

Biotic Province and in the Tethyan region of Europe. This consistent stratigraphy is evidence for the presence of a stable original magnetization. Furthermore, we found no evidence for inclination shallowing, as magnetic directions from early diagenetic carbonate concretions are statistically indistinguishable from siltstones and claystones in the section (Table 1 and Fig. 3). We note that even if such inclination shallowing did exist in our samples, it would still not change our basic finding of large-scale terrane movement: although inclination errors on the order of 10° have been documented in some clay-rich sediments (11), this would change our paleolatitude estimate from 25°N to 33°N . This is not enough to explain the latitude discrepancy we have observed unless large-scale tectonic transport took place. Our results show a mean paleolatitude value for the lower Campanian Texada sites of $26.7^\circ \pm 5.7^\circ\text{N}$, whereas the upper Campanian Hornby sites yielded a mean value of $23.5^\circ \pm 3.5^\circ\text{N}$. Because these mean directions are not statistically distinct (Table 1), we infer that there was no measurable translation of the Insular Superterrane during Campanian time. Our results place Vancouver Island off the coast of Baja California between 70 and 80 Ma, with an inferred geographic displacement of about 3500 km (Fig. 4). Within the error limits, our data imply that the Insular Superterrane occupied latitudes similar to those of the present-day Rosario Formation of Baja California, Mexico.

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Fossilized Metazoan Embryos from the Earliest Cambrian

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Small globular fossils known as *Olivoooides* and *Markuelia* from basal Cambrian rocks in China and Siberia, respectively, contain directly developing embryos of metazoans. Fossilization is due to early diagenetic phosphatization. A nearly full developmental sequence of *Olivoooides* can be observed, from late embryonic stages still within an egg membrane, to hatched specimens belonging to several ontogenetic stages. Earlier cleavage stages also occur, but cannot be identified to taxon. *Olivoooides* shows similarities to coronate scyphozoans and to their probable Paleozoic representatives, the conulariids. *Markuelia* eggs contain looped embryos of a segmented worm with short, conical processes covering the body.

Reports of fossilized eggs of marine invertebrates are rare. This may, however, largely be due to the difficulties of recognizing them. There is an abundance of small globular structures in the fossil record, including that of the Cambrian (1). Zhang and Pratt (2) reported Middle Cambrian spherical fossils, 0.3 mm in diameter, that under a smooth membrane preserved a polygonal pattern which the authors interpreted as remains of blastomeres belonging to 64- and 128-cell stages of arthropod embryos. In some other cases, at least a general resemblance to eggs has been noted. We report here that two such occurrences of globular fossils from basal Cambrian rocks are eggs containing identifiable embryos (3) of metazoans.

As the name implies, the Early Cambrian *Olivoooides* Qian, 1977, has been compared to eggs, and Zhang and Pratt (2) mentioned this fossil as a possible further example of fossilized eggs. We have found

that the globular fossils indeed contain developing embryos of the co-occurring fossil hitherto known as *Punctatus* He, 1980 (= *Pyrgites* Yue, 1984). The material (thousands of eggs and about 10 more or less complete hatched specimens) derives from limestones of an interbedded chert-limestone-phosphorite sequence in the upper part (beds 23 to 27) of the Dengying Formation in the Shizhonggou section, near Kuanchuanpu village, Ningqiang County, Shaanxi Province, China (4). The level is equivalent to the Kuanchuanpu Formation *sensu* Qian (5, 6). Associated fossils, *Anabarites trisulcatus*, *Siphononuchites triangularis*, and *Carinachites spinatus*, indicate that these are Lower Cambrian (Lower Meishucunian) rocks.

The hatched animal (Fig. 1, J and K) is conical, with rounded cross section and distinct transverse annulations. The largest specimen is 3.3 mm long. A characteristic surface pattern of star-shaped projections, stellae, in the apical part is replaced in the more apertural parts by fine longitudinal striae (6, 7). Growth seems to have taken place by addition of striated tissue: Smaller specimens (Fig. 1J) are dominated by stellate tissue, whereas larger ones may have

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half (Fig. 1K) or more of the surface covered by striae. The apical part, before the first annulation, has a pentaradial pattern of folds.

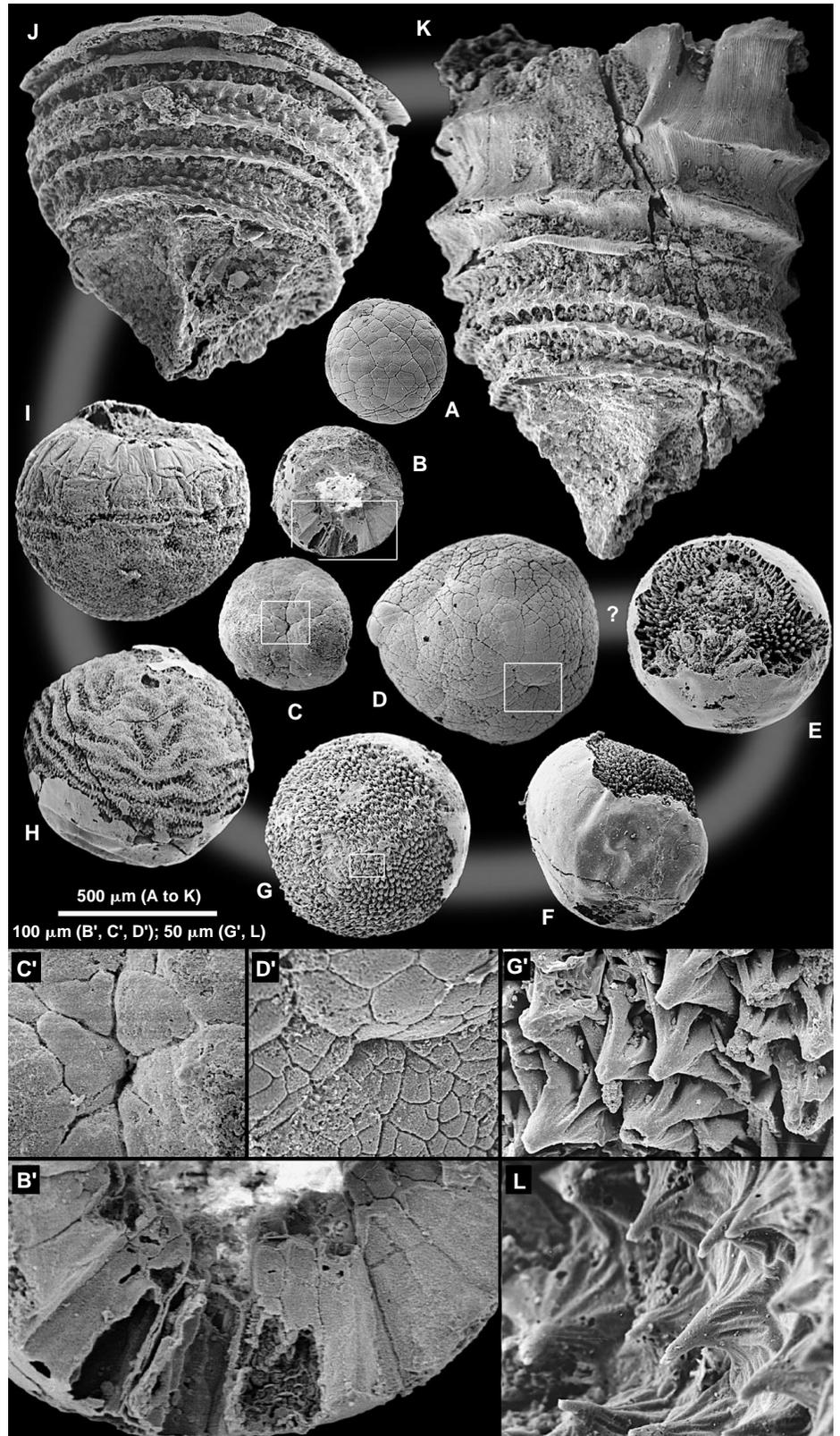
The test shows evidence of having been

flexible (7): It is commonly distorted without fracturing, and the surface is typically thrown into folds. The stellate cuticle has the appearance of a thin and flexible tissue being draped over a surface with regular

sharp protrusions, about 50 μm apart (Fig. 1L).

The co-occurring *Olivoides* globules that we interpret as the last prehatching stage of the animal show all these features

Fig. 1. Developmental stages of *Olivoides multisulcatus* Qian, 1977 (D?, E to L), and unidentifiable embryos of early cleavage stages (A to C) from the upper part (beds 23 to 27) of the Dengying Formation at Shizhonggou: (C) from 3 m above bottom of bed 24, sample N-Sh-26; (F and H) from 1.6 m below top of bed 24, sample N-Sh-31; (B, E, G, I to L) from 0.4 m below top of bed 25, sample N-Sh-35; (A and D) from top of bed 25, sample N-Sh-36. Specimens are deposited in the Institute of Geology, Chinese Academy of Geological Sciences (CAGS), Beijing, and the National Geological Museum of China (NGMC), Beijing. Scanning electron micrographs. Positions of details are indicated. Gray band indicates developmental sequence of *Olivoides*. (A) Approximate 256-cell stage (NGMC 9351). (B) Coeloblastula (?), approximate 256-cell stage (NGMC 9352). (C) Gastrula (NGMC 9353). (D) Stage with thousands of cells (NGMC 9354). (E to G) Early stellate embryos (NGMC 9355, 9356, CAGS 37733). (H and I) Late embryos (NGMC 9357, 9358). (J to L) Hatched individuals of different ontogenetic stages (NGMC 9359, CAGS 32372, 81011). (B') Detail of (B), showing prismatic blastomeres and surface of presumed blastocoel (top). (C') Detail of (C), showing blastopore. (D') Detail of (D), showing possible blastopore. (G') Detail of (G), showing stellae of embryo. (L) Detail of 3.3-mm long hatched individual showing stellae in apical region.



of conical “*Punctatus*,” but molded into a spherical structure 0.68 to 0.87 mm in diameter (Fig. 1, H and I). The area around one pole has an annulated surface beset with stellae, and around the opposite pole there is a tightly folded, finely striated tissue surrounding a rounded aperture (Fig. 1I, top). Allowing for the deformation of a flexible cuticle within a spherical egg membrane (visible in Fig. 1H, top), the globular fossils are identical with the smallest conical “*Punctatus*.”

The immediately preceding developmental stages seem to be represented by embryos, 0.60 to 0.87 mm in diameter, consisting mainly of nonannulated stellate tissue underlying a smooth outer membrane (Fig. 1, E to G). A narrow region of tightly folded nonstellate tissue is visible around a constricted aperture (Fig. 1E, lower part).

Co-occurring globules (Fig. 1, A to D) have a more or less regular polygonal surface pattern reflecting internal compartmentalization. Although this simple pattern may conceivably have arisen by nonbiological processes, the specimens occur with undoubted *Olivoooides* embryos and, furthermore, faithfully duplicate the morphology of modern metazoan embryos undergoing cleavage. We interpret them as early cleavage stages with preserved blastomere boundaries. Although *Olivoooides* is likely to be represented in this material, the size variation (0.28 to 0.73 mm) of these embryos suggests that other taxa may also be present.

Somewhat irregularly shaped embryos with a distinct polygonal pattern (Fig. 1D) seem to represent stages with a few hundreds to a few thousands of cells. More regular spheres (Fig. 1, A to C) may represent the 64- to 256-cell stages. The 0.42-mm specimen in Fig. 1C has a cellular pattern radiating from a pit (Fig. 1C', center). We interpret this fossil as a gastrula formed by polar ingression. [The larger specimen in Fig. 1D, the same size as the identifiable *Olivoooides* embryos, shows a somewhat similar pattern (Fig. 1D'), but this could be an effect of its lobate morphology.] A broken-open specimen reveals that the surface polygons extend as a prismatic layer toward a central hollow (Fig. 1, B and B'); this is similar to the packing of blastomeres around a blastocoel in, for example, sea urchin coeloblastulas (8). Earlier cleavage stages (fewer than about 64 cells) have not been identified with certainty.

“*Punctatus*,” with its flexible, annulated test, has been compared with the conulariids, a mainly Paleozoic group of biradially symmetrical fossils with a narrow-pyramidal phosphatic test. Although sometimes referred to as an extinct phylum (9), conulariids share a number of likely synapomor-

phies with scyphozoan cnidarians (10).

Olivoooides lacks the characteristic biradial symmetry of conulariids. The closely similar coeval hexangulaconulariids, of varying symmetry but frequently biradial, and the also coeval tetradial carinachiids, appear to provide morphological intermediates, however (7, 11). More significantly, the periderm of Recent coronate scyphozoan polyps (the basis for the proposed cnidarian affinity of conulariids) forms annulated chitinous tubes with circular cross section and fine longitudinal striations (12), that is, closely similar to *Olivoooides* tests.

Similarities also exist with certain acoelminths, in particular the loricate priapulid larvae. Priapulids constitute a small living phylum with a fairly diverse Cambrian record (13). Although bilaterians, they show both tetradial and pentaradial symmetry in parts of their anatomy, and the processes called scalids are formed by soft cuticle overlying a ciliated epithelium (14), somewhat similar to what is envisaged for the stellate tissue of *Olivoooides*. Priapulid adults and larvae, however, have a straight gut, and the larval lorica has an apical pore, in contrast to the closed apex of *Olivoooides*, hexangulaconulariids, conulariids, and scyphozoan polyp tubes. On balance, we consider that *Olivoooides* is more likely related to cnidarians than to priapulids.

The large, spherical eggs with clearly recognizable embryos indicate that *Olivoooides* had direct development, a large yolk content, and no free larval stage. Although it cannot be ruled out that the hatched *Olivoooides* in our samples represent larvae rather than juveniles, the evidence suggests that size increased regularly after hatching, and there is no sign of metamorphosis. This mode of development is not typical of marine cnidarians, which normally have a free-swimming planula larva from which a polyp (or in some cases a medusa) develops. However, in several marine cnidarians, the blastopore persists at the site of the future mouth during early planula stages (15); at the opposite end—the site of future attachment—there are concentrations of gland cells having a single cilium surrounded by villi. Thus, the stellate embryonic stages could correspond to a cuticularized “planula” contained within the egg membrane; metamorphosis is then subdued by the direct transformation of the blastopore into a mouth and the early establishment of a coelenteron. The stellate pattern of the cuticle may then reflect underlying gland cells with cilia surrounded by villi.

The other fossil embryos we have found are from the basal Pestrotsvet Formation (Lower Cambrian, Lower Tommotian) in the classical Dvortsy section on the Aldan River in southern Yakutia, Siberia (16). The

globular fossil *Markuelia* has been illustrated several times in the literature (17), interpreted as a chambered organism of unknown affinities. A closer investigation of a collection of 15 specimens (18) reveals that the chambers are segments of a wormlike animal that is tightly looped into a sphere, 0.48 to 0.55 mm in diameter (Fig. 2). The two ends of the body clinch to each other, yin-yang fashion, on one hemisphere (Fig. 2B). The median part of the body forms an inverted S-shaped double loop on the opposite hemisphere (Fig. 2A). The body broadens in the anterior- and posteriormost portions and is narrowest at 10 to 15 segments from the posterior end; this may, however, be an effect of the tight packing of the loops. It is not

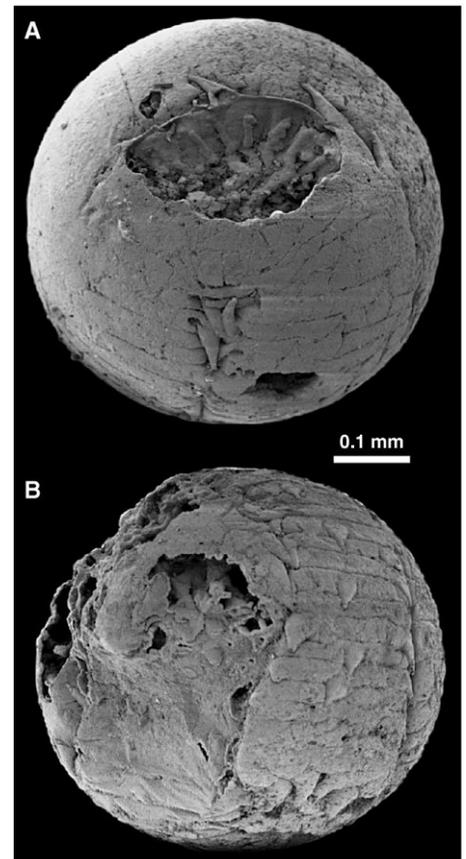


Fig. 2. Two embryos of *Markuelia secunda* Valkov, 1987, from the basal part of the Pestrotsvet Formation at Dvortsy, Siberia, sample Sib73-15-SB. Specimens are deposited at the Swedish Museum of Natural History (NRM), Stockholm. (A) Individual showing part of inverted S-loop in median part of body. Top bend of loop has body wall partially broken away, revealing internal rod-shaped organs correlated with segmentation. Lateral processes are visible along upper edge of loop as well as in the fold where one side of the animal meets itself at a 180° angle (bottom, middle) (NRM X2239). (B) Individual showing posterior segments and tail (right) as well as anterior end (left). Conical processes are visible along posterior part of body (NRM X2240).

clear whether the exposed side of the body is dorsal or ventral. The segments are narrow, about 30 to 50 μm , and the 0.19- to 0.38-mm-wide and \sim 3-mm-long embryonic body has about 75 segments.

The anterior end is not well preserved in the available specimens; it tends to expand laterally and be quite featureless externally. In Fig. 2B, the anterior region has a more complex type of preservation, with irregular phosphatization visible internally. This specimen shows a boss-like structure in the middle of the expanded anterior region (Fig. 2B, middle left).

The posterior end has two modified segments, each with two symmetrically placed processes that join into a kind of posterior comb (Fig. 2B, bottom right).

The segments carry conical processes that vary somewhat in shape but where most clearly exposed (Fig. 2B, right) are divided into an apical, narrow part and a basal, more flaring part. Typically, a process recurs in a similar position on every third segment. There seems to be no morphological difference between the processes occurring on the flat, exposed side and those that are laterally placed, except that the former tend to be flatter, presumably because they have been squeezed against an outer egg membrane. Judging from their distribution on the body, the processes cannot be interpreted as paired appendages or parapodia.

Broken specimens reveal internal rodlike structures (Fig. 2A, upper part), corresponding in number and position to the segments as visible on the body surface. The rods are about 10 μm in diameter, but as they consist of a diagenetic apatite crust, this dimension may not correspond to that of the original tissue. In Fig. 2A, some of the rods are at an angle to the segment boundaries, and elsewhere they have been observed to be detached from the body wall. Thus they seem to represent an organ system that is not part of body wall or mesenteries. There are several possible interpretations of these structures, including gut diverticules, blood vessels, muscles, nerves, nephridia, or gonads. On the basis of their regular distribution, thin rod shape, and presence in the embryonic state, however, we regard the structures most likely to be lateral nerve branches from a medial longitudinal nerve chord.

Markuelia is not unequivocally identifiable with any of the Cambrian segmented bilaterians known from soft-body preservation, although the regular pattern of processes should be recognizable if it persists into the adult stage. The development appears to be direct, with no evidence of a primary larva. The large number of equal segments and the wormlike body point to annelid affinity. The tendency of the rod-shaped organs to cut across segment bound-

aries suggests, however, that no transverse mesenteries were present, which would make the animal more comparable to arthropods or lobopods.

A notable feature of both *Olivoooides* and *Markuelia* is direct development. If a planula stage is at all present in *Olivoooides* (given the cnidarian interpretation), it is cuticularized and occurs within an egg membrane; what hatches appears to be a loricate polyp. If *Markuelia* is an annelid, it lacks the trochophore larva of polychaetes and would appear more similar to oligochaetes or leeches in mode of development. Likewise, terrestrial representatives of arthropods and lobopods favor direct development. Indirect development involving primary larvae is generally regarded as primitive among metazoans (19), direct development evolving independently when conditions do not favor the release of large numbers of larvae into the plankton. This may be the case in a harsh or unpredictable environment (reducing the survival chances for unprotected larvae), or where adult body size is small (preventing the production of large numbers of eggs). *Olivoooides* and *Markuelia*, however, may represent a biased sample of early metazoan development, because eggs of direct developers are generally larger (and yolkier) than those of indirect developers and thus may be more readily preserved as fossils and easier to identify.

Both instances of fossilized Early Cambrian embryos presented here are preserved as diagenetically phosphatized replacements and encrustations in marine limestones. Early diagenetic phosphatization has tremendous potential for replicating delicate biological tissues (20) but appears to take place under local conditions where pH and activities of P and HCO_3^- turn phosphatization on and off (21), and the conditions conducive to phosphatization are enhanced by bacterial activity. Metazoan eggs are readily phosphatized under experimental conditions (22), and the occurrences reported here and by Zhang and Pratt (2), from beds where other fossilized nonstructural tissues are absent, suggest that eggs are particularly susceptible to such phosphatization. Because several instances of this type of preservation have now been found, it may be that metazoan embryos are not uncommon as fossils but have simply been overlooked because of their minute size and nondescript morphology. If this is so, we will have a means of obtaining information on the early development of extinct organisms. Furthermore, we may have a method of searching for a missing metazoan record in the more than half a billion-year-long Proterozoic gap between the dates of metazoan diversification indicated by molecular divergence rates (23) and those suggested by a literal reading of the fossil record (24).

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