SPAWNING BEHAVIOR AND LARVAL DEVELOPMENT IN *MOPALIA LIGNOSA* AND *MOPALIA MUSCOSA* (MOLLUSCA: POLYPLACOPHORA) IN CENTRAL CALIFORNIA

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INTRODUCTION

The genus Mopalia (Mollusca, Polyplacophora) is represented by 14 species along the California coast (Burghardt and Burghardt, 1969). Among the common forms in central California are Mopalia muscosa (Gould, 1846), Mopalia lignosa (Gould, 1846), Mopalia ciliata (Sowerby, 1840), and Mopalia hindsii (Reeve, 1847). Though relatively well known taxonomically, little is known of the spawning behavior and larval development of this genus. Heath (1905) made brief mention of spawning in M. lignosa and M. muscosa in the field. Thorpe (1962) studied spawning in M. lignosa, M. muscosa, M. ciliata, M. hindsii, M. imporcata (Carpenter in Pilsbry, 1892), and M. porifera (Pilsbry, 1892). He also made some general observations on the larval development of M. ciliata. Comparable information on larval development in other species of this genus is not available. We chose to study development in M. muscosa and M. lignosa in part to fill this gap and because these species are common and known to spawn in the spring (Heath, 1899; Boolootian, 1964). Our aim was to determine the main sequence of events in larval development and its time schedule. The development of M. muscosa was followed by Cox, while that of M. lignosa was followed by Watanabe. A strong effort was made to standardize experimental procedures and presentation of results so that

comparisons between the two would be valid and clear. The work was carried out at Hopkins Marine Station of Stanford University during the months of April-June, 1974.

METHODS AND MATERIALS

Specimens of Mopalia lignosa were collected under low rocks at Mission Point, Carmel Bay, California. M. muscosa were collected at the same location and from rocks in the mid-tide zone of Point Pinos, Pacific Grove, California. Heath (1905, p. 392) maintains that Katharina tunicata (Wood, 1815) attains sexual maturity at two years, reaches a length of 25mm the firstyear and adds 8-11mm the second year. He states that this is also characteristic of both M. lignosa and M. muscosa, therefore only larger animals (50-60mm long) were taken, to insure sexual maturity. Once in the laboratory, the chitons were maintained in circulating seawater aquaria.

Embryos were reared in 5-inch finger bowls cleaned with concentrated nitric acid followed by detergent and thorough rinsing. Fertilized eggs were pipetted from the aquaria (see Spawning), rinsed in fresh sea water several times and placed in thin layers in bowls with one-half-inch of sea water. Both natural sea water filtered through coarse filter paper and artificial sea water (Instant Ocean Synthetic Sea Salts) were used. Little difference was found between the two and only filtered natural sea water was used for embryos from the late free-swimming stage on. From 0.1 to

0.3ml of a mixture of 0.5g streptomycin and 300,000 units of penicillin in one liter of distilled water was added to the bowls to control bacterial growth. Water in the bowls was changed by decanting off about one-half the volume of water and pouring the remainder of the culture, containing nearly all the larvae, into a clean finger bowl. This was done every 4 hours for the first 12 hours of development and twice daily for the later stages. The finger bowls were covered with glass plates and maintained partially immersed in running sea water at 13.5°-15.8°C. Around the time of settling, eroded fragments of Mytilus shell covered with a green algal film were added to most of the bowls as a settling surface.

Observations of the structure and behavior of living larvae were made in finger bowls under a dissecting microscope and in wet whole mounts under a compound microscope. For permanent whole mounts, larvae were fixed in Bouin's fluid and stained in dilute acidulated Grenacher's borax carmine (Galigher and Kozloff, 1964). Due to the large amount of yolk in the larvae, little internal differentiation could be discerned.

SPAWNING

To obtain gametes, attempts were made to induce spawning in the laboratory using methods which have produced positive results in gastropods and other invertebrates. The

methods tried were the following (M.l.= Mopalia lignosa, M.m.= Mopalia muscosa. Numerals preceding these indicate numbers tested):

1. Dilation of gonopores by insertion of glass probe, followed by placement of animals in standing seawater; 2 M.l., 1 M.m. No spawning in 1 hour.
   Ref. Gould (1967) for Urechis.
2. Electrical stimulation of gonopores (15v @ 50 cycles AC for 5 sec.) followed by placement in standing seawater; 3 M.l., 2 M.m. No spawning in 1.5 hours.
   Ref. Iwata (1950) for Mytilus edulis Linnaeus, 1758.
3. Electrical stimulation of exposed lateral nerve cord (15v @ 50 cycles AC for 5 sec.) followed by placement in standing seawater; 1 M.l., 1 M.m. No spawning in 1 hour.
   Ref. Harvey (1956) for echinoids.
4. Injection of 0.2ml 0.5M KCl into perivisceral hemocoel or through pallial groove followed by placement in standing seawater; 3 M.l., 3 M.m. Caused strong body contraction in 3 minutes but no spawning in 4 hours.
   Ref. Harvey (1939) for echinoids.
5. Injection of nerve tissue homogenate into perivisceral hemocoel, followed by placement in standing seawater; 1 M.m. No spawning in 1 hour.
   Ref. Davis, Mpitsos, and Pinneo (1973) for Pleurobranchaea.
6. Eggs dissected from ovaries and treated for one hour with 3ml 0.1N NaOH in 100ml seawater, inseminated with sperm obtained by dissection; 1 M.l., 1 M.m. Eggs not fertilizable with active sperm.
   Ref. Wolfsohn (1907) for Acmaea.

7. Several ml sperm solution obtained from dissected male gonad added to aquaria containing chitons; 7 M.l., 5 M.m. No spawning in 5 hours. Ref. Heath (1905) that sperm released by males may cause female spawning.
8. Water in tank containing chitons allowed to stand and become stale. Temperature slightly elevated (15°C.); 7 M.l., 7 M.m. Spawning occurred though not consistently. Ref. Grave (1932) for Chaetopleura apiculata (Say).

Still water at temperatures slightly above ambient ocean temperature seem to be common conditions for natural spawning. Ishnochiton magdalenensis (= Stenoplax heathiana Berry, 1946) was observed spawning in tide pools during early morning low tides (Heath, 1899, p. 5). Grave (1932) and Christiansen (1954) obtained spawning in Chaetopleura apiculata and Lepidopleurus asellus (Spengler), respectively, by allowing them to sit in non-circulating sea water at slightly elevated temperatures for several hours. While similar conditions were present when Mopalia lignosa spawned in the lab, these conditions were not sufficient for consistent release of gametes. Male and female Mopalia muscosa spawned together on one occasion in a tank with circulating seawater at a temperature of approximately 13°C. Isolated females spawned in finger bowls in which the water had been allowed to stand for a day. Thus, no coherent pattern of spawning conditions could be established.

Thorpe (1962) reports that Mopalia muscosa and Mopalia lignosa may spawn in the lab at times corresponding to certain phases of the local tidal cycle. We could not resolve any such correlation.

Detailed observations of spawning behavior were made only for Mopalia lignosa. In two instances, once in the late afternoon and once at night, 7 to 10 chitons placed in a large plastic dish pan partially filled with non-circulating seawater spawned after several hours. The pan was tilted so that the water reached only part way up the inclined bottom. During spawning, the girdle was elevated anteriorly and postero-laterally. In both sexes the posterior tip of the girdle margin was raised to form a spout through which a single stream of gametes was released. The four males observed spawning were more active than females during the process. They released intermittent spurts of sperm in long, thin streams which pooled in masses at the bottom of the tank and diffused into the water only slowly. The duration of each continuous sperm release was 3-5 minutes, separated by intervals of 5-15 minutes. Two of the three females observed spawning were partially out of water, with only their posterior ends submerged; all remained stationary. Eggs flowed slowly out in single file, loosely held together by a thin mucus sheath, and piled up behind the animal.

Small disturbances, including a brief removal from water, interrupted but did not permanently stop spawning. Thorpe (1962) reported that in his experience only the close proximity of a strong, hot light would halt spawning: agitation and inversion of the animals would not.

DEVELOPMENT OF MOPALIA LIGNOSA

A time schedule of development for Mopalia lignosa is given in Table I. The various stages of development are shown in Figure 1.

Early Development

The eggs were light green and about 0.2mm in diameter. They were very yolky and were surrounded by a transparent, frilly chorion (Figure 1 A). Once fertilization occurred, a small space appeared between the egg and the chorion (Figure 1 B). Cleavage was typically spiral (Figure 1 C-F).

Gastrulation begins with an invagination of the macromeres (Heath, 1899, p. 50). A slight invagination was observed in several embryos 10-12 hours after fertilization but was never positively identified as the blastopore. Beating of the prototrochal cilia began about 12 hours after fertilization. Just before hatching (19 hours), the strongly beating cilia stopped for several minutes. When beating resumed, small portions of the chorion broke away and the trochophore struggled out anterior end first using both muscular contractions of the body and ciliary beat (Figure 1 H). The hatching process occupied approximately 5

minutes.

Free Swimming Trochophore

The newly hatched trochophores were broadly egg-shaped with the protrochal band encircling the body at its greatest girth. Several long cilia at the anterior end of the body, which make up the apical tuft, were present at or before hatching (Figure 1 I). The apical tuft was surrounded by a field of much shorter cilia. A similar teleotrochal field of short cilia occurred around the posterior end of the body (Figure 1 I). By the third day after fertilization these fields had expanded to cover the body of the trochophore. About this same time the larval eyes appeared as simple pigment spots on the lateral margins of the body just posterior to the prototroch. They persisted until well after metamorphosis.

The prototrochal cilia beat such that the body was continually rotating around its axis in a clockwise direction when viewed from the anterior end. Sometimes the larvae halted their rapid swimming and hovered in a head-up position, maintaining their places in the water column with the slow beat of the prototrochal cilia. The apical tuft appeared in part to serve a sensory function, for when a swimming larva contacted an obstacle with it, it backed away and swam in another direction.

Mantle and Shell Development

Large epidermal cells, noted by Heath (1899) in Stenoplax heathiana and Okuda (1947) in Cryptochiton stelleri

(Middendorff, 1846), appeared scattered over the dorsal body surface 2 to 3 days after fertilization (Figure 1 K-L). Shortly after this, a series of alternating ridges and grooves, transversely oriented, began forming on the dorsal surface. Five days after fertilization, eight ridges and seven grooves were present. The large cells became aligned along the tops of the ridges (Figure 1 M-N). This system of ridges and grooves marked the site of the developing mantle. By 4.5 days, the mantle field had become well-delineated by the mantle fold (Figure 1 M). Short spicules appeared first at the anterior margin of the mantle and by six days after fertilization they completely encircled it (Figure 1 Q-R).

Herein, the term "settled" refers to larvae which have lost the prototrochal cilia and become permanent crawlers. "Metamorphosed" refers to larvae which have lost the apical tuft and have shell plates forming.

As the larvae began to settle (5.5 days), the head became partially covered by the mantle field. The shell plates first appeared after about 6.5 days. Plates 2-7 (counting the cephalic or head plate as number one), the first to form, appeared as thin, opaque slivers in the grooves between successive dorsal ridges(Figure 1 Q). The cephalic plate formed a day later, by which time the apical tuft had disappeared. The seven plates enlarged anteriorly and posteriorly until they overlapped one another (Figure 1 S-U),

and expanded laterally to completely obscure the body (Figure 1 V-W). A small pallial groove was formed (Figure 1 W), but no ctenidia were present. These began appearing approximately 8 weeks after fertilization, the posterior-most ones being formed first. By this time the larval eyes had disappeared. The eight (caudal) plate formed approximately 6 weeks after fertilization.

Foot Development

The foot began to form on the ventral surface of the body, just posterior to the prototroch and the mouth (Figure 1 M), about 4.5 days after fertilization. Within a day it was well-differentiated, and a heavily ciliated flap appeared at its anterior margin (Figure 1 O-P). Whether or not this structure aided in early feeding was not determined.

Approximately five days after fertilization, the larvae began to spend increasing amounts of time crawling on the bottom rather than swimming with their still-present prototrochs. This was accompanied by a dorso-ventral flattening of the body. The crawling larvae often attached with the posterior end of the foot and waved their free anterior end from side to side. They used the anterior portion of the foot to gain firmer attachment when needed. Once the prototroch cilia disappeared, the larvae became permanent crawlers and apparently began feeding, crawling slowly forward while moving their heads from side to side. Dark material became visable in the central region of the body.

Head Development

At hatching, the head region was clearly marked off by the prototroch. In the free-swimming trochophore, it was relatively undifferentiated, its most prominent feature being the apical tuft (Figure 1 I). As the foot and mantle formed, it became more flattened (Figure 1 R). Our studies did not determine whether the mantle grew forward over the head, or if the head itself formed new mantle tissue. At about 6.5 days, a groove appeared along the mid-ventral line of the head, being wider at the prototroch and tapering anteriorly (Figure 1 P). Its function was not determined. By 18 days after fertilization, the head had attained essentially its adult form (Figure 1 W). Feeding motions of the radula were observed under a compound microscope at this time.

By 8 weeks after fertilization, the juvenile chitons had all the features of an adult: eight shell plates were present, the girdle margin had grown out from under the plates and was covered with spicules, ctenidia had begun to form, and the larval eyes had disappeared.

DEVELOPMENT OF MOPALIA MUSCOSA

A schedule of development and illustrations of the various stages appear in Table I and Figure 2. Further details on the ontogeny of form and behavior are given below.

Early Development

The eggs of Mopalia muscosa are either green or golden brown, 0.29mm in diameter, and are encased in a bristly

chorion. The vitelline membrane of an unfertilized egg lies in close proximity to the chorion (Figure 2 A). A few minutes after fertilization,a gap was visible between the egg and chorion (Figure 2 B). Cleavage followed the typical spiral pattern (Figure 2 C-F). Division after the fourth cleavage and gastrulation were not followed in detail. The first prototroch cilia were seen at 10 hours and the ciliated ring appeared complete 12 hours after fertilization (Figure 2 G). The cilia beat slowly and feebly at first, but their movements increased in frequency and amplitude until hatching at 20 hours (Figure 2 H), when their action was sufficiently powerful to break away pieces of the chorion as the trochophore emerged. The trochophore larvae usually hatched with the apical tuft foremost, but some emerged with part of the prototroch first.

Free Swimming Trochophore

The trochophores were roughly egg-shaped with the prototroch a little above the equator (Figure 2 I). The apical tuft, developed prior to hatching,was surrounded by a field of smaller somatic cilia. A similar field of teleotrochal somatic cilia occupied the posterior end (Figure 2 J). These two patches of somatic cilia expanded anteriorly and posteriorly until they surrounded the body at 5.5 days. The larval eyes, two red pigmented spots embedded in the epithelium covering the body, appeared laterally just

posterior to the prototroch at 3.5 days, and were still visible at 32 days (Figure 2 J-Y). In swimming, the larvae rotated continuously in a clockwise direction (as viewed anteriorly); their bodies oriented vertically with the apical tuft up when hovering. Swimming of a larva was interrupted only when it ran into another larva or the side of the bowl, which caused an asynchronous beat. Ciliary action then stopped for less than a second and resumed slowly. Larvae usually swam along the bottom with the apical tuft in front, randomly moving both horizontally and vertically, but only occasionally swimming to the surface.

Mantle and Shell Development

The post-trochal region appeared elongated at 3.5 days (Figure 2 J). About 5 days after fertilization, it began to flatten dorso-ventrally, and large cells appeared, forming irregular rows on the dorsal surface (Figure 2 K). This was also reported by Heath (1899) in Stenoplax heathiana and by Okuda (1947) in Cryptochiton stelleri . A row of short, pointed spicules then formed anterior to the prototroch, and extended almost entirely across the dorsal surface of the head. A sparse scattering of spicules later appeared laterally on the periphery of the mantle field, and by 6.5 days, spicules formed a complete ring around the circumference of the mantle field. At 5.5 days, transverse grooves began to form dorsally, aligned between the bands of large cells

(Figure 2 M), and the latter formed more regular rows, except in the posterior region. The mantle field continued to expand, and by 11.5 days had extended over the posterodorsal head region. Mantle growth on the head was accompanied by the loss of the prototroch (Figure 2 P).

Shell plate formation began around 13.5 days with the deposition of seven thin lines of opaque material along the transverse grooves of the mantle field (Figure 2Q). During their early development, the order of size from the largest to the smallest (counting the cephalic plate as number one) was 2, 3, (4,1), 5, 6, 7 (Figure 2 Q). This order suggests the sequence of development. Enlargement of the plates continued until they came into mutual contact and extended laterally to the ring of spicules around the mantle field (Figure 2 R-Y). The mantle field itself extended until the rest of the larva was completely hidden. The eighth (caudal) plate did not form until approximately 6 weeks after fertilization. Ctenidia began to form in the pallial groove about two weeks after this, the posterior-most ones being the first to develop.

Foot Development

The foot began to form during the free swimming stage (6.5 days). It gradually extended as a ventral bulge, and a conspicuous ciliated flap formed on the anterior edge of the foot on the seventh day (Figure 2 N). By the tenth day,

the foot was well formed.

Development of the foot was accompanied by a gradual change in locomotion. The 3-day larvae swam rapidly, predominantly near the surface. However, at 6 days, they began to spend more time on the bottom, occasionally adhering to it with their posterior ends. Here they swung freely from the point of attachment or rotated due to prototrochal action for 1 to 2 seconds; then either they were knocked loose by movement of water in the bowl or freed themselves by swimming action of the prototroch. Once freed, they resumed swimming. As the foot developed further, the trochophores spent increasing periods of time on the bottom. At 9 or 10 days, they attached to the bottom by both the anterior and posterior ends of the foot and rocked from side to side from these two points. Their prototrochs were noticeably smaller and had disappeared by 12.5 days. The larvae were then considered "settled", crawling being their only means of locomotion.

Head Development

External differentiation of the head was minimal until the disappearance of the apical tuft at 11.5 days, which was about the same time as first deposition of the shell plates. As the mantle field extended, the head became flattened and was soon covered by the mantle dorsally (Figure 2 V). Radular movements were observed in the mouth at 21 days.

SETTLING STIMULI

Metamorphosis in both Mopalia lignosa and Mopalia muscosa was delayed or prevented by the lack of an appropriate settling substratum. Only two larvae out of several hundred observed underwent complete metamorphosis on glass.

In Mopalia lignosa, fully metamorphosed juveniles (shell plates present, no apical tuft, no prototroch cilia) appeared by seven days after fertilization when water-worn Mytilus shells with a film of microscopic algae were added 4.5 days after fertilization. In a bowl left without shells for 14 days, the apical tuft was still present and no shell plates had appeared, though most of the larvae had lost their prototroch cilia and had been crawling 6 days after fertilization. When Mytilus shells were added on day 14, fully metamorphosed juveniles were noted within a day.

Similarly, no substratum was added to three bowls containing seawater and Mopalia muscosa larvae, while pieces of Mytilus shell with an algal film were added to another three such bowls at 5 days after fertilization. In the bowls without the shells, only two larvae ever formed dorsal plates. The rest apparently stopped development, retained the prototroch cilia and never metamorphosed; all subsequently died 14 to 17 days after fertilization. Development in the bowls with Mytilus shell progressed normally.

The advantage of a substrate-sensitive settling response is clear. The ability to delay metamorphosis until a suit-

able substratum is present increases the chances that larvae will settle under conditions favorable for post-larval development. Such a settling response has been shown to exist in Tonicella lineata (Wood, 1815) by Barnes (1972) and was briefly mentioned by Heath (1899, pp. 62-63) for Stenoplax heathiana. It has also been found in other molluscs (Bayne, 1964; Thompson, 1964; Swennen, 1961; and Scheltema, 1961), as well as in other invertebrate groups.

DISCUSSION

Mopalia muscosa and Mopalia lignosa, while similar in many aspects of development, show some differences, particularly in the timing of events. They are compared below to each other, to Mopalia ciliata for which some details are available (Thorpe, 1962), and to a few more distantly related species.

Development from cleavage through hatching takes place at similar rates in Mopalia lignosa and M.muscosa, and at 13°C.,the larvae hatch roughly 20 hours after fertilization. Development of M. ciliata at "normal ocean temperature" is a little slower, and the larvae hatch 36-42 hours after fertilization (Thorpe, 1962). Structures arising during the free-swimming stage appear within 2 days of each other in M. lignosa and M. muscosa; details are not available for M. ciliata. Settling can be contrasted in all three species: M. lignosa loses its prototroch cilia at about 5.5 days, while M. ciliata and M. muscosa lose theirs on the 8th and 11th days, re-

spectively. For the remainder of development, M. lignosa adheres to a schedule 4 days ahead of that for M. muscosa.

A major difference in the development of these three species of Mopalia is in the ontogeny of the plates. Thorpe (1962) states that "the anterior valves are the first to be apparent" in M. ciliata. In both M. lignosa and M. muscosa, the cephalic plate did not form until after the appearance of the plates posterior to it. The caudal plate in M. ciliata develops on the 8th day (Thorpe, 1962). In contrast, in both M. lignosa and M. muscosa the caudal plated doesn't appear until the 6th week.

Mopalia lignosa and M. muscosa show sequences of developmental events similar to those of the few other chitons studied. The major differences appear in the timing rather than the nature or order of events. Tonicella lineata, according to Barnes (1972), hatches at 2 days and the larvae settle at 3 days. Christiansen (1954) reported that Lepidopleurus asellus hatched at 20 to 21 hours and settled at about 10 days. Heath (1899) reported a period of 7 days between fertilization and hatching in Ischnochiton magdalenensis (= Stenoplax heathiana). Okuda (1947) noted that Cryptochiton stelleri did not hatch until 70 hours or more after fertilization. The larvae emerged with external features which did not develop in M. lignosa and M. muscosa until the later free-swimming stages. Settling in Cryptochiton began 12 to 20 hours after hatching and liberation from the jelly mass.

A curious feature is the placement of the larval eye. In spiralian development, larval eyes usually occur anterior to the prototroch. The larval eyes of chitons are located more posteriorly, behind the head region proper. They apparently still serve a sensory function, since they are innervated by the pallial nerve cord (Heath, 1904). Heath (1904) puts forth the following interesting hypothesis:

> "Now it is obvious that if the chiton eye were situated in front of the velum, as in the annelids, it would be most unfavorably placed after metamorphosis. Under the circumstances the most available situation would be the furrow about the proboscis, where it would be continually obscured and would be practically useless even if provided with tentacles. It seems most reasonable to suppose that as the structures characteristic of the chitons appeared in the phylogenetic development, the eye-spots gradually shifted their position into the present more favorable location."

SUMMARY

1. Spawning behavior and external features of the larval development were studied in the chitons Mopalia muscosa and M. lignosa during the months of April-June, 1974, at Pacific Grove, California.

2. Specimens of M. lignosa spawned in the lab after several hours in containers of standing seawater. Males moved around during spawning while females remained stationary.
3. Electrical stimulation, injection of 0.5M KCl or homogenate of nervous tissue failed to induce spawning. Eggs obtained through dissection were unfertilizable, even after treatment with 3ml of 0.1N NaOH in 100ml seawater.
4. The sequence of events in the development of the two species is the same, though some differences in timing exist. First cleavage, second cleavage, third cleavage, and hatching occurred at about 1 hr., 1.5 hrs., 2.5 hrs., and 20 hrs., respectively, in both species.
5. After hatching, the larvae of both species swam freely for a period. M. lignosa settled about 5.5 days after fertilization and M. muscosa about 11.5 days after fertilization. During the free-swimming period, the larval eyes, mantle and foot developed.
6. Larvae were considered settled when the prototroch cilia were no longer present, and metamorphosed when the shell plates appeared and the apical tuft was lost. This happened at 6.5 days for M. lignosa and 13.5 days for M. muscosa. The shell plates of M. muscosa appeared to develop in the following order: 2, 3, 1&4, 5, 6, 7, 8. No such sequence was noted for M. lignosa. The caudal plate in both species did not form until about 6 weeks after fertilization.
7. Both species seemed to exhibit a substrate-sensitive

settling response, though further work is needed to verify this.

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TABLE CAPTIONS

Table 1. Time schedule of development for Mopalia lignosa and Mopalia muscosa in hours and days after fertilization. A vertical bar indicates the exact beginning and end of an event as observed. A dotted line indicates that the exact times were not determined. These times are representative and do not indicate the limits of individual variation.

A. First cleavage
B. Second cleavage
C. Third cleavage
D. Fourth cleavage
E. Gastrulation
F. Prototroch
   1. faint ciliary action within the chorion
   2. strong ciliary action within chorion
   3. swimming activity
   4. disappearance of cilia
G. Apical tuft
H. Hatching
I. Somatic cilia
   1. only at anterior and posterior ends
   2. distributed over body
J. Larval eyes
K. Mantle field
   1. Large cells appear on the dorsal surface
   2. Mantle fold develops
   3. Mantle field extends onto head
L. Foot
   1. initial bulge
   2. ciliated flaps develops anteriorly
   3. well-developed foot
M. Spicules
   1. across dorsal surface of head only
   2. all around mantle field
N. Shell plates
   1. $CaCO_3$ deposits first seen
   2. seventh plate forms
   3. plates expand and overlap one another

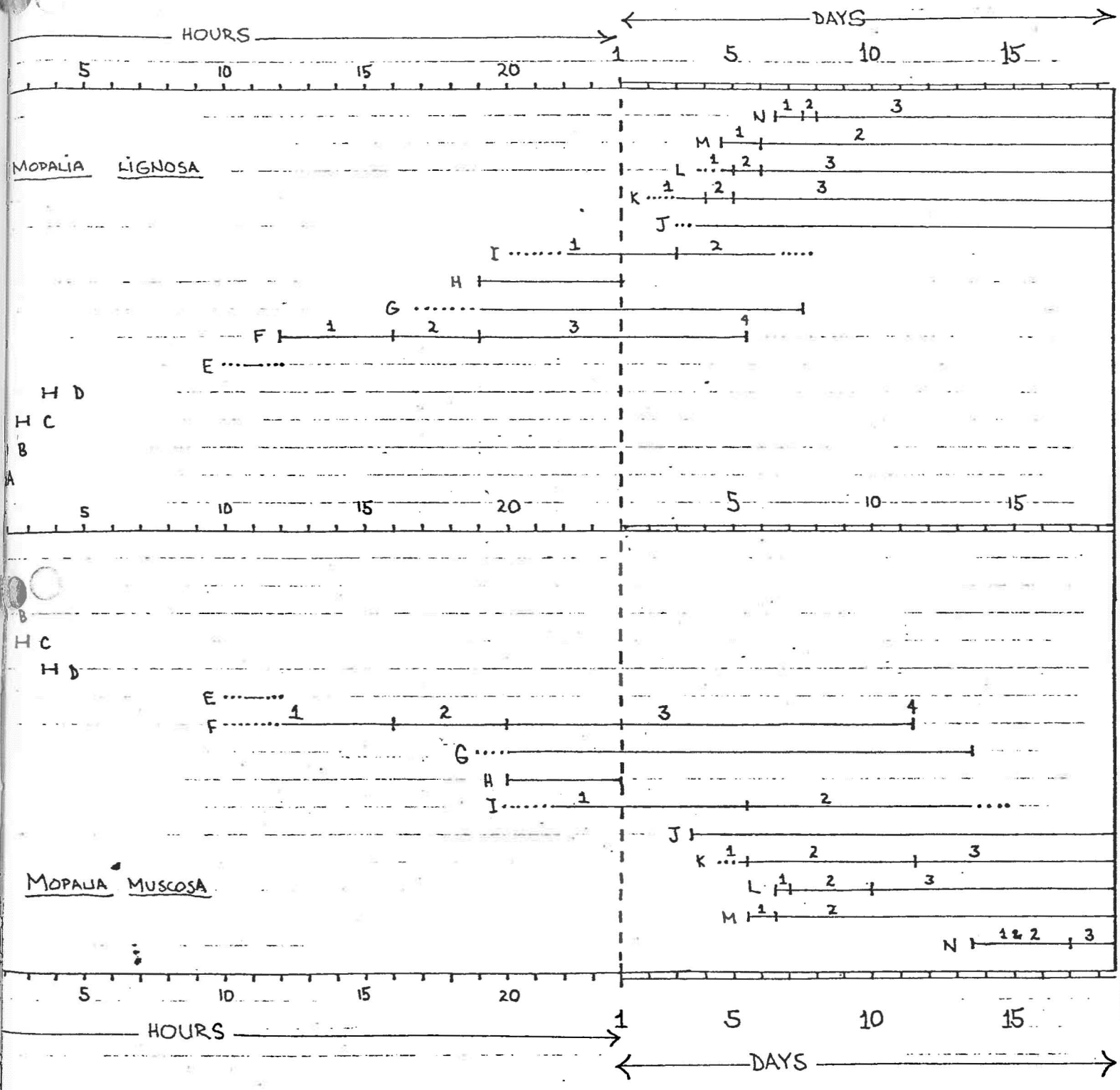


TABLE I. Time schedule of Development, etc.

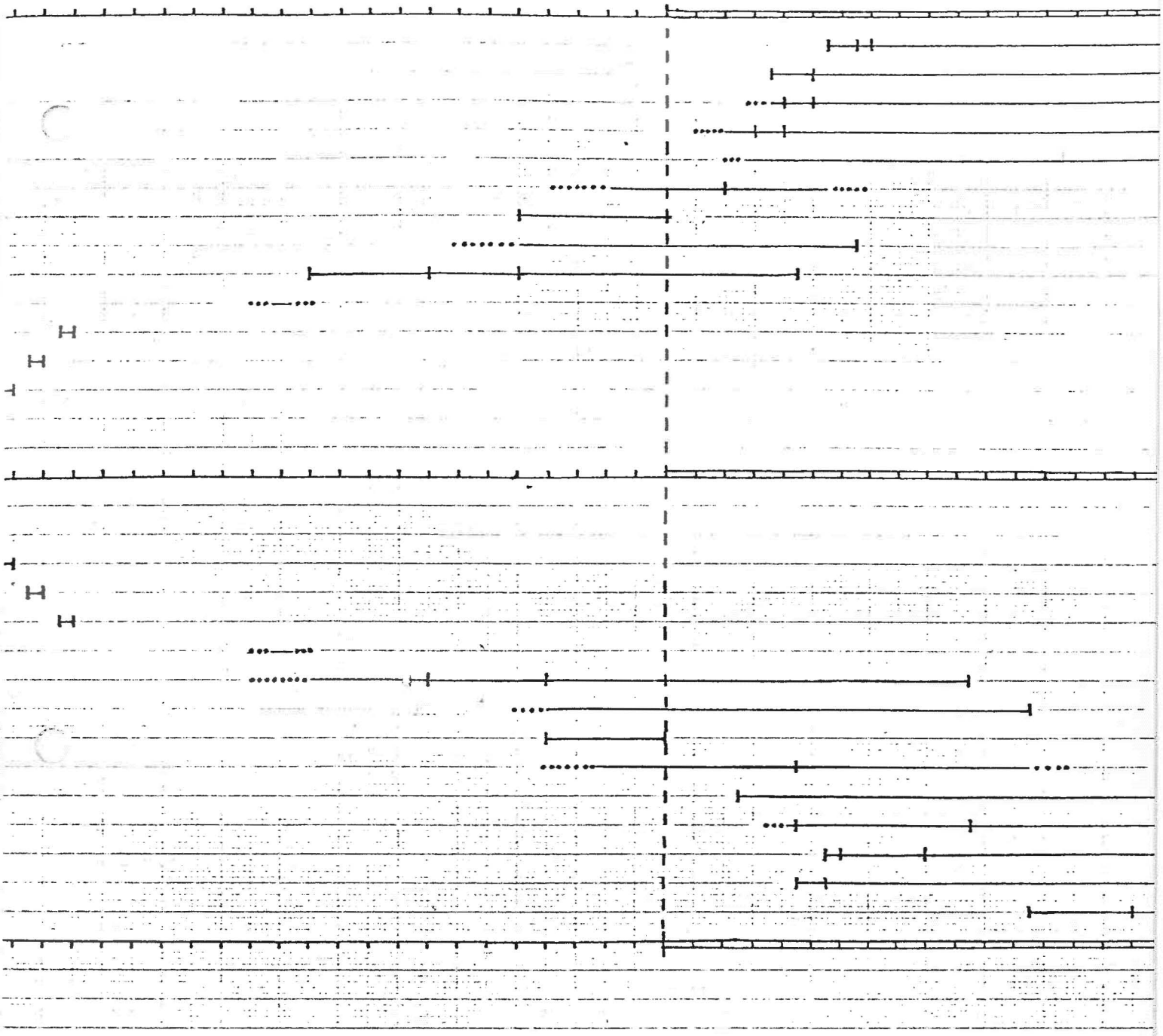
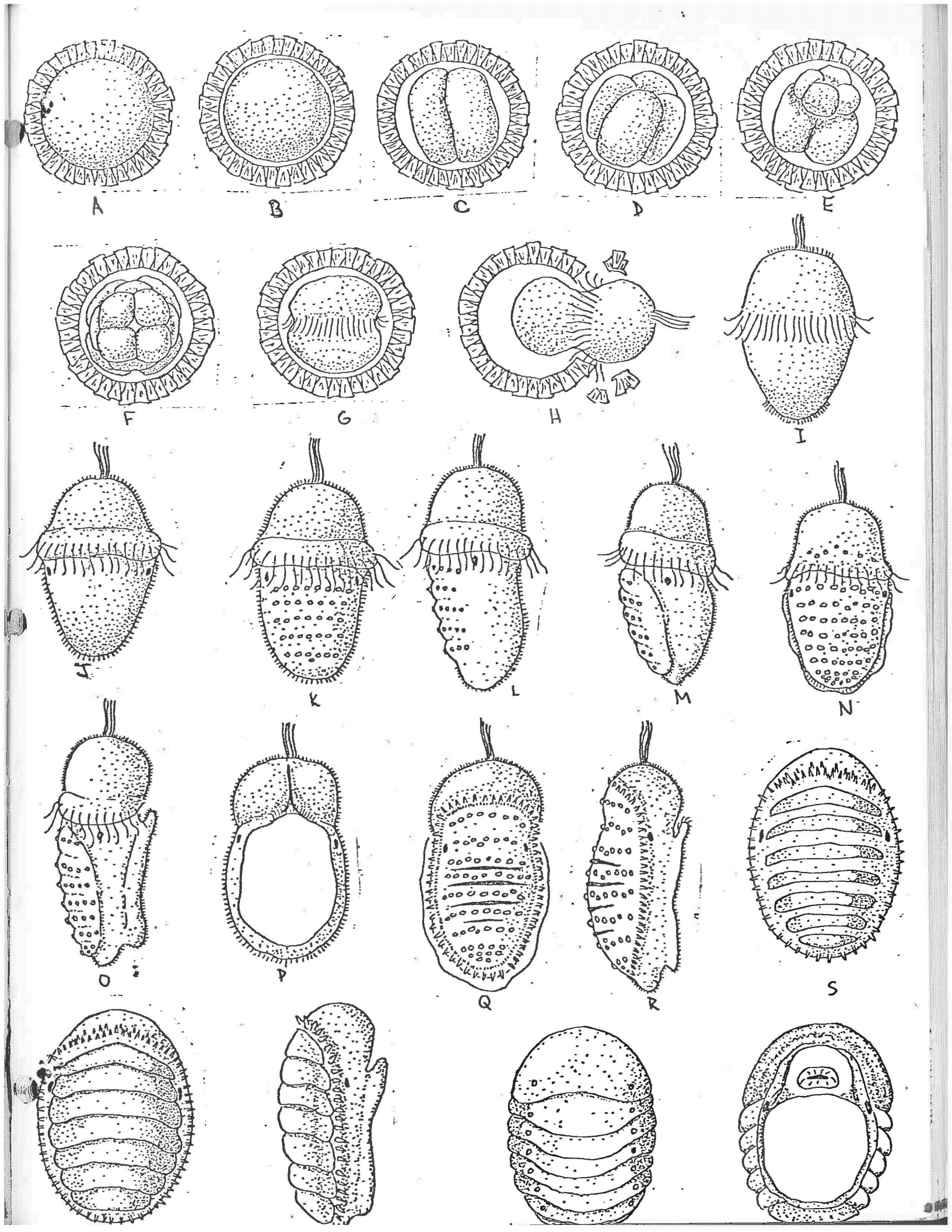


FIGURE CAPTIONS

Figure 1. Development of Mopalia lignosa.
A. Unfertilized egg within chorion. B. Fertilized egg showing the perivitelline space. C. First cleavage (1 hr.). D. Second cleavage (1.5 hrs.). E. Third cleavage (2.5 hrs.). F. Fourth cleavage (3.5 hrs.). G. Prototrochal cilia begin beating within chorion (12 hrs.). H. Hatching (19 hrs.). I. Newly hatched trochophore (about 1 day). J. Free-swimming trochophore. Eye spots appear (3-3.5 days). K,L. Dorsal ridges and foot forming (dorsal and lateral views, respectively; about 4 days). M. Mantle fold evident (lateral view; 4.5 days). N-P. Settling stage (dorsal, lateral, ventral views, respectively): eight dorsal ridges and ciliated flap of foot present (about 5 days). Q-R. Settled larva (dorsal and lateral views, respectively); shell plates 2-7 begin forming (6.5 days). S-U. Shell plates expand and apical tuft lost (dorsal, dorsal, lateral views, respectively; 7-8 days). V-W. Juvenile chiton (dorsal and ventral views, respectively; 24 days).

Figure 2. Development of Mopalia muscosa
A. Unfertilized egg within chorion. B. Fertilized egg, showing perivitelline space. C. First cleavage (1hr.). D. Second cleavage (1.5 hrs.). E. Third cleavage (2.5 hrs.). F. Fourth cleavage (3.5 hrs.). G. Prototroch complete (12 hrs.). H. Hatching (20hrs.). I. Early trochophore showing anterior and posterior fields of somatic cilia (1

day). J. Post-trochal region elongated; eye spots (3.5 days). K. Post-trochal region flattened dorsoventrally (5.5 days). L. Spicules on head and beginning of cell alignment on dorsal surface of mantle field (5.5 days). M. Grooves on dorsal surface of mantle field, foot beginning to bulge (6 days). N. Ciliated flap on anterior foot (7 days). O. Foot more differentiated (7 days). P. Settled larva, loss of prototroch (11.5 days). Q. Shell plate deposition, loss of apical tuft (13.5 days). R-S. Mantle field begins to extend onto head (14 days). T-U. Shell plates enlarging (15 days). V. Shell plates in mutual contact (17 days). W. Foot well developed (17 days). X. Juvenile chiton in curled position, 7th plate hidden from view (21 days). Y. Ventral view, head and mouth well formed, but neither eighth plate or first pair of ctenidia have appeared.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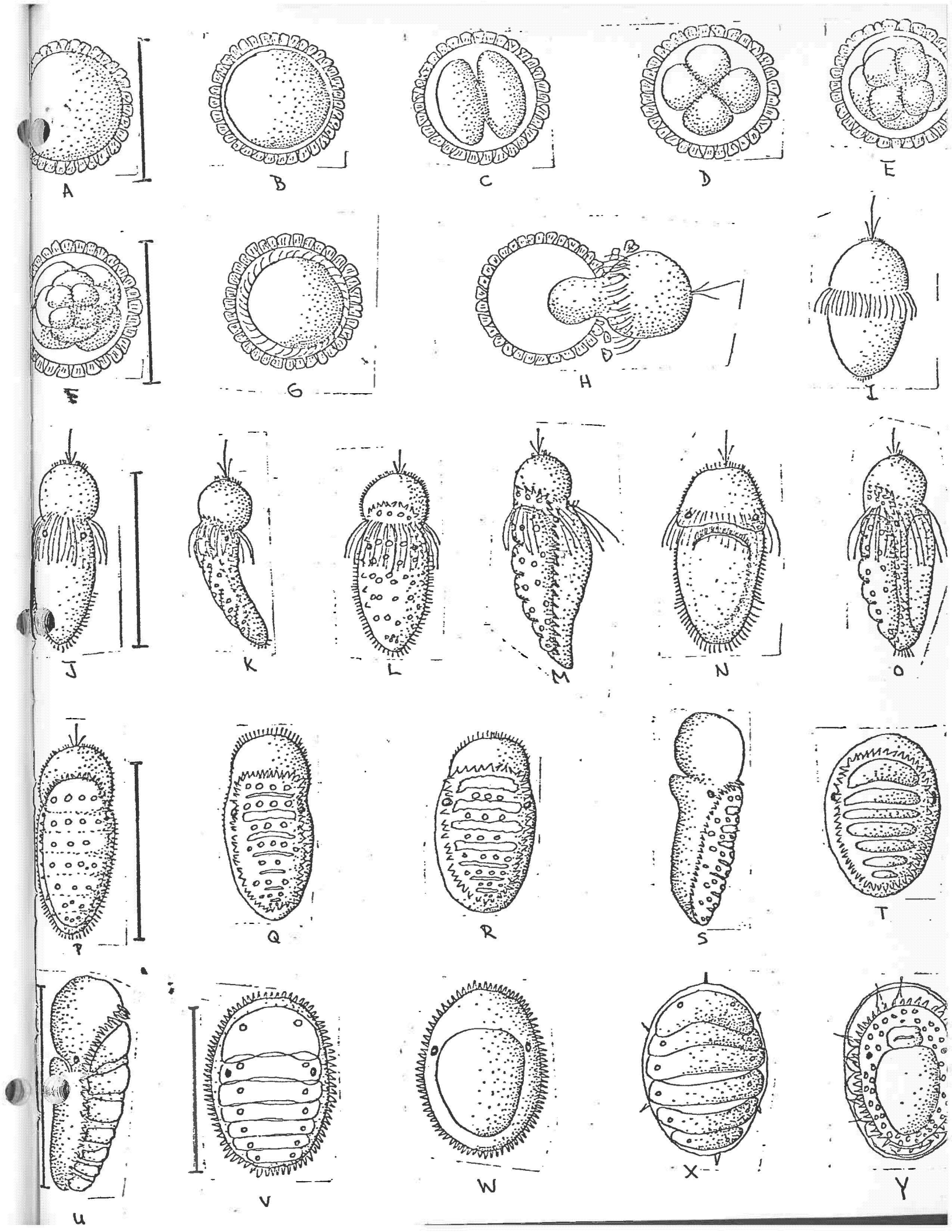
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