TERESCONULARIA GEN. NOV. FROM THE LOWER ORDOVICIAN OF THE CORDILLERA ORIENTAL OF SALTA (NW ARGENTINA): THE OLDEST CONULARIID (CNIDARIA) FROM SOUTH AMERICA

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Abstract

Teresconularia argentinensis, a new genus and species of conulariid (Cnidaria, Schyphozoa) from the Angosto de la Quesera conglomerates of the Santa Victoria Group (Ordovician), Cordillera Oriental of Salta, Argentina, is here described. *Teresconularia argentinensis* was found during standard laboratory procedures for conodonts. The new taxa present some striking features, such as: 1- the presence of rounded, smooth corners, without grooves, 2- very small size (1,4 mm) for an almost complete thecae, and 3- the occurrence of schott. These characters emphasize the idea that during the Ordovician conulariids were much diversified anatomically, adding new evidences to our understandings of some paleoecological issues, such as miniaturization. Finally, should be highlighted that *Teresconularia argentinensis* is the oldest conulariid known in South America.

Key words: Ordovician, Tremadocian, conulariid, Cnidaria, systematics, Argentina.

Resumen

Se presenta y describe *Teresconularia argentinensis,* un nuevo género y especie de conulárido (Cnidaria, Schypozoa) de los conglomerados del Angosto de la Quesera (Base del Grupo Santa Victoria, Ordovícico) en la Cordillera Oriental de Salta, Argentina. *Teresconularia argentinensis* fue hallado durante el procesamiento estándar de búsqueda por conodontos. El nuevo taxón presenta algunos caracteres destacables tales como: 1- La presencia de bordes tecales redondeados y lisos, sin surcos. 2- Tamaño muy pequeño, 1,4 mm para una teca casi completa. 3- La presencia de schott. Estos caracteres enfatizan la idea de que durante el Ordovícico los conuláridos presentaban una mayor diversidad morfológica a la antes conocida, aportando nuevas evidencias en temas vinculados al grupo, tales como miniaturización. Finalmente se destaca que *Teresconularia argentinensis* constituye el conularido más antiguo conocido en Sudamérica.

Palabras clave: Ordovícico, Tremadociano, conulárido, Cnidaria, sistemática, Argentina.

INTRODUCTION

Conulariids are extinct benthic cnidarians generally having a four-sided, elongate pyramidal theca (Van Iten, 1991a), ranging from the Neoproterozoic (Ivantsov and Fedolkin, 2002) to the Triassic. Conulariids are extremely rare components of the Neoproterozoic Vendozoan fauna (Ivantsov and Fedolkin, 2002), as well as in Cambrian rocks (Hughes *et al.*, 2000). By contrast, conulariids are much diversified in Ordovician deposits, including, at least, 12 genera. This is the highest diversity of any system (see Van Iten and Brabcová, in press). From these, only 6 genera (*Archaeoconularia, Conularia, Conulariella, Eoconularia, Exoconularia* and *Pseudoconularia*) have their first occurrence in the Lower Ordovician (Van Iten and Brabcová, in press).

In this paper we describe the first occurrence of conulariid remains in Tremadocian conglomerates of the Santa Victoria Group (Cambrian-Ordovician) (Aceñolaza *et al.*, 2003). This occurrence is important for multiple reasons. First, in South America conulariid remains are common only in marine Devonian strata of the Malvinokaffric Realm, particularly from the Central Andean area (e.g., Bolivia, Babcock *et al.*, 1987) and from the cratonic basins of Brazil (e.g., Paraná Basin, Clarke, 1913; Leme, 2002) forming the so called "*Conularia*" beds (Babcock *et al.*, 1987; Simões *et al.*, 2000). Other Devonian occurrences are also known from Uruguay (Méndez-Alzola and Sprechmann, 1973). Second, until now, the oldest conulariids recorded in South America were found in the Silurian Pitinga Formation (Clarke, 1899; Siviero, 2002), from the Amazon Basin and Silurian shales of the Vargas Peña Formation from Paraguay (Babcock *et al.*, 1990). The stratigraphic position of some conulariid occurrences in Lower to Middle Paleozoic rocks from the Amazon Basin (Manacapuru Formation) must be confirmed (Ramos *et al.*, 2003). Hence, the present found of a conulariid remain in Tremadocian strata from Angosto de La Quesera locality, Argentina is, according to our knowledge, the oldest in South America. Third, the detailed anatomical analyses carried out (see below) have revealed that the Argentinean specimen can not be ascribed to any previous known conulariid, adding a new element to the diversified conularian fauna of the Ordovician System.

MATERIAL AND METHODS

Recent detailed stratigraphic and paleontologic analysis of the conglomerates of the Angosto de la Quesera (Santa Victoria Group) showed that they represent a Lower Tremadocian incised valley system with an erosive contact respect to several Cambro-Ordovician units (Fig. 1, 2) (Aceñolaza *et al.*, 2003). The basal conglomerate member and the upper sandy member compose the sequence (Fig. 2) (*sensu* Aceñolaza *et al.*, 2003). Boulder conglomerates interbedded with coarse badly sorted and well-sorted conglomerates and minor sand lenses showing high stage plane bed and current-ripple laminations characterize the basal conglomerate (Aceñolaza *et al.*, 2003). This conglomerate was, deposited by an interaction of high-energy unidirectional cohesive and uncohesive flows powered by high slope and wave action. Few clasts in the conglomerate shows inherited glacial features, and some proglacial structures are also recognized (e.g. dropstones) (Aceñolaza *et al.*, 2003). On the other hand, the upper member is characterized by fine-grained sands alternating with turbidite-like medium to coarse sands (Aceñolaza *et al.*, 2003). Clasts of the conglomeratic unit proved to be highly fossiliferous, with conodonts, trilobites, brachiopods, echinoderms and conulariids mostly belonging to the reworked deposits of the Lampazar and Cardonal formations (Fig. 2) (Aceñolaza *et al.*, 2003).

The Lampazar Formation encompasses transgressive deposits of Tremadocian age and are represented by highly fossiliferous shales and sandstones with subordinated quartzites generated in a shoreface setting (from upper offshore to middle shoreface). On the other hand, the Cardonal Formation includes Tremadocian regressive deposits (mainly sandstones) that are correlated to the "Black Mountain Eustatic Event" and were generated in an upper offshore to transitional settings. Both units and their fossils are worthwhile recordings of cold, marine, high latitude conditions of the Lower Ordovician seas of the Gondwana margin, in South America.

The description of *Teresconularia argentinensis* presented below, is based on examination of one, almost completed specimen that was found during standard laboratory procedures for conodonts (Stone, 1987). The insoluble residue was recovered with sieves #100 and #200 IRAM. In order to recover fossil material greater than 1 and 3mm the coarse fraction (#100) was targeted, yielding the conulariid remain.

The specimen is very small, inflated, and laterally compressed, preserving the original thecae. In spite of their small dimensions, some diagnostic features, such as the transverse ribs, rib articulation type, interspace ridges and nodes (Fig. 3) can be identified and described. The specimen is reposited in the pale-
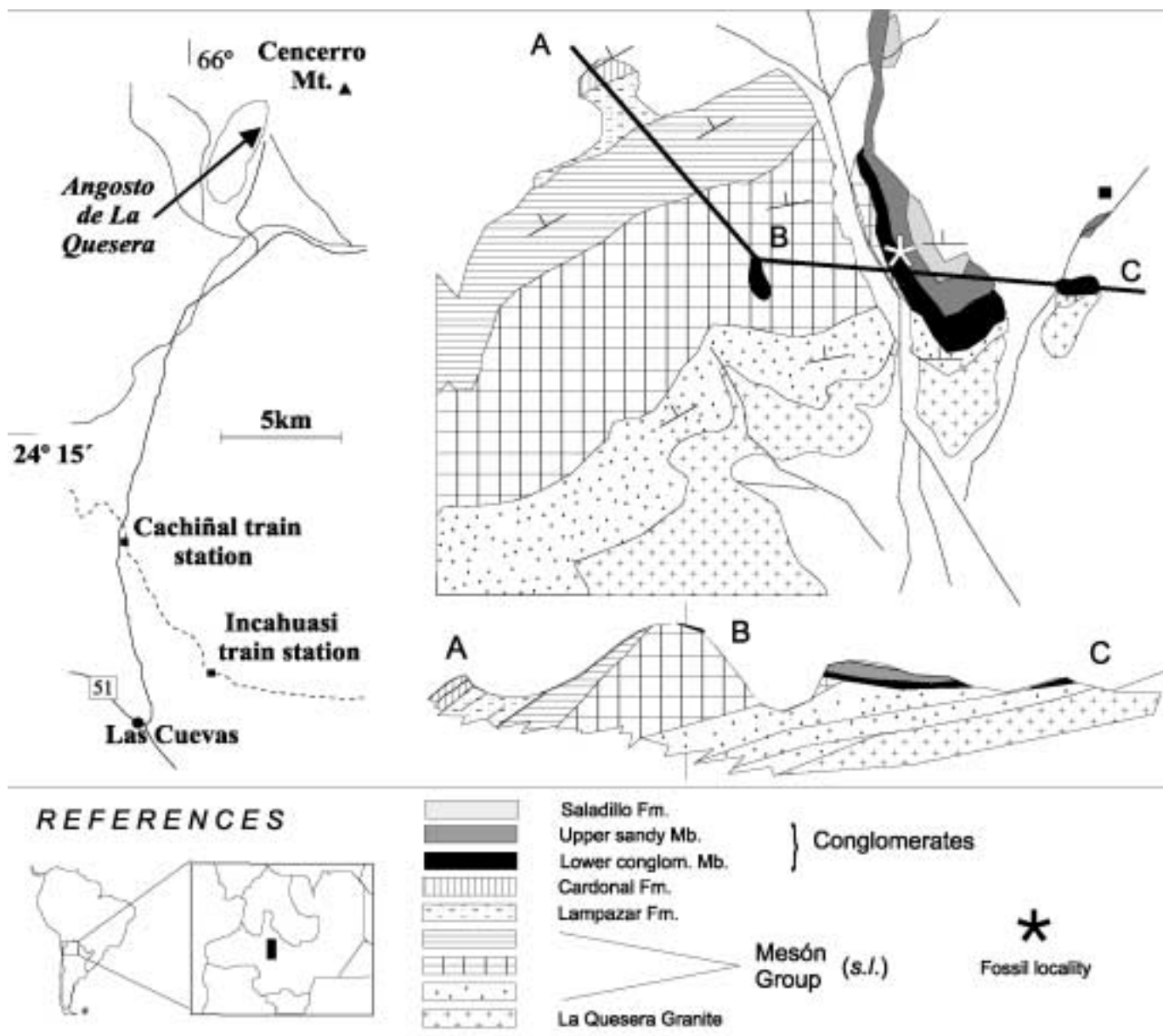
FIGURE 1–Location and geological map of the Angosto de la Quesera locality (Cordillera Oriental of Salta province, NW Argentina), modified from Aceñolaza *et al.* (2003).

ontological collection of Facultad de Ciencias Naturales and Instituto Miguel Lillo, Tucumán, Argentina under the code PIL (Paleontología Invertebrados Lillo).

The use of anatomical terminology (Fig. 3) in this paper is generally consistent with previous in Sinclair (1952), Moore and Harrington (1956), Babcock and Feldmann (1986), and Van Iten *et al.* (1996, 2000). In agreement with the following authors (e.g., Kiderlen, 1937; Werner, 1966; Bischoff, 1978; Van Iten, 1991a, 1992a, b; Jerre, 1994; Van Iten *et al.*, 1996; Hughes *et al.*, 2000), conulariids are interpreted as thecate cnidarians, and the conulariid exoskeleton is referred as thecae (Fig. 3).
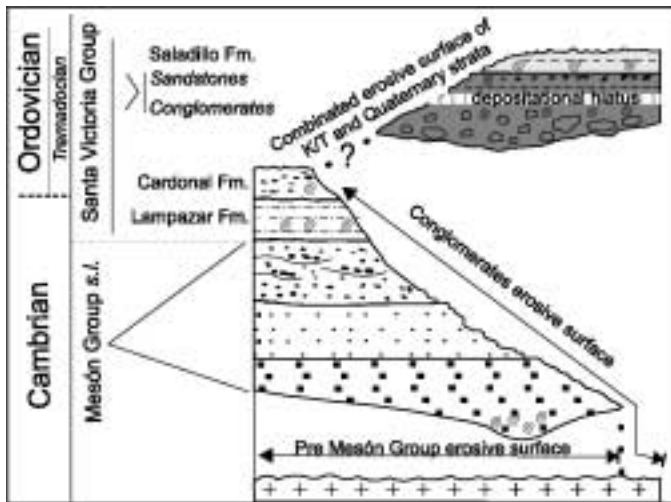
FIGURE 2–Lithostratigraphic chart of the Angosto de la Quesera area, according to Aceñolaza *et al.* (2003).

SYSTEMATIC PALEONTOLOGY

Phylum CNIDARIA Hatscheck, 1888
Class CONULATA Moore and Harrington, 1956
Order and family uncertain
Genus *Teresconularia* n. gen.
(Pl. 1)

Type species.–Teresconularia argentinensis n. sp.

*Diagnosis.–*Thecae with smooth and rounded corners. Corner grooves absent (Fig. 4; Pl. 1, Figs. 1, 2).

*Description.–*Conulariid with small four-sided thecae (Fig. 5; Pl. 1, Fig. 5). Corners without transversal ribs, interspace ridges and nodes (Pl. 1, Figs. 1, 2). The corners are rounded in cross section, lacking sulcus (Fig. 4; Pl. 1, Figs. 1, 2).

Derivation of name.–Teres (Latin) means rounded and is used in allusion to the shape (in cross section, Fig. 4) of the corners of the studied conulariid thecae.

*Occurence.–*Conglomeratic unit (Santa Victoria Group) of Aceñolaza *et al.* (2003), in the Angosto de la Quesera locality, Salta Province, NW Argentina.

*Discussion.–*The lack of corner sulcus distinguishes *Teresconularia* from most other conulariids. The exceptions are *Anaconularia* and *Baccaconularia* that also presents no traces of corner grooves (Fig. 4). However, in *Anaconularia* the corners elevate into a sharp ridge (Sinclair, 1952; Moore and Harrington, 1956). In other words, the corners are sharp in cross section (Fig. 4). This pattern is also shown in species of *Baccaconularia* (Hughes *et al.*, 2000). For example,

Baccaconularia robinsoni exhibits corners sharp, simple, and non-sulcate (Hughes *et al.*, 2000). However, a striking feature of *Teresconularia* is the presence of rounded corners (Fig. 4; Pl. 1, Figs. 1, 2). Additionally, the corners of *Teresconularia* are smooth, without cross ornamentation (transverse ribs, nodes and interspace ridges) (Fig. 4, Pl. 1, Figs. 1, 2). In spite of a lacking of corner grooves in *Baccaconularia,* in this genus the ornamentation crosses the corners (Hughes *et al.* 2000). Otherwise, no superficial ornamentation is shown in species of *Anaconularia.* Hence, the characters above add new anatomical information to the conulariid thecae, showing that during the Ordovician these invertebrates were, indeed, very diverse morphologically.

Teresconularia argentinensis n. sp.
(Pl. 1 1-6)

*Diagnosis.–*Thecae with transverse ribs without interspace ridges and nodes, always confluent at the midlines, terminating at the corner, and forming uniformly symmetrical, bell-shaped curves (or inflected circular curve style) (Pl. 1, Figs. 3, 4).

*Description.–*Inflated thecae having four faces, compressed laterally. Basal region complete (Pl. 1, Fig. 5). The length of nearly complete thecae is 1,4 mm (Fig. 5). Faces approximately equal in width; corner of a given face diverges at approximately 13 to 18 degrees. Midlines marked by slight deflection of the transverse ribs toward the aperture (Pl. 1, Figs. 3, 4). Transverse ribs always confluent at the midlines (Pl. 1, Figs. 3, 4), terminating at the corner; number 5,5 to 4 per 0,1 mm within about 5,5 per 0,1 mm of the former apex and from 4 to 3,5 per 0,1 mm elsewhere. Transverse ribs on the faces forming uniformly symmetrical, bell-shaped curves or inflected circular curve style (Pl. 1, Figs. 3, 4). Corner smooth, rounded, and without sulcus (Pl. 1, Figs. 1, 2). Schott present (Pl. 1, Fig. 6). Interspaces ridges, nodes, internal carina and midline thickening absent.

Derivation of name.–argentinensis, from Argentina the country where the conulariid was found.

*Type material.–*PIL 15099 holotype.

*Occurrence.–*Conglomeratic unit (Santa Victoria Group) of Aceñolaza *et al.* (2003), in the Angosto de la Quesera locality, Salta Province, NW Argentina.

Discussion.–Teresconularia argentinensis differs from all previously described conulariids species in having transverse ribs without interspace ridges and nodes, always confluent at the midlines, terminating at the corner, and forming uniformly symmetrical, bell-shaped curves or inflected circular curve style (Pl. 1,
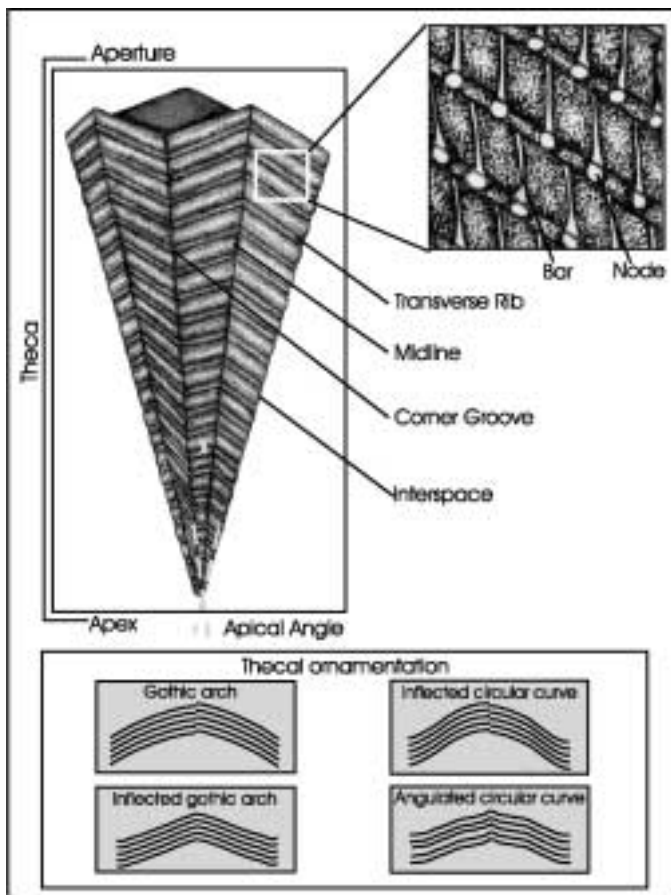
FIGURE 3–Conulariid thecal morphology, showing the main anatomical terms applied to the group.

Figs. 3, 4). Other species, *Conularia kaibabensis*, McKee; *Paraconularia alpenensis*, Babcock and Feldmann; *P. suarezriglosi*, Babcock; *P. arctica*, Babcock; *P. sciotovillensis*, Driscoll; *P. feldmanni*, Babcock *et al.*; *P. magna* (Ries); *Calloconularia strimplei*, Sinclair, exhibit the transverse ribs uniformly symmetrical, bell-shaped curves or inflected circular curve style, and nodes and interspace ridges are absent. However, in all these species the transverse ribs can be alternate at the midline. Similarly, *C. congregata*, Hall; *C. undulata*, Conrad; *C. splendida*, Billings; *P. missouriensis* (Swallow); *P. chesterensis* (Worthen); *P. derwentensis* (Johnston); *P. recurvatus*, Babcock and Feldmann; *P. ulrichana* (Clarke); *P. soreli*, Parfrey; *P. leonardensis* [Finks]), also show the same rib articulation style that *Teresconularia argentinenses* but nodes and interspace ridges are present, except in *P. recurvatus, P. ulrichana, P. soreli* and *P. leonardensis* which possess only nodes. Additionally, *C. congregata, P. missouriensis, P. chesterensis, P. derwentensis, P.*

recurvatus, P. ulrichana and *P. soreli* also exhibit transverse ribs alternate at the midline.

PALEOECOLOGY

One of the striking features of *Teresconularia argentinensis* is their small size, because the almost complete specimen (the apex, middle portion and part of the apertural region are) reaches 1,4 mm. Figure 5 shows the length of several conulariid thecae, ranging from the Neoproterozoic to Lower Paleozoic. The data was compiled from literature (Sinclair, 1940; 1942; 1948; Hessland, 1949; Moore and Harrington, 1956; Van Iten, 1994; Van Iten *et al.*, 1996; Hughes *et al.*, 2000; Ivantsov and Fedonkin, 2002). The *Teresconularia argentinensis* is 0,3 mm smaller than the *Climacoconus pumilus*, the smallest conulariid known (Sinclair, 1948) (Fig. 5). In addition, should be remembered that the aperture and apex of *Climacoconus pumilus* are unknown (Sinclair, 1942), and even in such conditions, Sinclair (1948) interpreted this as an "obviously dwarfed" species.

"Dwarfism" is a term applied to a reduction in size accompanied by morphological similarity to a reference taxon (Laurin and García-Joral, 1990). This is a particular case in which morphology (shape) is totally preserved. However, a reduction of size can also be the result of different types of alterations in ontogenetic development (heterocronies) (Gould, 1977; Alberch *et al.* 1979; Dommergues *et al.* 1986). These different processes have variable morphological, as well as evolutionary and adaptive, consequences (e.g., differences in adaptive strategies [Gould, 1977]).
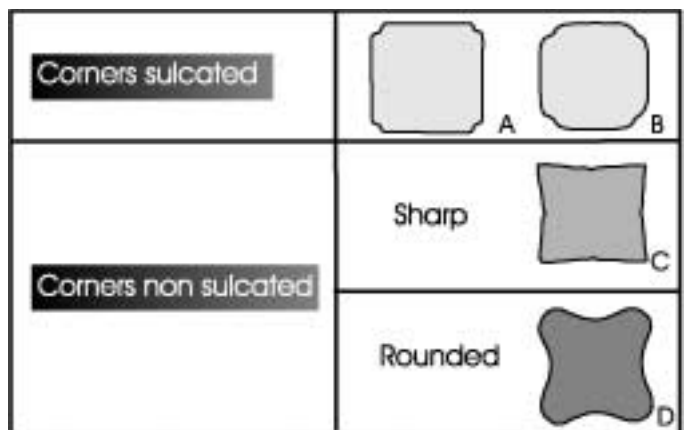

FIGURE 4–Schemes of the cross section of the conulariid thecae. A. *Climacoconus sinclairi*; B. *Eoconularia loculata*; C. *Anaconularia anomala*; D. *Teresconularia argentinensis*.
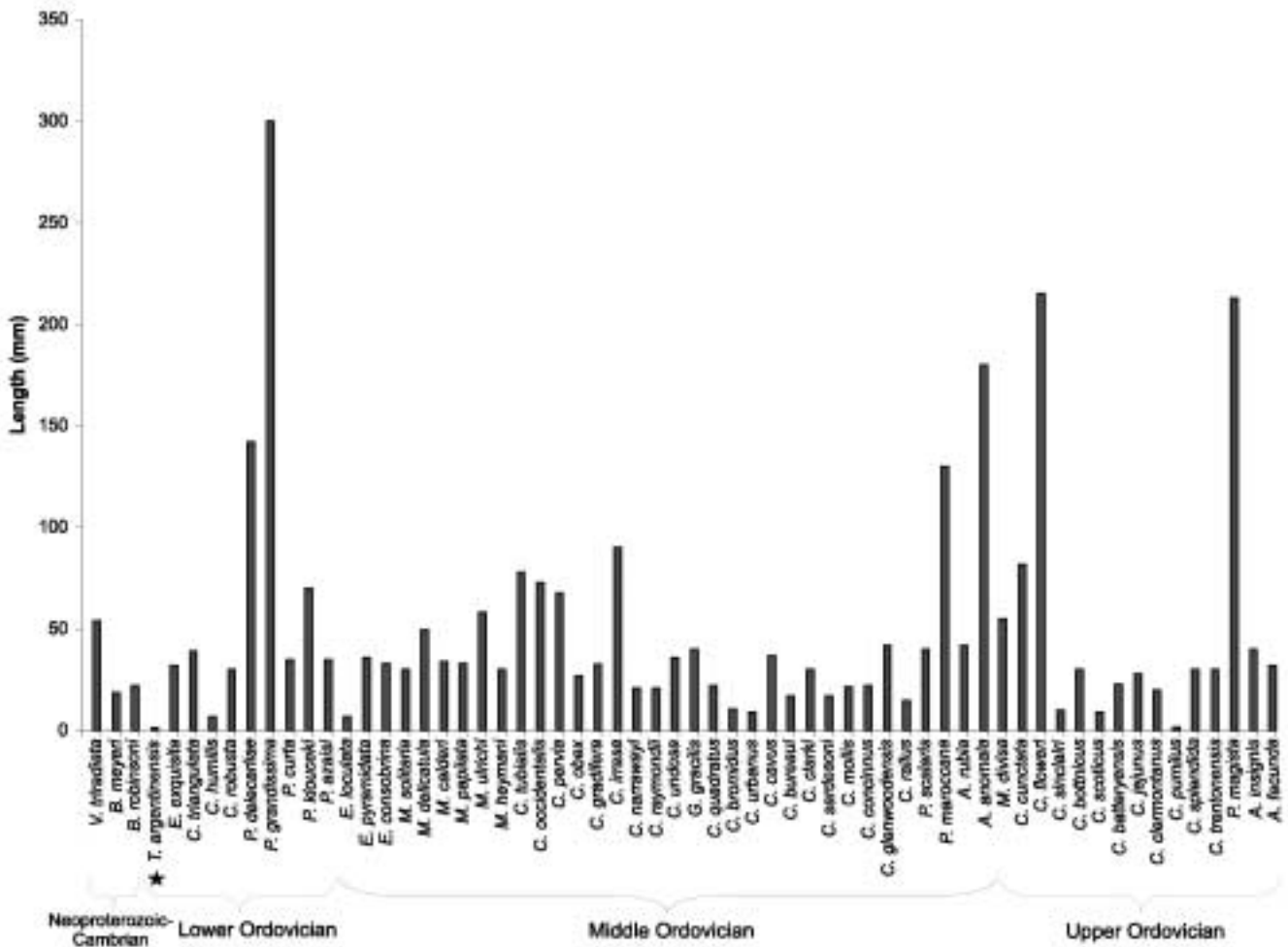
FIGURE 5–The length of several conulariid thecae, ranging from the Neoproterozoic to Ordovician. Black star indicates the total length of *Teresconularia argentinensis* gen. et sp. nov.

Multiple parameters are necessary to have information on ontogenetic change. These basic parameters are size, shape, age, and environment, which represent the manifestation of genetic variation and selection in the environment (McKinney, 1990). However, we have little information concerning the processes involved in the ontogenetic pathways of conulariids (e.g., growth pattern, individual's age, developmental stages, growth rates, age at sexual maturity, etc.). Even considering this some general comments can be done about the small size of the studied conulariid. For example, adult body size decrease may result from perturbations to ancestral ontogeny (ontogeny truncation, reduction in growth rates), causing heterocronic consequences (Hanken and Wake, 1993). Additionally, some environmental factors favor a small body size. Many specialized niches or habitats demand tiny body sizes, such as the spaces between sedimentary particles (the infauna) (Hanken and Wake, 1993). In unpredictable and unstable environments (e.g., glacial, deep-sea) the miniaturization is especially common. In these environments, early sexual maturation may be favored, and precocious reproduction is more common in small organisms. Smaller individuals require less food to support themselves, so they should have free energy and time for any activity that increase their mating and reproductive success, and can thus reproduce sooner, which supposedly confers a fitness advantage, especially in seasonal habitats that allow only one (or few) breeding attempts per year (Blanckenhorn, 2000).
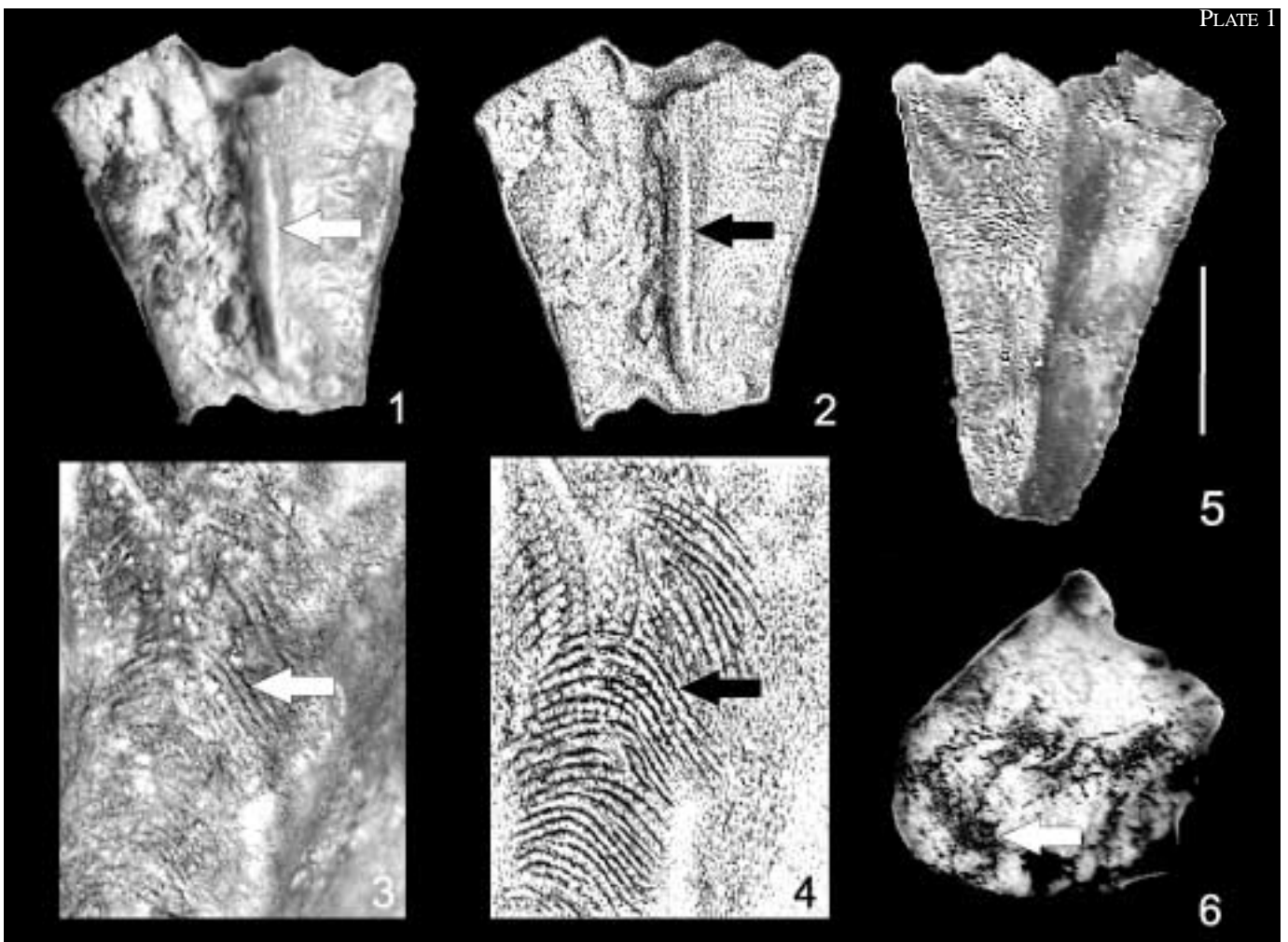
PLATE 1

PLATE 1–*Teresconularia argentinensis* gen. et sp. nov. *1,* Thecae showing a rounded smooth corner without grooves (white arrow), x 4,0; *2,* Drawing of the same thecae with the black arrow indicating the corner, x 4,0; *3,* Detail of the one face, showing the transverse ribs (white arrow), x 8,5; *4,* Drawing of the same face as in figure 3, where the "bell-shape" of the transverse ribs are highlighted (black arrow), x 8,5; *5,* General view of the almost complete thecae of the specimen PIL15099, bar size 0,5 mm, *6,* A superficial inferior view of the thecae base, showing the schott (white arrow), x 5,0.

Invertebrate faunas that are composed by minute species (Sanders and Allen, 1973), as those observed today in Antarctica characterize stressful environments. For example, maximum adult size for some modern Antarctic bivalve species (Protobranchia) is 1,1mm (Sanders and Allen, 1973).

Teresconularia argentinensis lived in high latitude, cold seas of the Gondwana margin. Thus, environmental stress may be one of the factors associated to their small size.

Another striking anatomical feature of the *Teresconularia argentinensis* is the presence of schott (Pl. 1, Fig. 6). Conulariids were sessile benthic marine cnidarians whose steeply pyramidal theca tapered to an extremely narrow apex or terminated in a more or less broad, generally outwardly convex transverse wall, called the schott (Van Iten, 1991b; Simões *et al.*, 2000; Rodrigues 2002). The conulariid schott has been interpreted as (1) a regular growth feature produced upon attainment of a certain age or size (Sinclair, 1948; Babcock and Feldmann, 1986); as (2) an autotomy scar produced when the conulariid polyp detached from its apical end and became a free-swimming medusa (Moore and Harington, 1956); or (3) as a scar produced in response to adventitious severance of the body by traction currents (Van Iten, 1991b).

Stratigraphic information of fossiliferous rocks indicates that they were deposited under high-energy conditions, supporting the view that conulariid schott may be a repair scar of thecae injured in high energy settings.

AGE

Conodont fauna suggest a Lower Ordovician, pre-*Paltodus deltifer* biozone (probably *Cordylodus angulatus*-base of *Rossodus manitouensis Zones*) for the rocks that yielded the studied conulariid specimen. In addition, the presence of *Rhabdinopora* sp. in sandstones of the upper conglomeratic unit corroborates a Lower Tremadocian age, but below *Bryograptus kjerulfi* biozone (Moya, 1988; Aceñolaza, 1997) of the Saladillo Formation. On the basis of the chronology information above, *Teresconularia argentinensis* is the oldest conulariid unearthed from South America Paleozoic rocks.

FINAL REMARKS

A new genus and species of conulariid (*Teresconularia argentinensis* gen. et sp. nov.) from Tremadocian (Lower Ordovician) rocks (Santa Victoria Group), from Argentina, is here described. This is the oldest conulariid from South America. Three main features presented by this new taxa are worthwhile to mention: 1- its small size (1,4mm), that accounts to miniaturization is here interpreted as related to environmental stress; 2- the presence of rounded, smooth corners, without grooves, adding new morphological features to the conulariid thecae anatomy, and 3- the presence of schott, probably a repair scar.

ACKNOWLEDGEMENTS

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PRIMEROS CONODONTOS KRALODVORIENSES (ORDOVÍCICO SUPERIOR) DE LA ZONA CANTÁBRICA, PORTILLA DE LUNA, LEÓN (ESPAÑA)

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Resumen

Se describen por primera vez en la Zona Cantábrica del Macizo Hespérico conodontos del Ordovícico Superior. La asociación consta de *Amorphognathus ordovicicus, Amorphognathus* sp., *Amorphognathus* sp. *A, Amorphognathus?* sp., *Scabbardella altipes, Birksfeldia* sp., *Icriodella* sp., *Dapsilodus* sp., *Panderodus* sp., y un elemento eocarniodiforme, y se adscribe a la Biozona de *Amorphognathus ordovicicus,* de edad esencialmente Kralodvoriense. Paleobiogeográficamente corresponde al Dominio Nordatlántico.

Palabras clave: Conodontos, Ordovícico Superior, Zona Cantábrica, Kralodvoriense, León, España.

Abstract

[First record of Kralodvorian (Upper Ordovician) conodonts from the Cantabrian Zone, Portilla de Luna, León province (Spain)]. Late Ordovician conodonts have been characterized for the first time in the Cantabrian Zone of the Hesperian Massif. The conodont association is formed for *Amorphognathus ordovicicus, Amorphognathus* sp., *Amorphognathus* sp. *A, Amorphognathus?* sp., *Scabbardella altipes, Birksfeldia* sp., *Icriodella sp., Dapsilodus* sp., *Panderodus* sp. and a eocarniodiform element, and is abscrited to the *Amorphognathus ordovicicus* Biozone, esencially of Kralodvorian age. Paleobiogeographically corresponds to the North-atlantic Domain.

Key words: Conodonts, Upper Ordovician, Cantabrian Zone, Kralodvorian, León, Spain.

INTRODUCCIÓN

En la mayor parte de la Zona Cantábrica, el Paleozoico Inferior presenta una amplia distribución, aflorando en la base de los mantos de cabalgamiento paralelos al Arco Asturiano (Aramburu *et al.*, 1992). Sin embargo, en muchas de estas áreas, los materiales correspondientes al Ordovícico Medio y Superior no existen, y cuando aparecen, presentan unas importan-tes variaciones litológicas y de espesor de unos puntos a otros. En la Región de Pliegues y Mantos, entre las pizarras silúricas de la Formación Formigoso y el Miembro Tanes de la Formación Barrios, constituido por cuarcitas de edad Arenigiense, suele existir una laguna estratigráfica que abarca el Ordovícico Medio y Superior; o bien entre ambas unidades se registran las Capas de Getino, una serie condensada de edad incier-ta (Aramburu y García Ramos, 1993).

Sin embargo, existen algunas excepciones, una de ellas es el afloramiento de Portilla de Luna, situado en la parte suroccidental de la Región de Pliegues y Mantos, cerca del Antiforme del Narcea. Los primeros trabajos realizados en esta sección corresponden a Leyva *et al.* (1984), quienes describieron sobre la Fm. Barrios, y concordante con ella, un paquete de areniscas, limonitas y fangolitas, al que asignaron una edad de Ordovícico Medio-Superior en función de su posición estratigráfica, litología, y unos escasos datos paleontológicos, equiparándola con el miembro basal de la Fm. Luarca. Aramburu *et al.* (1992) describen en la sección de Portilla de Luna, por encima de la Fm. Barrios, 65 m de pizarras negras y cuarzoarenitas alternantes, que estos autores comparan al Mb. Peñas de la Fm. Luarca, y 14 m de calizas grises. Posteriormente, Gutiérrez-Marco *et al.* (1996) llevan a cabo la descripción pormenorizada de estos materiales, denominándolos "unidad siliciclástica inferior" y "unidad calcárea superior", respectivamente.

En cuanto a los aspectos paleontológicos de los materiales post-Arenig presentes en Portilla de Luna, cabe destacar que la "unidad siliciclástica inferior" tiene un escaso contenido paleontológico (acritarcos, quitinozoos, trilobites, braquiópodos y ostrácodos), en función del cual se le atribuye una edad Ordovícico Superior (Gutiérrez-Marco *et al.*, 1996). La "unidad calcárea superior" presenta un abundante contenido fósil, reconociéndose una asociación de braquiópodos, equinodermos y trilobites característica del Kralodvoriense (equivalente al Ashgill pre-Hirnantiense de la escala regional Británico-Avalónica) [Aramburu *et al.* (1992); Gutiérrez-Marco *et al.* (1996)].

MATERIAL Y MÉTODOS

La sección de Portilla de Luna se localiza geográficamente en el talud de la carretera que enlaza desde la N-623 con la localidad de la que recibe su nombre, aproximadamente un kilómetro al SO de la misma (Fig. 1).

Debido a la dificultad que presenta el tratamiento físico/químico de materiales detríticos para la obtención de conodontos, se restringió el estudio a la "unidad calcárea superior", concretamente a los carbonatos poco alterados de un nivel situado 4 m por encima de la base de la unidad (Fig. 2).

La realización de láminas delgadas (Fig. 3) ha permitido la caracterización litológica detallada del material estudiado. Se trata de un packstone de equinodermos, briozoos, braquiópodos y trilobites, con la matriz
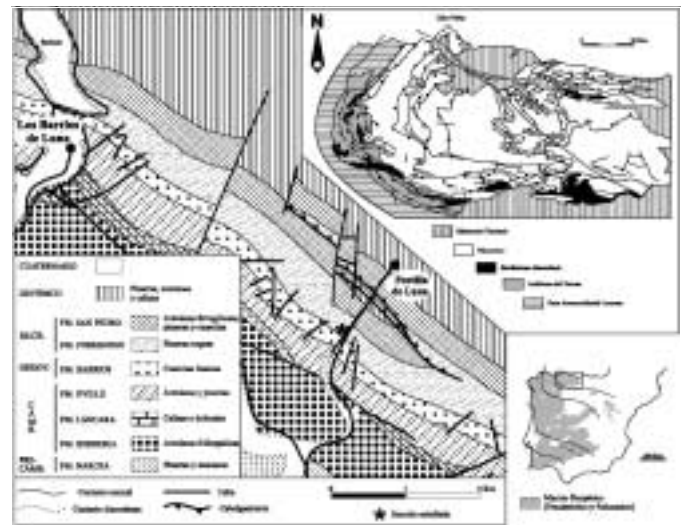
FIGURA 1–Situación geográfica y contexto geológico de la sección Portilla de Luna (tomada de Gutiérrez-Marco *et al.*, 1996).
FIGURE 1–Geographical situation and geological map of the Portilla de Luna section (after Gutiérrez-Marco *et al.*, 1996).
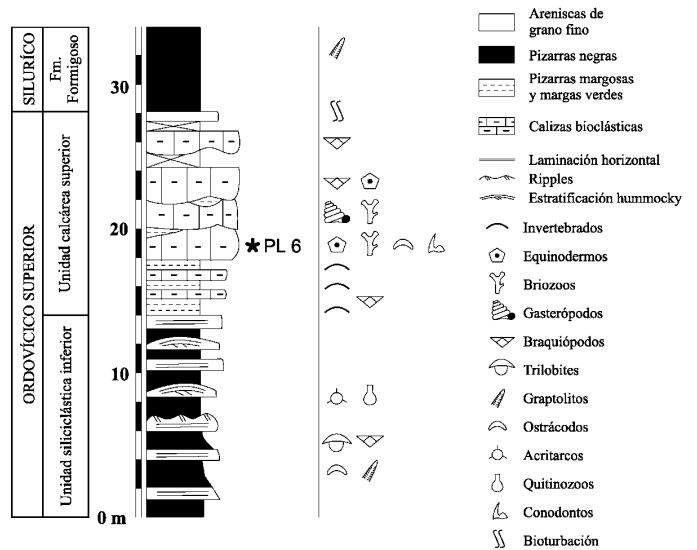
FIGURA 2–Columna estratigráfica con la localización del nivel estudiado (tomada de Gutiérrez-Marco *et al.*, 1996).
FIGURE 2–Stratigraphic column with the location of the studied level (after Gutiérrez-Marco *et al.*, 1996).

recristalizada, que a techo presenta una alta concentración de hierro.

De este nivel se habían procesado con anterioridad 4 kg de material, no habiéndose recuperado conodon-

FIGURA 3–Aspecto en lámina delgada de la muestra estudiada (x 6). Nícoles paralelos.
FIGURE 3–Aspect of the thin section of the studied sample (x 6). Plane-polarized light.

Peso de roca tratado (gr): 1.933,3

Peso del residuo (gr): 68,8

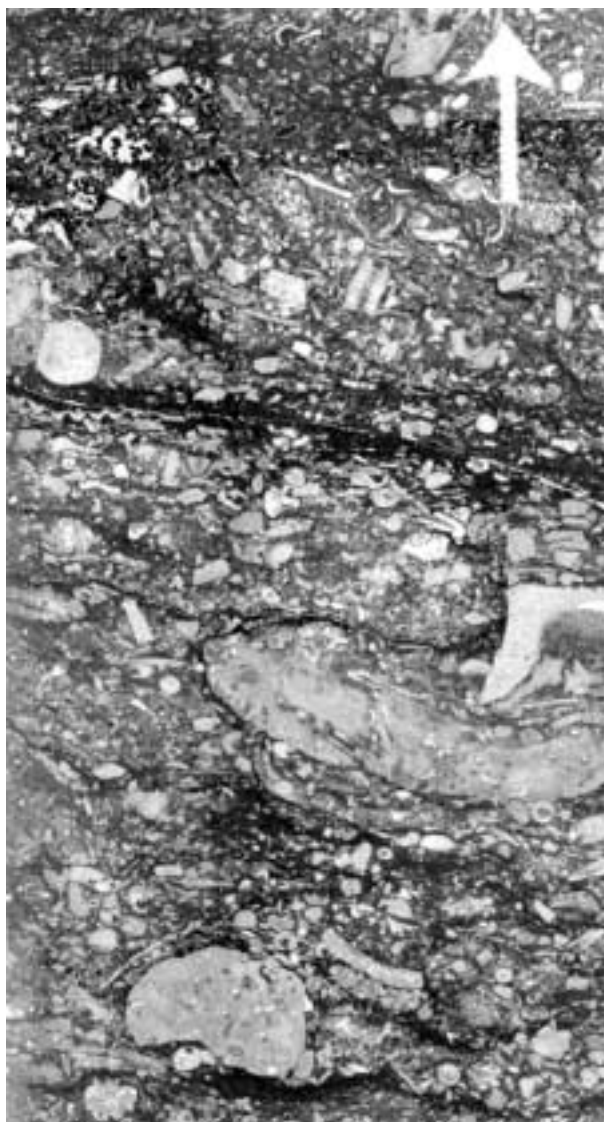| Especie	Elemento	Número ejemplares
Amorphognathus ordovicicus Branson & Mehl, 1933	M	1
	Pb	6
Scabbardella altipes Henningsmoen, 1948	a	3
Amorphognathus sp.	Pb	1
	P	3
Amorphognathus sp. A	Pb	1
Amorphognathus ? sp.	S	1
	P	1
Panderodus sp.	–	2
Dapsilodus sp.	a	1
Icriodella sp.	Pa	1
Birksfeldia sp.	P	1
Elemento eocarniodiforme	–	1
Elementos indeterminados	–	13
Total		**36**

TABLA 1–Relación de los taxones multielementales reconocidos en la asociación.
TABLE 1–Relation of multielemental taxa determined in the association.

tos. En este trabajo los elementos conodontales fueron extraídos de la matriz utilizando las técnicas clásicas, con 2 kg de muestra fragmentados y disueltos en una solución al 10% de ácido fórmico. La muestra se lavó después de tres días y el residuo insoluble se secó a 90 ºC. La fracción comprendida entre 80 µm y 1 mm fue triada con un pincel nº 0/5 bajo lupa binocular. La muestra ha proporcionado 36 elementos conodontales (Tabla 1).

Los conodontos más representativos fueron fotografiados con un microscopio electrónico de barrido (MEB) en el Centro de Microscopía Electrónica "Luis Bru" de la Universidad Complutense de Madrid. El material ilustrado se encuentra depositado en las colecciones de micropaleontología del Museo Geominero.

ASPECTOS TAFONÓMICOS

La característica común de todos los ejemplares que constituyen la colección de conodontos obtenida

es su mal estado de conservación. Entre los procesos tafonómicos observados destacan la fragmentación, la aparición de recubrimientos minerales y la disolución parcial. Sin embargo, el aspecto tafonómico más relevante es la maduración térmica de la materia orgánica presente en los conodontos. Esta maduración queda reflejada en una variación del color original de los elementos conodontales. Los ejemplares obtenidos en la sección de Portilla de Luna presentan tonalidades marrón oscuro, que equivalen, en el Índice de Alteración del color (CAI), al intervalo 3,5-4, rango que corresponde a paleotemperaturas de entre 190 y 300°C (Epstein *et al.*, 1977).

DESCRIPCIÓN SISTEMÁTICA

La inclusión de los distintos géneros y especies en categorías taxonómicas mayores se ha realizado siguiendo la clasificación propuesta por Sweet (1988) y las revisiones realizadas sobre la misma posteriormente por Dzik (1994; 1998). En cuanto a la asignación de las posiciones que ocuparían los elementos conodontales dentro del aparato, se ha utilizado la notación sugerida por Sweet (1988), dado su uso generalizado, si bien para algunas especies concretas se ha empleado la notación propuesta por Barnes *et al.* (1979).

Clase CONODONTA Pander, 1956
Orden BELODELLIDA Sweet, 1988
Familia DAPSILODONTIDAE Sweet, 1988
Género *Dapsilodus* Cooper, 1976
Dapsilodus sp.
(Lám. 1, Fig. 9)

Material.–1 elemento a (MGM-2459-O).
Descripción.–Corresponde a un cono simple asimétrico con cúspide erecta, comprimido lateralmente con bordes aquillados. Presenta una cavidad basal amplia y profunda. En el flanco externo aparece una costilla bien desarrollada en la porción media del elemento.
Observaciones.–Nowlan *et al.* (1988) definieron ejemplares similares al aquí descrito como *Besselodus borealis*, dado que consideraban a *Dapsilodus* una forma silúrica. Sin embargo, Carls (1975) ya reconoció la presencia de este género en materiales del Ordovícico tardío del Macizo Hespérico.

Orden PANDERODONTIDA Sweet, 1988
Familia PANDERODONTIDAE Lindström, 1970

Género *Panderodus* Ethington, 1959
Panderodus sp.
(Lám. 1, Fig. 10)

Material.–2 ejemplares (MGM-2457-O, MGM-2458-O).
Descripción.–Se trata de elementos cónicos simples, asimétricos y curvos. Toda su superficie aparece recorrida longitudinalmente por estrías. En uno de sus flancos presentan el característico surco panderodóntido.
Observaciones.–El estado de conservación de los ejemplares no permite precisar su asignación específica.

Orden PRIONIDONTIDA Dzik, 1976
Familia BALOGNATHIDAE Hass, 1959
Género *Amorphognatus* Branson & Mehl, 1933
Amorphognatus ordovicicus
(Branson & Mehl, 1933)
(Lám. 1, Figs. 1-3)

1933   *Phragmodus delicatus* Branson & Mehl, p. 123, Lám. 10, Fig. 22; elemento Sc.
*1933   *Amorphognathus ordovicica* Branson & Mehl, p. 127, Lám. 10, Fig. 38; elemento Pa.
1977   *Amorphognathus ordovicicus* Branson & Mehl - Lindström en Ziegler (ed.), pp. 35-40; multielemental (con sinonimias anteriores).
1980   *Amorphognathus ordovicicus* Branson & Mehl - Orchard, p. 16, Lám. 4, Figs. 1-13, 17-18; multielemental.
1981   *Amorphognathus ordovicicus* Branson & Mehl - Nowlan & Barnes, pp. 9-10; multielemental.
1983   *Amorphognathus ordovicicus* Branson & Mehl - Nowlan, pp. 660-662, Lám. 2, Figs. 16-17, 22, 25-27; multielemental.
1985   *Amorphognathus ordovicicus* Branson & Mehl - Savage & Bassett, pp. 691-692, Lám. 84, Figs. 1-21; Lám. 85, Figs. 1-26; Lám. 86, Figs. 1-13; multielemental.
1990   *Amorphognathus ordovicicus* Branson & Mehl-Uyeno, p. 55, Lám. 1, Figs. 1-7; multielemental.
1991   *Amorphognathus ordovicicus* Branson & Mehl-Ferretti & Serpagli, Lám. 1, Figs. 1-9; multielemental.
1993   *Amorphognathus ordovicicus* Branson & Mehl-Sarmiento, pp. 284-303, Lám. 1, Figs. 7, 9; Lám. 2, Figs. 2, 6; Lám. 3, Fig. 3; Lám. 16, Figs. 1-71; Lám. 17, Figs. 1-16; Lám. 18, Figs. 1-20; Lám. 23, Fig. 5; Lám. 25, Fig. 5; Lám. 27, Figs. 1-4; multielemental.

1997   *Amorphognathus ordovicicus* Branson &
Mehl-Ferretti & Barnes, pp. 26, 28, Lám. 1,
Figs. 1-15; multielemental.

1999   *Amorphognathus ordovicicus* Branson &
Mehl-Dzik, Lám. 2, Figs. 13-37.

1999   *Amorphognathus ordovicicus* Branson &
Mehl-Sarmiento, pp. 491-494, Lám. 1, Figs.
1-5; multielemental.

Material.–1 elemento M (MGM-2440-O) y 6 elementos Pb (MGM-2441-O, MGM-2442-O, MGM-2443-O, MGM-2444-O, MGM-2445-O, MGM-2446-O).

Descripción.–El elemento M presenta las características definidas por Ethingthon (1959) y redefinidas por Serpagli (1967). Corresponde a una forma robusta ramiforme, el proceso anterior es reducido y sin dentículos, el proceso lateral de nuestro ejemplar está fracturado, pero conserva parte de la denticulación.

Los elementos Pb presentan una amplia variabilidad morfológica, sin embargo todos exhiben características de la especie. Son formas robustas pectiniformes, con la cavidad basal profunda y estrecha y tres procesos denticulados, que no aparecen conservados en todos los ejemplares. Los procesos anterior y posterior se disponen perpendicularmente.

Distribución.–*Amorphognathus ordovicicus* es la especie índice del Kralodvoriense (Biozona de *A. ordovicicus*). En la Península Ibérica esta especie es bien conocida tanto en el Macizo Ibérico, como en los Pirineos orientales (e.g. Sarmiento, 1993; Sanz-López y Sarmiento, 1995).

<center>

Amorphognathus sp.
(Lám. 1, Fig. 4)

</center>

Material.–1 elemento Pb (MGM-2450-O) y 3 elementos P (MGM-2451-O, MGM-2452-O, MGM-2453-O).

Descripción.–Del elemento Pb se conservan el proceso posterior y anterior, estando ausente tanto la cúspide como el proceso lateral. Los elementos identificados como P corresponden a fragmentos de procesos con paredes gruesas, cavidades basales profundas y dentículos con bordes agudos.

Observaciones.–La asignación específica es imposible debido a que estos ejemplares corresponden a fragmentos y por tanto no exhiben todas las características necesarias para ello.

<center>

Amorphognathus sp. A
(Lám. 1, Fig. 5)

</center>

Material.–1 elemento Pb (MGM-2454-O).

Descripción.–Elemento pectiniforme con cavidad basal amplia y profunda, paredes gruesas y reborde basal. Presenta tres procesos en posición anterior, posterior y lateral, aunque sólo el posterior está completo.

Observaciones.–Todos estos rasgos nos permiten incluirlo en el género, sin embargo presenta algunas características que no coinciden con ninguna de las especies descritas para el mismo. Una de las más importantes es la existencia en el proceso posterior de un dentículo muy desarrollado. La falta de un número significativo de ejemplares impide realizar un estudio más detallado para determinar si se trata de una especie nueva o de una variedad morfológica de alguna ya existente.

<center>

Amorphognathus? sp.
(Lám. 1, Fig. 6)

</center>

Material.–1 elemento S (MGM-2455-O) y 1 elemento P (MGM-2456-O).

Observaciones.–Se incluyen aquí ejemplares cuya conservación dificulta la observación de las características diagnósticas.

<center>

Familia ICRIODELLIDAE Sweet, 1988
Género *Icriodella* Rhodes, 1953
Icriodella sp.

</center>

Material.–1 elemento Pa (MGM-2460-O).

Descripción.–El ejemplar corresponde a un fragmento de proceso anterior que presenta las dos hileras de dentículos divergentes que caracterizan al género.

Observaciones.–No es posible realizar la asignación específica debido al estado de conservación del elemento.

<center>

Orden PROTOPANDERODONTIDA Sweet, 1988
Familia PROTOPANDERODONTIDAE
Lindström, 1970
Género *Scabbardella* Orchard, 1980
Scabbardella altipes Henningsmoen, 1948
(Lám. 1, Fig. 7)

</center>

*1948   *Drepanodus altipes* Henningsmoen, p. 420,
Lám. 25, Fig. 14.

1980   *Scabbardella altipes* (Henningsmoen)-
Orchard, p. 25, Fig. 4c, Lám. 5, Figs. 2-5,
7-8, 12, 14, 18, 20, 23-24, 28, 30, 33, 35.

1983   *Scabbardella altipes* (Henningsmoen)-
Nowlan, p. 668, Lám. 1, Figs. 6-7, 11-14.

1984   *Scabbardella altipes* (Henningsmoen)-Chen
& Zhang, p. 131, Lám. 2, Figs. 29-30.

1988 *Scabbardella altipes* (Henningsmoen)-Nowlan *et al*. pp. 34-37, Lám. 16, Figs. 7-20; Lám. 17, Figs. 1-3, 5-6, 8-9.

1991 *Scabbardella altipes* (Henningsmoen)-Ferretti & Serpagli, Lám. 1, Figs. 12-14.

1992 *Scabbardella altipes* (Henningsmoen)-Bergström & Massa, pp. 1339-1340, Lám. 1, Figs. 1, 3-4.

1993 *Scabbardella altipes* (Henningsmoen)-Sarmiento, pp. 243-250, Lám. 1, Figs. 3-4, 6; Lám. 3, Fig. 9; Lám. 12, Figs. 1-18; Lám. 13, Figs. 1-22; Lám. 14, Figs. 1-15, 17, 19, 23; Lám. 27, Fig. 8; Lám. 30, Fig. 3; multielemental,

1994 *Scabbardella altipes* (Henningsmoen)-Dzik, p. 64, Fig. 6e, Lám. 11, Figs. 36-39.

1997 *Scabbardella altipes* (Henningsmoen)-Ferretti & Barnes, p. 34, Lám. 1, Figs. 17-22.

1999 *Scabbardella altipes* (Henningsmoen)-Sarmiento, pp. 489-490, Lám. 2, Figs. 6-8; multielemental.

Material.–3 elementos a (según Barnes *et al.*, 1979). (MGM-2447-O, MGM-2448-O, MGM-2449-O).

Descripción.–Los elementos a son cónicos simples con la cúspide suberecta a proclina; los bordes anterior y posterior son agudos y aquillados; en el flanco interno se desarrolla una costilla, que no llega hasta el ápice, y paralelo a ésta un surco, que se hace más estrecho y profundo hacia la cúspide; la cavidad basal es amplia y ocupa toda la base.

Observaciones.–Todos los ejemplares presentan fracturación de la cúspide y del borde inferior de la base, sin embargo es posible reconocer en todos ellos características propias de la especie.

Distribución.–En la Península Ibérica aparece en materiales del Kralodvoriense (Biozona de *A. ordovicicus*) en un gran número de localidades del Macizo Ibérico, en las Cadenas Costero Catalanas y en el Pirineo oriental (e.g. Sarmiento, 1993; Sarmiento *et al.,* 1995*;* Sanz-López y Sarmiento, 1995).

INCERTAE FAMILIAE
Birksfeldia sp.
(Lám. 1, Fig. 8)

Material.–1 elemento P (MGM-2461-O).

Descripción.–Elemento pectiniforme con un proceso anterior estrecho y denticulado. La cúspide es erecta con sección piramidal.

Observaciones.–No muestra todos los caracteres necesarios para incluirlo en una especie determinada.

Elemento eocarniodiforme
(Lám. 1, Fig. 11)

Material.–1 elemento (MGM-2462-O).

Descripción.–Elemento ramiforme con una cúspide central y dos procesos, anterior y posterior, denticulados.

Observaciones.–Nuestro ejemplar presenta muchas similitudes con la especie *Eocarniodus gracilis*, descrita por Rhodes (1955), pero la ausencia del reborde basal no permite su plena identificación, puesto que también podría corresponder a un fragmento de proceso ramiforme de otra especie.

CONCLUSIONES

La presencia de la especie índice *Amorphognathus ordovicicus* en la asociación descrita nos permite asignar los materiales estudiados a la Biozona de *A. ordovicicus* la cual tiene una edad Kralodvoriense en la Península Ibérica (e.g. Carls, 1975; Sarmiento, 1993;

→

LÁMINA 1–*1-3, Amorphognathus ordovicicus* Branson & Mehl, 1933; *1,* elemento M (MGM-2440-O); *2,* elemento Pb (MGM-2441-O); *3,* elemento Pb (MGM-2442-O). *4, Amorphognathus* sp., elemento Pb (MGM-2450-O). *5, Amorphognathus* sp. A, elemento Pb (MGM-2454-O). *6, Amorphognathus?* sp. elemento S (MGM-2455-O). *7, Scabbardella altipes* Henningsmoen, 1948, elemento a (MGM-2000447-O). *8, Birksfeldia* sp., elemento P (MGM-2461-O). *9, Dapsilodus* sp., elemento a (MGM-2459-O). *10, Panderodu*s sp. (MGM-2457-O); *a,* ejemplar completo; *b,* detalle de la microcostulación. *11,* elemento eocarniodiforme (MGM-2462-O). La escala gráfica representa 100 μm.

PLATE 1–*1-3, Amorphognathus ordovicicus* Branson & Mehl, 1933; *1,* M element (MGM-2440-O); *2,* Pb element (MGM-2441-O); *3,* Pb element (MGM-2442-O). *4, Amorphognathus?* sp., Pb element (MGM-2450-O). *5, Amorphognathus* sp. A, Pb element (MGM-2454-O). *6, Amorphognathus* sp., S element (MGM-2455-O). *7, Scabbardella altipes* Henningsmoen, 1948, a element (MGM-2447-O). *8, Birksfeldia* sp., P element (MGM-2461-O). *9, Dapsilodus* sp., a element (MGM-2459-O). *10, Panderodu*s sp (MGM-2457-O); *a,* complete exemplar; *b,* microcostulation detail. *11,* eocarniodiform element (MGM-2462-O). The graphic scale is 100 μm.
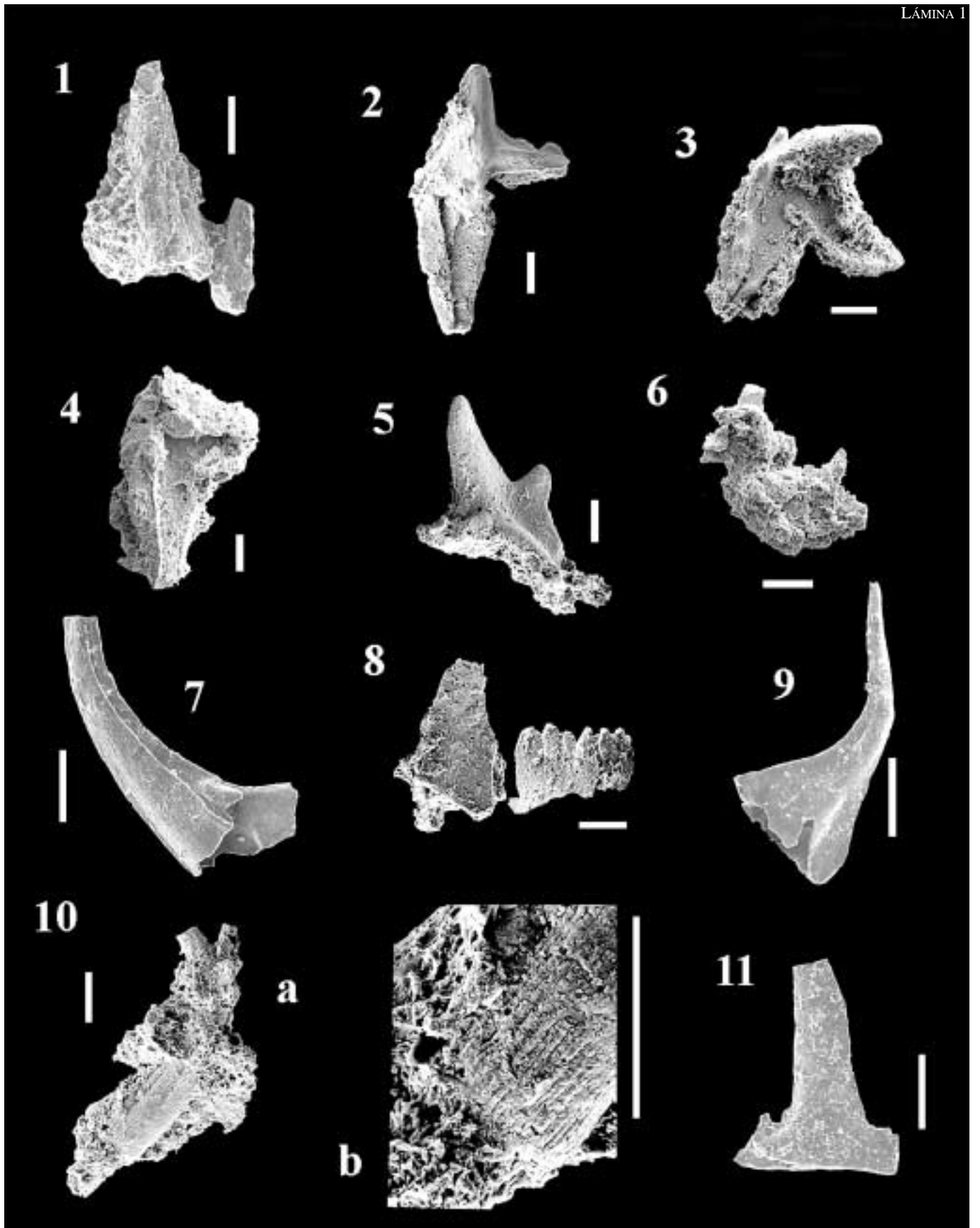
Sarmiento *et al.,* 1995*;* Sanz-López y Sarmiento, 1995). Ello confirma que los conodontos presentes en la "unidad calcárea superior" de Portilla de Luna concuerdan con la edad determinada anteriormente sobre la base de los braquiópodos y los equinodermos acompañantes de los conodontos (Aramburu *et al.*, 1992; Gutiérrez-Marco *et al.*, 1996).

La existencia de un marcado provincialismo en la distribución de los conodontos durante el Ordovícico ha permitido la diferenciación de dominios y provincias paleobiogeográficas (Sweet y Bergström, 1984). Los taxones presentes en la asociación estudiada permiten inscribirla dentro del Dominio Nordatlántico. Sin embargo, no es posible determinar a cuál de las provincias propuestas por estos autores, puesto que sólo el género *Amorphognathus* está suficientemente representado, y corresponde a una forma cosmopolita. Cabe destacar la ausencia en la asociación del género *Sagittodontina* endémico de la Provincia Mediterránea (Bergström, 1990) y muy abundante en asociaciones de la misma edad de otras regiones del Macizo Hespérico (e.g. Sarmiento *et al.*, 1999). Por otro lado, el registro de los géneros *Birksfeldia* e *Icriodella* dentro de la asociación*,* parece indicar una mezcla de faunas con elementos típicos de regiones templadas (Provincias Báltica y Británica: Sweet y Bergström, 1984).

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THE SILURIAN CEPHALOPOD LIMESTONE IN THE MONTE COCCO AREA (CARNIC ALPS, ITALY): CONODONT BIOSTRATIGRAPHY

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Abstract

The Orthoceras limestone of the Monte Cocco area has been studied in order to obtain new data on the stratigraphy and the depositional evolution of this unit. Pelagic and hemipelagic depositional processes are assumed for the limestones, on the basis of microfacies analysis, and faunistical and sedimentological considerations. The unit is highly fossiliferous, cephalopods, trilobites and bivalves being abundant. The fauna shows a close affinity with other areas of North Gondwana; furthermore, cephalopods suggest possible relationships with Kazakhstan, too. A quite rich conodont fauna allows to state a Ludlow-Prídoli age for the investigated rocks, where five conodont biozones are documented *(ploeckensis, snajdri, crispa, remscheidensis* and *detortus).*

Key words: Silurian, Carnic Alps, Monte Cocco, Orthoceras Limestone, conodonts.

Resumen

El estudio de la caliza de Orthoceras en el Monte Cocco pretende obtener nuevos datos estratigráficos y de evolución sedimentaria de esta unidad. La combinación de aspectos paleontológicos, sedimentológicos y el análisis de microfacies permite suponer la existencia de procesos deposicionales pelágicos y hemipelágicos para las calizas. La unidad es muy fosilífera, siendo muy abundantes los cefalópodos, trilobites y bivalvos. La fauna muestra una gran afinidad con la de otras áreas del norte de Gondwana; más aún, los cefalópodos sugieren también posibles relaciones con Kazakhstan. Una fauna considerablemente rica de conodontos permite datar las rocas estudiadas como Ludlow-Prídoli y reconocer cinco biozonas *(ploeckensis, snajdri, crispa, remscheidensis* y *detortus).*

Palabras clave: Silúrico, Alpes Cárnicos, Monte Cocco, Caliza de Orthoceras, conodontos.

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INTRODUCTION

This paper is the first report from a research project on the Silurian of the Carnic Alps arranged between several Italian universities (Modena and Reggio Emilia, Cagliari, Bologna) and institutions (Museo Friulano di Storia Naturale). Research includes geological mapping, palaeontology, stratigraphy
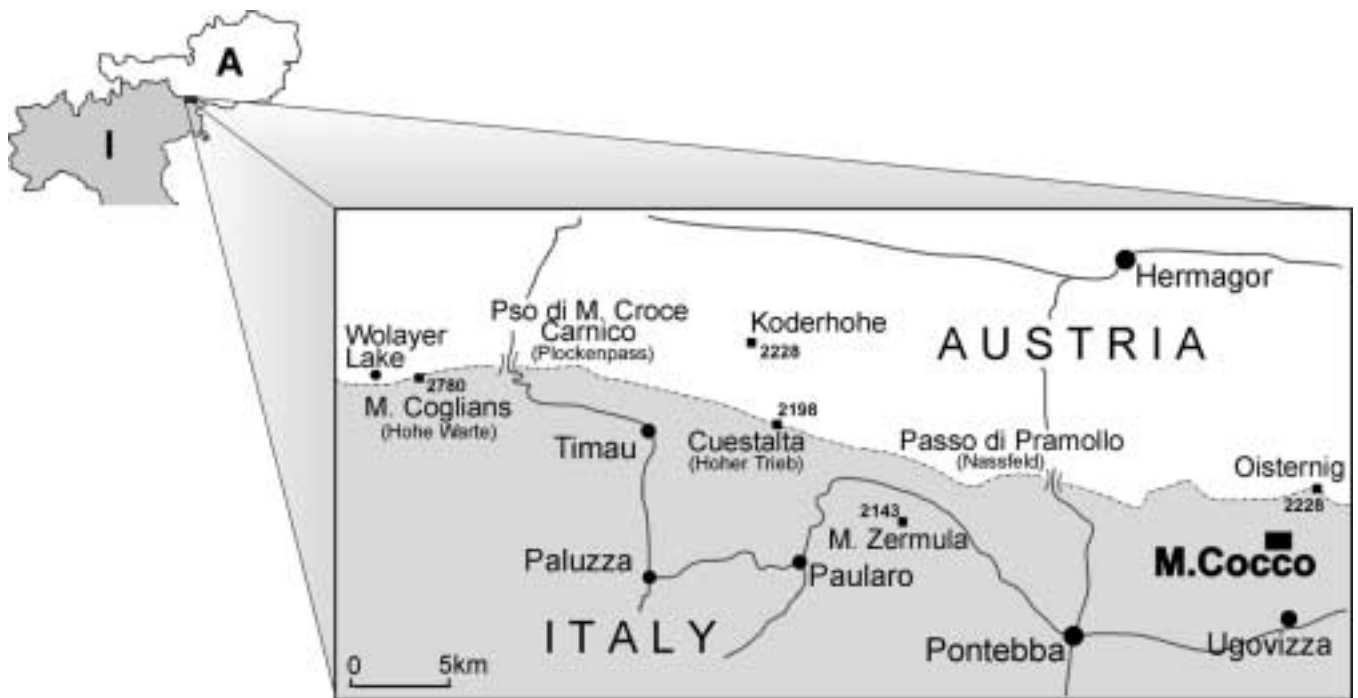
FIGURE 1–Location map of the studied area.

and depositional history of Silurian rocks, with special regard to carbonatic facies, in several sectors of the Carnic Chain. The final goal of the project is to provide a reconstruction of paleoenvironmental and paleogeographic evolution of the Carnic Basin during Silurian times.

Silurian calcareous sediments are mainly represented by cephalopod limestone cropping out discontinuously in many localities of the Carnic Alps, between Wolayer Lake and Uqua Valley. The western sector of the chain (Wolayer Lake and Passo di Monte Croce Carnico/Plöckenpaß areas) has been investigated and described in great detail by several authors, while only a few papers deal with Silurian topics from other areas of the Carnic Alps.

Monte Cocco is located in the eastern part of the Carnic Alps, close to the Italian-Austrian border (Fig. 1). This area has been known for a long time to geologists thanks to either the abundance of fossils (Frech, 1888) or the important mining activity, digging out iron and manganese, from 16th to the first half of the 20th century, but probably in roman age, too (Feruglio, 1970; Zucchini, 1998). However, geologic and stratigraphic studies on this area are quite old, and the only recent one (Herzog, 1988) has a structural approach only. It should be pointed out that, in old papers and by German speaking scientists, this locality is referred to by its Austrian name: "Kokberg"; in fact, even if it is an Italian speaking area, Monte Cocco was annexed to Italy only at the end of World War I.

The Silurian rocks of Monte Cocco are highly fossiliferous, therefore some papers deal with the taxonomy of selected groups. Many of these are devoted to nautiloid cephalopods: Heritsch (1929) described a rich collection from this area and Histon (1999) revised this material; Serventi (2001) described 38 taxa, while Gnoli & Histon (1998), Gnoli *et al*. (2000), Serventi *et al*. (2000) and Serventi & Gnoli (2001) described collections stored in Bologna and Udine museums, respectively. A few bivalves from Monte Cocco have been listed by Kříž (1999) in his monography of Silurian bivalves from the Carnic Alps. Finally, Manzoni (1965) and Herzog (1988) referred also on the occurrence of conodonts and listed, but not illustrated, some taxa of Wenlock and Ludlow age.

THE SILURIAN OF THE CARNIC ALPS

Silurian deposits are irregularly distributed within the Carnic Chain, and range from shallow water bioclastic limestones to nautiloid-bearing limestones, interbedded shales and limestones to black graptolitic shales and cherts. The overall thickness does not exceed 60 m. The Silurian transgression started at the base of the Llandovery, and, due to the disconformity separating the Ordovician and the Silurian, a varying pile of sediments is locally missing, which corresponds to several conodont zones of Llandovery and Ludlow age (Histon & Schönlaub, 1999).

The Silurian of the Carnic Alps is subdivided into four lithological facies (Fig. 2), representing different depths of deposition and hydraulic conditions (Wenzel, 1997). The Wolayer-facies is characterised by proximal sediments, the Bischofalm-facies by deep water deposits; the Plöcken-facies and the Findenig-facies are intermediate between the ones mentioned previously. In rough approximation, the four facies seem to be distributed north-west to south-east in the western-central sectors of the chain.

The depositional features suggest an overall transgressional regime from Llandovery to Ludlow. Uniform limestone sedimentation within the Prídoli suggests that more stable conditions were developed at that time (Schönlaub, 1997).

For a more detailed description of the Silurian of the Carnic Alps refer to Histon & Schönlaub (1999) and Schönlaub & Histon (2000).

Sediments of Late Ordovician to Late Devonian age are exposed in the Monte Cocco area (Fig. 3).

The basal part of the succession consists of dark grey and greenish pelites and siltstones grading to light grey sandstones, probably Caradocian in age. Locally a massive level, about 10 m thick, of presumably Ashgill crinoidal limestones is documented.

The Silurian transgressive Orthoceras limestones disconformably overlay these siliciclastic sediments. This succession will be described in the following section.

The Orthoceras limestones are conformably followed by about 10 m of well bedded light grey Lochkovian cephalopod wackestones and packstones which represent a marked shallowing of the sea level. The depositional processes are still pelagic and hemipelagic, but few tempestites reflecting major storm events are documented. Dark red nodular limestones of Pragian to Eifelian age are deposited on the top of this succession. This unit consists of more than 200 m of mudstones and wackestones reflecting pelagic and hemipelagic depositional processes. The very low amount of organic matter confirms that the carbonate buildups which developed from the Lochkovian-Pragian boundary in some places of the Carnic basin were quite distant. This unit originated as a response to a sea level fall across the Lochkovian-Pragian boundary, followed by a sea level rise up to the Eifelian.

A sequence boundary of middle Eifelian age testifies to a sea level fall, which is expressed in the Monte Cocco area by the deposition of about 20 m of

GEOLOGICAL SETTINGS

The structural setting of the Monte Cocco area is characterised by a kilometric-scale syncline generated by the slip along a thrust occurring in the southernmost part of the study area. The movement along this structure has been detected as top to the south by means of slickensides, while the age of the deformation has been constrained as Neoalpine through a mesoscale structures interference analysis. The structural setting of the whole area is probably connected to the exhumation of a fault-bounded block along the Gailtal Line during Miocene times (Läufer, 1996).

The slip along the N90°-105°E trending thrust brought to the development of an asymmetric syncline displaying a N105°E trending axial plane, dipping to the north of about 75°. The overall structure is partly disrupted by a younger system of strike-slip and extensive faults.
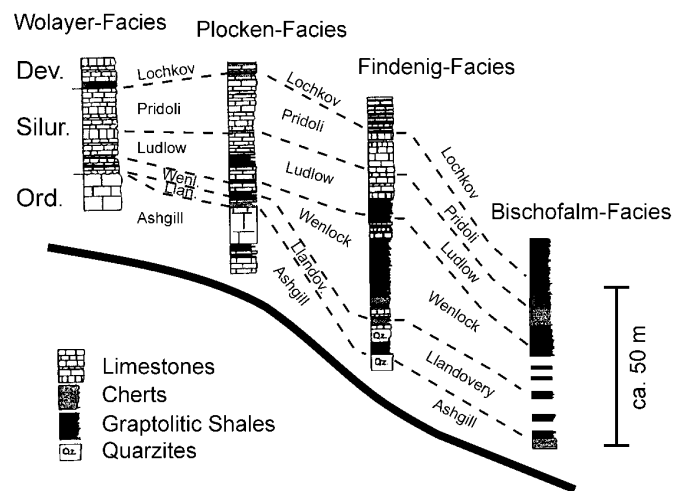

FIGURE 2–Lithology of Silurian sediments in the four different lithofacies of the Carnic Alps (after Wenzel, 1997).
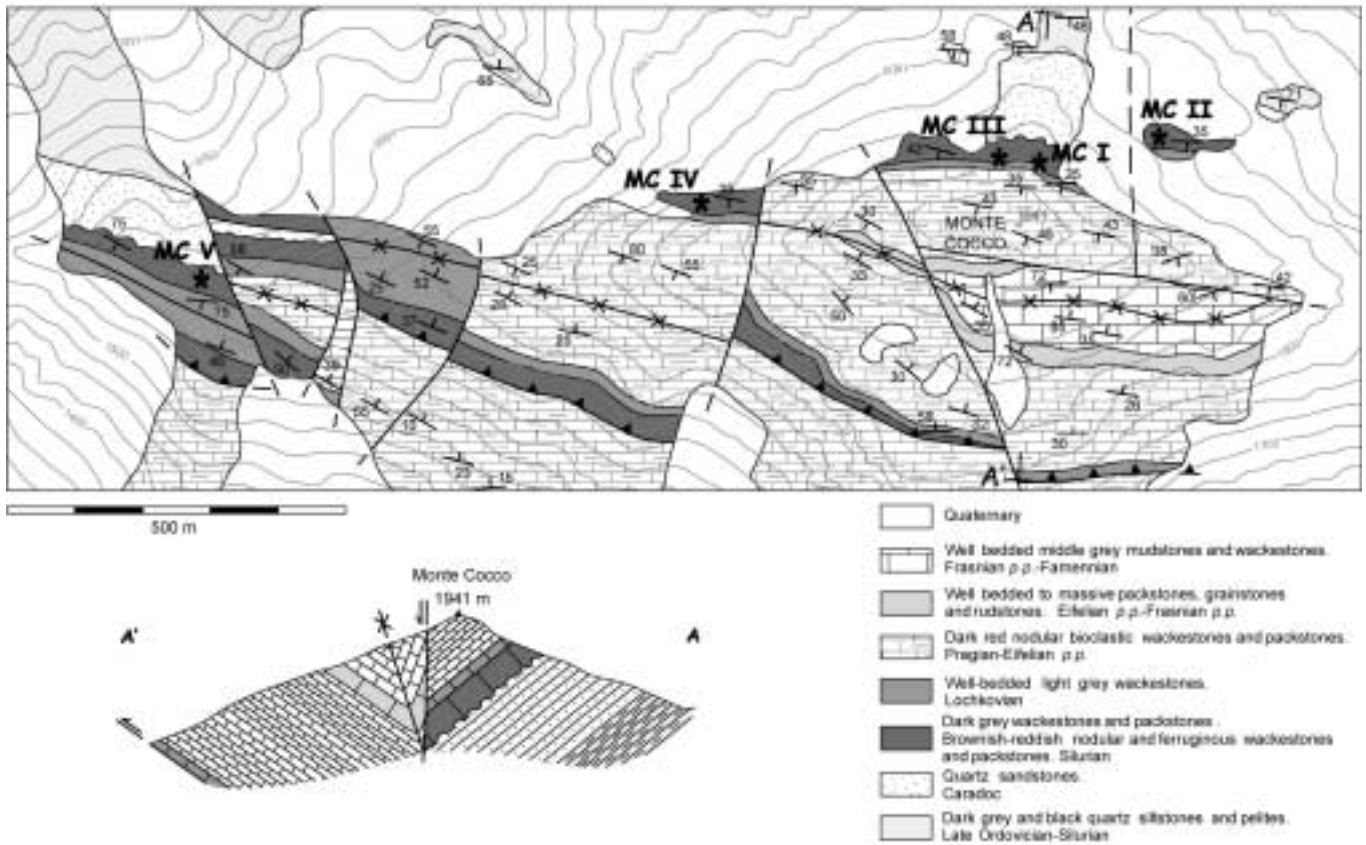
FIGURE 3–Geological map and N-S geological section of the Monte Cocco area. The mapping has been realised as part of the Geological Map of the Carnic Alps (Venturini *et al.,* 2002).

bioclastic grainstones and rudstones reflecting the presence of a stromatoporoid-coral reef complex in the proximal carbonate buildup areas. Starting from the upper Givetian, the progressive drowning of the reef complex probably by means of repeated transgressive-regressive pulses (Farabegoli *et al.,* in prep.) brought to the end of the detrital input to the basin. As a consequence, the Upper Devonian succession consists mainly of wackestones and packstones reflecting pelagic and hemipelagic depositional processes.

The topmost Devonian and Lower Carboniferous limestones as well as the middle Carboniferous siliciclastics units are not exposed in the Monte Cocco area.

THE SILURIAN OF THE MONTE COCCO AREA

The Silurian of Monte Cocco is quite widespread and mainly represented by a cephalopod limestone in Wolayer facies. However, the exposure is not very good, due to the abundant vegetation and Quaternary cover, and only a few meters of limestone crop out here and there: therefore, it is difficult to describe a complete succession.

The lower part of the Silurian sequences, up to the uppermost Gorstian, is known only thanks to some loose blocks, mainly collected from the debris close to mine galleries: in fact, up to date, we did not find any outcrop of this age. However, it seems to be represented by dark grey to black wackestone to packstone, with intercalations of millimetre thick black marl levels. The upper part of the succession consists of about twenty meters of wackestones and packstones, well stratified in beds 10-50 cm thick. The brownish-reddish colour frequently turns to dark red by weathering, due to the abundance of iron minerals, and progressively grades to light grey across the Silurian/Devonian boundary.

The palaeontological content, mainly represented by nautiloid cephalopods, trilobites and bivalves is always quite abundant, and is described in detail below.

The microfacies is mainly represented by a cephalopod wackestone to packstone, where the grains are mostly bioclasts deposited by means of pelagic and hemipelagic processes. Thin section analysis revealed echinoderms, gastropods, cephalopods, and small shells (ostracods, bivalves and brachiopods). A great concentration of small shells have been observed in some levels, suggesting reworking by means of redepositional processes, possibly tempestites.

Pelagic and hemipelagic depositional processes are supported also by the lack of structures documenting traction currents. Furthermore, the highly ferruginous limestones suggest a deposition in well oxygenated water.

PALAEONTOLOGICAL CONTENTS

As already pointed out, the limestones of Monte Cocco are almost always rich in cephalopods, while trilobites and bivalves are abundant in some levels only. Other fossil groups are much more rare. Furthermore, among microfossils, conodonts are abundant, and the residues yielded also bivalves, brachiopods, phyllocarid gnatal lobes, ostracodes, gastropods and spongae spiculae.

A rich macrofossil collection from Monte Cocco is stored in the Museo Friulano di Storia Naturale. However, it should be pointed out that most of this material has been collected in the debris from old mine galleries, and part of it belongs to historical collections from the first half of the 19th Century; therefore it is not possible to know precisely the stratigraphic horizon from which the fossil material was collected within the limestones.

Nautiloid cephalopods (Fig. 4) are the most abundant macrofossils. The association is dominated by orthocones and slender longicones: Orthocerida are dominant in the fauna, being the Orthoceratidae the bulk of the nautiloid cephalopod association; Sphooceratidae and Geisonoceratidae are also recognized. *Hemicosmorthoceras, Michelinoceras, Plagiostomoceras, Arionoceras* and *Geisonoceras* are the most common genera. Cyrtocone conchs are very rare, since only a few representatives of *Phragmoceras* have been collected.

Many juvenile specimens of genera *Sphaerorthoceras, Parasphaerorthoceras, Hemicosmorthoceras, Michelinoceras* and *Arionoceras,* with protoconchs, have been collected in the Monte Cocco area; nevertheless their preservation is poor.

The nautiloid fauna of Monte Cocco confirms the close faunal relationship between the Carnic Alps and

Southwestern Sardinia, Central Bohemia and Sahara-Morocco (Gnoli & Histon, 1998); furthermore, the occurrence of the genus *Andigenoceras* suggests a relationship with Kazakhstan, too: in fact, before the
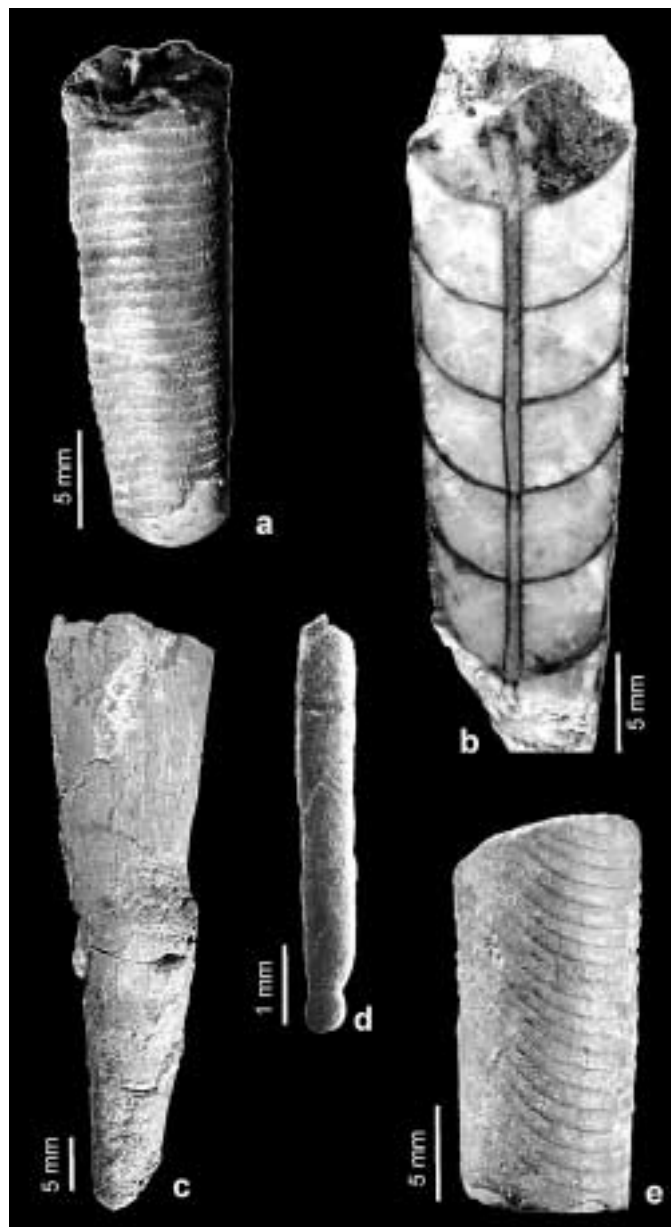

FIGURE 4–Nautiloid cephalopods from Monte Cocco. *a. Hemicosmorthoceras* sp., IPUM 24230; *b. Arionoceras affine* (Meneghini, 1857), IPUM 24229; *c. Vericeras*? cf. *dorulites* (Barrande, 1874), MFSNgp 26534; *d.* juvenile specimen of *Sphaerorthoceras beatum* (Ristedt, 1968), with the protoconch preserved, IPUM 24232; *e. Plagiostomoceras pleurotomum* (Barrande, 1860), IPUM 24231.
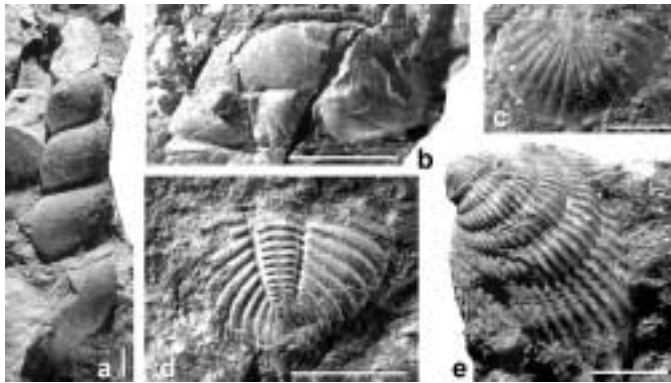
FIGURE 5–Macrofossils from Monte Cocco. Scale bar: 5 mm
a. Loxonematidid gastropod, MFSNgp 15753; b. Aulacopleura haueri (Frech, 1888), cephalon, MFSNgp 15059-1; *c. Scutellum* sp., pygidium, MFSNgp 16791; *d. Encrinurus novaki* (Frech, 1888), pygidium, MFSNgp 23161; *e. Cardiola* sp., MFSNgp 23116.

present report, up to date this taxon have only been found in central Asia.

Beside cephalopods, trilobites are the most abundant fossil group (Fig. 5b-d); however, almost all the fossil remains are represented by exuviae (isolated cephala and pygidia, and thorax fragments), complete specimens being very rare. The most common order is Phacopida, both with fam. Encrinuridae (mostly *Encrinurus novaki)* and fam. Cheiruridae *(Cheirurus sternbergi, Cerauroides quenstedti)*; ord. Ptychopariida is present with families Aulacopleuridae *(Aulacopleura*

haueri) and Tysanopeltidae *(Scutellum* is common). Ord. Odontopleurida is very rare, since a single fragmentary pygidium is dubitative referred to fam. Odontopleuridae.

Bivalves (Fig. 5e) are common in some levels, fam. Cardiolidae being the most represented, with genera *Cardiola*, *Carnalpia*, *Cominicula* and *Cardiolopsis;* also *Slava* is well represented.

Gastropods (Fig. 5a), mainly represented by members of the families Platiceratidae, Loxonematidae and Euomphalidae, are quite common, too. Crinoids are quite rare, and only a few articles are known. Finally, brachiopods are very rare: only a single poorly preserved undetermined specimen has been collected up to date.

CONODONT DATA

Five localities, located in the northern flank of Monte Cocco, have been sampled for conodonts in order to achieve a precise age setting for these limestones. The studied sections and outcrops are named "Monte Cocco I (MC I)" to "Monte Cocco V (MC V)" respectively (Fig. 3). The "MC II" Section is the more complete, spanning from late Ludlow to the Lower Devonian, and will be published in detail in the near future.

All samples have been processed with the conventional formic acid technique.

All the investigated limestones were fossiliferous, yielding a quite abundant fauna. The state of preservation is in general quite good, even if a few elements are

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PLATE 1–*1, Ozarkodina excavata excavata* (Branson & Mehl, 1933); IPUM 27671, lateral view of Pa element; sample MC II 1, *Oz. crispa* Zone. *2, Ozarkodina eosteinhornensis* s. l. (Walliser, 1964); IPUM 27672, upper view of Pa element; sample MC II 3D, *Oz. remscheidensis* Zone. *3, Ozarkodina eosteinhornensis* (Walliser, 1964); IPUM 27673, upper view of Pa element; sample MC II 3D, *Oz. remscheidensis* Zone. *4, Ozarkodina eosteinhornensis* (Walliser, 1964); IPUM 27674, upper (a) and lateral (b) views of Pa element; sample MC II 3D, *Oz. remscheidensis* Zone. *5, Belodella resima* (Philip, 1965); IPUM 27675, lateral view of Pa element; sample MC II 4, *Oz. remscheidensis* Zone. *6, Ozarkodina crispa* (Walliser, 1964); IPUM 27676, lateral view of Pa element; sample MC II 1, *Oz. crispa* Zone. *7, Ozarkodina crispa* (Walliser, 1964); IPUM 27677, upper (a) and lateral (b) views of Pa element; sample MC II 1, *Oz. crispa* Zone. *8, Pseudooneotodus beckmanni* (Bischoff & Sannemann, 1957); IPUM 27678, upper (a) and lateral (b) views; sample MC II 1, *Oz. crispa* Zone. *9, Kockelella absidata absidata* Barrick & Klapper, 1976; IPUM 27679, lateral view of Pa element; sample MC V 1, *A. ploeckensis* Zone. *10, Ozarkodina confluens* (Branson & Mehl, 1933); IPUM 27680, lateral view of Pa element; sample MC II 0, *Oz. snajdri* Zone. *11, Ozarkodina confluens* (Branson & Mehl, 1933); IPUM 27681, lateral view of Pa element; sample MC II 4A, *Oz. remscheidensis* Zone. *12, Kockelella variabilis variabilis* Walliser, 1957; IPUM 276782, upper-lateral (a) and upper (b) views of Pa element; sample MC I 2, *A. ploeckensis* Zone. *13, Coryssognathus dubius* (Rhodes, 1953); IPUM 27683, lateral view of Sc element; sample MC II 4, *Oz. remscheidensis* Zone. *14, Kockelella variabilis ichnusae* Serpagli & Corradini, 1998; IPUM 27684, upper view of Pa element; sample MC V 1, *A. ploeckensis* Zone. All specimens x90.

PLATE 1
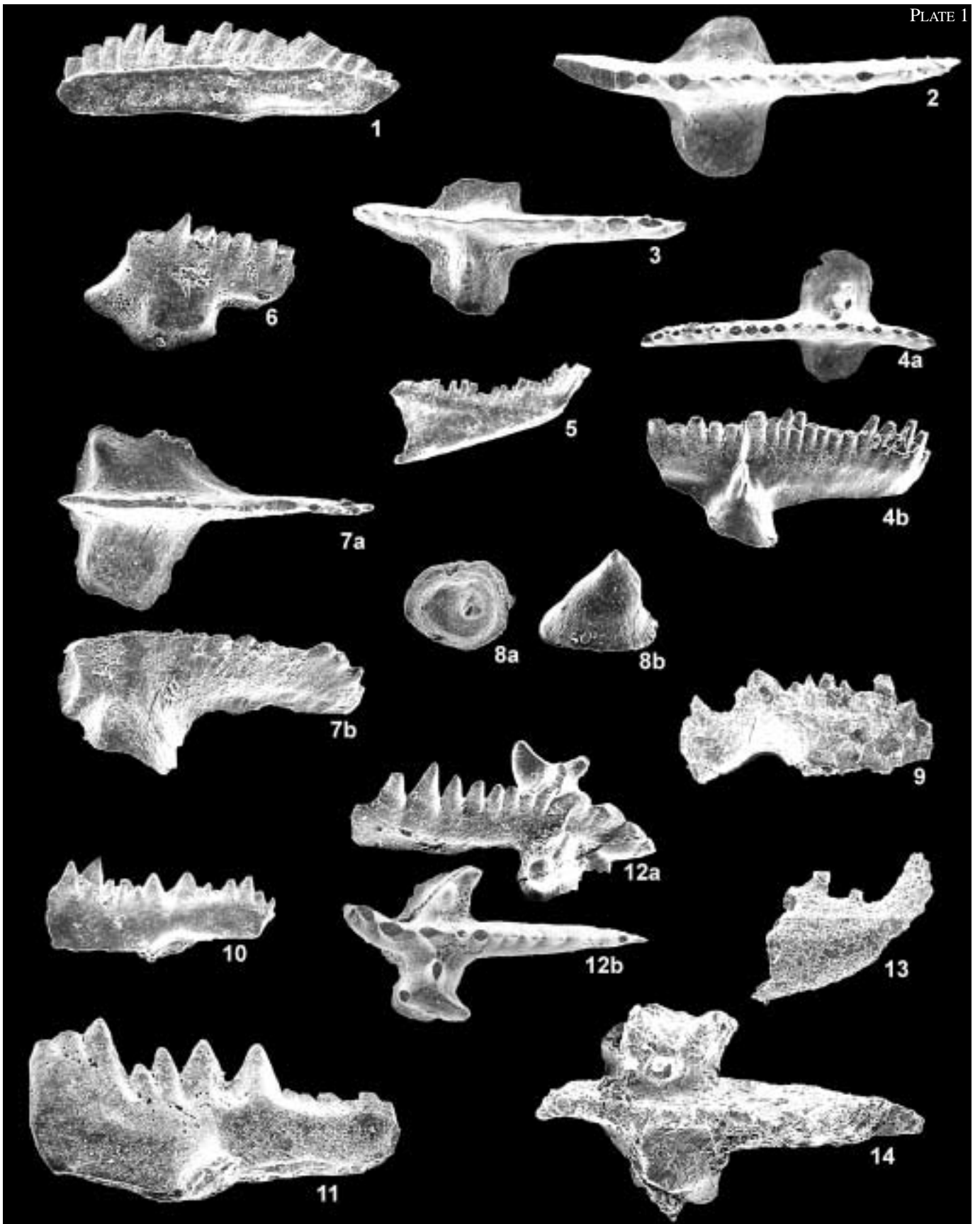
broken or slightly deformed; only in the MC V section, located in the western part of the studied area, conodonts are poorly preserved, broken and strongly encrusted.

Twenty-one taxa, belonging to eight genera have been found and are listed below:

Belodella resima (Philip, 1965)

Belodella sp.

Coryssognathus dubius (Rhodes, 1953)

Dapsilodus obliquicostatus (Branson & Mehl, 1933)

Kockelella absidata absidata (Barrick & Klapper, 1976)

Kockelella variabilis ichnusae (Serpagli & Corradini, 1998)

Kockelella variabilis variabilis (Walliser, 1957)

Oulodus elegans detortus (Walliser, 1964)

Oulodus elegans elegans (Walliser, 1964)

Oulodus siluricus (Branson & Mehl, 1933)

Ozarkodina confluens (Branson & Mehl, 1933)

Ozarkodina crispa (Walliser, 1964)

Ozarkodina eosteinhornensis s. s. (Walliser, 1964)

Ozarkodina eosteinhornensis s. l. (Walliser, 1964)

Ozarkodina excavata excavata (Branson & Mehl, 1933)

Ozarkodina remscheidensis remscheidensis (Ziegler, 1962)

Ozarkodina remscheidensis s. l. (Ziegler, 1962)

Panderodus recurvatus (Rhodes, 1953)

Panderodus sp.

Pseudooneotodus beckmanni (Bischoff & Sannemann, 1957)

Pseudooneotodus bicornis (Drygant, 1974)

The conodont fauna allowed a Late Silurian (Ludlow-Prídoli) age assignment for the investigated outcrops. The following biozones of the Silurian Conodont Zonation (Corradini & Serpagli, 1999) have been recognised: *ploeckensis, snajdri, crispa, remscheidensis* and *detortus.* It should be pointed out that, between *ploeckensis* and *snajdri* zones, no evidence of the *siluricus* and/or the *latialata* zones have been found (see discussion below).

A few loose blocks, collected close to old mine galleries, yielded a late Llandovery/early Wenlock fauna (*Pt. am. amorphognathoides* Zone), but no strata of this age have been found in place. Furthermore, Manzoni (1965) and Herzog (1988) reported also on the occurrence of Wenlock conodonts (*ranuliformis* and *sagitta* zones) in a few samples from this area, although the exact locality of their sampling is not known.

Finally, an Early Devonian fauna with icriodids has been collected from the light grey limestones in upper part of the MC II Section.

In general, *Ozarkodina* is the dominant genus, representing in some levels up to the 90% of the association. Only in a few samples from the *snajdri* Zone panderodids are very abundant, too; a similar dominance of panderodids have been observed also in other localities of the Carnic Alps (i. e.: Cellon) in the same stratigraphic horizons.

The colour of the conodont fauna is dark brown to black (CAI 4-5). A slight increasing of the CAI value has been observed across the area moving from West to East: samples located in the western part of the Monte Cocco display CAI values of 4-4.5, whereas, towards the east, CAI values range between 4.5 and 5.

DISCUSSION AND CONCLUSIONS

The age of the Silurian cephalopod limestones on the Monte Cocco area spans from latest Llandovery to end Prídoli. However, a complete sequence is documented only from middle Ludlow to the Silurian-Devonian boundary, whereas for lower intervals no outcrops have been found, and only some loose blocks, dating around the Llandovery/Wenlock boundary (*Pt. am. amorphognathoides* Zone) have been collected in debris from the old mines of the area.

It is worth noting that, within the exposed sequence, in the Ludfordian, no evidence of the *siluricus,* and of the *latialata* zones has been found. In other sectors of the Carnic Chain, the lower part of this interval corresponds to the "Cardiola Fm.", which is characterised by an alternance of black cephalopod limestones, marls and shales. This Unit always has a very limited thickness, from 3.5 m in Plöcken facies to a few centimetres only in Wolayer facies. Since the Silurian sediments of Monte Cocco present the typical features of the Wolayer facies, it is, therefore, highly possible that this thin interval is not exposed here, due to the Quaternary cover.

Concerning the *latialata* Zone, it is not always easy to recognise this interval, mainly because its time span is very short and sometime the marker is not abundant. However, only the upper part of the succeeding *snajdri* Zone has been documented, therefore this interval is likely unexposed, too.

Beside stratigraphic considerations, the main results up to date achieved with the present researches, still in progress, on the Silurian cephalopod limestone of Monte Cocco area can be summarized as follows:

— pelagic and hemipelagic sedimentation proces-
ses in well oxygenated waters can be supposed
for these limestones;

— the macrofauna confirms the close affinities bet-
ween the Carnic Alps and other areas of North
Gondwana; furthermore, the occurrence of nauti-
loid cephalopod genus *Andigenoceras* suggests a
possible relationship with Kazakhstan, too;

— the occurrence of juvenile nautiloids, bearing
the still preserved protoconch, is reported for the
first time from the Monte Cocco area.

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DEVONIAN ICRIODONTIDAE: BIOSTRATIGRAPHY, CLASSIFICATION AND REMARKS ON PALEOECOLOGY AND DISPERSAL

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Abstract

Stratigraphic ranges of ninety Devonian icriodontid species/subspecies from Western Europe-Morocco and North America have been analysed with regard to the Devonian standard conodont zonation. In the two areas diversification starts above the *woschmidti/hesperius* Zones and continues into about the *rhenanus/varcus* Zone. From the *ansatus* Zone on into the Upper *praesulcata* Zone diversification decreases except during the lower Famennian. During this mid-Givetian to upper Famennian period the most common icriodontid species occur in the two areas and their total range is longer than in the previous period. Icriodontids are a good tool for recognizing stages or substages in the absence of standard zone-defining species. The generic classification of Icriodontidae proposed by Sweet (1988), is in general, followed with the exception that also *Caudicriodus* is included. *Caudicriodus* and *Latericriodus* can be separated on the basis of the composition of the apparatus and the characteristics of the icriodontan Pa element.

Key words: Conodonts, Icriodontidae, Devonian, W. Europe-Morocco, N. America.

Resumen

Se analiza, respecto a la zonación estándar de conodontos, la distribución estratigráfica de noventa especies o subespecies de icriodóntidos del Devónico de Europa occidental-Marruecos y de Norteamérica. En ambas áreas la diversificación comienza por encima de las biozonas de *woschmidti/hesperius* y continúa aproximadamente hasta la de *rhenanus/varcus*. Desde la Biozona de *ansatus* hasta la de *praesulcata* Superior, la diversificación decrece salvo durante el Fameniense inferior. En este período del Givetiense medio al Fameniense superior, las especies de icriodóntidos más frecuentes aparecen en las dos áreas y su distribución total es más amplia que en el período anterior. Los icriodóntidos constituyen una buena herramienta para reconocer pisos o subpisos en ausencia de las especies guía de las zonas estándar. Se sigue la clasificación genérica de Icriodontidae propuesta por Sweet (1988), con la excepción de que también se usa *Caudicriodus*. *Caudicriodus* y *Latericriodus* pueden separarse basándose en la composición del aparato conodontal y características del elemento Pa icriodontiforme.

Palabras clave: Conodontos, Icriodontidae, Devónico, Europa occidental-Marruecos, Norteamérica.

INTRODUCTION

Icriodontidae is not the first group Devonian conodont workers are looking for. Icriodontids are commonly used for conodont biofacies analyses and considered as the "last straw" when other stratigraphically important conodont taxa are missing. However, Sweet (1988) wrote that members of Icriodontidae are important stratigraphically in shallow-water Devonian biofacies and that icriodonts have become famous as

Devonian "index fossils". We would even like to add to this that they can also be important stratigraphically also in more offshore environments during the Lower and Middle Devonian and that they provide a tool for correlation between shallower- and deeper-water facies. One of the prime purposes of this paper is to provide an overview of icriodont diversity through the Devonian as a tool for regional and inter-regional biostratigraphic correlation. Our analysis is based on data from Western Europe-Morocco and North America because the succession of icriodont faunas is most completely established and best documented in these areas. Occasionally we also refer to faunas from other areas. Thus the three range charts (Figs. 1-3) form the most important part of the paper. As already discussed in earlier papers (e.g. Klapper and Johnson, 1980), from the Lochkovian to about the mid-Givetian the succession of icriodont species/subspecies in Western Europe - North Africa (Fig. 1) is different from that in North America (Fig. 2). Icriodont data from western North America (Nevada, Utah, Canadian Rockies and North-western Canada) are separated from those of other North American areas, e.g. US Mid-Continent, Great Lakes region, Appalachians. During the late Givetian and the Late Devonian many members of Icriodontidae are almost cosmopolitan; ranges from the most common taxa in Western Europe - North Africa and North America are shown in Figure 3. For all areas ranges of the icriodont taxa are as far as possible controlled by co-occurrence of conodont-zone-defining taxa. One has to remember here that some parts of the Lower Devonian conodont zonation are still in a state of flux and are different in Western Europe-Morocco and North America.

For the Lower and Middle Devonian many of the data used herein are the same as those analysed by Klapper and Johnson (1980) and we refer the reader to this paper for most of the bibliography before 1980. The most important subsequently published Lower and Middle Devonian data used for the present analysis are grouped hereafter.

Western Europe
Ardenne.–Bultynck (1982, 1986, 1987); Borremans and Bultynck (1986); Bultynck and Hollevoet (1999); Gouwy and Bultynck (this volume).
Eifelian Hills - Rhenish Slate Mountains.- Weddige (1988); Weddige and Requadt (1985).
Barrandian.- Chlupac (2000); Chlupac and Hladil (2000); Chlupac and Lukes (1999); Chlupac *et al.* (1985); Kalvoda (1995); Slavik (2001); Weddige (1987).

North-western France.–Bultynck (1989); Bultynck and Morzadec (1979); Morzadec and Weyant (1982); Morzadec *et al.* (1991).
Spain.–Bultynck (1976a, 1979); Carls (1987, 1989); Carls and Valenzuela-Ríos (2002); García-López (1987); García-López and Alonso-Menéndez (1994); García-López and Arbizu (1993); García-López *et al.* (2002); García-López and Sanz-López (2002); Valenzuela-Ríos (1994).

Moroccan Anti-Atlas
Belka *et al.* (1997); Belka *et al.* (1999); Benfrika (1994,1999); Bultynck (1985, 1987, 1989); Bultynck and Walliser (1999); Gouwy *et al.* (2000); Lazreq (1990, 1999); Walliser *et al.* (1995).

North America
Nevada.–Johnson and Klapper (1981); Johnson *et al.* (1980, 1985); Murphy and Cebecioglu (1984); Murphy and Matti (1982); Kendall *et al.* (1983).
US Mid-Continent.–Barrick and Klapper (1992); Klapper and Barrick (1983); Klug (1983); Sandberg *et al.* (1994); Rogers (1998); Sparling (1983, 1984, 1988, 1995, 1999); Witzke *et al.* (1989).
Great Lakes.–Uyeno *et al.* (1982); Uyeno and Bultynck (1993).
Appalachians.–Denkler and Harris (1988); Kirchgasser (2000); Klapper (1981); Uyeno and Lespérance (1997);
North-western Canada.–Norris and Uyeno (1981); Uyeno (1991, 1998); Klapper (1991).
Canadian Arctic Archipelago.–Uyeno (1980, 1990).

The stratigraphic distribution of the most common Upper Devonian Icriodontidae (Fig. 3) in Western Europe and North America is primarily based on Sandberg and Dreesen (1984). Subsequently analysed literature includes Bultynck *et al.* (1998), Dreesen and Thorez (1994), Gouwy and Bultynck (2000), Johnston and Chatterton (2001), Klapper (1989), Klapper and Lane (1989), Metzger (1989), Norris *et al.* (1992), Sandberg *et al.* (1992), Schülke (1999), Vandelaer *et al.* (1989), Ziegler and Sandberg (1990), Weary and Harris (1994). Referring to the three range charts below special attention is drawn to recognition of innovations in the icriodontan element morphology, of species groups and morphologic lineages. Because of limited space we only occasionally fully discuss the systematics of species. The generic classification of the Icriodontidae used herein is discussed in the Systematic Paleontology section.
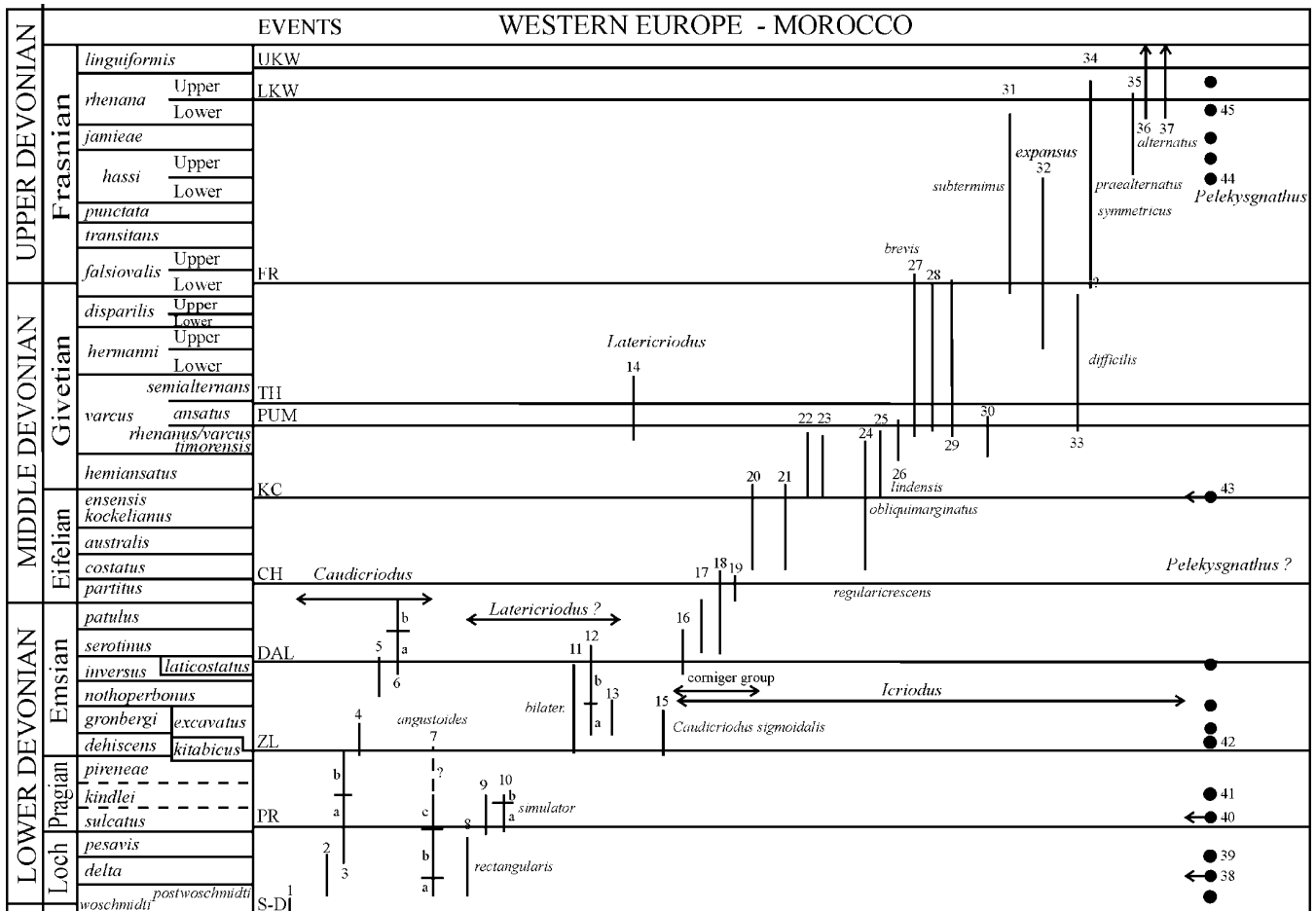
FIGURE 1–Ranges of selected Lochkovian-Frasnian icriodontid taxa in Western Europe and Morocco. 1. *Caudicriodus woschmidti woschmidti* (Ziegler) and *Caud. woschmidti hesperius* (Klapper and Murphy), Morocco; 2. *Caud. postwoschmidti* (Mashkova); 3a. *Caud. vinearum* (Carls) and *Caud.* aff *curvicauda*; 3b. *Caud. curvicauda* (Carls and Gandl); 4. *Caud. celtibericus* (Carls and Gandl); 5. *Caud. ultimus* (Weddige); 6a. *Caud. culicellus culicellus* (Bultynck); 6b. *Caud. culicellus altus* (Weddige); 7a. *Caud. angustoides bidentatus* (Carls and Gandl); 7b. *Caud. angustoides alcoleae* (Carls) and *Caud. angustoides angustoides* (Carls and Gandl); 7c. *Caud. angustoides castilianus* (Carls) and *Caud. angustoides angustoides*; 8. *Latericriodus? rectangularis rectangularis* (Carls and Gandl) and *Lat.? rect. lotzeï* (Carls); 9. *Lat. steinachensis* (Al Rawi); 10a. *Lat.? simulator* (Carls); 10b. *Lat.? simulator* and *Lat.* aff. *steinachensis*; 11. *Lat.*? *bilatericrescens* group including successivily *Lat.? bilat. gracilis* Bultynck, *Lat.? bilat. multicostatus* (Carls and Gandl) and *Lat.? bilat. bilat.* (Ziegler); 12a. *Lat.? beckmanni beckmanni* (Ziegler) and *Lat.? armoricanus* Bultynck; 12b. *Lat.? beckmanni sinuatus* (Klapper, Ziegler and Mashkova); 13. *Lat.? latus* (Al Rawi); 14. *Lat. latericrescens latericrescens* (Branson and Mehl); 15. *Caudicriodus sigmoidalis* (Carls and Gandl); 16. *Icriodus fusiformis* Carls and Gandl and *I. corniger ancestralis* Weddige; 17. *I. homorectus* Weddige (in this volume) and *I. rectirostratus* Bultynck; 18. *I. corniger corniger* Wittekindt; 19. *I. retrodepressus* Bultynck; 20. *I. struvei* Weddige; 21. *I. amabilis* Bultynck and Hollard; 22. *I. arkonensis* Stauffer; 23. *I. platyobliquimarginatus* Bultynck; 24. *I. regularicrescens* Bultynck; 25. *I. obliquimarginatus* Bischoff and Ziegler; 26. *I. lindensis* Weddige; 27. *I. brevis* Stauffer; 28. *I. latecarinatus* Bultynck; 29. *I. excavatus* Weddige; 30. *I. lilliputensis* Bultynck; 31. *I. subterminus* Youngquist; 32. *I. expansus* Branson and Mehl; 33. *I. difficilis* Ziegler and Klapper; 34. *I. symmetricus* Branson and Mahl; 35. *I. praealternatus* Sandberg, Ziegler and Dreesen; 36. *I. alternatus alternatus* Branson and Mehl; 37. *I. alternatus helmsi* Sandberg and Dreesen; 38. *Pelekysgnathus? serratus guadarramensis* Valenzuela-Rios and transitional forms with *Caud. angustoides alcoleae*; 39. *Pelekysgnathus? serratus serratus* Jentzsch; 40. Transitional forms between *Caud. angustoides* group and *Pelek.? serratus* group; 41. Earliest occurrence of *Pelek.? serratus serratus* in Bohemia (Weddige, 1987; Slavik, 2001); 42. Transitional forms between *I. regularicrescens* and *Pelekysgnathus*-like forms; 43. *Pelekysgnathus brevis* Sandberg and Dreesen; 44-45. *Pelekysgnathus* taxa. Black spots indicate occurrences of *Pelekysgnathus*(?) taxa.

Events: S-D = Silurian-Devonian boundary Event; PR = Pragian Event; ZL = Zlichov Event; DAL = Daleje Event; CH = Chotec Event; KC = Kacak Event; PUM = *pumilio* Event; TH = initial Thaganic Event; FR = Frasnes Event; LKW and UKW = Lower and Upper Kellwasser Event.
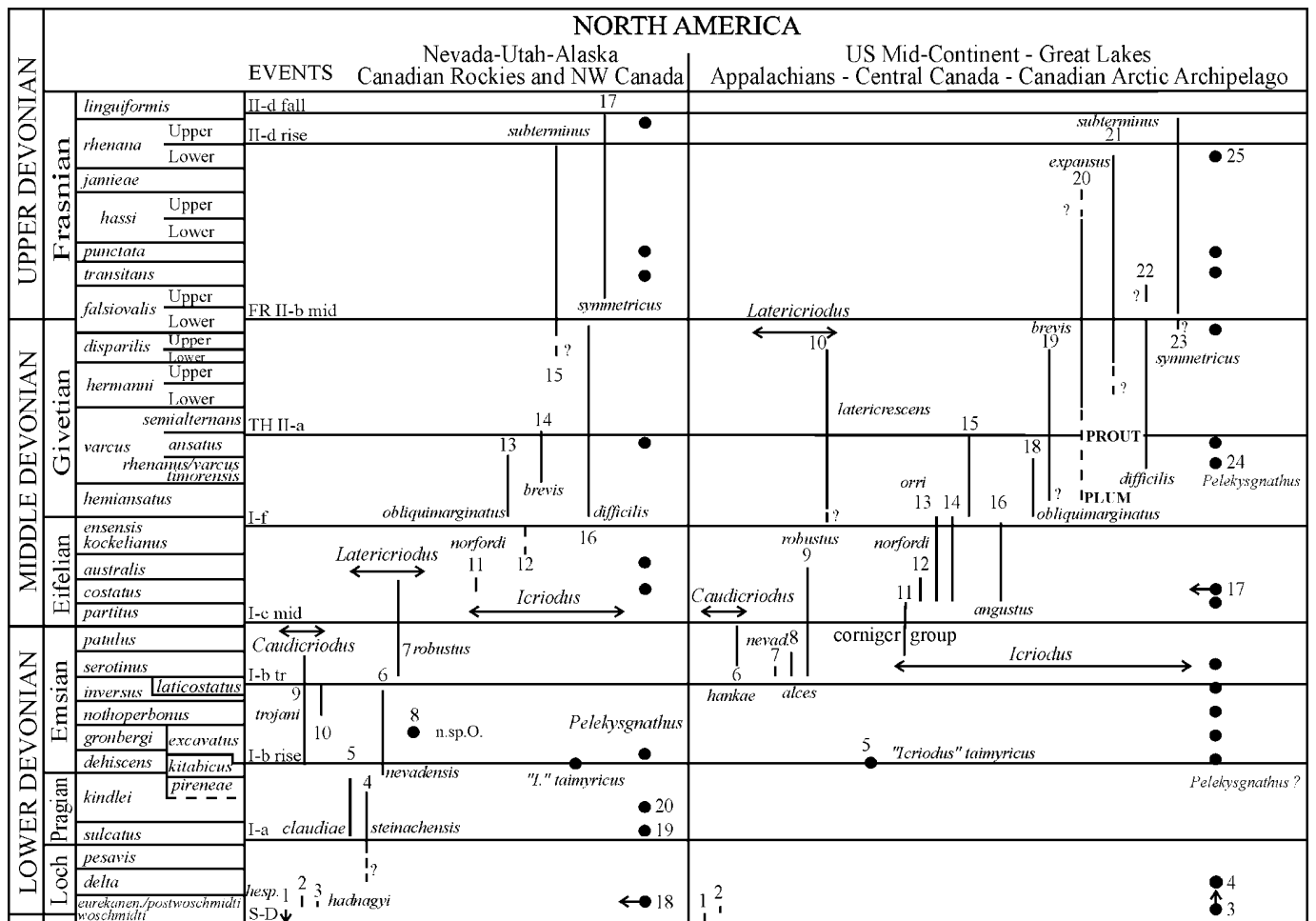
FIGURE 2–Ranges of selected Lochkovian-Frasnian icriodontid taxa in North America.

Nevada - Utah - Alaska - Canadian Rockies - NW Canada.

1. *Caudicriodus woschmidti hesperius* (Klapper and Murphy) and *Caud. woschmidti woschmidti* (Ziegler); 2. *Caud.* n.sp. G (Klapper 1977); 3. *Caud. hadnagyi* (Chatterton and Perry) including forms transitional with *Pelekysgnathus? csakyi* Chatterton and Perry; 4. *Latericriodus steinachensis* (Al Rawi); 5. *Lat. claudiae* (Klapper); 6. *Lat. nevadensis* (Johnson and Klapper); 7. *Lat. latericrescens robustus* (Orr); 8. *Lat.* n.sp. O (Johnson and Klapper 1981); 9. *Caudicriodus trojani* (Johnson and Klapper), costate form; 10. "*Caud. trojani*", with denticulate posterior-lateral process; 11. *Icriodus norfordi* Chatterton; 12. *I. stelcki* Chatterton; 13. *I. obliquimarginatus* Bischoff and Ziegler; 14. *I. brevis* Stauffer; 15. *Icriodus subterminus* Youngquist; 16. *I. difficilis* Ziegler and Klapper; 17. *I. symmetricus* Branson and Mehl; 18. *Pelekysgnathus? csakyi* (see n.° 3); 19-20. *Pelek.? serratus serratus* Jentzsch.

US Mid-Continent - Great Lakes - Appalachians - Central-Canada - Canadian Arctic Archipelago.

1. *Caud. woschmidti woschmidti* (Ziegler) and *Caud. woschmidti hesperius* (Klapper and Murphy); 2. *Caud. postwoschmidti* (Mashkova) and *Caud. eolatericrescens* (Mashkova); 3. *Pelekysgnathus*? n.sp.G Uyeno 1990; 4. *Pelek.? csakyi* Chatterton and Perry; 5. "*Icriodus*" *taimyricus* Kuzmin; 6. *Caud. hankae* (Uyeno); 7. *Lat. nevadensis* (Johnson and Klapper); 8. *Lat. alces* Uyeno and Bultynck; 10. *Lat. latericrescens latericrescens* (Branson and Mehl); 11. *Icriodus corniger* group (see Uyeno and Bultynck 1993 and Pl. 2, Figs. 30-33 herein); 12. *I. norfordi* Chatterton; 13. *I. orri* Klapper and Barrick; 14. *I. stephensoni* Sparling; 15. *I. arkonensis* Stauffer; 16. *I. angustus* Stewart and Sweet; 17. Transitional forms between *I. angustus* and *Pelekysgnathus*-like forms (see Pl. 3, Figs. 17-19); 18. *I. obliquimarginatus* Bischoff and Ziegler; 19. *Icriodus brevis* Stauffer; 20. I. *expansus* Branson and Mehl; 21. *I. subterminus* Youngquist; 22. *I. difficilis* Ziegler and Klapper; 23. *I. symmetricus* Branson and Mehl; 24. *Pelekysgnathus brevis* Sandberg and Dreesen; 25. *Pelek. planus* Sanneman.

Black spots indicate occurrences of *Pelekysgnathus*(?) taxa.

PLUM and PROUT indicate the diversified *Icriodus* faunas described by Sparling (1995, 1999) respectively from the Plum Brook Shale and the Prout Dolomite of Ohio.

Events are after Johnson and Sandberg (1989).

Series	stage	Standard Conodont Scale		Icriodus	"Icriodus"	Pelekysgnathus	Antognathus
DEVONIAN / UPPER	Famennian	praesulcata	Upper	HNG			
			Middle				
			Lower			inclinatus	volnovachensis |?
		expansa	Upper		raymondi		
			Middle				
			Lower				
		postera	Upper		darbyensis		
			Lower				
		trachytera	Upper		?		? mowitzaensis
			Lower				
		marginifera	Uppermost		costatus ←		
			Upper				
			Lower				
		rhomhoidea	Upper	CON	iowaensis iow.	chojnicensis	brevis
			Lower				
		crepida	Uppermost		?	planus	
			Upper				
			Middle				
			Lower				
		triangularis	Upper		cornutus	←	
			Middle		iow. ancylus		
			Lower	UKW			
		linguiformis		UKW			
	Frasnian	rhenana	Upper	LKW subterminus	alternatus helmsi alternatus alt.		
			Lower				
		jamieae		expansus ?|			
		hassi	Upper		praealternatus		
			Lower				
		punctata					
		transitans		diffic.			
		falsiovalis	Upper	FR	symmetricus		

FIGURE 3–Ranges of the most common Frasnian-Famennian icriodontid taxa that are almost cosmopolitan. The arrow in the range of *Pelekysgnathus planus* and *Pelek. inclinatus* indicates that *"Icriodus" cornutus* and *"I." costatus* respectively descend from the two former species.

Abbreviations: FR = Frasnes Event; LKW and UKW = Lower and Upper Kellwasser Event; CON = Condroz Event; HNG = Hangenberg Event.

Remarks on icriodontid paleoecology and dispersal are briefly expressed in a separate section.

All figured specimens, except Pl. 3, Fig. 30 are housed in the micropaleontological collection of the Royal Belgian Institute of Natural Sciences, Brussels to which the catalogue numbers prefixed "b" apply. The specimen of Pl. 3, Fig. 30 is deposited in the type collection of the Geological Survey of Canada, Ottawa (see Uyeno and Bultynck, 1993). The plates include new SEM photographs of previously figured specimens and previously unfigured specimens (b4202 - b4252) from our collections.

COMMENTS ON THE RANGE CHARTS
(Figs. 1-3)

Preliminary remark.–discussion of characteristics of icriodontid species relates to the Pa element.

The lowest Lochkovian icriodontid faunas (corresponding with lowest part of the *Monograptus uniformis* graptolite Zone) are widespread, however little diversified. *Caudicriodus woschmidti woschmidti* is known from many localities in W. Europe, in the Appalachians (Denkler and Harris, 1988) and in N.W. Canada (Chatterton and Perry, 1977). It is stressed that

the *Caud. woschmidti* fauna from the type locality in the Rhenish Slate Mountains includes specimens that are close to the *Caud. angustoides* group and the *Latericriodus? rectangularis* group (see systematic part and Pl. 1, Figs. 4-7) and therefore may be younger than the base of the Lochkovian. *Caud. woschmidti hesperius* occurs in western North America and in the Canadian Arctic Archipelago. This subspecies is also represented in the author's conodont collection from the Tafilalt (Morocco, sample TM 221 with *Monograptus uniformis angustidens* (see Hollard 1981, Tabl. 1, Rosfat-el-Hamra). Uyeno (1990, p. 51) describes a conodont fauna from the Arctic Archipelago that most likely belongs to the *hesperius* Zone and contains *Pelekysgnathus?* n. sp. G that he considers to be intermediate between the uppermost Ludlow-Pridolian *Pelek.? arcticus* and *Pelek.? csakyi* (*eurekanensis* to lowest *delta* Zone).

In W. Europe and Morocco diversification of the Icriodontidae starts in the *postwoschmidti* Zone. Two *Caudicriodus* lineages are recognized on the basis of successions in Celtiberia, the Guadarrama and the Cantabrian Zone (Spain). The main lineage includes *Caud. vinearum* → aff. *curvicauda* → *curvicauda* → *celtibericus* → *ultimus* → *culicellus* and ranges into the lowermost Eifelian. The succession within the *Caud. angustoides* group constitutes a second lineage. This group mainly occurs in the Lochkovian and the Pragian. However according to the new stratigraphic interpretation of the Santa Cruz Fm (Celtiberia) by Carls and Valenzuela-Ríos (2002) the latest forms of *Caud. angustoides angustoides* may range into the *excavatus* Zone. The *Latericriodus? rectangularis* group and the *Lat.? simulator* group make up a well separated lineage ranging from the lower Lochkovian into the middle? Pragian (= *serratus* Zone *sensu* Weddige, 1987 and Slavik, 2001). This lineage is well documented in Spain but some subspecies also occur in the Armorican Massif (Morzadec *et al.*, 1991) in Thuringia (Zagora and Zagora, 1978) and in Bohemia (Slavik, 2001).

In W. Europe and Morocco (Meseta) *Latericriodus steinachensis* enters slightly below or within the *sulcatus* Zone (e.g. Chlupac *et al.* 1985; Benfrika, 1999) whereas in western N. America this species first occurs distinctly below that zone (e.g. Klapper and Johnson, 1980: *pesavis* Zone; Murphy and Matti, 1983: *delta* Zone). Therefore migration of this species from N. America to W. Europe-Morocco may be considered.

In W. Europe the stratigraphic interval between the last occurrence of the *Lat.? simulator* group and the entry of the *Lat.? bilatericrescens* group and the *Lat.? beckmanni* group is poorly documented by icriodontids. Taxa belonging to the latter group have a broadly expanding basal cavity and may have more than one outer denticulate/costate lateral process. In *Lat.? beckmanni sinuatus* the junction between the posterior-lateral process and the main process is in a more anterior position than in the older representatives. Lochkovian-Pragian icriodontids are less diversified in N. America than in Europe. *Caudicriodus postwoschmidti* is only known from Oklahoma (Barrick and Klapper, 1992). *Caud. hadnagyi*, showing similarities with early subspecies of the *Caud. angustoides* group occurs in the *eurekanensis* Zone of Nevada and N.W. Canada. As mentioned above *Lat. steinachensis* appears in western N. America during the middle? - late Lochkovian and is respectively succeeded by *Lat. nevadensis* (from just below the *dehiscens* Zone on) and by *Lat. latericrescens robustus* ranging from the *serotinus* into the *costatus* Zone. In northern Ontario the *Lat. nevadensis* → *robustus* succession is accurately documented by the occurrence of an intermediate form, *Lat. alces*.

In the US Mid-Continent, the Great Lakes area and the Appalachians *Lat. latericrescens robustus* ranges into the *australis* Zone and its descendant *Lat. latericrescens latericrescens* enters in the *ensensis?* or equivalents of the *hemiansatus* Zone and may range into stratigraphic equivalents of the Lower *disparilis* Zone (Rogers, 1998).

Caudicriodus sigmoidalis is a characteristic taxon that is well represented in W. European and Moroccan successions. It is also known from Central Asia (Rzhonsnistskay *et al.*, 1990, Pl. 9, Figs. 3, 4).

In the Guadarrama the species co-occurs with *Polygnathus* specimens assigned by Bultynck (1976a) to *P. dehiscens*. Some specimens of this fauna (*ibidem,* Pl. 11, Fig. 7) are re-assigned here to *Polygnathus pannonicus* (Mashkova and Apekina) occurring within the *kitabicus* Zone and the lowest part of the *excavatus* Zone (Yolkin *et al.,* 1994). The wide range of variability observed in large *Caud. sigmoidalis* faunas from the Guadarrama suggests that the earliest *Icriodus* species, *I. fusiformis* and *I. corniger ancestralis*, could have evolved from this species (Pl. 2, Figs. 16-19, 23-25). Specimens with a more elongated spindle remind the *Lat.? bilatericrescens* group. *I. fusiformis* and *I. corniger ancestralis* first occur in the *laticostatus* Zone (Bultynck, 1979; Bultynck and Morzadec, 1979; García-López and Alonso-Menéndez, 1994; García-López and Sanz-López, 2002). The *I. corniger* group reaches an acme during the uppermost Emsian - early Eifelian.

Species of this group occur in the Appalachians and northern Ontario (Pl. 2, Figs. 30-33).

In other north American regions the first Eifelian *Icriodus* taxa enter in the *costatus* Zone and have not been recognized outside N. America. *I. norfordi* occurs in western N. America and in the Canadian Arctic Archipelago. *I. angustus*, *I. orri* and *I. stephensoni* are restricted to the US Mid-Continent and the Great Lakes area.

Icriodus regularicrescens is an innovative middle-upper Eifelian species. Typical specimens (Pl. 3, Figs. 1-3) occur in the *kockelianus* Zone. Early forms with a less regularly expanding outer basal cavity margin appear in the *costatus* Zone. The species is widespread, occurring in W. Europe-Morocco, US Mid-Continent (Sparling, 1995, *I. regularicrescens* subsp.), the Russian Platform (Kononova and Kim, 2001) and Australia (Mawson and Talent, 1989). Close to the base of the Givetian *I. regularicrescens* gives rise to *I. obliquimarginatus* that upward is succeeded respectively by *I. lindensis* and *I. brevis*. *I. obliquimarginatus* and *I. brevis* occur in western N. America and in the US Mid-Continent (Sparling, 1995 and herein Pl. 3, Figs. 11,12,14). The former species is also known from Central Asia (Bardashev, 1992). Together with these widespread *Icriodus* taxa several endemic *Icriodus* species of upper Eifelian and lower-middle Givetian age occur in W. Europe-Morocco and N. America (e.g. Klapper and Barrick, 1983; Sparling, 1995, 1999).

Diversity of *Icriodus* taxa decreases close to the initial Thaganic Event and is low during most of the Frasnian. From the uppermost Frasnian on and during the lower Famennian *Icriodus* diversity increases slightly. According to Sandberg and Dreesen (1984) the genus *Icriodus* died out in the Lower *rhomboidea* Zone. Frasnian and lower Famennian *Icriodus* taxa mentioned in the figures 1 to 3 occur in W. Europe-Morocco, N. America and also in other areas, e.g. the Frasnian of the Russian Platform (Ovnatanova and Kononova, 2001).

The polyphyletic nature of the genus *Pelekysgnathus* has been stressed by Chatterton and Perry (1977), Sandberg and Dreesen (1984) and Sweet (1988), mainly based on the occurrence of transitional forms between icriodontan and pelekysgnathan elements at very different stratigraphic levels. The irregular/discontinuous stratigraphic distribution of the genus has been also emphasized, however this may be explained by paleoecologic conditions. In Figures 1 to 3 the different stratigraphic levels from which *Pelekysgnathus* taxa are known are indicated and also some levels where inter-mediate forms between icriodontan and pelekysgnathan elements occur (see further in Systematic Paleontology section and Pl. 1, Figs. 12-19 and Pl. 3, Figs. 15-19).

SYSTEMATIC PALEONTOLOGY

Family ICRIODONTIDAE Müller and Müller, 1957

Members of Icriodontidae have a multimembrate apparatus including scaphate Pa elements (icriodontan) and various coniforms. Considering the total stratigraphic range of the Icriodontidae, the overall majority of coniforms co-occurring with Pa elements are acodiniform. Less frequent are nongeniculate coniforms with a more slender, high cusp of circular to oval cross section. Nongeniculate coniforms with a few ancillary denticles on the posterior margin of the cone (described as ramiforms by Serpagli, 1983) co-occur with other coniforms in a few lower Lochkovian species. Geniculate coniforms (oistodiform) have been found associated with other coniforms in two Famennian species. Except the geniculate coniforms, the cusp of the other coniforms can be striated or not. A formal assignment of these coniforms to Pb, M and S positions, that is well established in e.g. the Ozarkodinida on the basis of well-marked morphological characters, is avoided here. One of the reasons for doing so is that the morphology of the various coniforms can be very intergrading. Previously, Nicoll (1982) questioned the P-M-S series notational scheme for *Icriodus* and proposed a new one. Sandberg and Dreesen (1984) used a slightly different scheme and Schülke (1999) considers the multielement reconstruction of *Icriodus* as "far from being settled".

In the present paper Sweet's (1988, Fig. 5.17) generic classification of the Icriodontidae including the genera *Latericriodus, Icriodus, "Icriodus", Pelekysgnathus, "Pelekysgnathus"* and *Antognathodus* is followed, with the exception of *Caudicriodus* that is considered here as a valid genus, separate from *Latericriodus*.

In the genus *Pelekysgnathus* the upper surface of the Pa elements bears one longitudinal row with denticles or short transversal ridges. In all the other genera the upper surface of the main process or spindle is characterised by three longitudinal rows of denticles, nodes or ridges that can be laterally fused to form nearly transversal crests. The middle row extends behind the two lateral rows. Many species develop posteriorly a spur on the innerside and the genera *Caudicriodus*, *Latericriodus* and *Antognathus* have

one or more posterior-lateral processes. The genus *Pandoricriodus* Mawson, Talent and Furey-Greig (1995), characterised by a Pa element with a single row of denticles in the anterior part of the spindle and forming a fan-like crest, is not used here. This crest is a particular development, also occuring occasionally in Pa elements of other members of Icriodontidae e.g. *Icriodus rectirostratus* (Weddige, 1990, Pl. 3). The outline of the basal cavity of the Pa element of *Vjaloviodus taimyricus* (Kuzmin) is different from that of Pa elements of all other Icriodontidae by the absence of a posterior expansion and may be a valid criterion for the genus *Vjaloviodus* Gagiev. This systematic part is restricted to the discussion of the genera used herein.

Genus *Caudicriodus* Bultynck, 1976

Type species.–Icriodus woschmidti Ziegler, 1960.
Remarks.–Bultynck (1976a) introduced *Caudicriodus* for icriodontan Pa elements with either one or two prominent cusps in the posterior extension of the median row of the main process and with an outer posterior-lateral process emanating almost continuously from the posteriormost cusp. The posterior-lateral process can either be well developed and denticulated, e.g. *C. woschmidti*, or reduced to a distinct costa descending from the tip of the cusp, e.g. *C. angustoides* group. The other elements of the apparatus of the type species and of *C. woschmidti hesperius* are adenticulate and denticulate coniforms that have been discussed in detail by Serpagli (1983) and Simpson (1998). However, it has to be stressed that ornamentation of most coniforms of

C. woschmidti woschmidti and *C. woschmidti hesperius* is different. A similar apparatus composition can be reconstructed for *Caudicriodus postwoschmidti* on the basis of data from Drygant (1984) and Barrick and Klapper (1992). Weyant and Morzadec (1990) figure a Pa element of *Caudicriodus* cf. *postwoschmidti* co-occuring with denticulate coniforms. Carls and Gandl (1969) and Savage (1976) figure Pa elements of *Caudicriodus angustoides bidentatus* and denticulate and adenticulate coniforms respectively from the same stratigraphic level and sample. In other, younger species assigned here to *Caudicriodus* on the basis of the characteristics of the Pa element that element has been found only associated with adenticulate coniform series. Pa elements of *Caudicriodus sigmoidalis* show only a distinct cusp in early growth stages (Bultynck, 1976a, Pl. 8).

Typotype material from *C. woschmidti* (Pl. 1, Figs. 1 to 7) demonstrates that the characteristics of the Pa element as described herein, are developed in all growth stages and that the same sample produced Pa elements that are close to those of the *C. angustoides* group (Pl. 1, Figs. 6-7) and to the *Latericriodus? rectangularis* group (Pl. 1, Figs. 4-5) however without intergrading between the different forms. One Pa element has a main process with narrow transverse ridges as seen in *C. woschmidti hesperius* (Pl. 1, Fig. 1).

Genus *Latericriodus* Müller, 1962

Type species.–Icriodus latericrescens Branson and Mehl, 1938.

→

PLATE 1–(Figures 1-13, 24-26, X 30; Figs. 14-22, X 45; Fig. 23, X 100; Fig. 27, X 37). *1-3, Caudicriodus woschmidti woschmidti* (Ziegler), b806, b4202, b804. Hüinghaus-Schichten, type locality of the species, sample f, Ziegler (1960); *woschmidti* Zone. *4, 5, Latericriodus?* aff. *rectangularis* (Carls and Gandl) group, b811, b805. Same locality and lithostratigraphic unit as Figs. 1-3, sample e, Ziegler (1960); *woschmidti* Zone. *6, 7, Caudicriodus* aff. *angustoides* (Carls and Gandl) group, b4203, b807. Same locality and lithostratigraphic unit as Figs. 1-3, sample f, Ziegler (1960); *woschmidti* Zone. *8-11, Latericriodus? rectangularis lotzeï* (Carls), b552, b539, b540, b554. Cercadillo Fm, Guadarrama, localities Bultynck and Soers (1971). Fig. 8, sample Ce2-20, *pesavis* Zone. Figs. 9-11, sample Ce1-17; *pesavis* Zone. *12, 13, Caudicriodus angustoides alcoleae* (Carls), b644, b639. Same localities and formation as Figs. 8-11, sample Ce1-17; *pesavis* Zone. *14, Caudicriodus angustoides alcoleae → Pelekysgnathus? serratus guadarramensis* Valenzuela-Ríos, b630. Same localities and formation as Figs. 8-11, sample Ce1-12; *delta* Zone. *15-17, Pelekysgnathus? serratus guadarramensis,* b631, b632. Same localities and formation as Figs. 8-11, sample Ce1-15; *delta* Zone. *18, 19, Pelekysgnathus? serratus elongatus* Carls and Gandl, b4204, b4205. Same localities and formation as Figs. 8-11, sample Ce1-5, *delta* Zone. *20, 21, Caudicriodus angustoides castilianus* (Carls), b658, b662. Same localities and formation as Figs. 8-11, samples Ce 4-28 and Ce 4-71'; *kindlei* Zone. *22, 23, Pelekysgnathus? serratus serratus* Jentzsch, b655, b653. Same localities and formation as Figs. 8-11, sample Ce 4-29; *kindlei* Zone. *24, 25, Caudicriodus* aff. *curvicauda* ancestral to *Caud. curvicauda* (Carls and Gandl), b670, b668. Same localities and formation as Figs. 8-11, samples Ce 4-26 and Ce2-20; *pesavis* Zone. *26, Caudicriodus curvicauda,* b552. Same localities and formation as Figs. 8-11, sample Ce 6-35; *pyreneae*? Zone. *27, Caudicriodus celtibericus* (Carls and Gandl), b4206. Cercadillo Fm, Ce7, Guadarrama, locality Bultynck 1979, sample 1976-1; *dehiscens* Zone.

PLATE 1
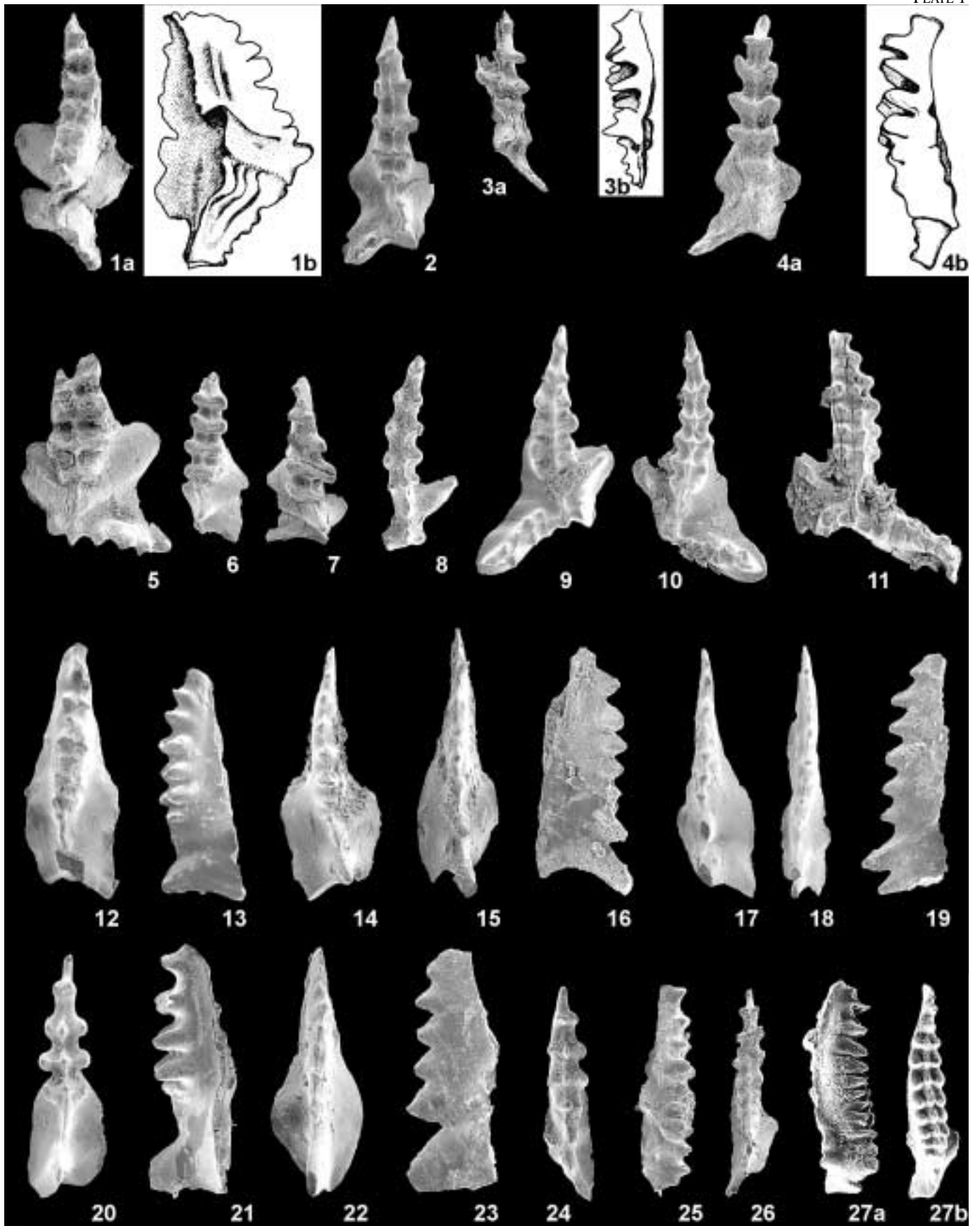
Remarks.–The Pa elements of *Latericriodus* are multisegminiscaphate and have at least an outer lateral process that joins laterally the main process either at the position of the posterior cusp or anteriorly of it, characteristic that is clearly shown from early growth stages on. The lateral process either bears one to three rows of denticles/nodes/transversal ridges or only a ridge corresponding to the axis of the process. *Latericriodus* Pa elements co-occur with adenticulate coniform series with acodinan and "M$_2$" elements e.g. *Lat. nevadensis* (Johnson and Klapper, 1981, pp. 1239, 1241) and *Lat. robustus* (Uyeno *et al.,* 1982, p. 32). Most N. American *Latericriodus* taxa belong to one morphophylogenetic lineage likely starting with *Lat. steinachensis* in the late Lochkovian, including successively *Lat. nevadensis, Lat. alces, Lat. robustus* and ending with *Lat. latericrescens* in the late Givetian (Johnson and Klapper, 1981; Murphy and Cebecioglu, 1984; Uyeno and Bultynck, 1993). In Europe-Morocco *Lat. latericrescens* is the only known species from this lineage and its stratigraphic range is restricted to the middle Givetian. The species probably migrated from N. America during the mid-Givetian.

The assignment of the European-Moroccan Lower Devonian Icriodontidae e.g. *Lat.? rectangularis, Lat.? simulator; Lat.? beckmanni* and *Lat.? bilatericrescens* to the genus *Latericriodus* is questioned because they may belong to a separate lineage and because the ontogeny and the characteristics of the lateral process(es) of the Pa element are unlike the lateral process of *Lat. latericrescens.*

Representative Pa elements of the *Lat.? rectangularis - Lat.? simulator* group have a large denticulate outer posterior-lateral process and an opposite short denticulate inner posterior-lateral process that both are developed from early ontogenetic stages on (Pl. 1, Figs. 8-11; Pl. 2, Figs. 1-4).

In early onogenetic stages Pa elements of the *Lat.? bilatericrescens – Lat.? beckmanni* group the outer posterior-lateral process is represented by a distinct ridge on the upper surface of the expanded basal cavity and only in later ontogenetic stages it grows into a denticulate process (Pl. 2, Figs. 7-8, 13-14).

Genus *Icriodus* Branson and Mehl, 1938

Type species.–*Icriodus expansus* Branson and Mehl, 1938.

Remarks.–The Pa element of *Icriodus* is uniscaphate with three longitudinal rows of denticles, nodes or ridges. The inner posterior expansion of the basal cavity may develop an oblique anteriorly directed spur that

$\rightarrow$

PLATE 2–(Figures 1-4, 23-25, X 45; Figs. 7-12, 15, X 40; 13, 14, 16-22, 29-35, X 33; 5, 6, X 65). *1-3, Latericriodus? simulator* (Carls), b567-b569. Cercadillo Fm, Guadarrama, localities Bultynck and Soers (1971), sample Ce5-32; *kindlei* Zone. *4, Latericriodus* aff. *steinachensis* (Al Rawi), b570. Same formation, locality and sample as Figs. 1-3; *kindlei* Zone. *5, 6, Latericriodus? bilatericrescens gracilis* Bultynck, b1677, b1678. Morocco, Ma'der, section Ou Driss Bultynck 1985, samples OD 3, 4; *dehiscens* Zone? *7, 8, Latericriodus? bilatericrescens multicostatus* (Carls and Gandl), b866, b867. Morocco, W Dra Plains, section Oui n' Mesdour Bultynck and Hollard (1980), sample 14-1; *dehiscens* $\rightarrow$ *gronbergi* Zone. *9-11, Latericriodus? bilatericrescens bilatericrescens* (Ziegler), b4207 (Figs. 9,11), b4208. Cercadillo Fm, Guadarrama, locality Bultynck (1979), sample Ce7-1976-4; *gronbergi* Zone. *12, Latericriodus? bilatericrescens* subsp. B Bultynck 1979, b4209. Same locality, formation and sample as Figs. 9-11; *gronbergi* Zone. *13-14, Latericriodus? beckmanni sinuatus* (Klapper, Ziegler and Mashkova), b747, b742. Suchomasty Lmst, Bohemia, Konéprusy; *serotinus* Zone. *15, Caudicriodus celtibericus* (Carls and Gandl) $\rightarrow$ *Caud. sigmoidalis* (Carls and Gandl), b4210. Cercadillo Fm, Guadarrama, locality Bultynck (1979), sample Ce7-1976-1; *dehiscens* Zone. *16-19, Caudicriodus sigmoidalis*, b736, b735, b731, b737, typical specimens. Same locality and formation as Fig. 15, sample Ce7-43a; *dehiscens* Zone. *20, 21, Caudicriodus sigmoidalis*, b741, b4211, specimens with elongated spindle tending to *Lat.? bilatericrescens* group. Same locality, formation and sample as Fig. 15; *dehiscens* Zone. *22, Icriodus corniger ancestralis* Weddige, b4212. Same locality and formation as Fig. 15, sample Ce8-1976-10; *laticostatus* Zone. *23-25, Caudicriodus sigmoidalis* $\rightarrow$ *Icriodus corniger* Wittekindt group, b4213-b4215. Same locality and formation as Fig. 15, sample Ce7-1976-4; *gronbergi* Zone. *26, 29, Icriodus corniger corniger* Wittekindt, b1707, b4216. Morocco, Ma'der, section Tizi n'Ikouach, sample TNA-15 Bultynck (1985); *partitus* Zone; Saint-Joseph Fm, Ardenne, section Béguinage Bultynck and Godefroid 1974, sample 1; *patulus* Zone. *27, 28, Icriodus retrodepressus* Bultynck, b4217, b4218. Eau Noire Fm, Ardenne, Eau Noire section Bultynck and Godefroid 1974, samples EN1-61-9 and 62-2; *partitus* Zone. *30-32, Icriodus corniger corniger*, GSC 100063, b4219, b4220. Stooping River Fm, Ontario, Uyeno and Bultynck (1993, pl. 2.3, figs. 8, 9); *serotinus* Zone; Nedrow Mbr, New York, section Oriskany Falls, sample 2, Klapper (1971); *partitus* Zone. *33, Icriodus retrodepressus*, b4221. Nedrow Mbr, New York, section Oriskany Falls, sample 2, Klapper (1971); *partitus* Zone. *34, 35, Icriodus orri* Klapper and Barrick, b4222, b4223. Dundee Lmst, Michigan, locality 1, sample 26, Bultynck 1976b; *costatus* Zone.

PLATE 2
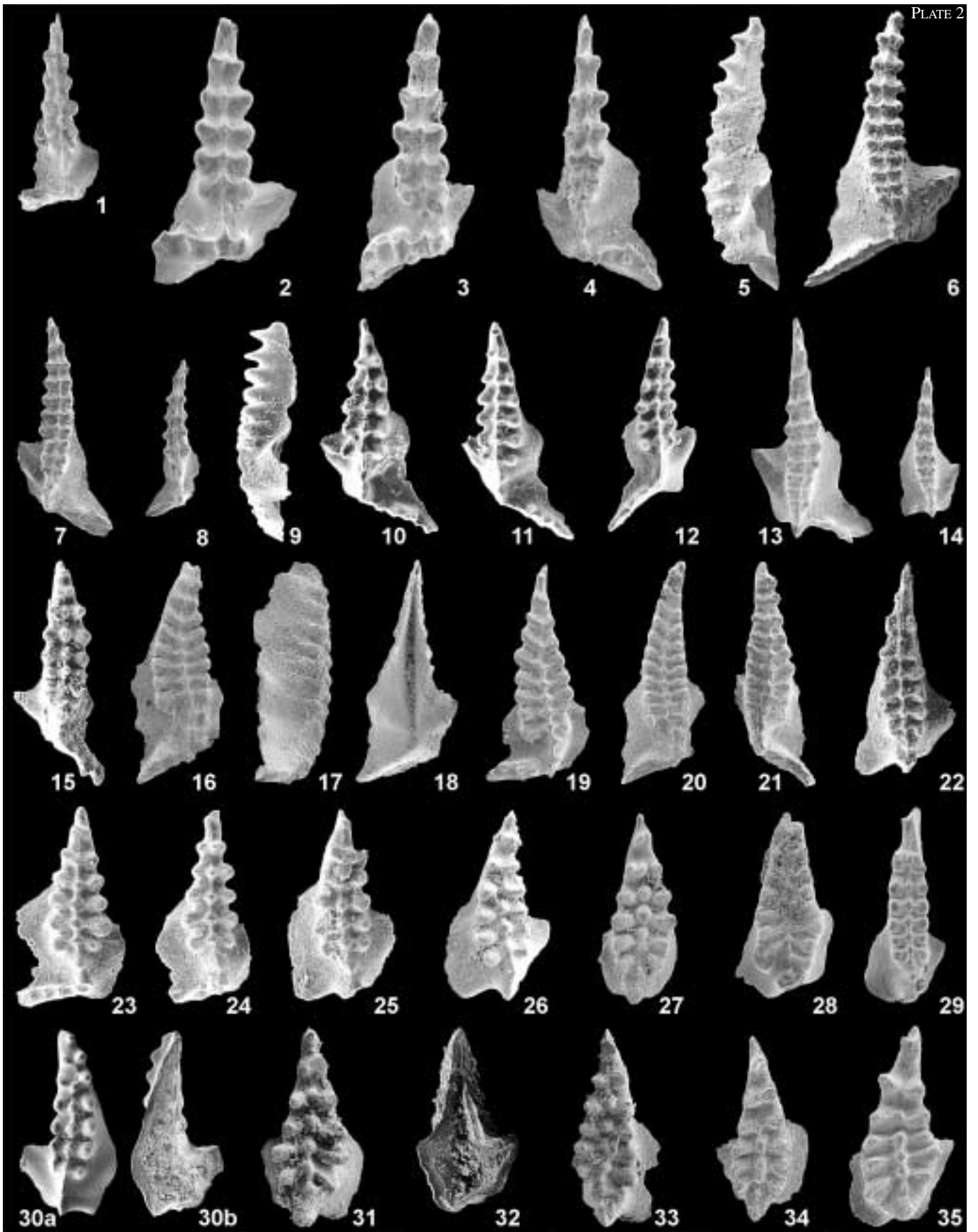
may bear a ridge or weakly developed denticles. In some taxa e.g. *Icriodus corniger* the outer posterior expansion of the basal cavity shows a small posterior lobe (Pl. 2, Fig. 22). Nicoll (1982) described fused clusters of *Icriodus expansus* containing Pa elements, a series of acodinan coniforms (Ca, Cb, Cc, Cd) and a series of nongeniculate coniforms with a circular to elliptical base and a slender more rounded cusp. All coniforms are striated. The association of these two types of coniforms with Pa elements of *Icriodus* has been documented elsewhere (e.g. Klapper and Barrick, 1983; Uyeno, 1990). However, the cusp of these cones is mostly not striated and co-occurrence of Pa *Icriodus* elements with only acodinan coniforms seems to be more common, as originally proposed by Klapper and Philip (1971). In our collections of *Icriodus corniger* and *I. regularicrescens* the Pa elements are associated with finely striated acodinan coniforms (Pl. 3, Figs. 8, 23-25). The oldest *Icriodus* taxa (*I. fusiformis* and *I. corniger ancestralis*) appear within the *inversus/laticostatus* Zone (see p. 5 herein). Sweet (1988) considers *Icriodus hadnagyi* from the Lochkovian Delorme Formation in N.W. Canada (Chatterton and Perry, 1977) as the oldest *Icriodus* species. That species is included

here in *Caudicriodus*. According to Sandberg and Dreesen (1984) *Icriodus iowaensis iowaensis* represents the youngest *Icriodus* taxon, ranging into the Lower *rhomboidea* Zone. Other "*Icriodus*" (e.g. "*Icriodus pectinatus*" and "*I.*" *costatus*) taxa ranging up into the *expansa* Zone should be treated as a different genus because they derive from *Pelekysgnathus* species.
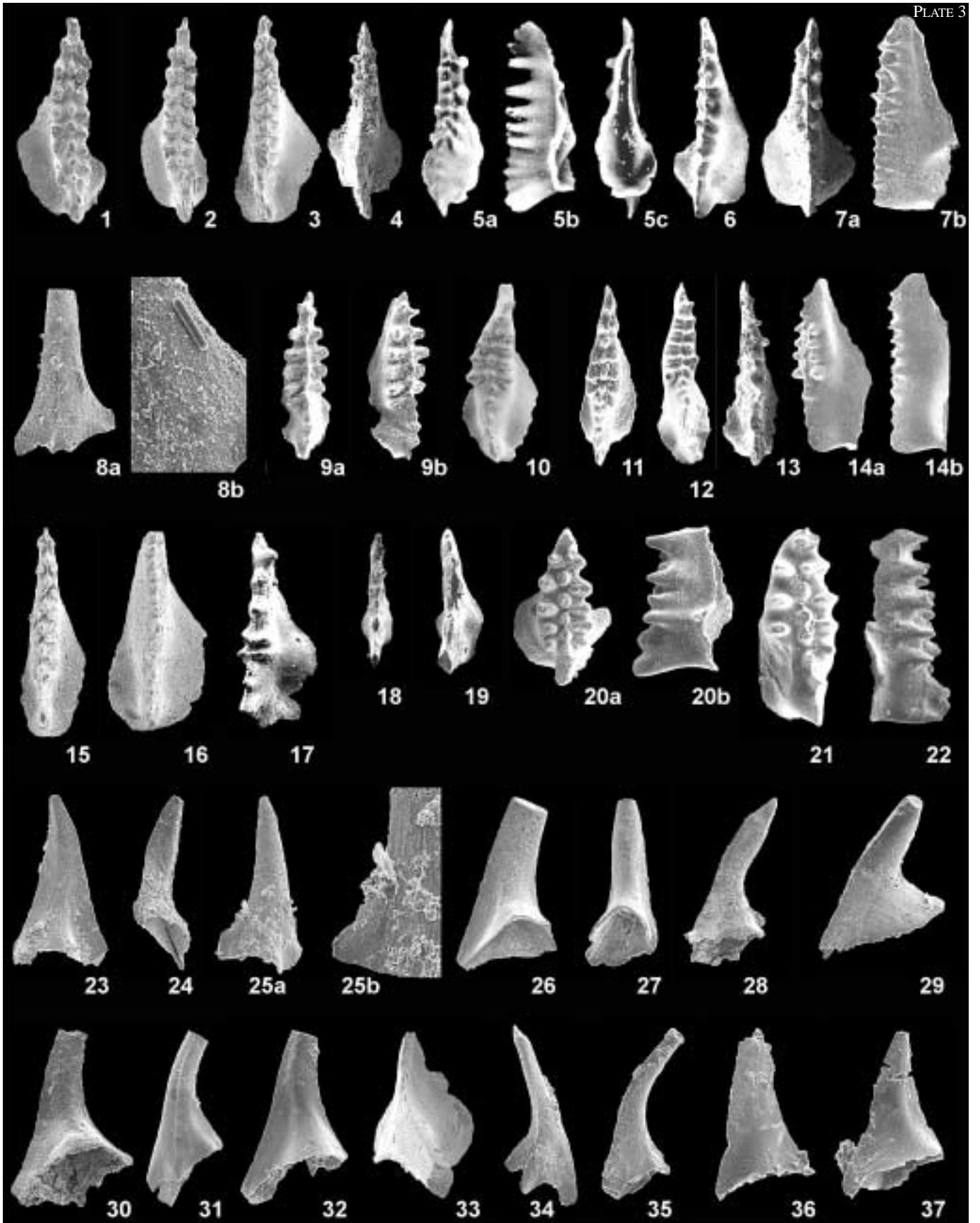
Genus *Pelekysgnathus* Thomas, 1949

Type species.–Pelekysgnathus inclinatus Thomas, 1949.

Remarks.–The Pa element of *Pelekysgnathus* is uniscaphate with one longitudinal row of denticles/ nodes or short transversal ridges on the upper surface. Sandberg and Dreesen (1984) described the complete apparatus of *Pelekysgnathus inclinatus* on the basis of a sample from the Dyer Dolomite (Colorado). Besides Pa elements it includes nongeniculate coniforms as in *Icriodus* and typical geniculate coniforms. Metzger (1989) found the same association of coniform elements in a sample with Pa elements of *P. inclinatus,* "*Icriodus*" *costatus* and "*I.*" *raymondi* from the Sheffield-Maple Mill Formation from Iowa-Nebraska.

$\rightarrow$

PLATE 3–(Figures 1-3, X 48; Figs. 4, 5, 13, 17-19, X 25; Fig. 6, X 32; Fig. 7, X 40; Figs. 8a, 23, 24, 25a, 26, 27, 29, 30, 32, 33, 36, 37, X 70; Figs. 9-12, 14, 21, 22, X 50; Fig. 15, X 85; Figs. 16, 20, 31, 34, 35, X 60; Fig. 28, X35; Figs. 8b, 25b, X250). *1, 8, Icriodus regularicrescens* Bultynck, b4224, b4225, Pa and acodinan elements. Unnamed limestone member in upper part of Jemelle Fm, Ardenne, section Nismes-212, sample N2, Bultynck and Godefroid (1974); *kockelianus* Zone. *2, 3, Icriodus regularicrescens*, b4226, b4227. Same lithostratigraphic unit, Ardenne, Wellin, sample FDV 3-2, Godefroid (1968); *kockelianus* Zone. *4-7, 13, Icriodus obliquimarginatus* Bischoff and Ziegler, specimens with either regular or irregular denticulation on the spindle and either an oblique or vertical border in lateral view. b1864, Hanonet Fm, Ardenne, Givet, section Mont d'Haurs, Bultynck (1987), sample MH 3; *hemiansatus* Zone; b939, b1867, b1873, b1869, Morocco, Tafilalt, section Bou Tchrafine, Bultynck (1987), samples BT 19, BT 19, BT 20 (*timorensis* Zone), BT 17 (*hemiansatus* Zone). *9, 10, Icriodus platyobliquimarginatus* Bultynck, b1885. Trois-Fontaines Fm, Ardenne, Menil, sample 67, Coen *et al.* (1974); *hemiansatus* Zone? b4228. Ferron point Fm, Michigan, locality 2a, sample 2, Bultynck (1976b); *timorensis* Zone? *11, 12, 14, Icriodus obliquimarginatus,* b4229, b4230, b4231. Same lithostratigraphic unit, locality and sample as Fig. 10. *15, 16, Icriodus regularicrescens* with narrow spindle and reduced lateral rows denticles compared with a *Pelekysgnathus*-like form from the same sample, b4232, b4233. Same lithostratigraphic unit, locality and sample as Figs. 2, 3. *17-19, Icriodus angustus* Stewart and Sweet with reduced denticulation on the spindle and two *Pelekysgnathus*-like forms from the same sample, b4234-b4236. Dundee Lmst, Michigan, locality 1, sample 01, Bultynck (1976b); *costatus* Zone? *20a, 20b, Icriodus lilliputensis* Bultynck, b1895, b1896. Fromelennes Fm, Ardenne, Flohimont, section W, Bultynck (1987), sample From W-4; *rhenanus/ varcus* Zone; Terres d'Haurs Fm, Ardenne, Givet, Mont d'Haurs section, Bultynck (1987), sample MH 42; *timorensis* Zone. *21, 22, Icriodus subterminus* Youngquist, b1132, b4237. Blacourt Fm, France, Ferques, section Brice *et al.* (1979), sample 18; Morocco, Tafilalt, section Bou Tchrafine, sample BT 37, Bultynck (1986); Lower *falsiovalis* Zone, with *Skeletognathus norrisi* (Uyeno). *23-25,* Acodinan elements, b4238-b4240. Co-occurring with Pa elements of *Icriodus corniger corniger* of Pl. 2, Fig. 29. *26, 27, 29,* Coniforms, b4241-b4243. Co-occurring with Pa elements of *Latericriodus? rectangularis* (Carls and Gandl) and *Pelekysgnathus? serratus elongatus* Carls and Gandl of Pl. 1, Figs. 18, 19. *28, 30-32,* Coniforms, b4244-b4247. Co-occurring with Pa elements of *Lat.? rectangularis lotzei* (Carls), *Caudicriodus angustoides alcoleae* (Carls) and *Pelekysgnathus? serratus guadarramensis* Valenzuela-Rios of Pl. 1, Fig. 14. *33,* Coniform, b4248. Co-occurring with Pa elements of *Pelekysgnathus? serratus* Jentzsch group, Cercadillo Fm, Guadarrama, localities Bultynck and Soers (1971), sample Ce1-15'. *34-37,* Coniforms co-occurring with Pa elements of *Pelekysgnathus? serratus elongatus*, b4249-b4252. Same localities and formation as Fig. 33, sample Ce1-11.

PLATE 3

Species generally assigned to the genus *Pelekysgnathus* range from the Ludlow-Pridolian (*P. arcticus* and *P. index)* into the Upper *praesulcata* Zone (*P. inclinatus*). However, the geniculate coniform has been only recognized in the type species of the genus. In some other Lower and Middle Devonian and Frasnian species assigned to *Pelekysgnathus* the Pa elements are associated with acodinan elements and coniforms with a circular or elliptical cross section, whether or not striated (e.g. Uyeno, 1981, 1990). There are also major gaps in the stratigraphic distribution of Devonian *Pelekysgnathus* taxa, mainly in the Middle Devonian and Lower to Middle Frasnian in Europe and Morocco (Fig. 1) and to a lesser degree in N. America (Fig. 2). Moreover, at different stratigraphic levels in the Lower Devonian and Eifelian occur transitional forms between icriodontan and pelekysgnathan elements (Pl. 1, Figs. 12-19; Pl. 3, Figs. 15-19). In the Famennian transitional forms between Pa elements of *Pelekysgnathus inclinatus* and *Icriodus? costatus* and Pa elements of *P. planus* and *I.? cornutus* occur. Sandberg and Dreesen only assign *P. brevis, P. planus* and *P. inclinatus* to the genus *Pelekysgnathus.*

The question whether or not the uppermost Silurian to lower Frasnian Icriodontidae with single-rowed Pa elements should be assigned to the genus *Pelekysgnathus* has been raised regularly (e.g. Chatterton and Perry, 1977; Sandberg and Dreesen, 1984; Sweet, 1988). Present understanding of the apparatus of these species does not provide a clear answer to the question. Therefore the generic assignment of all *Pelekysgnathus* taxa, except *Pelekysgnathus brevis, P. plana* and *P. inclinata*, is here questioned. In characteristic Pa elements of the two last mentioned species the rim of the enlarged posterior part of the basal cavity is clearly downcurved.

Genus *Antognathus* Lipnjagov, 1978

Type species.–Antognathus volnovachensis Lipnjagov, 1978.
*Remarks.–*See Sweet (1988).

REMARKS ON ICRIODONTID PALEOECOLOGY AND DISPERSAL

The widely used biofacies model confining Icriodontidae (*Icriodus* s.l.) to inshore shallow-water environments has to be considered as a generalized model. In the Emsian-Eifelian-early Givetian of the

N. Tafilalt *Latericriodus?* and *Icriodus* taxa are common, sometimes abundant, in condensed cephalopod limestone successions (Bultynck and Hollard, 1980; Bultynck, 1985, 1987, 1998) co-occurring with *Pandorinellina* and/or *Polygnathus* and *Tortodus* taxa, e.g. samples BT14 to BT15a (Bultynck, 1987, Fig. 4) in which *Icriodus regularicrescens* and *Tortodus kockelianus* are common to abundant. In the same section *I. obliquimarginatus* and *I. brevis* are common in the early Givetian. These two species also occur in early Givetian shallow-water platform carbonates of the Ardenne (ibidem), however they are accompanied there by other *Icriodus* taxa (e.g. *I. excavata*) that are not represented in the Tafilalt succession. Thus there certainly exists different environmental adaptations within *Icriodus* considering species. The Frasnian *Icriodus symmetricus* is another example of a conodont species that can be abundant in different environments. In the lower Frasnian of the Ardenne it can be abundant in an icriodid-polygnathid biofacies (Vandelaer *et al.*, 1989, Tabl. 9), whereas in an upper Frasnian sample (Bultynck *et al.*, 1998, Tabl. 3, sample C16) it is extremely abundant (778 Pa elements) together with 425 *Palmatolepis* Pa elements and 1278 *Polygnathus* Pa elements.

Diversity of Icriodontidae is lowest during the *woschmidti/hesperius* Zones and the two subspecies occur in the two major areas discussed. However, the former mainly occurs in W. Europe, the latter in western N. America. From the *postwoschmidti/eurekanensis* Zones to the *ansatus* Zone diversity increases, with different rates in the two areas. Klapper and Johnson (1980) came to the conclusion that almost all *Icriodus* (*Caudicriodus*, *Latericriodus*(?) and *Icriodus* herein) were endemic before the mid Middle Devonian. According to our data this level needs to be lowered into the upper part of the *serotinus* Zone. At that time species of the *Icriodus corniger* group, originating in W. Europe in the *laticostatus* Zone, occur in N. Ontario (Uyeno and Bultynck, 1993) and later, during the *partitus* Zone in New York (herein, Pl. 2, Figs. 31-33). Early forms of *I. regularicrescens* appear in W. Europe in the *costatus* Zone. *I. regularicrescens* subsp. and related forms occur in the US Mid-Continent during the early Givetian (Sparling, 1995). *Icriodus obliquimarginatus* is a good example of a widespread early Givetian *Icriodus* species (see p. 7).

From the initial Thaganic Event, diversity of Icriodontidae decreases and during the Frasnian and Famennian it is much lower than in the previously

discussed periods, except during the lower Famennian. In the late Givetian-late Famennian time interval the most common icriodontid species are widespread. The changing dispersal capabilities of icriodontidae during the Devonian can be explained by implying that they lived in the upper part of the water column mostly preferring inner shelf areas to outer shelf areas. During important sea-level rises some less specifically adapted species may have migrated freely, others not. We refer here to the upper *serotinus*-Zone eustatic rise I-c (Johnson *et al.,* 1985; Johnson and Sandberg, 1989) for the extensive dispersal of the *Icriodus corniger* group and to the *ensensis*-Zone eustatic rise I-f for the extensive dispersal of *Icriodus regularicrescens*. Endemism of Lower Devonian *Caudicriodus* and *Latericriodus*(?) species that occur in more outer shelf areas can be explained by the relatively low sea-level stand during most of the Lower Devonian in comparison to the Middle-Upper Devonian and the presence of important continental barriers, in N. America (Heckel and Witzke, 1979, Text-Fig. 3a) during this period.

CONCLUSIONS

Caudicriodus differs from *Latericriodus* in apparatus composition and characteristics of the posterior-lateral process of the Pa element.

Although the coniforms of the apparatus of *Latericriodus* and *Icriodus* are most likely of the same type the two genera can be distinguished by the posterior-lateral process in the Pa element of *Latericriodus*. A comparable criterion was used to distinguish *Pandorinellina* from *Ozarkodina*, the former having a Sa element with two lateral and one posterior denticulate process, the latter having a Sa element with only two lateral denticulate processes (Klapper and Philip, 1972).

The *Latericriodus steinachensis* → *nevadensis* → *alces* → *robustus* → *latericrescens* lineage recognized in N. America and the succession of *Latericriodus?* species/subspecies in W. Europe constitute two geographically separated evolving groups. *Pelekysgnathus* as currently used is certainly polyphyletic. The oldest *Icriodus* species are of late Emsian age (*inversus/laticostatus* Zone).

Ranges of Icriodontidae shown in Figures 1-3 demonstrate that they can be succesfully used for recognizing stages or subdivisions of stages in absence of standard-zone-defining species.

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CONODONT BASED GRAPHIC CORRELATION OF THE MIDDLE DEVONIAN FORMATIONS OF THE ARDENNE (BELGIUM): IMPLICATIONS FOR STRATIGRAPHY AND CONSTRUCTION OF A REGIONAL COMPOSITE

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Abstract

High-resolution correlation of nine Middle Devonian sections of the Belgian Ardenne is established using graphic correlation. The measured ranges of 76 conodont taxa, 70 coral taxa, 93 brachiopod taxa, 32 spore taxa and 19 acritarch taxa have been assembled into a chronostratigraphic framework. The developed regional composite subdivides the Middle Devonian into 1205 Composite Standard Units (Eifelian = 724 CSU, Givetian = 481 CSU). It provides a higher stratigraphic resolution than the traditionally used conodont zonation. The Ardenne chronostratigraphic diagram reveals the diachronous nature of some Middle Devonian sedimentary units. It shows a major transgression-regression cycle in the mixed siliciclastic-carbonate Eifelian succession. The transgression with the development of stromatoporoid biostromal limestone in the Couvin area occurs during the *costatus* and *australis* Zones. The regression that starts in the *kockelianus* Zone continues during the *ensensis* Zone and involves a sedimentary gap in the Aisemont area. This sedimentary gap might correlate with Struve's Great Gap (Struve, 1990). The regression continues during the lowermost part of the Givetian (*hemiansatus* Zone) but is interrupted by a small transgressive phase in the uppermost part of the *ensensis* Zone with development of limestone in the southern part of the Dinant Synclinorium (Couvin-Givet, Wellin and Jemelle areas). The rest of the Givetian carbonate platform succession shows a transgression comprising two phases. The first one takes place during the uppermost part of the *hemiansatus* Zone and the lower part of the *timorensis* (Lower *varcus)* Zone with the development of limestone in the southeastern part of the Dinant Synclinorium, the Vesdre nappe and the Namur Synclinorium. The second pulse, a deepening event with deposition of shales in the whole area, occurs slightly below the base of the *ansatus* Zone. The graphic correlation links the local brachiopod, coral, spores and acritarch ranges to the standard conodont zonation.

Key words: Middle Devonian, Ardenne, graphic correlation, conodonts.

Resumen

En el presente trabajo se ha realizado una correlación de alta resolución en nueve secciones del Devónico Medio de las Ardenas Belgas mediante técnicas de correlación gráfica. Los rangos de 76 taxones de conodontos, 70 de corales, 93 de braquiópodos, 32 de esporas y 19 de acritarcos han sido reunidos en un marco cronoestratigráfico. La composición regional permite subdividir el Devónico Medio en 1.205 unidades compuestas (Eifeliense = 724 UC, Givetiense = 481 UC), proporcionando una resolución estratigráfica más alta que la división en zonas de conodontos tradicionalmente utilizada. El diagrama cronoestratigráfico revela la naturaleza diacrónica de algunos depósitos del

Devónico Medio y muestra un ciclo importante de transgresión/regresión en la sucesión siliciclástica-carbonatada. La transgresión implica el desarrollo de calizas biostrómicas en el área de Couvin y abarca las zonas de *costatus* y *australis.* La regresión comienza en la zona de *kockelianus,* continúa en la zona de *ensensis* e implica finalmente una interrupción de la sedimentación en el área de Aisemont, que puede coincidir con el Great Gap de Struve. La regresión continúa durante la parte más baja del Givetiense (zona de *hemiansatus),* pero está interrupida por una transgresión menor al final de la zona de *ensensis,* con desarrollo de calizas en la parte meridional del sinclinorio de Dinant (áreas de Couvin-Givet, Wellin y Jemelle). El resto de la sucesión calcárea de la plataforma givetiense muestra una transgresión con dos etapas. La primera comprende la parte superior de la zona de *hemiansatus* y la parte más baja de la zona de *varcus,* con desarrollo de calizas en la parte sudeste del sinclinorio de Dinant, el manto de Vesdre y el sinclinorio de Namur. La segunda etapa implica una profundización con desarrollo de pizarras en toda el área y ocurre cerca de la base de la zona de *ansatus.* La correlación gráfica liga los rangos de braquiópodos, corales, esporas y acritarcos a la zonación estándar de conodontos.

Palabras clave: Devónico Medio, Ardenas, Correlación gráfica, Conodontos.

INTRODUCTION AND METHOD

The formational terminology and definitions for the Middle Devonian of the Ardenne revised by the Belgian National Subcommission on Devonian Stratigraphy (Bultynck *et al.,* 1991) were used.

The method used in this paper is Graphic Correlation developed by Shaw (1964) for biostratigraphical correlation of multiple sections and extended and discussed by Miller (1977), Sweet (1979) and Edwards (1984, 1989). In 1995 an SEPM special volume on graphic correlation was published (Mann & Lane, 1995). The method is primarily based on biostratigraphic fossil range data but can also be used with other data related to a vertical measured scale (geophysical log data, stable isotope data, lithological key marker beds…). It is a powerful tool for the analysis of the synchroneity and diachroneity of geological events. Compared to the traditional biostratigraphy using fossil zones for correlation, the method integrates all stratigraphic events. For graphic correlation of the Middle Devonian of the Ardenne, a software program for the PC (GraphCor 3.0) (Hood, 1998) was used.

GEOLOGICAL SETTING

During the Middle Devonian, the Ardenne region was situated in the subtropic regions of the Southern Hemisphere and constituted an area at the border of the Old Red Continent. A thick Paleozoic succession (Cambrium to Carboniferous) can be observed. The deposits have been deformed by Caledonian and Variscan compression and form mostly E-W and NE-SW oriented folds.

During the Eifelian an extensive ramp system characterized by a mixed siliciclastic-carbonate sedimentation was developed in the Ardenne region (Prèat, 1989). Differential subsidence and sea-level changes lead to distinct facies sequences (Prèat, 1989) with shale deposits with various bioconstructions in the SW of the Ardenne and more sandy deposits in the NE. The Eifelian ramp system evolved into a carbonate platform in the Givetian (Préat & Mamet, 1989) consisting of shallow-upward subtidal to supratidal cycles that locally pass into evaporite-carbonite cycles along an arid coastline (Préat & Rouchy, 1986).

DATA

The database for the Middle Devonian of the Ardenne includes 9 sections, illustrating the differences in the sedimentary development in the various depositional settings, and spread over the different structural units of the Ardenne: the Couvin-Givet area, the Pondrôme-Wellin-Resteigne area, the Jemelle area, the Villers-St-Gertrude area, the Remouchamps area and the Tailfer-Rivière area

in the Dinant Synclinorium, the Aisemont area and the Orneau area (Alvaux-Mazy) in the Namur Synclinorium and the Vesdre area (Fig. 1). In only two areas the Middle

Bultynck & Godefroid (1974) and Bultynck *et al.* (1982). The Eau Noire and Couvin Formations are described in a continuous section along the Eau Noire river
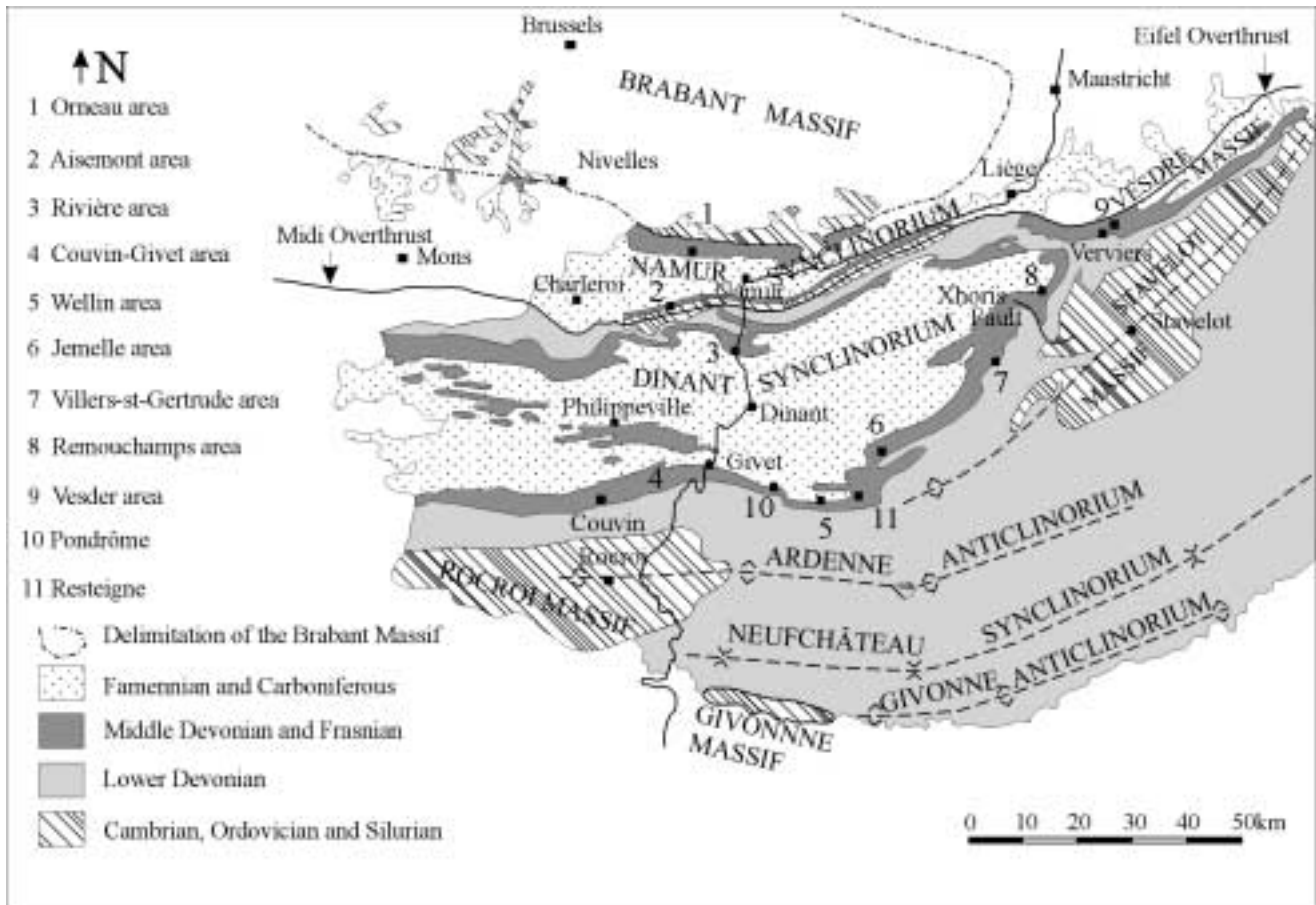
FIGURE 1–Location of the studied sections.

Devonian (Orneau and Aisemont) is exposed in a continuous outcrop, for the others areas, the sections were build from several outcrops allowing reconstruction of nearly complete columnar sections. Most data have been taken from literature exept for the additional conodont data in the railway section of Aisemont and the Moulin Boreux cliff (Givet) and the conodont data in the Orneau area. The conodont collections of the master thesis of Laenen (1982), of Bultynck & Boonen (1976) and of Coen-Aubert & Coen (1974) have been reviewed to obtain a uniform taxonomic approach.

Couvin-Givet area

    The conodont and brachiopod data of the St-Joseph Formation, studied in St-Joseph (Nismes) were taken from Bultynck (1970), Demeersseman (1980),

in Couvin (Bultynck, 1970; Bultynck & Godefroid, 1974; Bultynck *et al.,* 1982). Several small outcrops W of Couvin and the Chemin de Boussu roadcut represent the Jemelle Formation (Bultynck, 1970; Bultynck & Godefroid, 1974, Bultynck & Hollevoet, 1999). A bioherm type limestone body is located in the upper part of the formation (Bultynck, 1965). The Hanonet Formation, is exposed in the Couvinoise quarry (Bultynck & Hollevoet, 1999). The Mont d'Haurs sections in Givet expose the Trois Fontaines, the Terres d'Haurs and the Mont d'Haurs Formations (Bultynck, 1987). The uppermost part of the Givetian was studied along the road to Flohimont in Fromelennes (Bultynck, 1974; Bultynck, 1987; Bultynck *et al.,* 2001), in the Cul de Houille Quarry (Préat & Carliez, 1996) and on the Moulin Boreux cliff (Errera *et al.,* 1972).
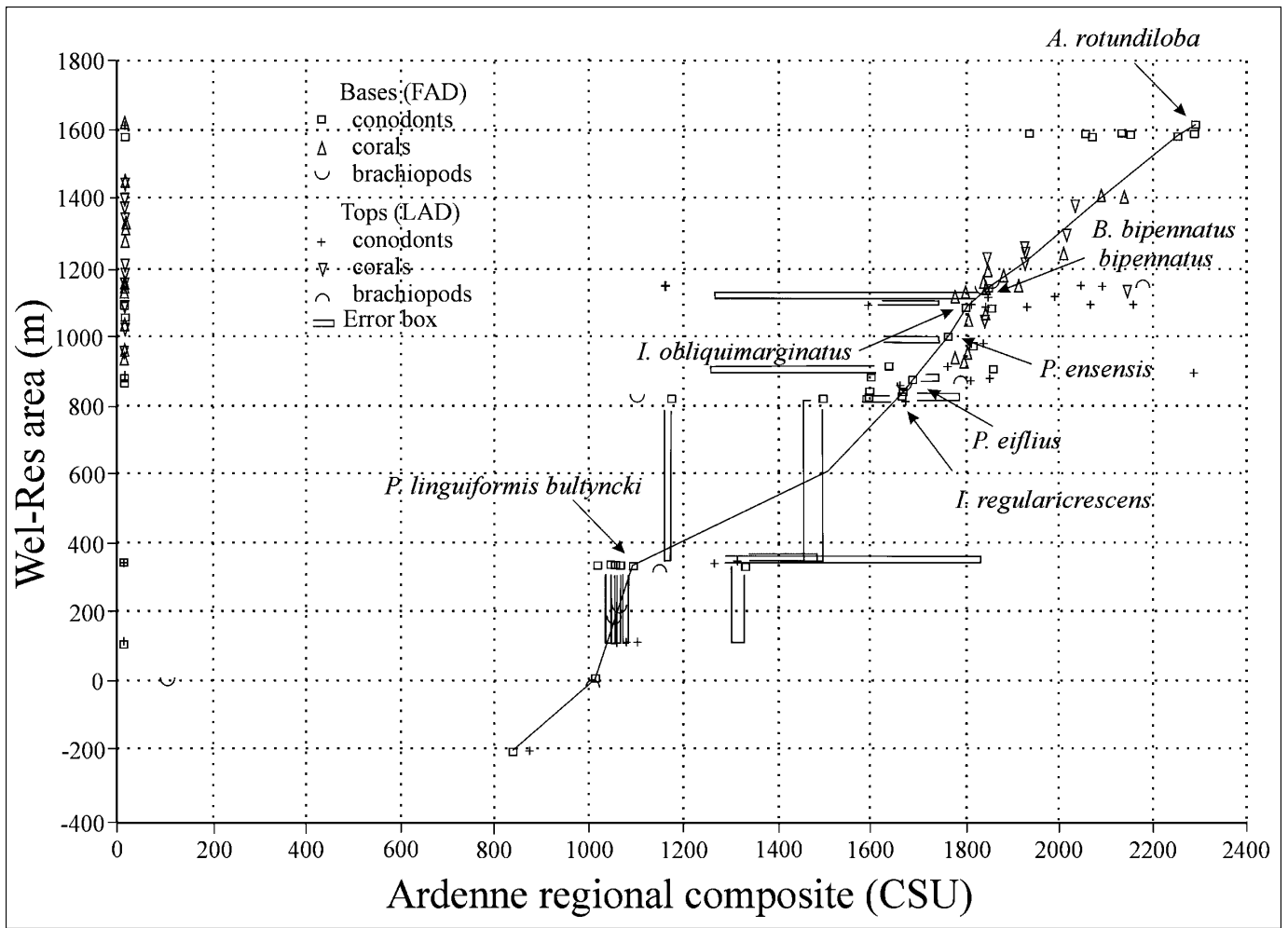
FIGURE 2–Graphic correlation of the Wellin-Resteigne (Wel-Res) area with the Ardenne regional composite.
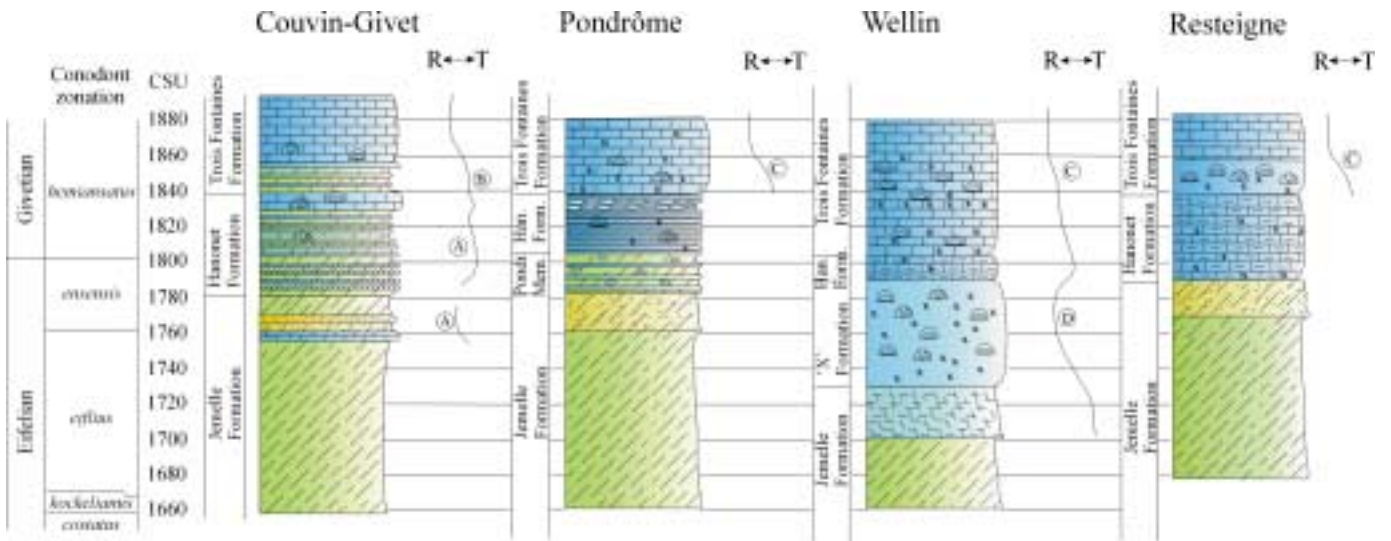
FIGURE 3–Time-rock chart of the lithologies around the Eifelian-Givetian boundary in the Couvin-Givet, Pondrôme, Wellin and Resteigne areas. T-R curves shown are based on calcareous microfacies evolution (B: Préat, 1989; C: Préat, 1984; D: Coen-Aubert *et al.,* 1990) and evolution in brachiopod assemblages (A: Bultynck & Hollevoet, 1999). Legend: see Fig. 11.
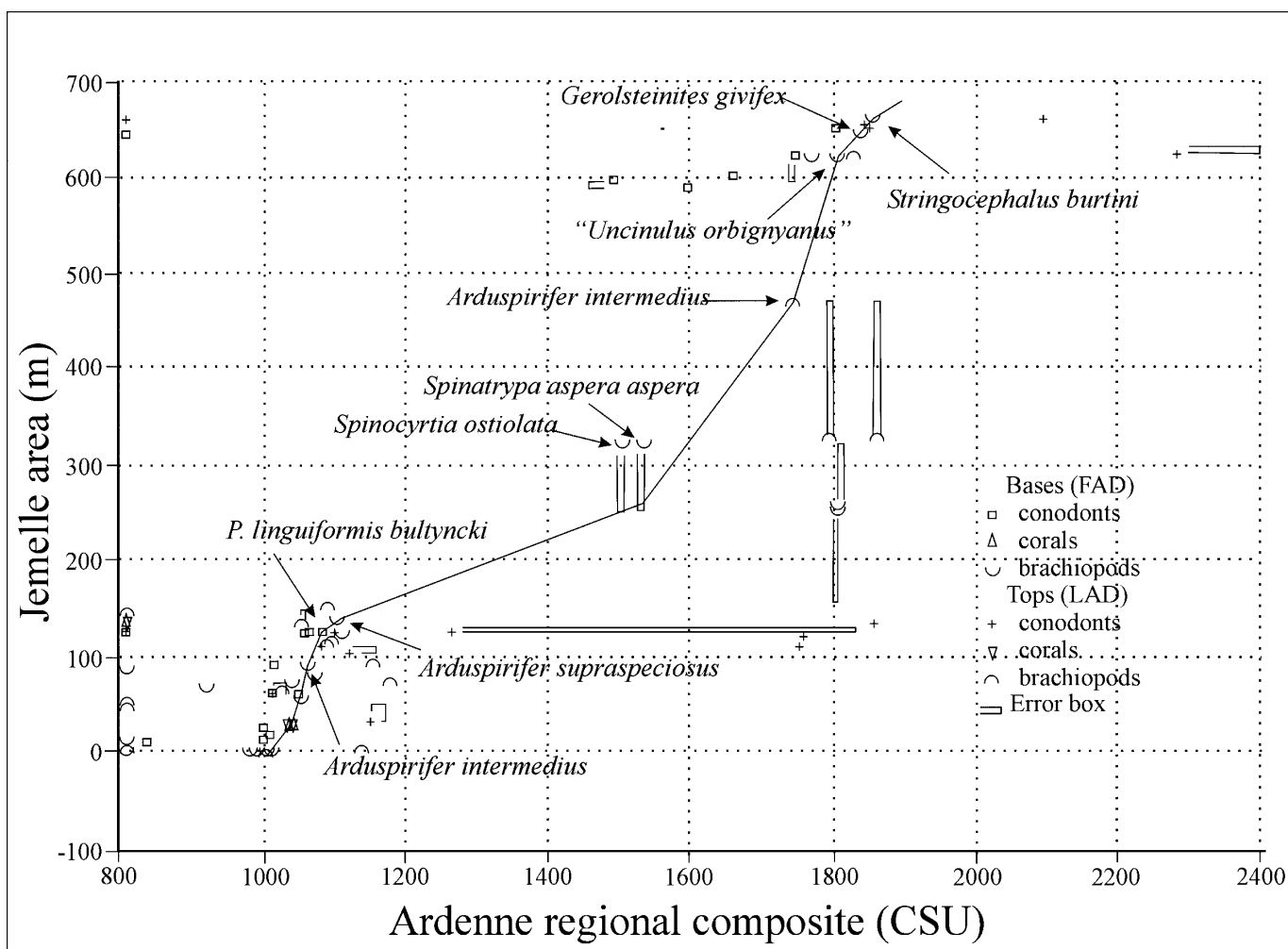
FIGURE 4–Graphic correlation of the Jemelle section with the Ardenne regional composite.

Pondrôme-Wellin-Resteigne area

The Halma 1-2 sections (Bultynck & Godefroid, 1974; Godefroid, 1968) expose the St-Joseph and Eau Noire Formations that are thicker than in the Couvin-Givet area. The Jemelle Formation was described in the Halma 7 and the Fond des Vaux 1 sections (Bultynck & Godefroid, 1974). In the Pondrôme area, the Jemelle Formation contains an extra member, the Pondrôme Member (Godefroid, 1995; Coen-Aubert, 1997). The 'X' Formation, described in the Fond des Vaux sections 2 and 4 is only found in the Wellin area (Coen-Aubert, 1989; Coen-Aubert *et al.,* 1991; Coen-Aubert, 1998). The Lomme Formation is present between the Jemelle Formation and the Hanonet Formation in the Resteigne area (Coen-Aubert, 1997; Tourneur, 1985). The Hanonet Formation is exposed in the eastern part of the Fond des Vaux quarry (Coen-Aubert, 1989). The Trois Fontaines Formation was studied by Tourneur, (1985), Coen-Aubert (1986, 1988, 1989, 1990, 1996, 1997, 1998) and Préat (1984) in the Limites quarry in Resteigne and in the Fond des Vaux quarry in Wellin. Préat (1984) and Tourneur (1985) described the Terres d'Haurs Formation in the Limites quarry in Resteigne. The Mont d'Haurs Formation is exposed in the same quarry (Préat, 1984; Tourneur, 1985;
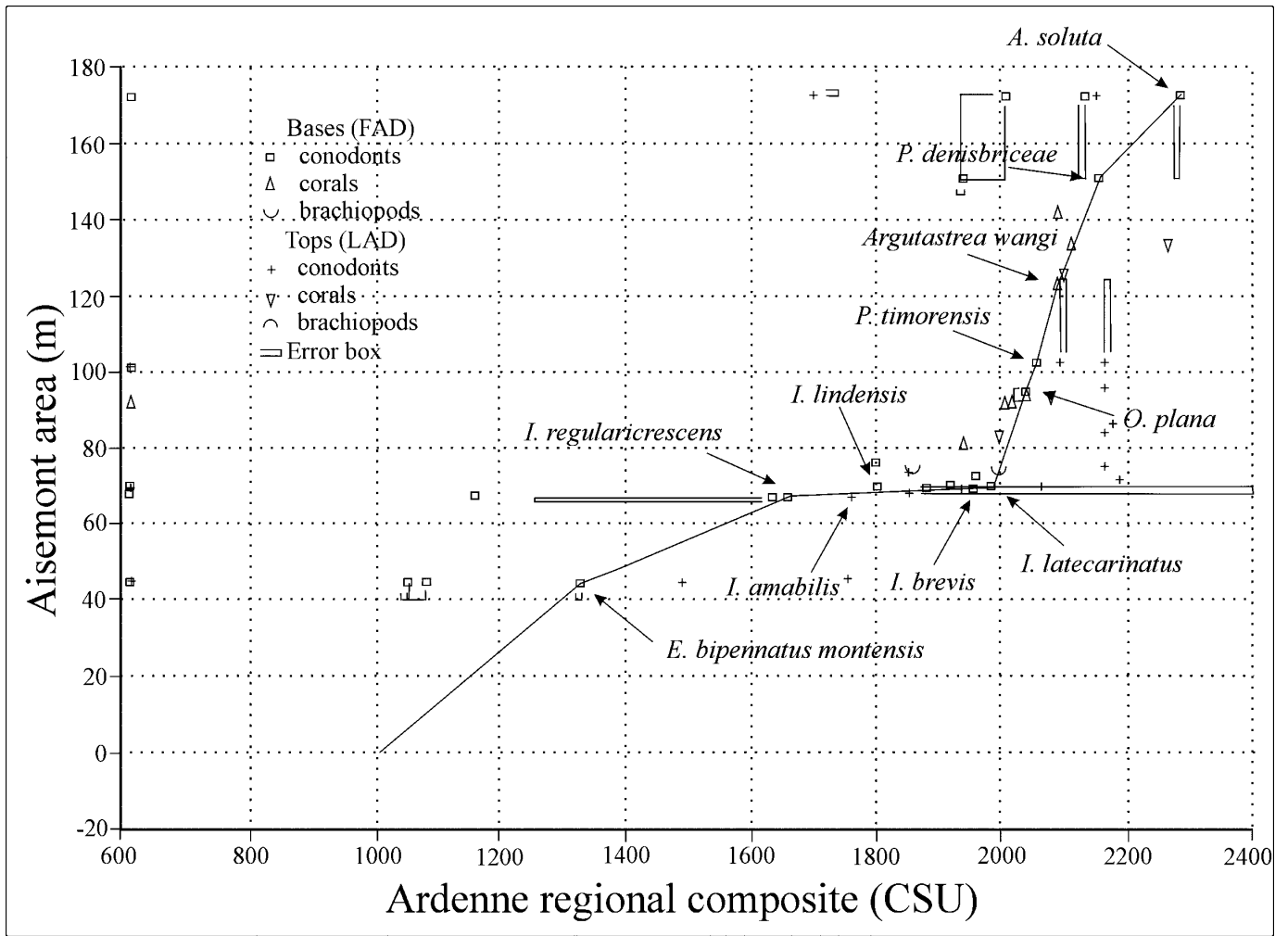
FIGURE 5–Graphic correlation of the Aisemont section with the Ardenne regional composite.

Coen-Aubert, 1999, 2002). In Sourd d'Ave a road-cut discloses the middle and upper member of the Frome-lennes Formation (Bultynck, 1974) and the Nismes Formation.

Jemelle area

The St-Joseph and Eau Noire Formations can be observed in the railway section in Grupont and along the road in Jemelle (Godefroid, 1968; Demeersseman, 1980). Both formations contain bentonites. The data used for the Jemelle, Lomme, Hanonet and Trois Fontaines Formations are taken from Godefroid (1968).

Villers-St-Gertrude area

The St-Joseph and Eau Noire formations were studied in the Hampteau road cut for conodonts and brachiopods by Demeersseman (1980) and for conodonts in the road-cut in Villers-St-Gertrude by Laenen (1982). The Jemelle Formation is exposed in the latter. The left bank of the Aisne, the sections in Sy (Burnotte & Coen, 1981) and the sections in Hampteau and Marenne (Lessuise *et al.*, 1979) reveal the Lomme Formation. In Marenne, the Lomme Formation contains a biohermal limestone level (Lessuise *et al.*, 1979). The Hanonet Formation here includes shales and limestones with some sandy intercalations. Only the lowermost 70
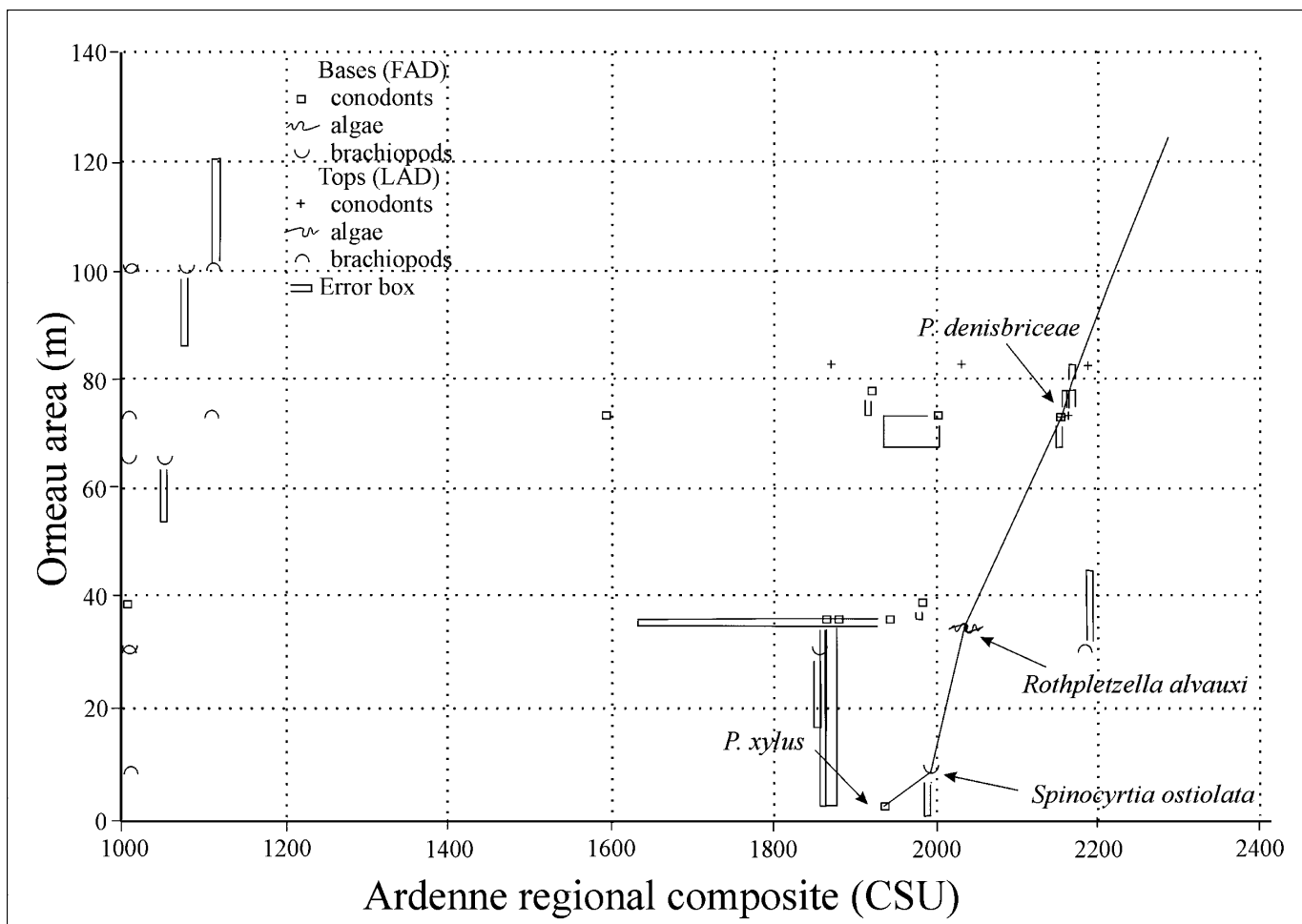
FIGURE 6–Graphic correlation of the Orneau section with the Ardenne regional composite.

meters of the Trois Fontaines Formation have been studied in Marenne (Meurrens, 1986; Coen *et al.,* 1974).

Remouchamps area

The Eifelian deposits in this area are quite different from the proceeding areas. The railway cut at the station of Remouchamps exposes the Pépinster Formation and the Névremont Formation studied for conodonts, ostracods and spores by de Decker (1994) (Dejonghe *et al.* in Bultynck *et al.,* 1991). The Flohimont Member of the Fromelennes Formation (railway section and Dieupart quarry, Aywaille) was examined by (Coen & Coen-Aubert, 1971).

Tailfer-Rivière area

In the northern part of the Dinant Synclinorium, the Rivière Formation represents the Eifelian. Several outcrops in the area were studied by Bultynck & Boonen (1976) for conodonts. The contact with the superimposing Névremont Formation is exposed in Godinne (Tantachau section) and Arbre. The Névremont Formation was described in Tailfer, Arbre, Godinne and Rivière (Coen-Aubert & Coen, 1974; Bultynck & Boonen, 1976). The Roux Formation completes the Givetian in the Tailfer and Rivière outcrops (Coen-Aubert & Coen, 1974).
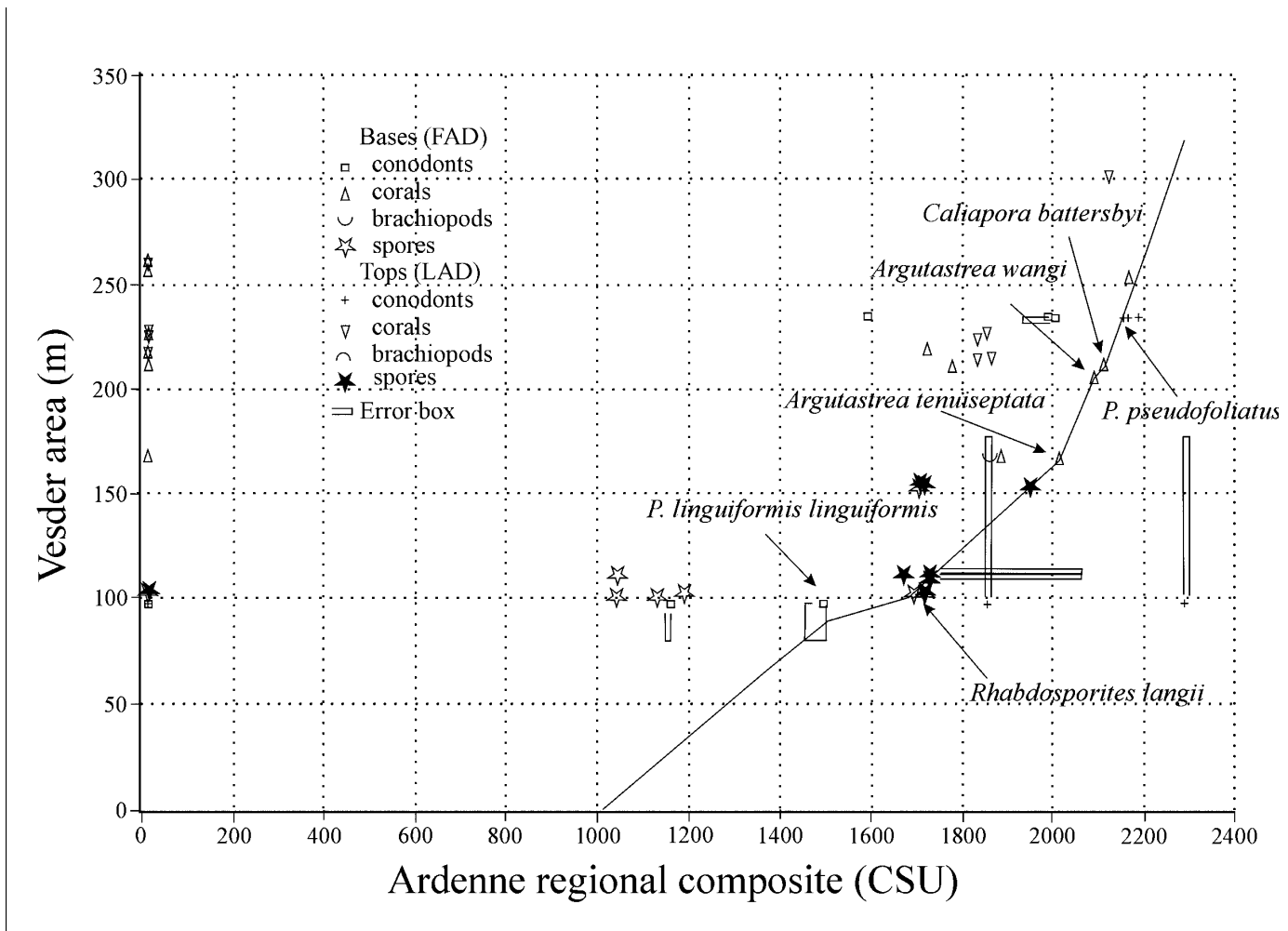
FIGURE 7–Graphic correlation of the Vesdre section with the Ardenne regional composite.

Aisemont area

The Middle Devonian of the southern part of the Namur Synclinorium is exposed in a continuous section along the old railway at Aisemont and was studied by several authors (Bultynck, 1970; Meurrens, 1986; Gouwy & Bultynck, 2002b).

Orneau area

The Bois de Bordeaux Formation represents the Middle Devonian in the northern part of the Namur Synclinorium. The formation is exposed along the left bank of the Orneau river (Bultynck *et al.*, 1991).

Vesdre area

In the Vesdre area, the Vicht Formation and the Pépinster Formation represent the Eifelian and the lower part of the Givetian and are exposed along the railway (Pépinster-Spa) (Bultynck *et al.*, 1991; de Decker, 1994). The overlying calcareous Névremont Formation was studied by Coen-Aubert (1970). The Givetian is completed by the Le Roux Formation, described in the Membach borehole (Coen-Aubert *et al.*, 1985).
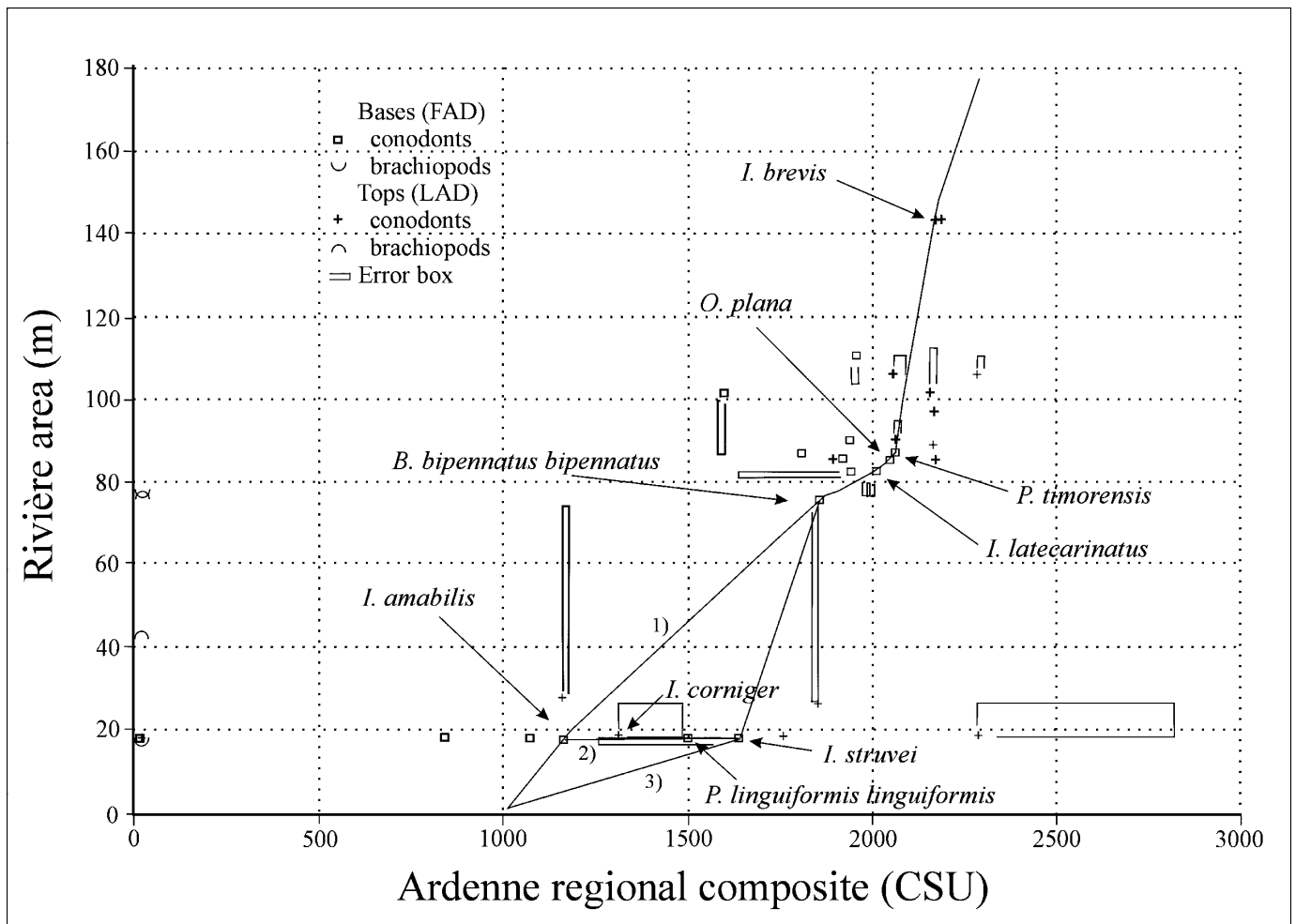
FIGURE 8–Graphic correlation of the Rivière section with the Ardenne regional composite.

CORRELATION GRAPHS

The section of the Couvin-Givet area was selected as the Standard Reference Section. Compared to the other sections it contains the highest number of conodont species and most of the type sections of the Southern Belgian Middle Devonian Formations, it is the most intensively studied one and does not contain any significant gaps or unconformities. The eight remaining sections were correlated in the following order: Wellin-Resteigne area (Welres), Villers-St-Gertrude area, Jemelle area, Aisemont area, Orneau area, Remouchamps area, Vesdre area and Tailfer-Rivière area. Our database consists of conodont, brachiopod, coral, spore and acritarch data. The first appearances of conodont taxa were preferably used for estimating the position of the LOC. To facilitate the correlation in some areas of the graphs, error boxes are used. They indicate the distance between the sample containing the first or last appearance of a species and the sample just beneath respectively above that does not contain the species. The true first or last appearance of the species lies in the error box. The lines stabilised after five correlation rounds.

Wel-Res graph (Fig. 2)

In the fifth round we have a segmented, in parts well constrained line of correlation that intersects the first appearances of *P. linguiformis bultyncki, I. regularicrescens, P. eiflius, P. ensensis, I. obliquimarginatus, B. bipennatus bipennatus* and *A. rotundiloba*. In addition the line also intersects the first appearances of a few brachiopod and coral taxa: *Arduspirifer intermedius, Gerolsteinites givefex, Acanthophyllum simplex* and *Argutastrea wangi*. Distinct outliers are the bases of *P. costatus costatus, P. linguiformis linguiformis* (at about 800 meters in the Wellin-Resteigne section) and the bases of *P. xylus, P. timorensis* and *P. varcus* (at about 1.600 meters in the section). These two levels are interpreted as horizontal sampling terraces, as opposed to unconformities for which there is no geological evidence. The sections of Wellin and Resteigne were first correlated with each other. The resulting database (Wel-Res) was used in the correlation of the Ardenne Middle Devonian. The Pondrôme data did not allow a correlation of the section with the Wellin and Resteigne sections. It was later correlated with the Ardenne regional composite. In order to recognize time equivalences in the different lithologies near the Eifelian-Givetian boundary in the Pondrôme, Wellin and Resteigne sections (Godefroid, 1995; Coen-Aubert, 1997), they were later recorrelated with the mature Ardenne regional composite.

Remark.–The Time-Rock chart (Fig. 3) shows the lithologies around the Eifelian-Givetian boundary in the three sections and the Couvin-Givet area. The Pondrôme Member of the Jemelle Formation in Pondrôme is time equivalent of the lower part of the Hanonet Formation in Resteigne and the Couvin-Givet area and the entire Hanonet Formation in Wellin. The 'X' Formation in Wellin corresponds to the upper part of the Jemelle Formation and the lowest part of the Hanonet Formation in the Couvin-Givet area. This correlation is supported by the T-R curves based on sedimentology. The Couvin-Givet and Wellin curves both show a distinct regression at CSU 1760-1780. At the same interval, the Jemelle Formation in the Pondrôme and Resteigne sections contains a more sandy shale deposit. The regression that takes place in the Trois Fontaines Formation coincides in all four regions.

Jemelle graph (Fig. 4)

The lowermost 150 meters of the Jemelle section can be accurately linked to the composite section by the first appearances of *Arduspirifer intermedius, P. linguiformis bultyncki* and *Arduspirifer supraspecio-*
sus. The upper 60 meters of the section are associated with CSU 1800-1870 through *"Uncinulus orbignyanus"*, *Gerolsteinites givefex* and *Stringocephalus burtini*. The middle 450 meters of the section are problematic. The Jemelle and Lomme Formations exposed in that part do not reveal any conodonts. The only available data are brachiopods: *Spinatrypa aspera aspera, Spinocyrtia ostiolata* and *Arduspirifer intermedius* indicate a possible location of this part of the LOC.

Aisemont graph (Fig. 5)

The most noteworthy feature in these graphs is the almost horizontal segment indicated by the bases of *I. brevis* and *I. latecarinatus* and the top of *I. amabilis*. This correlates an interval of 1 meter in the Aisemont section to a 185-meter thick interval in the Couvin-Givet reference section (Gouwy & Bultynck, 2002). The upper part of the LOC intersects the bases of *O. plana, P. timorensis, Argutastrea wangi, P. denisbriceae* and *A. soluta*. The lowermost part is indicated by the first appearance of *E. bipennatus montensis*.

Orneau graph (Fig. 6)

Only the bases of *P. xylus, Spinocyrtia ostiolata, Rothplezella alvauxi* and *P. denisbriceae* can be used to estimate the LOC for the Orneau area. The lowermost conodont appearance is *P. xylus*, found in the Mautiennes conglomerates immediately above the contact with the Silurian. This positions the oldest Devonian deposits in this area in the Givetian (CSU 1834). Poor sampling results cause the late entries of the other conodont species.

Vesdre graph (Fig. 7)

The bases of *P. linguiformis linguiformis, Rhabdosporites langii, Argutastrea tenuiseptata, Argutastrea wangi, Caliapora battersbyi, Thamnopora fromelennensis* and the top of *P. pseudofoliatus* indicate the possible position of the LOC. The terrace at about 100 meters in the section is a sampling terrace. The database of this section only consists of two conodont samples, two spore samples and a few brachiopod and coral data.

Rivière graph (Fig. 8)

The fifth round of the correlation shows a segmented LOC intersecting the bases of *I. amabilis, B. bipennatus bipennatus, I. latecarinatus, P. timorensis, O. plana* and the top of *I. brevis*. The line is rather well fixed in the upper half of the graph. The location of the LOC in the lower 70 meters of the section is problematic, because of only two levels providing data. The

lowermost sample contains specimens of *I. amabilis, I. corniger, I. struvei* and *P. linguiformis linguiformis,* species that do not overlap in the reference section of Couvin-Givet. Possible solutions to this problem are: 1) incompleteness of the ranges in the Couvin-Givet area for *P. linguiformis linguiformis* and *I. struvei*, 2) an unconformity and reworking of *I. corniger* in the Rivière area, and 3) the terrace should be considered as a sampling terrace. The first solution is the most probable one: the ranges of *I. corniger* and *I. amabilis* on one side and *P. linguiformis linguiformis* and *I. struvei* on the other side are found overlapping in the Middle Devonian composite standard of the Anti-Atlas (Belka *et al.,* 1997). This locates the sample at CSU 1158 in the composite standard. A terrace through the bases of *I. amabilis* and *I. struvei* would represent an unconformity, a hiatus in the section from CSU 1158 to 1632. This hiatus could be caused by non-sedimentation during that period or by erosion of the deposits, although in the direction of the Middle Devonian continent (to the north) no indications for a hiatus have been found (Aisemont area). So, therefore the second possible solution for the construction of the LOC is not acceptable. The third possibility would launch the last appearance of *I. corniger*, normally located in the lower part of the *costatus* Zone (Belka *et al.,* 1997; Bultynck, 1970), into the *australis* Zone. Therefore the third possibility is rejected.
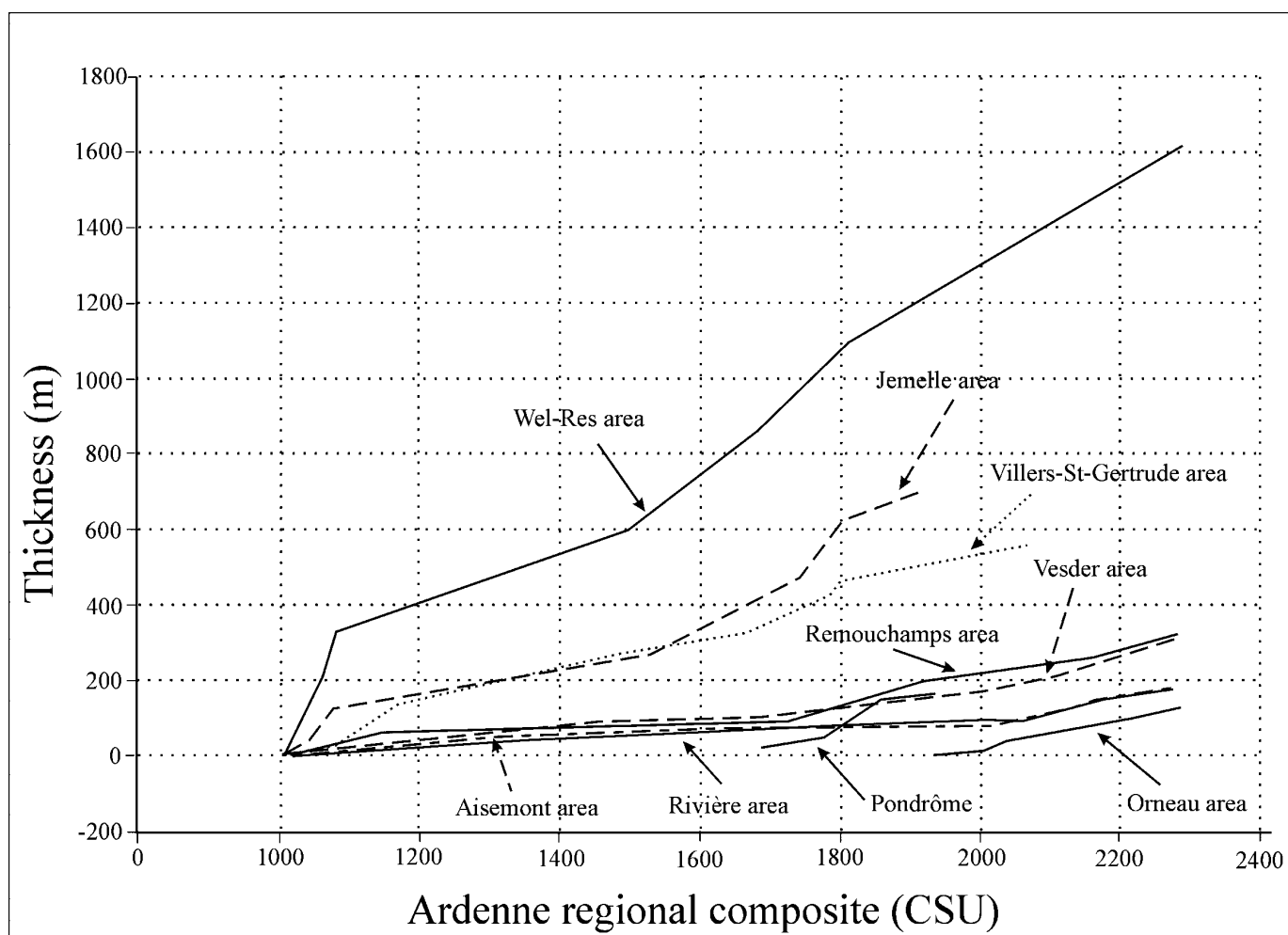

FIGURE 9–Stratigraphic nomograph of the different sections.

Stratigraphic nomograph (Fig. 9)

The stratigraphic nomograph of all sections from the Ardenne allows the comparison of the relative rates of rock accumulation during the Upper Emsian, Eifelian and Givetian. The higher slopes of the correlation lines of the sections from the southern part of the Dinant Synclinorium indicate a higher rock accumulation rate for that region. Because some changes in accumulation rates observed in the correlations lines occur simultaneously in several sections and considering the lithological differences in the reference section between the Eifelian and the Givetian, we should assume a non-linear fit to time of the regional composite. Therefore we suggest a more linear regional composite like the Anti-Atlas regional composite (Belka *et al.,* 1997) should be used as reference for an interregional composite standard (Gouwy & Bultynck, 2002a).

RESULTS

Middle Devonian Ardenne conodont composite standard and conodont zones (Fig. 10a-b)

The Middle Devonian regional conodont composite standard for the Ardenne contains 76 taxa. Eighty percent of the taxa were initially present in the reference section (Couvin-Givet). Only one third of the taxa have their first and last appearances controlled by the reference section. The conodont zones are now fixed in the Composite Standard Units scale. Most of the zone-defining conodonts are present in the reference section. The base of the *patulus* Zone is situated at CSU 1014 by the first appearance of *P. patulus* 6 meters above the base of the St-Joseph Formation in the Couvin-Givet section. The *partitus* Zone (first appearance of *P. partitus* in the Jemelle area) starts at CSU 1078, 30 meters above the base of the Eau Noire Formation in the Couvin-Givet section. *P. costatus costatus* appears at CSU 1169, 61 meters above the base of the Couvin Formation. The *australis* Zone cannot be located because of lack of zone defining species or associated species. *T. kockelianus* defining the base of the *kockelianus* Zone (CSU 1661) is found in a bioherm in the Jemelle Formation 173 meters above the top of the Couvin Formation in the Couvin area. The *eiflius* Zone (first appearance of *P. eiflius* in the Couvin-Givet area) starts at CSU 1667, 179 meters above the top of the Couvin Formation in the Couvin area. The *ensensis* Zone begins at CSU 1762 (first appearance of *P. ensensis*) 23 meters below the Hanonet Formation in the Couvin-Givet section. The

hemiansatus Zone defined by the first appearance of *P. hemiansatus* 17 meters above the base of the Hanonet Formation starts at CSU 1802. *P. xylus* locates the base of the *timorensis* Zone (lower part of the Lower *varcus* Zone) at CSU 1934, 16 meters above the base of the Terres d'Haurs Formation because of a delayed first appearance of *P. timorensis*. *P. varcus* (CSU 2129) indicates the base of the *rhenanus-varcus* Zone (upper part of the Lower *varcus* Zone) 141 meters above the base of the Mont d'Haurs Formation. The base of the *ansatus* zone (*middle varcus* Zone) is positioned at 9 meters above the base of the Fromelennes Formation in the Couvin-Givet section (CSU 2157, first appearance of *P. ansatus*. The *upper varcus* Zone (*latifossatus-semialternans* Zone) and *the hermanni-cristatus* and *disparilis* Zones cannot be located because the middle and upper member of the Fromelennes Formation contain only a limited number of significant conodont taxa. Gouwy & Bultynck (2002a, Fig. 5) correlated the Ardenne regional composite with the Anti-Atlas regional composite for the Middle Devonian. An approximate position of the base of the *australis* Zone, the *latifossatus-semialternans* Zone, the *hermanni-cristatus* Zone and the *disparilis* Zone in the Ardenne can be obtained through projection of the first appearances of the zone defining taxa from the Middle Devonian composite standard. This locates the base of the *australis* Zone (CSU 1518) at 30 meters above the base of the Jemelle Formation in the Couvin-Givet section and reveals the possible position of the base of the *latifossatus-semialternans* Zone (2225 CSU), the *hermanni-cristatus* Zone (2231 CSU) and the *disparilis* Zone (2241 CSU), all located in the Moulin Boreux Member (Middle Member of the Fromelennes Formation) at respectively 77, 83 and 93 meters above the base of the Formation. The projections of the bases of the *timorensis* Zone and the *rhenanus/varcus* Zone from the Middle Devonian composite standard suggest an adjustment of the position of the zones in the Ardenne composite. The stratigraphic first appearance of *P. timorensis* is projected on the Ardenne composite at 1900 Ardenne CSU, 18 m below the base of the Terres d'Haurs Formation in the Couvin-Givet section. The base of the *rhenanus/varcus* Zone is projected onto the Ardenne composite at 2038 Ardenne CSU, 50 m above the base of the Mont d'Haurs Formation.

The alternative *Icriodus* zonation (Bultynck, 1987, Fig. 9) can also be linked to the CSU's (also after correlation with the Anti-Atlas regional composite). The base of the *regularicrescens* Zone is situated at CSU 1218, 110 meters above the base of the Couvin
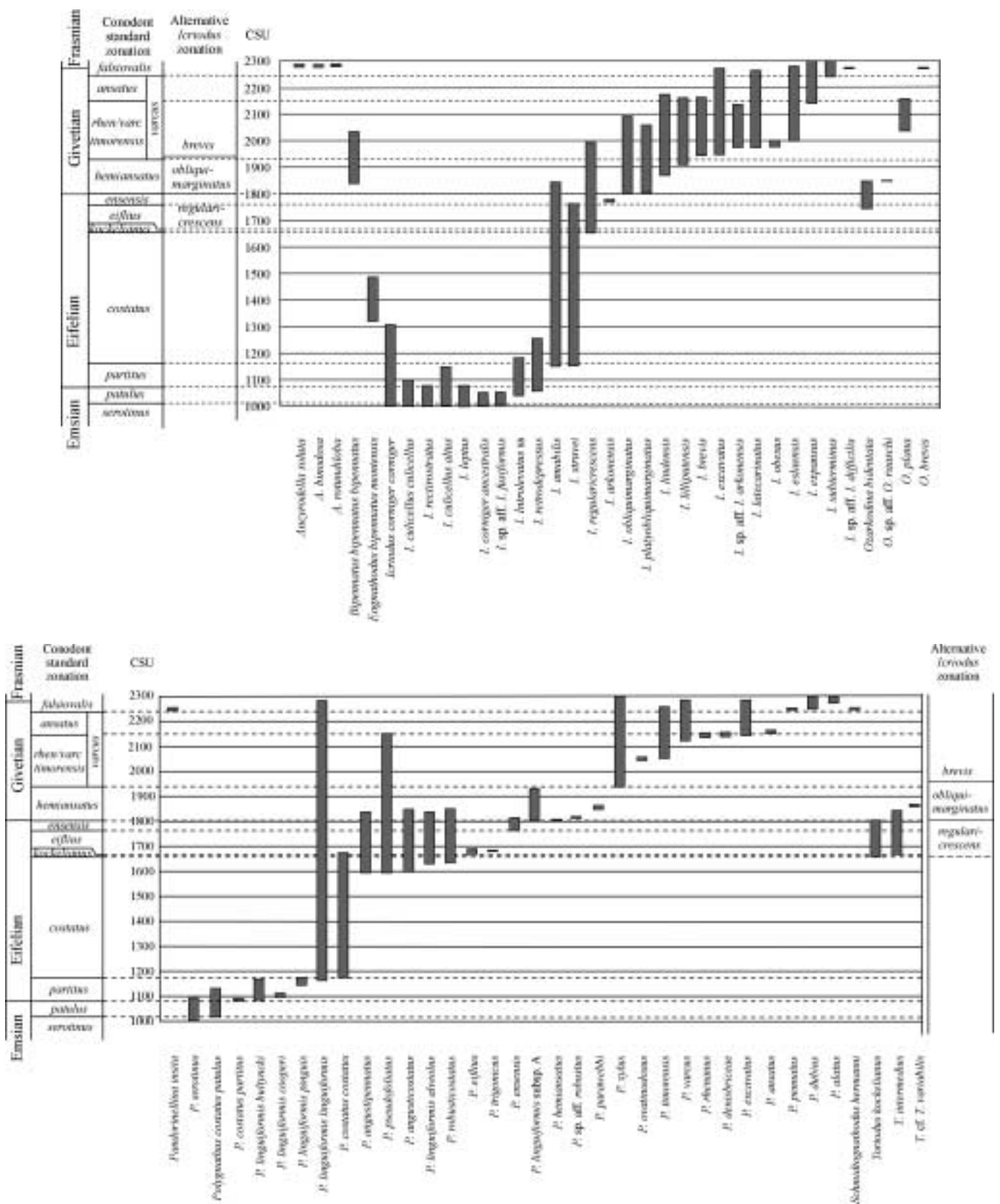
FIGURE 10a-b–Middle Devonian Composite standard conodont ranges of the Ardenne. The *australis, latifossatus/semialternans, hermanni-cristatus* and *disparilis* Zones are not recognized in the Ardenne due to lack of guide species.
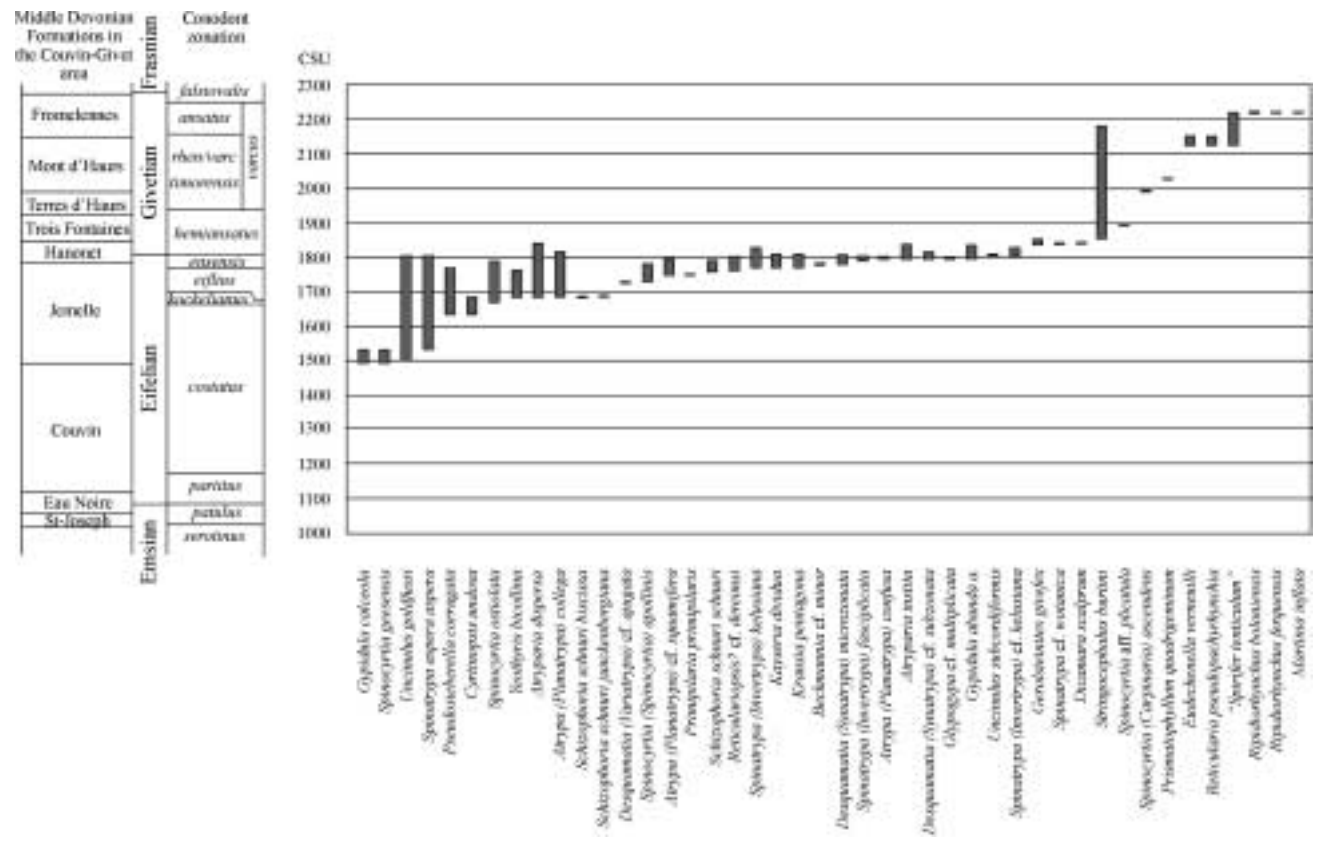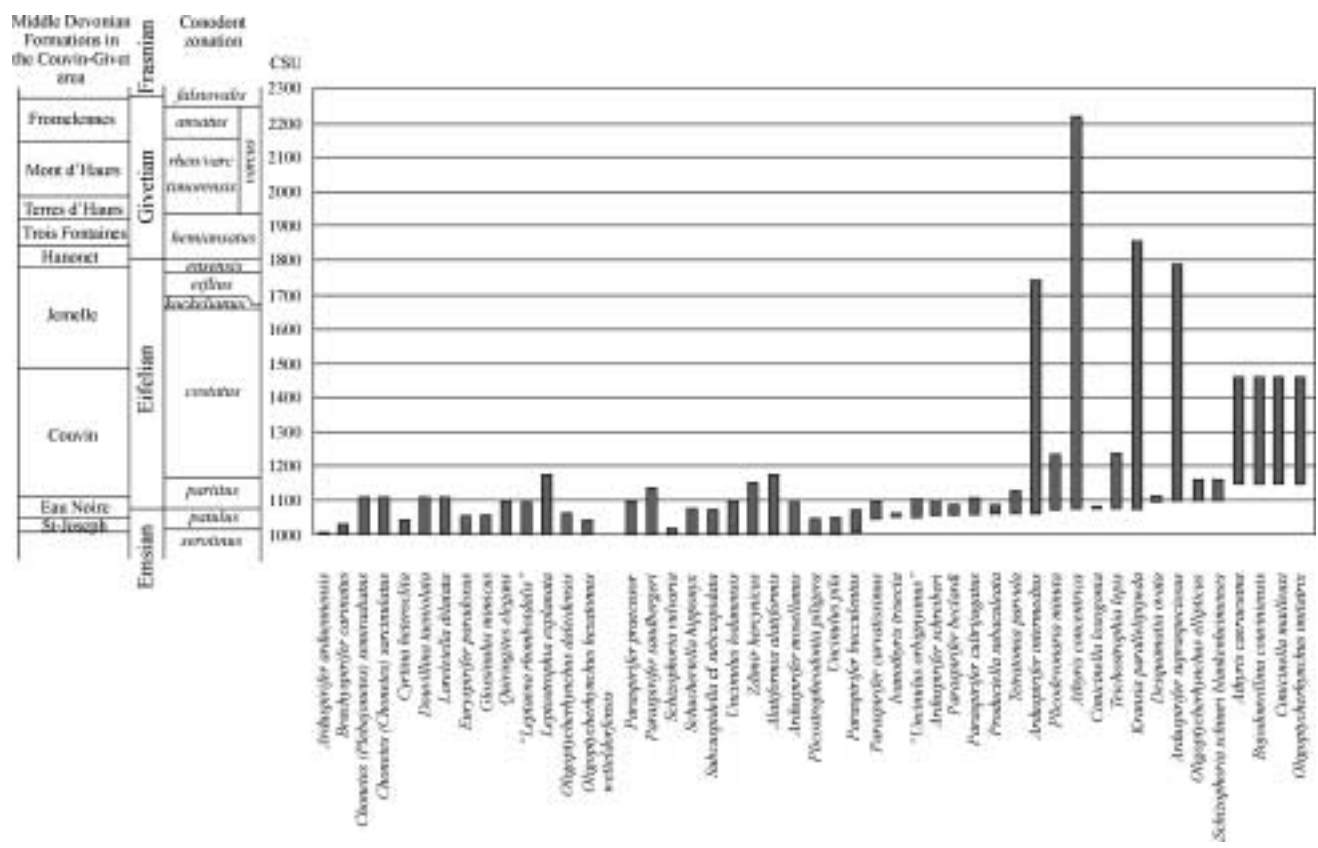
FIGURE 11a-b–Middle Devonian Composite standard brachiopod ranges of the Ardenne.

Formation, 49 meters above the base of the *costatus* Zone in the same Formation. The *obliquimarginatus* Zone begins at 11 meters below the top of the Jemelle Formation (CSU 1774), 28 meters below the base of the *hemiansatus* Zone in the Couvin-Givet section. This is lower than suggested by Bultynck (1987). The *brevis* Zone starts 17 meters above the base of the Terres d'Haurs Formation (CSU 1935), 35 meters above the base of the *timorensis* Zone in the Couvin-Givet section. The base of the *difficilis* Zone is placed 67 meters above the base of the Mont d'Haurs Formation (CSU 2055), 2 meters below the base of the *ansatus* Zone in the Couvin-Givet section.

Range charts of brachiopods (Fig. 11a-b), corals (Fig. 12), spores and acritarchs (Fig. 13)

Graphic correlation allows us to construct range charts for brachiopods, corals, spores and acritarchs and correlate the ranges of taxa with the internationally used conodont zones and with the high resolution CSU chart. These range charts of the Ardenne should be seen as a preliminary synthesis of the published data (see DATA, pp 2-3 of this paper). Most taxa ranges consist of only one or a few samples and are thus far from complete. Although the range charts give the impression of a possible high-resolution zonation, this is merely the result of incomplete ranges.

Time-rock charts (chronostratigraphic diagram), T-R cycles and events (Fig. 16)

SW-NE chart (Fig. 14)

The first thing that catches the eye is the diachronic nature of the sandy deposits. They are part of the St-Joseph Formation in the Villers-St-Gertrude area, the Pépinster Formation in the Remouchamps and Pépinster areas and the Lomme Formation in the Villers-St-Gertrude and Jemelle areas.
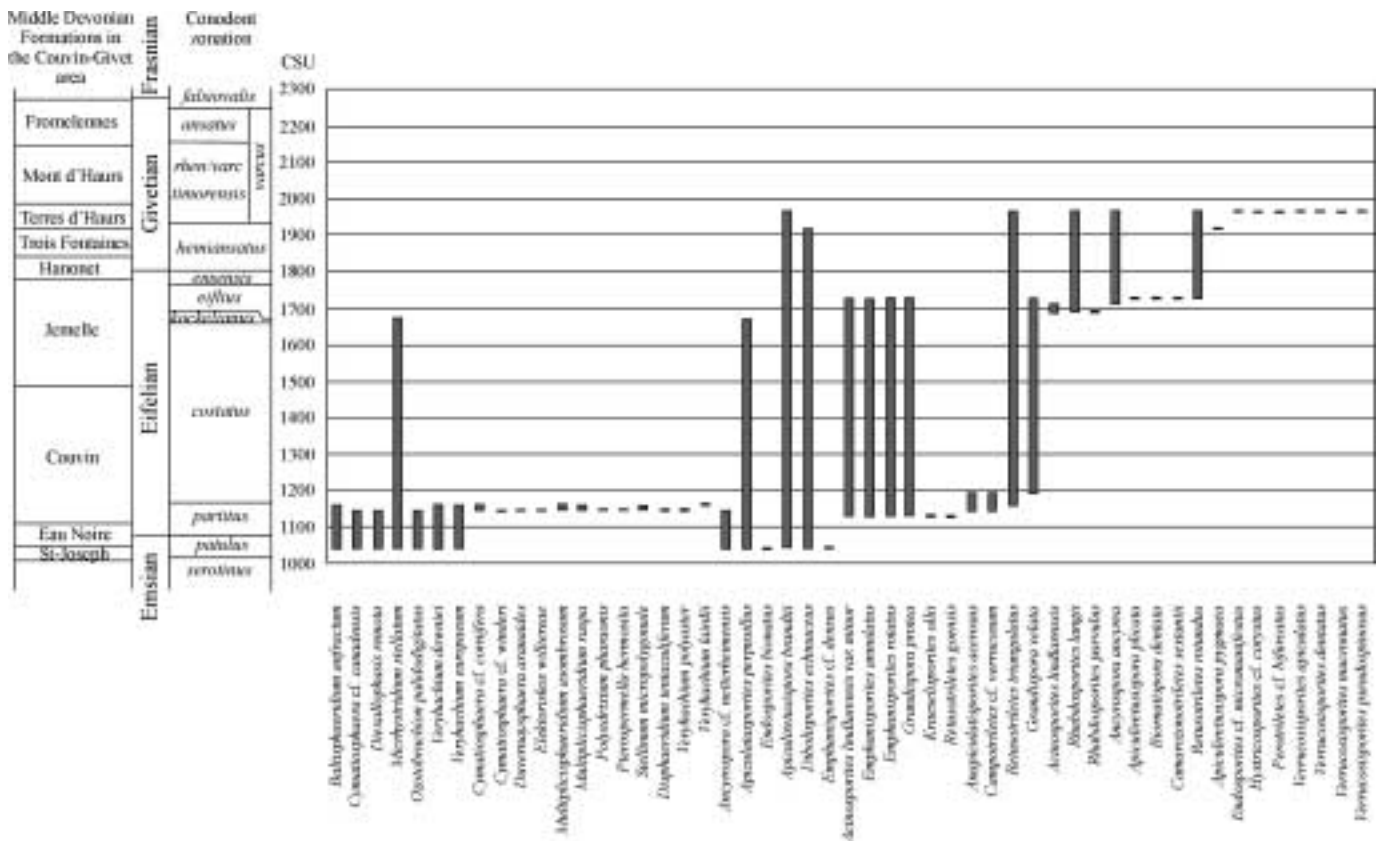
FIGURE 12–Middle Devonian Composite standard coral ranges of the Ardenne.
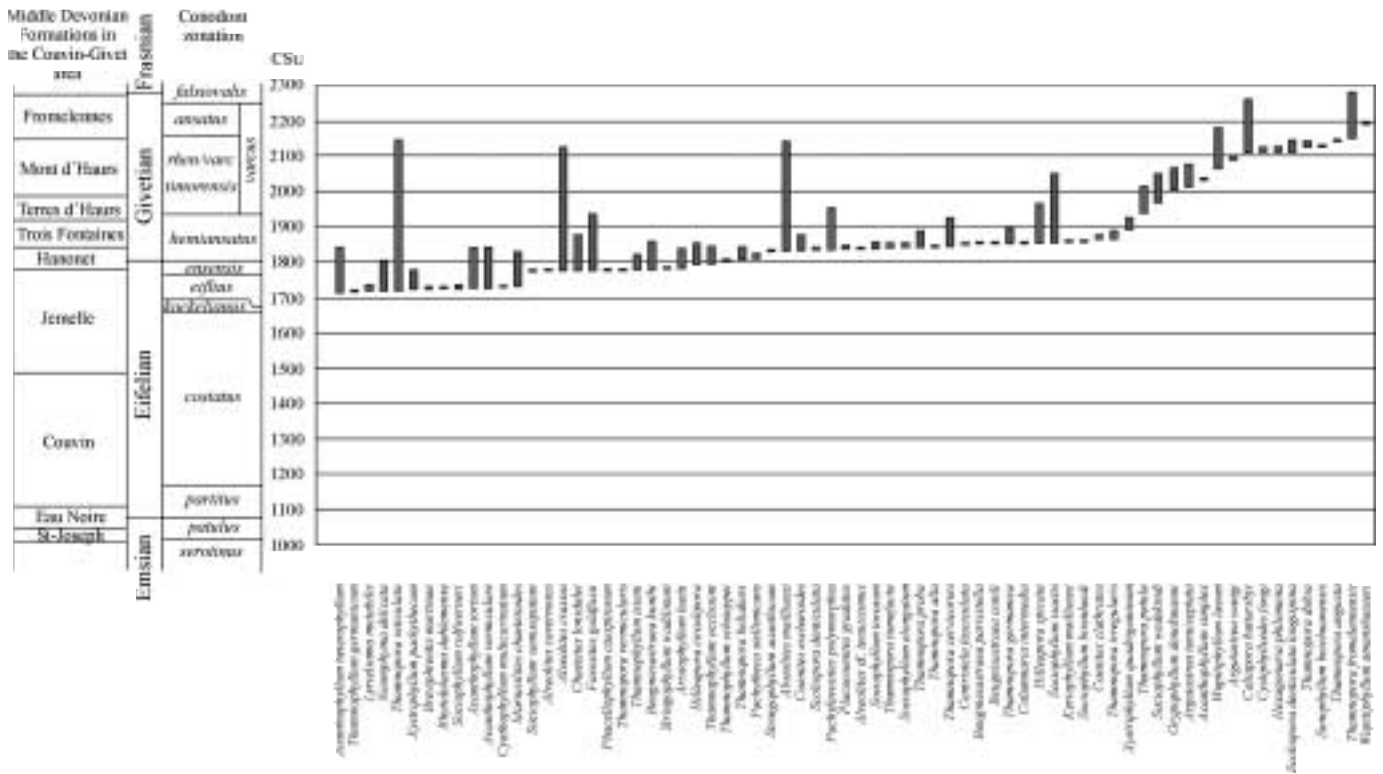
FIGURE 13–Middle Devonian Composite standard spore and acritarch ranges of the Ardenne.

The transgressive phase at the top of the Emsian (CSU 1008-1078) is noticed in the facies shift from sandstone/sandy shale deposits to shales in the Couvin-Givet, Wellin, Jemelle and Villers-St-Gertrude areas. The sandy shales at the base of the Jemelle Formation in the Jemelle area (CSU 1100-1125) indicate a minor regression during the lower part of the *partitus* Zone (CSU 1100-1120). At the same time, in the Couvin-Givet area, a stromatoporoid biostromal limestone with calcareous-argillaceous matrix (Lower Member of the Couvin Formation) develops, characteristic for a shallow environment (Préat, 1984). Around CSU 1130 in the *partitus* Zone, sandstone appears on top of red littoral siltstone containing calcretes and plant debris in the Remouchamps area. The limestone layer at the base of the sandstone contains the first conodonts of this area. This transgression is also manifested by a first interruption in the biostromal limestone development in the Couvin area: a brachiopod and conodont rich argillaceous limestone replaces the stromatoporoid limestone. This transgression could correspond with the sea-level rise that normally would be associated with the Chotec event, which occurs in the upper part

of the *partitus* Zone and the lowermost part of the *costatus* Zone. The reappearance of sandstone during the lower part of the *costatus* Zone in the Villers-St-Gertrude area marks a second minor regression (CSU 1200-1275). At the same time a second stromatoporoid biostromal limestone develops in the Couvin-Givet area. From CSU 1285 till CSU 1500, sandstone is only exposed in the Remouchamps area while in the Couvin-Givet area a third stromatoporoid biostromal limestone develops after a short interruption with more argillaceous limestone (CSU 1275-1285). From CSU 1500 on, a deepening event, a new pulse in the transgression is observed in the Vesdre area where sandstone is deposited onto red littoral siltstone and in the Couvin-Givet area where the biostromal limestone is replaced by shales. This pulse ranging from the upper part of the *costatus* Zone to the uppermost part of the *australis* Zone (the base of the latter is only an estimation after correlation with the Anti-Atlas because *T. kockelianus australis* is not found in the Ardenne) could correlate with the transgression at the base of Cycle Id of Johnson *et al.* (1996), located in the middle part of the *costatus* Zone. The sand deposit is located in the Vesdre area from CSU 1500-
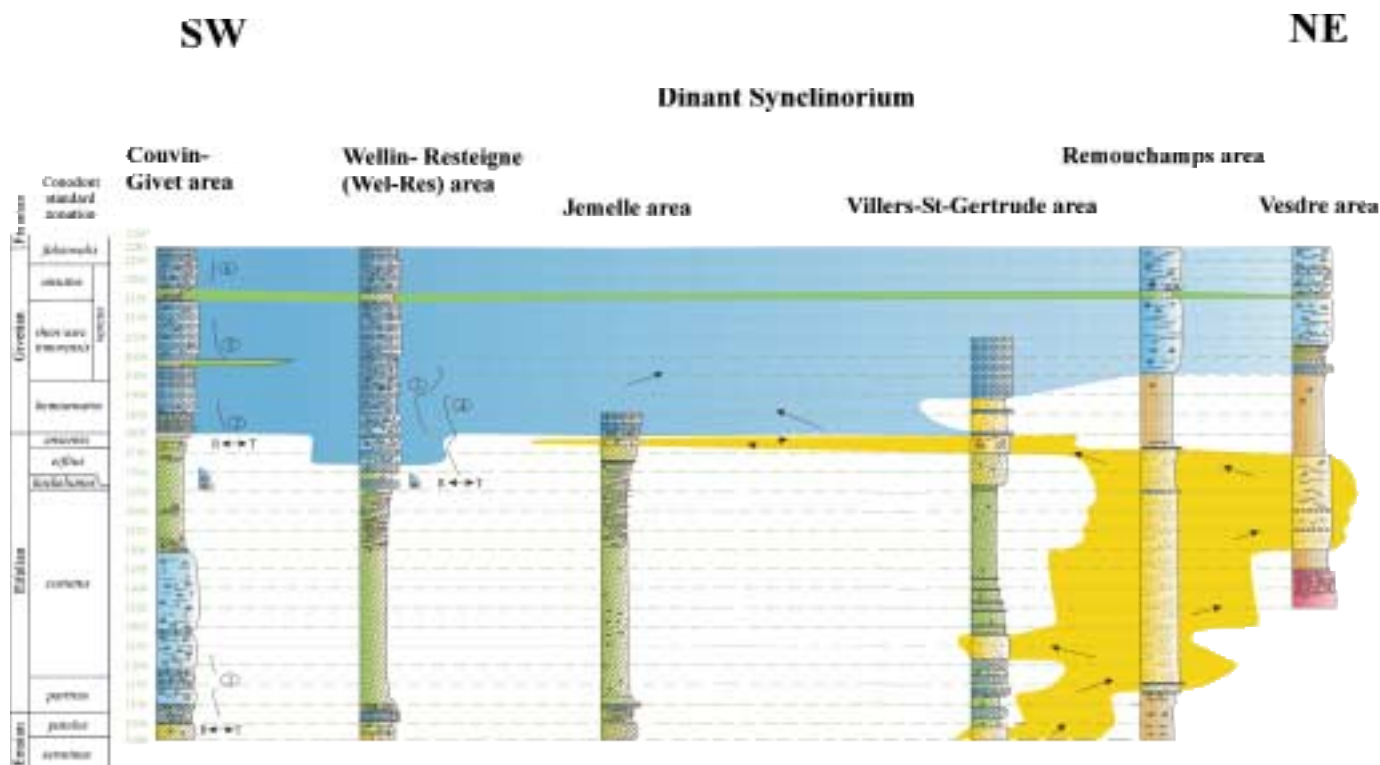
FIGURE 14–Chronostratigraphic diagram of the Middle Devonian deposits of the S-SE border of the Dinant Synclinorium. The sections are represented as vertical columns on the graph, with a vertical scale in composite standard units (or geological time). A vertical bar shows the chronostratigraphic intervals represented by deposits in a section; a hiatus is a blank area on the graph. The lithology is indicated in the vertical bars to study the facies relationships and the diachroneity of the lithological boundaries. Every horizontal line on the diagram is isochronous. Legend: see Fig. 15.

T-R curves: 1: Bertrand *et al.,* 1993; 2: Préat, 1989; 3: Casier & Préat, 1991; 4: Coen-Aubert *et al.,* 1991; 5: Errera *et al.,* 1972; 6: Préat & Carliez, 1996.

1750. Two conglomerate levels in the Vesdre area could indicate minor transgressive pulses. At the maximum extension of the transgression (CSU1650) small bioherms start to develop in the deepest area (Couvin-Givet and Wellin) in the *kockelianus* Zone. The regression at the top of the Eifelian is observed in the Remouchamps and Vesdre areas where the sandstone deposits are overlain by red littoral siltstone containing plant debris during the *eiflius* Zone and in the Villers-St-Gertrude and Jemelle areas where sandy shales and sandstone appear on top of the shales during the *ensensis* Zone. In the Couvin-Givet area this regression is indicated by the presence of siltstone with fine cross laminations in the uppermost part of the Jemelle Formation (Bultynck & Hollevoet, 1999). Locally, only in the Wellin area, crinoid-rich, stromatoporoid biostromal limestone is found. The regression continues in the lower part of the *hemiansatus* Zone after a transgressive interruption in the uppermost part of the *ensensis* Zone indicated by the evolution in brachiopod assemblages at CSU 1780-1800 in the lower part of the Hanonet Formation in the Couvin-Givet area (Bultynck & Hollevoet, 1999). The sedimentary gap in the Aisemont area (Gouwy & Bultynck, 2002b) caused by this regression might correlate with Struve's Great Gap, described as a period characterized by sedimentary gaps and not full marine deposits. In the Eifel area (Hillesheim syncline; Struve, 1988; Weddige, 1988) the acme of the gap is situated in the *ensensis* Zone. Some authors (Weddige, 1988) consider the Great Gap to be shallow water disorders caused in the *otomari* event. In the Ardenne, no evidence of the lower Kaçak event (*otomari* event) has been found. It corresponds to a deepening event (onset of back shales in pelagic environments) in the lower part of the *ensensis* Zone (Walliser, 1995) and a shallowing trend at the top of the event. Our T-R chart indicates a distinct regres-
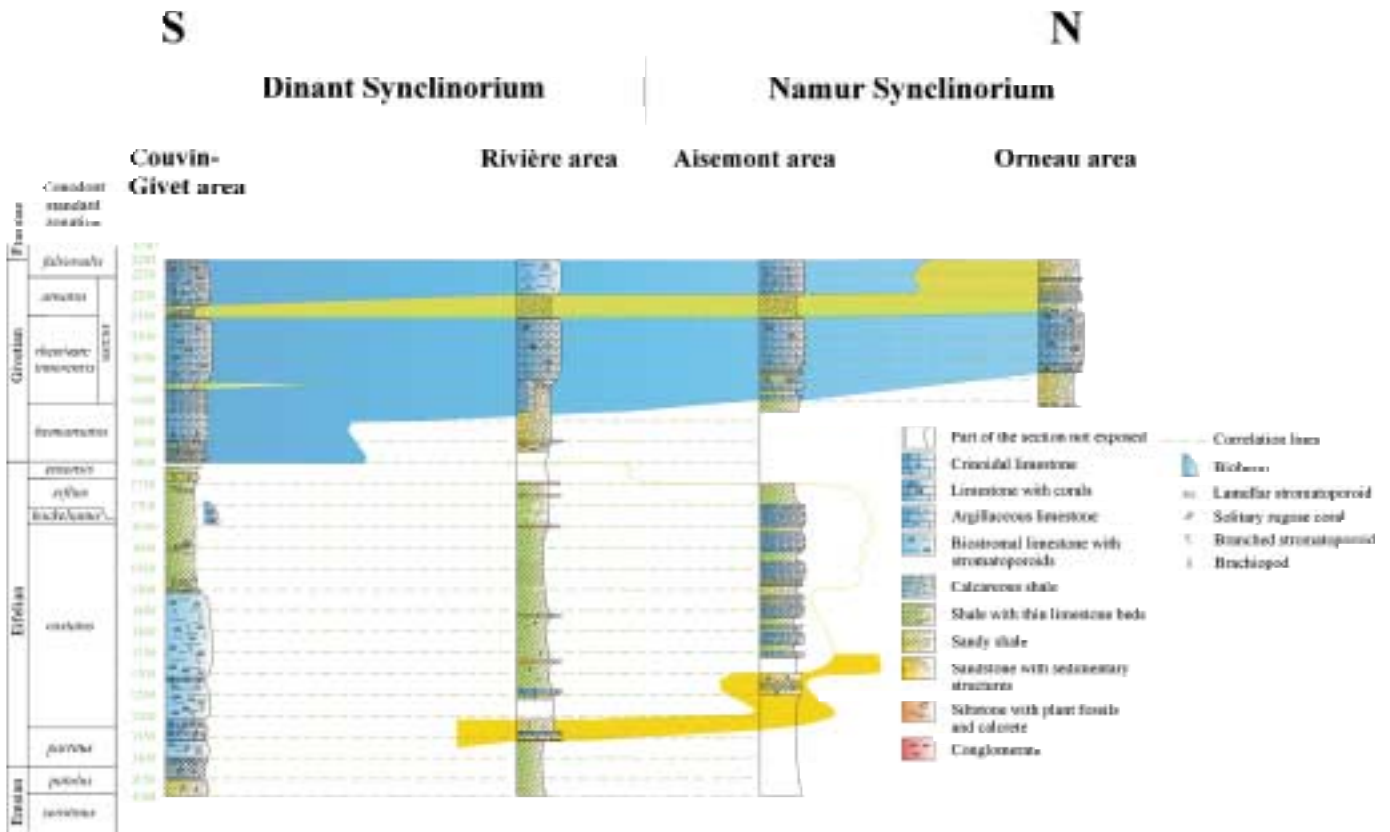
FIGURE 15–Chronostratigraphic diagram of the Middle Devonian deposits of the Ardenne from south to north.

sion in the lower part of the *ensensis* Zone. *I. arkonensis*, regarded as the marker of the event (Weddige, 1988), is only found in the Villers-St-Gertrude area, in the middle of a 20 meters thick sandstone deposit. No deepening trend is observed at that level. The lower Kaçak event recognized in the Bou Tchrafine section (Morocco, Bultynck, 1987) as a clear faunal break in shales with hematitic fauna is correlated (Gouwy & Bultynck, 2000a) with Ardenne CSU 1765-1797, a 32 meters thick unit in the top of the Jemelle Formation and the base of the Hanonet Formation in the reference area. The regression coincides with the lower part of this unit and so does not correspond to the shallowing trend at the top of the lower Kacak event. Like the Great Gap in the Eifel Mountains, this regression is connected with the 'ostiolatus' extinction event (Bultynck & Hollevoet, 1999) (Fig. 11 a-b).

Around the Eifelian-Givetian boundary (CSU 1802), limestone development initiates in a large region (Couvin-Givet, Wellin, Jemelle and Villers-St-Gertrude areas). In the Villers-St-Gertrude area shale and sandy shale deposits and sandstone overlie a thin deposit of that limestone, what indicates the continuance of the regression after the minor transgressive shift. At the same time, a stromatoporoid biostromal limestone is developed in the Couvin-Givet and Wellin areas (lowermost part of the Trois-Fontaines Formation). Limestone development restarts in the Villers-St-Gertrude area at CSU 1900 and covers the Remouchamps and Vesdre areas at CSU 1950, in Givet argillaceous limestone and shales of the Terres d'Haurs Formation (CSU 1910-1970) are found. This indicates the first pulse of the Givetian transgression during the upper part of the *hemiansatus* Zone and the *timorensis* Zone. In the time interval between CSU 2000 and CSU 2050, stromatoporoid limestone develops again in the whole region, coinciding with the major regression occurring in the *rhenanus-varcus* Zone (Johnson *et al.,* 1985). This stromatoporoid biostromal limestone should merely be understood as the limestone development keeping pace with or

going a little faster than the slight sea-level rise. The presence of shales overlying the limestone in the whole region (lower part of the Fromelennes Formation) reveals a second pulse in the transgression just below the base of the *ansatus* Zone. This does not coincide with the Taghanic event, a deepening event recognized in the Tully limestone of the New York region (Johnson *et al*., 1985) corresponding to the base of transgressive cycle IIa of Johnson *et al*. (1985) in the lower part of the *ansatus* Zone. Thus the base of the Fromelennes Formation probably corresponded with a smaller transgressive pulse below the Tully limestone in New York. On top of these shales the stromatoporoid limestone reappears for the last time in the region. Another transgressive pulse that will continue in the Frasnian is reflected in the presence of argillaceous limestone superimposing the stromatoporoid limestone in the Couvin-Givet and Wellin areas (Upper Member of the Fromelennes Formation).

S-N chart (Fig. 15)

On this chart the diachronic nature of the Eifelian deposits is not so clear. The sandstones and conglomerates of the Rivière and Aisemont areas do fit in the T-R-pattern based on the SW-NE chart. In the Aisemont area an angular unconformity is present between the Silurian and the Eifelian. The hiatus found in the Aisemont area at the Eifelian-Givetian boundary (Gouwy & Bultynck, 2002b) coincides with the regression in the upper part of the Eifelian and lower part of the Givetian, visualised on the SW-NE chart. The Eifelian-Givetian boundary is not exposed in the Rivière area. The first major transgressive pulse in the Givetian coincides with the start of the limestone development in the Rivière and Aisemont areas and with the first deposition of Devonian sediments directly onto the Silurian in the Orneau area. The development of stromatoporoid limestone in the Rivière, Aisemont and Orneau areas is time-equivalent with the second stromatoporoid limestone level in the southern part of the Dinant Synclinorium (CSU 2000-2050). The second transgressive pulse brings shales/sandy shales in the whole region (CSU 2150-2200). The minor regression in the uppermost Givetian brings sandy shales into the Orneau area and allows the development of dolomitic limestone in the Rivière and Aisemont areas.
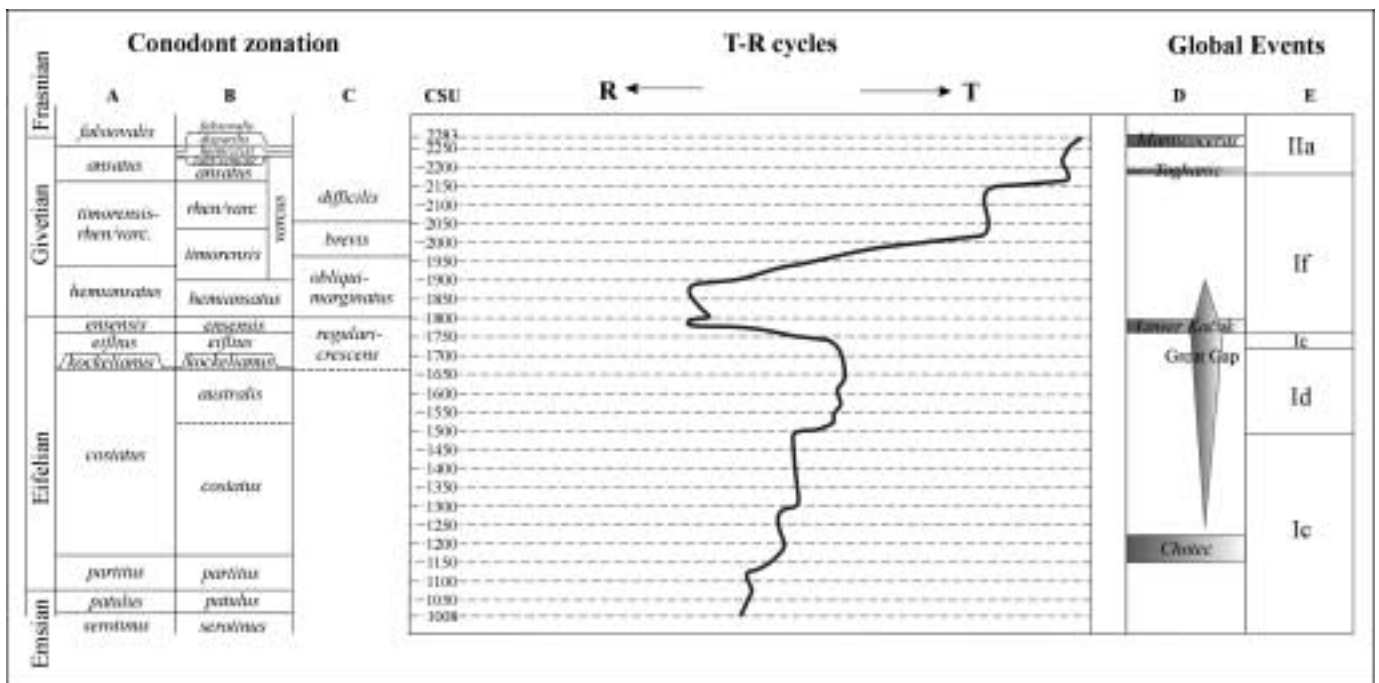
FIGURE 16–T-R cycles of the Middle Devonian of the Ardenne located in the conodont zonation and linked to the global events and T-R cycles of Johnson *et al*. (1985). A: conodont zonation based on the Ardenne regional composite. B: conodont zonation after correlation with the Anti-Atlas regional composite (Gouwy & Bultynck, 2002a). C: Alternative *Icriodus* zonation after correlation with the Anti-Atlas regional composite. D: Global events. E: T-R cyles (Johnson *et al.,* 1985).

Comparison with correlations based on sedimentary cycles (Fig. 14)

In the last twenty years several very detail sedimentological studies have been published on the Eifelian and the Givetian of Belgium (Bertrand *et al.,* 1993; Coen-Aubert *et al.,* 1986; Coen-Aubert *et al.,* 1991; Errera *et al.,* 1972; Kasimi & Préat, 1996; Préat, 1984, 1989; Préat *et al.,* 1984; Préat & Kasimi, 1995; Préat & Mamet, 1989; Préat & Rouchy, 1986) and cyclicity has been recognized based on microfacies evolution. Hereafter we discuss whether or not the correlation based on the sedimentary cycles is supported by the results obtained from graphic correlation. The first minor regression located near the base of the Eifelian coincides with a shift from an outer ramp to a middle ramp system from the base of the Eau Noire Formation to the lower part of the Couvin Formation, and to an inner ramp system in the second biostromal facies level in the Couvin Formation in the Couvin area (Bertrand *et al.,* 1993). The regression in the upper part of the Eifelian that is indicated by the migration of the sandstone deposits is also indicated in the 'X' Formation of the Wellin area by a shift from an outer ramp sedimentation in the Jemelle Formation to a middle ramp sedimentation in the lowermost part of the 'X' Formation and an inner ramp sedimentation in the upper part of the same Formation (Coen-Aubert *et al.,* 1991). The maximum of that regression coincides with the maximum regression indicated by the migration of the sandstone (CSU 1775) (Fig. 14). The minor transgression in the uppermost part of the Eifelian (CSU 1780-1800) is mentioned in Coen-Aubert *et al.* (1991) as an interruption of the inner ramp system by a middle ramp system in the Hanonet Formation. The facies evolution caused by the regression depositing the sandy shale and sandstone on top of the marine limestone succession at the base of the Givetian in Villers-St-Gertrude (Burnotte & Coen, 1981) is studied in two areas: Couvin and Wellin. In Couvin, the carbonate microfacies evolution in the Hanonet and Trois Fontaines Formations suggests an upward shallowing sequence (Errera *et al.,* 1972; Préat, 1989). In Wellin, the carbonate microfacies evolution in the Hanonet and Trois Fontaines Formations shows a decrease in water depth (Coen-Aubert *et al.,* 1991; Casier & Préat, 1991). The second regression in the Givetian indicated by the development of stromatoporoid limestones in the Mont d'Haurs Formation is recognized in the microfacies evolution in the Givet area (Errera *et al.,* 1972) and in the Rivière, Aisemont and Orneau areas (CSU 2010-2140) (Préat, 1984). Préat & Carliez (1996) analysed

the microfacies of the middle member of the Fromelennes Formation in Givet and concluded that the member consists of six 4th order sedimentary cycles, indicating a sea level rise in the lowermost 14 meters of the member, a stabilisation of the sea level in the next two thirds of the member and a new sea level rise in the uppermost part. This stabilisation of the sea level could correspond to the minor regression (CSU 2170-2220), indicated by the reappearance of sandy shales in the Orneau area.

The correlation between the Givetian formations of the southern part of the Dinant Synclinorium and the northern part of the Dinant Synclinorium by Préat (1984), based on sedimentological sequences is not supported by the results of the graphic correlation. Based on the sequences, the Névremont Formation in the northern part is correlated with the Trois Fontaines, the Terres d'Haurs and the Mont d'Haurs Formations in the southern part. The biostratigraphical correlation shows a time-equivalence between the Névremont Formation and the Mont d'Haurs Formation. This was also stated by Meurrens (1986) who concluded that the lower part of the Névremont Formation in Aisemont could be correlated with the upper part of the Trois
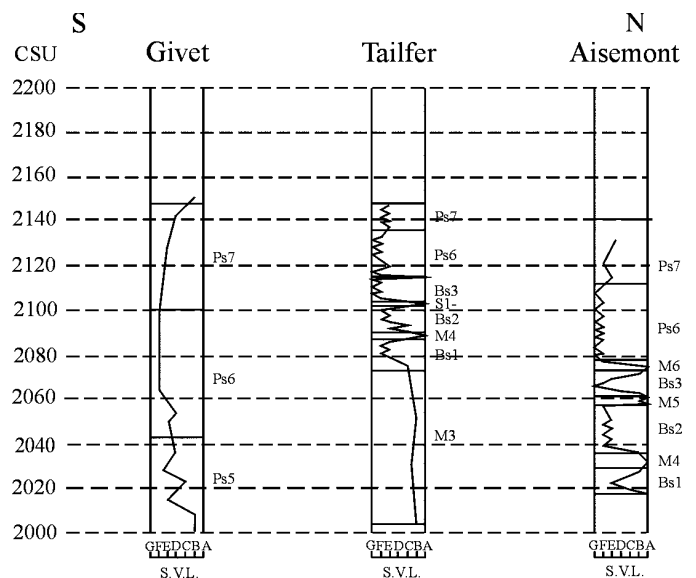
FIGURE 17–Sedimentary sequences of Préat (1984) in a chronostratigraphic framework. S.V.L.: Série virtuelle locale (Errera *et al.,* 1972).

Fontaines Formation in Givet and suggested that similar sequences of different phases have been correlated in the sequence correlation of Préat (1984). Gouwy & Bultynck (2002b) described a sedimentary hiatus in Aisemont, covering the upper part of the Jemelle Formation and the lower part of the Trois Fontaines Formation in Givet. When arranging the sedimentological sequences of Préat (1984) in a graphic correlation framework (CSU's), it is clear that the minor sequences in the different regions are not correlatable, despite the fact that the overall trend is the same (Fig. 17). Préat & Kasimi (1995) and Kasimi & Préat (1996) identify 5th order sedimentary cycles during the Eifelian – Givetian transition in the southern part of the Dinant Synclinorium. Lateral correlation of the vertical stacking of those cycles along the southern border of the Dinant Synclinorium connects the 'X' Formation in the Wellin area to the upper part of the Hanonet Formation in Couvin. Graphic correlation links the 'X' Formation to the upper part of the Jemelle Formation and the lower part of the Hanonet Formation in Couvin. So also in this case similar sequences of different phases have been correlated. The stacking of the cycles shows a decrease of water depth at the Eifelian-Givetian boundary.

Hance *et al.* (1992) describe a sedimentary gap below the Vicht Formation in the Vesdre area from the top of the Pragian till the top of the Eifelian, based on palynology. Detailed conodont research of the Pépinster Formation on top of the Vicht Formation in the Vesdre area (de Decker, 1994) indicated an Eifelian age for the Pépinster Formation. Graphic correlation places the lowermost part of the Pépinster Formation in the upper part of the *costatus* Zone (CSU 1450-1600). This reduces the gap in the Vesdre area to a maximum interval of Emsian and Lower Eifelian.

In the Villers-St-Gertrude (Hampteau section) and Jemelle (Grupont section) areas a few bentonite layers are recognized (Demeersseman, 1980) but cannot be used for precise correlation because of an unequal amount of layers in the different areas. However, projection of the layers onto the regional composite reveals that some of the bentonites coincide in the two areas: Grupont 164 and Hampteau 1 at CSU 1069, Grupont 181 and Hampteau 2 at CSU 1077 and Grupont 196 and Hampteau 7 at CSU 1100 (Fig. 10 a-b).
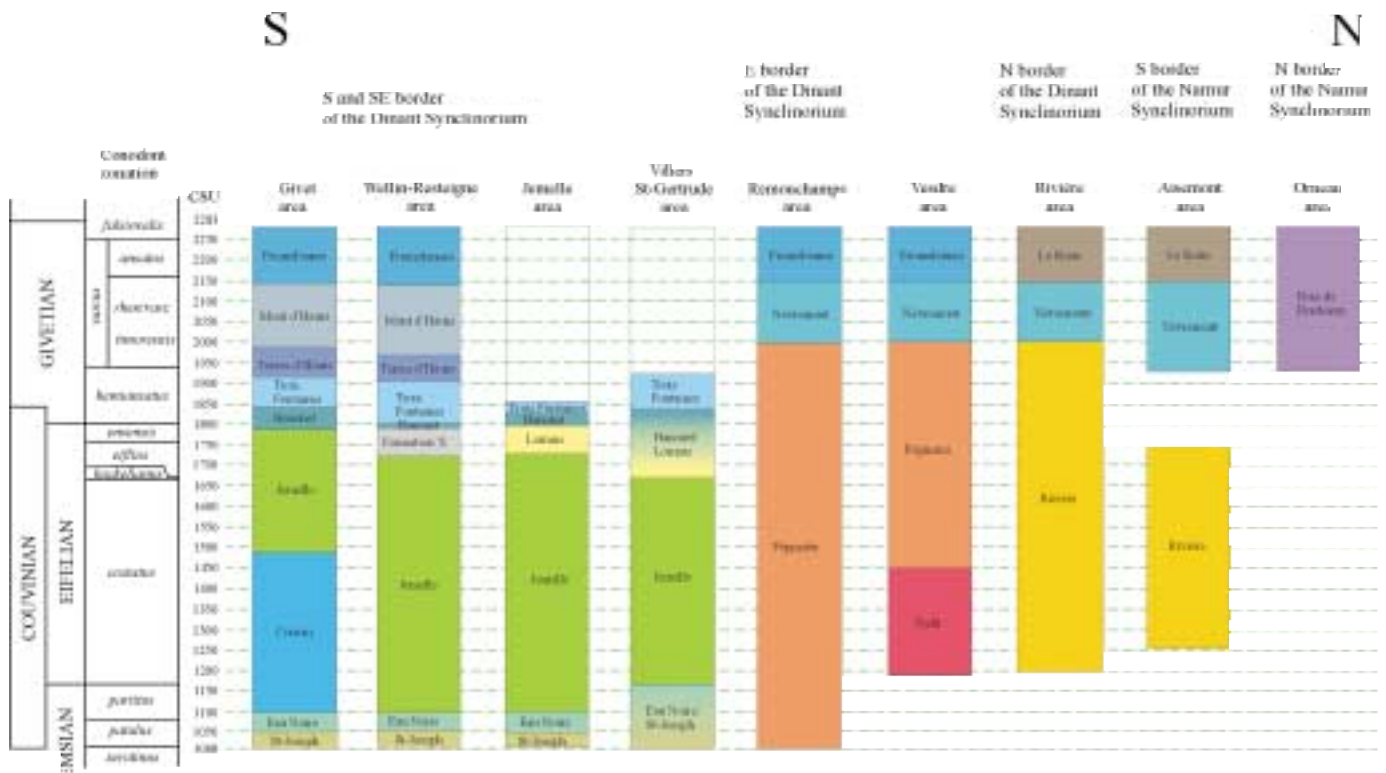
FIGURE 18–Chronostratigraphic diagram of the Middle Devonian Formations of the Ardenne.
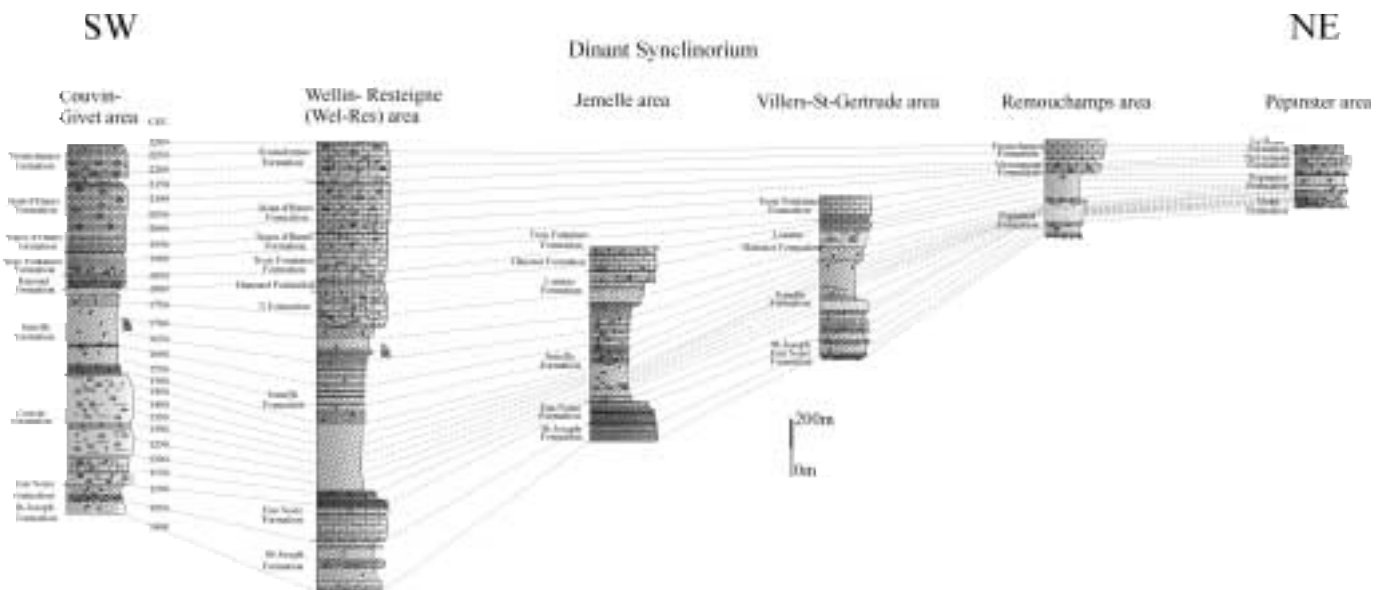
FIGURE 19–Correlation of the Middle Devonian sections of the southeastern part of Dinant Synclinorium and the Vesder area.

Chronostratigraphic diagram of the Middle Devonian formations in the Ardenne (Fig. 18)

One of the results of graphic correlation is that conodont zones can be projected into sections that either did not contain zone-defining species or did not at all contain conodonts. Figure 18 shows a chronostratigraphic diagram of the Middle Devonian formations of the Ardenne and their position in the conodont zonation. Graphic correlation indicates that the base of the Givetian limestone Formations (Trois Fontaines, Terres d'Haurs and Mont d'Haurs) are not isochronous in the Couvin-Givet, Wellin, Jemelle and Villers-St-Gertrude areas. The Névremont Formation in the northern and eastern border of the Dinant Synclinorium and the northern and southern border of the Namur Synclinorium is time-equivalent with the Mont d'Haurs Formation of the southern border of the Dinant Synclinorium. The lower position of the base of the Névremont Formation in the Aisemont area is only due to a relocation of that base to the first pure limestone layer (Gouwy& Bultynck, 2002b). The Vicht Formation is diachronous in the Vesdre area. In Figure 18 only the position of the Vicht Formation in the Pépinster section is indicated. In other sections of the Vesdre area, the base of the Pépinster Formation is placed at the base of the Givetian (Heusy, Hance *et al.,* 1989) or the middle part of the Vicht Formation is placed in the upper part of the Eifelian (Eupen, Bultynck *et al.,* 1991).

CONCLUSIONS

Conodont, coral, brachiopod, spore and acritarch data are used here to obtain a high-resolution correlation of nine Middle Devonian sections of the Ardenne based on graphic correlation. The Ardenne regional composite developed in this study allows a subdivision of the Eifelian into 724 CSU and of the Givetian into 841 CSU derived from the Couvin-Givet section selected as the standard reference section. This is a much higher resolution than obtained by the traditionally used conodont zones. Ranges of coral, brachiopod, spore and acritarch taxa can be

accurately correlated with the conodont zonation and to the CSU's. The chronostratigraphic charts reveal the diachronic nature of the Middle Devonian deposits. They show a major transgression-regression cycle in the mixed siliciclastic-carbonate Eifelian succession. The transgression covers the *partitus, costatus* and *australis* Zones. The first interruption of the biostromal facies of the Couvin Formation could correspond with the sea-level rise associated with the Chotec event that occurs in the upper part of the *partitus* Zone and the lower part of the *costatus* Zone. The transgression at the top of the Couvin Formation in Couvin may correlate with the deepening event in the *costatus* Zone (base of Cycle Id, Johnson *et al.,* 1996). The regression starts in the *eiflius* Zone, continues during the *ensensis* Zone and the lower part of the *hemiansatus* Zone, is interrupted by a minor transgressive pulse located in the uppermost part of the *ensensis* Zone and causes a sedimentary gap in the Aisemont area. This sedimentary gap might correlate with Struve's Great Gap. No evidence of the lower Kaçak event (*otomari* event) has been found.

In the rest of the Givetian, a transgression consisting of two pulses is recognized. The first one covers the upper part of the *hemiansatus* Zone and the *timorensis* Zone. The second pulse occurs slightly below the base of the *ansatus* Zone. None of these pulses coincide with the Taghanic event in the lower part of the *ansatus* Zone.

ACKNOWLEDGEMENTS
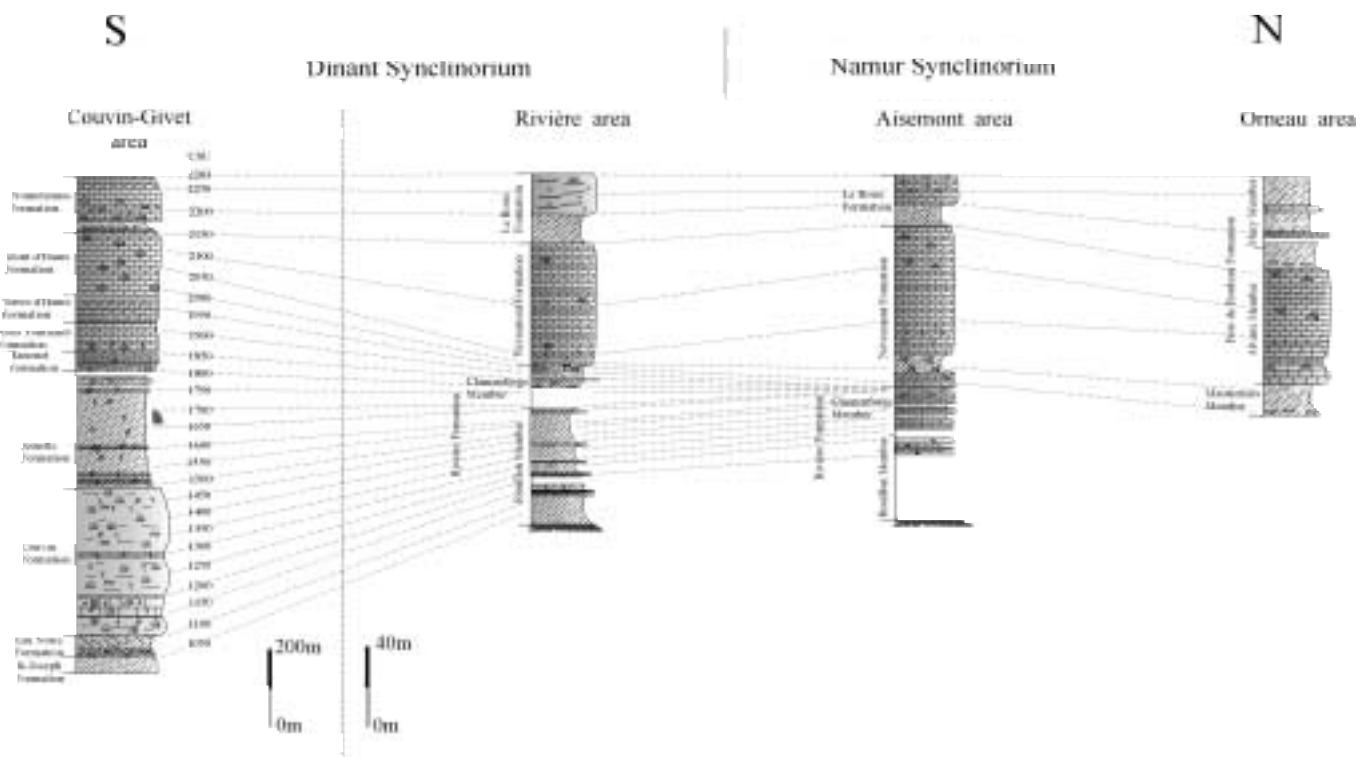
FIGURE 20–Correlation of the Middle Devonian sections from south to north.

Appendix of figured species

I. brevis Stauffer, 1940, p. 424, pl. 60, Figs. 30, 43, 44, 52. Bultynck 1987, Pl. 6, Figs. 1-14 (see Pl. Fig. 11 herein)

I. latecarinatus Bultynck, 1974, p. 19, Pl. II, Figs. 7, 8, Pl. III, Figs. 1-7, Pl. IV, Figs. 1-9 (see Pl. Fig. 13 herein)

I. lilliputensis Bultynck, 1987, p. 159, Pl. 5, Figs. 13-19 (see Pl. Figs. 6, 8 herein)

I. lindensis Weddige, 1977, pp. 293-294, Pl. 2, Figs. 38-39. Bultynck 1987, Pl. 4, Figs. 17-22 (see Pl. Figs. 9, 10 herein)

I. platyobliquimarginatus Bultynck, 1987, p. 160, Pl. 5, Figs. 1-9 (see Pl. Fig. 12 herein)

I. obliquimarginatus Bischoff & Ziegler, 1957, pp. 62-63, Fig. 14. Bultynck 1987, Pl. 4, Figs. 7-10, 12-16 (see Pl. Fig. 14 herein)

P. angusticostatus Wittekindt, 1966, p. 631, Pl. 1, Figs. 15-18 (see Pl. Fig. 7 herein)

P. costatus costatus Klapper, 1971, p. 63, Pl. 1, Figs. 30-36, Pl. 2, Figs. 1-7 (see Pl. Fig. 4 herein)

P. pseudofoliatus Wittekindt, 1966, pp. 637-637, Pl. 2, Figs. 19-23 (see Pl. Fig. 2 herein)

P. denisbriceae Bultynck in Brice *et al.,* 1979, p. 334, Pl. 27, Figs. 1-8 (see Pl. Fig. 1 herein)

P. linguiformis alveolus Weddige, 1977, p. 312, Pl. 5, Figs. 85-87 (see Pl. Fig. 3 herein)

P. xylus Stauffer, 1940, p. 430, Pl. 60, Figs. 54, 66, 72-74 (see Pl. Fig. 5 herein)

$\rightarrow$

PLATE –All magnifications are x90. *1, P. denisbriceae* Bultynck in Brice *et al*. 1979. Orneau area. Bois de Bordeau Formation, Alvaux Member. Alvaux 131. Upper view. I.R.Sc.N.B. N°b 4188. *2, P. pseudofoliatus* Wittekindt 1966. Orneau area. Bois de Bordeau Formation, Alvaux Member. Alvaux 131. Upper view. I.R.Sc.N.B. N°b 4189. *3, P. linguiformis alveolus* Weddige 1977. Villers-St-Gertrude area. Jemelle Formation. VSG 23. Upper view. I.R.Sc.N.B. N°b 4190. *4, P. costatus costatus* Klapper 1971. Villers-St-Gertrude area. Jemelle Formation. VSG 34. Upper view. I.R.Sc.N.B. N°b 4191. *5, P. xylus* Stauffer 1940. Orneau area. Bois de Bordeau Formation, Mautiennes Member. Poudingue. Upper view. I.R.Sc.N.B. N°b 4192. *6, 8, I. lilliputensis* Bultynck 1987. Orneau area. Bois de Bordeau Formation, Alvaux Member. Alvaux 133. Upper view. I.R.Sc.N.B. N°b 4193, Rivière area. Névremont Formation. Collection Coen-Aubert 095(341). Upper view. I.R.Sc.N.B. N°b 4195. *7, P. angusticostatus* Wittekindt 1966. Villers-St-Gertrude area. Jemelle Formation. VSG 33. Upper view. I.R.Sc.N.B. N°b 4194. *9, 10, I. lindensis* Weddige 1977. Orneau area. Bois de Bordeau Formation, Alvaux Member. Alvaux 126. Lateral view. I.R.Sc.N.B. N°b 4196, Villers-St-Gertrude area. Trois Fontaines Formation. Marenne 2. Lateral view. I.R.Sc.N.B. N°b 4197. *11, I. brevis* Stauffer 1940. Rivière area. Névremont Formation. Collection Coen-Aubert 059(277). Lateral view. I.R.Sc.N.B. N°b 4198. *12, I. platyobliquimarginatus* Bultynck 1987. Rivière area. Névremont Formation. Collection Bultynck and Boonen section 2 sample 7. Upper view. I.R.Sc.N.B. N°b 4199. *13, I. latecarinatus* Bultynck 1974. Orneau area. Bois de Bordeau Formation. Alvaux Member. Alvaux 131. Upper view. I.R.Sc.N.B. N°b 4200. *14, I. obliquimarginatus* Bischoff & Ziegler 1957. Rivière area. Névremont Formation. Collection Coen-Aubert 056(275). Upper view. I.R.Sc.N.B. N°b 4201.

PLATE

Nr	Conodonts	First Appearance Data (CSU)	Last Appearance Data (CSU)	Givet	Pondrôme	Wellin	Jemelle	Villers-St-Gertrude	Remouchamps	Vesder	Rivière	Aisemont	Orneau
1	*Ancyrodella rotundiloba binodosa*	2282	***	>	N.P.	×	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.
2	*A. rotundiloba rotundiloba*	2283	***	>	N.P.	×	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.
3	*A. soluta*	2281	***	×	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	>	N.P.
4	*Bipennatus bipennatus bipennatus*	1847	2039	×	N.P.	×	N.P.	×	N.P.	N.P.	><	N.P.	N.P.
5	*Eognathodus bipennatus montensis*	1328	1488	><	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	×	N.P.
6	*I. amabilis*	1158	1848	>	N.P.	N.P.	N.P.	<	×	×	×	×	N.P.
7	*I. arkonensis*	1768	1768	N.P.	N.P.	N.P.	N.P.	><	N.P.	N.P.	N.P.	N.P.	N.P.
8	*I. brevis*	1941	2162	<	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	×	>	×
9	*I. corniger ancestralis*	1014	1053	>	N.P.	N.P.	<	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.
10	*I. corniger corniger*	836	1309	>	N.P.	N.P.	×	<	N.P.	N.P.	N.P.	N.P.	N.P.
11	*I. culicellus altus*	1002	1149	>	N.P.	N.P.	×	N.P.	<	N.P.	N.P.	N.P.	N.P.
12	*I. culicellus culicellus*	836	1100	><	N.P.	×	×	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.
13	*I. eslaensis*	2003	2281	>	N.P.	N.P.	N.P.	N.P.	N.P.	×	×	<	×
14	*I. excavatus*	1954	2281	>	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	×	<	N.P.
15	*I. expansus*	2144	***	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	><	N.P.
16	*I. fusiformis*	837	872	><	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.
17	*I. introlevatus* ss	1048	1180	>	N.P.	<	×	N.P.	N.P.	N.P.	N.P.	×	N.P.
18	*I. latecarinatus*	1982	2285	><	N.P.	N.P.	N.P.	N.P.	N.P.	×	×	×	×
19	*I. leptus*	1002	1079	><	N.P.	N.P.	×	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.
20	*I. lilliputensis*	1918	2162	><	N.P.	N.P.	N.P.	N.P.	N.P.	×	×	×	×
21	*I. lindensis*	1877	2173	×	N.P.	N.P.	N.P.	>	N.P.	N.P.	N.P.	×	<
22	*I. obesus*	1982	2003	><	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.
23	*I. obliquimarginatus*	1802	2090	>	N.P.	×	×	×	N.P.	N.P.	<	×	N.P.
24	*I. platyobliquimarginatus*	1802	2060	>	N.P.	×	N.P.	×	N.P.	N.P.	<	×	N.P.
25	*I. rectirostratus*	837	1079	><	N.P.	×	×	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.
26	*I. regularicrescens*	1659	1990	×	N.P.	>	×	×	×	N.P.	N.P.	<	N.P.
27	*I. retrodepressus*	1065	1263	>	N.P.	×	×	×	×	N.P.	<	N.P.	N.P.
28	*Icriodus* sp. aff. *I. arkonensis*	1978	2148	><	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.
29	*I.* sp. aff. *I. arkonensis*	1978	2148	><	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.
30	*I.* sp. aff. *I. difficilis*	2281	2281	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	><	N.P.
31	*I.* sp. aff. *I. fusiformis*	1008	1058	N.P.	N.P.	><	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.
32	*I. struvei*	1161	1758	<	N.P.	×	N.P.	×	×	N.P.	>	×	N.P.
33	*I. subterminus*	2248	***	N.P.	N.P.	><	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.
34	*Latericriodus beckmanni sinuatus*	837	872	><	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.
35	*Ozarkodina* sp. aff. *O. raaschi*	1849	1849	N.P.	N.P.	N.P.	N.P.	><	N.P.	N.P.	N.P.	N.P.	N.P.
36	*O. bidentata*	1743	1843	×	N.P.	>	<	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.
37	*O. brevis*	2281	2281	><	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.
38	*O. plana*	2038	2161	<	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	×	>	N.P.
39	*Pandorinellina insita*	2249	2260	>	N.P.	<	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.
40	*Polygnathus ansatus*	2157	2160	><	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.
41	*P.* sp. aff. *P. ovatinodosus*	2050	2050	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	><	N.P.
42	*P.* sp. aff. *P. robustus*	1804	1804	><	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.
43	*P. alatus*	2282	***	N.P.	N.P.	><	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.
44	*P. angusticostatus*	1597	1848	>	N.P.	×	×	<	N.P.	N.P.	N.P.	N.P.	N.P.
45	*P. angustipennatus*	1595	1838	><	N.P.	×	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.

Nr	Conodonts	First Appearance Data (CSU)	Last Appearance Data (CSU)	Givet	Pondrôme	Wellin	Jemelle	Villers-St-Gertrude	Remouchamps	Vesder	Rivière	Aisemont	Orneau
46	P. costatus costatus	1169	1672	➤	N.P.	✗	N.P.	◄	N.P.	N.P.	N.P.	N.P.	N.P.
47	P. costatus partitus	1078	1078	N.P.	N.P.	N.P.	➤◄	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.
48	P. costatus patulus	1014	1123	➤◄	N.P.	✗	✗	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.
49	P. denisbriceae	2152	2162	◄	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	➤	✗
50	P. dubius	2257	***	➤◄	N.P.	✗	N.P.	N.P.	N.P.	N.P.	N.P.	✗	N.P.
51	P. eiflius	1667	1686	➤◄	N.P.	✗	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.
52	P. ensensis	1762	1806	➤	N.P.	◄	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.
53	P. hemiansatus	1802	1802	➤◄	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.
54	P. linguiformis alveolus	1632	1835	◄	N.P.	N.P.	N.P.	➤	N.P.	N.P.	N.P.	N.P.	N.P.
55	P. linguiformis bultyncki	1081	1162	✗	N.P.	➤◄	✗	✗	N.P.	N.P.	N.P.	N.P.	N.P.
56	P. linguiformis cooperi	1099	1102	N.P.	N.P.	➤◄	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.
57	P. linguiformis linguiformis	1161	2282	✗	✗	◄	✗	✗	✗	✗	➤	N.P.	N.P.
58	P. linguiformis pinguis	1142	1162	➤◄	N.P.	N.P.	N.P.	N.P.	✗	N.P.	N.P.	N.P.	N.P.
59	P. linguiformis subsp. A	1801	1927	✗	N.P.	➤	N.P.	◄	N.P.	N.P.	N.P.	N.P.	N.P.
60	P. parawebbi	1848	1863	N.P.	N.P.	N.P.	N.P.	➤◄	N.P.	N.P.	N.P.	N.P.	N.P.
61	P. pennatus	2251	2251	N.P.	N.P.	➤◄	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.
62	P. pseudofoliatus	1595	2153	➤◄	N.P.	✗	N.P.	✗	N.P.	✗	✗	N.P.	✗
63	P. rhenanus	2148	2162	➤◄	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.
64	P. robusticostatus	1632	1848	N.P.	N.P.	N.P.	N.P.	➤◄	N.P.	N.P.	N.P.	N.P.	N.P.
65	P. serotinus	***	1078	N.P.	N.P.	N.P.	➤◄	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.
66	P. timorensis	2053	2254	✗	N.P.	◄	N.P.	N.P.	N.P.	N.P.	✗	➤	N.P.
67	P. trigonicus	1681	1681	N.P.	N.P.	➤◄	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.
68	P. varcus	2129	2283	➤	N.P.	◄	N.P.	N.P.	N.P.	N.P.	N.P.	✗	N.P.
69	P. xylus	1934	***	◄	N.P.	✗	➤	N.P.	N.P.	N.P.	✗	✗	✗
70	Smithognathodus hermanni	2251	2251	N.P.	N.P.	➤◄	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.
71	Tortodus sp. cf. T. variabilis	1863	1863	N.P.	N.P.	N.P.	N.P.	➤◄	N.P.	N.P.	N.P.	N.P.	N.P.
72	T. intermedius	1667	1842	➤◄	N.P.	✗	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.
73	T. kockelianus	1661	1805	◄	N.P.	➤	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.	N.P.

TABLE–Conodont taxa ranges and their occurrences in the different regions. ✗ : present, ➤ : first appearance, ◄ : last appearance, N.P.: not present, ***: first appearance lower than 836 CSU or last appearance higher than 2285 CSU.

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OSTRACODES DU MIOCÈNE SUPÉRIEUR DU BASSIN DE TURIEC (SLOVAQUIE): FAMILLES DARWINULIDAE ET ILYOCYPRIDIDAE

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Resumé

Les espèces de *Darwinula, Vestalenula* et *Ilyocypris* ont été trouvées dans les dépôts d'eau douce du Miocène supérieur de Slovaquie (Europe Centrale). Les données paléobiologiques et sédimentologiques indiquent qu'elles ont vécu dans un milieu littoral et sublittoral. Les différences dans la vitesse de l'écoulement de l'eau ont influencé la distribution des genres. *Ilyocypris* se rencontre dans le nord du bassin de Turiec tandis que les Darwinulidae occupent un territoire plus large. Une espèce nouvelle, *Ilyocypris papilionacea*, à la morphologie et au bord externe inhabituel est décrite.

Mots clés: Ostracoda, Miocène supérieur, milieu d'eau douce, paléobiotopes, Slovaquie.

Abstract

[*Upper Miocene Ostracods of the Turiec basin (Slovakia): families Darwinulidae and Ilyocyprididae*]. *Darwinula, Vestalenula* and *Ilyocypris* species have been found in the freshwater Upper Miocene deposits of Slovakia (Central Europe). Both the paleobiological and sedimentological data indicate that they dwelt in a littoral to sublittoral environment. The differences in water flow velocity restricted the species of *Ilyocypris* to the northern part of the basin, while Darwinulidae occupy a larger area of the Turiec basin. A new species, *Ilyocypris papilionacea*, with unusual morphology and external margin is described.

Key words: Ostracoda, Upper Miocene, fresh-water environment, palaeobiotopes, Slovakia.

Resumen

Se describen especies de los géneros *Darwinula*, *Vestalenula* e *Ilyocypris*, procedentes de depósitos de agua dulce del Mioceno Superior de Eslovaquia (Europa central). Los datos paleobiológicos y sedimentológicos indican que habitaron en ambientes desde litorales a sublitorales. Las diferencias en la velocidad del flujo del agua restringieron las especies de *Ilyocypris* a la parte septentrional de la cuenca de Turiec, mientras que las de Darwinulidae ocuparon un territorio más extenso. Se describe una nueva especie, *Ilyocypris papilionacea*, que presenta una morfología y borde externo inusuales.

Palabras clave: Ostrácodos, Mioceno Superior, agua dulce, paleobiotopos, Eslovaquia.

INTRODUCTION

Une révision taxonomique des Darwinulidae sur la base des parties molles et des caractères des valves a permis de distinguer 5 genres au sein de cette famille (Rossetti et Martens, 1998).

Parmi ceux-ci, *Darwinula*, *Microdarwinula* et *Vestalenula* dont la distribution est cosmopolite sont rencontrés dans les écosystèmes européens depuis le Miocène inférieur (Straub, 1952; Danielopol, 1968; Martens *et al.*, 1997; Janz, 1997; Witt, 2000). La variabilité inter- et intraspécifique est peu importante chez *Darwinula stevensoni* (Brady et Robertson, 1870), seule sa taille varie d'une population à l'autre (Rossetti et Martens, 1996).

Les *Ilyocypris* sont fréquents dans les dépôts lacustres du Miocène d'Europe. Les espèces montrent une large variabilité de l'ornementation; de ce fait, une détermination spécifique des taxons fossiles s'appuie sur les rides situées au niveau postéro-ventral de la lamelle interne (Van Harten, 1979; Janz, 1994; Meisch, 2000).

Ces deux familles sont toutes deux minoritaires dans les dépôts d'eaux douces du Miocène supérieur du bassin de Turiec (Fig. 1). Leurs espèces ne présentent que 4,8% de la totalité des espèces de l'ostracofaune (Pipík, 2001).

DESCRIPTION SYSTÉMATIQUE

Abréviations utilisées dans le texte: BA, bord antérieur; BAD, bord antéro-dorsal; BD, bord dorsal; BPD, bord postéro-dorsal; BP, bord postérieur; BPV, bord postéro-ventral; BV, bord ventral; BAV, bord antéro-ventral; BE, bord externe; $H_{max.}$, hauteur maximale de la valve; $E_{max,}$ largeur maximale de la valve; n, quantité d'individus traités; l, longueur de la valve en mm; h, hauteur de la valve en mm; φ, moyenne; h/l, rapport hauteur versus longueur.

Tous les individus figurés sur les planches seront déposés au Musée National de Slovaquie à Bratislava.

Classe OSTRACODA Latreille, 1806
Ordre PODOCOPIDA Sars, 1866
Sous-ordre PODOCOPINA Sars, 1866
Famille DARWINULIDAE Brady et Norman, 1889
Genre *Darwinula* Brady et Robertson, 1885
Darwinula stevensoni (Brady et Robertson, 1870)
(Pl. 1, Figs. 1-4, Fig. 23)

1952 *Darwinula stevensoni* – Straub, p. 497, Figs. 17, 18.
1965 *Darwinula stevensoni* – Devoto, p. 346, Fig. 52.
1961 *Darwinula stevensoni* – Diebel, p. 539, Pl. II, Figs. 12, 13.
1973 *Darwinula stevensoni* – Malz et Moayedpour, p. 293, Pl. 1, Figs. 13-14, Pl. 5, Figs. 43-49.
1975 *Darwinula stevensoni* – Lister, p. 30, Pl. 3, Fig. 15.
1978 *Darwinula stevensoni* – Diebel et Pietrzeniuk, Pl. 26, Figs. 10, 11.
1978 *Darwinula stevensoni* – Sokac, p. 20, Pl. X, Figs. 9, 10.
1980 *Darwinula stevensoni* – Freels, p. 135, Pl. 1, Figs. 12-14.
1985 *Darwinula stevensoni* – Guillaume *et al.*, Pl. 115, Fig. 7.
1990 *Darwinula stevensoni* – Fuhrmann et Pietrzeniuk, Pl. 1, Figs. 9-10.
1996 *Darwinula stevensoni* – Rossetti et Martens, p. 77-83, Pl. 9, Figs. A-R, Pl. 10, Figs. A-M.
1997 *Darwinula stevensoni* – Janz, p. 12, Pl. 1, Fig. 4.

Matériel.–15 valves d'individus adultes, 7 valves d'individus juvéniles; les valves sont souvent cassées.
Dimensions.–(Localité Martin, échantillon MT 24) :

		n	l	φ	h	φ	h/l	φ
A	D	1	0,688	-	0,294	-	0,427	-
	G	7	0,647 - 0,69	0,674	0,258 - 0,294	0,278	0,399 - 0,426	0,412
A-1	D	2	0,549 - 0,573	-	0,235 - 0,239	-	0,418 - 0,429	-
	G	2	0,55 - 0,608	-	0,226 - 0,245	-	0,403 - 0,41	-

Rapports et différences.–La taille des valves des individus adultes se situe dans la limite inférieure de l'espèce (0,669-0,771 mm), selon Rossetti et Martens (1996) ou 0,63-0,80 mm (moyenne comprise entre 0,68-0,72 mm), selon Meisch (2000). Elle se rencontre rarement dans le bassin de Turiec.
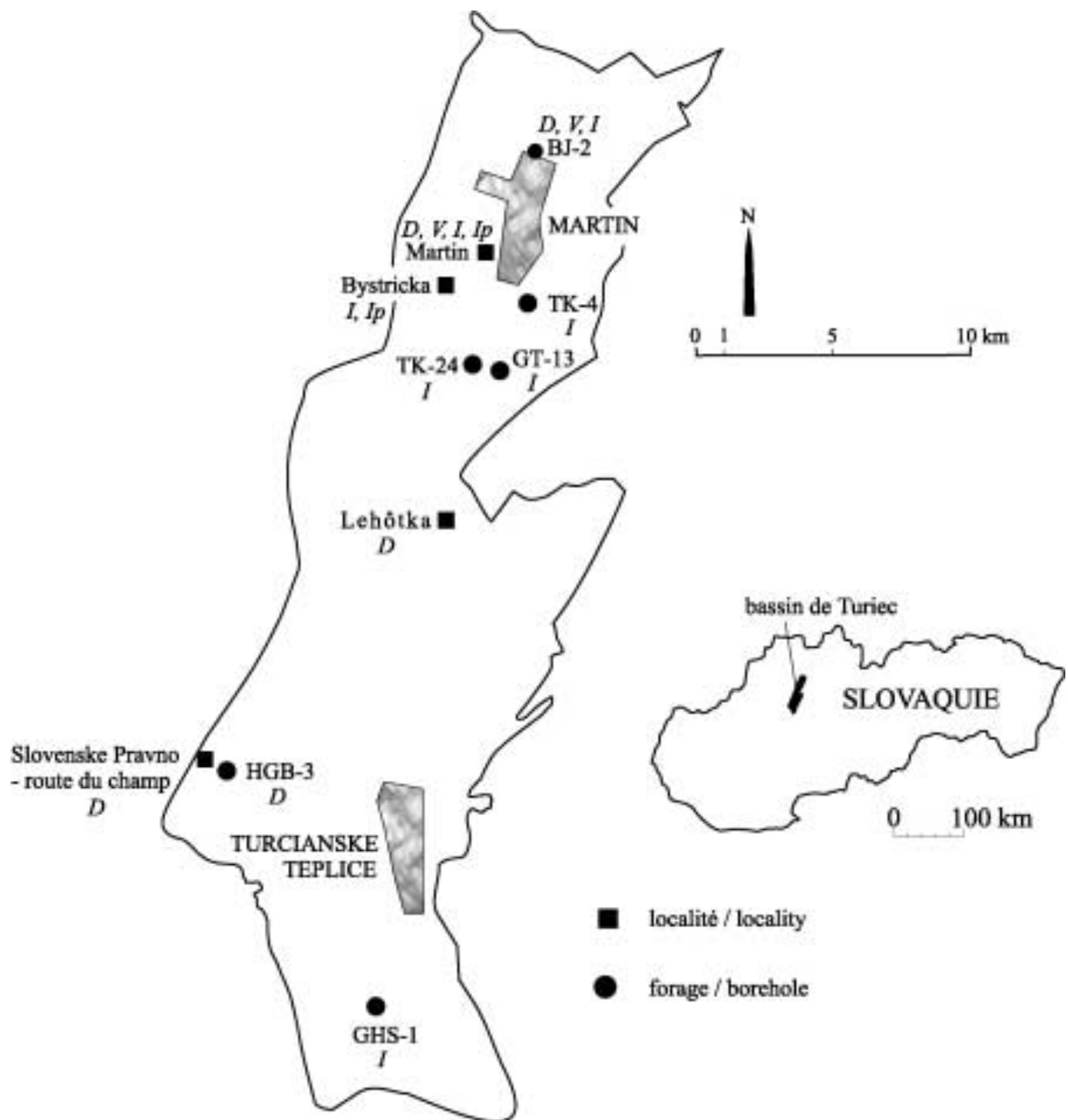
FIGURE 1–Le bassin de Turiec, sa position géographique en Slovaquie et répartition des espèces des familles Darwinulidae et Ilyocyprididae (*D, Darwinula stevensoni; V, Vestalenula pagliolii*; *I, Ilyocypris* sp. 1; *Ip, Ilyocypris papilionacea*).

FIGURE 1–The Turiec basin, its geographic position in Slovakia and distribution of the species of the families Darwinulidae and Ilyocyprididae (*D, Darwinula stevensoni; V, Vestalenula pagliolii*; *I, Ilyocypris* sp. 1; *Ip, Ilyocypris papilionacea*).

Répartition géographique et stratigraphique.–
Cosmopolite; Oligocène moyen jusqu'à l'Actuel
(Meisch, 2000).

*Répartition régionale.–*Martin, Slovenské Pravno
- route du champ, Lehôtka, forages HGB-3, forage
BJ-2.

Genre *Vestalenula* Rossetti et Martens, 1998
Vestalenula pagliolii (Pinto et Kotzian, 1961)
(Pl. 1, Figs. 5-10, Fig. 24)

1980 *Darwinula cylindrica* – Freels, p. 12, Pl. 1,
Fig. 1, 2, 6, non Pl. 1., Fig. 3, 4, 5.
1991 *Darwinula* cf. *pagliolii* – Pietrzeniuk, p. 108,
Fig. 1, 2, Pl. 5, Fig. 8, 9.
1997 *Darwinula pagliolii* – Martens *et al*. p. 106,
Pl. 3, Fig. M-P.
1998 *Vestalenula pagliolii* – Rossetti et Martens, p.
76-77, Pl. 25, Fig. Q-S, Pl. 28, Fig. A,B.

*Matériel.–*17 valves et une carapace d'individus
adultes, une valve d'individu juvénile.

Dimensions (localité Martin, échantillon MT 24).–
*Rapports et différences.–*JANZ (1997) a figuré les
individus de *Darwinula cylindrica* Straub, 1952 du
Miocène moyen; elle est très proche de *Vestalenula
pagliolii* mais sa quille postéro-ventrale est située plus
vers le BV sur la valve droite; la dent antéro-ventrale
interne sur la valve gauche, nécessaire pour la déter-
mination du genre *Vestalenula*, n'est pas visible sur les
individus d'Allemagne.

Darwinula flandrini Carbonnel, Weidmann et Berger,
1985 du Tortonien (Miocène Supérieur) (Carbonnel *et
al*., 1985) possède aussi la dent à l'intérieur sur la valve
gauche ainsi que les canaux de pores externes en rangée
commissurale sur le BP. La figuration détaillée de la par-
tie postérieure de *D. flandrini* ne présente pas le BPV
complet où se situe la quille postéro-ventrale à l'exté-
rieur de la valve de *Vestalenula paglioli*; en conséquen-
ce, il est difficile de se prononcer si *Darwinula flandrini*
est une espèce différente ou seulement synonymique.

D. chatti Malz et Moyaedpour, 1973 du Miocène
inférieur d'Hesse (Allemagne) ne présente pas non plus
la dent antéro-ventrale (Malz et Moyaedpour, 1973).

		n	l	φ	h	φ	h/l	φ
A	D	2	0,455 - 0,471	-	0,216 - 0,219	-	0,465 - 0,474	-
	G	10	0,471 - 0,496	0,488	0,216 - 0,235	0,229	0,453 - 0,48	0,469
A-1	G	1	0,408	-	0,198	-	0,486	-

Le bord externe de *V. pagliolii* est presque identique
à celui de *V. boteai* (Danielopol, 1970) des eaux soute-
rraines de Roumanie (Danielopol, 1970). Les indivi-
dus du bassin de Turiec ont une quille postéro-ventra-
le moins haute, plus longue et située plus vers la partie
ventrale (Pl. 1, Figs. 8, 9).

Répartition géographique et stratigraphique.–
Espèce actuelle, vivant au Brésil; en Afrique, en Asie
Mineure et en Europe Centrale se rencontre seulement
à l'état de populations fossiles. Elle est très rare dans
le bassin de Turiec. Miocène inférieur/moyen,
Pliocène, Pléistocène inférieur de Turquie, Miocène
supérieur de Slovaquie, Pléistocène (Eemien)
d'Allemagne, Holocène du Soudan, Actuel du Brésil.

*Répartition régionale.–*Martin, forage BJ-2.

*Litérature.–*Freels (1980); Pietrzeniuk (1991);
Griffiths et Butlin (1994); Martens *et al*. (1997);
Rossetti et Martens (1998).

Famille ILYOCYPRIDINAE Kaufmann, 1900
Sous-Famille ILYOCYPRIDINAE Kaufmann, 1900
Genre *Ilyocypris* Brady et Norman, 1889

Ilyocypris papilionacea n.sp.
(Pl. 1, Figs. 11-17, Fig. 25)
*Derivatio nominis.–*Lat. *papilionaceus* – en forme
de papillon; d'après la forme en papillon du bord
externe.

*Holotype.–*VG, Pl. 1, Fig. 11 (No. RP9-41).

*Paratypes.–*Pl. 1, Fig. 12 (No. RP9-42) ; Pl. 1, Fig. 13
(No. RP9-44) ; Pl. 1, Fig. 14 (No. RP9-45) ; Pl. 1, Fig.
15 et 25. (No. RP9-43) ; Pl. 1, Fig. 16 et 17 (No. RP8-2).

*Locus typicus.–*Bystrička.

*Stratum typicum.–*Miocène supérieur.

*Lieu de dépôt.–*Musée National de Slovaquie à
Bratislava.

*Diagnose.–*Espèce en forme de papillon à BV très
concave et à surface ornée; ornementation constituée
de fossettes rondes, d'épines, de quatre tubercules et
d'une forte crête située sur la deuxième moitié du BD
recouvrant le BI; lamelle interne couverte de faibles et
courtes rides dans sa partie distale sur le BP.

*Description.–*VG - BA haut et largement arrondi,
BD long et droit, angles cardinaux coudés et bien pro-
noncés, BP largement arrondi, BV très fortement con-

cave au milieu, profil latéral irrégulier en forme de papillon; deuxième moitié du BD recouverte par la crête longitudinale; H_{max} se situe à l'avant, E_{max} sur le postérieur.

VD - BA haut et largement arrondi passant régulièrement au long et droit BD; angles cardinaux soit arrondis, soit faiblement coudés; BP largement arrondi et plus bas que BA; BV très fortement concave au milieu, profil latéral faiblement allongé et irrégulier en forme de papillon; deuxième moitié du BD recouverte par la crête longitudinale; H_{max} se situe à l'avant; E_{max} sur le postérieur.

Dimorphisme sexuel: non observé.

Recouvrement: non observé.

Empreintes musculaires: petites, faibles, celles d'*Ilyocypris*.

Charnière: adonte.

Canaux de pores normaux: simples, peu nombreux.

Ornementation: se compose d'une crête, de tubercules, d'épines, de sillons et de fossettes. La forte crête à surface lisse est située sur la deuxième moitié du BD. Elle recouvre le BI. Quatre tubercules lisses inclinés vers l'arrière se situent au milieu de la valve dans l'ordre suivant: T1 avant le premier sillon; T2, le plus petit et moins prononcé, entre les sillons; T3, le plus haut et le plus important derrière le deuxième sillon; T4 au-dessous de T3. La taille des tubercules T2

et T4 est variable. Leur présence sur la surface est stable. De nombreuses, faibles, courtes et petites épines recouvrent la zone marginale du BA et du BP. Deux sillons verticaux, subparallèles et profonds situés au milieu descendent du BD. Le sillon S1 est plus court que S2 qui se termine au niveau du tubercule T4. Les fossettes peu profondes et rondes recouvrent la surface entière créant l'ornementation principale de la valve.

Zone marginale: zone de fusion large et de même largeur sur toute la longueur de la zone marginale; lamelle interne large à l'avant, plus courte au BV et au BP et fusionnée avec la lamelle externe sur le BV; elle est lisse sur le BP sauf sa partie distale qui porte les faibles et courtes rides; vestibule très bas à l'avant et haut à l'arrière; ligne de concrétion et BI parallèles à BE; canaux de pores marginaux droits, simples et denses; le faible repli et le rebord interne sont plus fortement développés sur la valve droite que sur la valve gauche.

Matériel.–14 valves complètes dont 7 proviennent de la Collection du Professeur Pokorný et une dizaine de valves cassées d'individus adultes, 3 individus juvéniles.

Dimensions.–(Localité Martin, échantillon MT34, localité Bystrička, échantillon BY4.1 et les échantillons de la Collection de Pokorný).

		n	l	φ	h	φ	h/l	φ
A	VG	3	0,892 - 0,931	-	0,502 - 0,53	-	0,563 - 0,569	-
	VD	11	0,882 - 0,975	0,929	0,471 - 0,549	0,503	0,512 - 0,563	0,542
A-1	VG	1	0,775	-	0,446	-	0,576	-
	VD	2	0,768 - 0,825	-	0,432 - 0,465	-	0,563 - 0,564	-

Rapports et différences.–*Ilyocypris slavonica* Sokac et Van Harten, 1978 possède aussi une ornementation particulière mais celle-ci présente seulement des épines nombreuses distribuées à l'arrière. Les tubercules sont moins exprimés. Les morphotypes illustrés sont moins concaves sur le BV et la différence de hauteur entre l'avant et l'arrière est moins importante (Sokac, 1978; Sokac et Van Harten, 1978). Des rides sur le BPV d'*Ilyocypris slavonica* ressemblent à celles observées chez *I. gibba* (Ramdohr) (Van Harten, 1979). *I. binocularis* Sieber, 1905 du Miocène moyen paraît être l'espèce la plus proche de *I. papilionacea* n.sp., mais il existe plusieurs caractères morphologiques permettant de distinguer ces deux espèces. Ses BA et BP sont moins arrondis, BP est plus grand comparé à celui de *I. papilionacea* n.sp. Son BD forme avec le BP vertical un angle postéro-dorsal presque droit. Il montre le repli bien développé sur la lamelle interne. De même il ne porte qu'une faible crête

longitudinale dans la deuxième moitié de la longueur du BD les rides sont bien développées (Janz, 1992, 1994).

Répartition régionale.–Martin, Bystrička; connu également de la Collection du Professeur Pokorný (Prague, Rép. Tchéque) de la localité Martin – briqueterie de Schulz.

Ilyocypris sp. 1
(Pl. 1, Figs. 18-22, Fig. 26)

Description.–VG - BA largement arrondi, BAD peu concave et court, BD long et droit, angles cardinaux coudés et bien visibles, BP faiblement arrondi et presque vertical, BPV fortement arrondi, BV fortement concave au milieu; forme rectangulaire; H_{max} se situe à l'avant, E_{max} au milieu de la valve.

VD - BA largement arrondi, BAD peu concave et court, BD long et droit, angle antérieur coudé, angle

postérieur fortement arrondi, BP faiblement arrondi et presque vertical, BPV fortement arrondi, BV fortement concave au milieu; forme rectangulaire; H_{max} se situe à l'avant, E_{max} juste derrière le deuxième sillon.

Dimorphisme sexuel: non observé.

Recouvrement: non observé.

Empreintes musculaires: petites, faibles, celles d'*Ilyocypris*.

Charnière: adonte.

Canaux de pores normaux: simples, peu nombreux.

Ornementation: se compose d'une crête, d'épines, de deux sillons, de fossettes et de tubercules. La faible crête se situe sur la deuxième moitié du BD; elle est plus déve-

$\rightarrow$

PLANCHE 1–*1-4, Darwinula stevensoni* (Brady et Robertson, 1870). *1,* – VG, l = 0,667 mm, h = 0,259 mm, Lehôtka DX3. 2 No. RP1-12, vue latérale interne; *2,* – VG, l = 0,686 mm, h = 0,292 mm, Martin MT24, No. RP4-25, vue latérale externe; *3,* – VD, l = 0,688 mm, h = 0,294 mm, Martin MT24, No. RP4-23, vue latérale externe; *4,* – VG, l = 0,667 mm, h = 0,272 mm, Martin MT24, No. RP4-24, vue latérale externe. *5-10, Vestalenula pagliolii* (Pinto et Kotzian, 1961). *5,* – VG, l = 0,494 mm, h = 0,235 mm, Martin MT24, No. RP4-20, vue latérale interne; *6, 7,* VD, l = 0,455 mm, h = 0,216 mm, Martin MT24, No. RP4-22; *6,* – vue latérale interne; *7,* – détail de la quille au niveau postéro-ventral; *8, 9,* VG, l = 0,496 mm, h = 0,235 mm, Martin MT24, No. RP4-19; *8,* – vue latérale interne; *9,* – détail de la dent au niveau antéro-ventral; *10,* – VG, l = 0,48 mm, h = 0,222 mm, Martin MT24, No. RP4-21, vue latérale externe. *11-17,* Ilyocypris papilionacea *n.sp. 11,* – VG, holotype, l = 0,904 mm, h = 0,511 mm; Bystricka 4.1, No. RP9-41, vue latérale externe; *12,* – VD, paratype, l = 0,903 mm, h = 0,492 mm; Martin MT34, No. RP9-42, vue latérale externe; *13,* – VD, paratype, l = 0,941 mm, h = 0,5 mm; Martin - Collection du Professeur Pokorn_, No. RP9-44, vue latérale externe*; 14,* – VD, paratype, l = 0,906 mm, h = 0,5 mm; Martin - Collection du Professeur Pokorn_, No. RP9-45, vue latérale externe; *15,* – VD, paratype, l = 0,882 mm, h = 0,484 mm; Martin MT34, No. RP9-43, vue latérale interne; *16, 17,* VG, paratype, l = 0,892 mm, h = 0,502 mm; Bystricka 4.1, No. RP8-2 ; *16,* – vue latérale interne, *17,* – *détail de la lamelle interne au bord postéro-ventral. 18-22, Ilyocypris* sp. 1. *18,* – VD, l = 0,794 mm, h = 0,452 mm; forage BJ-2, 189,0-190,0 m, No. RP10-17, vue latérale externe; *19,* – VG, l = 0,878 mm, h = 0,529 mm; forage BJ-2, 204,0-205,0 m ; No. RP8-3, vue latérale externe; *20,* – VG, l = 0,778 mm, h = 0,42 mm; Martin MT-6, No. RP10-18, vue latérale externe; *21,* 22, VG, l = 0,845 mm, h = 0,453 mm; Martin MT-6, No. RP8-1; *21,* – vue latérale interne; *22,* – détail de la lamelle interne au bord postéro-ventral; *23,* – *Darwinula stevensoni* (Brady et Robertson, 1870) ; VG, l = 0,667 mm, h = 0,259 mm, Lehôtka DX3.2, No. RP1-12, vue latérale externe; *24,* – *Vestalenula pagliolii* (Pinto et Kotzian, 1961); VG, l = 0,496 mm, h = 0,235 mm, Martin MT24, No. RP4-19, vue latérale externe; *25,* – Ilyocypris papilionacea *n.sp.;* VD, paratype, l = 0,882 mm, h = 0,484 mm ; Martin MT34, No. RP9-43, vue latérale externe; *26,* – *Ilyocypris* sp. 1; VG, l = 0,778 mm, h = 0,42 mm ; Martin MT6, No. RP10-18, vue latérale externe.

PLATE 1–*1-4, Darwinula stevensoni* (Brady & Robertson, 1870). *1,* – LV, l = 0,667 mm, h = 0,259 mm, Lehôtka DX3.2, No. RP1-12, intern lateral view; *2,* – LV, l = 0,686 mm, h = 0,292 mm, Martin MT24, No. RP4-25, extern lateral view; *3,* – RV, l = 0,688 mm, h = 0,294 mm, Martin MT24, No. RP4-23, extern lateral view; *4,* – LV, l = 0,667 mm, h = 0,272 mm, Martin MT24, No. RP4-24, extern lateral view. *5-10, Vestalenula pagliolii* (Pinto & Kotzian, 1961). *5,* – LV, l = 0,494 mm, h = 0,235 mm, Martin MT24, No. RP4-20, intern lateral view; *6, 7,* RV, l = 0,455 mm, h = 0,216 mm, Martin MT24, No. RP4-22, 6, – intern lateral view; *7* – detail of the postero-ventral keel; *8, 9,* LV, l = 0,496 mm, h = 0,235 mm, Martin MT24, No. RP4-19, 8, – intern lateral view; *9,* – detail of the antero-ventral tooth; *10,* – LV, l = 0,48 mm, h = 0,222 mm, Martin MT24, No. RP4-21, extern lateral view.*11-17,* Ilyocypris papilionacea *n.sp. 11, – LV, holotype, l = 0,904 mm, h = 0,511 mm; Bystricka 4.1, No. RP9-41, extern lateral view; 12,* – RV, paratype, l = 0,903 mm, h = 0,492 mm; Martin MT34, No. RP9-42, extern lateral view; *13,* – RV, paratype, l = 0,941 mm, h = 0,5 mm; Martin – Pokorný's Collection, No. RP9-44, extern lateral view; *14,* – RV, paratype, l = 0,906 mm, h = 0,5 mm; Martin – Pokorný's Collection, *No. RP9-45, extern lateral view; 15*, – RV, paratype, l = 0,882 mm, h = 0,484 mm; Martin MT34, No. RP9-43, intern lateral view; *16, 17,* LV, paratype, l = 0,892 mm, h = 0,502 mm; Bystricka 4.1, No. RP8-2; 16, – intern lateral view; *17,* – detail of the inner lamella on postero-ventral border. 18-22, *Ilyocypris* sp. 1. *18,* – RV, l = 0,794 mm, h = 0,452 mm ; borehole BJ-2, 189,0-190,0 m, No. RP10-17, extern lateral view; *19,* – LV, l = 0,878 mm, h = 0,529 mm ; borehole BJ-2, 204,0-205,0 m ; No. RP8-3, extern lateral view; *20,* – LV, l = 0,778 mm, h = 0,42 mm; Martin MT-6, No. RP10-18, extern lateral view; *21, 22,* LV, l = 0,845 mm, h = 0,453 mm; Martin MT-6, No. RP8-1; *21,* – intern lateral view; *22,* – detail of the inner lamella on postero-ventral border; *23,* – *Darwinula stevensoni* (Brady & Robertson, 1870); LV, l = 0,667 mm, h = 0,259 mm, Lehôtka DX3.2, No. RP1-12, extern lateral view; *24,* – *Vestalenula pagliolii* (Pinto & Kotzian, 1961); LV, l = 0,496 mm, h = 0,235 mm, Martin MT24, No. RP4-19, extern lateral view*; 25,* – Ilyocypris papilionacea *n.sp.; RV, paratype, l = 0,882 mm, h = 0,484 mm ; Martin MT34, No. RP9-43, extern lateral view*; *26,* – *Ilyocypris* sp. 1; LV, l = 0,778 mm, h = 0,42 mm ; Martin MT6, No. RP10-18, extern lateral view.
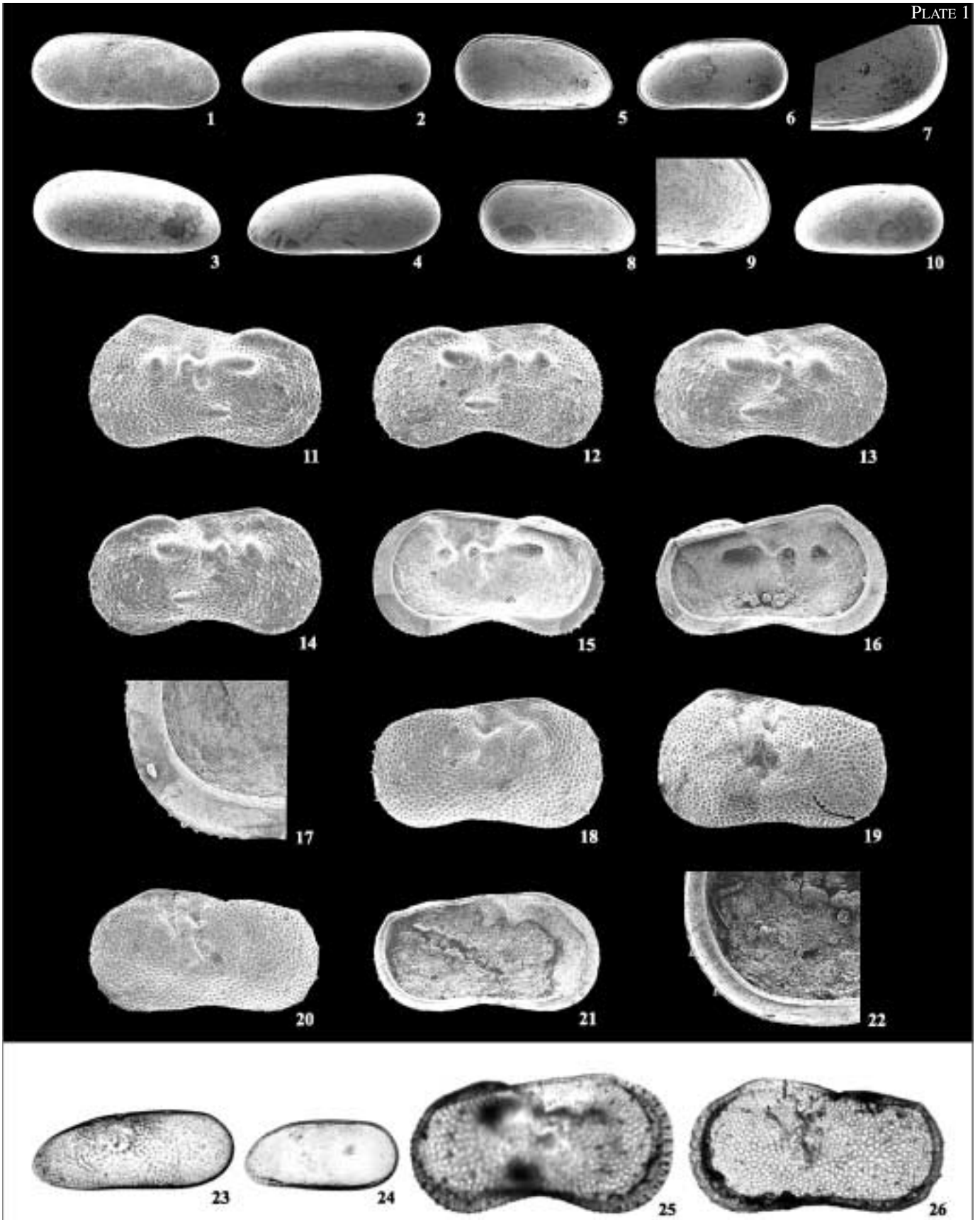
loppée sur la valve gauche que sur la valve droite. Deux sillons inclinés vers l'arrière, parallèles, profonds et situés en avant descendent du BD. Le sillon S1 est plus court que S2 se terminant sur la partie centrale de la valve. Des épines petites, courtes et faibles se retrouvent sur la partie postérieure et postéro-dorsale. La surface est entièrement recouverte de fossettes peu profondes et arrondies. Les tubercules sont rarement présents sur les valves.

Zone marginale: zone de fusion large et de même largeuer sur toute la longueur de la zone marginale; lamelle interne large à l'avant, plus courte au niveau

du BV et du BP et fusionnée avec lamelle externe sur le BV; elle porte les courtes et faibles rides qui se présentent sur la partie distale et proximale du BPV; elles sont partagées par le faible repli; vestibule bas; ligne de concrétion et BI sont parallèles à BE; canaux de pores marginaux droits, simples et denses; le rebord interne est bien visible à l'avant et au niveau du BPV.

Matériel.–Plusieurs dizaines de valves d'individus adultes, mais en majorité endommagées.

Dimensions.–(Localité Martin, échantillon MT-6; forage BJ-2).

		n	l	φ	h	φ	h/l	φ
A	VG	8	0,706 - 0,878	0,823	0,414 - 0,529	0,465	0,536 - 0,603	0,566
	VD	1	0,794	--	0,452	--	0,569	--

Rapports et différences.–Les rides situées sur le BPV de la lamelle interne constituent le caractère qui définit bien les différentes espèces d'*Ilyocypris* proches par leur BE; en même temps, elles révèlent la variabilité intraspécifique assez importante au niveau de la morphologie de la surface (Van Harten, 1979; Janz, 1994). L'arrangement des rides chez *I.* sp. 1 ne correspond pas tout à fait à celui déjà connu chez les autres espèces. D'après la distribution, la forme et la taille des rides, cette espèce se rapproche de *I. binocularis* Sieber, mais les rides proximales de cette dernière sont peu nombreuses et avant tout bien développées, même à l'avant (Janz, 1992, 1994). *I.* sp. 1 montre une certaine ressemblance avec *I.* sp. Janz (Janz, 1994), mais les rides proximales de cette dernière sont plus calcifiées et peu nombreuses et l'espace entre les rides reste lisse. *I. gibba* (Ramdohr) a au maximum 7 courtes rides proximales. Elles sont arrangées comme chez *I. slavonica* Sokac et Van Harten et chez *I. biplicata* (Koch, 1838) mais les rides de cette deuxième sont très fortement développées. *I. bradyi* Sars, 1890 a cinq, ou moins, large rides distales; les proximales sont moins développées. Chez *I. decipiensis* Masi, 1906 la lamelle interne porte de nombreuses et faibles rides dans la zone médiane de la lamelle interne (Van Harten, 1979; Janz, 1994).

Les autres espèce telles que *I. inermis* Kaufmann, 1900, *I. nitida* Lerner-Seggev, 1968 ou *I. steegeri* Kempf, 1967 n'ont pas de rides (Van Harten, 1979; Janz, 1994).

I. getica Masi a de 5 à 6 rides mal développées, sphériques et allongées sur la lamelle interne (Meisch *et al.*, 1996).

La forme spectaculaire, *I. tuberculata* Lienenklaus, 1905 du Miocène inférieur, à surface recouverte de

nombreux tubercules, a été décrite par Lienenklaus (1905) mais son profil latéral est rectangulaire à BV peu concave.

Répartition stratigraphique.–Miocène supérieur.

Répartition régionale.–Forage BJ-2, forage Martin TK-4, forage Martin-Koštany TK-24, forage GT-13, forage GHŠ-1, Martin, Bystrička; connu également de la Collection du Professeur Pokorný (Prague, Rép. Tchéque) de la localité Zemné.

RÉPARTITION DES ESPÈCES DANS LE BASSIN DE TURIEC – CONCLUSION

Les observations paléoécologiques dans le bassin de Turiec confirment les connaissances actuelles sur *Darwinula stevensoni, Vestalenula pagliolii* et sur les espèces du genre *Ilyocypris*. Elles se rencontrent principalement dans la partie septentrionale des dépôts littoraux jusqu'à sublittoraux (Fig. 1). Seulement 5 individus de *Darwinula stevensoni* parmi plus de 4 600 valves ont été recueillis dans le forage HGB-3 et dans localité Slovenské Pravno – route du champ (Pipík, 2001). *Ilyocypris* sp. 1 est signalé aussi du forage GHŠ-1 (Gašparík *et al.,* 1974). La présence de deux espèces dans le sud du bassin est donc occasionnelle.

Les Darwunulidae et les Ilyocyprididae se rencontrent ensemble dans un milieu peu profond situé dans le nord du bassin de Turiec mais les Darwinulidae ont une extension bathymètrique légèrement plus importante (Fig. 1). Les particularités paléoécologiques des biotopes expliquent les faibles différences entre la distribution des Darwinulidae et des Ilyocyprididae.

Pour comprendre les différences constatées dans la distribution des Darwinulidae et des Ilyocyprididae, nous rappelons brièvement les caractéristiques écologiques des espèces:

– *Darwinula stevensoni* préfère les mares, les ruisseaux au cours lent et les lacs, où elle vit entre 0-12 m de profondeur sur le fond argileux ou sableux; cosmopolite, en général dulçaquicole et eurythermique, elle tolère une salinité allant jusqu'à 15‰ (Griffiths et Butlin, 1994; Rossetti et Martens 1996; Meisch, 2000).

– *Vestalenula pagliolii* habite des lacs et des mares de la plaine fluviatile ; les individus fossiles sont connus des formations limniques et estuariennes (Martens *et al.*, 1997 ; Rossetti et Martens, 1998). Dans le bassin de Turiec (localité Martin), elle s'associe aux sédiments argileux et organo-détritiques du littoral (Pipík, 2001).

– les espèces d'*Ilyocypris* préfèrent un milieu à courant faible (littoral des lacs, sources, rivières) et boueux; elles occupent souvent des étangs parfois liés au sources et peuvent être oligohalines. Au niveau thermique, elles sont plutôt polythermophiliques; elles sont rares dans le milieu stagnant (Meisch, 2000).

Le milieu dans le nord du bassin livre des ostracodes habituellement rencontrés dans des environnements peu profond [*Pseudocandona compressa* (Koch, 1838), *Fabaeformiscandona balatonica* (Daday, 1894)], des racines d'arbres et des plantes aquatiques telles que *Typha latissima, Nelumbium protospeciosum, Potamogeton martinianus, Phragmites oeningensis,* et des characées. Une sédimentation paralique supporte cette hypothèse. La tanathocénose de mollusques témoigne aussi de la présence d'un milieu marécageux et peu profond en position proximale par rapport au rivage d'un grand lac (gastéropodes *Ancylus, Gyraulus, Helix* cf. *occlusa, Carychium* sp., *Succinea* sp., *Vertigo* sp.) (Pokorný, 1954; Ondrejíčková, 1974). Ce milieu a subi des fluctuations écologiques importantes. Hormis les espèces d'ostracodes déjà mentionnées, l'ostracofaune comporte des espèces du genre *Euxinocythere* mais aussi *Candonopsis arida* Sieber, 1905 et les différentes espèces nouvelles de *Candona* (Pipík, 2001).

Selon Sitár (1966), la flore de la localité Martin a été transportée dans le lac par un ruisseau. L'origine des calcaires massifs à structure de pisolithes (localité Vrútky, au nord-ouest du forage BJ-2) s'associe aussi avec les eaux courantes (Andrusov, 1954) qui ont pu remonter vers la surface à partir de sources

signalées par la présence d'espèces psychrophiles (*Caverno-cypris subterranea* (Wolf, 1920) (Pipík, 2001).

L'assemblage de *Candona clivosa* caractérise un biotope de la localité Lehôtka. Il se compose surtout des individus de *C. clivosa*, Fuhrmann, 1991, mais aussi d'espèces nouvelles de Candoninae ou déjà connues – *Candonopsis arida, Fabaeformiscandona balatonica, Heterocypris salina* (Brady, 1868) - mais moins représentées.

La macroflore de la localité Lehôtka indique un milieu d'eaux douces et peu profond (*Typha latissima*). Il correspondrait à un environnement de baie, plutôt calme pouvant passer à un marécage et se situant au voisinage d'une forêt humide couverte par *Acer tricuspidatum* et *Platanus aceroides* et des *Ulmus* (Sitár, 1966, 1969; Němejc, 1967). Le milieu de baie stagnante a pu favoriser le développement d'une flore microbienne (Pipík, 2001).

Nous supposons que des différences dans la vitesse de l'écoulement de l'eau ont influencé la distribution des Darwinulidae et des Ilyocyprididae. Du fait que les représentants des deux familles supportent un milieu à faible courant, ils se rencontrent associés dans le nord du bassin de Turiec. Le milieu a également favorisé une faune rhéophilique. Les Darwinulidae supportent aussi un biotope stagnant qui leurs a permis de peupler la baie á Lehôtka. Dans l'Actuel, les *Ilyocypris* sont souvent rares dans le milieu stagnant (Meisch, 2000). Il est intéressant de constater que les *Ilyocypris* n'ont pas été observés au sud-ouest du bassin de Turiec (Fig. 1); les dépôts de cette partie livrent plusieurs espèces d'étangs, de sources et du milieu souterrain qui pourrait signaler l'eau courante *(Candona neglecta* Sars, 1887, *Darwinula stevensoni*, *Pseudocandona* aff. *eremita* (Vejdovsky, 1882), *Fabaeformiscandona* ex gr. *breuili* (Paris, 1920), 3 espèces de *Psychrodromus*).

Bien que *Darwinula stevensoni* soit oligorhéophilique (Meisch, 2000), ses individus dans la localité Martin ont dû subir des conditions environnementales difficiles. En effet, ils sont remarquables par leur petite taille (0,647-0,69 mm) qui se situe dans la limite inférieure de l'espèce (0,63-0,80 mm), selon Meisch (2000). Les différences de nourriture et de salinité de l'eau du milieu de vie, mais également de température, pourraient affecter le développement larvaire et provoquer des différences de la longueur des individus adultes mais pas la morphologie de leurs valves (Rossetti et Martens, 1996). Une quantification de ces facteurs dans un milieu actuel aiderait aux reconstitutions paléoenvironnementales.

REMERCIEMENTS

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REASSESSMENT OF *SOLENOMERIS AFONENSIS* MASLOV, 1956 (FORAMINIFERA): FORMERLY CONSIDERED A CORALLINE RED ALGA

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Abstract

The type specimens of *Solenomeris afonensis* Maslov, 1956 are reassessed and compared with the *Solenomeris* species known in the literature. The controversial nature of *Solenomeris* as a calcareous red alga or foraminifer is discussed. Differences in the juvenile stage of *Solenomeris* and *Acervulina* allow the genus *Solenomeris* Douvillé, 1924 (represented by the type species *S. ogormani* Douvillé, 1924) to remain valid in the family Acervulinidae. *Solenomeris afonensis* Maslov is considered a junior synonym of *S. ogormani* as emended on the ground of the types. The early juvenile stages of *S. afonensis* are true nepiont stages demonstrating their free-living juvenile life by adding chambers on both lateral sides prior to their permanent encrusting, adult stage.

Key words: Foraminifera, encrusting forms, Acervulinidae, *Solenomeris*, systematics.

Resumen

Se revisan los tipos de *Solenomeris afonensis* Maslov, 1956 y se comparan con las especies de *Solenomeris* conocidas en la literatura. Se discute la controvertida naturaleza de *Solenomeris* como un alga roja calcárea o un foraminífero. Las diferencias en el estadio juvenil de *Solenomeris* y *Acervulina* permiten mantener como válido *Solenomeris* Douvillé, 1924 (representado por la especie tipo *S. ogormani* Douvillé, 1924) en la familia Acervulinidae. *Solenomeris afonensis* Maslov se considera un sinónimo posterior de *S. ogormani* (enmendado de acuerdo con sus tipos). Los estadios juveniles tempranos de *S. afonensis* son verdaderos estadios nepiónticos, lo que indica un modo de vida libre con crecimiento lateral previo al estadio encrostante permanente del adulto.

Palabras clave: Foraminíferos, formas encostrantes, Acervulinidae, *Solenomeris*, sistemática.

INTRODUCTION

Encrusting lamellar perforate foraminifera (Acervulinidae) represent common benthic components in Upper Cretaceous to Recent shallow water marine carbonates (e.g., Poignant, 1974; Deloffre *et al.*, 1977). Since the Paleocene, acervulinids have contributed to reef frameworks and monospecific biostromes (e.g., Perrin, 1992) as well as to free-living macroids (e.g.,

Hottinger, 1983). They are also important producers of carbonate sediments (Minnery, 1990; Zankl, 1993). They are often associated with larger benthic foraminifera, coralline red algae, bryozoans, and corals in Paleogene shallow water carbonate depositional sequences (e.g., Garavello & Ungaro, 1982; Brugnatti & Ungaro, 1987; Moussavian & Höfling, 1993). The systematics of the family Acervulinidae Schultze (1854) is particularly confusing, especially at the

genus level. The growth-forms of these encrusting foraminifera are not well known and they have been often misidentified as red algae (Solenoporaceae, Corallinaceae). For instance, Eocene *Solenomeris* build-ups of the Pyrenean region (Plaziat & Perrin, 1992) have been considered as «*Lithothamnium* reefs» by Gaemers (1978) and Eichenseer (1988), and the Eocene *Solenomeris* assemblages of northern Italy as «solenoporacean levels» (De Zanche, 1965).

There is evidently a high degree of confusion regarding the systematic ascription of these fossil-encrusting forms to foraminifera or to calcareous red algae. The present study is a re-description of *Solenomeris afonensis* Maslov, 1956 (Late Eocene, Aphon region) in order to define its taxonomic status. This species, the types of which are deposited at the Geological Institute of the Academy of Sciences in Moscow, was considered of "undefined systematic position" by Maslov (1956).

Douvillé (1924) created the genus *Solenomeris*, with the type species *Solenomeris O'Gormani* [sic] from the Early Eocene of the Béarn region (southwestern France). This author interpreted the specimens of *S. ogormani* as an isolated branch of "Lithothamniae" (Douvillé, 1924, p. 170) emphasizing the greater size of *Solenomeris* "cells" compared with "Lithothamniae". He identified it as a red alga because he had not seen the embryo produced by chamber-wise growth. The new genus was not included in the algae Solenoporaceae because of the difference in "cell" shape in transverse section; the described specimens formed "small calcareous balls more or less mammilated with a smooth surface" (Douvillé, 1924; p. 169).

Pfender (1926) described another *Solenomeris* species, *S. douvilléi*, from the Early Eocene of the Spanish Pyrenees (Camarasa, Province of Lérida). According to the latter author, this species differs from the type species in its encrusting growth-form alternating with red algal crusts and because it never forms isolated calcareous nodules. Pfender (1926) also recorded *Solenomeris* sp. which forms "globular masses" in the Middle Eocene of Venetian area (north-eastern Italy). She compared *Solenomeris* with hydrozoans owing to the similar aspect of the "tissue".

Rao & Varma (1953) reported a new species, *Solenomeris ? douvillei* (non Pfender), from the Early Eocene of Pakistan and assigned this taxon to the coralline red algae "melobesians". Such an assignment was paradoxically based on "cell" size and on the more characteristic presence of conceptacles including reproductive cells (Rao & Varma, 1953, p. 22). The

species of Rao & Varma (1953) was later named *Solenomeris pakistense* by Johnson & Konishi (1960).

Maslov (1956) described the new species *Solenomeris afonensis* (Early Eocene of Abkhazia) and ascribed it to coralline red algae; he noted the similarity of *Solenomeris* "cells" with those of «discocyclines» and stromatopores. Elliott (1960) recorded *S. ogormani* and *S. douvillei* in the Paleocene and Early Eocene of Iraq and placed them into the Solenoporaceae. Elliott (1964) argued that the algal nature of *Solenomeris* is supported by the existence of uniporate conceptacles, underlined the scarcity of reproductive organs, and considered the conceptacles described by previous authors (Rao & Varma, 1953; Maslov, 1956) as foraminifera belonging to the genus *Bullopora* (Polymorphininae, Webbinellinae) subsequently encrusted by *Solenomeris*. Since then, *Solenomeris* has been misidentified as calcareous alga (Schalekova, 1963; Boulanger & Poignant, 1969; Poignant & Du Chaffaut, 1970) and classified among the Rhodophyceae (Samuel *et al*, 1972; Poignant, 1975, 1977; Dieni *et al*, 1979; Deloffre *et al*, 1977; Garavello & Ungaro, 1982), and more precisely as Solenoporaceae (De Zanche *et al*, 1977; Wray, 1977; Tappan, 1980), or among Corallinaceae (Gaemers, 1978).

Although some authors noted the similarity of *Solenomeris* to orthophragminids («discocyclines» in Maslov, 1956) or orbitoids (De Zanche, 1965), Hagn (1967) was the first, after Trauth (1918), to ascribe Lower Eocene *Solenomeris* from the Bavarian Alps to the foraminifera, comparing it with the Acervulinid genera *Acervulina* and *Gypsina*. Trauth (1918), in fact, ascribed nodular forms of *Solenomeris* from the Eocene of Austria (Province of Pongau) to the encrusting foraminifer *Polytrema planum* (= *Acervulina inhaerens* var. *plana* according to Hanzawa, 1957). Trauth's publication was, however, overlooked by subsequent authors until Hagn (1967). Hagn & Wellnhofer (1967) placed the genus *Solenomeris* in the Family Acervulinidae and considered it as a possible synonym of *Gypsina*. Subsequently, this new combination has been used for *Gypsina ogormani* (Hagn, 1972, 1978, 1983; Hagn & Moussavian, 1980; Moussavian, 1984). Moussavian (1989) attributed *Solenomeris* to the genus *Acervulina* since he considered *Gypsina* to be a synonym of *Acervulina*. Nonetheless, Brugnatti & Ungaro (1987) and Barbin *et al.* (1989) identified *Solenomeris* from the Middle Eocene of north-eastern Italy as *Gypsina*.

In spite of the Hagn's publications, most of the authors have not considered *Solenomeris* as a forami-

nifer and it is persistently placed among the red algae. In Tappan's (1980) synthesis of plant protists, *Solenomeris* appears in the Family Solenoporaceae (p. 140). Considering *Solenomeris* Douvillé as a younger synonym of *Acervulina* Schultze, Moussavian & Höfling (1993) redescribed *Acervulina ogormani* (Douvillé, 1924) placing *S. douvilléi* and *S. afonensis* as its synonyms. Afterwards, comparison of the structural features of the *Solenomeris* test with those of *Acervulina* from Plio-Quaternary reefs of Mururoa Atoll (French Polynesia) led to the conclusion that the genus *Solenomeris* belonged to the Family Acervulinidae and has to be kept separated from *Acervulina* and *Gypsina* (Perrin, 1987, 1994). Such a conclusion was based on the identification of the juvenile stages with a geometry and arrangement of chambers which confirm the assignation to the Family Acervulinidae (Perrin, 1987, 1994; Perrin & Plaziat, 1987).

The stratigraphic distribution of *Solenomeris ogormani* is said to range from the Late Cretaceous (Poignant & Blanc, 1974; Poignant, 1975; Deloffre *et al*, 1977) to the Miocene (Elliott, 1960, 1964; Hagn, 1972, 1978; Beckmann *et al*, 1982; Poisson & Poignant, 1975; Moussavian, 1984, 1989; Moussavian & Höfling, 1993; Plaziat & Perrin, 1992; Perrin, 1994).

SYSTEMATIC PALAENTOLOGY

Family ACERVULINIDAE Schultze, 1854
Genus *Solenomeris* Douvillé, 1924
Solenomeris ogormani Douvillé, 1924
(Figs. 1, 2)

1924 *Solenomeris O'Gormani* n. gen. n. sp.; Douvillé, 1924, pp. 169-170, Figs. 1-5.
1956 *Solenomeris afonensis* sp. nov.; Maslov, 1956, pp. 140-141, Pl. 43, 44, 45.
1964 *Solenomeris o'gormani* Douvillé; Elliott, 1964, pp. 697-698, Pl. 105-107.
1972 *Solenomeris ogormani* (Douvillé); Hagn, 1972, pp. 116-117, Pl. 8, Fig. 2.
1975 *Solenomeris douvillei*; Poisson & Poignant, 1975, Pl. 1, Fig. 2.
1980 *Gypsina ogormani* (Douvillé); Hagn & Moussavian, 1980, pp. 148-149, Pl. 12, Fig. 2.
1984 *Gypsina ogormani* (Douvillé); Moussavian, 1984, Pl. 5, Fig. 4.
1989 *Acervulina ogormani* (Douvillé); Moussavian, 1989, pp. 77-78, Pl. 6.

1989 *Gypsina ogormani* (Douvillé); Hagn, 1989, pp. 14-15, Pl. 5, Fig. 1.
1992 *Solenomeris ogormani* (Douvillé); Plaziat & Perrin, 1992, Fig. 3a (C).
1993 *Acervulina ogormani* (Douvillé, 1924); Moussavian & Höfling, 1993, Pl. 2, Figs. 2-7; Pl. 3, Figs. 2-6.

Description.–Lamellar, very large, encrusting test composed of numerous chamberlet layers producing large sheets coalescent with encrusting, foliose and layered coralline red algae, other encrusting foraminifera (acervulinids), and bryozoans, coating solid substrate often overgrowing tests of its own specimens. Branching growth-forms develop as lumpy and fruticose protuberances. Lumpy forms have more or less swollen protuberances that may vary in length, are usually crowded and contiguous. Fruticose forms have protuberances that are mostly over 3 mm long, are usually branched, and are free from one another or laterally coherent to varying degrees.

Early growth spiral consisting of less than 8 spiral subspherical chambers forming a complete whorl around the comparatively large proloculus (Figs. 1, 2).

Each layer of the test consists of an expanse chamber subdivided into small, low chamberlets connected by tubular passages (tp; Fig. 1) with imperforate walls. In the broad, marginal sector of the shell, the chamberlets may be radially elongate and interconnected with regularly spaced, tubular connections. No chamberlet sutures are recognised.

Apertures multiple. Each marginal chamberlet bears several tubular apertures. In random sections, the lowest chamberlet layers produce very irregular intersections, while higher layers tend to organise the superposed chamberlets in more or less regular stacks. Vertical random sections of such stacks show a seemingly confusing wealth of connections between neighbouring chamberlets. Passages connecting chamberlets of the same cycle in horizontal direction from oblique stolons (st; Fig. 1) are produced by transformation of interiormarginal apertures.

Remarks.–The calcareous red algal nature (Rhodophyta, Corallinaceae, Solenoporaceae) of *Solenomeris* proposed by some authors (e.g., Rao & Varma, 1953; Maslov, 1956; Elliott, 1964; Samuel *et al*, 1972; Poignant, 1975, 1977; Dieni *et al*, 1979; Deloffre *et al*, 1977; Gaemers, 1978; Garavello & Ungaro, 1982) on the base of the existence of uniporate conceptacles cannot be supported. No illustration of these features shows pore canals (either multiporate and uniporate) which are exclusive of these reproduc-
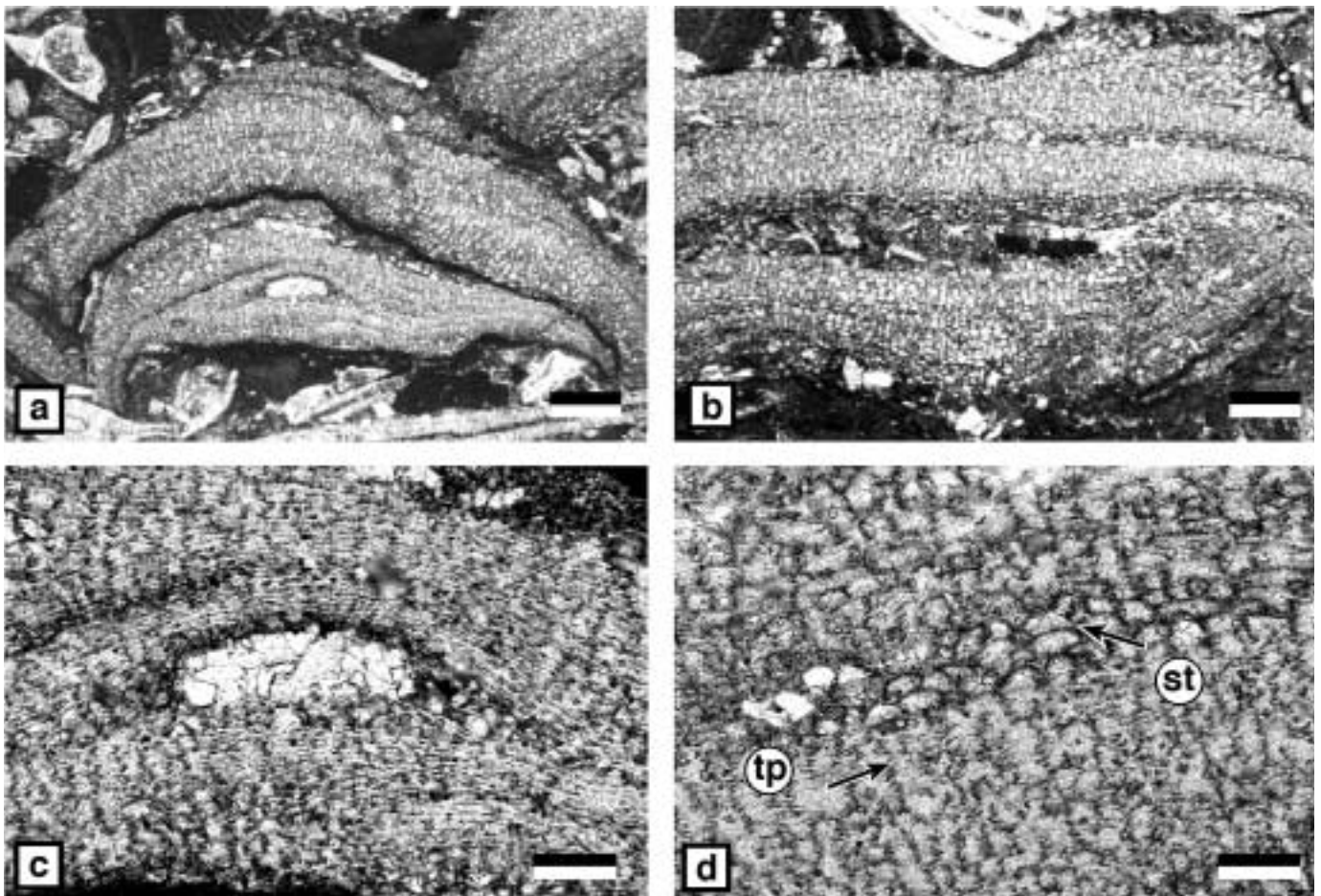
FIGURE 1–*Solenomeris ogormani* Douvillé, 1924. Tangential sections of encrusting growth-forms ascribed by Maslov to *Solenomeris afonensis* (1956). The illustrated specimens are from the original Maslov's collection (1956); sample no. S3/2, Early Eocene, Aphon region, deposited at the Geological Institute of the Academy of Sciences in Moscow. a, b. superimposed growths of two specimens. Scale bar= 0.500 mm. c. magnification of (a) showing a possible nepionic apparatus defined by Maslov as a coralline multiporic conceptacle. Scale bar= 0.150 mm. d. tangential oblique section showing test layers each of which consists of an expanse chamber subdivided into small, low chamberlets connected by tubular passages (tp) with imperforate walls. Passages connecting chamberlets of the same cycle in horizontal direction from oblique stolons (st). Scale bar= 0.150 mm.

tive organs. The illustrated chambers represent in fact the nepionic apparatus (proloculus) of the encrusting foraminifer. The calcified thalli of Corallinaceae are composed of cell filaments which are mostly pseudo-parenchymatously united into a plant body with a characteristic internal structure (e.g., Woelkerling, 1988). This is not shown by the studied material nor by the illustrated specimens of the literature.

Some authors noted the similarity of *Solenomeris* to orthophragminids («discocyclines» in Maslov, 1956; or «orbitoids» in De Zanche, 1965). This group of large benthic, hyaline perforated foraminifera is characterised by a lenticular test with a median layer of rectangular chamberlets arranged in concentric rings and lateral layers of chamberlets on both sides (e.g., Ferràndez-Cañadell, 1999). *Solenomeris* does not have such architectural shell features and, therefore, it cannot be assigned to the orthophragminids.

Maslov (1956, p. 141) stated that, in spite of the Pfender's opinion (1926), *Solenomeris afonensis* has much closer affinities with foraminifera or stromatoporoids than to hydractinids. A detailed structure analysis of *Solenomeris* has been made by Moussavian (1989) who proposed the new combination *Acervulina ogormani*, as *Solenomeris* shows the same shell characters of *Acervulina* and *Gypsina*.

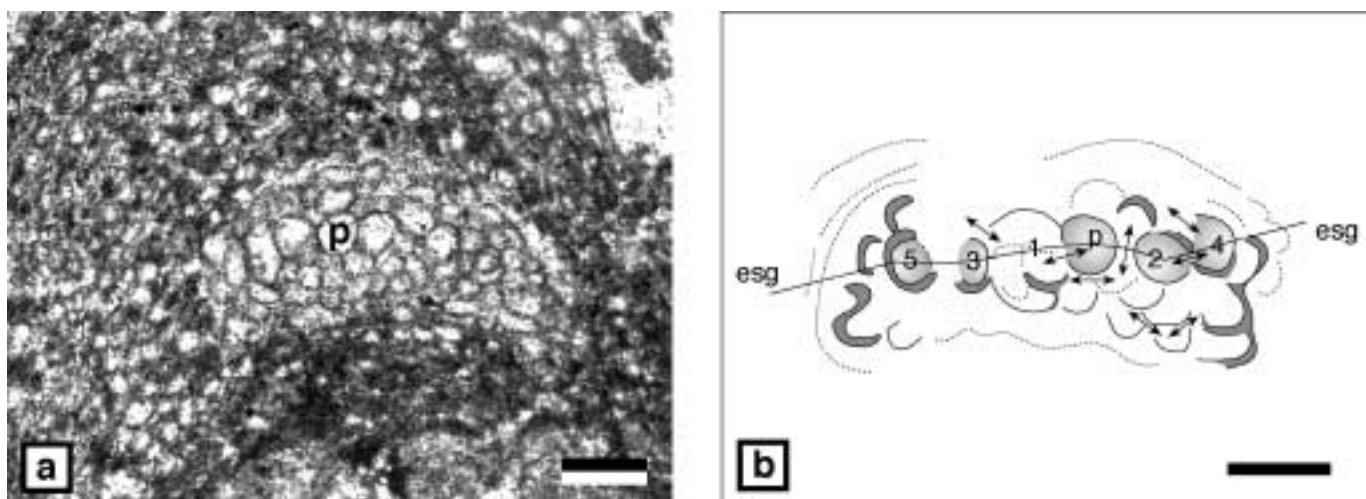Perrin (1994) separated *Solenomeris* from *Acervulina* on the basis of the existance of a differentiated

FIGURE 2–Structural analysis of *Solenomeris ogormani* Douvillé. Scale bar= 0.150 mm. a. Nepionic apparatus consisting of an early spiral growth with subspherical chambers forming a complete whorl around the comparatively large proloculus (p); original Maslov's collection (1956); sample no. S3/2, Early Eocene, Aphon region, deposited at the Geological Institute of the Academy of Sciences in Moscow. b. Based on a type of *Solenomeris afonensis* Maslov (1956), illustrated in Maslov (1956), Pl. 45, Fig. 1, interpretation of the ontogeny (esg: early spiral growth) of the nepiont by an oblique-centered section from the proloculus (p) through the first to the fifth spiral whorl. Arrows point to stolons connecting chamberlets of successive generations.

nepiont consisting of possible spiral, inflated juvenile chambers followed by chamberlet cycles ("equatorial layer") whose diameter decreases in size towards the periphery (p. 440). The early growth stages of *S. ogormani* show similarities with *Planorbulinella* Cushman (1927) by cycles of alternating chamberlets in the equatorial plane. *S. ogormani* differs from the latter in having lateral chamberlets at both sides of the equatorial chamberlet layers. The subsequent development of incipient layers with small chamberlets stacked perpendicular to the substratum can then take place. The almost abrupt change in chamberlet size from a free to encrusting growth stage documents the existence of a true nepiont. As pointed out by Perrin (1994), the geometry and arrangement of *S. ogormani* adult chamberlets are similar to *Acervulina inhaerens*; in tangential section the adult chamberlets have a rounded and irregular shape, the lateral walls are imperforated and the presence of stolons has been observed (Perrin, 1994). Free-living juvenile stages of *Solenomeris* have been described from the Early Eocene of the Pyrenean domain (Plaziat & Perrin, 1992). Differences in juvenile stage of *Solenomeris* and *Acervulina*, according to Perrin (1994), thus allow

Solenomeris, which is represented by the species *S. ogormani*, to be kept as a valid genus. *S. afonensis* Maslov is considered a junior synonym of *S. ogormani* as it does not show any distinctive characters.

ACKNOWLEDGEMENTS

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UPWELLING-RELATED DISTRIBUTION PATTERNS OF RADIOLARIANS IN HOLOCENE SURFACE SEDIMENTS OF THE EASTERN EQUATORIAL PACIFIC

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Abstract

Temporal studies have identified a radiolarian assemblage characteristic of upwelling that has been used to construct an Upwelling Radiolarian Index (URI) and which appears to correlate with the spatial upwelling pattern (thermocline depth) in the present day eastern equatorial Pacific (EEP). In the present study, 92 radiolarian taxa were counted in surface sediment samples from the EEP and the distribution of 14 species interpreted as upwelling-related have been individually mapped (rather than compiled into a URI) and described. Some of the species have previously been considered upwelling-related (*Acrosphaera murrayana*, *Eucyrtidium erythromystax*, *Lamprocyrtis nigriniae* and *Pterocorys minythorax*), but others have not (*Amphirhopalum ypsilon*, *Anthocyrtidium zanguebaricum*, *Botryostrobus auritus*, *Carpocanarium papillosum*, *Eucyrtidium octocolum*, *Lamprocyclas maritalis*, *Phormospyris scaphipes*, *Pterocorys clausus* and *Cycladophora davisiana*), and correlation analysis confirms the upwelling relationship of these species.

Key words: Radiolaria, oceanography, upwelling, productivity, Eastern Pacific, Holocene.

Resumen

Estudios temporales han identificado una colección de radiolarios característicos de los ascensos de aguas profundas que ha sido utilizada para construir un Índice Radiolario de Ascenso de Aguas Profundas (Upwelling Radiolarian Index, URI) y que parece tener correlación con el patrón de ascenso de aguas profundas espacial (profundidad metalimnia) actual del Pacífico ecuatorial oriental (EEP, Eastern Equatorial Pacific). En el presente estudio se contaron 92 taxones de radiolarios en muestras de sedimentos superficiales del EEP, y la distribución de 14 especies interpretadas como relacionadas con ascensos de aguas profundas fue trazada en mapas individuales (en lugar de recopilada en un URI) y descrita. Algunas de las especies han sido previamente consideradas especies relacionadas con ascensos de aguas profundas (*Acrosphaera murrayana*, *Eucyrtidium erythromystax*, *Lamprocyrtis nigriniae*, y *Pterocorys minythorax*), pero otras no (*Amphirhopalum ypsilon*, *Anthocyrtidium zanguebaricum*, *Botryostrobus auritus*, *Carpocanarium papillosum*, *Eucyrtidium octocolum*, *Lamprocyclas maritalis*, *Phormospyris scaphipes*, *Pterocorys clausus*, y *Cycladophora davisiana*), y un análisis de correlación confirma la relación de estas especies con el ascenso de aguas profundas.

Palabras clave: Radiolarios, oceanografía, ascenso de aguas profundas, productividad, Pacífico Este, Holoceno.

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INTRODUCTION

Polycystine radiolaria have been used extensively in oceanographical reconstructions of the eastern equatorial Pacific (Pisias and Moore, 1995; Molina-Cruz, 1977, 1984; Romine and Moore, 1981; Schramm, 1985; Hays *et al.,* 1989; Haslett, 1992, 1994, 1996; Haslett *et al.,* 1994; Haslett and Funnell,

1996, 1998). Nigrini and Caulet (1992) described a radiolarian assemblage characteristic of upwelling environments from the Somalian Gyre, Oman Margin, and the Peru Current region. A similar assemblage has also been noted from upwelling areas off the west coast of Africa (Haslett, 1995a; Zhao *et al.*, 2000). Caulet *et al.* (1992) constructed an Upwelling Radiolarian Index (URI) by summing the percentage abundances of the upwelling assemblage component species within their down-core samples. This provided an upwelling record of the Somalian Gyre for the Late Pleistocene. Subsequently, Haslett (1995b) carried out a spatial survey of upwelling radiolarian species in core-top samples from the eastern equatorial Pacific. When a URI was constructed for the core-top dataset, it was found to correlate well with thermocline depth in the region, with high URI values corresponding to shallow thermocline depths, and low URI values with a deeper thermocline. This study reconfirmed the applicability of the URI method to palaeo-upwelling studies (see Haslett, 2002 for review).

Thermocline depth is preferred to productivity as an upwelling indicator because new production has been shown to occur in some downwelling areas in the eastern equatorial Pacific (Fiedler *et al.*, 1991), where productivity is stimulated by horizontal advection of unused nutrients from adjacent upwelling areas. Also, the effects of upwelling may not always reach the surface leading to low concentrations of surface nutrients and productivity (Fiedler *et al.*, 1991), although deeper dwelling radiolarian faunas may be influenced by this upwelling.

Nigrini and Caulet (1992) used the radiolarian species listed in Table 1 to characterise the Holocene upwelling assemblage of the Peru margin. These species were counted by Haslett (1995b) in core-top samples from the eastern equatorial Pacific and the numbers converted to a percentage of 92 radiolarian counting groups defined for the study (Haslett, unpublished data); however, of the 18 species listed in Table 1, only 14 were eventually included in the URI by Haslett (1995b) due to the extremely rare occurrence of four of the species in eastern equatorial Pacific surface sediments.

Category	Species	Stratigraphic Range
Endemic Upwelling Species	*Collosphaera* sp. aff. *C. huxleyi*	Miocene-Recent
	Cypassis irregularis	Pleistocene-Recent
	Dictyophimus infabricatus	Pliocene-Recent
	Eucyrtidium erythromystax	Pleistocene-Recent
	Inversumbella macroceras	Miocene-Recent
	Lamprocyclas hadros	Miocene-Recent
	Lamprocyclas maritalis ventricosa	Pleistocene-Recent
	Plectacantha cremastoplegma	Pleistocene-Recent
	Pseudocubus warreni	Miocene-Recent
	Pterocanium grandiporus	Miocene-Recent
Displaced Temperate Species	*Acrosphaera murrayana* group	Miocene-Recent
	Pentapylonium implicatum	Miocene-Recent
	Pterocanium auritum	Miocene-Recent
Enhanced Tropical Species	*Lamprocyrtis nigriniae*	Pleistocene-Recent
	Lithostrobus cf. *L. hexagonalis*	Miocene-Recent
	Phormostichoartus caryoforma	Pliocene-Recent
	Phormostichoartus crustula	Miocene-Recent
	Pterocorys minythorax	Miocene-Recent

TABLE 1–List of radiolarian species considered characteristic of Peru Current upwelling by Nigrini & Caulet (1992). Endemic Upwelling Species are forms that are commonly found only in sediments deposited in areas of upwelling; Displaced Temperate Species are forms that are commonly found in temperate waters, but are not usually found in tropical areas; and, Enhanced Tropical Species are tropical forms that are more abundant and/or robust in areas of upwelling (from Nigrini & Caulet, 1992).

In this paper, the distribution of the 92 species counted were individually mapped (rather than compiled into a URI) and a number of them were found to positively correlate with upwelling (depth of thermocline) in the region. Some of these individual species were described by Nigrini and Caulet (1992), but there are additional species whose relationship to upwelling has previously been uncertain. This paper describes these distribution patterns and considers their relationship to upwelling in the eastern equatorial Pacific.

OCEANOGRAPHIC SETTING

The eastern equatorial Pacific (Fig. 1) is dominated by two water masses (Tropical and Equatorial Surface Water, separated by the Equatorial Front) and several latitudinally aligned surface and subsurface currents (Wyrtki, 1967; Mann and Lazier, 1991). The South Equatorial Current (SEC) flows westward on the surface and extends from approximately 3°N to 10°S. It is driven by the southeast trade winds, and at the equator the Coriolis Force causes divergence-driven upwe-

lling. The mixed layer deepens westward from 10-20 m thick at 100°W to 80 m or more at 155°W. Therefore, nutrient-rich water is upwelled from beneath the shallow thermocline in the east, but further west partly from nutrient-depleted water from within the mixed layer.

The North Equatorial Counter Current (NECC) flows eastward on the surface, extending from approximately 3°N, at its convergence with the SEC, to 10°N at its diverging boundary with the North Equatorial Current (NEC). The NEC, like the SEC, flows westward extending from 10° to 20°N, and is driven by the northeast trade winds. Other surface currents entering the eastern equatorial Pacific include the Peru and California Currents. These are cold equatorward flowing currents, driven by offshore winds, conveying entrained high-latitude water, along the eastern Pacific boundaries. As these currents enter the equatorial Pacific they flow westward, parallel to the equator until they merge with the SEC and NEC.

The SEC and NECC are fully developed during August to December when the southeast trade winds are strongest, effectively pushing the Intertropical
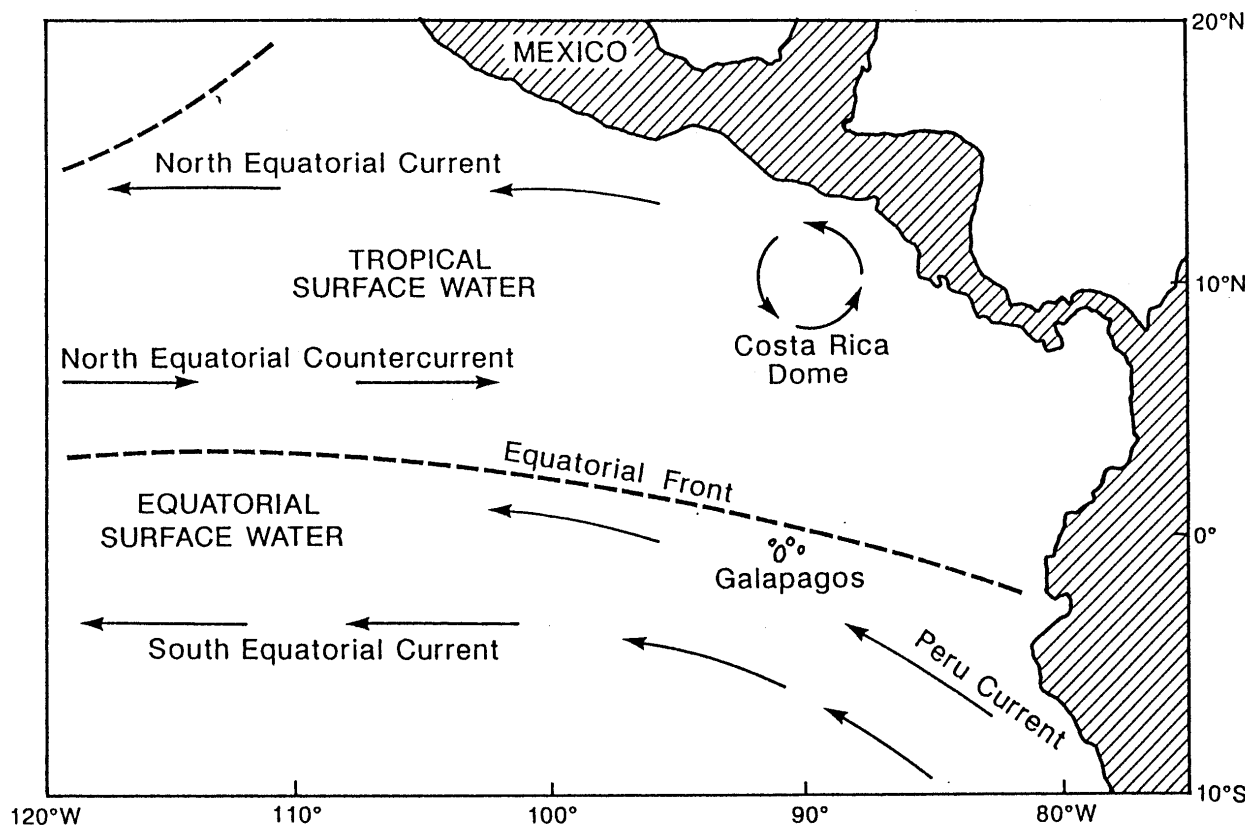

FIGURE 1–Oceanography of the eastern equatorial Pacific (based on Fiedler *et al.*, 1991).

Covergence Zone (ITCZ) to a northerly position parallel to 10°N. Between February to April however, the ITCZ attains a more southerly position around 3°N as the southeast trade winds weaken, resulting in the poor development of both the SEC and NECC. Through May to July a transition period ensues as the ITCZ migrates northward.

Subsurface currents include those associated with the Costa Rica Dome, a physiographic high in the northeast of the region which causes deep turbulence, deflecting other currents which leads to local upwelling. However, the main subsurface current in the equatorial Pacific is the Equatorial Undercurrent (EC) or Cromwell Current. This current flows eastward beneath the westward flowing SEC, extending from 1°N to 1°S (c. 200 km wide) and is approximately 100 m thick.

The regional thermocline (Fig. 2) shallows from west to east; however, imprinted on this general pattern is a system of latitudinally aligned thermocline ridges and troughs. The ridges reflect the propagation of upwelled waters westward into the central Pacific, whilst troughs

reflect eastward incursion of warmer water. The Equatorial Ridge (ER), marking the axis of the Peru Current and diverging zone of the South Equatorial Current, can be traced eastward to the coastal upwelling cell off the Ecuador and Peru coast. The Countercurrent Trough (CCT) lies within the eastward flowing North Equatorial Countercurrent. The Countercurrent Ridge (CCR) extends westward, from the Central American coastline and Costa Rica Dome, along latitude 10°N where divergence-driven upwelling occurs. The North Equatorial Trough (NET) extends eastward to the southeast coast of Mexico, where minimal upwelling occurs.

MATERIAL AND METHODS

The samples selected for this study were obtained from cores housed in Scripps Institution of Oceanography, La Jolla, California, USA. The cores, their location (latitude and longitude), water depth (m), interval (cm) from which sample was taken, and basic
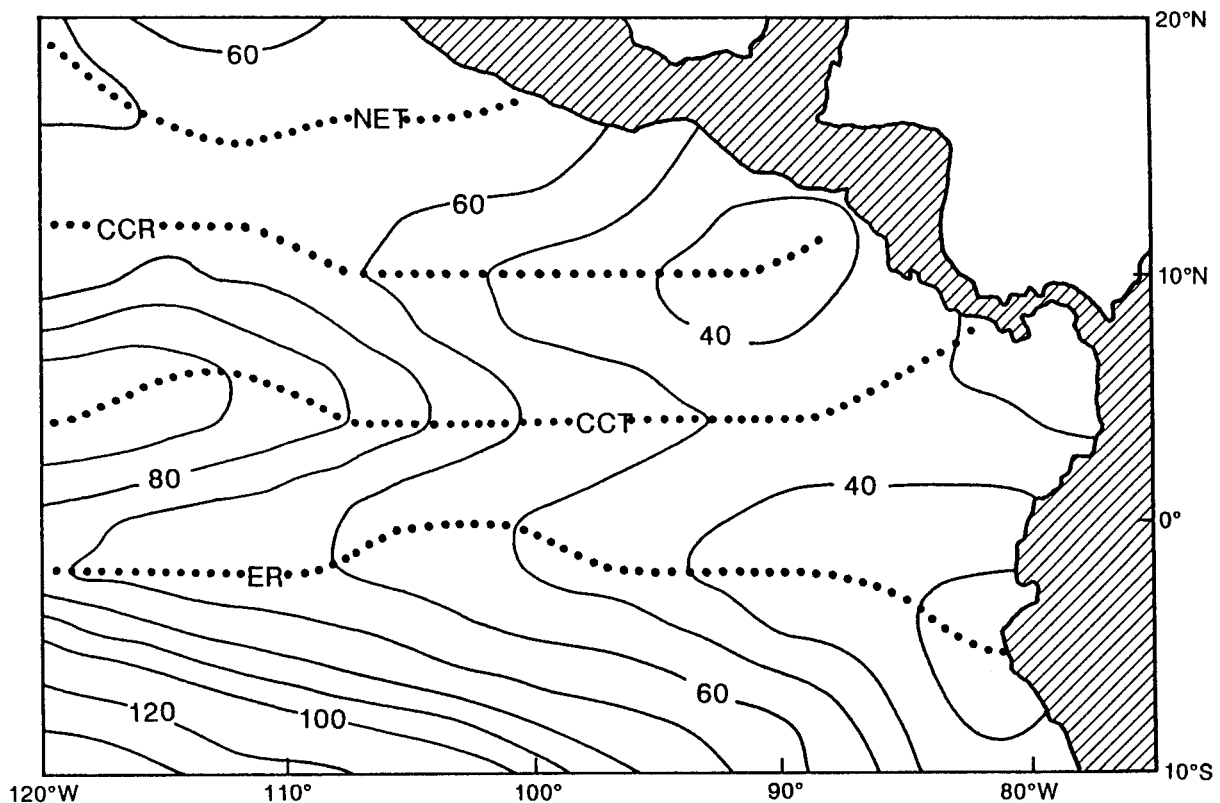
FIGURE 2–Thermocline depth (m) (depth to 20° C isotherm) in the eastern equatorial Pacific. Data obtained during August-November in one year (based on Fiedler *et al.*, 1991). ER = Equatorial Ridge; CCT = CounterCurrent Trough; CCR = CounterCurrent Ridge; NET = North Equatorial Trough. The depth of the thermocline is an indication of the degree of upwelling that occurs within the water column. In areas of strong upwelling the thermocline lies at a shallow depth. Where upwelling is weak or absent the thermocline extends to greater depths.

Sample	Latitude	Longitude	Depth	Interval	Lithology
AMPH 10PG	7°31'S	117°43'W	4284m	2-3cm	calc-clay
AMPH 11P	7°28'S	113°32'W	3728m	0-2cm	calc-mud
AMPH 15PG	7°43'S	109°20'W	3391m	0-1.5cm	calc-mud
BNFC 4G	14°30.6'N	106°02.0'W	3268m	0-1.5cm	silic-clay
BNFC 14PG#1	10°42'N	109°06.0'W	5118m	0-1cm	silic-ooze
BNFC 56BX	13°22.1'N	114°05'W	4105m	0.5-1cm	rad-clay
BNFC 82BX	14°50.2'N	119°39.8'W	4224m	0-1cm	silic-clay
CCTW 8PG	0°24.4'S	85°34.1'W	2944m	0-1cm	foram-ooze
CCTW 9PG	0°33.2'S	81°09.3'W	3127m	0-1cm	green-mud
CCTW 42PG	3°08.8'N	83°39.1'W	2767m	0-2cm	silic/calc-clay
CCTW 43PG	2°39'N	87°28.7'W	3604m	0-2cm	brown-clay
CCTW 47PG	16°32.6'N	100°39'W	5198m	0-2cm	olive/grey-silt/clay
CHUB VIIG	11°30'N	88°04'W	c.5100m	0-5cm	clay/ooze
DWHH 89	4°02'S	113°18'W	4140m	0-6cm	clay/ooze
INMD 14P	8°48'N	103°59.8'W	3138m	4-5cm	calc-sediment
INMD 24PG	6°33.5'N	92°47.7'W	3558m	4-5cm	brown-mud
PAPA 4Go	09°56'N	119°42'W	4321m	4-6cm	brown-clay
PAPA 39Go	8°43'N	92°24'W	3647m	0-4cm	brown/red-clay
PAPA 72Go	10°34'N	95°22'W	4010m	2-4cm	green-mud
PAPA 88Go	13°45'N	98°30'W	3375m	4-6cm	grey/green-mud
PAPA 103Go	17°27'N	104°48'W	3052m	0-4cm	red-clay
PAPA 118Go	19°00'N	113°33'W	3545m	0-4cm	brown-mud
PLDS 12P	3°45.6'S	102°52.3'W	4085m	2-4cm	calc/metal-ooze
PLDS 67PG	0°55.4'N	104°12.1'W	3507m	2-3cm	silic/calc-clay
PLDS 73PG	1°00.4'N	109°18.9'W	3672m	4-5cm	calc-clay
PLDS 76PG	1°02.7'N	113°53.4'W	3948m	7-8cm	calc-clay
PLDS 78PG	1°04.9'N	119°55.5'W	4098m	2-4cm	calc-clay
RIS 13G	6°46'N	117°52'W	3970m	0-4cm	brown-clay
RIS 17G	4°44'N	111°32'W	4110m	0-6cm	brown/calc-clay
RIS 19G	5°12'N	106°36'W	3720m	6-7.5cm	brown-mud
RIS 23G	5°36'N	101°15'W	3310m	0-6cm	brown-mud
RIS 34G	2°46'S	85°28'W	3210m	3-10cm	brown-mud
RIS 36G	9°07'S	81°32'W	4810m	3.5-10cm	brown-mud
SCAN 85P	2°25.6'N	106°55.8'W	3679m	4-5cm	brown/calc-clay
SCAN 86P	3°32.7N	99°28.8W	3441m	5.5-7.5cm	brown/foram-clay
SCAN 87P	4°15.6'N	95°39'W	3438m	2-4cm	brown/foram-clay
SCAN 96PG	1°29'N	113°52'W	3856m	5-7cm	brown/calc-clay
SDSE 39	2°44'S	92°45'W	3609m	8-10cm	brown-clay
SOTW 14PG	2°25'N	80°37.2'W	2470m	2-3cm	brown/rad-clay
SOTW 18PG	0°35.4'N	86°11'W	2723m	4-6cm	foram/rad-clay
ZAP 9G	6°38'N	86°39'W	2860m	0-2cm	brown-clay

TABLE 2–Location of sample sites, with water depth (m), interval in the core from which the sample was taken (cm), and a general description of lithology (usually from the cruise core-log).

lithology are given in Table 2. Their location is shown in Fig. 3. The age of all the samples is considered to be late Holocene (see Table 2) as the sediment surface was seen to be intact.

Samples were prepared for radiolarian analysis by dissolving the carbonate fraction in dilute hydrochloric acid, and treating the remainder with hydrogen peroxide to remove organic material and disperse the sediment constituents. The entire residue was sieved at 63 μm and the >63 μm pipetted onto glass microscope slides, allowed to dry, and mounted in Canada Balsam. 92 counting groups were defined, counted, and converted to percentages (Haslett, unpublished data). The preservation of radiolarian faunas was good to excellent and upward of 300 specimens were counted in each sample. Data relevant to species discussed in this paper are given in Table 3 and plotted on individual maps.

RADIOLARIAN DISTRIBUTION PATTERNS

Fourteen species distributions were found to correlate positively with upwelling (thermocline depth) and are discussed individually below (in alphabetical rather than taxonomic order).

Acrosphaera murrayana (Haeckel) group
(Fig. 4a)

1887 *Choenicosphaera murrayana* Haeckel, p. 102, Pl. 8, Fig. 4.
1994 *Acrosphaera murrayana* (Haeckel), Haslett, p. 130, Pl. 1, Fig. 6.

Nigrini and Caulet (1992) noted that it is difficult to discriminate consistently between the three members of the *A. murrayana* group as defined by Goll (1980), and they are therefore included here in a single counting group. Nigrini (1968) first suggested a link between the occurrence of this species in the eastern equatorial Pacific and the regional oceanography. Subsequently, Molina-Cruz (1977) included this species in his Peru Current assemblage and later emphasised its importance as a coastal upwelling proxy (Molina-Cruz, 1984). Romine and Moore (1981) also included this species in a Peru Current assemblage and related it to coastal upwelling. Nigrini and Caulet (1992) consider *A. murrayana* to be a displaced temperate species (*i.e.* a temperate species only encountered in equatorial regions where cool water occurs, *via* upwelling). The present study clearly indicates that the
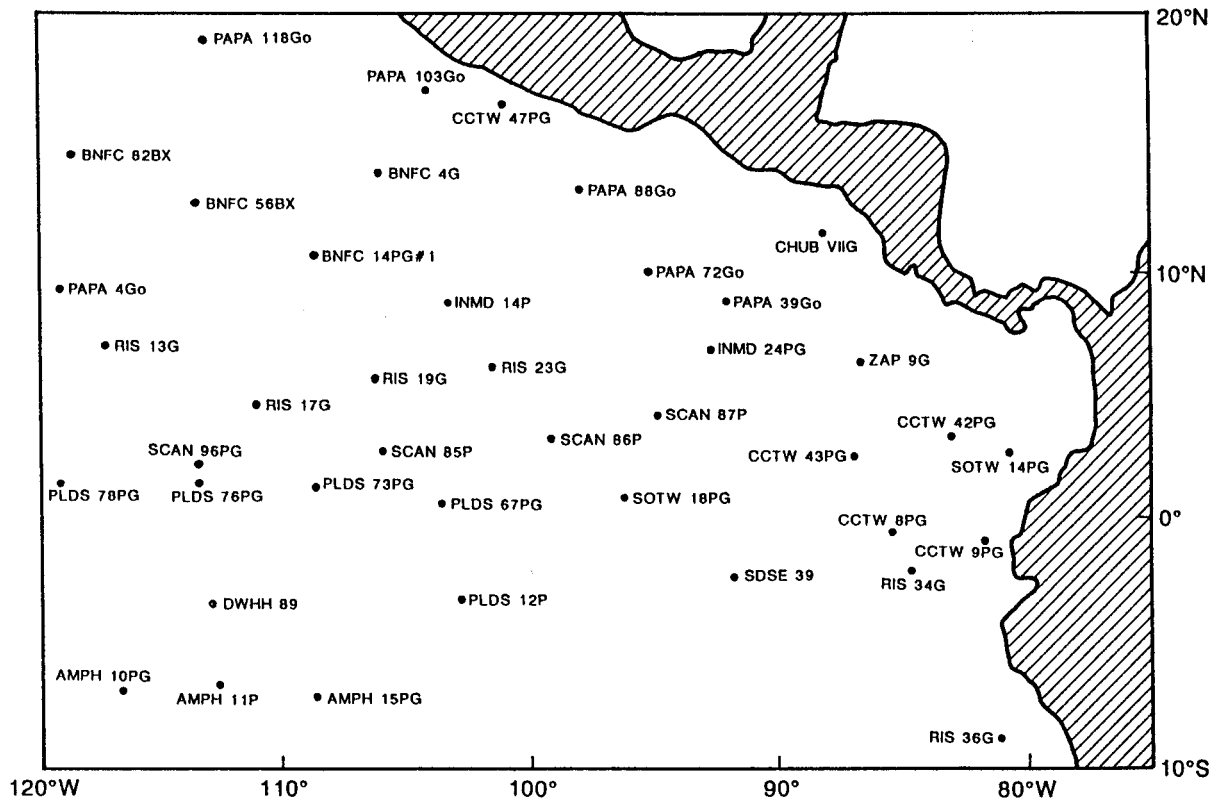

FIGURE 3–Location of sample sites in the eastern equatorial Pacific (see Table 2 for details).

sample	A.zanguebaricum	A.ypsilon	A.zanguebaricum	B.auritus	C.papillosum	C.davisiana	E.erythromystax	E.hexagonatum	E.octocolum	L.maritalis	L.nigriniae	P.scaphipes	P.clausus	P.minythorax
AMPH 10PG	0	0,28	0	0,11	0,28	0,28	0	0,84	0	0,84	0	0	0	0
AMPH 11P	0,62	0,31	0	1,24	0,62	0,18	0	0,93	0	0,62	0,09	0	0	0,31
AMPH 15PG	0	0,22	0,22	0,22	1,1	0,44	0	0,22	0	0,22	0,44	0	0	0
BNFC 4G	4,64	0,7	0,13	7,19	0,7	2,78	0,1	0,46	0,23	0,46	0,07	0,7	3,01	8,58
BNFC 14PG#1	4,52	1,73	0	6,03	1,29	1,29	0,22	0,65	1,29	0,43	0,86	0,65	0,86	4,52
BNFC 56BX'A'	2,46	1,23	0	10,82	0,02	0,49	0	0,07	0,49	0,02	0,74	0,49	1,23	3,94
BNFC 82BX#1	1,66	0,74	0,37	9,94	0,37	0,55	0,11	0,37	0,74	0,24	0,74	1,1	0,74	5,71
CCTW 8PG(A)	1,32	1,05	2,11	2,9	1,05	1,32	0,53	3,43	0	3,95	0,53	0,79	3,43	4,22
CCTW 9PG	1,91	0,76	5,73	3,44	0,38	13,74	1,15	0,38	0,38	0,76	1,15	2,67	3,05	2,29
CCTW 42PG	0,82	0,49	3,27	5,4	1,31	0,65	0,33	1,47	0,07	1,47	0,82	1,8	0,65	2,78
CCTW 43PG	0,59	1,37	2,15	5,07	0,78	1,76	0,39	2,34	1,17	1,56	0,59	0,98	2,15	2,93
CCTW 47PGA	0	0	0	8,97	0	3,85	0	1,28	0	0	0	1,28	5,13	3,85
CHUB 7G	6,15	1,54	0	9,23	3,08	1,54	0	1,54	1,54	0	3,08	3,08	6,15	10,77
DWHH 89	0	0,97	0,49	2,44	0,97	1,22	0,11	1,95	0,49	0,35	0,73	0	0,97	2,19
INMD 14P	6,84	0,55	0,27	4,65	0,55	1,91	0,55	0,31	0,16	0,27	1,09	0,55	1,64	6,84
INMD 24PG	1,18	0,24	1,42	7,09	1,18	0,95	0,71	1,89	0	0,95	2,13	0,24	2,36	7,56
PAPA 4GO	0,95	1,75	0,32	0	2,54	0,48	0,64	0,16	0,79	0,25	0,64	0,64	3,49	9,05
PAPA 39GO	3,7	0,74	0,99	8,14	1,23	0,74	0,49	1,48	0,99	1,48	1,23	0,25	0,99	6,17
PAPA 72GO	6,78	0,81	1,35	4,88	1,09	0,81	1,09	0,54	0,81	0,27	1,9	1,63	1,63	10,85
PAPA 88GO	2,71	1,58	0,45	4,74	0,45	9,47	1,8	0,68	0,23	0	0,9	2,93	2,25	5,64
PAPA 103GO	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PAPA 118GO	2,76	4,93	1,58	1,97	1,18	0,99	0,59	0,59	0,59	0,2	0,79	0	0,39	3,16
PLDS 12P	1,33	1	1,33	5,98	0,66	1	0,66	4,32	0,14	1	1	0,17	1,83	5,81
PLDS 67PG	0,46	0,33	1,39	3,95	0,23	1,16	0,46	4,64	0,4	1,86	0,23	0,46	2,55	5,81
PLDS 73PG	0,47	0,16	1,73	5,68	0,63	0,47	0,16	4,41	0,09	1,58	0,16	0,32	3,15	4,26
PLDS 76PG	0,17	1,39	1,59	3,17	0,2	0,4	0,17	2,97	0,59	0,99	0,59	0,4	0,99	3,57
PLDS 78PG	0,26	0,26	0,78	3,12	0,26	0,26	0,26	2,86	0,15	1,04	0,3	0,07	1,82	1,04
RIS 13G	0,18	1,05	0,21	3,77	1,05	0,42	0,21	1,26	0,12	0,54	0,63	0,21	0,84	1,05
RIS 17G	0,81	0,27	0,54	3,25	0,81	0,54	0,27	2,17	0,23	0,54	0,27	0,54	1,35	1,35
RIS 19G	0,26	0,77	0,26	1,03	1,03	0,26	0,14	1,03	0,26	1,03	0,26	0,26	2,06	2,83
RIS 23G	0,86	0,12	1,5	4,93	1,72	0,43	0,25	0,64	1,07	0,21	0,64	0,12	0,64	3
RIS 34G(B)	6,12	1,44	1,08	5,4	1,08	2,7	0,18	3,24	0,72	1,44	0,72	0,9	1,8	0,54
RIS 36G(B)	21,71	3,29	0	5,92	5,26	7,23	1,97	3,29	0,66	1,97	1,97	0,66	0,66	11,18
SCAN 85P	0,85	0,17	1,02	4,09	0,34	3,58	0,51	3,07	0,68	1,36	2,9	1,02	3,07	5,12
SCAN 86P	0,65	0,98	0,98	2,44	1,14	0,49	0,09	1,14	0,33	1,14	0,33	0,33	1,3	3,74
SCAN 87P	1,22	0,61	0,41	6,1	1,22	1,42	0,2	1,83	0,81	0,81	1,63	0,06	1,63	2,85
SCAN 96P	1,8	0,18	0,9	2,34	1,08	0,72	0,36	4,67	0,18	1,98	0,9	0,18	1,8	3,06
SDSE 39	0,45	1,75	0,44	14,83	0,65	1,75	0,09	3,05	0,44	1,09	0,87	0,87	3,49	5,67
SOTW 14PG	0,89	0,89	1,56	4,02	0,89	0,45	0,22	0,89	0,29	1,56	0,22	0	2,23	2,46
SOTW 18PG	0,74	0,56	4,64	3,53	0,74	2,79	0,37	3,71	0,56	1,49	1,49	1,11	2,41	3,16
ZAP 9G	2,74	0,75	0,5	1,75	1	0,75	0,54	1	0,25	3,24	0,75	0	1,25	4,24

TABLE 3–Counts of radiolarian species discussed here as a percentage of 92 taxonomic counting groups.

occurrence of this species in the eastern equatorial Pacific is related to coastal upwelling, particularly the Peru Current. The scarcity of this group outside coastal upwelling areas tends to confirm its status as a displaced temperate species.

Amphirhopalum ypsilon Haeckel
(Fig. 4b)

1887 *Amphirhopalum ypsilon* Haeckel, p. 552.
1994 *Amphirhopalum ypsilon* Haeckel, Haslett, p. 131, Pl. 1, Fig. 14.

Fig. 4b indicates that the abundance of *A. ypsilon* increases in coastal upwelling areas. Not previously considered to be associated with upwelling, Nigrini (1970) includes it in her tropical assemblage and Benson (1966), in his study of the Gulf of California, states that this species (syn. *Amphicraspedium wyvilleanum*) "undergoes no marked increase at stations located within regions of upwelling"; however, Nigrini (1968) does note that this species exhibits a westward decline in abundance in the eastern equatorial Pacific. It is clear from the present study that, although found throughout tropical waters, *A. ypsilon* abundance increases in upwelling zones (at least in the eastern equatorial Pacific), and so in the terminology of Nigrini and Caulet (1992), should be considered as an enhanced tropical species (*i.e.* a tropical species with an enhanced abundance in upwelling areas).

Anthocyrtidium zanguebaricum (Ehrenberg)
(Fig. 4c)

1872 *Anthocyrtis zanguebarica* Ehrenberg, p. 301.
1994 *Anthocyrtidium zanguebaricum* (Ehrenberg), Haslet, p. 139, Pl. 4, Fig. 3.

The present study indicates that this species has a widespread occurrence throughout the eastern equatorial Pacific; however, its abundance increases in some coastal upwelling areas. Its higher abundance off South America may be a local phenomenon, as Haslett (1992) included this species in an assemblage that characterised early Pleistocene isotopically-defined 'glacial' maxima at ODP Site 677 (Panama Basin), suggesting that it is indicative of cold-water conditions. However, at ODP Site 658 in the eastern tropical Atlantic, Haslett (1995a) noted a high abundance of this species in an assemblage dominated by species described by Nigrini and Caulet (1992) as being characteristic of upwelling.

Botryostrobus auritus (Ehrenberg)
(Fig. 4d)

1844 *Lithocampe aurita* Ehrenberg, p. 84.
1994 *Botryostrobus auritus* (Ehrenberg), Haslett, p. 141, Pl. 4, Figs. 14, 15, Pl. 7, Figs. 2, 3.

This species is abundant in the study area and exhibits a complex distribution pattern, however, the maximum abundances of this species occur in areas affected by upwelling. Romine and Moore (1981) included *B. auritus/australis* in their Equatorial assemblage associated with divergence-driven upwelling along the equator, and Schramm (1985) found it to be the dominant species in her Upwelling assemblage. Furthermore, Pisias *et al.* (1986) considered this species to be indicative of high productivity conditions in the Peru Current region and in the eastern equatorial Pacific in general. However, Nigrini and Caulet (1992) did not include *B. auritus/australis* in their upwelling assemblage because Boltovskoy and Vrba (1989) regarded the species group as a single cosmopolitan taxon. Subsequently, Haslett (1994) has placed the species of this group in synonymy with *B. auritus*, which on the present and previous evidence should be considered an enhanced tropical species.

Carpocanarium papillosum (Ehrenberg)
(Fig. 4e)

1872 *Eucyrtidium papillosum* Ehrenberg, p. 310.
1994 *Carpocanarium papillosum* (Ehrenberg), Haslett, p. 134, Pl. 2, Fig. 9, Pl. 5, Fig. 9.

The distribution of *C. papillosum* has not previously been connected to upwelling. Nigrini (1967) stated that this species (syn. *Dictycryphalus papillosus*) is very sparsely distributed in both low and middle latitudes of the Indian Ocean, comprising less than 1% of her described population. However, the present study reveals that it has high abundances associated with upwelling conditions of the Peru Current and off the Central American coastline. In the eastern equatorial Pacific, at least, this species may be regarded an enhanced upwelling species.

Cycladophora davisiana Ehrenberg
(Fig. 4f)

1861 *Cycladophora? davisiana* Ehrenberg, p. 297.
1994 *Theocalyptra davisiana* (Ehrenberg), Haslett, p. 136, Pl. 3, Fig. 4, Pl. 6, Fig. 2.
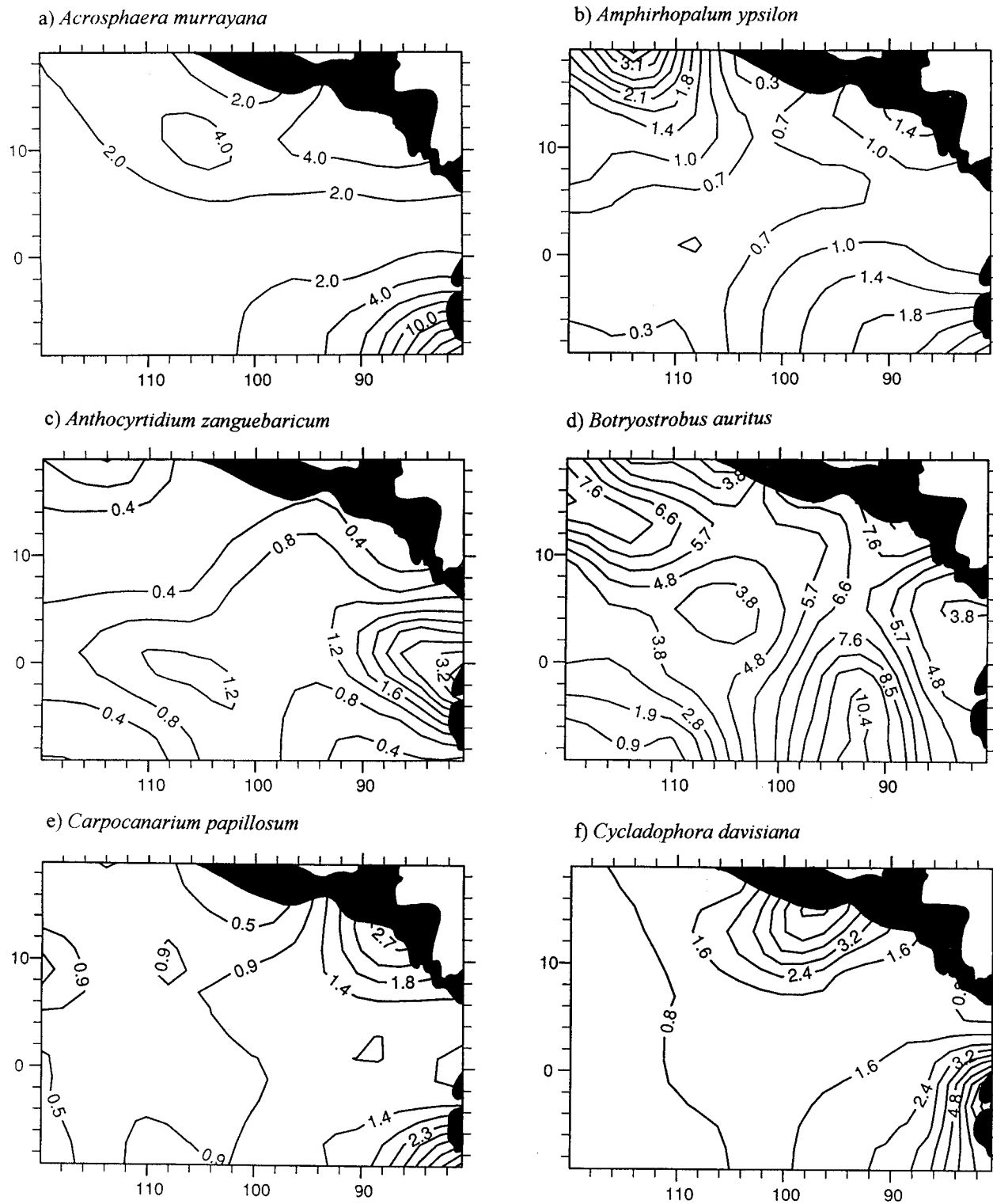
FIGURE 4–Latitude-longitude distribution (%) maps of radiolarian species in the eastern equatorial Pacific: a) *Acrosphaera murrayana*, b) *Amphirhopalum ypsilon*, c) *Anthocyrtidium zanguebaricum*, d) *Botryostrobus auritus*, e) *Carpocanarium papillosum*, f) *Cycladophora davisiana*.

Molina-Cruz (1977) and Romine and Moore (1981) include this species in their Peru Current assemblages, and Schramm (1985) includes it in her Upwelling assemblage. Haslett (1992) showed the affinity of this species to cold-water conditions at isotopically-defined Pleistocene glacial maxima in the Panama Basin. However, Nigrini and Caulet (1992) excluded this species from their upwelling assemblage on the grounds that its abundance does not vary downcore in concert with the other upwelling species they describe. The present study clearly indicates that this species is associated with the environmental conditions provided by upwelling during the Holocene in the eastern equatorial Pacific.

Eucyrtidium erythromystax (Nigrini and Caulet)
(Fig. 5a)

1992 *Eucyrtidium erythromystax* Nigrini and Caulet, p. 154, Pl. 4, Figs. 9, 10.

Nigrini and Caulet (1992) consider *E. erythromystax* to be an endemic upwelling species, although it is rare in their Peru Current material. The abundances encountered in the present study are low, but although specimens are recorded throughout the study area, this species is clearly more abundant in the Peru Current region, off the Central American coastline, and around the Costa Rica Dome. Its widespread occurrence throws some doubt on its status as an endemic upwelling species.

Eucyrtidium hexagonatum Haeckel
(Fig. 5b)

1887 *Eucyrtidium hexagonatum* Haeckel, p. 1489, Pl. 80, Fig. 11.
1994 *Eucyrtidium hexagonatum* Haeckel, Haslett, p. 137, Pl. 3, Fig. 8, Pl. 6, Fig. 7.

Generally considered a low-latitude species, included in Nigrini's (1970) tropical assemblage. It commonly occurs in the eastern equatorial Pacific, although its abundance distribution appears to correspond to the Peru Current and equatorial divergence-driven upwelling system, with a 'tongue' of high abundances extending westwards along the equator. The present study also suggests that *E. hexagonatum* is an enhanced tropical species.

Eucyrtidium octocolum (Haeckel)
(Fig. 5c)

1887 *Lithocampe octocola* Haeckel, p. 1508, Pl. 79, Fig. 6.

1994 *Eucyrtidium octocolum* (Haeckel), Haslett, p. 138, Pl. 3, Fig. 7, Pl. 6, Fig. 8.

This species is often considered a subspecies of *E. acuminatum*, but can be distinguished by its heavy and narrower test (Haslett, 1994). *E. acuminatum* is considered characteristic of middle latitudes (Nigrini, 1967, 1970), but *E. octocolum* occurs in the eastern Pacific at least through the Pliocene-Pleistocene (Haslett, 1994; De Wever *et al.,* 1990). It occurs throughout the study area, but its numbers are enhanced off the Central American coastline, around the Costa Rica Dome complex and, to a lesser extent, in the Peru Current region; so *E. octocolum* may be an enhanced tropical species.

Lamprocyclas maritalis Haeckel
(Fig. 5e)

1887 *Lamprocyclas maritalis* Haeckel, p. 1390, Pl. 74, Figs. 13 and 14.
1994 *Lamprocyclas maritalis* Haeckel, Haslett, p. 139, Pl. 4, Fig. 11, Pl. 6, Fig. 15.

The subspecies *L. m. ventricosa* (Nigrini) was counted separately in this study and therefore, *L. maritalis* here includes all other subspecies *e.g. L. m. maritalis* (Hae-ckel) and *L. m. polypora* (Nigrini). *L. m. ventricosa* is considered to be an endemic upwelling species by Nigrini and Caulet (1992) but, although widespread, it is generally too rare in the present study to warrant an individual interpretation (although see Haslett, 1995b). *L. maritalis* however, is fairly abundant throughout the study area, but with its maximum abundances occurring in the east and along the equator associated with the Peru Current and equatorial divergence upwelling. Nigrini (1970) included *L. m. maritalis* in her North Pacific tropical assemblage, yet in the Indian Ocean it is more abundant in middle latitudes (Nigrini, 1967). *L. m. polypora* was also included by Nigrini (1970) in her tropical assemblage and Nigrini (1967) found it was more abundant in low, than middle, latitudes of the Indian Ocean. The amalgamation of these two subspecies in the present study makes categorising this taxon as either a displaced temperate or enhanced tropical species difficult.

Lamprocyrtis nigriniae (Caulet)
(Fig. 5d)

1971 *Conarachnium nigriniae* Caulet, p. 3, Pl. 3, Figs. 1-4; Pl. 4, Figs. 1-4.
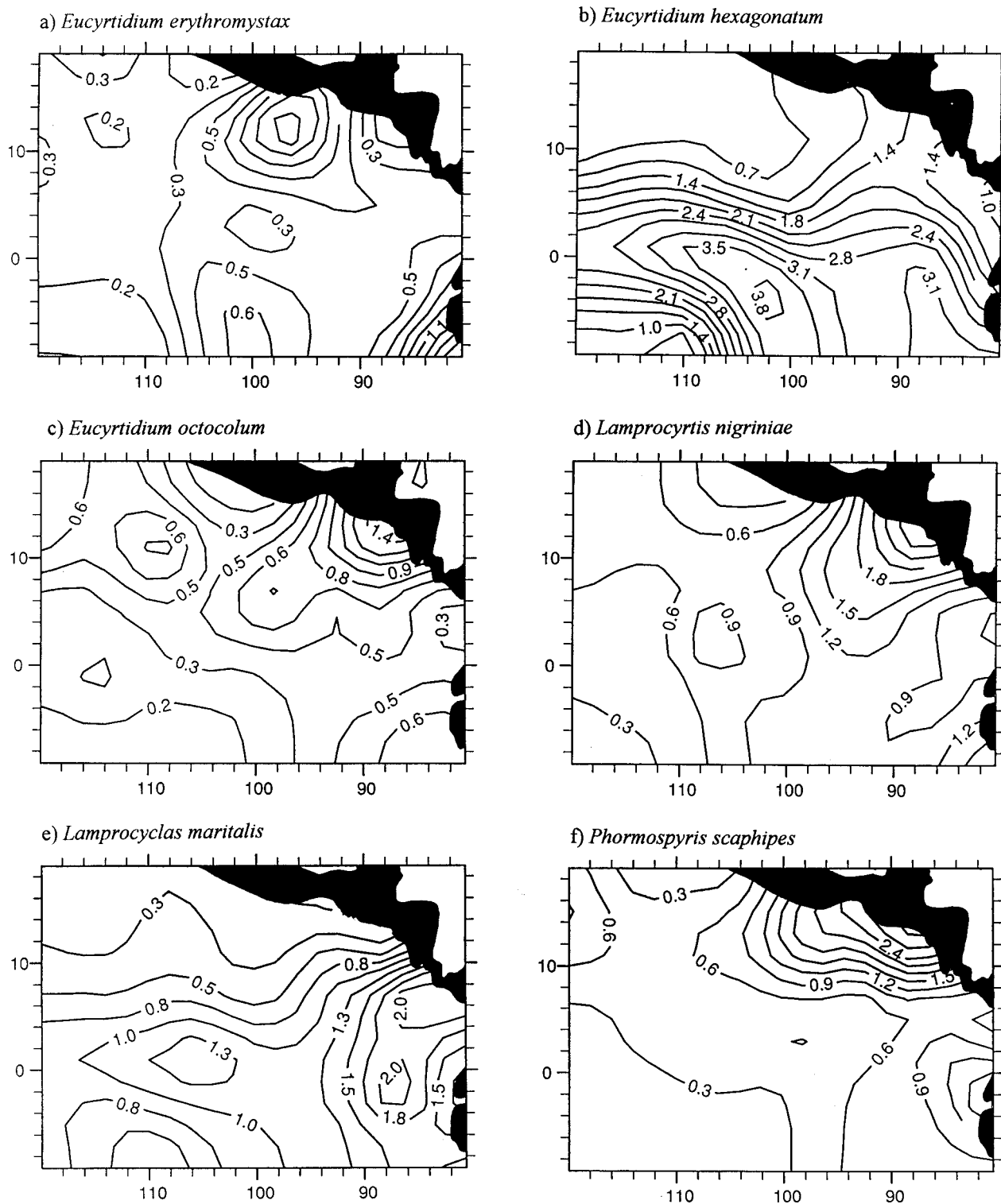1995b *Lamprocyrtis nigriniae* (Caulet), Haslett, p. 478, Fig. 5.9.

FIGURE 5–Latitude-longitude distribution (%) maps of radiolarian species in the eastern equatorial Pacific: a) *Eucyrtidium erythomystax*, b) *Eucyrtidium hexagonatum*, c) *Eucyrtidium octocolum*, d) *Lamprocyrtis nigriniae*, e) *Lamprocyclas maritalis*, f) *Phormospyris scaphipes*.

L. nigriniae is considered an enhanced tropical species by Nigrini and Caulet (1992) and the present study corroborates this view. It is widely distributed in the eastern equatorial Pacific, but with highest abundances off the Central American coastline, around the Costa Rica Dome, and in the Peru Current region.

Phormospyris scaphipes (Haeckel)
(Fig. 5f)

1887 *Tristylospyris scaphipes* Haeckel, p. 1033, Pl. 84, Fig. 13.
1994 *Phormospyris scaphipes* (Haeckel), Haslett, p. 133, Pl. 5, Fig. 6.

This species has not previously been considered to be associated with upwelling, although Haslett (1995a) did speculate on a possible relationship between the occurrence of this species and cold-water upwelling during the Pleistocene in the eastern equatorial Atlantic. The present study clearly shows that, although widespread, it attains maximum abundances in association with Central and South American coastal upwelling cells. From previous studies on the distribution of this species (*e.g.* Goll and Björklund, 1971) it is not clear whether it should be considered a displaced temperate or enhanced tropical species, although the present study suggests it may be an enhanced tropical species.

Pterocorys clausus (Popofsky)
(Fig. 6a)

1913 *Lithornithium clausum* Popofsky, p. 393, text-Fig. 11.
1994 *Pterocorys clausus* (Popofsky), Haslett, p. 140, Pl. 4, Fig. 6, Pl. 6, Fig. 16.
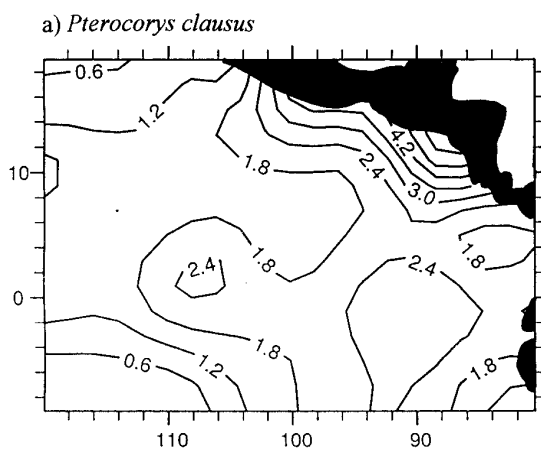
Caulet and Nigrini (1988) state that this species is "common in both tropical Indian and tropical Pacific Ocean sediments. Few to common in temperate and subarctic sediments" (p. 229). It occurs throughout the study area, but with significant abundance increases off the Central American coastline and the equatorial divergence-driven upwelling system; however, it does not appear to be associated with the Peru Current, so it is likely to be an enhanced tropical species.

Pterocorys minythorax (Nigrini)
(Fig. 6b)

1968 *Theoconus minythorax* Nigrini, p. 57, Pl. 1, Fig. 8.
1995b *Pterocorys minythorax* (Nigrini), Haslett, p. 478, Fig. 5.11.

Considered by Nigrini and Caulet (1992) to be an enhanced tropical species, the present study confirms this view. It is common throughout the study area, but its abundance is markedly increased off the Central American coastline, around the Costa Rica Dome, and Peru Current region.

DISCUSSION

A number of discrepancies exist between the present study and that of Nigrini and Caulet (1992). However, Nigrini and Caulet (1992) was essentially a temporal study, based on Late Neogene cores from three different upwelling areas. By contrast, the present study and those of Molina-Cruz (1977, 1984), Romine and Moore (1981), and Schramm (1985) are spatial studies based on Holocene sediments. Nigrini
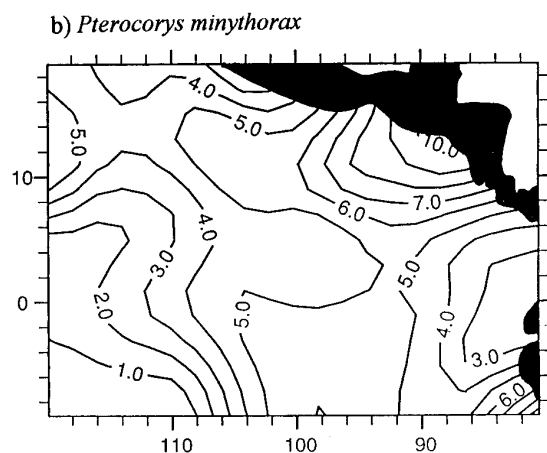

FIGURE 6–Latitude-longitude distribution (%) maps of radiolarian species in the eastern equatorial Pacific: a) *Pterocorys clausus*, b) *Pterocorys minythorax*.

and Caulet (1992) imply, judging by their comment about *Cycladophora davisiana*, that they only considered a species characteristic of upwelling if it co-varied downcore with the other upwelling species they discuss. It may be that the species identified here as upwelling related, but not considered as characteristic of upwelling by Nigrini and Caulet (1992), are responding to oceanographic parameters that are only incidentally associated with upwelling, such as cold sea-surface temperatures (SST's). This hypothesis may be tested to a degree because for each sample station investigated here, SST's and depth of thermocline (20°C isotherm) is known (Table 4). Standard correlation analysis can help to elucidate the relationship between species abundance distribution and oceanographic parameters and is often used in microfossil distribution studies using surface sediments (e.g. Giraudeau, 1993). The results of this statistical analysis, which should be viewed in conjunction with the visual interpretations, are shown in Table 5. Generally the scores are low, however, those >+0.3 or <-0.3 are considered significant (Giraudeau, 1993). Given that the oceanographic information is based on modern observations and that the microfossil data is undoubtedly time-averaged, perhaps over millennia, this low threshold does not seem unreasonable, particularly when correlation is supported by visual comparisons.

Species can be grouped according to their correlation with oceanographic variables, and four groups may be defined:

*Group 1.–*Comprises *A. zanguebaricum, B. auritus, E. erythromystax, E. octocolum, L. nigriniae, P. clausus, P. minythorax* and *C. davisiana*. These species show significant negative correlation with thermocline depth, and thus correlate with a shallow thermocline and upwelling conditions.

*Group 2.–*Comprises *A. murrayana, A. ypsilon, C. papillosum* and *L. maritalis*. These species show significant negative correlation with both thermocline depth and July SST and therefore, indicate a shallow thermocline and cool July SST's. These parameters suggest that these species are upwelling-related as upwelling during July results in cool SST's.

*Group 3.–*Comprises *P. scaphipes* only. This species shows significant negative correlation to thermocline depth, but a significant positive correlation to January SST, suggesting a correlation with a shallow thermocline (upwelling) and warm January SST's. This species probably indicates upwelling, as SST's in

major upwelling areas (*e.g.* Peru Current) become warmer during January.

*Group 4.–*Comprises *E. hexagonatum* only. This species shows significant negative correlation to both January and July SST's, suggesting its distribution is

sample	sstw (°C)	ssts (°C)	thermocline depth (m)
AMPH 10PG	24,9	27	119
AMPH 11P	24,8	27,1	100
AMPH 15PG	25,1	25,5	94
BNFC 4G	27,1	28,4	62
BNFC 14PG#1	27,1	28	65
BNFC 56BX'A'	26,4	28,1	65
BNFC 82BX#1	24,3	27,1	62
CCTW 8PG(A)	25,5	23,3	35
CCTW 9PG	25,9	23,8	33
CCTW 42PG	26,6	25,8	45
CCTW 43PG	24,4	25	41
CCTW 47PGA	28,4	28,9	64
CHUB 7G	26,6	29,1	41
DWHH 89	23,5	25,4	72
INMD 14P	27,2	27,4	55
INMD 24PG	25,9	26,6	42
PAPA 4GO	26,6	27,4	70
PAPA 39GO	25,2	26,8	38
PAPA 72GO	26,7	28,4	41
PAPA 88GO	27,8	28	56
PAPA 103GO	27,9	28,9	65
PAPA 118GO	24,3	21,9	59
PLDS 12P	24,3	23,7	59
PLDS 67PG	24,8	24,9	56
PLDS 73PG	24,1	24,2	67
PLDS 76PG	23,2	23	75
PLDS 78PG	22	24,9	85
RIS 13G	27,1	27	90
RIS 17G	23,3	27	86
RIS 19G	26,6	28,4	75
RIS 23G	26,4	26,7	60
RIS 34G(B)	24,2	19,9	32
RIS 36G(B)	24,6	17,5	30
SCAN 85P	25,2	27,3	69
SCAN 86P	26,1	26,1	56
SCAN 87P	26,4	25,8	52
SCAN 96P	23,2	23	80
SDSE 39	25,8	18,7	39
SOTW 14PG	25,9	25,8	42
SOTW 18PG	25,2	24,7	47
ZAP 9G	26,4	26,8	43

TABLE 4–Present day oceanographic conditions at sample stations. sstw = January SST, ssts = July SST.

Species	sstw (°C)	ssts (°C)	thermocline depth (m)
A.murrayana	0,05	-0,35	-0,43
A.ypsilon	-0,07	-0,47	-0,30
A.zanguebaricum	-0,16	-0,27	-0,42
B.auritus	0,16	-0,12	-0,45
C.papillosum	0,02	-0,32	-0,33
C.davisiana	0,18	-0,21	-0,38
E.erythromystax	0,07	-0,29	-0,44
E.hexagonatum	-0,59	-0,59	-0,14
E.octocolum	0,01	0,01	-0,38
L.maritalis	-0,29	-0,45	-0,34
L.nigriniae	0,07	-0,05	-0,44
P.scaphipes	0,33	0,12	-0,43
P.clausus	0,23	0,07	-0,38
P.minythorax	0,25	0,02	-0,50

TABLE 5–Correlation coefficients between species abundance and oceanographic data. sstw = January SST, ssts = July SST.

related to cool SST's, but not necessarily the result of upwelling.

This analysis indicates that the abundance distribution of species in Groups 1-3 are upwelling-related, at least in the spatial dimension, but that *E. hexagonatum* (Group 4) is related to cold-water conditions whether or not these conditions are associated with upwelling.

Establishing the array of radiolarian species available to palaeoceanographers as potential indicators of upwelling conditions is of great significance for two main reasons:

1) To enhance the geographic application of Radiolaria as upwelling indicators. The occurrence of species in different upwelling regions varies, for example, Nigrini & Caulet (1992) only encounter some species in a single upwelling region, such as *Pseudocubus warreni* in the Peru Current, but other species occur in all three regions investigated (Peru Current, Oman Margin and Somalian Gyre). This means that the species that are selected as upwelling indicators, and inclusion in a URI, are dependent on location. Therefore, a wide selection of species indicative of upwelling would enhance the likelihood of obtaining statistically significant abundances for inclusion in a URI, so producing a more reliable upwelling record. An example of this is apparent from Haslett's (1995a) study of the NW African upwelling cell off Cap Blanc. Six species considered to be characteristic of upwelling by Nigrini & Caulet (1992) were encountered, but appeared to co-vary with six other species not previously linked to upwelling. Haslett (1995a) suggested that these additional species may also be indicative of upwelling, and indeed three of those species (*A. zanguebaricum*, *C. davisiana* and *P. scaphipes*) are now considered as such based on the results of the present study.

2) To stratigraphically extend the application of Radiolaria as upwelling indicators. Table 1 shows the stratigraphic range of species listed by Nigrini & Caulet (1992), and although a number of them extend back to the Miocene, most do not evolve until the Pliocene or Pleistocene, or are rare over their range. Indeed, most studies which have so far employed a URI (Caulet *et al.,* 1992; Haslett, 1995b; Venec-Peyre *et al.,* 1995; Zhao *et al.,* 2000) have investigated Middle to Late Quaternary sediments, whilst in compiling a URI for the Late Pliocene-Early Pleistocene of

Species	Stratigraphic range	Source
Amphirhopalum ypsilon	Pliocene-Recent	Moore et al. 1993
Anthocyrtidium zanguebaricum	Pliocene-Recent	Nigrini & Caulet 1988
Botryostrobus auritus	Miocene-Recent	Nigrini 1977
Carpocanarium papillosum	Pliocene-Recent	Haslett 1996
Cycladophora davisiana	Pliocene-Recent	Moore et al. 1993
Eucyrtidium hexagonatum	Miocene-Recent	Nigrini & Lombari 1984
Eucyrtidium octocolum	Pliocene-Recent	Haslett 1996
Lamprocyclas maritalis	Miocene-Recent	Nigrini & Lombari 1984
Phormospyris scaphipes	Miocene-Recent	Nigrini & Lombari 1984
Pterocorys clausus	Miocene-Recent	Caulet & Nigrini 1988

TABLE 6–Stratigraphic ranges of the species here considered for the first time to be indicative of upwelling.

the eastern equatorial Pacific, Haslett & Funnell (1996) explain how they were only able to include four species in their URI. One of these species, *Lamprocyrtis neoheteroporos* Kling (the ancestor of *L. nigriniae*) was included because a previous study indicated that its occurrence was related to palaeoproductivity (Haslett *et al.,* 1994). Table 6 shows the general stratigraphic ranges of the species here considered for the first time to be indicative of upwelling. All ranges extend at least back to the Pliocene and many to the Miocene, thus extending the potential application of the URI into the Neogene. At the same time all these species are extant, allowing their palaeoecological attributes to be based on Holocene studies. This is preferable to using extant descendant ecology alone as a basis for inferring extinct ancestor palaeoecology.

It is not suggested that these newly upwelling associated species be indiscriminately used in the construction of a URI immediately, but rather that their availability for inclusion should be evaluated further. This may be through comparing the temporal abundance distribution of these species alongside established upwelling proxies to examine co-variance.

CONCLUSION

The present study examined the spatial distribution of 14 radiolarian species in surface sediment samples from the eastern equatorial Pacific and corroborates the interpretation of Nigrini and Caulet (1992) that *A. murrayana*, *E. erythromystax*, *L. nigriniae*, and *P. minythorax* are species characteristic of upwelling; however, *B. auritus* and *C. davisiana*, which were discounted by Nigrini and Caulet (1992) but considered upwelling-related by previous authors, are also shown to relate to upwelling, at least spatially. The distribution of seven other species, not previously connected to upwelling, are also shown to be upwelling-related, and whilst *E. hexagonatum* is statistically shown to correlate with cool SST's, it may or may not be upwelling-related.

ACKNOWLEDGEMENTS

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NOMENCLATURAL NOTE

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The name *Icriodus rectus* Weddige 1985 (in Weddige & Requadt, 1985) is a junior homonym of *Icriodus rectus* Youngquist & Peterson, 1947 and thus according to ICZN, art. 39, 56 invalid. Therefore, the new name *Icriodus homorectus* nov. spec., Weddige, 2003, is introduced now for the species cited firstly.

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