Variation in the outline and distribution of epithelial cell imprints on the surface of polygnathacean conodont elements

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The elements of many conodont taxa exhibit a polygonal surface micro-ornamentation. Four main types are recognized (striation, linear texture, regular (idiomorphic) texture and granular texture) and their distribution over the conodont elements of different morphology is considered. The intraspecific (ontogenetic and ecological) and interspecific (phylogenetic) causes of the reticulation texture variations are also considered. □*Cell imprints, Conodonta, Polygnathacea*

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Conodont element histology has been conducted in two main ways: through studying the tissues from which the elements are composed and through examining surface micro-ornamentation. The first method has been investigated by a number of researchers (see Donoghue (1998) for a comprehensive review), but structures of secretory epithelium imprint are less well known (Burnett 1988; Conway Morris & Harper 1988; von Bitter & Norby 1994b). The imprint is composed of micro-reticulation and is known on 'oral' surfaces of different types of conodont elements (Pierce & Langenheim 1970; Budurov 1976; Burnett 1988; Conway Morris & Harper 1988; von Bitter & Norby 1994a, b; Zhuravlev 1994). The texture of the reticulation on conodont elements is considered to reflect the structure of the secretory epithelium (Conway Morris & Harper 1988). Some aspects of the micro-ornamentation can be used as features of taxonomic significance (Budurov 1976; Zhang 1998). Burnett (1988) proposed the differentiation of cell imprints on functionally active and passive surfaces that are closely related to conodont element morphology. Prominent inter- and intraspecific variations in shape and size of the cell imprints have been observed (Conway Morris & Harper 1988; von Bitter & Norby 1994b; Zhuravlev 1994; Zhuravlev 1997). These have been examined at the interspecific level on a geological time-scale by Conway Morris and Harper (1988) and interpreted as controlled by genome size. On the intraspecific level, modifications of cell imprint shape are linked to conodont element relief (Pierce & Langenheim 1970; Budurov 1976; McCracken & Nowlan 1989; Burnett & Hall 1992; Zhuravlev 1994); variations in imprint size have been attributed to varying ecological factors (Zhuravlev 1994, 1997). Imprint patterns demonstrate weak dependence on ontogeny (von Bitter & Norby 1994a, b; Zhuravlev 1995).

The aims of this paper are: (1) to describe the main types of cell imprints and micro-reticulation textures; these are taken to reflect the structure of the conodont secretory epithelium; (2) to consider distribution of the textures over the conodont elements of different morphology, and (3) to determine the main causes of variation at both intraspecific and interspecific levels.

Material and methods

The reticulation patterns composed by epithelial cell imprints have been studied in conodont elements of various geological age and morphological type (Fig. 1). Main attention has been focused on Pa conodont elements of the Late Devonian (Early–Middle Frasnian of the East European Platform, Late Famennian of the Northern Urals) and Early Carboniferous (Tournaisian of the Northern Urals). Some Late Permian conodonts (Far East and Trans-Caucasus) have also been included in the study.

Reticulation was studied using a scanning electron microscope (S.E.M.) and a reflected light microscope at magnifications between ×160 and ×2000. Unfortunately, in some cases it was not possible to obtain a good image of the reticulation (for example, on S and M elements) because of the low contrast between the boundaries and contents of cell imprints.

Cell imprints were measured to a standard error of 1.5–2.5%. Statistics were obtained from a database containing information on cell imprint sizes from more than 800 conodont elements (database available from the author).

Classification of micro-reticulation textures

Cell imprints covering the 'oral' surface of conodont elements are of different shape and size. Four main morphological types of cell imprint shape have been discerned (Fig. 2A–D): elongate rod-like, elongate sub-rectangular, sub-triangular and sub-isometric (mainly rounded or sub-hexagonal). All the types can be observed on a single conodont element. Cell imprints of various shapes compose reticulation textures, characterized by superimposition of cell imprints. Four main types of textures were recognized (Fig. 3): striation (Fig. 2A), linear texture (Fig. 2A, B), regular (idiomorphic) texture (Fig. 2C) and granular texture (Fig. 2C, D). Transitions between the textures occur as well.

Striation is composed of alternation of rounded costa and hollows, and in some cases by highly elongated rod-like imprints. Linear texture is characterized by elongated cell imprints. Sub-hexagonal cell imprints of nearly equal size are characteristic of regular texture; this is the most common texture found on conodont elements of various types. Granular texture is a complex reticulation composed of rounded agglomerations of cell imprints of various shape and size. As a rule, the agglomerations correspond to nodes or denticles on the 'oral' surface of elements (Figs. 2C, 4).

Morphologically similar textures of the micro-reticulation are known on ostracode shells (FitzGerald 1983), the loop of terebratulide brachiopods (Mckay *et al.* 1994), dermal plates, scales and teeth of dipnoans (Smith 1977), heterostracans (Blieck 1982), actinopterigians (Schultze 1977), etc.

Distribution of the micro-reticulation over conodont elements

The textures composed by cell imprints are closely related to relief of conodont element: flat surfaces, as a rule, are covered by regular reticulation, but complex surfaces often bear granular and linear textures of reticulation. Also, some morphological features of conodont elements have specific reticulation textures (see Fig. 4). Superimposition of reticulation textures of a conodont element composes its reticulation structure (Fig. 5), which probably corresponds to the structure of the secretory epithelium. Pa and Pb conodont elements display the most variable structure of reticulation. Free blades of platform Pa elements and blades of some Pb elements are covered by regular (in lower part) and linear (in upper part) textures that

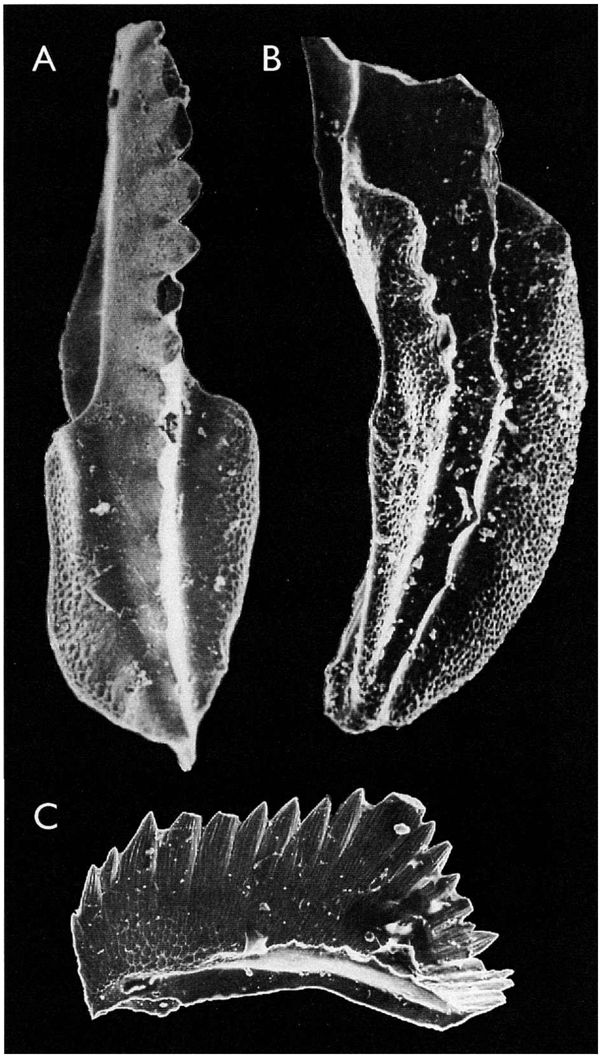

Fig. 1. Epithelial cell imprints on the various types of conodont elements. ☐A. Pa element of *Polygnathus zikmundovae* Zhuravlev, Polar Urals, Kozhym River section, Lower Carboniferous, Tournaisian, *duplicata* Zone; specimen 332/23, ×180. ☐B. Pa element of *Polygnathus communis lectus* Kononova, Northern Urals, Podcherem River section, Lower Carboniferous, Tournaisian, *sulcata* Zone; specimen 332/35, ×165. ☐C. Pb element of *Siphonodella* sp. ('*Elictognathus*' *laceratus* (Branson & Mehl) s.f.), Polar Urals, Konstantinov Creek section, Lower Carboniferous, Tournaisian, *quadruplicata* Zone; specimen 337/9, ×115.

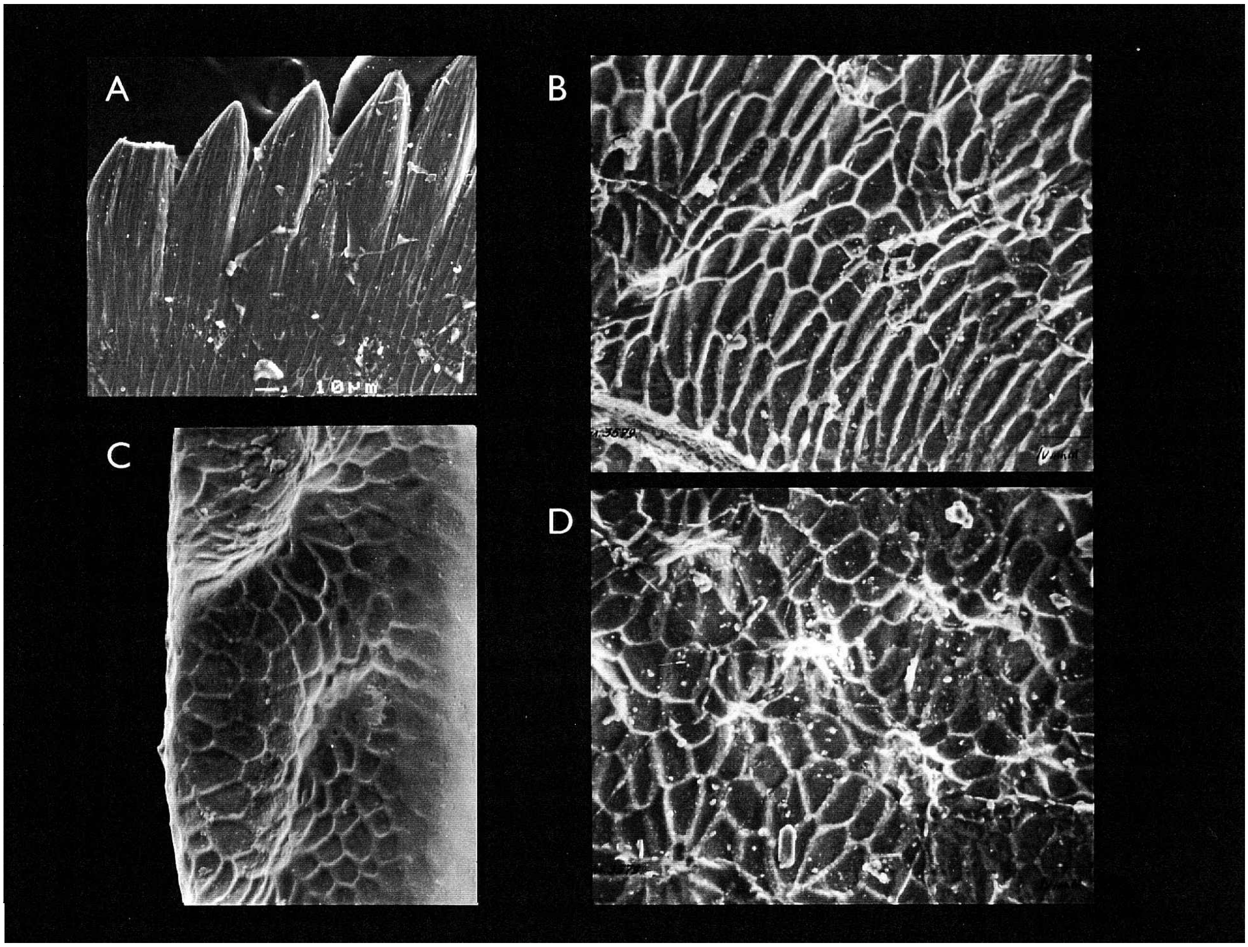

Fig. 2. Main morphological types of cell imprints shape and reticulation textures. □A. Elongate rod-like imprints composing linear texture and striation, blade of Pb element of *Siphonodella* sp. (*'Elictognathus' laceratus* (Branson & Mehl) s.f.), Polar Urals, Konstantinov Creek section, Lower Carboniferous, Tournaisian, *quadruplicata* Zone; specimen 337/9, ×300. □B. Elongate sub-rectangular imprints comprising linear reticulation texture, outer part of platform of *Siphonodella crenulata* (Cooper), Northern Urals, Podcherem River section, Lower Carboniferous, Tournaisian, *quadruplicata* Zone; specimen 332/13G-6-2, ×680. □C. Sub-triangular and sub-isometric imprints composing regular and granular textures, platform margin of *Polygnathus drucei* Zhuravlev, East-European Platform, Lake Ilmen section, Lower Frasnian, specimen 11/13019, ×570. □D. Sub-triangular and sub-isometric imprints composing granular texture, outer part of platform of *Siphonodella crenulata* (Cooper), Northern Urals, Podcherem River section, Lower Carboniferous, Tournaisian, *quadruplicata* Zone; specimen 332/13G-6-2, ×680.

grade into striation on denticles. The carina of platform Pa elements bear, as a rule, linear texture on the lower part, and striation or granular texture on denticles (nodes). Nodose parts of platform are covered by granular texture. Concave surfaces (for example, adcarinal troughs) bear linear texture. Convex surfaces are covered by regular or granular textures. M and S elements, characterized by simpler reticulation structure, bear regular texture on processes and linear texture grading into striation on denticles (Fig. 5).

Size variation on individual elements can reach almost 40% (*Siphonodella quadruplicata* Branson &

Cell imprint morphology	Textures			
	Striation	Linear	Regular	Granular
Elongate rod-like (prolate)	common	common		
Elongate sub-rectangular	rare	common	rare	rare
Sub-triangular		rare	occur	common
Sub-isometric			common	common

Fig. 3. Types of cell imprints and reticulation textures.

Morphological features	Textures			
	Striation	Linear	Regular	Granular
Denticle	common	common		
Node			rare	common
Ridge (sharp)		common	common	occur
Ridge (round)			common	
Trough (groove)		common	common	
Flat surface		rare	common	
Platform margins		common	common	occur

Fig. 4. Dependence of textures of the reticulation on relief of a conodont element.

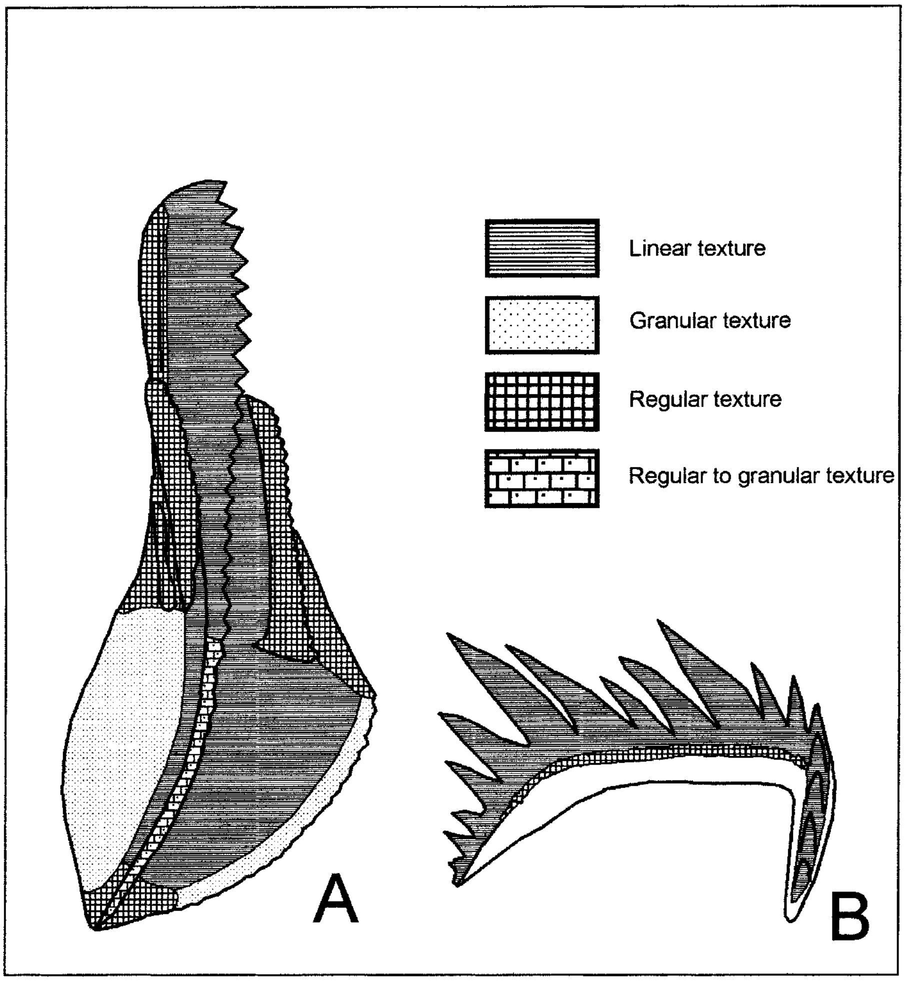

Fig. 5. Distribution of the reticulation textures on the different types of conodont elements. □A. Pa element (*Siphonodella quadruplicata* (Branson & Mehl)). □B. Sc element ('*Polygnathus*' ex gr. '*P.*' *angustidiscus* (Youngquist)).

Mehl) and intraspecific variation can reach 200% (see also Zhuravlev 1994). Cell imprint sizes (CIS), measured as median diameter of isometric cell imprints, vary significantly among the individuals of a species (Fig. 6; distribution of CIS for *Polygnathus communis communis* Branson & Mehl, *Siphonodella obsoleta* Hass, and *Palmatolepis gracilis* Branson & Mehl). These variations are caused, in some degree, by variations of the cell imprint form, and by several other factors.

Variation of the micro-reticulation

Variation of the micro-reticulation structures can be subdivided into several groups: (1) ontogenetic variations, (2) individual non-ontogenetic variations (probably ecologically induced), (3) interspecific (taxonomic) variations.

Ontogenetic variations in cell imprint form and size are not prominent (von Bitter & Norby 1994b; Zhuravlev 1995), although Burnett (1988) noted dependence between the appearance of cell imprints and ontogeny. This study has found that conodont elements of all ontogenetic stages exhibit cell imprints.

Ontogenetic changes in reticulation textures were considered for Pa elements of the Tournaisian species *Polygnathus purus* Voges and *Siphonodella quadruplicata* (Branson & Mehl). These species are characterized by different morphology of Pa elements.

Polygnathus purus has a platform element with simple morphology: wide flat platform and denticulated carina. Element morphology does not change during ontogeny. Juveniles differ from adult forms both in size and proportion of the platform (see Zhuravlev 1995, text-fig. 5). Ontogenetic changes in reticulation textures are absent: the platform is covered by regular texture and the carina by regular and linear textures; the free blade bears regular reticulation in the lower part and linear reticulation in the upper part.

Siphonodella quadruplicata shows complex morphology of the Pa element. Adult forms have a set of

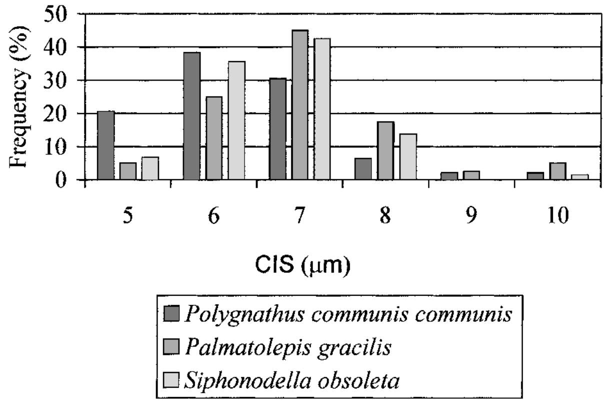

Fig. 6. Frequency distribution of cell imprint size (CIS) for *Polygnathus communis communis* Branson & Mehl ($n = 141$), *Siphonodella obsoleta* Hass ($n = 73$), and *Palmatolepis gracilis* Branson & Mehl ($n = 40$).

longitudinal ridges in the anterior part (rostrum), nodes on the inner part of the platform and transverse costae on the outer part. Juveniles of this species demonstrate simpler morphology: they do not have a full set of rostral ridges and are characterized by a smooth platform surface (without prominent nodes and costae). During ontogeny, the rostral structure develops (by adding of the ridges) and meso-ornamentation of the platform appears (see Zhuravlev 1995, text-fig. 5). Changes in reticulation structures during ontogeny are represented mainly by an increase in complexity and a decrease in the elongation of reticulation (Fig. 7). In adult forms, isometric structures (composed mainly by regular and granular textures) dominate.

Analysis of the relationship between average (for conodont element) CIS and element size (as a proxy for age) suggests that CIS does not increase during ontogeny (Fig. 8) (see also Zhuravlev 1995, text-fig. 6).

Variations in reticulation that are not attributable to ontogeny appear mainly as variations in CIS. Aberrations in reticulation structure are not common; they are induced mainly by injuries and subsequent regeneration of the conodont element. For example, in the regeneration area of denticle of the free blade, striation and linear texture are replaced by regular texture (Fig. 9). Ecologically induced CIS variations have been considered for the latest Famennian–Tournaisian species *Palmatolepis gracilis* Branson & Mehl ($n = 48$, CIS ranges from 4.3 μm to 9.9 μm), *Polygnathus communis communis* Branson & Mehl ($n = 156$, CIS ranges from 3.95 μm to 10.1 μm) (Fig. 10), *Polygnathus purus* Voges ($n = 76$, CIS ranges from 4.2 μm to 11.2 μm) and *Siphonodella obsoleta* Hass ($n = 73$, CIS ranges from 4.4 μm to 7.8 μm).

Median CIS of *Polygnathus communis communis* Branson et Mehl in the Lower Tournaisian varies from 5.5 μm in oxygen-depleted condition (Izyayu River section, Polar Urals, facies of shelf depression with stagnated water circulation; $n = 42$, standard deviation 0.13) to 6.5 μm in the shallow-water carbonate shelf condition (Kamenka River section, North Urals; facies of carbonate platform, $n = 22$, standard deviation 0.25).

Changes in reticulation structure in phyletic lineages were also observed. For example, in the lineage from *Siphonodella sulcata* to *Siphonodella quadruplicata*, median CIS increases slightly from 6.3 μm to 6.5 μm (the difference is statistically insignificant) and reticulation structure becomes more differentiated. In the *Polygnathus zikmundovae*–*Polygnathus proprius* lineage, median CIS also demonstrates an absence of statistically significant differentiation. They are distributed as follows: *Polygnathus zikmundovae* – 7.3 μm ($n = 16$, standard deviation 1.05); *Polygnathus purus* – 7.2 μm ($n = 78$, standard deviation 1.00); *Polygnathus proprius* – 6.1 μm ($n = 18$, standard deviation 1.44). Reticulation structure on the platform changes slightly in this lineage from mainly regular in *Polygnathus zikmundovae* to regular and granular in *Polygnathus proprius.*

Congeneric species demonstrate some variation in CIS. For example, average CIS for the Early Carboniferous genus *Siphonodella* is about 6.3 μm ($n = 281$,

Stage of ontogeny	**Part of Pa conodont element**						
	Outer platform margin	**Outer platform**	**Outer adcarinal trough**	**Carina**	**Inner adcarinal trough**	**Inner platform**	**Inner platform margin**
Juvenile	regular & linear	linear & regular	mainly linear	linear & granular	regular & linear	regular	linear
Adult	granular	regular & linear	mainly linear	linear, regular & granular	regular & linear	granular & regular	linear & regular
Herontic	granular	mainly regular	linear	linear & granular	linear & regular	granular	regular

Fig. 7. Distribution of reticulation textures in *Siphonodella quadruplicata* (Branson & Mehl) and its ontogenetic changes.

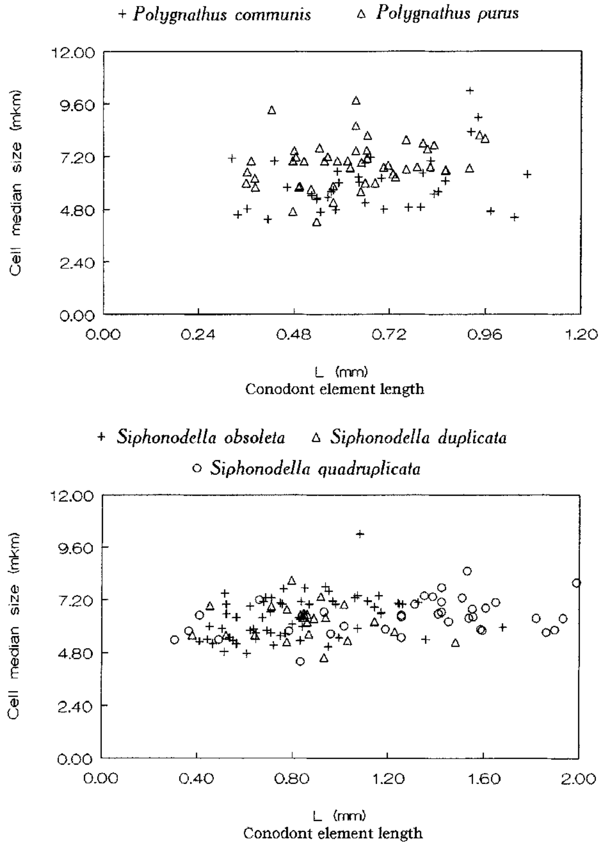

Fig. 8. Ontogenetic changes in cell imprint size (CIS).

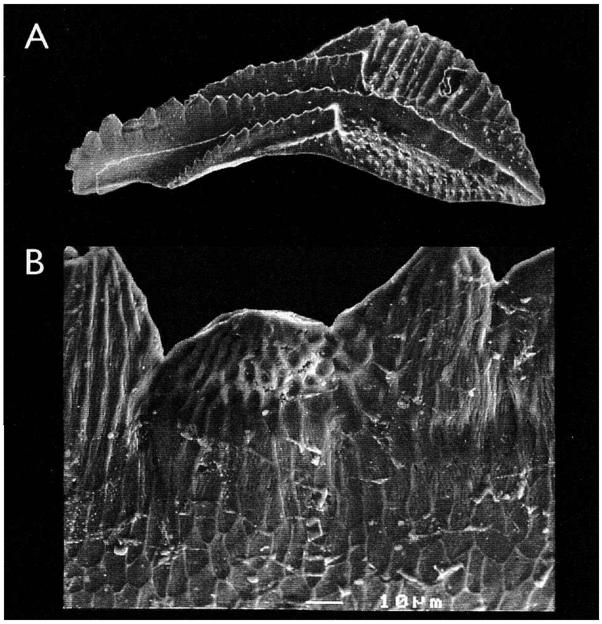

Fig. 9. Siphonodella quadruplicata (Branson & Mehl) Pa element, Polar Urals, Konstantinov Creek section, Lower Carboniferous, Tournaisian, *quadruplicata* Zone; specimen 332/Tn20-4. □A. ×50. □B. ×470. Reticulation texture in the area of regeneration of free blade denticle. Striation and linear textures are replaced by a regular one.

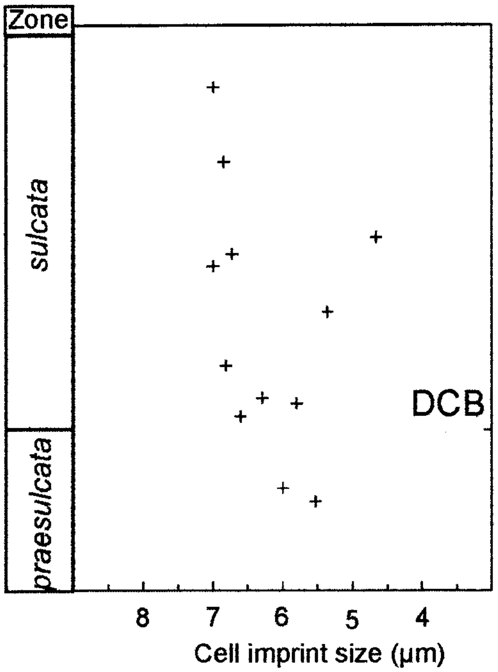

Fig. 10. Polygnathus communis communis Branson & Mehl CIS measurements for time-series record from the Devonian/Carboniferous boundary (DCB) beds in Northern and Polar Urals sections. The measurements represent generalized data from three sections (12 samples, 31 specimens).

standard deviation 0.99), and *Siphonodella duplicata* is characterized by median CIS of 6.2 µm ($n = 30$, standard deviation 0.61), *Siphonodella obsoleta* – 6.3 µm ($n = 81$, standard deviation 0.37, minimum CIS 4.4 µm), *Siphonodella uralica* – 6.9 µm ($n = 13$, standard deviation 1.02), and some individuals of *Siphonodella lobata* demonstrate CIS up to 11.6 µm. So CIS varies in individuals of siphonodells from 4.4 µm (*Siphonodella obsoleta*) up to 11.6 µm (*S. lobata*).

Interpretation

Close relations between relief of a conodont element and the reticulation textures support the conclusion that the textures reflect the structure of the secretory epithelium. The presence of cell imprints on the surface of 'adult' and 'gerontic' conodont elements, as well as the occurrence of traces of regeneration of carina in these elements, suggests full covering of the elements by secretory epithelium (during growth periods) at all the stages of ontogeny, contrary to the opinion of Burnett (1988). It also assumes growth of the elements during the whole the life of the conodont animal. Observed ontogenetic changes of micro-reticulation structure and the absence of ontogenetic control on CIS supports the conclusion of von Bitter and Norby (1994b) about multiplicative cellular growth in the conodont secretory epithelium.

It has been assumed that the factors affecting intraspecific CIS variations were water temperature, salinity and oxygen content (Zhuravlev 1997). There are no direct evidences of this suggestion. Only limited data exist on positive correlation between the water temperature and CIS of *Polygnathus communis communis* Branson & Mehl (7 samples, Late Famennian–Tournaisian) and *Polygnathus praepolitus* Kononova & Ovnatanova (11 samples, Early–Middle Frasnian; Zhuravlev, in prep.). Also, some circumstantial evidences occur. Environmental control on cell size is documented for recent and Mesozoic foraminifers (Hecht 1976) – in this case cell size is equivalent to the test size. Hecht (1976) assumed the maximum size for the optimal condition and cell size decreasing in unfavorable conditions (abnormal salinity and/or temperature). In spite of their being certain differences between foraminifers and conodonts, a common mechanism of environmental control on cell size through metabolic rate can be assumed.

Taxonomic variation in CIS can be explained by the variation in genome content (Conway Morris & Harper 1988). Despite the wide range of CIS variation in the genus, CIS cannot be used alone as a taxonomic feature because of significant intraspecific variation and overlap of CIS distributions of different species and even of different genera (see Fig. 6).

Conclusions

Four reticulation textures of conodont element micro-ornamentation composed from four types of cell imprints can be recognized on the surface of all the types of conodont elements (not just on Pa and Pb). Ontogeny, element meso-morphology and taxonomic position control distribution of the textures over the surface of conodont elements. The most variable parameter is cell imprint size, which appears to be constrained by species and, probably, environment.

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