

# Conodonts in Silurian hypersaline environments: Specialized and unexpectedly diverse

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## ABSTRACT

**Hypersaline environments are commonly assumed to be barren of metazoans and therefore are avoided by paleontologists, yet a number of early Paleozoic jawless vertebrate groups specialized to live in such settings. Sampling bias against restricted settings resulted in substantial underestimation of their diversity. Rare studies venturing into such environments yielded multiple new species of conodonts, suggesting that the diversity and habitat range of these hyperdiverse predators of the early oceans are equally underestimated. We describe here autochthonous conodont fauna from evaporite-bearing horizons from the middle Silurian of Estonia that provide evidence for efficient osmoregulation in this group. Based on a global compilation of coeval conodont assemblages, we show that marginal-marine, periodically emergent environments were characterized by higher conodont diversity than open-marine shallow settings. This diversity is due to a high number of species occurring in these environments only. The high degree of specialization is also reflected by the highest within-habitat variability ( $\beta$  diversity) in marginal settings. Most conodont species had narrow environmental niches and, unlike in marine invertebrates, extreme environments were inhabited by the most specialized taxa. Such environments represent a large proportion of early Paleozoic tropical epicratonic basins. Our analysis allows quantification of the degree to which mid-Silurian conodont diversity is underestimated as a result of sampling bias against marginal-marine settings.**

## INTRODUCTION

Shallow-water hypersaline and schizohaline settings are difficult to identify in the geological record, they are commonly assumed to be barren of fossils and consequently undersampled. This results in a strong negative sampling bias against taxa specialized to live in such settings. Stenotopic shallow-marine early Paleozoic jawless vertebrates such as galeaspids and osteostracans are subject to strong recovery bias, and the magnitude of this bias is proportional to the environmental restriction of a group (Sansom et al., 2015). The development of restricted epicratonic water masses and wide peritidal areas in the inter-tropical zone, favored by the continental configuration during the Silurian, created vast sabkhas across the Baltic Basin and Laurentia (e.g., Etensohn and Brett, 1998; Jarochowska et al., 2016). Monotonous and microbially dominated, these hostile environments have been avoided by paleontologists on the assumption that they are bound to be barren of fossils. Dolomite, the dominant lithology in such settings, constitutes only ~10%–15% of lithologies sampled for conodont studies (Purnell and Donoghue, 2005). However, several studies that ventured into the peritidal environment yielded new species of conodonts,

increasing their estimated diversity substantially (e.g., the Homerian–Gorstian of Saaremaa, Estonia: Viira, 1994; Viira and Einasto, 2003; the Silurian of Gotland, Sweden: Strömberg, 1997; the Middle Ordovician Winneshiek Lagerstätte of Iowa, USA: Liu et al., 2006; the middle Silurian Eramosa Lagerstätte of Ontario, Canada: von Bitter et al., 2007). This makes conodonts vulnerable to the same type of recovery bias as galeaspids and osteostracans and obscures a large share of early Paleozoic vertebrate diversity.

We investigated the upper Homerian (Wenlock) Rootsiküla Formation at Soeginina on the Estonian island of Saaremaa (Viira and Einasto, 2003; Meidla et al., 2014), the type unit for a number of new conodont species described from marginal-marine facies. We present sedimentological evidence that these species occurred in evaporite-bearing strata (Fig. 1) and evaluate the contribution of these evaporitic assemblages to total conodont diversity. To achieve this, we combined new field data with a literature-derived compilation of global Homerian–Gorstian (approximately coeval with the Saaremaa and Eramosa Lagerstätte assemblages) conodont occurrences provided with their environmental context. Two hypotheses are tested: (1) conodont assemblages

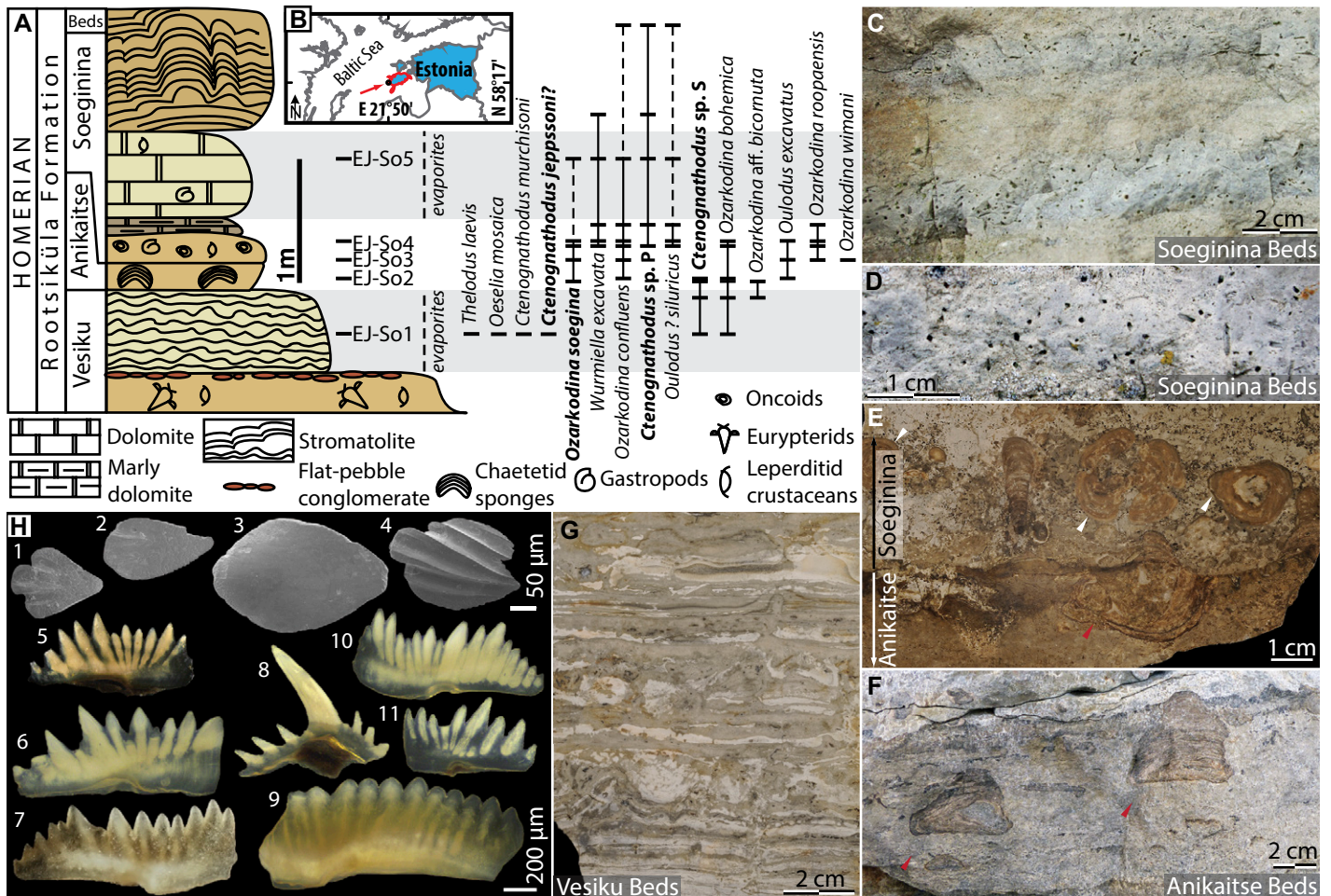
found in hyperhaline or schizohaline habitats represent allochthonous fauna transported there from open-marine settings; (2) these assemblages are formed by sink populations of open-marine faunas; i.e., by autochthonous conodonts representing a subset of open-marine species.

In both cases, the diversity in these habitats is expected to be lower than in their open-marine counterparts. We also calculate niche breadths to identify whether highly variable marginal-marine environments are occupied by species with the widest environmental niches, as it is in the case of benthic invertebrates (Jackson, 1974; Tomašových et al., 2014), or by stenotopic taxa. The distribution of niche breadths allows prediction of the magnitude of sampling bias incurred on diversity data by undersampling of extreme environments.

## METHODS

We compiled published data on conodont assemblages across the Homerian (Wenlock) through Gorstian (Ludlow). Conodonts distinguishing these stages are rare and it was often not possible to assign a sample to either Homerian or Gorstian; therefore, both stages were included in the compilation. The compilation has been submitted to the Paleobiology Database (<https://paleobiodb.org/#/>) and the full list of references is provided in Item DR2 of the GSA Data Repository<sup>1</sup>. We excluded collections with no environmental information, as well as uncertain identifications (e.g., aff., cf.), and analyzed presence-absence data for a total of 45 species and 376 samples. Assemblages were assigned to one of seven environmental categories along an onshore-offshore gradient (Figs. 2 and 3). Peritidal assemblages were identified as those from sites with evidence of periodic emergence, sedimentological evidence of desiccation, and salinity

<sup>1</sup>GSA Data Repository item 2017001, Item DR1 (new conodont occurrences from the Soeginina section), Item DR2 (supplementary information on analytical methods), and Item DR3 (supplementary results), is available online at <http://www.geosociety.org/pubs/ft2016.htm> or on request from editing@geosociety.org.



**Figure 1.** Soeginina section (Estonia). **A:** Lithology and microvertebrate distribution, modified from Meidla et al. (2014). New occurrences are shown in bold and gray areas indicate levels with evaporites. **B:** Position of the Soeginina section (arrow) in Estonia (blue infill). **C, D:** Vugs after gypsum crystals. **E:** Erosional boundary between the Anikaitse and Soeginina beds. Red arrow indicates a truncated chaetetid, and white arrows indicate oncoids. **F:** Chaetetid floatstone. **G:** Stromatolite with vugs after evaporites. **H:** Microvertebrates from the upper Rootsiküla Formation. 1, 2—*Oeselia mosaica* Märss 2005, EJ-So1/1–2; 3, 4—*Thelodus laevis* (Pander, 1856), EJ-So1/3–4; 5, 6—*Ctenognathodus* sp. S Viira and Einasto 2003; 5—GIT 715–1; 6—EJ-So2/1; 7—*Ozarkodina soegina* Viira and Einasto 2003, GIT 715–2; 8—*Ctenognathodus* spp., EJ-So1/2; 9—*Oz. roopaensis* Viira 1994, EJ-So3–1; 10—*Oz. anika* Viira and Einasto 2003, EJ-So3/2; 11—*Ctenognathodus* sp. P Viira and Einasto 2003, EJ-So1/1.

fluctuations, including data newly collected in this study (Table DR1 in the Data Repository).

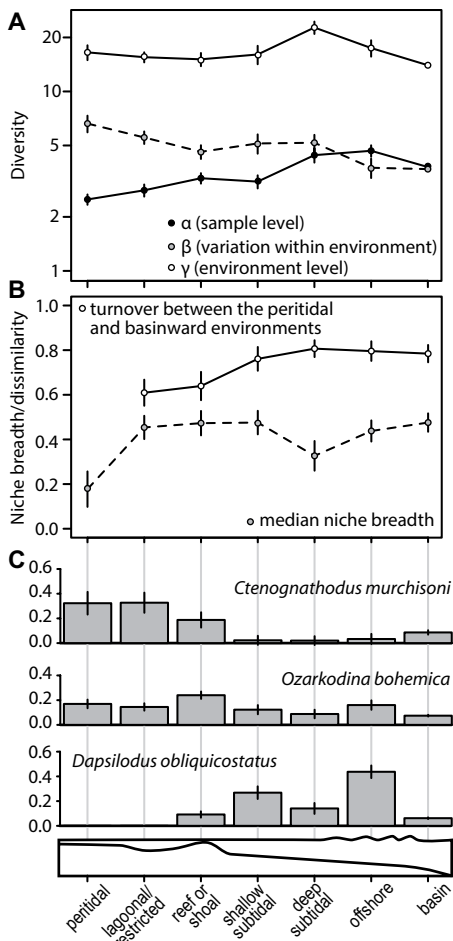
Peritidal assemblages were compared to those from other environments in terms of species richness, taxonomic composition, and environmental specialization of constituent species. To understand the contribution of local (assemblage level) diversity and within-habitat (between assemblage) variation in species composition to total richness of each environment we used multiplicative diversity partitioning. Ordination of assemblages containing more than one species (326 in total) was performed using multidimensional scaling (metaMDS). Species turnover at the habitat scale between peritidal and successive environments along the bathymetric gradient was measured as the Jaccard dissimilarity. To test the contribution of species with different degrees of environmental specialization in each environment and in the turnover between them, we calculated the niche breadth of individual species using

standardized Levins measure, which takes into account the frequency of occurrence across the environmental range (Hurlbert, 1978). To limit the effects of uneven sampling intensity, all analyses were performed on a data set subsampled to 24 collections per environment. (Details on analytical methods are given in Item DR2; details on results are in Item DR3.)

### SOEGININA HYPERSALINE ASSEMBLAGE

The Rootsiküla Formation at Soeginina shows multiple karstified erosional boundaries (e.g., Fig. 1E) and flat-pebble conglomerates indicative of periodic emergence and flooding. Stromatolites and oncoids are the dominant structures, whereas the macroscopic biota is dominated by euryhaline organisms. A partly reworked rudstone with eurypterids, bryozoans, and the nonvascular putative land chlorophyte *Parka decipiens* is found in the Vesiku Beds at the base of the

section. Two intervals contain vugs after gypsum crystals (Figs. 1C and 1D): (1) the upper part of the Vesiku Beds, formed by planar stromatolites with alternating organic-rich and micritic dolomite layers (Fig. 1G), and (2) the middle part of the Soeginina Beds, represented by massive micritic dolomite with regularly distributed intervals with gypsum vugs (upper gray band in Figs. 1A and 1C). The chaetetid and oncoidal floatstones (Figs. 1E and 1F) found between these two units have an erosional contact stained with iron oxides, which indicate subaerial weathering (Fig. 1E). The lower part of the Soeginina Beds hosts the most diverse biota dominated by oncoids, solenoporacean algae, and microproblematica. Proliferation of algae and stromatolites is typical of the intertidal and supratidal zones, in which periodic emergence, as well as temperature and salinity fluctuations, restricted the activity of grazing organisms. In contrast to depauperate macrofauna, conodonts recovered across the

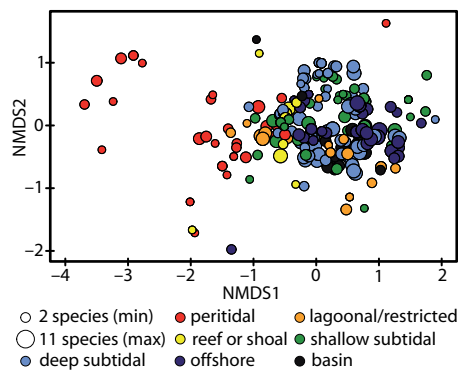


**Figure 2. Homerian through Gorstian conodont diversity across the onshore-offshore gradient. Vertical bars are standard errors. A: Multiplicative diversity partitioning. B: Species turnover (Jaccard dissimilarity) between the peritidal zone and subsequent environments and median niche breadth in each zone. C: Relative proportions of example conodont species.**

section were represented by 13 species (Fig. 1); of these, four (*Ctenognathodus jeppsoni*, *Ozarkodina soeaina*, *Ctenognathodus* sp. P, and *Ctenognathodus* sp. S; Viira and Einasto, 2003) are known only from the upper Rootsiküla Formation and coeval deposits that form the evaporitic facies belt extending along the paleoshore of the Baltic Basin. These deposits include, for example, the Širvinta and Neris Formations in Lithuania (Radzevičius et al., 2016), the Ustya Formation in Ukraine (Jarochovska et al., 2016), and peritidal strata within the Klinteberg Formation and Hemse Group in Gotland, Sweden (Strömberg, 1997). The lower evaporitic horizon yielded more than 100 scales of thelodont species *Oeselia mosaica* and *Thelodus laevis* (Fig. 1H).

#### DIVERSITY ACROSS THE ONSHORE-OFFSHORE GRADIENT

Our global compilation depicts the lowest average local (assemblage level) species richness



**Figure 3. Multidimensional scaling (MDS) ordination of Homerian through Gorstian conodont assemblages.**

in peritidal environments ( $\bar{\alpha} = 2.5$  species, Fig. 2A; Item DR3), in accordance with a general decrease from the peak in the offshore zone ( $\bar{\alpha} = 4.7$ ) toward more onshore environments. However, between-assemblage (habitat level) variation in species composition shows an opposite trend and reaches the highest values in the peritidal zone ( $\beta$  diversity = 6.6), compared to minimum values in basinal environments ( $\beta = 3.7$ ). Consequently, in spite of low diversity of individual assemblages, the total pooled peritidal fauna is more species rich (habitat-level diversity  $\gamma = 16.5$ ) than in any other shallow-water habitat ( $\gamma = 15.5$  in the lagoonal and/or restricted,  $\gamma = 15.1$  in the reef or shoal, and  $\gamma = 16.1$  in the shallow subtidal environment). The variation among peritidal conodont assemblages is reflected by a strong dispersion of samples from this environment in the metaMDS ordination space (Fig. 3). The limited overlap with other habitats resulted from a distinct species composition indicated by, on average, very narrow niche breadths of species inhabiting this zone (Fig. 2B). The turnover between the peritidal zone and other shallow-water environments is very high ( $>0.61$ ) and increases up to 0.81 for the deep subtidal zone, i.e., only 19% of species occurring in these environment are shared between them (Fig. 2B).

Contrary to what may be expected from nektonic fossils, specialist species (with narrowest niches,  $<0.1$ ) are the most common in the data set (27 of 45). The proportion of stenotopic and eurytopic species varies substantially between environments, the peritidal and deep subtidal zones having the highest proportion of specialists (median niche breadth 0.14 and 0.3, respectively; Fig. 2B). Seven species (15% of total diversity) are confined to the peritidal zone only (Strömberg, 1997; Viira and Einasto, 2003), allowing us to exclude shoreward transport of conodonts from open-marine waters. Environmental niches obtained from our data set (e.g., Fig. 2C) agree with previous observations on the ecology of individual species, for example that the Wenlock index taxon *Ozarkodina bohemica* shows no facies affinity, supporting its utility as an index taxon (e.g., Märss and Männik, 2013).

#### IMPLICATIONS FOR CONODONT ECOLOGY

The high conodont diversity in evaporitic sabkha-like settings contrasts with the apparent lack of macrofauna in these environments. Precipitation of gypsum requires brines more than three times concentrated with respect to seawater (Warren, 2016). Living in such hypersaline conditions requires efficient osmoregulation, which allows us to better constrain conodont physiology. The closest living relatives of conodonts are hagfishes and lampreys (Donoghue et al., 2000), which show contrasting osmoregulatory strategies. Hagfishes are exclusively stenohaline osmoconformers, whereas lampreys are efficient osmoregulators, but both have the genes for suitable ionic transporters; therefore, stenohalinity in hagfishes is inferred to be a derived trait (Edwards and Marshall, 2013). This suggests that effective osmotic control was present in the common ancestor of conodonts and cyclostomes.

Between-habitat variation of  $\beta$  diversity might result from differences in spatial (ecological) or temporal (evolutionary) turnover (e.g., Sepkoski, 1991). The narrow temporal scope of our study (~5 m.y.) minimizes the contribution of evolutionary turnover within the studied interval. In marine invertebrates, known onshore-offshore variation in the rates of origination and extinction does not appear at this time scale (Tomašových et al., 2014). This allows attributing high  $\beta$  diversity in peritidal settings to spatial turnover. The reasons for this spatial heterogeneity must be sought in the mode of life of conodonts. Oxygen isotope data from studies spanning the Ordovician through Early Triassic indicate that conodont species living in the same area could have permanently occupied different depths of the water column (e.g., Sun et al., 2012; Quinton and MacLeod, 2014). However, depth-stratification models fail to predict all observed variability of conodont distribution, revealing a more complex relationship with different water masses (Herrmann et al., 2015). This is supported in our study as variability within the water column can be excluded in the case of peritidal environments. Spatial variation in species composition of peritidal assemblages must be attributed to other factors, e.g., tolerance to highly variable temperature and oxygen supply, or limited metazoan food base available to conodonts, which fed as predators or scavengers (Purnell, 1993).

#### IMPLICATIONS FOR THE CONODONT FOSSIL RECORD

The dominance of species with narrow niches in our data set contradicts environmental distribution patterns expected from nektonic organisms. Twelve species (27% of total diversity) have been found in one environment only. Spatial distribution of individual species across environmental gradients translates into their uneven collection probability in a stratigraphic succession,

and results in a systematic facies bias in conodont occurrence data used for biostratigraphic and evolutionary reconstructions (e.g., Holland and Patzkowsky, 2002; Barrick and Männik, 2005). Exclusion of the peritidal zone would result in a loss of 15% of species from the data set. Although no provincialism in Silurian conodonts has been reported, substantial differences exist between low-latitude basins. Many Laurentian and Baltic taxa, such as *Ctenognathodus*, have never been reported from Avalonia or Perunica, and the diversity of peritidal conodonts in Laurentia represents only a fraction of that recognized in Baltica. This may be due to differences in their dispersal and abundance, but also in taxonomic practice such as the use of open nomenclature (e.g., von Bitter et al., 2007).

Apart from addressing allochthonous input into peritidal environments, our study did not consider taphofacies or environment-specific postmortem processes affecting species composition (reviewed by Purnell and Donoghue, 2005). Sampling bias against restricted settings might be compensated by the favorable preservation conditions that they offer. Thanks to limited bioturbation and scavenging, as well as trapping in biofilms, marginal-marine settings have provided the largest number of articulated conodont skeletons (Mikulic et al., 1985; Liu et al., 2006; von Bitter et al., 2007). Nonetheless, high diversity represented in these settings is not due to species being particularly delicate or distinguished based on features requiring exceptional preservation. Therefore, the Lagerstätten effect can be excluded as the main cause for high species richness in peritidal settings, but it may contribute to preservation of spatial patchiness and low  $\alpha$  diversity. Lower within-habitat variability ( $\beta$  diversity) in open-marine environments may reflect more intensive hydrodynamic and biotic transport and destruction. Consequently, restricted environments may be a taphonomic window into environmental conodont distribution.

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