Early Cambrian Ostracode Larvae with a Univalved Carapace

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Phosphatized univalves, recovered from the Lower Cambrian (~530 million years old) Qiongzhusi Formation in southern China, are recognized as early instars belonging to bradoriid ostracodes whose later instars are bivalved. The univalved form is the primitive larval character for shell-secreting crustaceans, although most post-Cambrian ostracodes bypassed this developmental phase. The univalved-bivalved transition during early ontogeny represents an important evolutionary event in ostracodes, with implications for crustacean classification, and implies that the ostracode ancestor achieved this bivalved capacity before the appearance of mineralized skeletons during the "Cambrian explosion."

The Ostracoda are small crustaceans that widely inhabit marine, brackish, hypersaline, and freshwater environments. As fossils, the earliest bradoriid ostracodes are associated with the oldest redlichiid trilobites near the base of the Cambrian in China (*1*). Phosphatized Cambrian Bradoriida and Phosphatocopida that have preserved delicate appendages and soft body parts show no departure from the basic ostracode *Bauplan* (*2–5*). However, such extraordinary preservation is confined to just a few *Lagerstätten* within the long geological range of this group. Most fossil ostracodes are merely calcareous or phosphatized carapaces, which show a greater diversity than all other crustacean groups but shed little light on their early ontogeny, especially how they developed from an egg through the nauplius larval stage to a bivalved juvenile. This lack of information is likely a result of the tiny size of the initial larvae and the fact that the juvenile carapaces were too poorly mineralized to withstand post-ecdysial disintegration. Nonetheless, it has long been accepted that a bivalved nauplius is common to both fossil and extant ostracodes (*5–7*). Here, we show that at least some Early Cambrian bradoriid ostracodes had univalved larval and juvenile instars before the youngest bivalved ones.

By dilute (~5%) acetic acid digestion of thin-bedded limestones of the Qiongzhusi Formation from two sections exposed 760 km apart in Zhenping, Shaanxi (8), and Jinyang, Sichuan, China, we extracted secondarily phosphatized carapaces that represent rare univalved instars of two bradoriid taxa and abundant bivalved later instars. The rocks are fine-grained and were deposited in a deep-water environment. The two ostracode assemblages consist of different bradoriid taxa: *Kunmingella douvillei* (Mansuy 1912) occurs in Jinyang and many other places in southern China but not in Zhenping, whereas *Duibianella* sp. nov. is restricted to Zhenping. In addition, both assemblages contain inarticulate brachiopods, sponge spicules, and small shelly fossils but have so far yielded neither trilobite protaspides nor meraspides. Many adult redlichiid trilobites, preserved in the same strata with their original calcareous exoskeletons, indicate that both faunas belong to the Lower Cambrian *Eoredlichia-Wutingaspis* zone, Qiongzhusi (Chiungchussu) stage, approximately equivalent to the upper Atdabanian of Siberia.

The small univalved carapaces recovered from Zhenping (Figs. 1 and 2) and Jinyang (Fig. 3) can be linked to cooccurring larger bivalved bradoriid carapaces that belong to subsequent ontogenetic stages; they each represent at least one of the earliest instars preceding the youngest bivalved ones. The univalved instar may therefore be equivalent to the nauplius or metanauplius larva of extant Crustacea.

The purported pre-protaspid larva of a Lower Ordovician trilobite (9) is similar in shape and ornament to our bradoriid larvae. However, the early protaspis of trilobites commonly bears paired border spines, and although some taxa may be domical (*10*), most exhibit variably distinct furrows as evidence of the axial lobe. The axial furrows and paired eye ridges develop during subsequent growth, but no such furrows and ridges could be seen on the external surfaces of the univalved carapaces we isolated (Figs. 1, A to C, and 3A). These basic features are the main criteria that distinguish univalved ostracode instars from trilobite protaspides.

The first naupliar instar of almost all extant ostracodes, whose ontogenies are

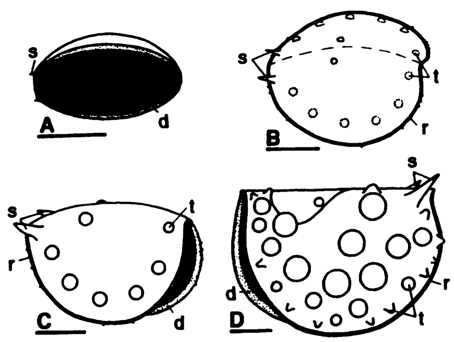

Fig. 2. Reconstruction of *Duibianella* sp. nov., showing the transformation from a univalved carapace (**A** through **C**) to a bivalved one (**D**); d, duplicature; r, marginal rim; s, posterior spine; and t, tubercle. Scale bars, 0.1 mm.

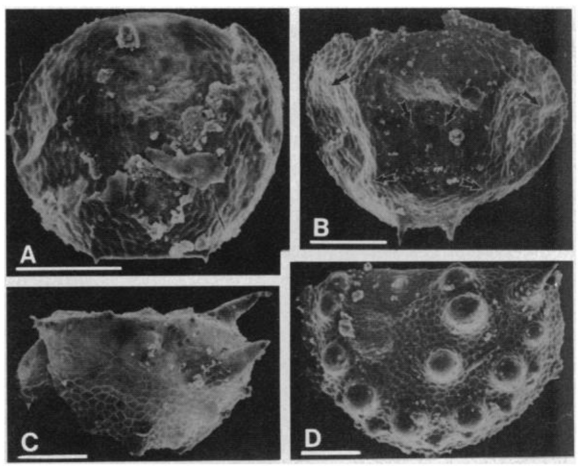

Fig. 1. *Duibianella* sp. nov. from the Lower Cambrian Qiongzhusi Formation of Zhenping, Shaanxi, China. Scale bars, 0.1 mm. (**A**) Dorsal view of the smallest (youngest) univalved carapace (ZP 0001), which is circular in outline, moderately convex, and surrounded by a narrow rim along which developed fine denticles and a pair of backward-directed posterior spines. The exterior surface of the carapace is covered with a reticulate network of fine ridges that produce an ornament of irregular but equant polygons. (**B**) Dorsal view of a later univalved instar (ZP 0002). The carapace extends more laterally than sagittally, becoming strongly convex transversely. The posterior spines become more prominent and separated from the rim. The reticulate ornament has more polygons, and several symmetrically paired tubercles appear on either side of the carapace (arrows). (**C**) Dorso-lateral view of a later univalved instar (ZP 0003). The carapace becomes more curved transversely and expands ventrally to develop a nascent bivalved shape, leaving a gape along the free margin. The hinge is still invisible, and the dorsal margin remains moderately arched. The dorsally directed posterior spines increase in size and advance farther from the margin, and more fine tubercles appear in the reticulate surface. (**D**) Lateral view of a pre-adult left valve (ZP 0004), showing the appearance of the truly bivalved structure. The paired posterior spines shift somewhat toward the anterior.

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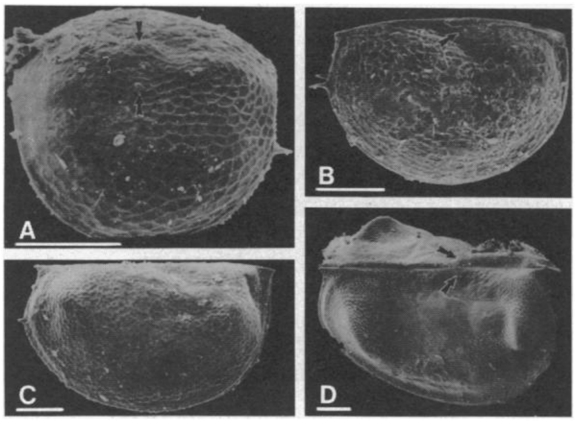

Fig. 3. *Kunmingella douvillei* (Mansuy 1912) from the Lower Cambrian Qiongzhusi Formation of Jinyang, Sichuan, China. Scale bars, 0.1 mm. (**A**) Dorso-lateral view of the only univalved carapace (JY 0006), which resembles the univalved instar of *Duibianella* sp. nov. but is more convex transversely and bears a straighter anterior margin. We assign it to *K. douvillei*, whose bivalved juveniles and adults are common in the same bed. Its youngest bivalved instar shares certain features that appear to have been derived from the domical univalved form: (i) The smallest bivalved carapace bears a pair of posterior spines that still project from the narrow marginal rim; and (ii) the exterior surface is similarly covered with a reticulate ornament. (**B**) Right view of a juvenile bivalved carapace (JY 0007). The appearance of a hinge made it possible for the carapace to close tightly along the free margin, but the dorsal margin is still arched. (**C**) Right view of a further growing juvenile carapace (JY 0008), showing the straightened hinge, posterior spine, and indistinct anterior node and posterior lobe. (**D**) Dorso-lateral view of a bivalved pre-adult carapace (JY 0009) with a prominent anterior node and posterior lobe. In addition, a pair of dorsal pores (possible gland exits) is present in all instars (arrows).

known, is bivalved and resembles the adult form (*11*, *12*). The only known exception to this is the punciid *Manawa staceyi* (Swanson 1989), whose nauplius and metanauplius carry single carapaces. In this species, the univalved-bivalved transformation results from the development of the sagittal hinge during early ontogeny (*13*), which thus indicates that this species exhibits a growth history similar to that of our Cambrian bradoriids. The transition shown by bradoriid and punciid ostracodes is more or less a progressive, gradual process rather than one involving abrupt changes. This development history argues against the possibility that the transition from univalves to bivalves is a metamorphosis linked to changes in life habit. Adult carapaces of Lower Cambrian *Phaseolella dimorpha* (Zhang 1987) from China (*14*) and Middle Cambrian *Svealuta* sp. A from Australia (*15*) vary from this process in that they achieved an overall bivalved shape but retained the single shell and never developed a hinge at all. Therefore, we regard the univalved phase as the primitive character, an inheritance from a single-shelled ancestor, rather than as a special feature that arose in early instars as an adaptation to unusual ecological conditions. The primitive nature of the univalved phase is supported by other crustacean groups like the Cirripedia and Branchiopoda, whose larvae also carry a single carapace regardless of whether it originated from the naupliar head, akin to a specialized head shield (*16*), or from the thoracic region (*17*).

The transition from a univalved to a bivalved shape represents an important event in ostracode evolution, because it may have been motivated by the need of the ancestor of bradoriids to adapt to complex surroundings. For example, one of the selection pressures that is thought to have played an important role in the earliest phases of evolution of animal skeletons is predation (*18*). Because this transition during ontogeny is displayed by some of the earliest known bradoriids, the advantage of a bivalved carapace may have been realized before the onset of mineralization near the beginning of the Cambrian.

The smallest bivalved instars of those Recent ostracodes that have been studied, as well as those of phosphatized Cretaceous *Pattersoncypris micropapillosa* (Bate 1972) from Brazil (*4*), are considerably larger than their corresponding egg cases. The smallest bivalved instar of Upper Cambrian *Falites* sp. from Sweden is spheroidal in shape like the first instar of Recent cyprid ostracodes (*11*) and was therefore interpreted as the first molt stage (*2*). Nevertheless, it remains possible that other young instars of extant and fossil ostracodes with a univalved shell might be present but still await discovery.

The absence of the univalved phase in most post-Cambrian ostracodes suggests that development of the organism was accelerated while it was still in the egg stage. If so, the bivalved ostracode nauplius can then be regarded as an autapomorphy that unites members of this class as a divergent group, whereas bradoriid and punciid ostracodes bearing univalved carapaces would be separate branches in the class. However, the phylogenetic relation between Recent punciid and Cambrian bradoriid ostracodes is uncertain, because the univalved naupliar stage is only a symplesiomorphic (shared primitive) character and the geological interval between the known occurrences of the two groups is very long. It is still unknown whether the bradoriids formed the stem group for all later ostracodes or a sister group derived from a generalized crustacean ancestor. Bradoriids may comprise a polyphyletic group (*1*, *15*). The classification of ostracodes is further unsettled because of the possibility that the Phosphatocopida were secondarily phosphatic in composition; their limb structure differs from that of other ostracodes and suggests a closer affinity to barnacles (*6*, *19*), but this may simply be the result of convergence.

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