

An ontogenetic analysis of changes in morphology during phylogeny of some *Lamprocyrtis* spp. from deep sea sediments

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ABSTRACT: The ontogenetic patterns of skeletal development that may account for variations in morphology of the mature skeleton during evolution of *Lamprocyrtis heteroporos* to *L. nigrinae* and *L. heteroporos* to *L. gamphonycha* have been determined using scanning electron microscopy. Ontogenetic patterns of development are inferred from examination of mature stages exhibiting features characteristic of rim growth or bridge growth. The characteristic differences in pore size and shape between the cephalo-thoracic segments (round pores with thick rims) and third segment (polygonal pores with thin, bar-like rims) in mature specimens of *L. heteroporos* are explained by differences in ontogenetic growth patterns. A process of rim growth during deposition of the first two segments produces the nearly circular pores and wide rims in the cephalo-thoracic regions. This is followed by bridge-growth during formation of the third segment producing large, polygonal pores with thin bars. The septal ring at the juncture of the second and third segment is the terminal apertural rim deposited at the orifice of the second segment before bridge growth commences. The gradual shift toward more polygonal pores throughout the skeleton and the loss of the septal ring during evolution toward *L. nigrinae* is explained by increasing amounts of bridge growth occurring during morphogenesis of the cephalo-thoracic segments. This is further exemplified by the bridge-like buttresses supporting the offset apical spine in *L. nigrinae*. These analyses of ontogenetic growth patterns combined with classical methods of analyzing mature skeletons of fossil radiolaria may yield significant additional information in elucidating phylogenetic pathways and discriminating among species.

INTRODUCTION

The purpose of this paper is to examine skeletal ontogenesis in five species of the genus *Lamprocyrtis* Kling 1973, and determine to what extent the well-established phylogenetic changes in morphology of these species (Hays and Gross, in prep.) can be explained by differences in growth patterns. The *Lamprocyrtis* lineage extends back at least to the Lower Miocene, but the descendent species we have examined arose approximately 6.9 million years ago in the upper Miocene. This evolutionary series is of further interest as it proceeds from *L. heteroporos* (Hays 1965), confined to subpolar water, to *L. nigrinae* (Caulet 1971), most abundant in sediments underlying tropical and subtropical water. It also appears that *L. nigrinae* evolved from *L. neoheteroporos* Kling 1973, in low latitudes. Hence, a thorough understanding of the ontogenetic processes accounting for the mature morphology of these species may eventually contribute to our understanding of the environmental selection pressures that could account for speciation events at these different geographical locations. A summary of major morphological changes that occurred in the various speciation events is presented as background information for the ontogenetic analyses.

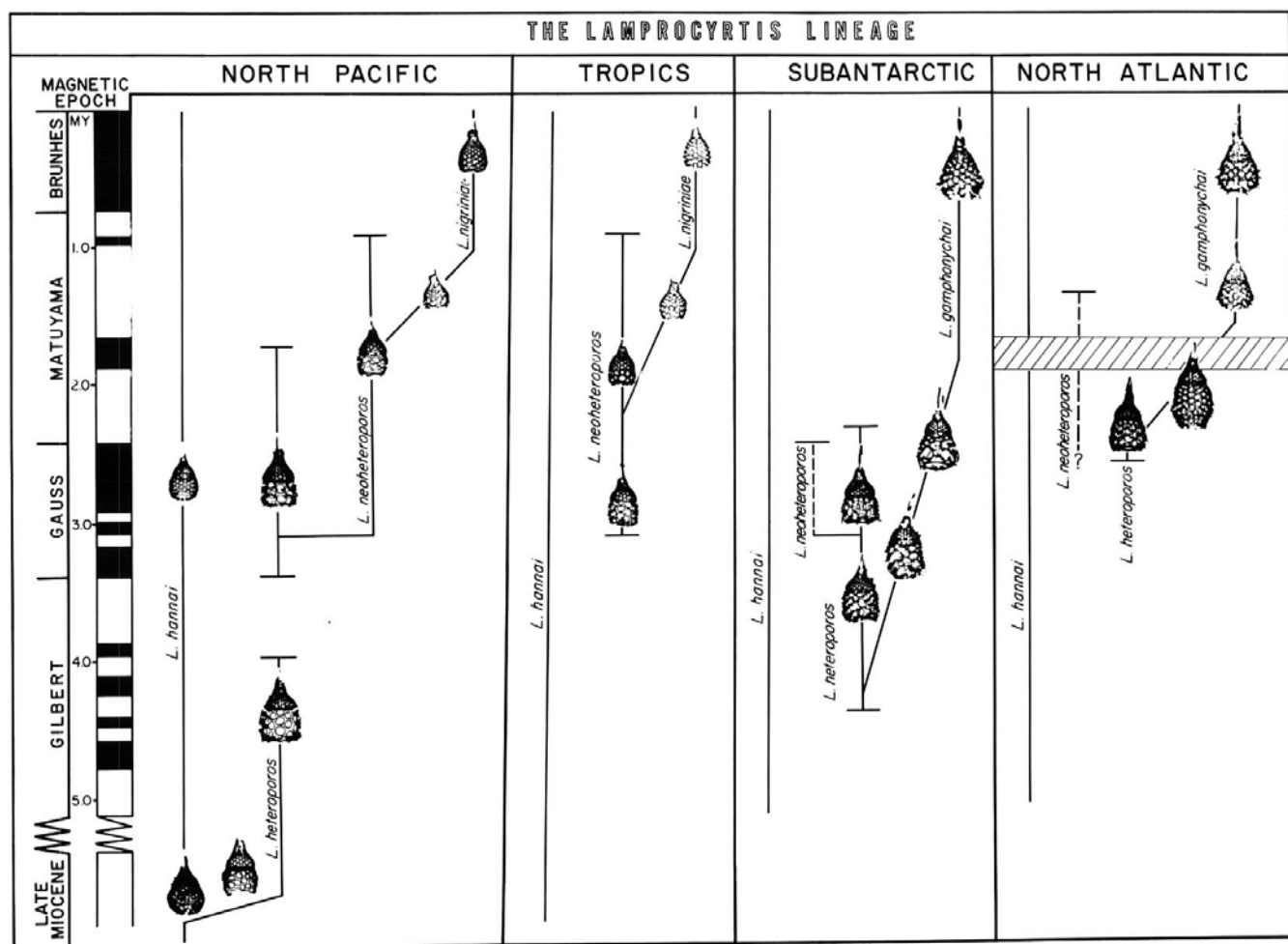
The genus *Lamprocyrtis* was erected by Kling (1973) to include three- and two-segmented Pterocoryidae Nassellaria. The first segment (cephalis) is generally conical and weakly three-lobed with either a single or double, three-bladed apical spine. If the spine is single, it may be centered or offset; if double, both spines are parallel to the major skeletal axis. The shape of the second segment is campanulate with evenly

spaced circular pores. The pore size in this segment is uniform among species. An internal septal ring marks the boundary between the second and third segment when the latter is present. A number of species within the genus are distinguished on the basis of pore variations in the third segment. Pore pattern variations range from circular pores similar to those in the thorax, to those of irregular shape and several times the size of the thoracic pores. Some species possess a thickened peristomal ring often with terminal spines; in others it is absent and the periphery of the third segment is smooth or bears subterminal spines.

The study of Hays and Gross (in prep.) provides a global coverage of the evolution of the genus and therefore only a brief overview (summarized in text-fig. 1) is given here. The extant ancestral species extends back to at least the lower Miocene. At 6.9 million years in the far north Pacific (north of 40°N), individuals appear in the *Lamprocyrtis* (?) *hannai* (Campbell & Clark 1944) population with larger abdominal pores. These morphotypes, marked by increasing abdominal pore size, are destined to become *L. heteroporos* that proliferate and eventually far outnumber *Lamprocyrtis hannai*. *L. heteroporos* migrates out of the subpolar water to northern subtropical waters at 4.9 million years and to the subantarctic by 4.4 million years. Soon after arrival in the antarctic, the *L. heteroporos* population produced morphotypes with more conical abdomens and subterminal spines that eventually evolved into *Lamprocyrtis gamphonychai* (Jørgensen 1905) by 1.6 million years ago. *L. heteroporos* became extinct at 2.3 million years in the Antarctic and North Atlantic and 1.8 million years in the North Pacific.

By 3.2 million years ago, the *L. heteroporos* population was abundant in both the north Pacific and subantarctic. At this time, individuals without a septal ring at the juncture be-

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TEXT-FIGURE 1

Lamprocyrtis lineages in the North Pacific, tropics, subantarctic, and North Atlantic as proposed by Hays and Gross (in prep.)

tween the second and third segment appeared simultaneously in both the far north Pacific and subantarctic; and morphotypes without the septal ring migrated to the tropical Indo-Pacific. These individuals, lacking a septal ring but resembling *L. heteroporos* in all other respects, are *L. neoheteroporos*. In the tropical Indo-Pacific, the *L. neoheteroporos* population gradually produced smaller individuals with smaller abdominal pores. These individuals eventually became *L. nigriniae* by 1.1 million years and continued to live in tropical and subtropical Indo-Pacific locations. Therefore according to the interpretation of Hays and Gross, the *L. heteroporos* diverges into two evolutionary paths: *L. heteroporos* to *L. nigriniae* in the North Pacific/Indian Tropics, and *L. heteroporos* gives rise to *L. gamphonychia* in the Antarctic/North Atlantic.

We have applied some current knowledge of radiolarian ontogenetic patterns (e.g. Anderson and Swanberg 1981; Anderson 1983; Anderson and Bennet 1985; Anderson et al. 1986; Thurow and Anderson 1986) toward an explanation

of the rather clear changes in skeletal morphology during phylogenetic development from *L. heteroporos* to *L. nigriniae*. Previous transmission and scanning electron microscopic investigations of skeletal morphogenesis in some extant species have shown that the skeleton is deposited within a living sheath "cytokalymma" secreted by the cytoplasm of the cell. This mold-like cytoplasmic sheath determines the ultimate morphology of the skeleton. The form of the skeleton is produced both by the configuration of the internal hollow space where the initial silica is deposited, and in some cases also by the dynamic flowing process (cytoplasmic streaming) of the cytokalymma that in effect sculpts the shape of the growing skeleton. The spatio-temporal organization of the cytokalymmal activity thus determines the sequential pattern of development of the skeleton. Analyses of living polycystine radiolarian species during ontogeny have shown that there are at least two fundamental patterns of growth that can account for skeletal morphology of a wide range of species: (1) Rim growth, a process of silicogenesis resulting in relatively massive silica deposition forming substantial

walls with circular or nearly circular pores; and (2) Bridge growth, a process of forming cross-bridges within a lattice skeleton producing usually a rather light-weight mesh consisting of polygonal spaces bordered by thin, bar-like skeletal elements. In some cases, secondary rim growth may occur upon the margins of the initially polygonal pores, increasing the bulk of the silica and producing pores of smaller diameter with more circular outlines. Ontogenetically, rim growth can occur by several different patterns of cytotakymmal activity. This paper describes the most common form observed in skeletons with predominant rim growth from the outset of ontogeny. Based on evidence of the skeletal form deposited within the cytotakymma, the rather ameboid flowing activity of the cytotakymma first streams outward from at least two locations forming a crescent-like configuration. This is the initial stage in the development of a pore rim. As the cytotakymma further expands, the two streaming arcuate lobes recurve toward one another and coalesce producing a circular pore surrounded by silica deposited within the sheath of the cytotakymma. By repeated steps of this kind (i.e. outward projection of arcuate cytoplasmic lobes, their recurving toward one another, and coalescence at the forward edge) additional porous areas are added onto the growing skeletal wall (pl. 2, fig. 1). Bridge growth by contrast involves the elaboration of a net-like pseudopodial framework of the cytotakymma, which at first is rather open with large polygonal pores. The hollow space within the cytotakymmal network is the site of silica deposition thus determining the form of the skeletal lattice. Further elaboration of the developing skeleton occurs by additional cross-bridge formation within the pores partitioning them into two smaller pores usually with decidedly elliptical outline. The cytotakymma forms finger-like protrusions from the edge of a pore thus initiating the bridge growth. In some cases, only one protrusion grows across the pore and eventually fuses with the opposite side, or in other cases, two diametrically opposed protrusions may be formed that grow toward one another and meet to produce a complete bar partition. By repeated cross-bridging of this kind, an initially large, open-lattice skeleton is transformed into a finer pore construction. In some species, either rim growth or bridge growth is the predominant form of ontogenesis. In others, however, combinations of these two fundamental growth patterns, varying spatio-temporally and in magnitude of form, account for the morphology of the mature skeleton. Evidence is presented here that variations in spatio-temporal patterns of rim and bridge growth can account for the changes in morphology of the *Lamprocyrtis* spp. as diagrammed in text-figure 1.

METHODS

Cores were selected for SEM study from the following geographic locations (table 1): North Pacific (DSDP Site 579A), the Indian Ocean (piston core V29-40) and the subantarctic (DSDP Site 514, and piston core RC13-252). Samples were taken at levels where the various *Lamprocyrtis* species were relatively abundant and well preserved, corresponding in age to 3.5–4 my (early Pliocene), 3 my (middle Pliocene), 1 my (mid Pleistocene) and Late Pleistocene.

The samples were disaggregated chemically using HCl and H₂O₂, and mechanically through boiling and ultrasonic clean-

TABLE 1
Core samples.

Sample source	Lat.	Long.	Water depth (meters)
DSDP Site 579A	38°37.6'N	153°50.28'E	5736
DSDP Site 514	46°02'S	26°51'W	4318
Piston core V29-40	10°29'S	78°03'E	5325
Piston core RC13-252	45°05'S	09°09'E	4523

ing. The cleaned and dried radiolarian samples were hand picked using a low-power dissecting microscope and mounted on SEM stubs with double adhesion tape as a substrate. Images were made of 90 specimens and many more were examined as a basis for description of growth patterns reported here.

To recover juvenile radiolarian specimens to document early growth stages, a 2 cm sample was taken from V21-148 (North Pacific) at a depth of 772 cm, disaggregated and washed through 63 μ m, 38 μ m, and 20 μ m screens. The collected radiolarian skeletons were strewn onto SEM stubs. The stubs were plated with a thin film of gold, and observed with a Cambridge Stereoscan 250 Mk2 scanning electron microscope. Individuals were identified to species based on the shape and pore configuration of the cephalic region. Only early stages of *Antarctissa* were found in sufficiently intact condition to make analyses.

RESULTS

Detailed scanning electron microscopic images yield evidence of growth patterns that may explain the changes in morphology accompanying the evolution of *L. heteroporos* to *L. nigriniae* as summarized in text-figure 1, and the general morphological features of the succession of species as displayed in plate 1, figures 1–6. Although no clearly identifiable very early stage of *Lamprocyrtis* was found, an early ontogenetic stage of a juvenile specimen of *Antarctissa* showing only the cephalo-thoracic region, was discovered fortuitously among sedimentary samples containing mature *Lamprocyrtis* skeletons. This species has a porous cephalis when mature with circular pores resembling those of *Lamprocyrtis* spp. Since there are some similarities in the mature skeletons of *Antarctissa* and *Lamprocyrtis*, it is described here to document early stages of growth to complement the detailed analyses of more mature stages found for *Lamprocyrtis* spp. The SEM images provide clear evidence of rim growth. The arcuate lobes of silica deposited at the periphery of the incomplete thorax (pl. 2, fig. 1, see arrow) and the thin wall with circular pores in the completed region near the apical spine are characteristic of early stages of rim growth (Anderson 1983). A high magnification view of a mature cephalic pore of *L. heteroporos* (pl. 2, fig. 2) exhibits the thickened wall and thin flange-like border within the circular pores characteristic of mature stages of rim growth. These signs appear throughout the cephalic and thoracic segments of *L. heteroporos*. The abdominal segment, however, shows clear evidence of bridge growth. The lattice consists of polygonal

pores separated by thin bar-like partitions (pl. 2, fig. 3). In some specimens (e.g. pl. 2, fig. 4), incomplete stages of bridge growth are observed exhibiting the characteristic finger-like projection within the lumen of the pore (Anderson 1983) further corroborating the conclusion that abdominal ontogenesis occurs by bridge growth. Thus, these two phases of ontogenesis (rim growth followed by bridge growth) can account for the two kinds of pores in *L. heteroporos*: circular pores in the cephalo-thoracic region resulting from predominantly rim growth, and large irregular pores in the abdomen formed largely by bridge growth. A septal ring (pl. 2, figs. 5 and 6) separates the two regions of growth and forms a substantial rim within the skeleton (pl. 2, fig. 6). These data suggest that the completion of thoracic ontogenesis is marked by deposition of an apertural rim, which becomes the septal ring when bridge growth subsequently deposits the attached abdominal lattice. The lattice growth, moreover, commences at the margin of the thoracic apertural rim where the bar-like elements are initiated and grow distally to form the lattice elements.

By contrast to the sharp delineation of rim growth from bridge growth at the thoracic-abdominal septum in *L. heteroporos*, a gradual transition of bridge growth into the thoracic region is observed in *L. neoheteroporos* (pl. 3, fig. 1). The clearly polygonal quality of the lattice and the relative absence of strong circular pore development is evidence of the transition toward bridge growth throughout the skeleton. *L. nigrinae* (pl. 3, figs. 2-4), observed in high magnification, shows strong evidence of bridge growth throughout the entire skeleton. The cephalic region contains elliptical pore outlines with evidence of bridging bars across their diameter (pl. 3, fig. 3) indicating a transition away from rim growth toward bridge growth. The offset spine (pl. 3, fig. 4) is buttressed laterally by bridge-like bars (arrow) connecting it to the surrounding lattice. This offset spine compared to the centrally located spine of *L. heteroporos* and *L. neoheteroporos*, may result from the increasing trend toward bridge growth. The lateralization of the spine, as observed in *L. nigrinae*, could reflect a change in ontogenetic plan with the initial spine serving as an anchor point from which the initial buttress-like bridge framework originates during ontogeny. Thus the lateral position may arise from constraints imposed by the initial geometry of the cephalic lattice early in ontogeny. The degree of lateral buttressing and the presence of arch-like bridge growth is more apparent when compared to the centrally-located spine of *L. heteroporos* (pl. 3, fig. 5). The thickened edge may represent the phylogenetic precursor for the initial part of the lateral spine in *L. nigrinae*. However, we have no analysis.

The high magnification views of *L. gamphonychai* also support the conclusion that this species could have arisen from *L. heteroporos* by increasing development of bridge growth in the cephalo-thoracic region (pl. 3, fig. 6). The loss of a sharp delineation of the thoracic-abdominal septum and the tendency toward elliptical pore outlines in the thoracic segment with clear bridge-like links into the abdominal segment, further support this conclusion. The spine-like projections at the base of the abdomen (pl. 4, fig. 1) and the varying stages of bridge growth observed within pores of the abdomen (pl. 4, figs. 2-4) provide strong evidence for bridge-growth on-

togeny in this species. Some rim growth also accompanies the bridge growth, especially in the cephalo-thoracic regions, as signs of rim thickening are still evident on the edges of the pores (pl. 3, fig. 6).

DISCUSSION

The clearly identifiable morphological changes during the evolution of the lineage *Lamprocyrtis heteroporos* to *L. nigrinae* (text-fig. 1) as documented by Hays and Gross (in prep.) can be understood in part as the product of a gradual shift in ontogenetic growth patterns from largely rim growth toward increasing amounts of bridge growth, commencing first in the abdominal segments. This change of growth produces larger more polygonal pores in the abdomen while circular pores remain in the cephalo-thoracic region as in *L. heteroporos*. Increasing dominance of bridge growth spreads also to the thoracic region in later evolutionary stages as observed in *L. nigrinae*. The offset spine reinforced by buttress-like bridge connections to the cephalis provides further evidence for the increasing contribution of bridge growth in later evolutionary stages of this sequence. Evidence for rim-growth is based largely on characteristic pore patterns in the mature forms. Additional insights may be obtained by searching for incomplete juvenile stages of *Lamprocyrtis* spp. that exhibit early stages of pore development. The potential for this kind of analysis is demonstrated by our finding at least one juvenile *Antarctissa* specimen (pl. 2, fig. 1) with evidence of rim growth in the cephalic segment. This is the first time that we have observed evidence of rim growth in an early stage of nassellarian ontogenesis in a sediment sample. Although this cannot provide conclusive evidence for rim growth in early stages of *Lamprocyrtis* spp., we note that both genera have similar pore construction in mature stages and therefore may have similar early stages of development. Clearly, more research is needed to clarify these relationships.

In the *Lamprocyrtis* spp., the gradual shift from rim-growth patterns with massive silica deposition toward a more open framework of bridge-growth construction produces lighter-weight structures and apparently conserves silica. The physiological and/or environmental factors accounting for this change are not known. Yet, it is interesting to note that this feature appears in both *L. heteroporos* and *L. nigrinae*, even though they evolved in very different geographical locations. This suggests that there is a strong genetic contribution in this morphological change during evolution rather than a major contribution by environmental factors. Clearly, the gradual shift toward bridge growth results in more efficient use of silica and is accompanied by a reduction in complexity of the skeleton as marked by the disappearance of the septal ring and loss of segmentation as in *L. nigrinae*. The accelerating depletion of silica content in the oceans over geological time, due to diatom fixation of silicate and the constant deposition of biogenically fixed opal on the seafloor, favors the development of organisms that utilize silica more efficiently. This may explain the gradual shift toward more lightweight constructional patterns in these *Lamprocyrtis* spp. However, some of these species occur in high latitudes where silica depletion is less pronounced than other regions of the oceans thus lessening the strength of the silica-depletion hypothesis as a major driving force in their evolution. Bjørk-

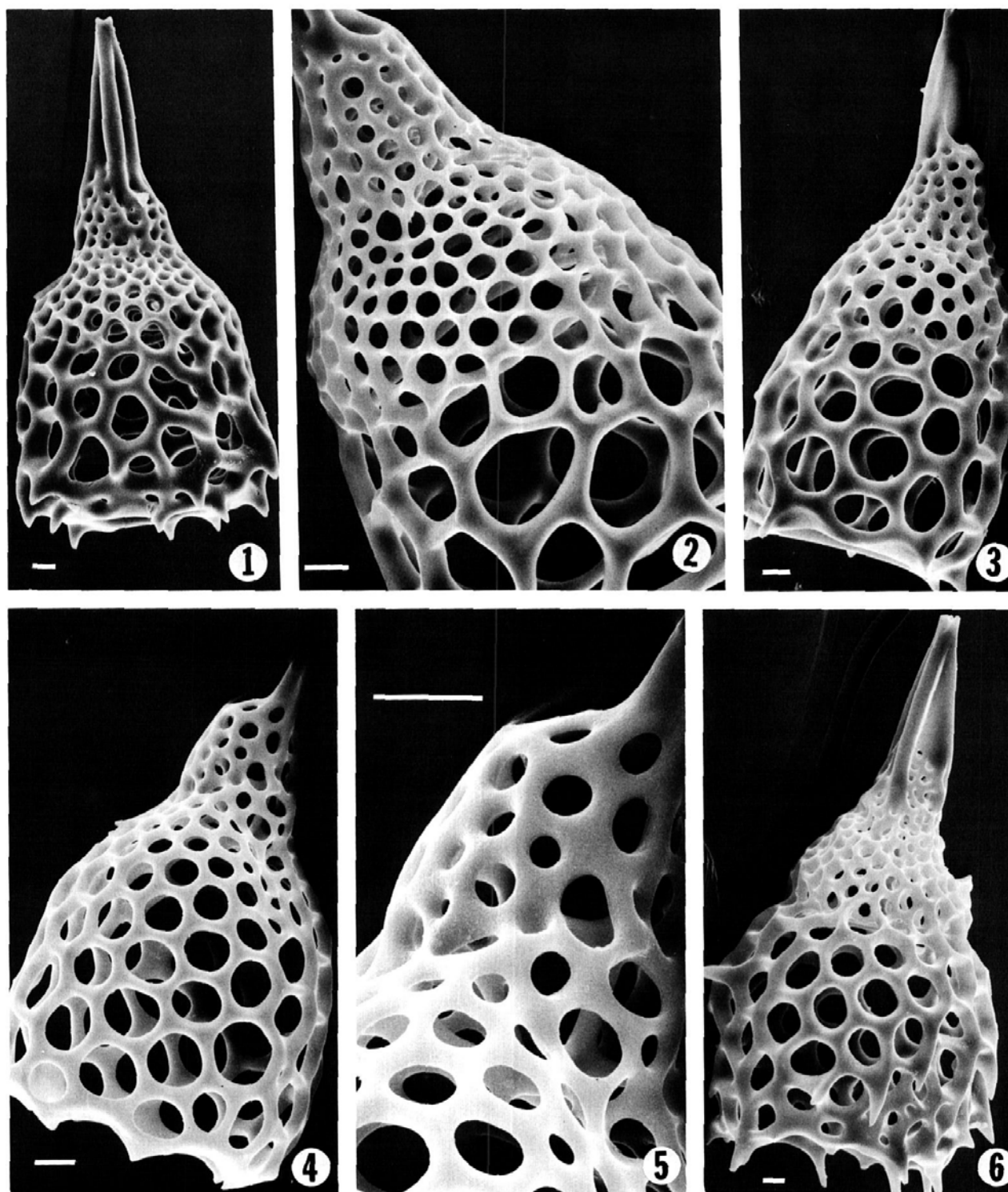


PLATE 1

1-6 Representative views of skeletal structure. 1 and 2, *Lamprocyrtis heteroporos*; 3, *L. neoheteroporos*; 4 and 5, *L. nigrinae*; 6, *L. gamphonychai*. Note the nearly circular pores in the cephalo-thoracic region, and polygonal pores with irregular bars between them in the

abdominal region of *L. heteroporos*. Increasing numbers of polygonal pores occur in the cephalo-thoracic regions of *L. neoheteroporos* and *L. nigrinae*. Scale = 10 μ m.

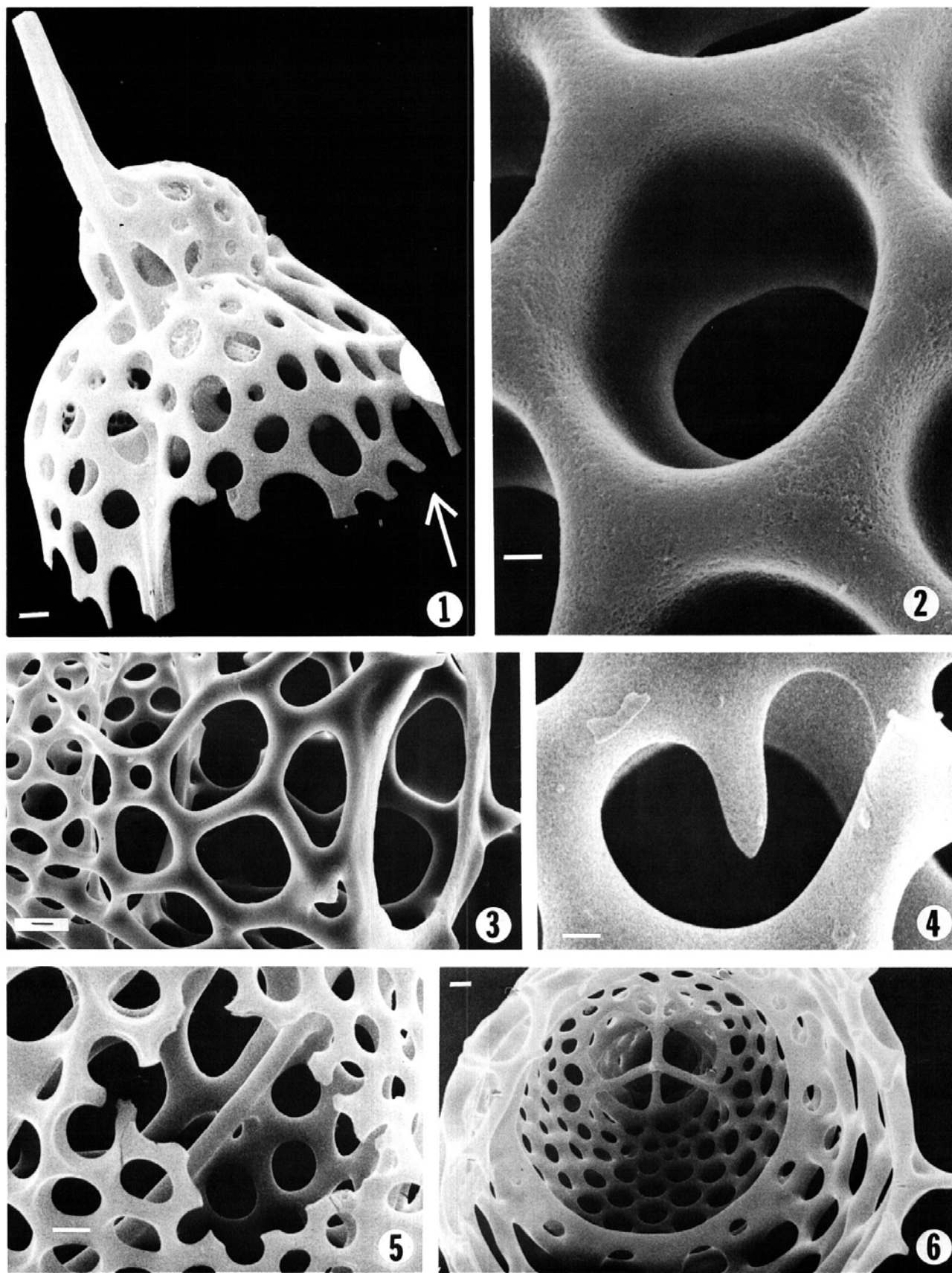
lund and Swanberg (in press) have hypothesized that the degree of genetic control over skeletal ontogenesis may vary with different stages of growth and that at some stages environmental variables such as temperature and nutrition may be significant variables in determining the amount of silica deposited. Further research is needed to determine how genetic control and environmental variables interact to produce the final shape of the radiolarian skeleton, and to ascertain their relative contributions with varying environmental conditions. Among the possible explanations for changes in skeletal pattern during evolution of *Lamprocyrtis* spp. is the gain

in mechanical advantage in capturing prey provided by the more open lattice in later evolutionary stages reported here. The gradual shift to bridge growth with fewer skeletal segments may permit the organism to mature more rapidly as there are fewer segments to be constructed during ontogeny. This may increase the rate of maturation of the skeleton and provide an advantage in snaring prey through early development of larger skeletal size. This hypothesis, however, cannot be fully evaluated until we have more data on the ontogenetic patterns of development in living specimens of this genus. At present, we also know little about the range and

PLATE 2

- 1-6 High magnification views of skeletal features representing patterns of growth. 1, An early growth stage of *Antarctissa* sp. showing the predominately round pores in the cephalic region and lobe-like curved processes at the incomplete apertural rim (arrow) indicating rim growth in the early development of the cephalo-thoracic region; 2, Cephalic pore of *L. heteroporos* showing clear signs of a mature stage of rim growth for a

pore in the cephalic region. The nearly circular pore outline and inner flange-like border are characteristic products of rim growth; 3, Irregular pores with narrow bars and angular outline; 4, Incomplete bridge growth exemplified by spine-like projections indicating bridge-growth patterns in the abdominal segment of *L. heteroporos*; 5 and 6, septal ring of *L. heteroporos*. Scales (1, 4 μm ; 2, 1 μm ; 3, 5 μm ; 4, 2 μm ; 5 and 6, 5 μm).



sizes of prey accepted by these species, thus making it difficult to establish strong biological hypotheses to explain the changes in ontogenetic patterns.

Within these limitations in understanding the evolutionary selection pressures influencing phylogenetic changes in skeletal morphology, it is clear that the use of ontogenetic pattern analyses helps to explain the major morphological changes observed during phylogeny. Clarification of evolutionary pathways and refinement of taxonomic categories may be enhanced by combining ontogenetic pattern analysis with gross morphology of radiolaria.

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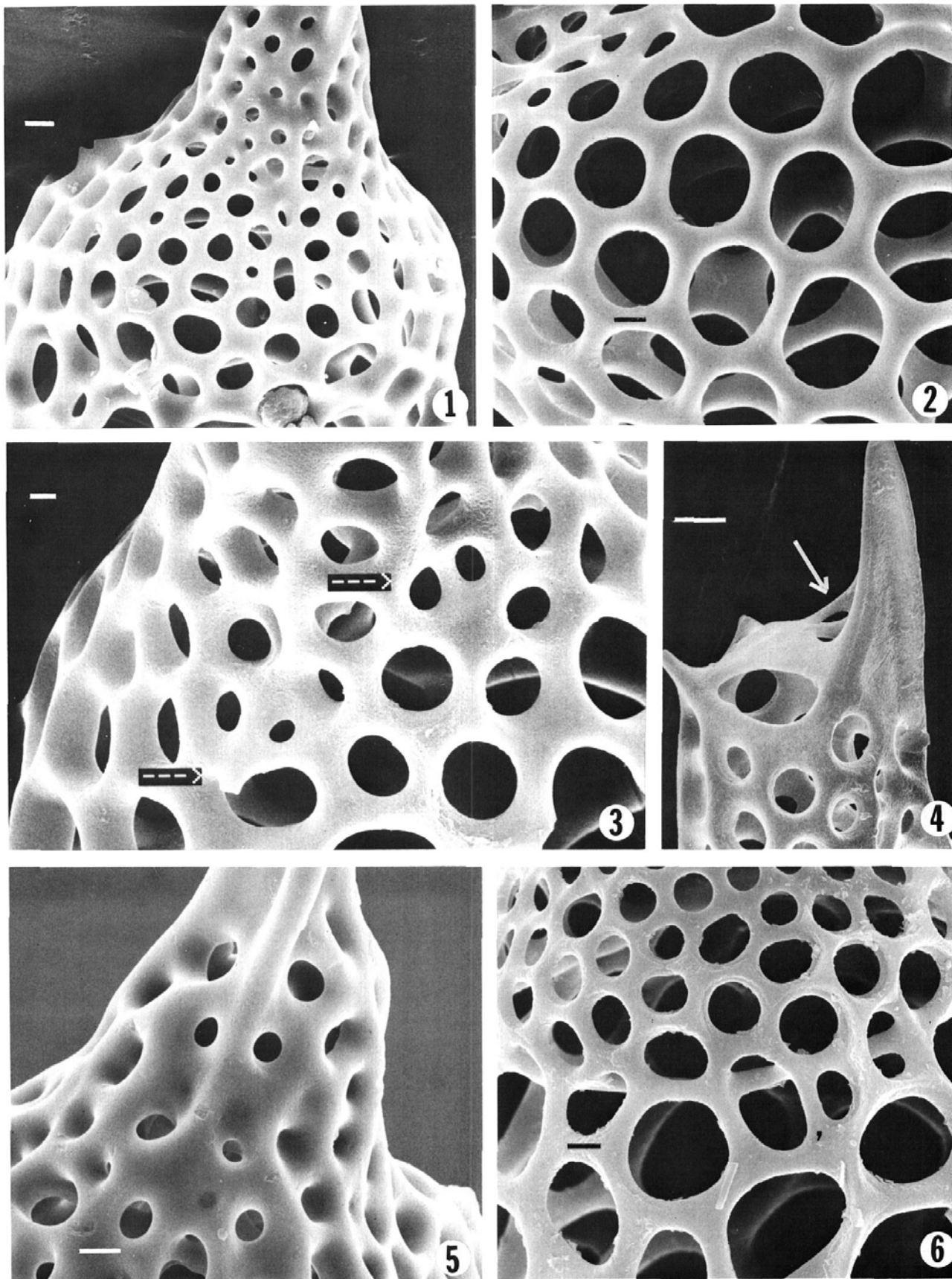
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PLATE 3

Figures 1-6: *Lamprocyrtis* species. 1, *L. neoheteroporos* cephalo-thoracic region showing strong polygonal pore development indicating increasing amounts of bridge growth; 2-4, *L. nigrinae* showing the polygonal pores in the cephalo-thoracic region (2), evidence of bridge growth as exemplified by bar-like partitions across pores (arrows) producing two oval pores (3), and offset spine with bridge-like buttresses

(4). This is compared to the more centrally located spine (5) of *L. heteroporos* with more circular pores. Evidence of increasing bridge growth into the thoracic region of *L. gamphonychai* (6) is indicated by the bridge-like extensions from the abdominal region across the septum with underlying septal ring. Scales (1, 5 μm ; 2, 4 μm ; 3, 2 μm ; 4, 5 μm ; 5, 5 μm ; 6, 4 μm).



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PLATE 4

1-4 High magnifications of *L. gamphonychai* showing evidence of bridge-growth; including spine-like projections from the apertural rim (1) and incomplete bridge-growth resulting in spikes (2). Complete stages of bridge

growth (3 and 4) produce oval pores with a distinct linear bar between them. Scales (1, 10 μ m; 2, 2 μ m; 3, 1 μ m; 4, 2 μ m).

