this stage, the opisthe pm begins to form kinetosomes which originate from the parental pm, and a distinctive array of three membranellar primordia is apparent. The membranellar primordia are longitudinally oriented and of increasing length from right to left (Figs. 3a, 7).

Following the appearance of distinct membranellar primordia, parental buccal dedifferentiation is concluded with parental membranelles found as narrow fields of densely packed kinetosomes. In both parental and opisthe mouths the terminal portions of the pms begin to form from the scutico-fields (sf) found near the posterior



FIGS. 2a-2d. — Early and mid-stomatogenic stages of *Peniculistoma mytili* based on camera lucida sketches of protargol-stained specimens. pf: primordial field. (× 1 000).



FIGS. 3a-3e. — Mid- and late stomatogenic stages of *Peniculistoma mytili* based on camera lucida sketches of protargol-stained specimens. om: opisthe membranellar primordia; sf: scuticofield; scv: scuticovestige. (× 1 000).

terminus of each developing pm; near-parity of development between the two mouths is evident (Fig. 3b). The parental mouth is hereafter referred to as the proter.

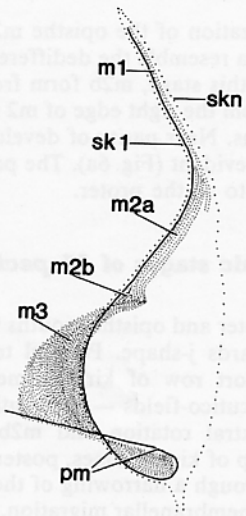
Late stomatogenic stages of *P. mytili*

The terminal curves of both the proter and opisthe pms are formed from the scutico-fields of kinetosomes. During this and subsequent stages, development of the opisthe appears to be slightly more advanced than that of the proter (Fig. 3c). Differentiation of membranelles follows. M1, m2a and m3 attain the characteristic form and position of fully differentiated buccal organelles. M3 rotates approximately 45° dextrally; m2b is formed from kinetosomes which originate from the right edge of m2 and migrate posteriorly (Fig. 3d).

The final stage of stomatogenesis follows with the appearance of a short row of kinetosomes, apparent remnants of the scutico-field — the scuticovestige (scv), along the terminal portion of the pm (Fig. 3e). The characteristic buccal structure of *P. mytili* is reached with either the absorption of the scuticovestige or its integration into the terminal portion of the pm.

Mytilophilus pacificae

A detailed description of this organism appears elsewhere (ANTIPA and DOLAN, 1985). Buccal organelles consist of a pm and three membranelles (m1, m2, m3) (Fig. 4). The pm parallels the right margin of the oral area for most of its length, then abruptly curves around the posterior margin of the oral area and extends deep into the buccal cavity. M1 originates near the anterior end of the pm, parallels the pm and then curves slightly toward the left. The origin of m2a is found between the pm and the terminus of m1. It parallels the pm and joins the anterior margin of m3 at the anterior aspect of the buccal cavity. M3 originates at a 'v' formation adjacent to the terminus of m2a and forms a sheet of kinetosomal rows which

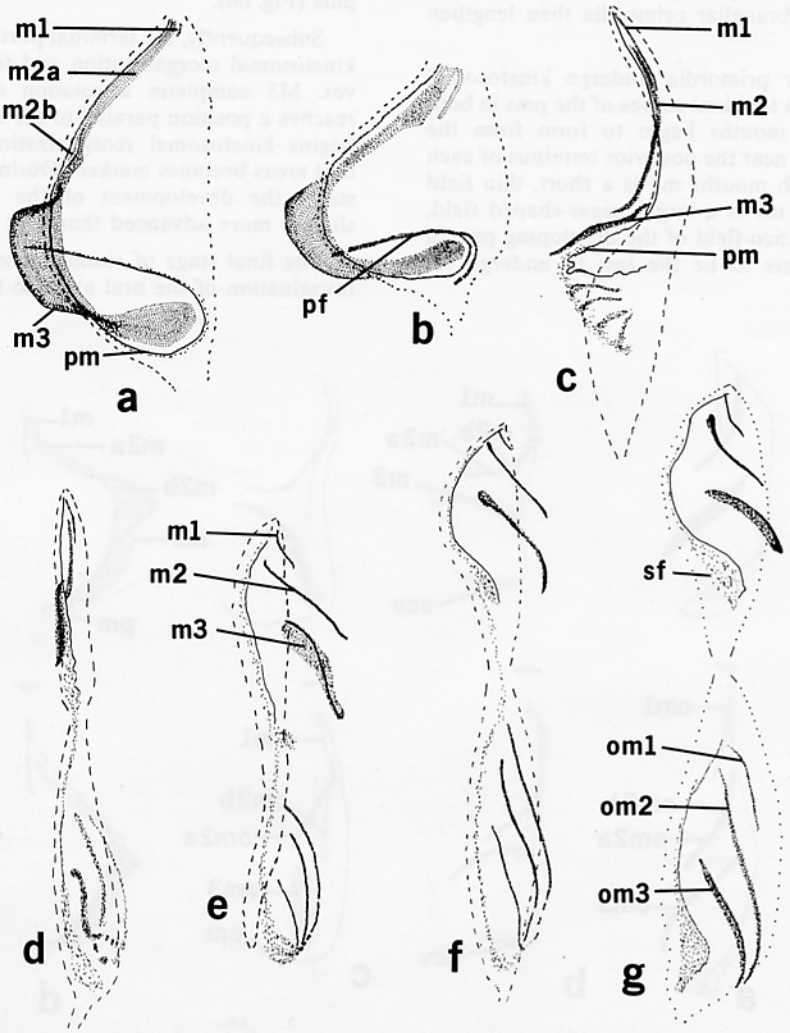


encircle the right side of the buccal cavity. M2b appears as three rather inconspicuous and loosely organized rows of kinetosomes which bridge the 'v' formed by the terminus of m2a and the origin of m3.

Early stomatogenic stages of *M. pacificae*

Stomatogenesis begins with the replication of kinetosomes along the length of the pm (Fig. 5a). Subsequently, the formation of the primordial field (pf) begins as a dense bar of kinetosomes along the terminal portion of the pm. Also, parental buccal dedifferentiation begins as the

FIG. 4. — Buccal structure of *Mytilophilus pacificae* based on protargol-stained specimens. sk1 : somatic kinety 1; skn : somatic kinety n; other abbreviations as in Fig. 1 (× 1 000).



FIGS. 5a-5g. — Early and mid-stomatogenic stages of *Mytilophilus pacificae* based on camera lucida sketches of protargol-stained specimens. Abbreviations as in Fig. 2. (× 1 000).

terminus of m2a, the origin of m3 and the kinetosomes of m2b become indistinguishable from each other (Fig. 5b).

The primordial field develops in the posterior half of the oral area with kinetosomal contribution from the pm. At this stage m3 has formed a cigar-shaped field and has become distinct from m2. M1, m2 and m3 occupy the anterior half of the enlarged oral area (Fig. 5c).

The primordial field now begins to become organized into distinct membranellar primordia as dense groups of kinetosomes form, and the parental buccal membranelles are greatly reduced in size (Fig. 5d).

Mid-stomatogenic stages of *M. pacificae*

The opisthe pm begins formation from kinetosomes which originate from the parental pm. Simultaneously, a distinctive array of three membranellar primordia is apparent. The membranellar primordia are longitudinally oriented and of increasing length from right to left (Figs. 5e, 8). The membranellar primordia then lengthen (Fig. 5f).

Next, membranellar primordia undergo kinetosomal re-organization, and the terminal curves of the pms in both parental and opisthe mouths begin to form from the scutico-field (sf) found near the posterior terminus of each developing pm. In both mouths m1 is a short, thin field located anteriorly and m3 is a larger, cigar-shaped field, found opposite the scutico-field of the developing pm. In the opisthe, m2 appears to be the last to undergo re-organization (Fig. 5g).

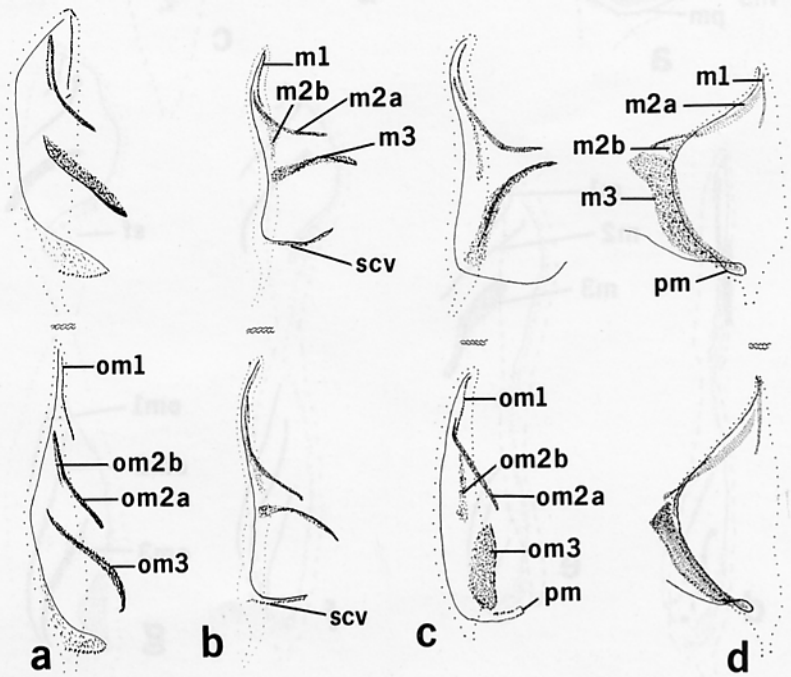
After re-organization of the opisthe m2, opisthe membranellar primordia resemble the dedifferentiated parental membranelles. At this stage, m2b form from kinetosomes which originate from the right edge of m2 in both parental and opisthe mouths. Near parity of development between the two mouths is evident (Fig. 6a). The parental mouth is hereafter referred to as the proter.

Late stomatogenic stages of *M. pacificae*

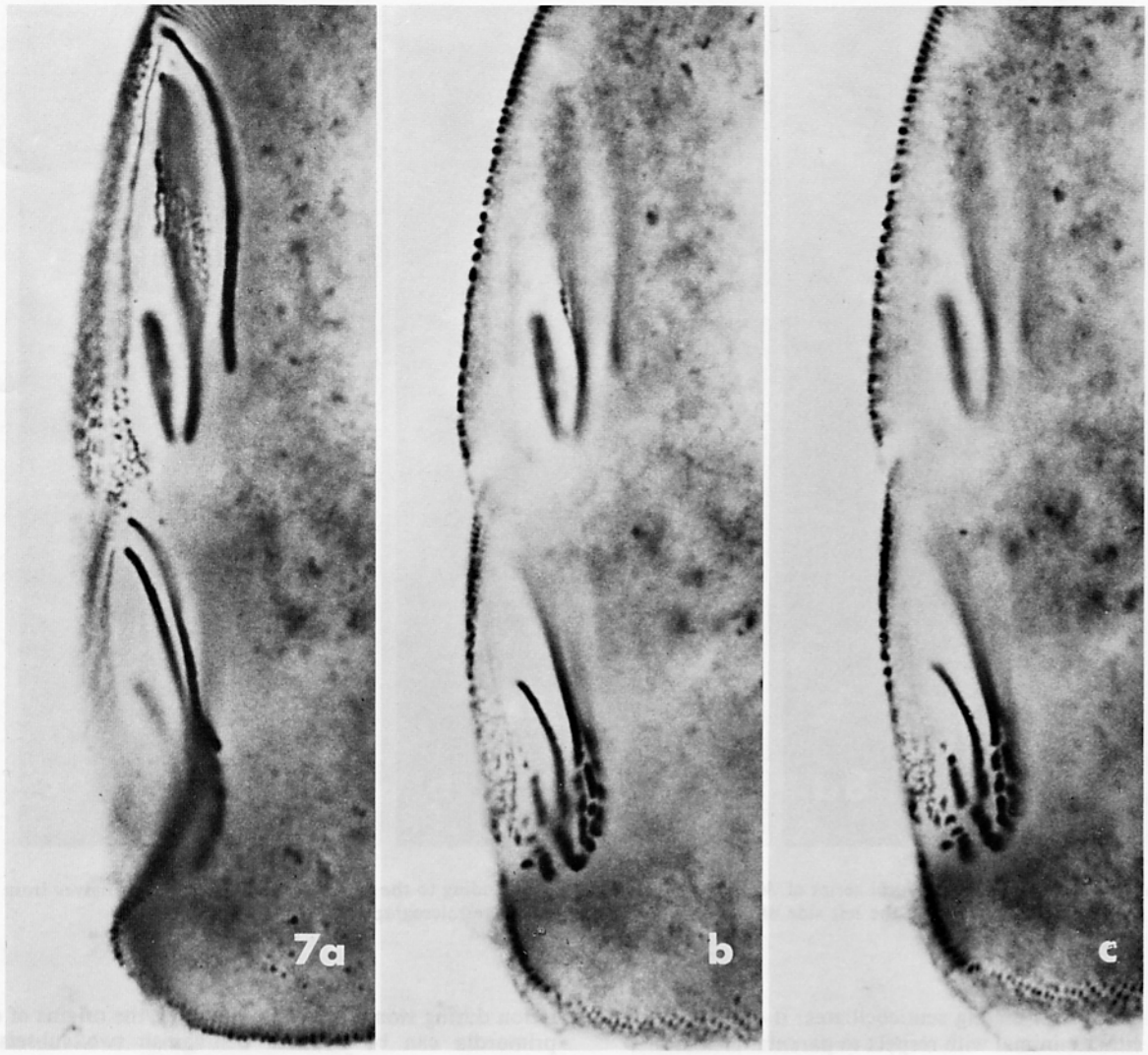
In both the proter and opisthe mouths the pms begin to take on a backwards j-shape. Parallel to the termini of each pm is a short row of kinetosomes, the apparent remnants of the scutico-fields — the scuticovestiges (scv). M3 begins a dextral rotation and m2b appears as an unorganized group of kinetosomes, posterior to the center of m2a. Either through a narrowing of the anterior end of the oral areas or membranellar migration, or both, m1 and the origin of m2a comes to lie parallel to the respective pms (Fig. 6b).

Subsequently, the terminal portions of the pms undergo kinetosomal reorganization and form their posterior curves. M3 completes a rotation of approximately 180°, reaches a position parallel to the long axis of the pm, and begins kinetosomal reorganization. Invagination of the oral areas becomes marked. During this and the following stage, the development of the opisthe appears to be slightly more advanced than that of the proter (Fig. 6c).

The final stage of stomatogenesis includes the further invagination of the oral areas to form the buccal cavities



FIGS. 6a-6d. — Mid- and late stomatogenic stages of *Mytilophilus pacificae* based on camera lucida sketches of protargol-stained specimens. Wavy lines represent progressively larger spaces removed from original drawings. Abbreviations as in Fig. 3. (× 1 000).



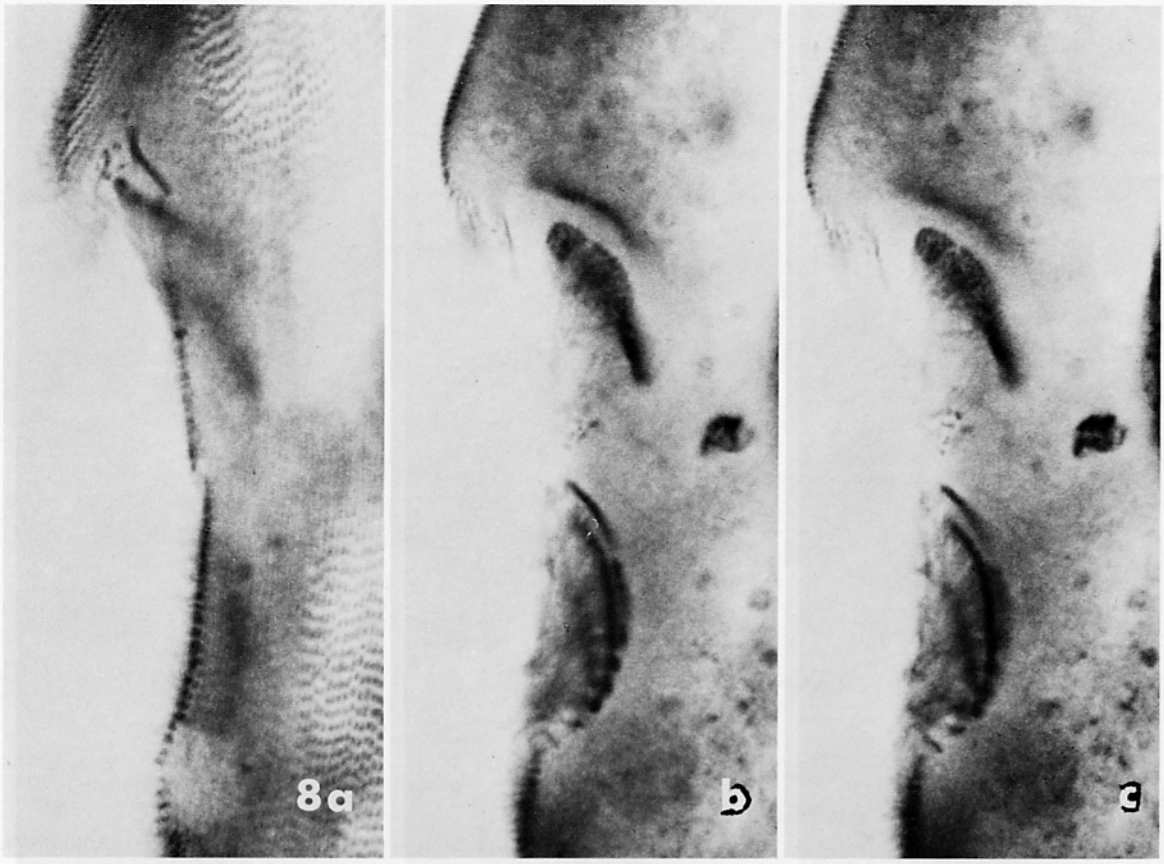
FIGS. 7a-7c. — Photomicrograph focal series of *Peniculistoma mytili* corresponding to the stage seen in Fig. 3a. Focus moves from the right to the left side of the oral area in the respective micrographs a-c. (× 1 600).

characteristic of trophic cells. The differentiation of the buccal cavities is probably responsible for the orientation of buccal organelles in the position of fully developed buccal organelles. The characteristic buccal structure of *M. pacificae* is reached with the completion of the kinetosomal reorganization of m3 (Fig. 6d).

DISCUSSION

Three major characteristics of the stomatogenesis of *P. mytili* and *M. pacificae* are seen in all patterns of scuticociliate stomatogenesis : 1) Oral primordia derived from buccal organelles, 2) Scutico (hook) configuration of the developing pm, and 3) Parental buccal dedifferentiation (ANTIPA and HATZIDIMITRIOU, 1981; HATZIDIMITRIOU and BERGER, 1977; PECK, 1974). Thus, *P. mytili* and *M. pacificae* may be identified as scuticociliates. Two characteristics of the stomatogenic pattern, the exact origin of oral primordia and the extent of parental membranellar dedifferentiation, provide a means of easily distinguishing the major groups of scuticociliates. These characteristics have been employed in the diagnosis of specific scuticociliate stomatogenic patterns and to determine generic affinities (EVANS 1969; RAMSEY *et al.*, 1980; SMALL, 1967).

The oral primordia of scuticociliates are derived either from the pm *and* a separate set of kinetosomes located posterior or parallel to the pm or solely from the pm (ANTIPA and HATZIDIMITRIOU, 1981; HATZIDIMITRIOU and BERGER, 1977). The degree of parental buccal dedifferen-



FIGS. 8a-8c. — Photomicrograph focal series of *Mytilophilus pacificae* corresponding to the stage seen in Fig. 5e. Focus moves from the right to the left side of the oral area in the respective micrographs a-c. (× 1 600).

tiation also varies among scuticociliates; it can be identified as either minimal with respect to parental membranelles or involving changes in both the shape and orientation of the parental membranelles.

Philasterine stomatogenesis is marked by oral primordia derived from the pm and kinetosomes located posterior to the pm plus minimal parental membranellar dedifferentiation. These stomatogenic pattern attributes have been seen in all genera of the suborder Philasterina studied to date (*Anophryoides* DE PUYTORAC and GROLIÈRE, 1979; *Cinetochilum* DE PUYTORAC *et al.*, 1974; *Cohnilembus* DIDIER and DETCHEVA, 1974; *Dexiotricha* PECK, 1974; *Metanophrys* DE PUYTORAC *et al.*, 1974; *Paralembus* GROLIÈRE, 1974; *Paranophrys* DIDIER and WILBERT, 1976; GROLIÈRE and LEGLISE, 1977; *Pauronema* GROLIÈRE, 1974; *Philaster* GROLIÈRE, 1974; COATS and SMALL, 1976; *Philasterides* GROLIÈRE, 1980; *Potomacus* RAMSEY *et al.*, 1980; *Pseudocohnilembus* EVANS and CORLISS, 1964; *Sathrophilus* GROLIÈRE, 1973; *Uronema* FOISSNER, 1972; *Urozona* GROLIÈRE, 1975).

All non-philasterine scuticociliates exhibit considerable parental membranellar dedifferentiation with the parental membranelles showing changes in shape as well as orientation during stomatogenesis. However, the origins of oral primordia can be used to distinguish two subsets of non-philasterine scuticociliates. The derivation of oral primordia from the pm *and* segments of kinetosomes posterior or parallel to the pm have been found in three genera; *Ancistrum* (HATZIDIMITRIOU and BERGER, 1977), *Conchophthirus* (ANTIPA and HATZIDIMITRIOU, 1981) and *Cyclidium* (GROLIÈRE, 1980). Two genera of scuticociliates studied thus far have been found to exhibit both great parental membranellar dedifferentiation and oral primordia derived solely from the pm : *Pleuronema* (GROLIÈRE and DETCHEVA, 1974; SMALL, 1967) and *Histiobalantium* (DRAGESCO and IFTODE, 1972). The *Pleuronema-Histiobalantium* stomatogenic pattern set which is defined by the paroral origin of all oral primordia and great parental membranellar dedifferentiation includes both *P. mytili* and *M. pacificae.*

The *Pleuronema-Histiobalantium* stomatogenic pattern set can be subdivided according to characteristics of opisthe membranellar development. *Pleuronema, P. mytili* and *M. pacificae* all develop a bipartite m2 and do so in a similar manner: a small segment of kinetosomes separates from the main body of the m2 primordium and

migrates posteriorly. *Histiobalantium* stomatogenesis does not display this characteristic. Additionally, *P. mytili* and *M. pacificae* share a characteristic of membranellar development which distinguishes them from *Pleuronema* and all other scuticociliates with known stomatogenic patterns. Buccal membranelles in *P. mytili* and *M. pacificae* arise from a distinct array of three, longitudinally oriented membranellar primordia which increase in length from left to right (Figs. 3a, 5e).

Based on parental membranellar dedifferentiation, origin of oral primordia and development of a bipartite m2, *P. mytili* and *M. pacificae* appear most similar to *Pleuronema*. Thus, Small's placement of *P. mytili* within the suborder Pleuronematina (SMALL, 1967) appears justified as well as Jankowski's earlier inclination to remove *P. mytili* from the Thigmotrichida *(sensu lato)* (JANKOWSKI *in* FENCHEL, 1965). The provisional placement of *M. pacificae* in the family Peniculistomatidae, originally based on grounds of gross morphology and habitat (ANTIPA and DOLAN, 1985), also appears justified. If the degree of correlation in stomatogenic pattern is considered as a direct indication of phylogenetic relation, then *M. pacificae* is most closely related to *P. mytili* of all known scuticociliates.

The use of stomatogenic data to show homology in buccal structure and thus common descent is well established (CORLISS, 1974). Historically, stomatogenic data have been used to establish homology in buccal structure among the thigmotrichs (CHATTON and LWOFF, 1949), between hymenostomes and spirotrichs (FURGASON, 1940) and unite as well as divide the hymenostomes (FAURÉ-FREMIET, 1950; SMALL, 1967). More recently, stomatogenic data have led to hypotheses of homologous buccal organelles among nassulids and peniculines (SHI, 1980), peniculines and scuticociliates (ANTIPA and HATZIDIMITRIOU, 1981) and scuticociliates and peritrichs (ANTIPA and HATZIDIMITRIOU, 1981; EPERON, 1980). However, within the order Scuticociliatida, the sole ciliate order united primarily by stomatogenic pattern (CORLISS, 1979), the use of stomatogenic data to establish relations has presented some problems.

Many variations of scuticociliate stomatogenic patterns are now known to exist, most of which were unknown to Small when he created the order (RAMSEY *et al.*, 1980). Differences in pattern have been found within a single family (DE PUYTORAC and GROLIÈRE, 1979) and similarities in pattern have been found among members of different suborders previously believed to be pattern distinct (GROLIÈRE, 1980). However, the present study reiterates Small's assertion that among scuticociliates divergent buccal structures can mask phylogenetic relationships (SMALL, 1967). The evidence presented here indicates that *P. mytili* and *M. pacificae* correspond in stomatogenesis as well as general morphology and ecology. Thus the conclusion that *P. mytili* is most closely related to *M. pacificae* appears justified despite obvious differences in buccal structure. Investigations now underway, utilizing different kinds of evidence, attempt to further test character correspondence between *P. mytili* and *M. pacificae* and perhaps shed light on precisely how the two species may be related.

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