# Species Diversity of Silurian Gastropods Related to Abiotic Events

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**ABSTRACT**—*Species diversity dynamics of Silurian gastropods reveal an intimate relationship to sea-level fluctuation. In turn, sea-level fluctuation during the Silurian was associated with glacio-eustatic change in the Early Silurian and gradual shoaling of most Silurian basins as a final stage of Caledonian tectonism. This picture was complicated by other minor fluctuations of sea-level, the specific reasons for which are not always clear. Sea-level fluctuations and resultant changes of gastropod species diversity were cyclic. Four important cycles are recognized in the Silurian, and correspond to the Llandovery, Wenlock, Ludlow, and Pridoli Series. The Llandovery cycle has four subcycles. The most important changes in species diversity occurred at the boundaries between major cycles. It is assumed that species diversity was related to the total area occupied by shallow seas. A decrease this area resulted in higher interspecific competition and produced a fall in diversity, while increase in the area of shallow marine shelves caused a reduction in competition and a corresponding rise in speciation.*

## Introduction

Paleozoic gastropods, especially those from the Silurian, have been little studied, though they played an important role in paleoecosystems and are of interest in evaluation of abiotic environmental factors on the benthos. It has been established (Gubanov, 1985) that gastropod intraspecific variation during the Silurian was associated with basin hydrodynamics. Changes in species diversity also depended strongly on sea-level fluctuation and water depth of basins.

## Data

The stratigraphic range of Silurian gastropods in Avalonian Britain (Murchison, 1839; Donald, 1899, 1902, 1905, 1906; Longstaff, 1909; Reed, 1920–1921; Pitcher, 1939), Nova Scotia (Peel, 1977, 1978), eastern Siberia (Gubanov, 1985, 1988, 1992, 1994 a, 1994b; Gubanov and Yochelson, 1994), Estonia (Isakar et al., 1990), Gotland (Lindström, 1899; Peel and Wängberg-Eriksson, 1979), and Podolia, western Ukraine (Mironova, 1987) provides the basis for the study of their diversity through this geological period. It also provides data on the possible relationship between species diversity and abiotic events, including sea-level fluctuation and water depths. Preliminary work for this study placed all available data into a modern stratigraphical framework. Great difficulties still remain for the Barrandian in the Prague Basin and some regions of North America, where Silurian gastropods are well studied but refinement of the stratigraphic range of gastropods in individual sections remains to be done.

## Results

Comparison of species diversity curves of gastropods from different regions based on their stratigraphic range has shown that periods of diversity variation coincide with boundaries between major chronostratigraphic units (Figure 1). The most significant changes in gastropod phylogeny took place at the Ordovician–Silurian boundary. The Late Ordovician biotic crisis, one of the most important in earth history (Raup and Sepkoski, 1982), resulted in a nearly complete change of gastropods at the species level. Unfortunately, poor knowledge of gastropods from the boundary beds, the relative dominance of Ordovician–Silurian boundary sections from deep-water deposits where gastropods are usually absent, and a significant lack of Upper Ordovician shallow-water facies make it impossible to evaluate the number of surviving species.

The Late Ordovician glaciation resulted in a marked lowering in sea-level and narrowing of shelf areas that induced a biotic crisis. Subsequent increase in tempera-

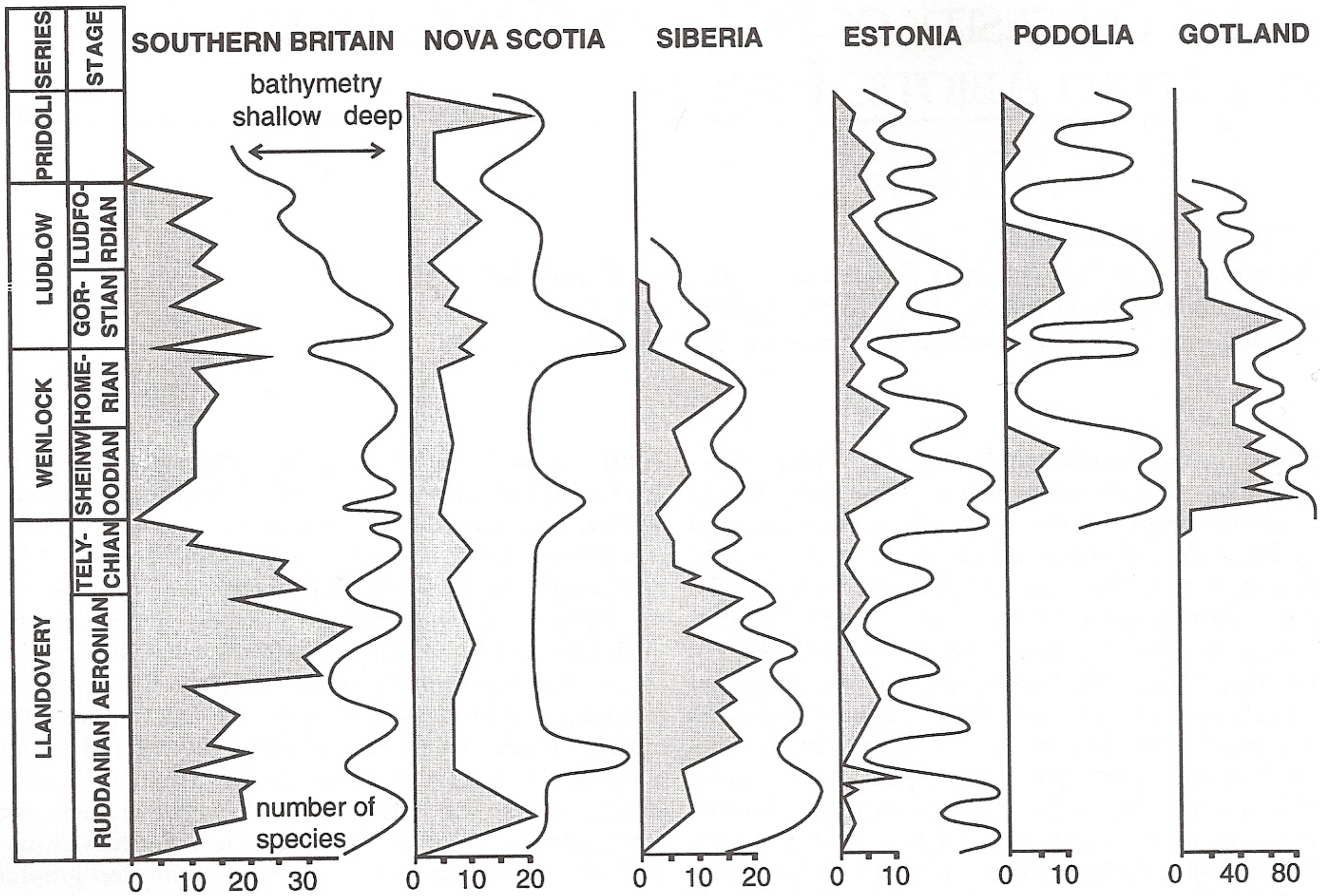


FIGURE 1—Change in gastropod species diversity and relative water depth in the Silurian of southern Britain, Nova Scotia, Gotland (after McKerrow, 1979), Estonia (after Kyrts et al., 1991), Podolia (after Gritsenko et al., 1986), and Siberia (author's unpublished data).

ture and deglaciation caused a dramatic sea-level rise at the beginning of the Early Silurian (Berry and Boucot, 1973; McKerrow, 1979; Brenchley, 1988). This event is associated with an important "anoxic event" that brought about the widespread deposition of thick black limestones and graptolite shales at the base of the Silurian (Berry and Wilde, 1978; Jeppsson, 1990).

Another important change in gastropod diversity occurred at the Llandovery–Wenlock boundary, but this change is expressed differently in different regions. In southern Britain and eastern Siberia, gastropod assemblages decrease in diversity through the upper Llandovery, and there is wide variation in the diversity of gastropods in the lower Wenlock (Figure 1). In Estonia, Gotland, and Podolia, the early Wenlock rise in diversity was explosive in character and far exceeded that of the Llandovery (Peel and Wängberg-Eriksson, 1979; Mironova, 1987; Isakar et al., 1990). A change in species composition also took place in Nova Scotia (Peel, 1977, 1978).

A major extinction of gastropods accompanied by a sharp decrease in species diversity occurred at the boundary between the Wenlock and Ludlow in southern Britain and eastern Siberia (Figure 1). In Nova Scotia and Estonia, the extinction was less profound (Peel and Wängberg-Eriksson, 1979; Isakar et al., 1990). In Podolia, gastropods disappeared from the record somewhat earlier in the middle Wenlock (Mironova, 1987). On Gotland, the diversity did not diminish in the late Wenlock. However, in the early Ludlow, the number of species increased almost twofold during a short interval (Figure 1). A significant increase in diversity at this point is observed in southern Britain, Nova Scotia, and Estonia (Peel, 1977, 1978; Isakar et al., 1990). Only *Catazone* sp. appeared in the earliest Ludlow of Podolia, but the sharp increase in the number of species occurred somewhat later there (Mironova, 1987). On the Siberian platform only *Prosolarium cirrosa* joined several species (*Murchisonia cingulata* and *Straparollus alacer*) known after the late Wenlock extinction, but by the end of the

Gorstian they also became extinct (Gubanov, 1988). Somewhat later, at the end of the early Ludfordian, the gastropods disappeared from the Podolian record, but their diversity decreased considerably for a short time in Estonia and on Gotland (Mironova, 1987).

After the late Ludfordian, the gastropods of southern Britain underwent a considerable decrease in diversity followed by an insignificant increase before they disappeared by the middle early Pridoli (Figure 1). In Nova Scotia after a 50% reduction in the number of species in the late Ludlow, the number of gastropod species was stable until the middle Pridoli, when diversity more than doubled (Peel, 1977, 1978). At the boundary between the Ludlow and Pridoli in Estonia, the number of gastropod species was reduced, but to a lesser extent than during the event at the Gorstian–Ludfordian boundary; in early Pridoli times the diversity increased for a short period (Isakar et al., 1990). In Podolia, gastropods are absent in the upper Ludfordian, but reappear in the early Pridoli and progressively increase in diversity (Mironova, 1987). Unfortunately, where gastropods are recorded up to the end of the Silurian, Devonian examples are very poorly known, and nothing is known about the change of the species composition at the Silurian–Devonian boundary.

The variations in species composition described above were closely related to fluctuations of sea-level and increase in basin depth. Such a relationship is evident when the curves for species diversity, sea-level fluctuation, and basin depth are compared for different regions (Figure 1). The data on sea-level and basin water depth changes in the Silurian of southern Britain, Nova Scotia, and Gotland are taken from McKerrow (1979). The curves for Estonia were constructed by the author using the data of Kyrts et al. (1991), and for Podolia with data from Gritsenko et al. (1986). Data for the Siberian Platform are based on the author's research. Increases in gastropod diversity are associated with transgression, and diversity decreases with regressions and changes in basin water depth. The relationship between cyclic changes of species composition, sea-level changes, and basin water depth is easily seen. The general nature of sea-level changes in the Silurian includes a sharp rise in the early Llandovery and a slow lowering through the latest Silurian. The general lowering of sea-level was affected by cyclic changes of higher-order magnitude. Four cycles are recognized in the Silurian, and correspond to the Llandovery, Wenlock, Ludlow, and Pridoli. Each cycle started with major sea-level rise. The same periodicity is noted in the species diversity of gastropods.

In well-studied Llandovery sequences in Britain, four more minor cycles of gastropod species diversity changes can be established. The first cycle involves the lowermost Rhuddanian (A2–A4 of British standard) and ends with a 52% decrease in species diversity. Comparatively greater changes took place at this point in Estonia (100%) and Nova Scotia (65%). The lowest decrease in diversity occurred in Siberia (10%).

The second cycle comprises the upper Rhuddanian and lowermost Aeronian (B1–B3). It began with the complete replacement of gastropod species in Estonia. In Siberia, the number of species doubled. In southern Britain, the species diversity remained stable, but with an almost 50% change in species composition. In Nova Scotia, the diversity remained unchanged. The cycle ended with a considerable decrease in diversity in Britain (43%) and eastern Siberia (22%), but in Nova Scotia and Estonia, this event is not recognized.

The third cycle (middle Aeronian, C1–C3) begins with a threefold increase in diversity of gastropod species in southern Britain, and with an increase of 50% in Siberia; it ends with diversity dropping to almost half (49%) in southern Britain. In other regions, this level of change is not seen. A more significant change occurred in the gastropod composition in Estonia, with a complete disappearance of earlier species and appearance of five new ones (*Boiotremus longitudinalis*, *Kjalromphalus* new sp., *Murchisonia* sp., *Stenoloron aequlatera*, and a new pleurotomariacean). In eastern Siberia, 57% of the species disappeared before the diversity again increased by half. This happened somewhat earlier than in the British Isles. In Nova Scotia, the diversity decreases are 33% and 40%, respectively, and occurred somewhat later than in the British Isles.

The fourth Llandovery cycle is only easily recognized in British sections, and is characterized by an increase of gastropod species diversity by 30% at the beginning and by a nearly complete disappearance of Llandovery species at the end. The upper boundary of the cycle, which coincides with a boundary between cycles of a higher order, is clearly defined in all of the regions discussed.

The change in sea-level and basin water depth had a similarly cyclic recurrence in the Llandovery of southern Britain, eastern Siberia, and Estonia, and was apparently characteristic of many other regions worldwide (Johnson et al., 1991; Johnson and McKerrow, 1991; Johnson, 1996). A somewhat different situation occurred in Nova Scotia, where the cyclic changes in gastropod species diversity were minor and cyclic changes in sea-level and basin water depth are not well defined. The basin water depth remained the same throughout the Silurian. Short periods of deepening of the basin in the middle Rhuddanian and at the Llandovery–Wenlock, Wenlock–Ludlow, and

Ludlow–Pridoli boundaries were quickly compensated for by sedimentation and aggradation.

For the Wenlock, only one cycle of gastropod diversity change exists, although species composition changed diachronously in different regions. In southern Britain during the Homerian, diversity was reduced by 25% before doubling. Wenlock variation is recorded through the upper Sheinwoodian of Estonia, with a drop and rise in diversity of 75% and 300% respectively. On Gotland, this variation occurred to a somewhat lower degree than in Estonia, with a 34% and 25% change, respectively. In eastern Siberia and Podolia, the change took place at the Sheinwoodian–Homerian boundary, with diversity first dropping by 22% and then increasing by 100% in Siberia, and a complete extinction in Podolia. This level also is definable in southern Britain and on Gotland, but is rather inconspicuous. During the Ludlow and Pridoli, these smaller cycles are difficult to define. Nevertheless, a relationship between the change in species diversity of gastropods and the fluctuation of sea-level and basin water depth is clearly seen.

A special feature should be noted. In the British Isles and on the Siberian Platform, the highest species diversity occurs during the late stages of important cycles that correspond to the epochs. In the southwest and northwest Russian Platform (Podolia, Estonia, and Gotland), this high diversity coincides with the initial stages of cycles. The close match between the species diversity of Silurian gastropods and fluctuation of sea-level and basin water depth in different regions indicates a close relationship between species diversity and the events that effected the change in sea-level and water depth.

## Discussion

Fluctuations of sea-level and water depth were probably associated with changes in climate and tectonic regimes. A general regressive trend in sea-level change is associated with the final stage of the Caledonian cycle (Seslavinskij, 1987, 1991), and early Llandovery transgression followed Late Ordovician glacio-eustatic events (McKerrow, 1979). The subsequent Early Silurian glaciation, which is known in South America (Grahn and Caputo, 1992), apparently was considerably less important than the Late Ordovician glaciation, and the consequence for changes of sea-level and gastropod diversity were not as severe. Although the general relationship between major changes in gastropod species diversity and these events is evident, the mechanism behind it remains unclear. One possibility is MacArthur and Wilson's "theory of balance" (R.H. MacArthur and E.O. Wilson *in* Hallam, 1983). By this model, sea-level lowering reduced the area of shallow seas. The basins on the platforms were reduced in size, and the size of the biotopes decreased simultaneously. This resulted in increased K-selection that brought about a decrease in taxonomic diversity. Conversely, an increase in sea area favored the appearance of new biotopes and extension of previous ones. The result of radiation of biotopes produced a burst of speciation.

## Conclusions

Four global cycles of species diversity changes among gastropods are defined for the Silurian. The boundaries of diversity cycles coincide with those of the series. Four lower-magnitude diversity cycles are established in the Llandovery. The reasons behind these changes are as yet unclear. The change in the area of shallow seas probably had a direct influence on species diversity. Decreases in shallow-sea area led to decreases in biotopes (because of increased biological competition) and species diversity. Conversely, increased shallow-sea area resulted in radiation of new biotopes, a decrease in competition, and intense speciation.

There existed a close relationship between the change in species diversity of gastropods and sea-level changes. The most important events which caused global sea-level fluctuations were glacio-eustasy in the early Llandovery and the final stage of Caledonian tectonism. The latter was responsible for regression in the Silurian.

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