Lanea carlsi conodont apparatus reconstruction and its significance for subdivision of the Lochkovian

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A cosmopolitan spathognathodontid taxon "*Ancyrodelloides carlsi*" is not regarded in this paper as one of the earliest known representatives of *Ancyrodelloides* according to former concepts, but is considered as conspicuous member of the genus *Lanea*. The taxon shows distinct morphological innovation of the upper surface of the Pa element within the *Lanea* lineage which makes it easily recognizable worldwide and suitable for global correlation. Presented stratigraphic correlation using conodonts and other faunal groups qualifies a short-lived *Lanea carlsi* as probably the best marker of the middle Lochkovian base. This paper presents reconstruction of the apparatus of *L. carlsi* which is the first complete reconstruction in the genus *Lanea*. The comparison of the *Lanea* apparatus and assumed apparatus of early *Ancyrodelloides* from the Požáry Quarries (Barrandian, Czech Republic) resulted to proposal of an alternative concept of evolution of these two genera. The relatively short-lived genus *Ancyrodelloides* is considered to split off from the *Lanea* clade in the late middle Lochkovian by the entry of *Ancncyrodelloides transitans*.

Key words: Conodonta, apparatus reconstruction, biostratigraphy, Lochkovian, Barrandian, Prague Synform.

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Introduction

Since the introduction of multielement taxonomy, conodont apparatuses are the basis for classification and completed reconstructions of conodont taxa essential for understanding of conodont phylogeny. Reconstructed multielement taxa show range of morphological innovations and characters in individual elements of entire apparatus and thus also enhance the possibility for their correct identification. Recent studies revealed that even ramiform elements have a great potential in tracing morphological trends in conodont clades and may also help in suggesting evolutionary lineages in spite of heterochronous (mosaic) evolution within some apparatuses. An example of the advantages of using morphological changes in ramiform elements has recently been provided by Dzik (2002), who studied Frasnian palmatolepidids, with evidence that changes in ramiform elements can be even more diagnostic than those in the platform ones. For a long time, the platform elements have been, however, practically the only ones used for taxonomy of late Silurian–early Devonian Spathognathodontidae and morphologies of Pa element also were considered fundamental for lineage reconstructions. But, the major problem among spathognathodontid conodonts, especially in the Přídolí, is relatively small pace of distinct morphological changes in Pa elements of certain taxa. This means that most of the Pa elements in individual clades show outwardly only relatively slight changes in denticulation, whereas there are no pronounced morphological changes of platform lobes or general features of the blade. Moreover, some typical morphologies in late Silurian–early Devonian are recurrent, e.g., occasional appearance of ornamentation on platform lobes and higher degree of similarity in denticulation. As a consequence of difficult delimitation of taxa in past decades, many spathognathodontids were lumped into single genus ("*Ozarkodina*"). For distinguishing of two stratigraphically important taxa *Spathognathodus eosteinhornensis* (Walliser, 1964) and *Ziglerodina remscheidensis* (Ziegler, 1960) only regularity of denticulation of the blade was used in most cases as pointed out Murphy et al. (2004) who provided a new perspective of classification of a great part of late Silurian–early Lochkovian Spathognathodontidae which is based also on characteristic morphologies in ramiform elements. This new taxonomy thus also points to significance of non-platform members of spathognathodontid apparatus around the Silurian–Devonian boundary.

In most cases, numbers of individual element-types in conodont samples are not balanced and the effect of primary bio-production (original numbers of elements) is biased by subsequent post-mortem processes, e.g., hydrodynamic sorting of sediment particles, material lost during deposition and diagenesis. Accordingly, the number of obtained platform elements which often show highest morphological change rates are not always sufficient and/or diagnostic for biostratigraphic and evolutionary implications.

In spite of the number of indices or important guiding conodonts and relatively well-working zonal scale for the

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middle and the upper Lochkovian (Valenzuela-Ríos and Murphy 1997, and later modified by Murphy and Valenzuela-Ríos 1999), the number of completely reconstructed taxa of the most substantial genera is still not sufficient. An exception is the reconstruction of *Zieglerodina remscheidensis* (Ziegler, 1960) and *Wurmiella excavata excavata* (Branson and Mehl, 1933) by Murphy et al. (2004); these reconstructions were recently applied with some modifications by Suttner (2007). The biggest constrain for the apparatus reconstructions in the Lochkovian is apparently too many resembling ramiforms co-occurring and overlapping stratigraphically which often causes apparatus mixing in conodont samples. A probability of dealing with natural assemblages or numerically well-balanced and strikingly distinct multispecies or even a single-species bearing conodont samples which is ideal for apparatus reconstruction is undoubtedly a good deal of luck. This may, however, happen in densely sampled sections—by bed-by-bed sampling or selective resamplings of large intervals.

The aim of this paper is to present reconstruction of the apparatus of *Lanea carlsi* (Boersma, 1973)—a conspicuous member of the middle Lochkovian Spathognathodontidae; to demonstrate its stratigraphic application for the subdivision of the Lochkovian stage and to discuss its systematic position among known spathognathodontid genera in the early Devonian.

Remarks on nomenclature.—The generic affiliations of some conodont taxa mentioned in this paper have been changed repeatedly or their inclusion in the genus is doubtful. These taxa are treated in quotation marks because no better affiliation to the genus is possible. This applies, for example, to "*Ozarkodina*" *planilingua*, "*Pandorinellina*?" *boucoti*, and "*Ozarkodina*" *optima*.

Institutional abbreviation.—NM, National Museum Prague, Czech Republic.

Other abbreviations.—Pa, Pb, Sa, Sb, Sc, M, locational notation for conodont apparatuses.

Geological setting

The apparatus of *Lanea carlsi* has been discovered 22 m above the base of the section Požár-3. The section is situated in an active quarry which forms a part of a larger mining locality of the Požáry Quarries. The section Požár-3 lies 1 km E of Řeporyje-a village WSW of the city of Prague (GPS location: N 50°01'66", E 14°19'63") (see Fig. 1). The Požáry Quarries represent one of the most prominent localities for biostratigraphy in the Prague Synform (Barrandian area) which is also famous for the GSSP of the lower boundary of the Přídolí Series (Kříž et al. 1986). The abundance of pelagic faunal component together with sedimentological features mentioned below indicate a strong influence of oceanic conditions (Hladíková et al. 1997, 1999) and allows a world-wide biostratigraphic correlation. The great advantage for biostratigraphy is an uncovered succession of the major part of Lower Devonian carbonates without major tectonic disturbances. Fundamental biostratigraphic information in the Devonian was provided by conodonts, dacryoconarids and many graptolites. Previous conodont studies in the Ludlow–Zlíchovian interval of the Požáry Quarries (Slavík 2004a, b; Carls et al. 2005, 2007; Slavík et al. 2007, 2010) revealed that conodont faunas are relatively abundant, with a great potential for refinement of global conodont time scales. In past years an intensive biostratigraphic research was carried out and provided an extensive conodont data-set from the basal Lochkovian to the basal Zlíchovian (almost 100 conodont samples were taken in past 7 years only from the Lochkovian). A complex mineralogical and sedimentological study using various physical methods of Lower Devonian carbonates of the Požár-3 section have recently been carried out by Koptíková et al. (2010a, b).

The major part (0–77.6 m) of the carbonate succession at the Požár-3 section belongs to the Kotýs Limestone of the

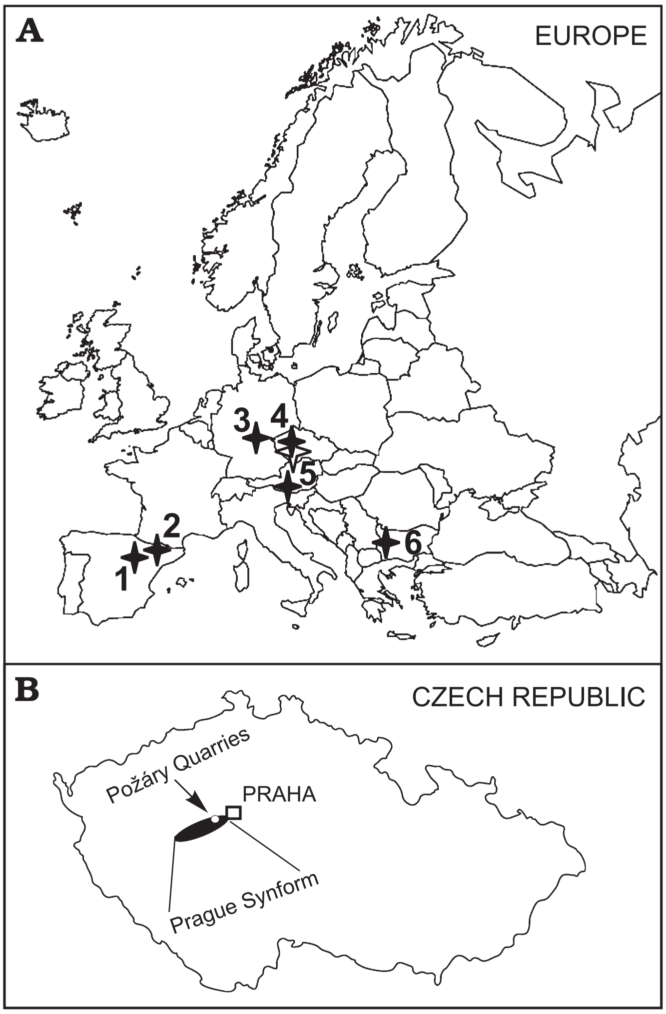

Fig. 1. **A**. Map with marked ocurrences of *Lanea carlsi* in Europe: 1, Eastern Iberian Chains; 2, Spanish Central Pyrenees; 3, Frankenwald; 4, Prague Synform (Barrandian); 5, Carnic Alps; 6, Western Bulgaria. **B**. Location of the Požáry Quarries in the Prague Synform (Barrandian, Czech Republic).

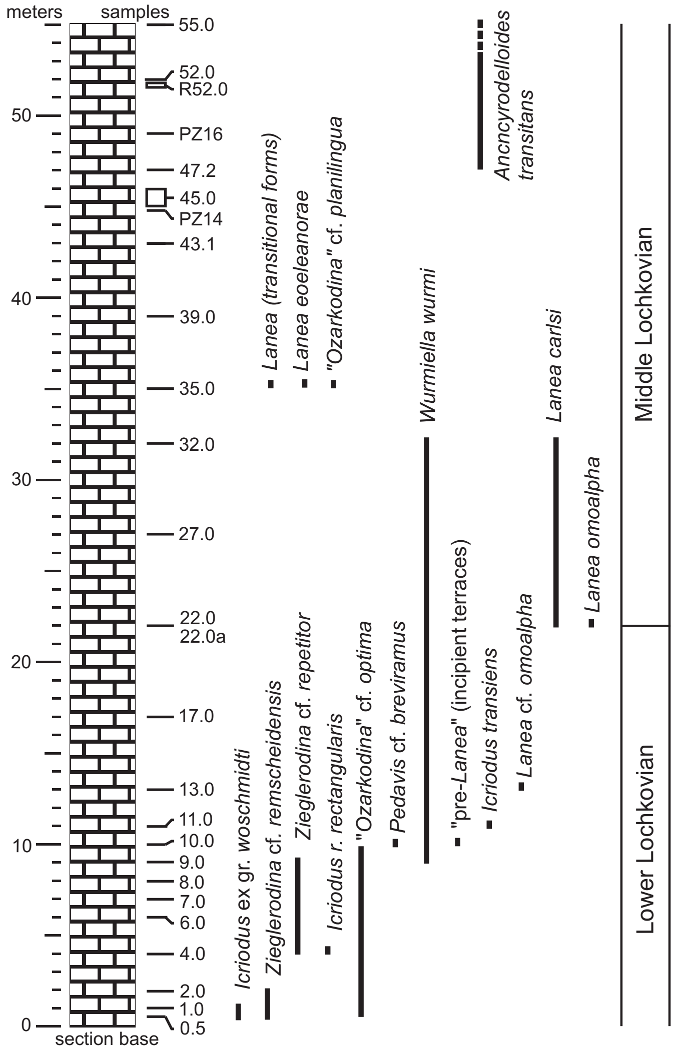

Fig. 2. Stratigraphy of the lower and middle part of the Požár-3 section with ranges of stratigraphically most important cosmopolitan conodonts in relation with the range of *Lanea carlsi*. The samples are marked on the right side of the column. The sample numbers are marked on the right side of the column. For convenience the sample prefix (4Po) is omitted. The samples with other prefixes (from different samplings and re-samplings) are given in full (i.e., PZ14, PZ16, and R52.0).

Lochkov Formation (Chlupáč et al. 1998). The rocks are mostly thin bedded with some intercalations of nodular calcarenite and calcisiltite beds; cherts are very scarce occurring at few horizons only. Echinoderms, bryozoans, brachiopods, mollusks, trilobites, corals, algae, ostracods, sponge spicules, tentaculites, and scolecodonts dominate among bioclasts. In order to have multiple control and better orientation in time in the locality, Lochkovian conodonts were obtained from two parallel sections (Požár-1–2 and Požár-3); both sections are a short distance from each other (ca. 100 m). In spite of unfinished processing of conodont data and incomplete biostratigraphic analysis from the Požár-3 section, a piece of data from the Lochkovian in this stage already can be presented. Detailed comparison of conodont data from both parallel sections showed that the Lochkovian in the Požár-3 section starts approximately 5 m above the Silurian–Devonian boundary. This boundary is well exposed in the neighboring section Požár-1–2, where the basal Devonian conodont *Icriodus hesperius* marks the first Devonian bed (Carls et al. 2007). Advanced development and radiation in icriodid faunas can be seen in the first 4 m in the section Požár-3. In general, conodont faunas in the middle and upper part of the Lochkov Formation include a number of index taxa and other important guide conodonts supporting (still only partly developed) global Lochkovian zonation suggested by Valenzuela-Ríos and Murphy (1997). Their concept covers the formal subdivision of the Lochkovian Stage into the three parts—the lower, the middle, and the upper Lochkovian. The middle Lochkovian zonation is mostly based on evolution of conspicuous members of the genera *Lanea* Murphy and Valenzuela-Ríos, 1999 and *Ancyrodelloides* Bischoff and Sannemann, 1958. The upper Lochkovian zonation, which is "basically without *Ancyrodelloides*", is characterized by *Masaraella pandora* beta (Murphy, Matti, and Walliser, 1981) and the evolution of late Lochkovian *Pedavis* clade. The faunas obtained from the Lochkovian of the Požáry Quarries have a great potential for even more detailed subdivision of the Lochkovian Stage, but it still depends on prospective increase of density of data by repeated samplings. The lower part (0–22 m) is characterized by several important taxa—*Icriodus* ex gr. *woschmidti* Ziegler, 1960, *Zieglerodina* cf. *remscheidensis* (Ziegler, 1960), *Pedavis* cf. *breviramus* Murphy and Matti, 1983 and possible predecessor of *Lanea* with incipient terraces (herein named tentatively as "pre-*Lanea*", see Fig. 2). The middle part of the Lochkov Formation (22–73 m) starts with typically developed *Lanea omoalpha* Murphy and Valenzuela-Ríos, 1999 and *Lanea carlsi* (Boersma, 1973). The latter taxon in its upper range (at 32 m above the base of the section) co-occurs with embryonal bulbs of the oldest dacryoconarids (*Homoctenowakia senex* Alberti, 1983). At 35 m above the base, *Lanea eoeleanorae* Murphy and Valenzuela-Ríos, 1999 appears. At 47.2 m, *Ancyrodelloides transitans* (Bischoff and Sannemann, 1958) appears, followed by *A. trigonicus* Bischoff and Sannemann, 1958, higher up (at 60 m). In the uppermost part of the Lochkov Formation several morphotypes of *Masaraella pandora* Murphy, Matti, and Walliser, 1981 and *Pedavis gilberti* Valenzuela-Ríos, 1994 occur. The total thickness of the Lochkov Formation (i.e., the original Lochkovian) at the Požár-3 section is 77.6 m. The overlying Praha Formation starts with marked lithological change (lighter color) and contains already typical Pragian benthic and pelagic faunal elements.

Remarks on classification of the Lochkovian Spathognathodontidae

The specific paleoenvironmental conditions in the Lochkovian time and presence of several facies types ranging from typically shallow-water to pelagic deeper-water environments, also influenced the composition of Lochkovian conodont faunas which are very diverse. The Lochkovian taxa belong to several families in the sense of Sweet (1988). Apart from abundant but stratigraphically difficult to apply simple cones, the most important Lochkovian conodonts belong to the families: Prioniodinidae—represented by genus *Delotaxis* Klapper and Philip, 1971 and *Erika* Murphy and Matti, 1983, Icriodontidae—with genera *Icriodus* Branson and Mehl, 1938, *Pedavis* Klapper and Philip, 1971 and *Pelekysgnathus* Thomas, 1949; and to relatively large and varied group of conodonts that constitutes family Spathognathodontidae. This paper is partly focused on stratigraphically significant Lochkovian genera included in the last mentioned family whose members are the most common at this stratigraphic level. The concept of supra-generic classification made by Sweet (1988) has been partly modified by Dzik (1991) who relocated several genera—*Ancyrodelloides* Bischoff and Sannemann, 1958, *Pandorinellina* Müller and Müller, 1957, and *Eognathodus* Philip, 1965 into the family Polygnathidae. In the present paper these genera are considered to be rather separated from polygnathids, following the reasons summarized by Murphy et al. (2004). The comprehensive review of all spathognathodontid genera in the Přídolí–Lochkovian, and its upgraded classification is presented in the same paper. The concept of spathognathodontid genera by Murphy et al. (2004) is in principle followed in this paper apart from modification presented in next chapters. As it was already remarked in above mentioned paper, in Sweet's (1988) classification were many of the late Silurian–early Devonian Spathognathodontidae incorporated in the genus *Ozarkodina* Branson and Mehl, 1933.

The new concept of Murphy et al. (2004) preserves many formerly proposed genera and includes also newly introduced ones. Their classification of Spathognathodontidae that cross the Silurian–Devonian boundary includes: *Ozarkodina* Branson and Mehl, 1933 (a genus that is largely restricted), *Wurmiella* Murphy, Valenzuela-Ríos, and Carls, 2004, *Zieglerodina* Murphy, Valenzuela-Ríos, and Carls, 2004, "new genus *W*" Murphy, Valenzuela-Ríos, and Carls, 2004 and *Amydrotaxis* Klapper and Murphy, 1980. Among the most conspicuous Lochkovian genera of Spathognathodontidae were also included: *Flajsella* Valenzuela-Ríos and Murphy, 1997, *Lanea* Murphy and Valenzuela-Ríos, 1999, *Pandorinellina* Müller and Müller, 1957, *Ancyrodelloides* Bischoff and Sannemann, 1958, *Kimognathus* Mashkova, 1978, *Masaraella* Murphy, 2005, and early eognathodontid taxa. The most recent classification by Donoghue et al. (2008) who applied computer generated cladistics based on topology of elements in skeletal apparatuses represents undoubtedly a novel approach with many inspiring ideas using also those characters that have never or only partly been applied in previous classifications. This concept is not, however, followed in this paper because the basic principles of this approach treating selected characters are herein still regarded problematic until more explanations and refinements are provided—for example, little attention has been paid to slight and subsequent morphological changes which can be observed in large stratigraphic successions in time—these observations are usually fundamental for suggestions of evolutionary lineages and their relations. Their concept thus includes many surprising changes that concern also Lochkovian taxonomic ranks: e.g., family Spathognathodontidae was abandoned, "*Nicollidina* (= *Zieglerodina*) *remscheidensis* (Ziegler, 1960)" is assumed to be closely related to Frasnian polygnathid *Nicollidina brevis* Dzik, 2002. Explanation of all problematic points, contra virtues of their concept is not, however, aim of this paper as it would require a separate thorough discussion. Accordingly, for the purpose of this paper and transparency of given results, the original concept of late Silurian–early Devonian Spathognathodontidae modified by Murphy et al. (2004) is applied.

Lanea carlsi apparatus position and its generic classification

Reconstruction of a spathognathodontid apparatus based on a natural assemblage from the Lochkovian of Podolia was presented by Mashkova (1972). Although two elements were lacking in her apparatus, this reconstruction and later discovered natural assemblages were the basis for the completed model of skeletal apparatus of ozarkodinid conodonts. It was presented by Purnell and Donoghue (1998) as a sexmembrate apparatus having 15 elements that includes seven mirror image pairs and one symmetrical element. Similarly like in the other spathognathodontid taxa, the reconstruction of *Lanea carlsi* apparatus is based on this concept.

The apparatus has been found in the sample 4Po22 (Fig. 2) in the Požár-3 section. Apart from some elements of *Belodella* the sample contains only two spathognathodontid taxa. These are strikingly different. The first taxon is represented by 4 juvenile elements: 1x Pa, 1x Pb, 1x Sa and 1x M. Considering the size proportionality and common morphological features, all these elements probably belong to the same apparatus and possibly even to the same organism. The denticulation of the spathognathodontid Pa element with prominent cusp and cockscomb at the anterior end of the blade resemble *Zieglerodina remscheidensis*, but it slightly differs from *Z. remscheidensis* by stronger inclination of denticles towards the posterior. The other elements of the apparatus show typical characters of the *Zieglerodina* apparatus that was described in Murphy et al. (2004). The Pb element is very short, the Sa element shows a very sharp angle between lateral processes which are rather high. Almost regular alternation of denticle size is seen also in the M element.

The second taxon in the sample is *L. carlsi* which is represented by 12 Pa, 7 Pb, 5 M, 5 Sa, 4 Sb, 7 Sc, and 28 fragments of diverse elements. The complete material of the taxon is 68 complete or fragmentary elements in total showing various stages of maturity. *L. carlsi* was also found in sample 4Po32 (only 2 Pa elements were identified) in the same section in association with fragments of *Lanea* sp., *Wurmiella* cf.

wurmi (Bischoff and Sannemann, 1958), and *Zieglerodina* sp. More specific determination of platform and ramiform elements of *Lanea* is difficult because these have siliceous grains fused to their surfaces.

At the same stratigraphic level as the appearance of *Lanea carlsi* (22 m above the base of the section) but in a different sample (4Po22a) taken during previous sampling has been detected one characteristic Pa element of *Lanea omoalpha* Murphy and Valenzuela-Ríos, 1999. This is accompanied by a few fragments of ramiform elements which belong to the apparatus of *Lanea* and resemble very much the ramiforms of the apparatus described in this paper. The range of *L. carlsi* in the Požár-3 section is only 10 m (i.e., the interval between samples 4Po22 and 4Po32). The taxon occurs also in the parallel section Požár-1–2 at about the same stratigraphic position with roughly corresponding range (four succeeding samples in 8 m interval). The total number exceeds 80 Pa elements in this section. In association with the Pa elements of *L. carlsi* in the samples co-occur also other taxa of *Lanea* (*L. omoalpha*, *L. eoeleanorae*, *L.* cf. *omoalpha*), "*Pandorinellina*?" *boucoti* Klapper, 1969, and *Wurmiella wurmi*. The ramiform elements are thus mixed in samples, but assignation to the genus is possible.

Regarding the history, the taxon originally named as "*Spathognathodus carlsi*" has been coined by Boersma (1973) who studied condonts from the Spanish Central Pyrenees. He collected 41 specimens from "*Orthoceras* limestones" at Bahent locality and established a new spathognathodontid taxon for these Pa elements with a widely open and asymmetrical basal cavity with one ornamented lobe. The associated conodonts found by Boersma (1973) in the Pyrenees together with *Lanea carlsi* are icriodids of the *Icriodus woschmidti* group (*I. woschmidti postwoschmidti* Mashkova, 1968), *I. angustoides bidentatus* Carls and Gandl, 1969, *I. rectangularis* Carls and Gandl, 1969, and the taxa "*Spathognathodus remscheidensis*" (Ziegler, 1960) and "*Spathognathodus steinhornensis repetitor*" (Carls and Gandl, 1969). The platform elements of *L. carlsi* were previously described from the Lochkovian of Frankenwald (Bischoff and Sannemann 1958) and from Aragón (Carls and Gandl 1969). In accordance with the past nomenclature, the *L. carlsi* was assigned originally to *Spathognathodus* and later was also transferred to *Ozarkodina* as was the case of most spathognathodontid taxa in the eighties and early nineties of the last century. Klapper et al. (1991) assigned the *L. carlsi* to the genus *Ancyrodelloides* Bischoff and Sannemann, 1958 mainly due to the presence of distinct ornamentation on the platform lobes, and provided a complete synomymy. A relatively large number (50 of Pa elements) of "*Ozarkodina carlsi*" were found by Valenzuela-Ríos (1994) in the section Geri 1.1 (Pyrenees) where its range is well controlled stratigraphically by the succession of diagnostic taxa. It appears below morphotypes of "*Ancyrodelloides omus*" including *Lanea omoalpha* (= *A. omus* delta morph Valenzuela-Ríos, 1994, according to Murphy and Valenzuela-Ríos 1999) which are well below *Ancncyrodelloides transitans* and *A. trigonicus*. Valenzuela-Ríos and Murphy (1997) in their zonation of the middle Lochkovian kept some diagnostic taxa with *Ancyrodelloides* (including *A. omus* alpha Murphy and Matti, 1983 and *A. eleanorae* Lane and Ormiston, 1979). Later, Murphy and Valenzuela-Ríos (1999) proposed a new genus *Lanea* for several rather robust species of the middle Lochkovian Spathognathodontidae sharing numerous morphological characters. The authors presented the hypothesis of a separate history for the two stratigraphically closely related genera—*Lanea* and *Ancyrodelloides*. *Lanea* was separated from the latter genus mostly on the basis of "normally unornamented basal platform lobes" equipped with terraces. According to Murphy and Valenzuela-Ríos (1999), in more derived members of *Lanea* (i.e., *L. eleanorae* and *L. telleri* (Schulze, 1968), and *Ancyrodelloides* (i.e., *A. transitans*) the basal grooves and basal cavities are already restricted to some extent. Although the overall characteristic of the new genus is robust, the authors remarked that at the dawn of the *Lanea* clade, its early members show similarities to coeval taxa. An example of such a strong similarity can be the identically developed basal cavity in the taxa *L. carlsi* and *L. omoalpha*. The authors included in the new genus *Lanea* several distinct taxa—*L. omoalpha* Murphy and Valenzuela-Ríos, 1999, *L. eoeleanorae* Murphy and Valenzuela-Ríos, 1999, *L. eleanorae* Lane and Ormiston, 1979, and *L. telleri* (Schulze, 1968). *L. carlsi* was not discussed in that paper and in their interpretation remained it within *Ancyrodelloides* (Murphy and Valenzuela-Ríos 1999: table 1). Their concept also left *L. omus* Murphy and Matti, 1983 within *Ancyrodelloides* mainly because of ornamentation of the platform lobes (see Murphy and Matti 1983: pl. 2: 21–29). To sum up, the interpretation by Murphy and Valenzuela-Ríos (1999) supposes stratigraphically close or almost corresponding origin of both genera and the branching point should be expected close to the lower/middle Lochkovian boundary (cf. the ranges of taxa *carlsi* and *L. omus* in Pyrenees: section Gerri 1.1., Valenzuela-Ríos 1994 and Segre 1, Valenzuela-Ríos 2002, and ranges of taxa *omus* alpha, *L. omus* beta and "*A. omus* sp. nov.—*A. transitans*" (Murphy and Matti 1983: table 2, pl. 2: 13, 15, 17) = ?*L. carlsi* (this paper). The figured Nevadan specimen that might probably be *L. carlsi* in the Simpson Park Range Section VII coexists with *L. omoalpha* Murphy and Valenzuela-Ríos, 1999, *Amydrotaxis johnsoni* Klapper, 1969, and *L. eleanorae*, and is well below *A. transitans*. The faunal succession in the sections of the Požáry Quarries that were obtained by relatively dense sampling in the Lochkovian (almost 100 conodont samples) also confirms the stratigraphic succession of these important members of *Lanea* and *Ancyrodelloides*.

The main reason for re-allocation of *L. carlsi* to the genus *Lanea* in this paper is the strong similarity to representatives of *Lanea* clade and faunal successions that may point to modified concept of *Ancyrodelloides* and *Lanea* lineage. The striking similarity does not apply to the platform elements only, but is also observed in the entire apparatus, which is probably almost undistinguishable from *Lanea omoalpha* and its immediate

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descendants within the *Lanea* clade. Moreover, it is possible to distinguish certain elements of the apparatus from those of *Ancyrodelloides* (*A. trigonicus, A. kutscheri,* and especially, *A. transitans*). Murphy and Valenzuela-Ríos (1999) remarked that the entire apparatus of *Lanea*, *Ancyrodelloides*, and *Kimognathus* have not been reconstructed yet mostly because of their common co-occurrence, element mixing, and scarcity of certain ramiforms. The apparatus of early *Lanea* member—*L. carlsi* reconstructed in this paper may elucidate the relation between respective genera.

Stratigraphic relation between *Ancyrodelloides* and *Lanea* in the Požáry sections

The following succession of *Lanea* can be seen in the Požár-3 section (Fig. 2): The first form that strongly resembles *Lanea* (named herein provisionally as "pre-*Lanea*") appears at 10 m above the base of the section and co-occurs with *Pedavis* cf. *breviramus* (it is left in open nomenclature because of breakage of the specimens) and last forms of *Zieglerodina* that declines at this level. The "pre-*Lanea*" Pa elements in mature stage are robust, showing already incipient terraces on rounded but slightly asymmetrical platform lobes and an unrestricted basal cavity. In the following sample, at 11 m, *Icriodus transiens* Carls and Gandl, 1969 was recorded. Probably the first *Lanea omoalpha* (unfortunately, the single Pa element obtained is broken posteriorly) enters at 13 m above the section base. The platform lobes bear well developed terraces that do not occupy the entire upper surface of the platform lobes; they are smooth without ornamentation and the basal cavity is completely opened.

The dawn of *Lanea* in the Požáry Quarries thus can be approximated close to this level, i.e., well above the radiation of the earliest icriodids (*Icriodus* ex gr. *woschmidti*), close above the decline of typical early Devonian *Zieglerodina*; taxa *Z. remscheidensis* (Ziegler, 1960) and *Z. repetitor* (Carls and Gandl, 1960) and just above the range of "*Ozarkodina*?" *optima* (Moskalenko, 1966). The following 9 m interval is very poor in conodonts, *Lanea omoalpha* is confirmed at 22 meters above the base of the section, i.e., at the same level that *L. carlsi* enters. In the following 10 m of its range it seems that only *L. carlsi* dominates; *Lanea omoalpha* has no longer been found above the level 22 m. At 35 m, forms with sub-quadrate platform lobes with less developed ornamentation were found; they correspond well to specimens figured from Copenhagen Canyon Section IV (Nevada) and from U topolů section (Barrandian area) by Murphy and Matti (1983: pl. 2: 21–29) as "*A. omus* beta morph". This taxon shows a great variability in ornamentation of the upper surface of the platform lobes: in some forms there is only one lobe ornamented, other variants have both lobes with tubercle that may pass into a faint ridge and the tubercles are sometimes twisted aside or inclined posteriorly or anteriorly. These transitional forms, that are also considered to belong to the genus *Lanea*, seem to replace *Lanea carlsi* at this level, showing stepwise disappearance of ornamentation (pronounced nodes on outer lobe are thus substituted by weak irregular tubercles or ridges) whereas the basal cavity does not show any change from its predecessors. The same sample (4Po35) contains "*Ozarkodina*" cf. *planilingua* Murphy and Valenzuela-Ríos, 1999 and *Lanea eoeleanorae* Murphy and Valenzuela-Ríos, 1999, the latter with incipient closing of the basal grooves. The section Požár-1–2 shows the same conodont succession, but includes also the transitional forms between *L. eoeleanorae* and *L. eleanorae*, in which the basal cavity is more constricted and the platform starts to be extended along the posterior blade. But true *L. eleanorae* and *L. telleri* have not yet been found in the Požáry Quarries. Genus *Ancyrodelloides* (*A. transitans*) was first recorded at 47.2 m above the base of the section, at the level, where no representatives of *Lanea* have been recorded. The ranges of some members of *Lanea*, however, partly overlap with *Ancyrodelloides* in Nevada and Pyrenees (cf. Murphy and Valenzuela-Ríos 1999: text-fig. 1) and thus show clear coexistence in time. The alternative phylogenic hypothesis in this paper suggests a branching of the *Lanea* clade that gave rise to the specific and relatively short lived genus *Ancyrodelloides* in the late middle Lochkovian (i.e., above the entry of dacryoconarid tentaculites); the *Lanea* branch in global scale is then shortly continued by a few advanced members with a more constricted basal cavity (*L. eleanorae*). These late members of *Lanea*, however, has not yet been found in the Požáry Quarries.

Discussion of phylogenic concepts and stratigraphy

The original concept of *Ancyrodelloides* supposes that the oldest member of the clade is probably *A. carlsi*. In the Segre 1 section in the Pyrenees (Murphy and Valenzuela-Ríos 1999: text-fig. 4), the taxon co-occurs (possibly in its upper range) with *L. omoalpha*, *L. eoeleanorae*, and "*Ozarkodina*" *planilingua*. Its origin is, however obscured, because of an underlying interval without conodonts. In the section Gerri 1.1, taxon *carlsi* was recorded in a sole limestone bed in association with *Icriodus transiens* Carls and Gandl, 1969 and *Icriodus angustoides bidentatus* Carls and Gandl, 1969; taxa belonging to *Lanea* (morphotypes of *L. omus*, *L. eleanorae*) were recorded above. The forms from Nevadan Simpson Park Range Section VII, considered here as *L. carlsi*? (Murphy and Matti 1983: table 2, pl. 2: 13, 15, 17), are within the range of *L. omoalpha* and coexist also with *Amydrotaxis johnsoni* (Klapper, 1969) alpha morphotype Murphy and Matti, 1983, *L. eleanorae* and *Pedavis breviramus* Murphy and Matti, 1983. Similarly as in the Pyrenees, *L. carlsi* disappears well below the forms with a distinctly closing basal cavity (*L. eleanorae* and *A. transitans*). The same stratigraphic succession of *L. carlsi* and *A. transitans* is seen in the Požár-3 section and also in the parallel section Požár-1–2. In the latter section part of the *L. carlsi* range overlaps with *L. eoeleanorae*. A similar situation is present in the Segre 1 section (Murphy and Valenzuela-Ríos 1999: text-fig. 4). Transitional forms between *L. eoeleanorae* and *L. eleanorae* appear 2 meters above the end of *L. carlsi* range in the Požár-1–2 section. As *L. eleanorae* has not yet been found in the Požáry section, it is only possible to suppose tentatively its origin might be very close to the appearance of *A. transitans* and shortly overlapping with these early *Ancyrodelloides* (according to the concept in this paper). As it was shown in Murphy and Valenzuela-Ríos (1999: text-fig. 1), *A. transitans* starts earlier than *L. eleanorae*. According to their interpretation of the genus *Ancyrodelloides*, the immediate known descendant of *L. carlsi* is *A. omus*, followed by *A. transitans* in the same clade (no other intermediate forms has been discovered). Then there would exist, however, relatively large intervals without recorded intermediate forms, or taxa in evolutionary stasis within the assumed clade, where individual members subsequently appearing and disappearing without inter links. These intervals might be estimated up to several hundred thousand years according to rather stable accumulation rate in the middle Lochkovian carbonates of the Požáry Quarries. The common characters that have taxa *L. carlsi* and *L. omus* beta with early members of *Lanea* are considered herein to be more significant than those with *Ancyrodelloides*. Although, there is some variability, the pattern of denticulation of the blade in *L. carlsi* is almost identical with that of. *L. omoalpha*. Denticles in *L. carlsi* at the posterior blade are just a little smaller than the ones at the anterior, which are palisade and form an incipient cockscomb, a cusp that is less developed and not well recognizable in the area above the basal cavity where smaller denticles proceed towards anterior. The basal cavity is completely opened and unrestricted with basal grooves showing no difference from that of *Lanea*. The basal lobes in *L. carlsi* are, however, distinctly asymmetrical, more than those of *L. omoalpha*. The terraces on the lobes are well developed and the brim is large and wide. All these characters can be seen on Fig. 3. According to original diagnosis of the genus *Lanea*, the platform lobes are "normally unornamented" (Murphy and Valenzuela-Ríos 1999: 326). The presence of distinct ornamentation on the terraces above the basal platform lobes seems to be the only marked difference of taxa *carlsi* and *L. omus* beta from other *Lanea* members. The generic assignment of taxon *L. carlsi* to *Lanea* supports also the similarity of apparatuses mentioned in the systematic part, as well as the described stratigraphic succession in regions with well developed Lochkovian conodont stratigraphy (Nevada, Pyrenees, Carnic Alps, and Barrandian).

A very important morphological innovation suddenly appears in the *Lanea* clade; the characteristic ornamentation of the upper surface of the outer lateral basal lobe in taxon *L. carlsi* is undoubtedly also a conspicuous stratigraphic and correlation mark. In the subdivision of the Lochkovian by Valenzuela-Ríos and Murphy (1997), the middle Lochkovian starts with the appearance of *A. omus* alpha (= *Lanea omoalpha* Murphy and Valenzuela-Ríos, 1999). Although this taxon is well characterized, it is not probably the most diagnostic marker for the lower/middle Lochkovian boundary, particularly if there might be a possibility of a better alternative. The taxon *L. omoalpha* was described as the earliest member of the *Lanea* clade. According to Murphy and Valenzuela-Ríos (1999) the genus *Lanea* is considered a successor of the "*eosteinhornensis* group of taxa", that was later assigned to the "new genus *W*" (Murphy et al. 2004). The origin of *L. omoalpha* in the Pyrenees is not clear because it is either recorded at the first bed with conodonts in the section (Segre 1, Valenzuela-Ríos 2002) or it is obscured by lithology (Gerri 1.1, 1.2, Valenzuela-Ríos 1994). In Nevada the taxon is well documented in several sections (Murphy and Matti 1983: tables 1–3) with a large overlap of forms, in that time named as "*Ozarkodina remscheidensis*". The range of the entire *Lanea* clade is well-controlled stratigraphically in the Simpson Park Range VII Section where it is delimited also by cosmopolitan graptolites (Murphy and Valenzuela-Ríos 1999: 325). In my opinion the taxon *L. carlsi* is probably also present there (cf. figured specimen of Murphy and Matti 1983: pl. 2: 13, 15, 17).

To locate precisely the origin of *Lanea omoalpha* in the Požáry sections is, however, difficult due to many intermediate forms ("pre-*Lanea*", mentioned above). According to experience from Požáry Quarries, the same situation, with an abundance of earlier transitional forms that are not unambiguously distinguishable from *L. omoalpha* sensu stricto might also occur in other regions like Nevada or Pyrenees. These intermediate forms may thus preclude the precision of placement of the intra-stage boundary. The authors of the genus *Lanea* have also mentioned the problems of distinguishing the early members of a clade from their closest ancestors. Therefore, in spite of the very good stratigraphic control of the *Lanea* range in Nevada, the precise recognition of the base of the middle Lochkovian, by the entry of its earliest representative (*L. omoalpha*), can still be difficult worldwide. On the other hand the distinct morphological change in the early part of the range of *Lanea* (just represented by taxon *L. carlsi*) seems to be more eligible for the approximation of the middle Lochkovian base.

Taxon *Lanea carlsi* has a relatively short range and is easily distinguishable in many regions. Besides European regions like the Pyrenees, Frankenwald, Carnic Alps, Eastern Iberian Chains, and Barrandian; it has also been recorded in the middle Lochkovian of Western Bulgaria (the Gorna Vrabcha sections, Boncheva et al. 2007). It occurs in similar association in the Pyrenees and Frankenwald (e.g., with *Icriodus angustoides bidentatus*) close to the base of *Monograptus hercynicus* Graptolite Zone (Boncheva et al. 2007: fig. 2). The taxon *L. carlsi* has been formerly reported from the Barrandian by Schönlaub (in Chlupáč et al. 1980: pl. 20: 15–20) who found several specimens in the tectonically disturbed section U topolů in the *Monograptus hercynicus*

Zone; the big part of stratigraphic succession in this folded section is, however, largely disturbed (see Vacek 2007) and therefore not recommended for stratigraphic correlation, regardless of occurrence of many important taxa. In addition to the described conodont succession, the stratigraphic control of the *L. carlsi* range in the Požáry sections in the Barrandian area is underpinned by entry of the earliest dacryoconarids. The embryonal bulbs of *Homoctenowakia senex* Alberti, 1983 were recorded in the middle of the range of the taxon in the Požár-1–2 section. In the Požár-3, dacryoconarids were recorded at the corresponding position (30 m above the base of the section). Lukeš (1991) described the earliest dacryoconarid faunas from the Lochkov Formation in the section Radotín Valley that co-occur with *Monograptus hercynicus*. *Homoctenowakia senex* was recorded, however, close above the tectonic distrbance in the section. Accordingly it is not possible to detect in which part of the *M. hercynicus* range this oldest dacryoconarid enters. In the Carnic Alps the faunal successions are almost identical with those in the Barrandian. In the section Oberbuchach II (Schönlaub 1985: fig. 2) *L. carlsi* (described therein as "*Ozarkodina masara*") co-occurs with "*Pandorinellina optima*" in the lower part of the *M. hercynicus* Zone and marks also a conspicuous facies change that is also characterized by the onset of dacryoconarids that start to dominate at this level (Schönlaub 1985: 355). A very reliable stratigraphic alignment of *L. carlsi* can be seen also in the Eastern Iberian Chains, Celtiberia where this taxon was found at the base of d1c-gamma (top of Luesma Formation) (e.g., Carls 1987, 1999). Above this record of *L. carlsi* which co-occurrs with *Icriodus transiens* Carls and Gandl, 1969 is about 45 m of middle and upper Lochkovian sediments (Nogueras Formation). According to Carls and Valenzuela-Ríos (2002), above the record of *L. carlsi* is a well-described succession of brachiopods and trilobites. According to Carls (1999) a typical middle Lochkovian marker, *Acastella tiro* Trilobite Zone starts 1 m above this only find of *L. carlsi* in the d1c-gamma, and the range of this trilobite zone practically overlaps with the middle Lochkovian in the sense of Valenzuela-Ríos and Murphy (1997).

Conclusions

To conclude, this alternative hypothesis of the relationship of *Ancyrodelloides* and *Lanea* lineages follows the original concept of these genera by Murphy and Valenzuela-Ríos (1999) but differs in regard to the origin of *Ancyrodelloides* and corresponding generic assignment of some early middle Lochkovian taxa. In this paper the origin of *Ancyrodelloides* is suggested in the late middle Lochkovian and characterized by the entry of *A. transitans*, which has a distinctly restricted basal cavity, almost identically developed in *L. eleanorae*. *Ancyrodelloides* as a separate clade split off from the *Lanea* clade probably close the level of origin of *L. eleanorae*. The partly coeval taxa *A. transitans* and *L. eleanorae* share some similarities as may be expected close above the branching point (in this case the common characters are, e.g., general robustness of the Pa and Pb elements, similar pattern of denticulation and restriction of the basal cavity). The relatively short-lived genus *Anycrodelloides* includes *A. asymmetricus* Bischoff and Sannemann, 1958, that follows *A. transitans* and completely disappears soon after the radiation close to the end of the middle Lochkovian. That radiation gave rise to *A. trigonicus* and *A. kutscheri* in association with their numerous coeval variants (mostly described as new taxa—e.g., *A. cruzae* Valenzuela-Ríos, 1994, *A. murphyi* Valenzuela-Ríos, 1994, *A. sequeirosi* Valenzuela-Ríos, 1999). The time of *Ancyrodelloides* is also characterized by the appearance of probably the very short-lived clade of *Kimognathus* Mashkova, 1978. According to the classification of Murphy and Valenzuela-Ríos (1999) this Lochkovian genus is represented by *K. delta* Klapper and Murphy, 1974 (Nevada, Klapper and Murphy 1974; Murphy and Matti 1983), *K. limbacarinatus* Murphy and Matti, 1983 (Nevada: Murphy and Matti 1983; Pyrenees: Valenzuela-Ríos 1994; Barrandian: the taxon has been recorded in the upper part of the Lochkov Formation in the Požár-3 section) and *K. alexei* Mashkova, 1978 (Urals: Mashkova 1978; NSW: Australia, Wilson 1989). Following the data by Murphy and Valenzuela-Ríos (1999) the *Lanea* lineage terminated within the *Ancyrodelloides* range. The genus is then probably replaced by the *Masaraella pandora* lineage that is characterized by slender Pa elements, repeated complete opening of the basal cavity, disappearance of terraces and re-appearance of ornamentation of the basal platform lobes. This alternative and modified concept of the origin of the genus *Ancyrodelloides* and its relation to *Lanea* is evidently only hypothetical and suffers with insufficiency of material that would be necessary for its testing e.g., by morphometric studies that were successfully applied to other early Devonian taxa (e.g., Murphy and Cebecioglu 1984; Murphy and Springer 1989; Roopnarine et al. 2004). The possible availability of more material and future apparatus reconstructions of bigger number of Lochkovian taxa will, however, help succeeding conodont workers to verify or refuse these concepts.

To summarize the stratigraphic information—probably the oldest dacryoconarids were recorded in the Barrandian and Carnic Alps within the short range of *Lanea carlsi* that enters in the lower part of the *Monograptus hercynicus* Graptolite Zone (recorded e.g., in the middle part of the Lochkovian successions in Barrandian, Carnic Alps, and West Bulgaria). *L. carlsi* occurs just below the middle Lochkovian *Acastela tiro* Trilobite Zone (in the Eastern Iberian Chains). The taxon appears in the early part of the *Lanea* lineage and its entry is close to the entry of *L. omoalpha* which is probably a little older. The *Lanea* lineage starts in the early Lochkovian. The stratigraphic position of *L. carlsi* among other conodont taxa and its correlation with available data about dacryoconarids, graptolites and trilobites qualifies this morphologically expressive conodont taxon as the most eligible marker for the base of the middle Lochkovian.

Systematic paleontology

The terminology for description of platform elements is adopted from Murphy and Valenzuela-Ríos (1999) who proposed an elaborated and extended descriptive nomenclature in connection to introduction of their new genus *Lanea*.

Phylum Chordata Bateson, 1886

Class Conodonta Pander, 1856

Order Ozarkodinida Dzik, 1976

Family Spathognathodontidae Hass, 1959

Genus *Lanea* Murphy and Valenzuela-Ríos, 1999

Type species: *Ozarkodina eleanorae* Lane and Ormiston, 1979, Salmontrout River Area, East-Central Alaska, Lochkovian.

Remarks.—Murphy and Valenzuela-Ríos (1999) proposed this genus based on recurrent characteristics in several species of the middle Lochkovian Spathognathodontidae. Although the overall characteristic of their new genus is robust, the authors admitted that at the dawn of the *Lanea* clade, its early members show similarities to coeval taxa. The genus *Lanea* in the sense of this paper is extended to include *Lanea carlsi* (Boersma, 1973) and "*Lanea omus* beta" Murphy and Matti, 1983. As was mentioned above, the main reason for generic relocation of these taxa is their stronger similarity with the *Lanea* clade, showing more common characters than with *Ancyrodelloides*. Most of the typical features in Pa element of *L. carlsi* are identical with the coeval *L. omoalpha*. The characteristics of the apparatus described below and its differences from the assumed apparatus of *A. transitans* support the modified taxonomical concept of both genera. The distinct morphological changes are well expressed in both apparatuses in spite of their relative stratigraphic proximity in the section. The suggested stratigraphic succession of the taxa in the *Lanea* clade is follows: *L. omoalpha, L. carlsi, L. eoeleanorae* + "*L. omus* beta", *L. eleanorae*, *L. telleri*.

Lanea carlsi (Boersma, 1973)

Figs. 3–8.

1958 *Spathognathodus steinhornensis* Ziegler; Bischoff and Sannemann 1958: 106, pl. 13: 3, 7, 9.

1969 *Spathognathodus* cf. *asymmetricus* Bischoff and Sannemann; Carls and Gandl 1969: 197, pl. 19: 1.

1973 *Spathognathodus carlsi* sp. nov.; Boersma 1973: 289–290, pls. 3: 1–6, 4: 1–9.

1980 *Ozarkodina masara* Murphy, Matti, and Walliser, 1981 (beta morphotype); Schönlaub 1980: pls. 2: 10, 16, 17; 3: 24–30; 7: 3.

1980 *Ozarkodina masara* Murphy, Matti, and Walliser, 1981 (beta morphotype); Chlupáč et al. 1980: pl. 20: 15–20.

?1983 *Ancyrodelloides omus* sp. nov.–*A. transitans*; Murphy and Matti 1983 (imprint 1982): pl. 2: 13, 15, 17.

1994 *Ozarkodina carlsi* (Boersma); Valenzuela-Ríos 1994: pls. 1: 19; 3: 3, 9, 10, 14.

2007 *Ozarkodina masara* Schönlaub; Boncheva et al. 2007: fig. 5L.

Material.—12 Pa, 7 Pb, 5 M, 5 Sa, 4 Sb, 7 Sc, and 28 fragments of diverse elements were obtained from sample 4Po22; 2 Pa elements from sample 4Po32 (both samples are from Požár-3 section, Požáry Quarries near Řeporyje, Czech Republic). All figured and supplementary specimens (40 specimens) are catalogued and deposited in the National Museum Prague, Czech Republic under catalogue numbers: NM L40532–40571. All figured specimens are from sample 4Po22.

Pa element (diagnostic)

Fig. 3.

Original diagnosis.—A species of *Spathognathodus* with broadly flaring lips of the basal cavity. The inner lip is rounded and unornamented in upper view. The outer lip is slender, ornamented at the upper side with 1–3 thick denticles, and roughly perpendicular to the blade (from Boersma 1973).

Emended diagnosis.—A species of *Lanea* with weakly developed terraces on basal platform lobes. The basal cavity is shallow, strongly asymmetrical and unrestricted. The outer platform lobe is considerably larger than the inner one and its upper side is ornamented with 1 to 3 nodes interconnected with the cusp by a faint ridge.

Description.—The emended diagnosis has been added in order to refine the distinction by listing few more clearly observable characters of this taxon of *Lanea*. Boersma (1973) provided a very precise description of Pa elements in his material from Bahent locality. An even more detailed description of the material from the same area was later made by Valenzuela-Ríos (1994). Even though these descriptions are exhaustive, just a few observations of the material from the Požáry Quarries are given in this chapter using terminology which complies with the *Lanea* nomenclature of Murphy and Valenzuela-Ríos (1999: text-fig. 2).

The blade is often distinctly inclined at the posterior end, both in juvenile and adult specimens. The entire length of the Pa element (the main axis) varies from 0.4 mm in juvenile specimens up to 1.3 mm in adult specimens. The posterior part of the blade is much shorter than the anterior part and forms approximately 1/3 of the whole unit. Denticles on the blade are lenticular in cross section, stout or even triangular or palisade in lateral view; they are closely arranged, usually not too deeply inserted into the blade. The number of denticles depends on the ontogeny but mostly fluctuates from 12 to 17. The anterior 2–4 denticles are higher than the ones in the middle part of the blade and form an incipient fan-structure. The cusp located right above the basal pit is not always distinct; the denticles on the anterior blade between cusp and fan (cockscomb) are markedly smaller and irregular in size. The basal cavity is completely open and shallow, anterior basal groove is opened along the entire length of the anterior blade, it is deep, narrow and appressed close to anterior end. Posterior basal groove is also opened, and like in *L. omoalpha* tapers to the posteriormost point of the blade. It is medium deep, but gradually shallows towards the posterior end. The platform lobes are strongly asymmetrical; the outer lobe is larger than the inner lobe, sub-quadrate to round and expanded perpendicularly to the blade or slightly to the ante-

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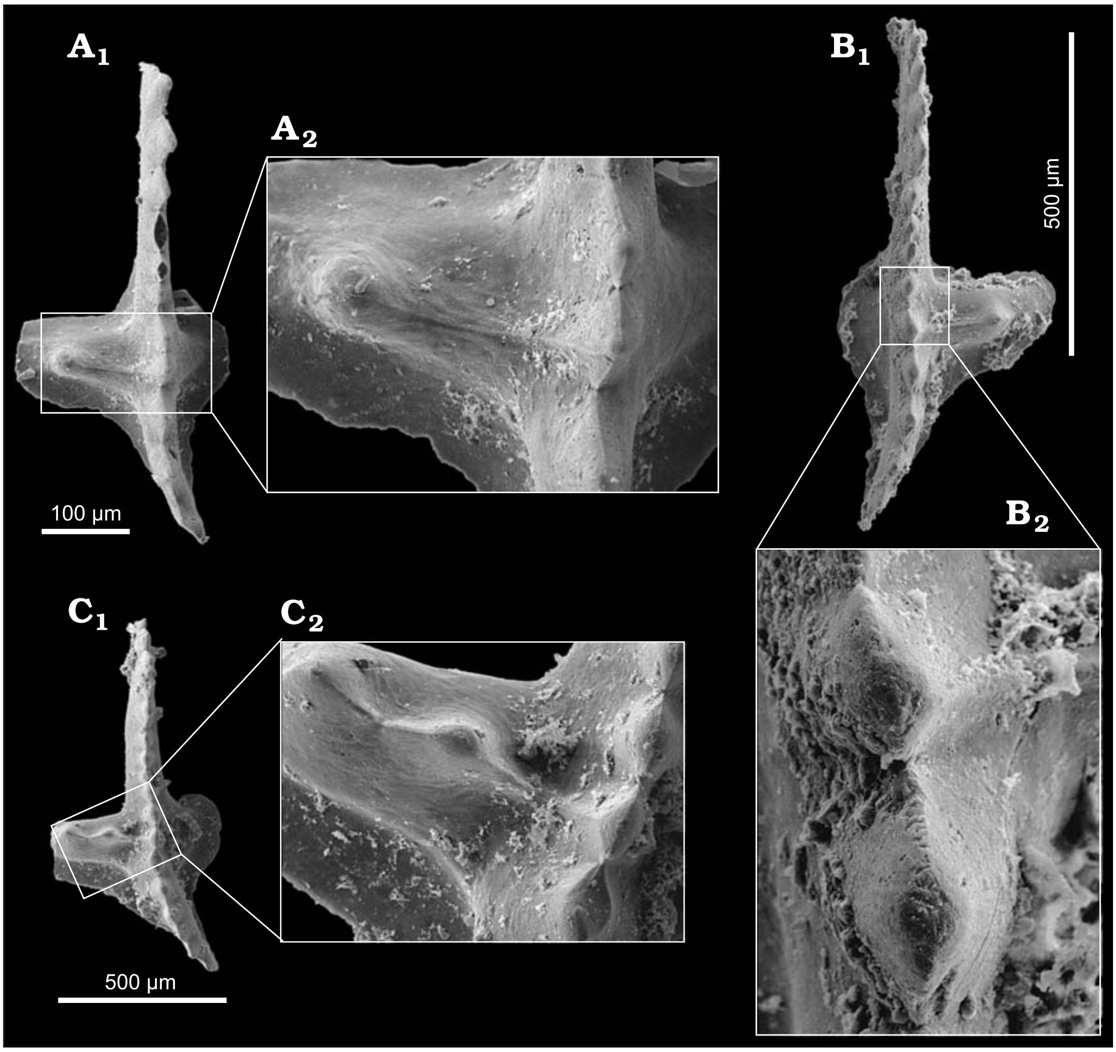

Fig. 3. SEM photographs of Pa elements of spathognathodontid conodont *Lanea carlsi* (Boersma, 1973). **A**. NM L40532, upper view (A_1), detail of the platform lobe denticulation (A_2), the terrace on platform lobe with single node connected by ridge with cusp. **B**. NM L40533, upper view (B_1), detail of the cusp and neighboring denticle (B_2). **C**. NM L40534, upper view (C_1), detail of the ornamentation of the outer platform lobe (C_2). All figured specimens are from sample 4Po22.

rior. Brim and terrace are distinctly developed, the angle between the surface of the terrace and the brim is obtuse. The brim is narrower than the terrace as in other early *Lanea* species, brim sulcus is not developed. The terrace occupies less than 50% of platform lobe area and is equipped with 1–3 denticles which are elliptical to oval in cross-section. They are interconnected by a faint ridge that connects this ornamentation with cusp. In adult specimens these denticles are the same height as the cusp. The inner platform lobe is smaller, semicircular, unornamented and terraced. The terrace occupies usually 30% of the area of the inner lobe.

Remarks.—The above described characters of the platform element of *L. carlsi* point to a great similarity with *Lanea omoalpha*, from which differs practically only by the presence of ornamentation on one platform lobe and by increased irregularity of the lobes. The other slight differences (e.g., inclination of posterior blade, variation in denticulation and size of platform lobes) are relatively so inconspicuous that would be ordinarily regarded as variability (which is relatively high) in *Lanea omoalpha*. Degree of similarity in these taxa is probably at the same level or even higher than in some coeval taxa of *Ancyrodelloides* (e.g., *A. kutscheri* versus *A. transitans*). *L. carlsi* differs from its possible immediate successor—*L. omus* beta by stronger inclination of posterior blade, increased asymmetry of platform lobes and by absence of denticulation of inner lateral lobe in all cases.

Pb element

Fig. 4.

These pectiniform elements resemble to Pb elements of *Zieglerodina* figured by Murphy et al. (2004: figs. 2-42, 3-29). The entire unit in lower view is often S-shaped and slender. Both anterior and posterior branches are slender, of compressed lenticular shape in cross-section without any development of ledges below denticles. Although denticulation show variability, in adult specimens the number of needle-like

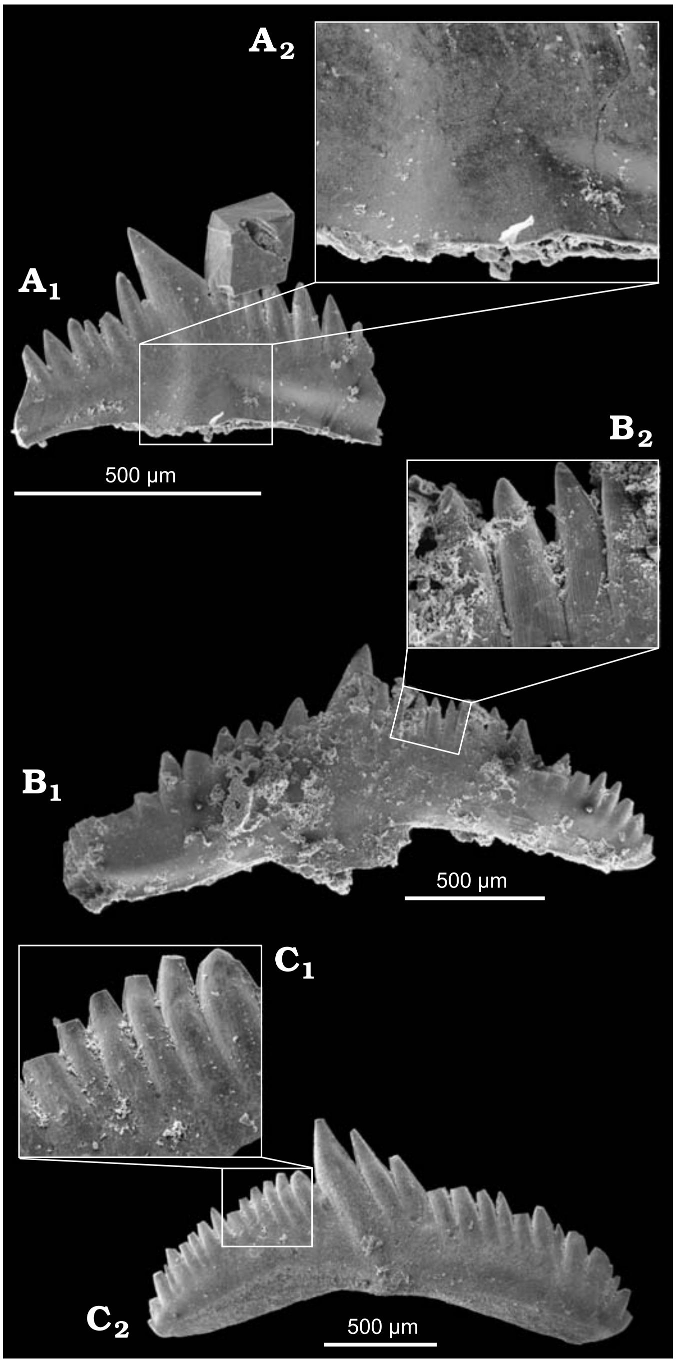

Fig. 4. SEM photographs of Pb elements of spathognathodontid conodont *Lanea carlsi* (Boersma, 1973). **A**. NM L40535, incomplete element, inner lateral view (A_1), detail of the basal area (A_2). **B**. NM L40536, adult element, outer lateral view (B_1), detail of denticles on posterior blade (B_2). **C**. NM L40537, detail of denticulation on posterior blade (C_1), outer lateral view (C_2). All figured specimens are from sample 4Po22.

denticles is relatively high (up to 18 on the posterior blade, up to 15 on the anterior blade). The denticles in the anterior are normally seemingly larger and less numerous than the posterior ones. The cusp is robust, stout and deeply inserted to the blade and strongly inclined posteriorly. The angle between the line segment connecting extreme points at the lower margin with axis of the cusp is up to 50°. The blade is very high from lateral view. Denticles including their insertion into the blade form usually around 1/3 of the total height of the blade in the middle areas of the anterior and posterior blade. This character differs from Pb of *Zieglerodina*, where this proportion is different—denticles are much higher, reaching half of total height of branch or even more. The pinch zone close to the lower margin is very high and may extend up to 1/3 of the total height of the posterior blade. The lower margin is regularly curved in lateral view. Basal cavity is small (approximately 1/5 of the entire lower margin length) and shallow.

Specimens of possible *Ancyrodelloides* apparatus were found in several samples in the section Požár-3, from 52 m to 69 m above the base of the section. In this interval, no Pa elements of *Lanea* were found, but *A. transitans* abounds at the 52 m. The Pb elements from this level strongly differ from the ones of *L. carlsi*: they have extremely inflated blades forming wide benches of the platform in upper view. They may almost reach the proportion of the platform in some Pa elements of *A. transitans*, where denticles occupy less than one third of the entire platform surface. The platform lobe of almost triangular shape protrudes in inner side and is slightly directed anteriorly (at angle around 80°). The whole unit is slightly curved and the inflated blades are wider than higher (irrespective denticles) and oval to sub-angulate in cross-section. In lateral view, denticles are in general higher than the remaining basal part. The basal cavity is deep and larger than in *Lanea carlsi*. Similar Pb elements figured Lane and Ormiston (1979: pl. 1: 47) from Salmontrout (Alaska) and Murphy and Matti (1983: pl. 3: 21–24) from Nevada. These specimens in samples co-occur with Pa elements of *A. transitans*, *A. kutscheri*, *A. trigonicus*, and *L. eleanorae*. Although the apparatus of *Ancyrodelloides* has not yet been completely reconstructed, these specimens most probably belong to its apparatus. The specimens from Požár-3 section that probably belong to *A. transitans* differ from those mentioned above by having more inflated blade (wider benches) and larger lateral lobe. The Pb elements figured by Murphy and Matti (1983: pl. 4: 1–3) probably belong to late members of *Lanea* (*L. eleanorae*); they differ from the assumed Pb elements of *A. transitans* from the Požár-3 section by having more symmetrical basal cavity, two equal lateral lobes and less developed benches that are in much lower position below denticles in lateral view.

Sa element

Fig. 5.

The two specimens figured (Fig. 5A, B) are typical representatives of the Sa element of *L. carlsi* in the material. The branches are relatively low with denticles alternating in size and form an angle of 110–120°. The cusp is stout and triangular close to tip in cross section. The basal cavity below the cusp is small and shallow; it slightly ascends along the cusp and passing into faint ridge that continues along the inner side of the cusp. In outer side, the basal area of the cusp is concave.

The specimens are superficially a little similar to those of *Zieglerodina* sp. figured by Murphy et al. (2004: fig. 3: 30,

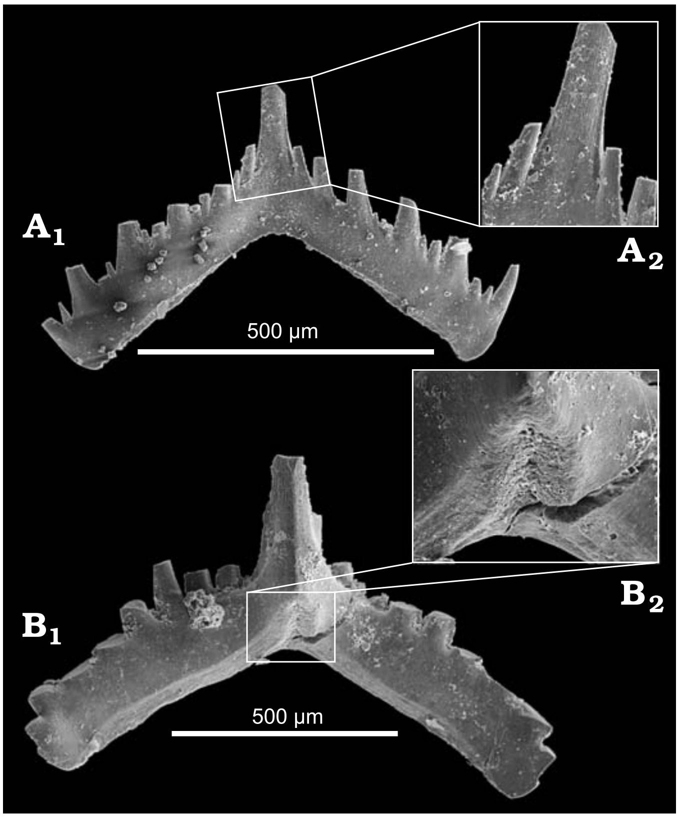

Fig. 5. SEM photographs of Sa elements of spathognathodontid conodont *Lanea carlsi* (Boersma, 1973). **A**. NM L40540, complete element, anterior view (A_1) , detail of cusp area (A_2). **B**. NM L40541, posterior view (B_1), detail of basal cavity (B_2). All figured specimens are from sample 4Po22.

31), but the specimens of *L. carlsi* are more robust and the angle between branches is markedly more obtuse. In the sample (at 52 m) with possible *Ancyrodelloides transitans* apparatus were found distinctly different Sa elements from *L. carlsi*. The angle between the branches ranges 90–100°, the basal cavity is deeper and shortly extends laterally into appressed grooves that are closed near the basal cavity. In inner view the basal cavity does not ascend along the cusp which is strongly projected out from the blade towards the inner side in upper view. In lateral view it seems to be somehow separated from the blade. In outer lateral view, the basal area of the cusp is flat. The blades are markedly inflated, not flat like in *L. carlsi*.

Sb element

Fig. 6.

Although the figured elements (Fig. 6) have broken denticles, in general the anterior branch shows higher irregularity in denticle size than the posterior branch which bears three big and strongly posteriorly inclined denticles forming a fan-structure. The branches are relatively low and flat, they form an angle 140–150° in lateral view; in upper view the extreme parts of processes are deflected inward. The basal cavity is deep, rounded to sub-rectangular in lower view, no open grooves are developed. The basal part of the cusp from outer lateral view is slightly concave; the cusp is semicircular in cross section (cf. Fig. 6A_1).

At the level 55 m above the base of Požár-3 section several incomplete Sb elements were found in association with *A. transitans* and *Wurmiella*. The Sb elements have many identical characters with the other transition series elements of *A. transitans* mentioned above (e.g., inflated blade and sharper angle between the processes). Due to breakage and scarcity of material, it is not possible to generalize other characteristics, but the difference from the Sb elements of *L. carlsi* is evident.

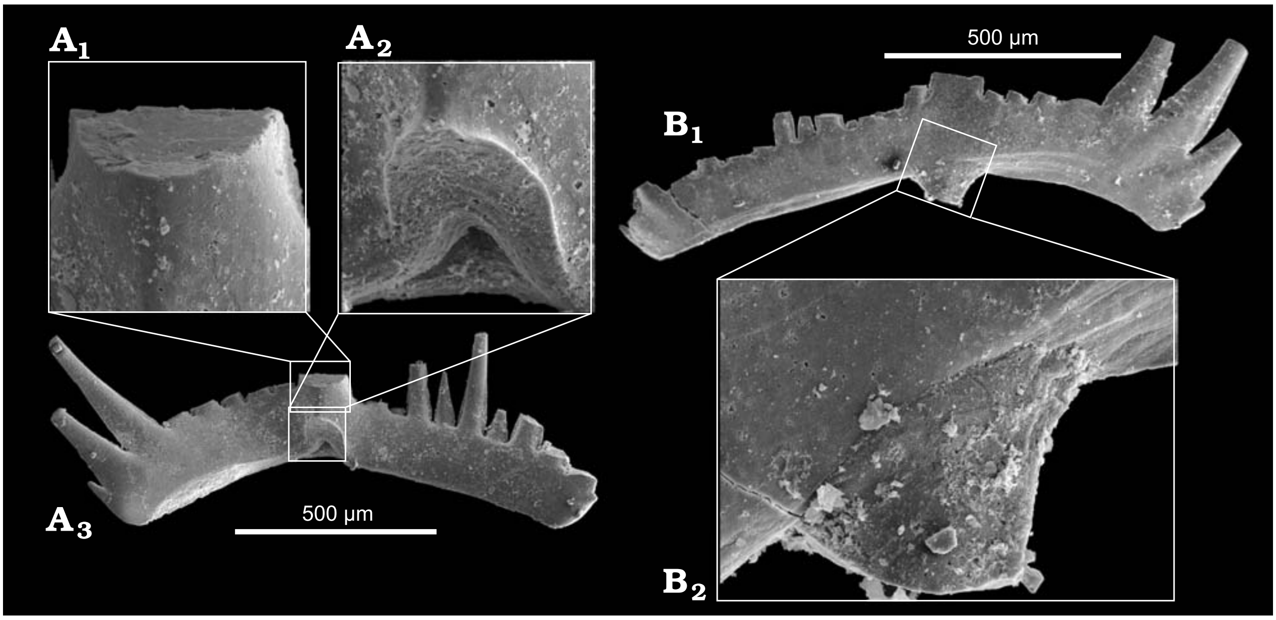

Fig. 6. SEM photographs of Sb elements of spathognathodontid conodont *Lanea carlsi* (Boersma, 1973). **A**. NM L40542, detail of cusp in cross section (A_1), detail of basal cavity (A_2), inner lateral view (A_3). **B**. NM L40543, outer lateral view (B_1), detail of basal area (B_2). All figured specimens are from sample 4Po22.

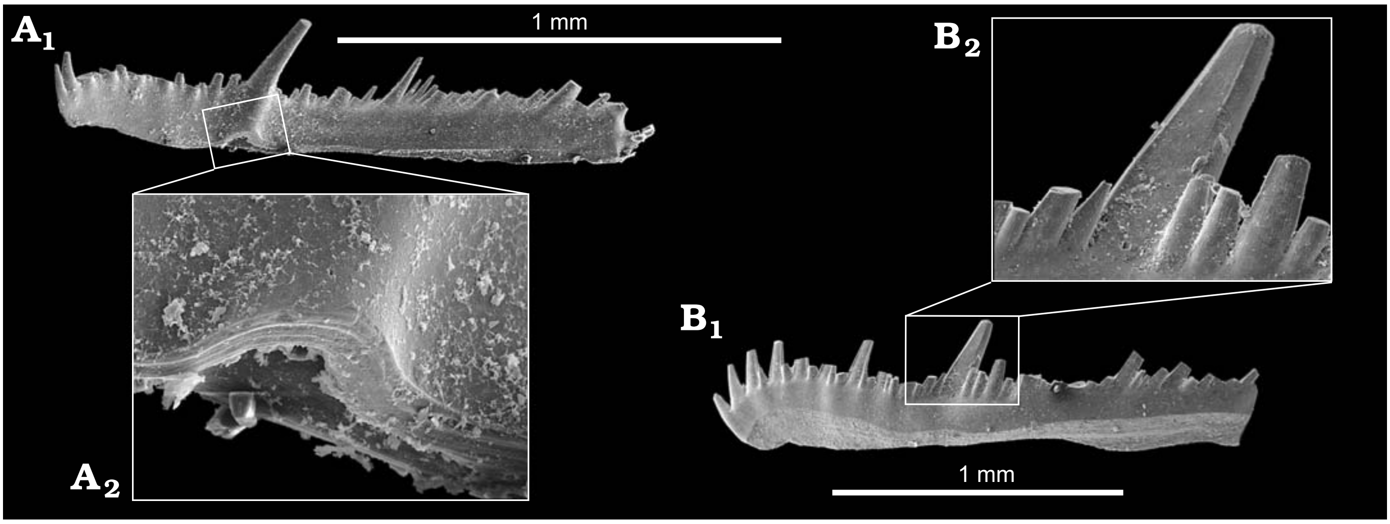

Fig. 7. SEM photographs of Sc elements of spathognathodontid conodont *Lanea carlsi* (Boersma, 1973). **A**. NM L40544, inner lateral view (A_1), detail of basal cavity (A_2). **B**. NM L40545, outer lateral view (B_1), detail of cusp area (B_2). All figured specimens are from sample 4Po22.

Sc element

Fig. 7.

The Sc elements are probably twice as long as Pa elements, they are strongly curved in upper view; both processes are forming an angle of 140°. The branches are medium high in lateral view. The posterior branch bears bigger number (up to 30) of denticles, strongly alternating in size, than the anterior branch (up to 15 denticles). The anterior-most 3 or 4 denticles at the end of the anterior blade form a fan. The lower margin in lateral view is straight; the posterior branch may be slightly undulated. Branches are flat and thin as in other ramiform elements of the *L. carlsi* apparatus, without inflations or ledges below denticles. The cusp is strongly inclined posteriorly and slightly curved backwards, semicircular to circular in cross section; it is somewhat stepping out from array of denticles (see the detail on Fig. 7B_2).

The general habitus is very close to Sc element of *Zieglerodina* (cf. Murphy et al. 2004: fig. 3-40) but variation in denticle sizes is more irregular, not reaching rhythmicity or more regular alternation of denticle sizes like in typical *Zieglerodina*. The only two badly preserved Sc elements found in the sample from the level 60 m above the base of the Požár-3 section (in association with only Pa elements of *A. transitans*) show conspicuous inflation of the blade which has also lower profile in lateral view.

M element

Fig. 8.

The M elements of *L. carlsi* are characterized by irregular denticulation and by development of stout cusp which is semicircular to sub-triangular in cross section. The cusp bears a faint ridge in area close to the basal cavity in inner lateral view (see Fig. 8). This ridge may form a sharp edge of the cusp. The cusp does not terminate at the anterior of the element, but is accompanied by 1 to 3 denticles that form incipient anterior process. The blade is medium high, flat and regularly arched. The number of denticles on the posterior process may reach 22. The basal cavity is small and almost triangular in shape.

The only one complete M element that possibly belongs to *A. transitans* was found at the same sample as the other mentioned ramiforms in the Požár-3 section. It strongly differs from the M element of *L. carlsi* by typical thickening (inflation) of the posterior process, more regular denticulation and larger and deeper basal cavity that continues shortly as a groove towards posterior. The basal cavity of this specimen is widely open below the cusp and forms small but distinctly developed lateral lobe in the inner lateral side.

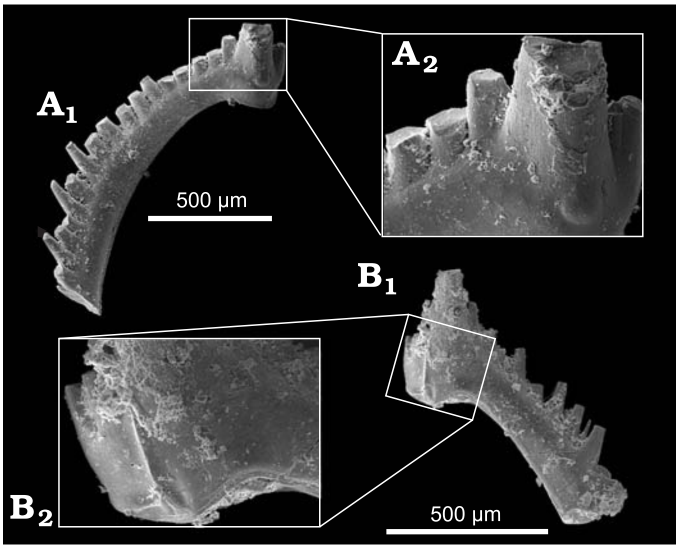

Fig. 8. SEM photographs of M elements of spathognathodontid conodont *Lanea carlsi* (Boersma, 1973). **A**. NM L40538, incomplete element, inner lateral view (A_1) detail of broken cusp (A_2). **B**. NM L40539, inner lateral view (B_1), detail of basal area with ridge (B_2). All figured specimens are from sample 4Po22.

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