SOME LATE EO- AND MESOTRIASSIC CONODONT-MULTI-ELEMENTS: NOTES ON THEIR TAXONOMY, PHYLOGENY AND DISTRIBUTION

BY

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RÉSUMÉ

L'étude comparative d'assemblages de conodontes d'âge Eotriasique supérieur et Mésotriasique d'Amérique du Nord et de la région circumméditerranéenne, indique que ces assemblages peuvent être dérivés de deux souches: ellisoniide et xaniognathide. La distribution paléogéographique des multi-éléments naturels était contrôlée par des facteurs paléo-écologiques en relation avec la nature de leurs habitats: néritique, épi- et mésopélagiques.

ABSTRACT

Comparative study of late Eotriassic and Mesotriassic conodont assemblages from North America and the circum-mediterranean region, indicates their derivation from two major stocks: ellisoniid and xaniognathid. The paleogeographic distribution of these groups was probably controlled by paleoecologic factors relating to their habitat.

INTRODUCTION

Described conodont-collections of Late Early and Middle Triassic age from the circummediterranean realm are compared with material from the North American Great Basin and adjacent cratonic margin (Collection J. W. Collinson, O.S.U., Columbus, Ohio).

A multi-element approach is used to revise some earlier conclusions concerning their age and taxonomic classification.

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MULTI ELEMENT TAXONOMY AND PHYLOGENY

Unlike form-taxonomy, which considers the morphology of single elements and their derivation from earlier appearing single elements, multi-element taxonomy attempts to reconstruct the original apparatus by assembling individual elements within natural units that have been derived, as a whole from earlier units. P elements are considered to have been rapidly evolving parts of an apparatus whose other elements were evolving slowly. The latter elements represent a control module that may be useful in working out the phylogeny of evolving species and arranging them within natural genera and suprageneric taxa. Therefore a natural subdivision of conodont-elements within suprageneric, generic and specific categories depends not only on the ultrastructure of single elements, but also on the morphology of multi-elements as units and their geographic and stratigraphic distribution.

1. THE ELLISONIID — DERIVED STOCK

Genus *Ellisonia* MÜLLER, 1956; emend. SWEET, 1970.
Generotype: *Ellisonia triassica* MÜLLER, 1956.
Plate I, Fig. 7-10.

Sweet (1970) has erected the first Triassic multielement taxon *Ellisonia*. Later publications by the same author show the development of his thinking with the separation of elements, earlier described as belonging to multielements of *Ellisonia* by their assignment to the genera *Hindeodus* and *Ellisonia* (Sweet, 1977, in Catalogue of Conodonts).

The apparatus of *Ellisonia* is composed of 6 elements in the following positions (Croft, J. S., 1978, unpubl. M.S.; Sweet, in Treatise of Invertebrate Paleontology, part W, in press): Pa (Xaniognathid), Pb (Lonchodinid), M (Lonchodinid), Sa (Hibbardellid), Sb and Sc (Hindeodellid). (Nomenclatory system after Sweet and Schoenlaub, 1975). White matter varies strongly.

Distribution : Upper Carboniferous — Triassic, Worldwide.

Genus *Furnishius* CLARK, 1959.
Generotype: *Furnishius trisseratus* CLARK, 1959.

Plate I, Fig. 1-6.

The apparatus of this genus has been reconstructed by Sweet (Treatise, in press) and is similar to that of *Ellisonia* with the exception of its Pa element. White matter varies strongly.

Distribution : N. America and Malaysia, Smithian.

Genus *Pachycladina* STAESCHE, 1964.
Generotype: *Pachycladina obliqua* STAESCHE, 1964.

The apparatus of *Pachycladina obliqua* consists of a xaniognathid Pa element *(inclinata)*, a lonchodinid M element *(obliqua)*, and Sa, Sb and Sc elements (resp. *tricuspidata, symmetrica* and *longispinosa*). Hyaline elements dominant.

Distribution : Spathian, Europe, Middle East.

Remark : Sa-Sb elements found in N.America (Mosher, 1973) and described as *Pachycladina* are homeomorphs that possibly belong to the apparatus of *Furnishius*. An entire apparatus of *Pachycladina* has never been encountered in this realm.

Genus *Hadrodontina* STAESCHE, 1964.
Generotype *Hadrodontina anceps* STAESCHE, 1964.

Hadrodontina anceps has a xaniognathid Pa element *(biserialis)* with a double row of denticles on the carina, the M element *(anceps)* and Sa element *(adunca)* are lonchodinid, the Sb element is hindeodellid. Distribution of *H. anceps* is the Spathian of Europe and the Middle East. Albid elements dominant.

Hadrodontina aequabilis has a xaniognathid Pa element and a lonchodinid M or Sa element. Distribution: ? late Dienerian- Smithian in Europe.

Genus *Parachirognathus* CLARK, 1959.
Generotype: *Parachirognathus ethingtoni* CLARK, 1959.
Plate I, Fig. 11-13.

Only 2 elements, one alate (Sa) and another hindeodellid (Sc).
Unit is palmate, no discrete denticles developed. All elements are hyaline, fibrous-like in structure.

Distribution : Smithian of N. America.

Remark : Specimens described as *P. geiseri* by Staesche (1964, p. 285) from Italy lack the fibrous structure of the N. American species, as well as their palmate shape.

DISCUSSION OF THE STRUCTURE AND DISTRIBUTION OF ELLISONIID GENERA

Comparing the ultrastructure of the elements of genera *Ellisonia, Furnishius* and *Parachirognathus* with that of the genera *Hadrodontina* and *Pachycladina* reveals that the lamellar structure, well visible in hyaline elements (*Pachycladina* and *Parachirognathus*) and obliterated in albid elements (*Hadrodontina* and *Ellisonia*) are a

less exclusive generic character than as evaluated in the past by Staesche (1964) and Hirsch (1975). Several hyaline to albid specimens have been observed within the apparatus of *Ellisonia* and *Furnishius*, indicating variability in the distribution of white matter. The ratio of white matter within a unit was probably controlled by paleoecological factors that affected rather shallow marginal waters more than open seas, from which conodonts show more constant distribution of white matter.

Clark and Rosser (1976) emphasize the high energy environment in which *Furnishius* is believed to prevail, whereas Collinson and Hasenmueller (1978) made the observation that *Furnishius* is more likely to occur in dark-gray fossiliferous limestones, that are believed to indicate open-marine conditions, and that *Parachirognathus* occurs in yellowish-gray silty limestone representing very shallow water, possibly with restricted circulation.

Evidence of the concurrent range of species of *Platyvillosus* and *Neospathodus* in N.America, Europe and Asia led to the conclusion that a so-called "cousinage" (sensu Sweet, in Hirsch, 1975) seems still possible between *Furnishius* and the early *Hadrodontina aequabilis* (Smithian). However, such a relationship seems now doubtful for *Parachirognathus* (Smithian of N.America) and *Pachycladina*. The latter's Spathian age together with *Hadrodontina anceps* derives from their concurrence with *Neospathodus triangularis* and *N. homeri* in Asia Minor (Gedik, 1975) and Greece (Ardaens & al., 1979), as well as by their occurence above and partial concurrence with *Platyvillosus costatus* in N. Italy (Staesche, 1964). *Platyvillosus costatus* is common at the base of the Spathian of Utah and Nevada (Sweet & al., 1971; Collinson & Hasenmueller, 1978) together with *Neospathodus triangularis*.

In summary homeomorphy of Sa and Sb elements can occur between *Ellisonia* and *Hadrodontina* on one hand, and *Furnishius* and *Pachycladina* on the other hand. Distribution of white matter varies strongly in *Ellisonia* and *Furnishius*, whereas albid elements in *Hadrodontina* and hyaline elements in *Pachycladina* are dominant, although not exclusive, whereas *Parachirognathus* is characterised by its exclusive hyaline and fibrous structure. The genera of the Ellisoniid stock seem generally related to shallower marine shelf environments, and their reduced white matter indicates more extreme shallow water conditions.

2. THE XANIOGNATHID-DERIVED STOCKS
PHYLOGENY

Bender (1969) has shown two possible phylogenetic lineages for the late Spathian through Middle Triassic. He derives several genera, such as *Neogondolella* and *Epigondolella* from *Neospathodus*. In addition, Sweet (1970) has proposed a similar relationship for *Neospathodus* and *Neogondolella*, but has them originated from *Xaniognathus*.

Both observations have to be considered complementary and the Permo-Triassic "permanent" xaniognathid stock may have generated several apparatuses described individually as *Neospathodus, Neogondolella, Carinella, Pseudofurnishius* and *Epigondolella.*

Derivation of P elements from a Pa element (xaniognathid) might have repeated at different times, the Pa element being the "permanent" slowly evolving one, generating P elements that do not necessarily derive directly from one another.

In the Middle Triassic, early Late Ladinian *Carinella truempyi* appears in Sardinia and Provence, and *C. hungarica* in Hungary and S. Turkey, from which is derived *Carinella mungoensis* of worldwide distribution. The derivation of *Epigondolella* took place directly from the late Neogondolellid apparatus of *Neogondolella polygnathiformis*, as was proposed by Bender (1969). Bender (1969) also supposes a lineage deriving *Gladigondolella* from xaniognathid Pa elements of the Late Spathian (*turgida-saginata* type).

2.1. *The xaniognathid-neogondolellid-stock*

Conodonts of this stock developed an apparatus composed of the following elements: P (platform), Pa (xaniognathid-type *tortilis*), Pb (Enantiognathid-type *ziegleri*), M (lonchodinid-type *muelleri*, or cypridodellid), Sa (Roundyid-type *magnidentata*), Sb (prioniodinid-type *latidentata*), Sc (hindeodellid-type *triassica*). From this stock the following genera are derived: *Neospathodus, Neogondolella, Pseudofurnishius, Carinella, Epigondolella* and possibly *Platyvillosus*. The number of elements within the latter apparatus may be reduced to only one single element.

Genus *Pseudofurnishius* VAN DEN BOOGAARD, 1966.
Generotype: *Pseudofurnishius murcianus* VAN DEN BOOGAARD, 1966.

The apparatus of *Pseudofurnishius* has been reconstructed by RAMOVS (1977). It comprises a P element (with small platform on internal or both sides, variable number of denticles on carina and platforms), Pb, Pa, M, Sa, Sb, and Sc elements.

The following species belong to *Pseudofurnishius*: *P. murcianus* VAN DEN BOOGAARD 1966, Ladinian, and *P. huddlei* VAN DEN BOOGAARD 1973, ? Early Ladinian. Some of the biplatform specimens of *P. murcianus* have been assigned erroneously by some authors into *P. huddlei* VAN DEN BOOGAARD, 1973. This apparently moved Ramovs (1977) to put *P. huddlei* into synonymy with *P. murcianus*. *P. huddlei* is the fore-runner of *P. murcianus* and occurs stratigraphically below the latter in stratigraphic sequence.

Pseudofurnishius murcianus occurs in the Ladinian of Spain (including Balearic islands), the Pyrenees, Israel, Chios and Slowenia. Together with *Carinella mungoensis* this species defines the typical late Ladinian association of the sephardic realm (HIRSCH, 1972).

Genus*Carinella* BUDUROV, 1973.
Generotype *Carinella mungoensis* (DIEBEL, 1956).

The apparatus of *Carinella* consists of elements P, Pa, Pb, M, Sa, Sb and Sc. The platform element has a short free blade ($^4/_5$ to $^1/_3$ of the unit length), low carina with well developed denticles, basal cavity amygdaloid with small pit. The platform is bordered by a variable number of denticles ranging from none *(C. truempyi)* to many *(C. mungoensis mungoensis)*. The unit is incurvated. The following species belong to *Carinella*:

Carinella truempyi (HIRSCH) 1971, early Late Ladinian, Provence (S. France), and Sardinia; *C. hungarica* (KOZUR) 1972, early Late Ladinian, Hungary and Turkey; *C. mungoensis* (DIEBEL) 1956, Late Ladinian — earliest Carnian, worldwide. *C. hungarica* differs from *C. truempyi* by its smaller basal cavity only, whereas *C. mungoensis* (including *C. mungoensis catalana*) differs from the earlier species by a variable number of denticles bordering the platform and by its free blade that occupies $^1/_3$ of the unit length. *C?. ciernensis* KOZUR & MOCK, 1972 from the Ladinian of Slovakia is probably related to early forms of the genus (Catalogue, III, p. 159, 1977).

Remark : The attribution of *C. catalana* (HIRSCH) 1966 to the genus *Gondolella* instead of *Polygnathus* was motivated by the "gondolelloid" apparatus in Hirsch's material from Coll de Jou, Spain, expressing the author's view of the importance of "natural assemblage" (apparatus), above mere morphology of the platform element alone.

2.2. *The xaniognathid-gladigondolellid-stock*

Conodonts of this stock belong to a lineage proposed by Bender (1969) that starts in the very late Spathian with *Gladigondolella carinata*, that is derived from the Late Spathian xaniognathid element of the *turgida-saginata* type.

The apparatus comprises the following elements: P (platform, no free blade, basal pit amygdaloid, carina with low denticles, platform smooth), Pa (xaniognathid-type *saginata*), Pb (cypridodellid-type *venusta*), M (Roundyid-type *lautissima*), Sa (prioniodinid-type *petrae-viridis*, alate), Sb (hindeodellid-type *multihamata*), Sc (prioniodellid-type *pectiniformis*).

The following species belong to *Gladigondolella*:
Gladigondolella carinata BENDER 1969, late Spathian — earliest Anisian;
Gladigondolella tethydis HUCKRIEDE 1958, Early Anisian-early Carnian;
Gladigondolella malayensis NOGAMI 1968, Late Ladinian-earliest Carnian.

Budurov (1973) described *Gladigondolella arcuata* from the Ladinian to earliest Carnian, this form being separated from *G. tethydis* by its more "xaniognathid" shape, may represent a variation within *G. tethydis*.

BIOFACIES AND PROVINCIALISM

The concept of provinces, emphasized mainly in the Triassic by Mosher (1968), Kozur and Mostler (1972) and Hirsch (1972) has been partly reinterpreted under the paleoecological concept of Biofacies (Hirsch, 1976).

The distribution of several conodont-assemblages leads to the recognition of at least three basic types of conodont-habitats.

I. *Neritic*

On cratonic margins or on large epicontinental shelves, shallow, still open marine, carbonatic with high clastic ratios, sometimes fossiliferous limestones with high marl ratio dominate, as the late early Triassic Werfen and Campil beds of the alpino-dinarid realm, the Zafir Formation in the levantine region, or the Thaynes and Moenkopi Formations of Utah and Nevada. In the circum-mediterranean Middle Triassic the sephardic muschelkalk fossiliferous limestones with evaporitic or clastic interlayers are of the same type. Similar environment was the habitat of Smithian forms *Ellisonia*, *Furnishius*, and *Parachirognathus* in the North American *Meekoceras*- and *Anasibirites* beds, that are partly concurrent with *Neospathodus dieneri*, *N. conservativus*, *N. waageni* and *Neogondolella milleri*.

Ellisonia further dominates this environment during the Spathian of North America, whereas in Europe and the Middle East *Hadrodontina* and *Pachycladina* often occur in this habitat. Common concurrent forms are *Platyvillosus costatus*, *Neospathodus triangularis*, *N. homeri* and *Neogondolella jubata*.

The shallow epicontinental shelf of the sephardic realm is characterised by a biofacies composed of endemic cephalopod taxa, abundant ostracodes and the conodont multi-elements *Pseudofurnishius murcianus* and *Carinella mungoensis* only.

A special endemic lineage derived from *Neogondolella mombergensis* dominates the Ladinian conodont-assemblages of the Polish-Germanic Muschelkalk realm (Kozur, 1968; Zawidzka, 1975).

II. EPIPELAGIC

Open marine, little affected by the depth of the water column (except in very shallow, rather high energy environments) this habitat had worldwide distribution and was most likely to be the one in which the most permanent conodont-stocks lived, from which new genera were repeatedly derived. *Neospathodus*, *Platyvillosus*, *Neogondolella*, *Carinella* and *Epigondolella* dominated this habitat during the Triassic.

Ramovs (1977) has found the complete apparatus of *Pseudofurnishius murcianus* in a dark fossiliferous limestone with *Posidonia*, whereas in somewhat younger

tuffaceous limestones of the same locality in Slovenia, *Posidonia* occurs with *Neogondolella*.

Kozur (1979 & pers. comm. 1980) mentioned *P. murcianus* in a Raibl-type facies together with *Neogondolella*, *Epigondolella* and even *Gladigondolella*, emphasizing the facial independence of *Pseudofurnishius* but underlining the "southern" origin of the tectonic unit in which his fauna was found.

III. MESOPELAGIC

More basinal, with waterdepth ranging below that of the continental margin, such facies types are like the "ammonitico rosso", Hallstatt or other thin bedded, nodular, often strongly condensed limestones with chert nodules or flint intercalations, with thin-shelled molluscs, ammonites and few foraminifers (e.g. *Turitelella mesotriassica*) and represent the lithotype that contains both *Neogondolella* and an equivalent or dominant ratio of *Gladigondolella* elements.

The limited geographic distribution (Neotethys of Europe and Asia, rare circumpacific occurences) infers that this biofacies represents the most basinal and farest offshore habitat, whose record is less comon among Triassic sediments.

Migration, as emphasized by Kozur and Mostler (1972) for *Gladigondolella tethydis* is more due to the absence of the proper environment in the alpine realm during the major part of the Anisian than to any other possible barrier, since *Gladigondolella tethydis* already prevails in appropriate sediments from the Far East to Asia Minor during the Anisian.

PLATE I

FIG. 1-6. — *Furnishius triserratus* CLARK.
    1. Pa element, lateral view, albid structure, sample 68JC48, × 80;
    2. same specimen in upper view, × 85;
    3. Sb element, lateral view, albid structure, sample 68JC3, × 30;
    4. Sb element, lateral view, albid structure, sample 68JC67, × 50;
    5. Sa element, lateral view, partly hyaline structure, sample 68JC3, 40 × ;
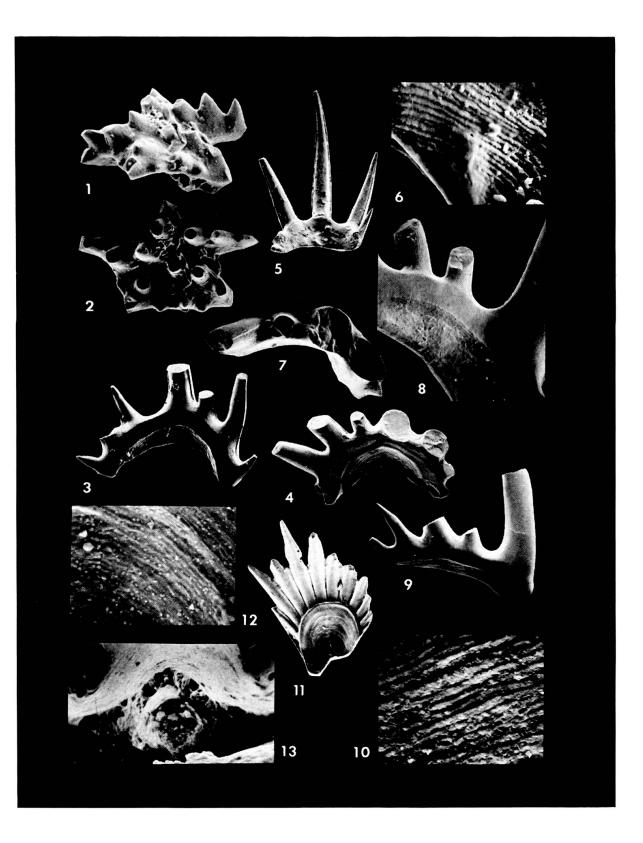   6. same specimen, detail of basal attachment, × 335.

FIG. 7-10. — *Ellisonia triassica* MUELLER:
    7. M element, upper view, albid structure, sample 68JC3, × 50;
    8. Sc element, detail of unit, lateral view, sample 68JC67, × 60;
    9. Sb element, lateral view, albid structure, sample 68JC3, × 24;
    10. same specimen, detail of basal attachment, × 500.

FIG. 11-13. — *Parachirognathus ethingtoni* CLARK:
    11. symmetric element, lateral view, hyaline structure, sample 68JC21, × 24;
    12. same specimen, detail of basal attachment, × 295;
    13. same specimen, detail of palmate denticle with lamellar structure, view from above, × 295.

(Material deposited in O.S.U. dept. of Geology and Mineralogy, Columbus, Ohio-U.S.A.)

PLATE I — F. Hirsch   (All samples from Smithian, Confusion Range, Utah)

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