Rates of evolution in the Emsian (Early Devonian) conodont and trilobite lineages

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ABSTRACT—Evolutionary rates within Emsian trilobite and conodont lineages are considered against the background of precise alignments of regional stratigraphic units and sea-level fluctuations, according to the standard conodont zonation. Three steps of morphological change of equal magnitude within the Ganinella lineage coincide with three successive eustatic T-R cycles. These steps are aligned with three stages in change of basin cavity and adaxial trough of polygnathids. At the base of the kitabicus and nothoperbonus zones (Zinzil’ban and Daleje event levels) the evolutionary rate of this fossil group accelerates, resulting in short-range species lineages. Two-fold and three-fold divisions of the Emsian Stage into substages are discussed.

INTRODUCTION

Comparative analysis of evolutionary rates of pelagic and benthic fossil groups, in the present case conodonts and trilobites, requires a substantial corpus of data, preferably from a single sedimentary basin in order to exclude factors specific to various basins. Such data have been accumulated during four decades from the well-studied richly fossiliferous shallow water Emsian terrigenous-carbonate sequences of the Salair and Gorny Altai regions of southwestern Siberia (Rzhon-snitkaya, 1968; Yolkin & Kanygin, eds., 1986, 1987; Yolkin et al., 1989). Diverse trilobite associations are common in these deposits, among them dechenellids, particularly lineages of Ganinella (Yolkin, 1968). Conodonts are relatively scarce because of shallow water environments, but sustained field and laboratory investigations have been successful. All Emsian and Eifelian polygnathid zonal index species, except Polygnathus costatus patulus Klapper and P. costatus partitum Klapper, Ziegler & Mashkova, have been found (Yolkin & Izokh, 1988; Izokh, 1998) permitting precise stratigraphic alignment of stratigraphic units, and of trilobite and conodont zones (Yolkin, 1983, and abovementioned papers). In this report we use conodont data from the Zinzil’ban and other sections in Central Asia where early polygnathid lineages are better known (Yolkin et al., 1994c) and where the International Committee on Stratigraphy has fixed the GSSP for the base of the Emsian Stage (Yolkin et al., 1997b).

The regional stratigraphic background for the analysis (Text-fig. 1) embraces three Emsian horizons—Salairka, Belovo and Shanda (Yolkin et al., 1989, inter alia). The base of each horizon coincides with the start of a transgression-regression couple. There are three such cycles within the Emsian (Yolkin et al., 1997a); in marginal basin sections they are combined into a single second order cycle (Yolkin, 1998). Two of these T-R events are assumed to be global biotic/sedimentary events; these have specific names Zinzil’ban (kitabicus) Event for the base of the Khodzha-Kurgan Formation in Central Asia (and Salairka Horizon as well; Yolkin et al., 1994a), and the well-known Daleje (nothoperbonus) Event at the base of the Shanda Horizon (House, 1985; Chlupac & Kukal, 1988; Yolkin et al., 1997c). The chronostratigraphic framework for the analysis is thus based on readily recognizable global event levels.

A major objective of this paper is to show that during Emsian the evolutionary rate for conodonts was rather variable, in contrast with the rate for trilobites. This follows from comparison of morphological changes within Emsian lineages of the genera Ganinella and Polygnathus with sea-level fluctuations.
THE GANINELLA LINEAGE

The evolutionary succession in the genus Ganinella Yolkin involves seven species and subspecies (Yolkin, 1967, 1968). Four of them developed within the Emsian Altai-Salair shelf-basin (Text-fig. 1; Yolkin et al., 1994b). The general morphology of this trilobite group is quite simple; the basic change through time concerns the glabellar furrows and degree of separation of axial and pleural parts of the pygidium into rings and ribs. The Emsian portion of the Ganinella lineage displays a progressive evolutionary trend directed towards simplification of morphology (Yolkin, 1968, 1983). It is expressed in shallowing of glabellar furrows and decrease of axial and pleural rib numbers.

The appearance of Ganinella dombrowiensis ( Gurich), the first species of Emsian lineage under consideration, is connected with relatively sharp but progressive morphological changes that exhibits a beginning of new stage in transformation of the initial ganinellan morphotype. The praecapitall furrows of the glabella of the Pragian species G. diversa Yolkin are deep, but in Ganinella dombrowiensis all glabellar furrows become deep and there are additional ones. The pygidium becomes elongated with one additional pleural rib - an increase from 7 to 8.

Entry of the subspecies Ganinella dombrowiensis brevis Yolkin occurs at the base of middle Salairka Horizon, within the kitabicus-Zone (Text-fig. 1). This is the first step in a pattern of regressive morphological change in the Emsian part of the Ganinella lineage. All three glabellar furrows, except the additional ones, become slightly shallower - viewed on internal moulds - but are still deep. Additional furrows are visible only on the external glabellar surface as small spots without microsculpture. The number of pygidial pleural ribs decreased to 7.

The first occurrences of the next species of the lineage, G. bacheates (N. Tchernysheva, 1951), are at the base of the Belovo Horizon. Its morphology demonstrates further simplification of glabellar and pygidial features, as well as elements of neotony. This is indicated by the presence of a fourth pair of glabellar furrows - as occurs in the oldest species of the lineage, G. gurijetskiensis Yolkin. Only the praeocapitall furrows are quite deep; the others are poorly developed. On the pygidium, the 12 axial rings of G. dombrowiensis have decreased to 11 in G. bacheates; and pleural ribs have reduced from 7 to 5-6.

The range of the last member of the Ganinella lineage, G. schebalinoensis Yolkin, corresponds to the entire Shanda Horizon. The main morphological changes concern the glabella (Text-fig. 1). If microsculpture is present, it is possibly to recognize three pairs of weak glabellar furrows. The pygidium has 11 axial rings and 5 (sometimes 6) pleural ribs.

Thus, change in morphostructure in Emsian ganinellans is clearly expressed as having occurred in 3 well expressed stages of equal magnitude (Text-fig. 1), represented by the morphotypes of (1) G. dombrowiensis, (2) G. bacheates and (3) G. schebalinoensis. Each of these evolutionary stages corresponds exactly with the 1st order eustatic cycles, 3a, 3b and 3c (Yolkin, 1998), combined as a 2nd order cycle (number 3). It should be noted that the entry of G. dombrowiensis brevis marks a minor event within the first Emsian ganinellan evolutionary stage.

POLYGNATHUS LINEAGES

There is much modern data on Emsian Polygnathus; several easily-recognizable lineages can be combined into a single tree. Many such "trees" occur in the literature, all based on the first phylogenetic scheme proposed by Klapper & Johnson (1975). This has been followed (Yolkin et al., 1994c) incorporating lineages and trees of Weddige (1977), Bardashev (1986), Mawson (1987), Yolkin & Izokh (1988), Bultynck (1989) and others. In doing so, we have illustrated the clarified phylogeny of early polygnathids based on materials from Central Asia, particularly from the Zinzi basin section where the majority of lineages are relatively complete (Text-fig. 1). Reference should be made to a previous paper (Yolkin et al., 1994c) for characterization of the levels of more important morphological change in Emsian polygnathid evolution considered against the background of trilobite evolution and sea-level fluctuations. Use of the Central Asian and West Siberian Emsian sections is reasonable because they are well correlated (Yolkin et al., 1982); they document the same global events and T-R eustatic levels (Kim et al., 1978; Yolkin et al., 1994a).

Phylogenetic relationships of species shown in Text-figure 1 demonstrate two principal event-levels in Emsian polygnathid evolution. These are located near the bases of the kitabicus and nothoperbonus zones; both levels are related to radiation of forms and the inception of significant global transgressions. They may be considered to be exemplary levels for biotic sedimentary events (Walliser, 1996; Yolkin, 1998). It could be noted here, that the general direction of change in early polygnathid morphology in time involves, first of all, two important features - the basal cavity and the adcarinal troughs.

In both radiations three lineages appeared. Near the base of the kitabicus Zone these are (Text-fig. 1): (1) the pireneae to tamara lineage, (2) the kitabicus (main stock) and (3) pannonicus lineages. All included species are characterized by relatively deep basal cavities and flattened upper sides of the platform elements. The entry of P. excavatus coincides with divergence in characters, specifically gradual decrease in size of the basal cavity and deepening of adcarinal troughs in the successive taxa P. excavatus excavatus - P. excavatus gronbergi - P. perbonus of the P. excavatus-group. The
next radiation event at the base of the nothoperbonus Zone brought about three short-ranged species lineages (Text-fig. 1). Species of P. laticostatus also have a group of short-ranged taxa. Evolution of Emsian polygnathids thus has three well expressed stages, recalling those of the Ganinella lineage. The first and third stages are characterized by rapid morphologic change interpreted as examples of high rates of polygnathid speciation. The second evolutionary stage however is one of gradual change within the one morphostructure, P. excavatus.

SUMMARY AND CONCLUSIONS

Morphological evolution of ganinellid trilobites and polygnathid conodonts has, as shown above, a high degree of both similarity as well as dissimilarity. The similarity is that the two fossil groups under consideration display precisely synchronous evolution in three stages, coinciding with three eustatic T-R cycles, but evolution of the two groups, trilobites and conodonts, have their own peculiarities. The stages in trilobite evolution concern successive species appearing with comparable magnitude of morphologic transformations. This is true also for morphological change during evolution of the main polygnathid stock, pireneae-kitabicus-excavatus, resulting in change of the most important features, the basal cavity and adcarinal troughs (Text-fig. 1, median cross-sections). On the other hand, the first and third polygnathid stages are characterized by lineages of short-range taxa. This could be taken as evidence of variable evolutionary rates within individual lineages, i.e. the time-intervals between entries of P. kitabicus, P. excavatus and P. nothoperbonus are longer (and comparable with ganinellian evolutionary stages) than between entry of species in successive polygnathid lineages: nothoperbonus-bulynckii and mashkovae-serotinus. The duration of the kitabicus and excavatus zones would thus appear to be longer than nothoperbonus, inversus and serotinus zones.

Of special interest is the top of the lower Salaikanka Horizon and its equivalents in the Zinziiban section. At this level there is a well expressed extinction of the branch polygnathid lineage, P. pireneae to P. tamara, and entry (innovation) of the trilobite subspecies Ganinella dombrowsiensis brevis (Text-fig. 1). This seems to be the actual bioevent level. It can have biochronologic significance for dividing the kitabicus Zone into two informal units.

The conclusions presented have potential value for division of the Emsian Stage into substages, Zlichovian and Dalejean, a current focus of discussion by the Subcommission on Devonian Stratigraphy. A threefold division (Lower, Middle, Upper) of the Emsian may have more value (compare Text-fig. 1), in which case the substages Dalejean and Zlichovian could be supplemented by a Zinziiban Substage.
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