

DESCRIPTIONS AND PHYLOGENETIC SIGNIFICANCE OF THE FRONTO-LATERAL GLAND PORES AND DORSAL LATTICE ORGANS OF CYPRID LARVAE OF SEVEN SPECIES OF BARNACLES (CIRRIPEDIA: THORACICA: PEDUNCULATA)

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A B S T R A C T

The paired fronto-lateral gland pores and lattice organs (LO1, 2, 3, 4, and 5) of seven species of pedunculate barnacles belonging to two thoracican suborders, Heteralepadomorpha (family Heteralepadidae: *Heteralepas* sp. 1 and 2) and Lepadomorpha (families Poecilasmatidae: *Poecilasma inaequilaterale* and *Octolasmis aymonini geryonophila*; and Lepadidae: *Lepas pacifica*, *Dosima fascicularis*, and *Conchoderma virgatum*), were investigated by scanning electron microscopy (SEM). While the fronto-lateral gland pores exhibit slight variation among species, with only *L. pacifica* showing a different morphology, the variations in the arrangement of LOs are phylogenetically instructive. The lattice organs in the foregoing species correspond in general to the inferred advanced type (Type C), but the distinct keel in the pore field in *P. inaequilaterale* and *L. pacifica* is reminiscent of, but not necessarily identical with the less advanced Type B. The arrangement of the anterior LOs (1-2) is rhomboidal in the two heteralepadomorph species, the two poecilasmatid species, and two of the three lepadid species, as it is in all previously and presently known lepadomorph cyprids except *D. fascicularis*. In this last species, they are deployed linearly along the hinge line. A linear arrangement of all the lattice organs is presumably the plesiomorphic condition for the Thoracica; an obvious exception being the pattern seen in *Ibla cumingi*. The arrangement of the first two pairs of posterior LOs (3-4) in *O. a. geryonophila* and *C. virgatum* differs from that of all previously described Lepadomorpha in being rhomboidal rather than aligned linearly along the hinge line. This same arrangement of LOs 3 and 4 in the two heteralepadomorph species is notable since it is not known in other thoracicans. Our results concerning variation in lattice organs of the lower Pedunculata are more or less consistent with current phylogenetic speculations and genetic information that ally Heteralepadomorpha with Lepadomorpha. Significance of this variation at lower taxonomic levels is also evident in the two similar forms of *Heteralepas*.

KEY WORDS: Cirripedia, cyprid larvae, frontal lateral glands, lattice organs

INTRODUCTION

Larval morphology has been studied extensively in many invertebrate groups in search of characters that can serve as evidence of homologies that help elucidate relationships as well as aid in species identification. Cirripedia have two larval forms: the generally planktotrophic nauplius, and the non-feeding cypris. The naupliar development of numerous species is moderately well known (Newman and Ross, 2001), and comparative morphological studies of cyprids are increasing, a field in which the most useful results have come from advanced techniques, such as SEM.

Cyprid characters such as size and carapace color, shape, and ornament have been useful in species identification. Antennular morphology and the structure of the thoracic appendages and caudal rami have been of some importance in phylogenetic analyses, as has the form of the paired fronto-lateral gland pores located on the antero-ventral surface of the carapace. Morphological variation in the lattice organs, which are sensory organs situated on the dorsal surface of the carapace (Jensen et al., 1994), has so far proven to be the most phylogenetically illuminative source of data.

The cyprids of cirripedes examined in previous studies at the ultrastructural level have come from the North Atlantic and North Pacific (Glennier et al., 1989; Jensen et al., 1994; Elfimov, 1995; Høeg and Rybakov, 1995; Moyses et al.,

1995; Høeg et al., 1998; Alvarez et al., 2003; Yan et al., 2005; Ponomarenko et al., 2005; Buckeridge and Newman, 2006), but those of many cosmopolitan and wide-ranging species, as well as those from distant shore remain unknown.

The phylogenetic conclusions derived from such studies can be tested by comparing them to phylogenies based on adult morphology, molecular genetics, and the fossil record. Since the number of species for which detailed larval descriptions are available is still quite limited, such results have yet to be rigorously tested. Nonetheless, the value of larval characters has been great. For example, Rhizocephala are parasites, largely of decapod crustaceans, and their adults have a very limited number of characters. Yet it has been possible to place them, as well as the thoracicans, in a phylogenetic scheme on the basis of larval characters (Jensen et al., 1994; Høeg et al., 2004). In the present study we examine, using SEM, the paired fronto-lateral gland pores and lattice organs of cyprids belonging to seven species of the suborders Heteralepadomorpha and Lepadomorpha. The seven species treated herein are epibionts, while it seems unlikely, it is not known whether this way of life can influence cyprid morphology, such as the distribution of lattice organs. At this stage generalizations across Thoracica based on cyprid morphology thus should be carefully evaluated.

Table 1. Number of cyprids examined, cyprid total length (mean, standard deviation and range), mean length of LOs (\pm standard deviation), and ratio of the two measurements for the seven species of barnacles examined in this study.

	N	Cyprid total length (μm)	Mean LO length (μm)	Mean LO length/cyprid total length
<i>Heteralepas</i> sp. 1	5	1131.4 \pm 112.3 (1000-1238)	12.04 \pm 1.19	0.009
<i>Heteralepas</i> sp. 2	4	1054 \pm 86.1 (990-1152)	8.58 \pm 1.59	0.007
<i>Poecilasma inaequilaterale</i>	5	1237 \pm 128.4 (1048-1333)	23.66 \pm 4.21	0.017
<i>Octolasmis aymonini geryonophila</i>	5	844.6 \pm 164.3 (661-1066)	20.14 \pm 1.90	0.018
<i>Lepas pacifica</i>	4	1866.3 \pm 71.4 (1800-1942)	31.26 \pm 3.43	0.017
<i>Dosima fascicularis</i>	5	1297.2 \pm 90.7 (1177-1393)	23.37 \pm 4.35	0.019
<i>Conchoderma virgatum</i>	4	1584.5 \pm 48.7 (1550-1619)	27.31 \pm 5.52	0.017

MATERIAL AND METHODS

Cyprids of the species studied were obtained from several sources as follows:

- 1) *Heteralepas* sp. 1, an epibiont on the carapace of the scyllarid lobster *Evivacus princeps* Smith, 1869. ATLAS IV cruise, off the coast of Michoacan, Mexico; 17°35'06"N, 102°24'00"W, depth 100 m.
- 2) *Heteralepas* sp. 2, an epibiont on the diogenid crab *Dardanus sinistripes* (Stimpson, 1859). ATLAS IV cruise, off the coast of Michoacan, Mexico; 18°00'45"N, 102°24'07"W, depth 96 m.
- 3) *Poecilasma inaequilaterale* Pilsbry, 1907, epibiont on the carapaces of the crabs *Chaceon ramosae* Manning, Tavares and Albuquerque, 1989, off the southern Brazilian coast; 27°11'10"S, 46°52'18"W, depth 350-550 m, and of *C. notialis* Manning and Holthuis, 1989, 34°41'40"S, 51°56'45"W, depth 647 m.
- 4) *Octolasmis aymonini geryonophila* (Pilsbry, 1907), epibiont on the same host crabs as *P. inaequilaterale* but on their gills, and the crab *Benthochascon schmitti* Rathbun, 1931, SIGSBEE 5 cruise, Gulf of Mexico, 21°14'04"N, 96°55'57"W, depth 330 m.
- 5) *Lepas pacifica* Henry, 1940, on *Velella* from off La Jolla, California, 32°51'N, 117°16'W.
- 6) *Dosima fascicularis* (Ellis and Solander, 1786), same host and locality as *L. pacifica*.
- 7) *Conchoderma virgatum* (Spengler, 1790), an epibiont on the sea snake *Pelamis platurus*, off Chamela Bay, Jalisco, Mexico (Alvarez and Celis, 2004).

Cyprids were detached from the surfaces of the adult barnacles or from points immediately adjacent to the latter on their hosts. Hosts from different sources were initially fixed in different ways, but all cyprids were transferred to 70% ethanol as the first step in processing for SEM. They were hydrated, postfixed in 1% OsO₄, dehydrated, mounted, critical-point dried with CO₂, coated with gold, and observed in a Hitachi S-2460N scanning electron microscope. Four and five cyprids of each species were processed for SEM and observed (Table 1). We follow Jensen et al. (1994) for nomenclature of the lattice organs (LOs): Type A, a seta-like keel lying prostrate in an elongate depression; Type B, same as Type A but with numerous pores on the keel; and Type C, the keel is absent remaining the pore-field. The five pairs being referred to as LOs 1-5.

RESULTS

The distribution of LOs follows the general pattern of two anterior pairs and three posterior pairs straddling the hinge line on the dorsal surface of the cyprid carapace; whereas the paired fronto-lateral gland pores are located on the antero-ventral border of the carapace.

- 1) *Heteralepas* sp. 1. The general shape of the cyprid in dorsal view is oval and elongate, with a total length of 1238 μm and a maximum width of 417 μm (Fig. 1A). The surface of the carapace is relatively smooth with scattered shallow depressions, these increasing in number towards the anterior end. The fronto-lateral gland pore on each side has a single thick, elevated border with secondary ventral foldings and a ventral notch (the pore obstructed by debris; Fig. 8A). The LO

pore fields, located in shallow depressions and consisting of irregularly shaped pores of non-uniform sizes are Type C (Fig. 1D, G). The LO1 and LO2 pairs are strongly curved, converge anteriorly and posteriorly (toe-in and out), respectively (a pattern referred to as rhomboidal), and there is a distinct central pore on the hinge line in the middle of the area they demark (Fig. 1B, C). LOs 3 and 4 are similar in size, the former being straight, the latter curved (Fig. 1E). They are located near the posterior end of the hinge line, before the two valves separate, and toe-in and out, respectively (Fig. 1F). A central pore is located in the middle of these two pairs (Fig. 1F). The posteriormost LO5 pair are straight and lie parallel to the hinge line (Fig. 1E).

- 2) *Heteralepas* sp. 2. In dorsal view the cyprid is oval-shaped with the anterior region rounded and the posterior end acute; total length is 1152 μm with a maximum width of 266 μm (Fig. 2A). The surface of the carapace is smooth with regularly distributed shallow depressions, these increasing in number anteriorly. The fronto-lateral gland pore has a single elevated border, a well-marked ventral rounded cleft, and a slit-like opening (Fig. 8B). The LOs are of Type C. LOs 1 and 2 are slightly curved, similar in size, and located in shallow depressions; and toe-in and -out, respectively (Fig. 2B). The pore fields are composed of pores of subequal diameter (Fig. 2C, D); the associated central pore is between the anterior parts of the LO2s (Fig. 2B). LOs 3 and 4 are located posteriorly, anterior to the end of the hinge line, and also toe-in and -out, respectively (Fig. 2E); the LO4s are straight and larger than the LO3s and a double central pore is situated at the level of the anterior tips of the LO4s (Fig. 2E, F). The LO5s are straight, parallel to the longitudinal axis of the body, and similar in size to the LO3s. The pore fields of LOs 3-5 consist of pores of subequal size (Fig. 2G).

- 3) *Poecilasma inaequilaterale*. The cyprid is elongate, slightly oval-shaped, with its maximum width in the posterior half (263 μm) and a total length of 1333 μm . The surface of the carapace adjacent to the hinge line is smooth, but the rest appears striated due to numerous narrow, longitudinal undulations (Fig. 3A-E). The fronto-lateral gland pore, approximately circular in section, has two irregular elevated borders dorsally, which become a single irregular border ventrally (Fig. 8C). The LOs consist of nearly-regular rows of pores with the central portion elevated (Fig. 3B-D) and while being somewhat reminiscent of Type B, are Type C. LO1s are straight, elongate, run parallel to the hinge line

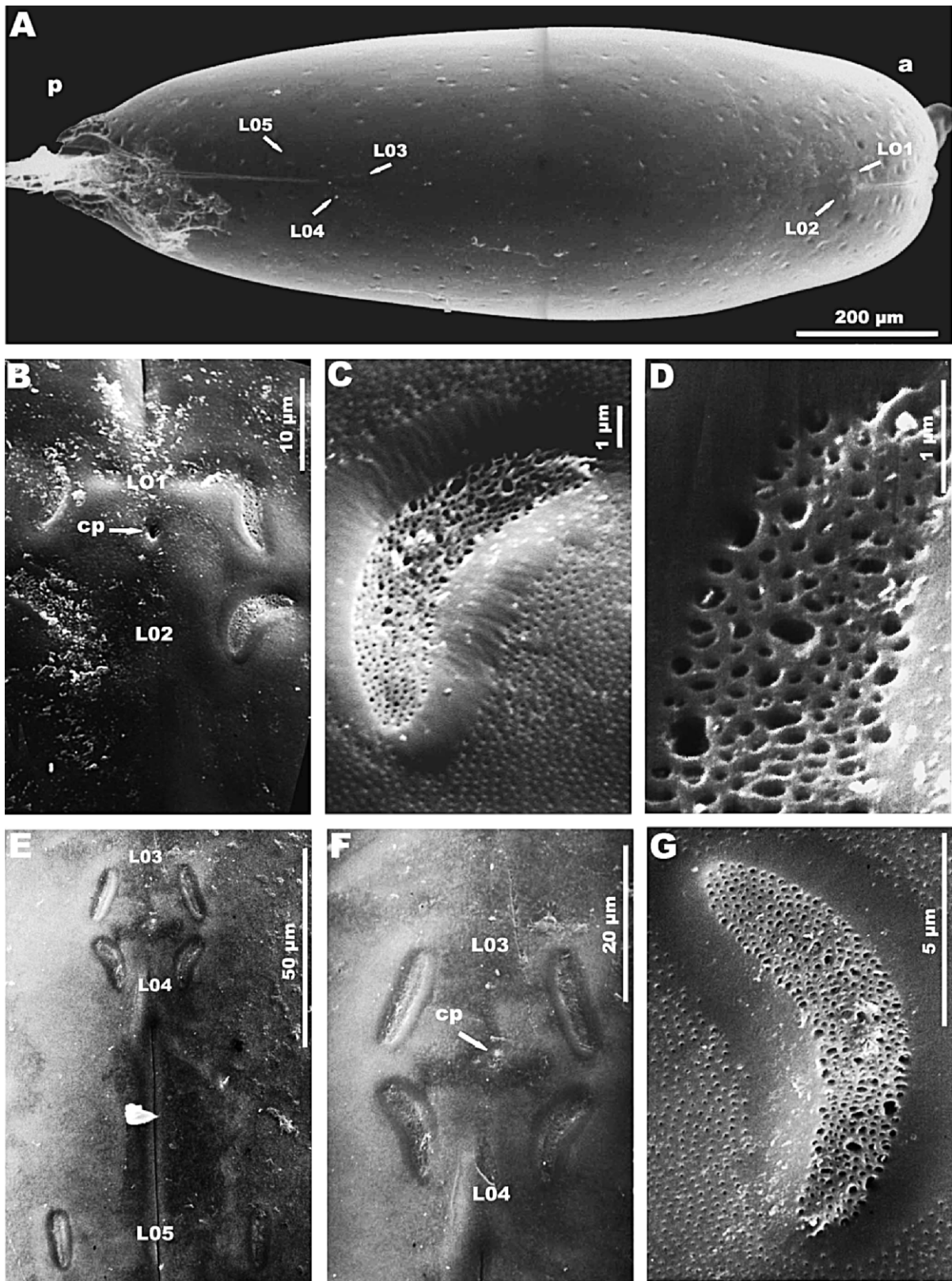


Fig. 1. *Heteralepas* sp. 1, cyprid: A, dorsal view showing the distribution of the five pairs of LOs, (a) anterior end, (p) posterior end; B, LO1 and LO2 with central pore (cp); C, right LO2; D, detail of LO2; E, LO3-LO5; F, detail of LO3s and LO4s with central pore (cp); G, detail of left LO4.

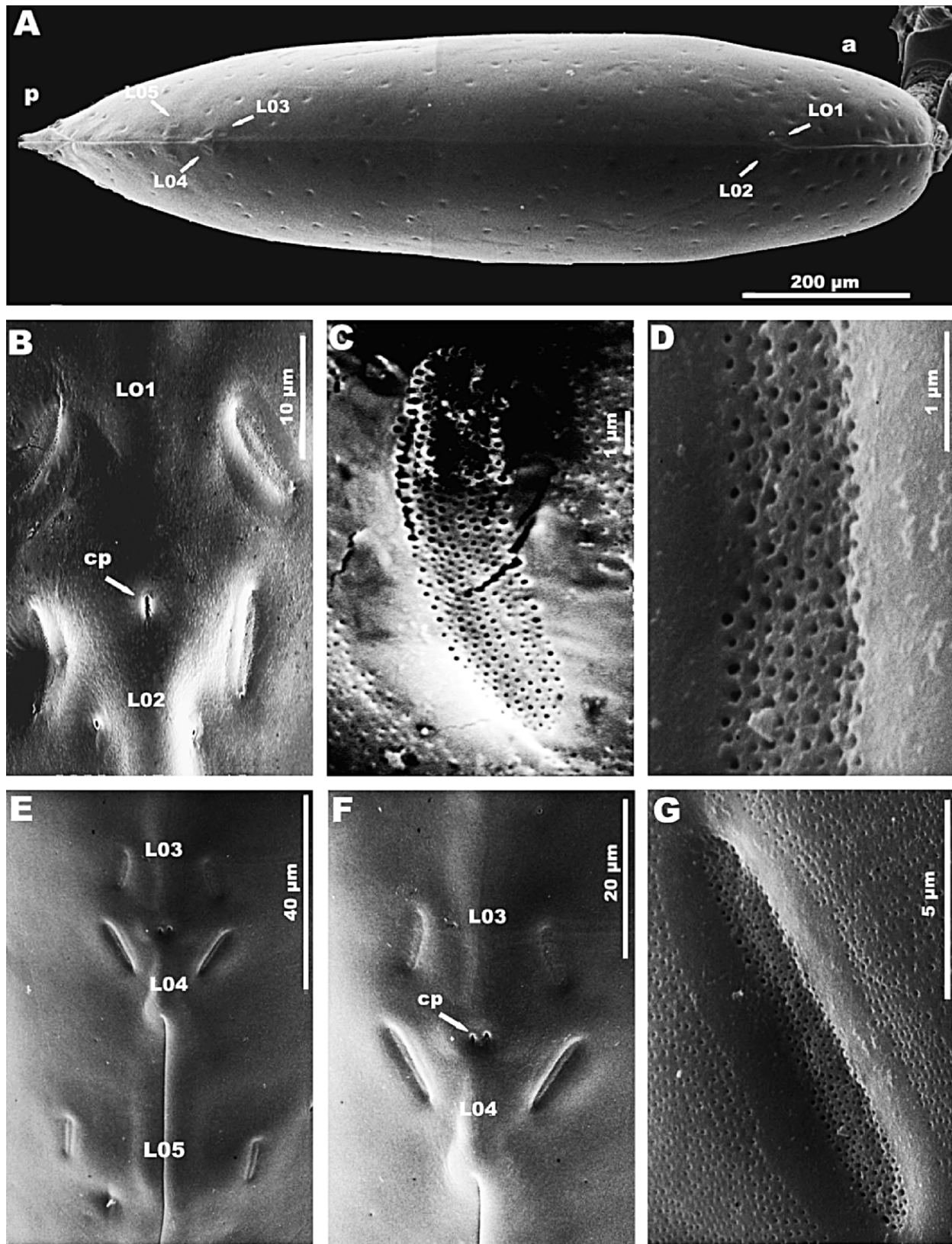


Fig. 2. *Heteralepas* sp. 2, cyrid: A, dorsal view showing the distribution of the five pairs of LOs, (a) anterior end, (p) posterior end; B, LO1s and LO2s with central pore (cp); C, left LO2; D, detail of LO2; E, LO3-LO5; F, LO3s and LO4s with central pore (cp); G, detail of left LO4.

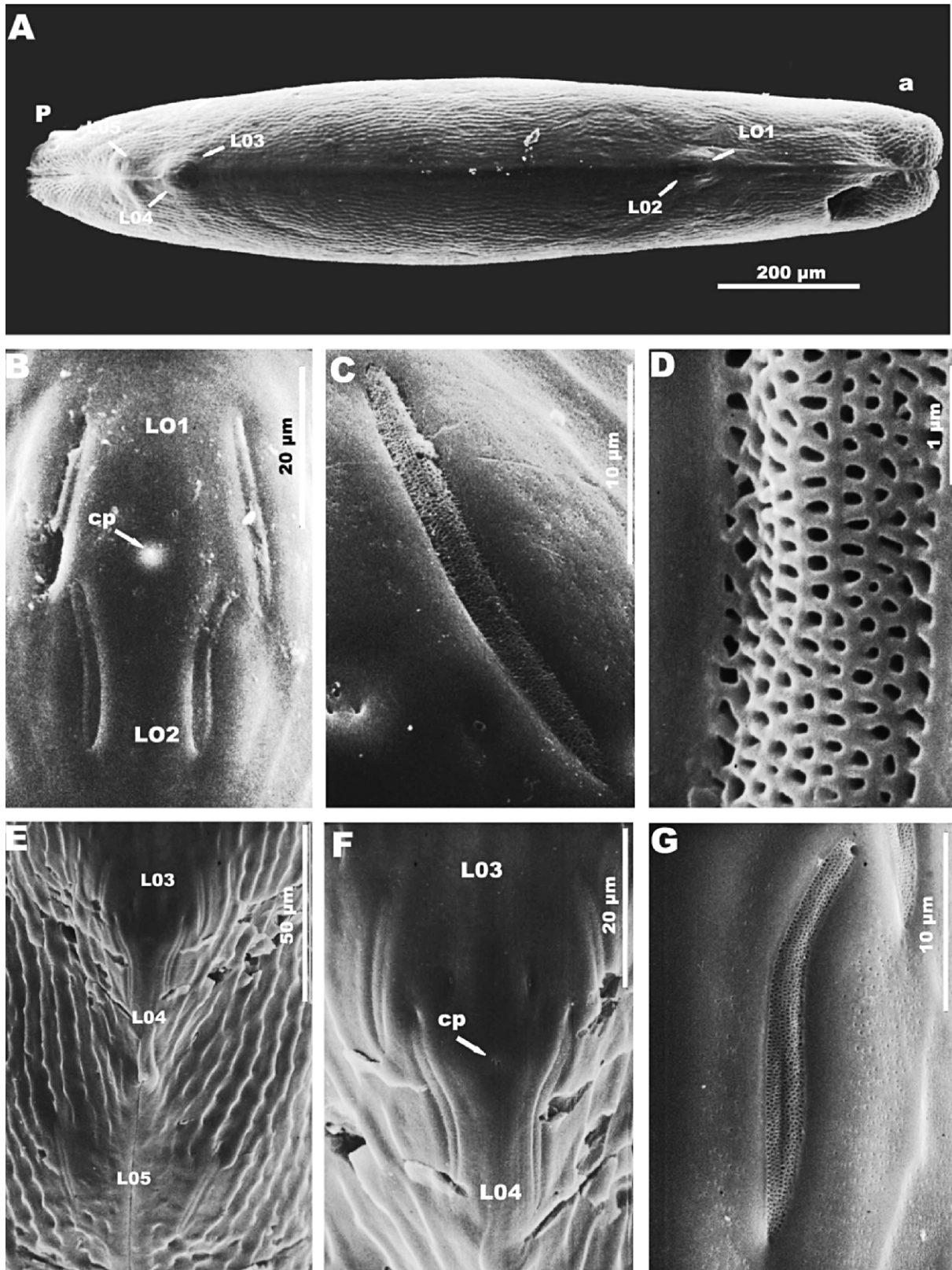


Fig. 3. *Poecilasma inaequilaterale*, cyprid: A, dorsal view showing the distribution of the five pairs of LOs, (a) anterior end, (p) posterior end; B, LO1s and LO2s with central pore (cp); C, left LO2; D, detail of LO2; E, LO3-LO5; F, detail of LO3s and LO4s with central pore (cp); G, right LO4 showing terminal pore and pit in pore field at end opposite to terminal pore.

and overlap with the LO2s, which are shorter, slightly curved, and run closer to the hinge line; the associated central pore is between the posterior parts of the LO1s (Fig. 3B). LOs 3 overlap LOs 4 by approximately 1/4 of their length, are almost straight and lie lateral to the LO4s, which are closer to the hinge line but diverge anteriorly from it (Fig. 3E, F). The central pore is at the level of the anterior third of LO4, and antero-lateral to it are two similar pores (Fig. 3F). The LO5s are the most posterior pair, toe-out from the midline (Fig. 3E).

- 4) *Octolasmis aymonini geryonophila*. In dorsal view, the cyprid is elongate and oval-shaped; the maximum width (200 μm) is attained in the posterior half, and the total length is 1066 μm . The surface of the carapace is smooth with scattered shallow depressions, and the hinge line is faintly marked (Fig. 4A). The fronto-lateral gland pore is surrounded by irregular and incomplete concentric borders of different thicknesses, and the opening is oval-shaped (Fig. 8D). LO1s are straight, converging anteriorly (Fig. 4B); the LO2s are slightly curved anteriorly, and lateral to and longer than the LO1s, which they overlap somewhat on the outer side (Fig. 4B, C); the pore fields are composed of more or less organized rows of pores (Type C) (Fig. 4D); and the associated central pore sits on the hinge line in the center of the area demarcated by both pairs (Fig. 4B). LOs 3 and 4 toe-in and -out, respectively, similar to the arrangement of LOs 1 and 2 (Fig. 4E-G). LO5s, toe-out, are well separated from LOs 3 and 4, and lie well posterior to the end of the hinge line (Fig. 4E).
- 5) *Lepas pacifica*. The anterior and posterior ends of the oval-shaped cypris show the two valves agape with a total length of 1800 μm and a maximum width of 512 μm ; the hinge line is smooth, standing out from the carapace ornamentation as a shallow trench. The surface of the carapace is covered with short longitudinal striations (formed aggregations of tubercles) and short, socketed setae (Fig. 5A, B). The fronto-lateral gland pore sits on a projection formed by fused tubercles; the opening is small and oval-shaped (Fig. 8E). The LOs in this species are of Type C, but they have a pore field with a distinct keel reminiscent of Type B (Fig. 5C). LOs 1 and 2 are not completely symmetrical, those of the right side being slightly curved and those of the left side straight (Fig. 5B). They toe-in and out, respectively, and the associated central pore lies in a central position (Fig. 5B-D). LOs 3 and 4 are almost straight (Fig. 5G), and run parallel to the hinge line (Fig. 5E-G). The associated central pore is located within a slit-like excavation on the hinge line (Fig. 5F). The LO5s toe-out, and the right one being slightly anterior to that on the left (Fig. 5E).
- 6) *Dosima fascicularis*. The cyprid is oval-shaped but globose in dorsal view with the anterior and posterior ends gaping; the maximum width is attained in the anterior half (604 μm), and the total length is 1177 μm (Fig. 6A). The surface of the carapace has some setae and is covered with low, closely spaced, rounded tubercles, the hinge line is more or less well defined, and a row of large pores with setae in sockets runs parallel to the anterior portion of the valves (Fig. 6A). The fronto-

lateral gland pore exhibits two irregular external borders and one complete internal border, and the opening is circular in section (Fig. 8F). The cluster formed by LOs 1 and 2 is located farther back on the carapace than in the other species described herein. The LOs are of Type C with a keel, with a prominent terminal pore and pore-field pores of various sizes and shapes (Fig. 6C, D). LOs 1 and 2 are slightly curved and toe-in; the LO2s are longer than the LO1s, and together run nearly parallel to the hinge line; the associated central pore is located between the posterior ends of LO1s (Fig. 6B). While LOs 3-5 are short, straight, subequal in size, and toe-out, they run more or less in a straight line; both LOs 4 and 5 straddle the gape beyond the end of the hinge line (Fig. 6E-G).

- 7) *Conchoderma virgatum*. In dorsal view, the cyprid presents the usual bluntly pointed anterior and posterior ends, but with a central region of varying width (464-500 μm); the total length is 1550 μm . The surface of the carapace is smooth, with a few scattered socketed setae and an evident hinge line (Fig. 7A). The fronto-lateral gland pore has a complete external border, several minor foldings, and a complete internal border; the opening is circular in section (Fig. 8G). The LOs are keel-bearing, Type C (Fig. 7C-G), and the pores of their pore fields vary in size (Fig. 7D); the associated central pore is slit-like. LOs 1 and 2 are straight and do not overlap, and all of them have a prominent anterior terminal pore (Fig. 7B, C). Slightly curved LOs 3 and 4 toe-in and out, respectively, as do LOs 1-2; the associated central pore is slit-like (Fig. 7E-G). LO5s toe-out and are deployed asymmetrically in the four cyprids observed, the right one being in a more anterior position (Fig. 7E).

DISCUSSION

Jensen et al. (1994) and subsequent authors (cf. Høeg et al., 2004) have described and discussed the phylogenetic value of the LOs of cyprids in Facetotecta/Ascothoracida and Cirripedia (Acrothoracica/Rhizocephala/Thoracica). These authors generally agree that the few hitherto described Ascothoracida, with the LOs arranged linearly along the hinge line, display the plesiomorphic condition. Taking this as a departure point, Jensen et al. (1994) developed plausible evolutionary pathways to explain the observed patterns. The original LO type and the main departures from it were characterized as follows: Type A, a depression with a seta-like structure lying on its floor found in the ascothoracicans, becomes Type B, a seta-like structure with pores within the depression in acrothoracicans and some lower pedunculate barnacles such as *Capitulum*, and then changes to Type C, a pore field integrated into the carapace and nearly flush with its surface or with no depression, as found in most pedunculate barnacles, rhizocephalans, and balanomorphs. Furthermore, the terminal pore at the apex of a Type A LO changes from a posterior to an anterior position in thoracicans, or it may disappear. Also, the distribution of LOs on the carapace changes from a linear arrangement along the hinge line (ascothoracicans and some lepadomorphs) to other arrangements such as the anteriorly converging or diverging (toeing in or out). When two pairs

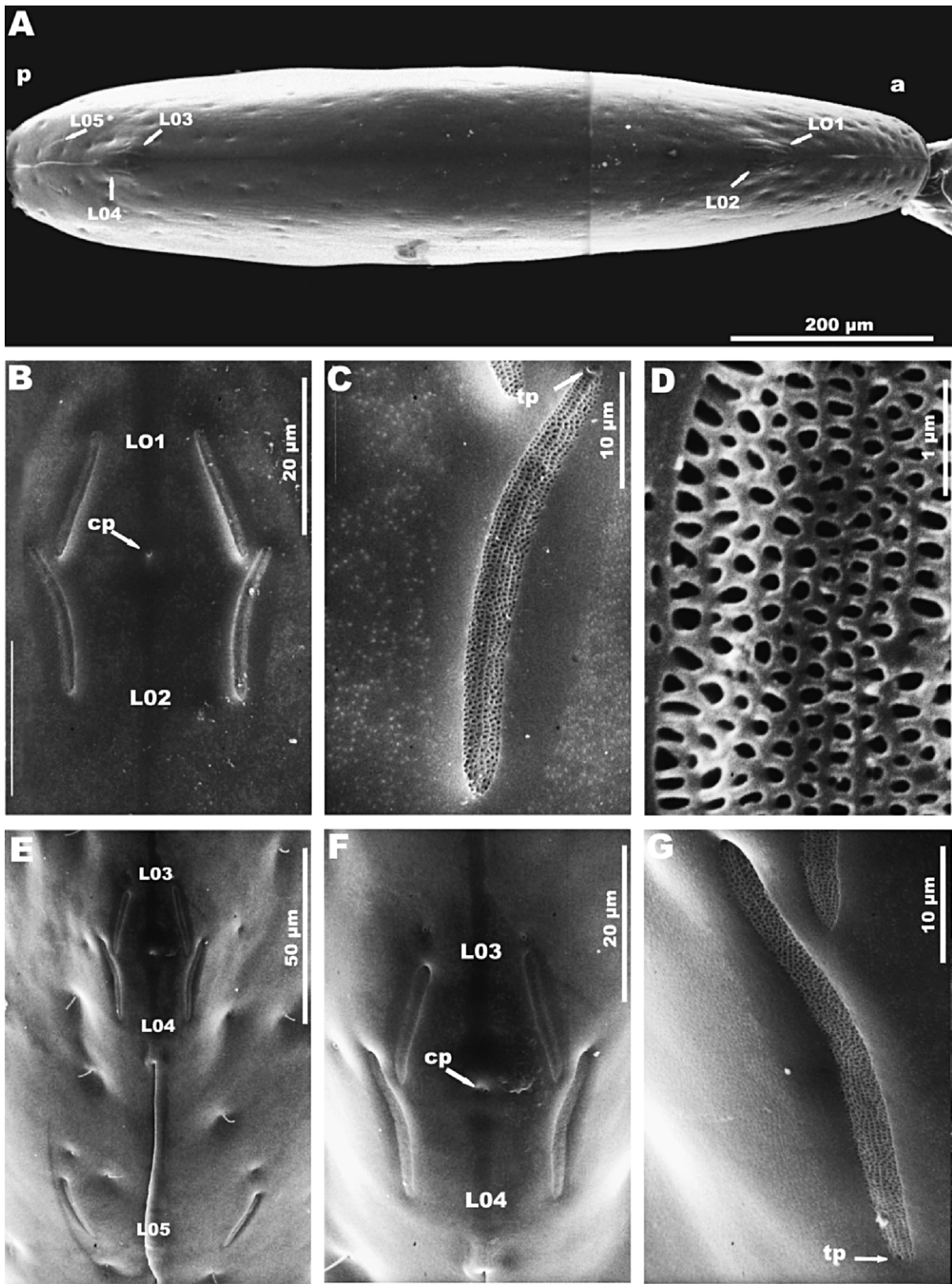


Fig. 4. *Octolasmis aymonini geryonophila*, cyprid: A, dorsal view showing the distribution of the five pairs of LOs, (a) anterior end, (p) posterior end; B, LO1s and LO2s with central pore (cp); C, right LO2 showing terminal pore (tp); D, detail of LO2; E, LO3-LO5; F, detail of LO3s and LO4s with central pore (cp); G, left LO4 showing terminal pore (tp).

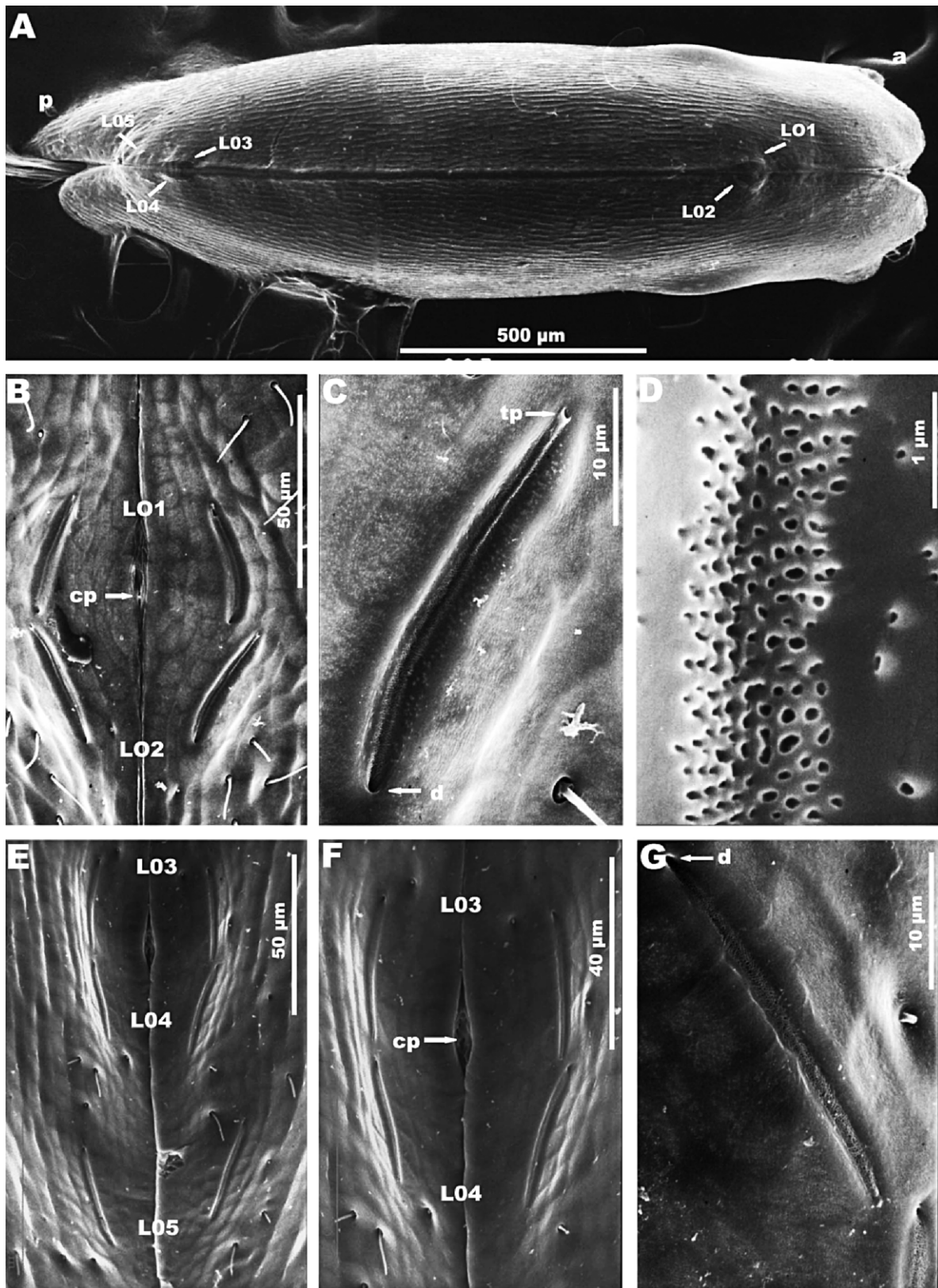


Fig. 5. *Lepas pacifica*, cyprid: A, dorsal view showing the distribution of the five pairs of LOs, (a) anterior end, (p) posterior end; B, LO1s and LO2s with central pore (cp); C, right LO2 showing terminal pore (tp) and pit in pore field at end opposite to terminal pore (d); D, detail of LO2; E, LO3-LO5; F, detail of LO3s and LO4s with central pore (cp); G, detail of right LO3 showing pit in pore field at opposite end of terminal pore (d).

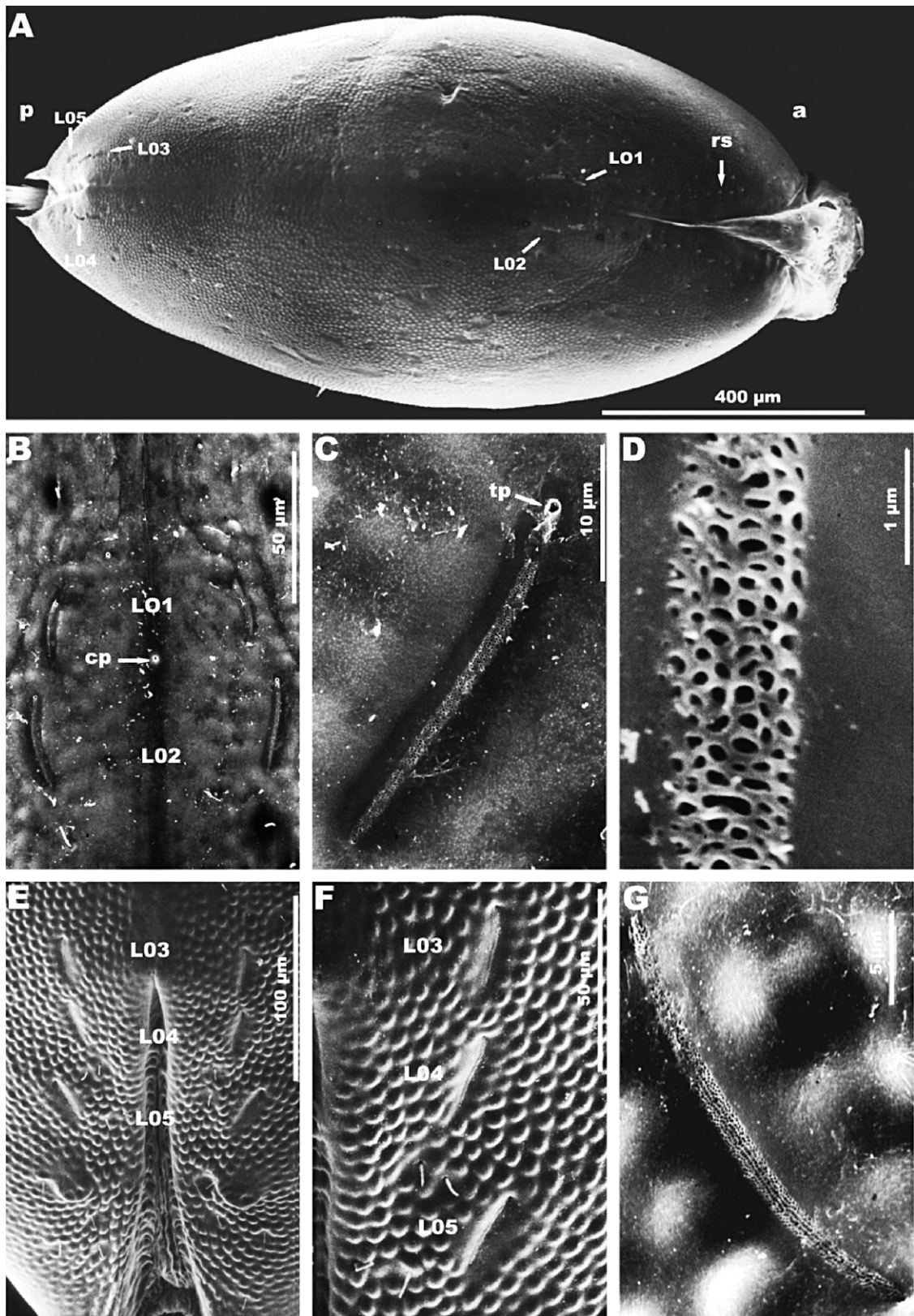


Fig. 6. *Dosima fascicularis*, cyprid: A, dorsal view showing the distribution of the five pairs of LOs, (a) anterior end, (p) posterior end, (rs) row of setae; B, LO1s and LO2s with central pore (cp); C, right LO2 showing terminal pore (tp); D, detail of LO2; E, LO3-L05; F, detail of LO3-L05; G, LO4.

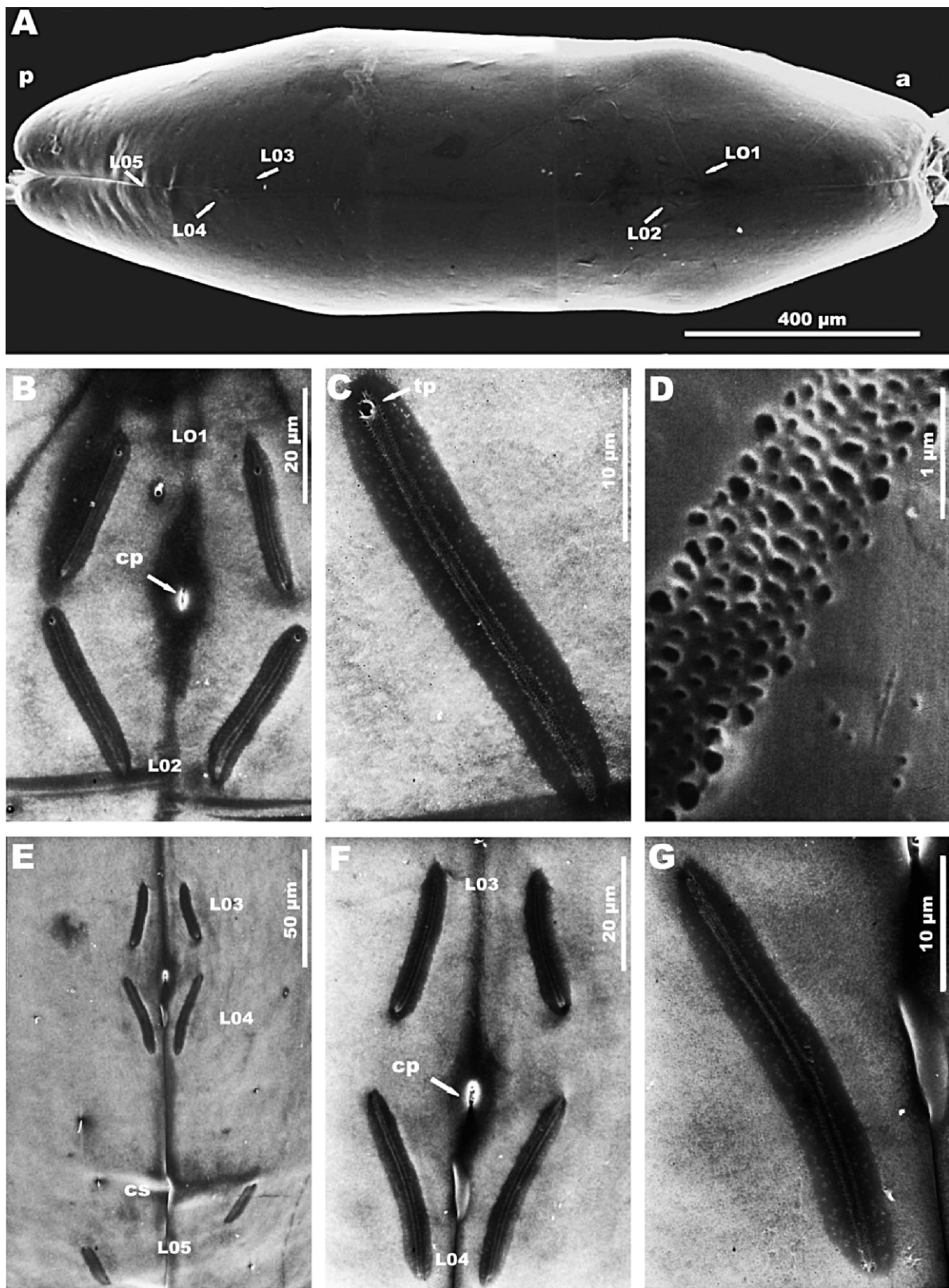


Fig. 7. *Conchoderma virgatum*, cyprid: A, dorsal view showing the distribution of the five pairs of LOs, (a) anterior end, (p) posterior end; B, LO1s and LO2s with central pore (cp); C, left LO2 showing terminal pore (tp); D, detail of LO2; E, LO3-LO5 with central slit (cs); F, LO3 and LO4 with central pore (cp); G, LO4 showing terminal pore.

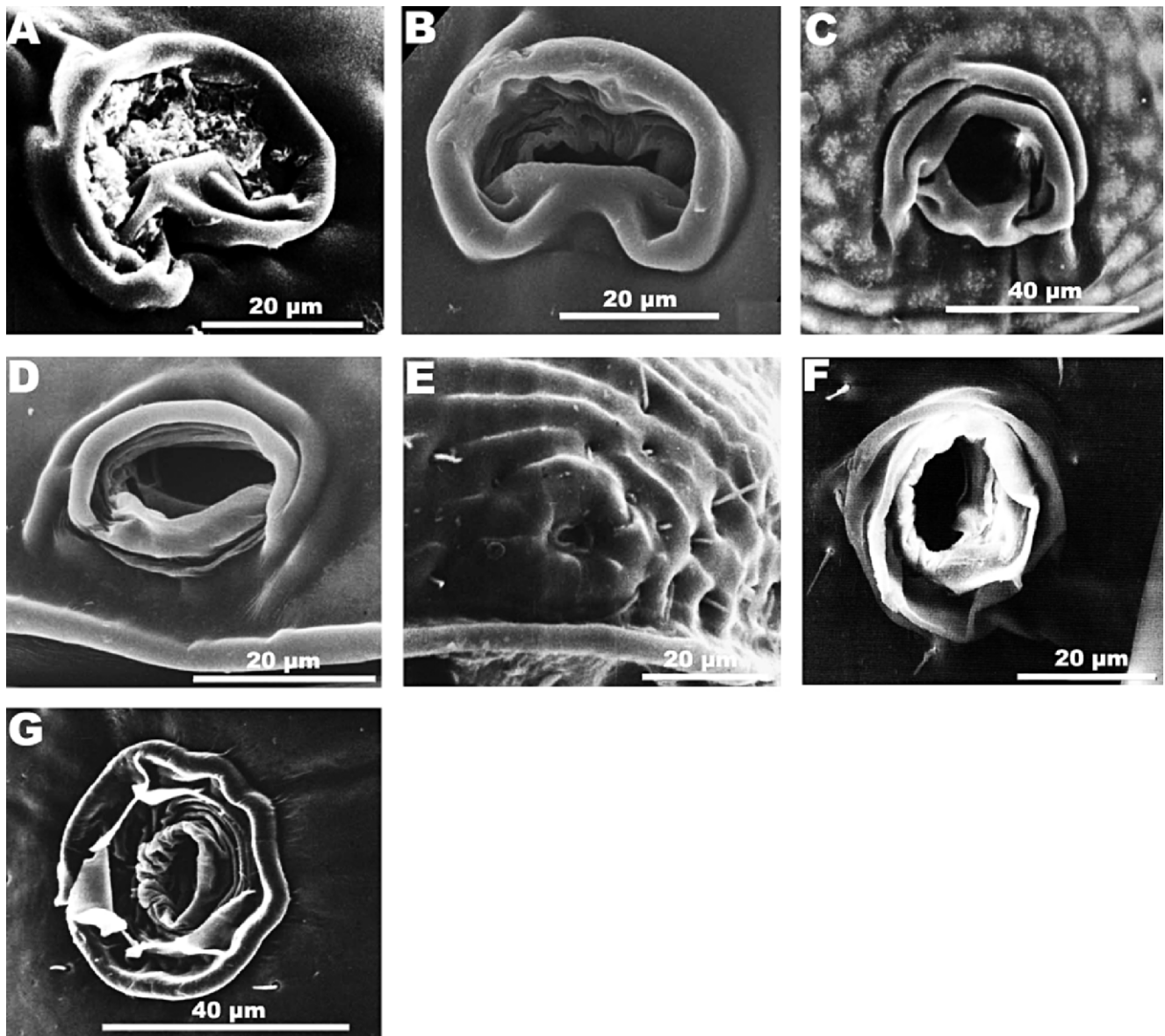


Fig. 8. Fronto-lateral gland pores of cypris larvae: A, *Heteralepas* sp. 1; B, *Heteralepas* sp. 2; C, *Poecilasma inaequilaterale*; D, *Octolasmis aymonini geryonophila*; E, *Lepas pacifica*; F, *Dosima fascicularis*; G, *Conchoderma virgatum*.

toe-in and -out respectively, the configuration is termed rhomboidal, as LOs 1 and 2 in heteralepdomorphs and some lepadomorphs (herein), the advanced diverging-diverging (toe-out/toe-out) configuration being found in iblomorphs, scalpellomorphs, verrucumorphs, and balanomorphs (Buckeridge and Newman, 2006). In light of genetic data (Perez-Losada et al., 2004) and adult morphology, one might expect the rhomboid condition of the first two pairs of LOs to be plesiomorphic for the thoracicans. However, it is not found in the most plesiomorphic of all thoracicans, Iblomorpha as Buckeridge and Newman (2006) noted, based on Yan et al. (2005), nor in the lepadids *Dosima fascicularis* and perhaps *Poecilasma inaequilaterale*, which herein have been shown to have something closer to the generalized, all-linear arrangement. The significance of these morphological variations has yet to be resolved.

In this study, seven species belonging to three families in Pedunculata were examined. We showed that a greater degree of variation exists in the LO patterns of this group than previous studies have indicated (Fig. 9). Jensen et al. (1994) and Buckeridge and Newman (2006) based their interpretations of Lepadomorpha on observations from *Lepas australis* Darwin, 1851, *L. pectinata* Spengler, 1793, an undescribed species of *Lepas*, and *Dosima fascicularis*, in Lepadidae. In this study new information is presented with the inclusion of species from among the heteralepdomorphs (*Heteralepas* sp. 1 and 2), the lepadomorph family Poecilasmatidae (*Poecilasma inaequilaterale* and *Octolasmis aymonini geryonophila*), and two additional species of Lepadidae (*Lepas pacifica* and *Conchoderma virgatum*). The pattern we found is one in which the anterior two pairs of LOs appear in much the same rhomboidal

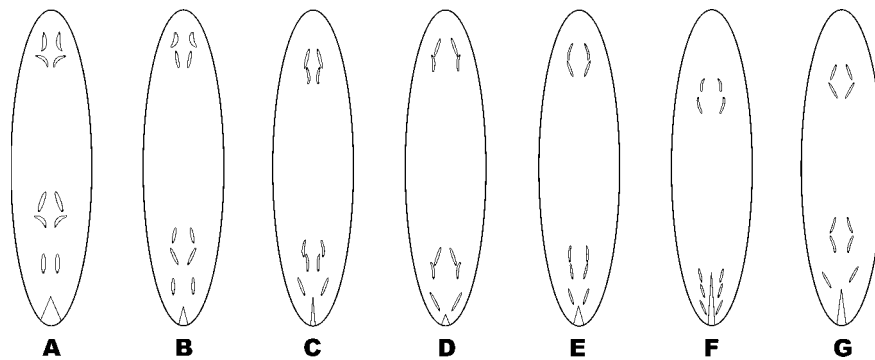


Fig. 9. Schematic representation of LOs: A, *Heteralepas* sp. 1; B, *Heteralepas* sp. 2; C, *Poecilasma inaequilaterale*; D, *Octolasmis aymonini geryonophila*; E, *Lepas pacifica*; F, *Dosima fascicularis*; G, *Conchoderma virgatum*.

arrangement in the heteralepadids, poecilasmatids, and some lepadids. However, there are differences in detail between species, for the LO1s in *O. californiana* Newman, 1960 described by Alvarez et al. (2003) are strongly curved inward, whereas those of *O. aymonini geryonophila* are virtually straight. This may be a new important feature among those distinguishing shallow and deep-water *Octolasmis* (Newman, 1967). It is necessary to view such similarities and differences with caution, but because, while Jensen et al. (1994) described the configuration of LOs 1 and 2 in *C. virgatum* as converging-diverging (toeing in and out), we found them to be essentially linear in specimens from a different water mass.

Buckeridge and Newman (2006) considered a non-linear arrangement of LOs 3-5 along the hinge line to be the apomorphic condition in thoracicans, including Lepadidae and some scalpellomorphs. If so, departures from this pattern seen in species of Iblomorpha, and now Heteralepadomorpha (Heteralepadidae), Poecilasmatidae, and *C. virgatum* (Lepadomorpha) by this interpretation would be more derived states. The arrangement of the posterior three pairs of LOs in *C. virgatum* differs from what has been published previously in that LOs 3 and 4 are rhomboidally arranged (Jensen et al., 1994). The location of the LO5s in this species also differs from previous accounts in that they are well separated from the clustered LOs 3 and 4 along the hinge line (Jensen et al., 1994). The mix of plesiomorphic and apomorphic conditions in the lower pedunculate barnacles diminishes the phylogenetic resolving power of these characters.

The “type” of lattice organs found in all the studied species closely corresponds to Type C of Jensen et al. (1994). This is the most advanced type and consists of an elongate pore field lying within a shallow depression surrounded by a band of smooth cuticle. A small variation of this is seen in *P. inaequilaterale* and *L. pacifica*, in which the LOs have a distinct keel reminiscent of, but not necessarily homologous with, the keel of Type B of Jensen et al. (1994), which is purported to be the plesiomorphic type within Cirripedia. Such a keel is present in the LOs of some higher thoracicans such as Verrucomorpha (Jensen et al., 1994), so it may not after all be of any particular phylogenetic significance.

The length of the LOs relative to cyprid total length is highly conserved in Lepadomorpha, as was noted by

Alvarez et al. (2003), always amounting to about 2% despite a two-fold difference in cyprid length. The data from the species examined herein confirm this pattern for Lepadomorpha but show a significantly different pattern in Heteralepadomorpha, where they reach only about 1% of total length in the examined species (Table 1). Although it is hard to infer the significance of size differences in these sensory organs, the pattern represents an additional character that strengthens current taxonomic classifications.

The fronto-lateral gland pores have not been examined in detail in many species. Apparently, they display just a moderate amount of variation. Together with major differences in shape, as in *Lepas pacifica* (Fig. 8E), and in combination with other cyprid structures such as the first antennae, they may be useful in discriminating among species (Yan, 2003; Alvarez et al., 2003).

Cyprid characters may prove to be useful aids in species identification in the future. Both samples of *Heteralepas* reported on here would likely have been reported as *Heteralepas quadrata* (Aurivillius, 1894) if it had not been for the observed differences between their cyprid larvae. The data presented on these species may contribute to elucidate their specific status considering the high degree of variation found in some species of *Heteralepas* (Buhl-Mortensen and Newman, 2004).

Finally, let us consider whether knowledge of the LOs of *Dosima* assists in our understanding of its origins. Did it evolve from the pelagic lepadids as is generally supposed, or from some benthic ancestor among the poecilasmatids, or even from the oxynaspidids as Memmi (1989) attempted to demonstrate? As shown here, *Dosima* seems to have the generalized linear arrangement of LOs, a pattern only partially evident in various species of *Lepas* and completely lost in *C. virgatum* and the poecilasmatids. The lattice organs of the oxynaspidids have yet to be observed, so while *Dosima* still could have arisen from them, LO morphology seems to rule out an origin among the lepadids.

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