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BENTHIC BRACHIOPOD COMMUNITY CHANGES THAT REFLECT SILURIAN BIOEVENTS

Project 216
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Abstract. The Silurian shelly benthos shows evidence of five bioevents: late Aeronian major dispersal item, early Wenlock extinction, late Wenlock radiation, end-Ludlow Pentamerid Event and end-Silurian extinction. Late Aeronian community changes correspond with the beginning of the "late" Llandovery transgression; causes of the other events are difficult to find out.

Despite the fact that the Silurian is the shortest Phanerozoic Period its shelly benthos shows evidence of five bioevents. All five involve a significant amount of community change, commonly involving the results of minor extinction and/or adaptive radiations, and dispersal in one case (Boucot, 1990; Talent, in prep.). All these changes are at a far lower level than is the case of community change at the major Phanerozoic marine extinction and/or adaptive radiation horizons, such as the Permo-Triassic or end-Ordovician extinctions on the one hand, and the beginning-Carboniferous, beginning-Middle Triassic, or beginning-Jurassic on the other hand. I emphasize the role of articulate brachiopods in this account because at the moment their community roles are better understood. It is obvious, however, that when the corals, both tabulates and rugosans, trilobites and pelmatozoans plus bryozoans, have been more extensively considered coenologically this situation will alter substantially.

During the Silurian we lack the capability of recognizing any Malvinokaffric Realm bioevents. Whether or not this is due to lack of information or reflects the real situation is unclear.

During the entire Silurian, like in the whole period from the upper Arenig through the Permian (Boucot, 1991), there is a marked, high taxonomic contrast in diversity between the carbonate platform, level-bottom communities (high diversity) and the siliciclastic, off-platform communities (low diversity). The carbonate platform communities tend to be rich in varied rugosans, tabulates, stromatoporoids, sponges, calcareous algae, bryozoans, nautiloids, and pelmatozoans; whereas the reverse is true for the siliciclastic, off-platform communities where brachiopods, trilobites, plus less abundant bivalves and gastropods are the dominant taxa in terms of both specimens and species — with most of these taxa also commonly occurring on the carbonate platforms. The siliciclastic off-platform also lacks the reef and mound complexes that add so much to overall carbonate platform diversity.

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Earlier Llandovery

Following the massive end-Ordovician global extinction event preceding the *G. persculptus* Zone there is a relatively lengthy low diversity interval in the Rhuddanian and much of the Aeronian, up to the C_2—C_3, later Aeronian interval. This initial interval sees the quieter water introduction of the high dominance, low diversity, BA (Benthic Assemblage) 4 *Stricklandia* Community Group, which persists into the early Wenlock except for central North America, where the *Microcardinalia-Plicostricklandia* lineage persists into the later, but not latest Wenlock.

In BA 4—5 this initial interval contains higher diversity, lower dominance representatives of the *Dicoelosia-Skenidioides* Community Group. These units lost much of their diversity during the Ashgillian extinction interval. The still higher diversity, so characteristic of this community group, will not be regained until the C_2—C_3 dispersal event sees the addition of many taxa from the Uralian-Cordilleran Region into the North Atlantic Region.

Also characteristic of this interval are the rough water, high dominance, low diversity Virgianid Community Group communities of BA 3, that feature *Virgiana* so prominently on both the North American and Siberian-Kolyma platforms. During the C_2—C_3 bioevent these virgianid communities are replaced by smooth pentamerinid communities, consequent with the extinction of most of the virgianid genera (except for *Borealis*, which phyletically evolved into *Pentamerus*).

In the BA 1 position this interval is characterized by the typical low diversity, high dominance, poorly studied orbiculoid-linguloid community complex, and by the equally poorly known rhynchonellid community complex. Both of these units persist through the entire Period. A high dominance, low diversity nuculoid bivalve community is also characteristic of BA 1 during the Silurian, as is a hughmillerid-stylonurid-eurypterid community complex that occurs both in BA 1 and in the nonmarine environment during the entire Silurian. Also present here, as well as throughout the Period, are BA 1 homalonatid-dominated trilobite and *Plectonotus*-dominated bellerophontid units.

BA 2 during this interval is characterized by several low diversity communities, including the *Mendacella*, *Cryptothyrella*, and *Dalmanella* communities and ecoclinal mixtures thereof.

BA 3 during this interval is characterized by a number of moderate diversity *Janius* Community Group units, in which the lack of the C_2—C_3 dispersalists such as *Atrypa "reticularis," Howellella*, *Eospirifer*, and *Cyrtia* is notable, although the presence of such taxa as *Leptaena*, *Protatrypa*, *Eospirigerina*, and various stropheodontids, orthids, and dalmanellids is prominent.

Late Aeronian—Telychian—Early Wenlock

The C_2—C_3 bioevent is the major item within the Silurian. It does not reflect great adaptive radiation, following a lengthy post-Ordovician extinction event low diversity interval as is commonly the case following some of the major bioevents, such as the Permo-Triassic with its major Middle Triassic level bottom adaptive radiation following the Lower Triassic all time low diversity. Rather, it appears to reflect a massive dispersal event of many taxa previously endemic within the Uralian-Cordilleran Region into the North Atlantic Region (Wang Yu et al., 1984).

The next set of communities, those spanning the C_2—C_3 to early Wenlock interval, mark the beginnings of what is commonly thought of as the

Silurian benthic fauna, because of their globally far greater abundance and geographic distribution which correlates positively with overall Silurian transgression from a Rhuddanian low point.

During this second interval the virgianid communities are replaced by large, smooth Pentamerinid Community Group units featuring first *Pentamerus*, commonly of the *P. oblongus* type, followed by *Pentameroides*, except for central North America where other smooth pentamerinids also co-occur with *Pentameroides*, and parts of the Russian Platform as well.

In the BA 2 position a prominent feature is the high dominance, low diversity *Eocoelia* communities, which began here at a low level late in Aeronian time, but start to really flourish only in the C_2—C_3 through early Wenlock of eastern North America, Britain, Norway, and the Siberian-Kolyma platforms. *Eocoelia* does extend seawards into BA 4 as an uncommon component of higher diversity communities, but never in the densely packed, "pearly layers" so characteristic of BA 2 during this interval in the North Atlantic and Siberian regions.

BA 4 *Stricklandia* Community Group faunas maintain their characteristics unchanged until the end of this interval when *Costistricklandia*, the costate member of the *Stricklandia-Costistricklandia* lineage, finally disappears.

During this interval east-central Asia sees the first appearance, and persistence through most of the Silurian of the *Tuvaella* dominated and *Tuvaella* associated communities so characteristic of this BA 2—3 biogeographically unique region.

The BA 4—5 *Dicoelosia-Skenidioides* Community Group high diversity, low dominance communities show a marked diversity increase during C_2—C_3 that persists through the end of the Period, with many of the additional taxa being immigrants from the Uralian-Cordilleran Region into the North Atlantic Region.

The BA 3 *Janius* Community Group, areally the most widespread set of Silurian communities, now attains its maximum diversity with the addition of the immigrants from the Uralian-Cordilleran Region into the North Atlantic Region. This high diversity situation persists through the end of the Period.

Post-Early Wenlock, Pre-Late Wenlock

The early Wenlock, post-*amorphognathoides* Zone extinction is minor in terms of shelly taxa, but notable in terms of shelly biomass and abundance relations for several previously important groups. The *Stricklandia* Community Group now disappears except for central North America, part of the American Province, where the *Microcardinalia-Plicostricklandia* lineage persists into the late Wenlock. The *Eocoelia* communities disappear except for a limited area of the European Province where *E. angelini* persists a little longer in dominant condition. Notable in the *Dicoelosia-Skenidioides* Community Group is the disappearance of *Porpites*, as well as the addition, presumably by adaptive radiation of ambocoelids in the Uralian-Cordilleran Region. There are still a number of nearer shore, low diversity, BA 2 units such as the *Meristina* Community.

In North America several smooth pentamerinid communities persist into the later Wenlock, in the normal BA 3 position.

By and large this interval merely sees, particularly in the high diversity units of the *Janius* and *Dicoelosia-Skenidioides* Community Groups, a continuous sequence of evolving communities featuring phyletic changes within varied generic lineages. There were a few extinctions immediately prior to the late Wenlock, such as that of *Leangella.*

Late Wenlock—Ludlow

The next community event is the late Wenlock adaptive radiation of the pentamerinids and subrianinids, especially the ribbed forms, all of them being low diversity, high dominance BA 3, rough water items. This late Wenlock interval also sees the adaptive radiation responsible for the Silurian reefs (not just mud mound type bioherms, which are present throughout the Period) with their many unique taxa. These reef complexes persist through the Pridolian, but their community ecology is poorly known. The precise age of the late Wenlock event in graptolitic terms is uncertain, because zonal graptolites (see Jaeger, 1991, for discussion concerning the lack of key graptolites occurring with the shelly faunas in the late Wenlock) are not interbedded with the shelly faunas, and curiously enough the major extinction event affecting the graptolites at the very end of the Wenlock (Jaeger, 1991) is not reflected by the benthic shelly faunas. In terms of conodonts the late Wenlock, as the term is being used here, would be essentially the Homerian, i. e., within the *Ozarkodina bohemica bohemica* conodont biozone (Aldridge and Schonlaub, 1989). Rexroad et al. (1978) provide information on the conodonts of the late Wenlock from North America in terms of material recovered from the Louisville Limestone; they conclude that the material represents the *Kockelella variabilis* Zone, with a late Wenlock—early Ludlow (up to the lower Leintwardine Formation and its equivalents elsewhere) range indicated.

The most marked event at the end of this interval is what Talent (in prep.) has termed the Pentamerid Event, since it sees the extinction of almost all of the Pentameridae and the Subrianidae, together with the many communities they dominated.

This interval sees more local community features such as the Ludlow—Pridoli *Dayia* dominated communities of the European Province and the *Gracianella* dominated communities of the Uralian-Cordilleran Region.

During the late Wenlock—Ludlow interval the high diversity community groups undergo little prominent alteration, as is also true through the Pridolian. The end of this interval presumably corresponds with the end of the Ludlow in both graptolitic and conodont terms, as is evident in such regions as central Nevada (Roberts Mountains Formation).

Beginning in this interval and continuing through the Pridoli, within the European Province of the North Atlantic Region, there is an extensive development of *Salopina* and *Protochonetes* dominated BA 2 communities, as well as the continuation of course, of the rhynchonellid, nuculoid bivalve, orbiculoid-linguloid dominated BA 1 community types.

Pridoli

Following Talent's end-Ludlow Pentamerid Event gypidulid dominated communities take over the same BA 3, rough water role in a Gypidulid Community Group that persists through the Frasnian. In the pre-Pridolian Silurian gypidulinids were low abundance members of high diversity BA 3—4 communities, and in the late Wenlock—Ludlow of rough water, high dominance pentamerinid communities.

Pridolian communities have much in common with those of both the Ludlow and the Gedinne-Lochkov, with the qualification that Pridolian faunas are most easily recognized by the absence of pentamerinid communities, presence of gypidulinid communities, and *Janius* Community Group faunas lacking key Devonian items such as *Cyrtina*, terebratuloids (*Podolella, Mutationella, Nanothyris*), and containing such forms as halysitid corals and *Merista*.

The end-Pridoli Event, an extinction at the Silurian—Devonian boundary, eliminated a few lineages in the higher diversity community groups, but by and large it was a minor, although recognizable event both taxonomically and ecologically.

Causation

The C_2—C_3 community changes correspond in many places with the beginning of the "late" Llandovery transgression. Correlatives of a potentially causative nature are difficult to find for the other items. This problem accords, of course, with the overall Phanerozoic difficulty of finding truly convincing causation for the varied extinctions and adaptive radiations, despite the spate of recent controversial publications that try to deal with the topic. It is largely the old question about whether or not one should seize on this or that correlation between several phenomena and interpret one of them as causal.

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SILURI BIOSÜNDMUSI KAJASTAVAD BENTILISTE BRAHHIOPOODIKOOSLUSTE MUUTUSED

Siluris on täheldatud viit olulist põhjafaunas kajastuvat biosündmust, mis toimusid Hilis-Aeronianis, Vara- ja Hilis-Wenlockis, Hilis-Ludlow's ja siluri lõpul. Peale esimese, mis langeb kokku transgressiooni algusega, on teiste arvatavad põhjused ebaselged.

Артур Дж. БУКО

ИЗМЕНЕНИЯ СООБЩЕСТВ БЕНТОСНЫХ БРАХИОПОД, ОТРАЖАЮЩИЕ БИОТИЧЕСКИЕ СОБЫТИЯ В СИЛУРЕ

По составу бентосной фауны в силуре установлено пять биотических событий, которые произошли в позднем эроне, в раннем и позднем венлоке, в позднем лудлове и в конце силура. Первое из них совпадает с началом трансгрессии в позднем лландовери. Возможные причины остальных подлежат выяснению.