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EVOLUTIONARY TRENDS OF FAMENNIAN ICRIODIDS IN THE DINANT AND VESDRE BASINS (CONODONTS, BELGIAN UPPER DEVONIAN) [1]

by

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(2 figures and 8 plates)

RESUME.- Deux groupes morphologiques différents, probablement liés à la profondeur et/ou au faciès, sont reconnus dans le genre, d'eau peu profonde, *Icriodus* du Famennien belge : le "groupe *Icriodus alternatus*" domine dans les sédiments marins "offshore" en eau relativement calme du Famennien inférieur ("Groupe des schistes de la Famenne") tandis que le "groupe *Icriodus cornutus-costatus* caractérise le faciès plus proche du rivage et turbulent du Famennien supérieur ("Groupe des Psammites du Condroz"). Une évolution morphologique probablement endémique est suggérée pour le dernier groupe. Une lignée phylomorphogénétique a été observée entre *I. alternatus* BRANSON & MEHL et *I. cornutus* SANNEMANN à la base du Famennien. Les relations morphologiques interspécifiques et la variabilité morphologique intraspécifique dans les différents stocks d'*Icriodus* sont discutées. Trois nouveaux morphotypes d'*I. alternatus*, une nouvelle sous-espèce de *I. cornutus* et deux nouvelles sous-espèces de *I. costatus* (THOMAS) sont décrits ; leur extension stratigraphique est discutée.

ABSTRACT.- Two different probably depth- and/or facies-related morphological groups are recognized within the "shallow water" genus *Icriodus* of the Belgian Famennian : the "*Icriodus alternatus* group" dominates in the relatively quiet offshore marine sediments of the Lower Famennian ("Groupe des Schistes de la Famenne"), where as the "*Icriodus cornutus-costatus* group" characterizes the more nearshore, turbulent facies of the Upper-Famennian ("Groupe des Psammites du Condroz"). A probable endemic morphological evolution is suggested for the latter group. A phylomorphogenetical lineage has been observed between *I. alternatus* BRANSON & MEHL and *I. cornutus* SANNEMANN at the base of the Famennian. The interspecific morphological relations and the intraspecific morphological variability within the different *Icriodus*-stock are discussed. Three new morphotypes of *I. alternatus*, one new subspecies of *I. cornutus* and two new subsepcies of *I. costatus* (THOMAS) are described ; their stratigraphical range is discussed.

1.- INTRODUCTION

Different workers have already drawn attention to the fact that the distinctions between the different species of *Icriodus* (I elements) are in a state of considerable confusion.

This is particularly true for the taxonomy of Upper-Devonian Icriodids (lacking lateral processes), which is based essentially on the morphological features of the oral surface.

DRUCE (1976) suggested that for this group of Icriodids, some of the morphological characteristics of the oral ornament (denticulation pattern) on which species had been characterized, might possibly be controlled by facies and/or water depth. This would explain the plastic nature of the group (including homeomorphic development at different stratigraphic levels) and the great problems of systematics.

He demonstrated further that an artificial classification of morphological characteristics (used in subdividing the Late Devonian Icriodids) furnished information on the ecological conditions rather than on phylogenetic relationships.

WEDDIGE & ZIEGLER (1979) demonstrated that the complex phylogenetic development of *Icriodus*

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in the Middle Devonian is closely associated with, and dependent on a complicated interplay of ecological, adaptive, and facies factors (delimiting so-called "eco-phenotypic groups").
The same authors stated further that "no key for systematic identification of *Icriodus* can be given other than that the outline of the spindle (= the main platform excluding the posteriorly extended median row) and the nodes of the platform and the carina, including the cusp, are significant taxonomic features. Innerspur, antispur, sinus and posterior margin, i.e., the outline of the posterior basal cavity, are no longer regarded as of overriding significance for taxonomic subdivisions".

Recently, one of us (DREESEN, 1978, Ph. D. Thesis, K.U. Leuven) recognized two different, probably depth- and/or facies-related morphological groups, within the *Icriodus* populations of the Belgian Famennian : the "*I. nodosus-alternatus* group" is typical of the relatively quiet and deeper marine environments of the Lower Famennian ("Famenne Shales") where as the "*I. cornutus-costatus* group" characterizes the more shallow and more turbulent facies of the Upper Famennian "Psammites du Condroz".

The author also suggested a probable endemic morphological evolution within the latter group, as some subspecies of *I. cornutus* and *I. costatus* appear to occur only in some Upper Famennian lithofacies. A phylomorphogenetic lineage moreover, has been observed at the base of the Belgian Famennian, between *I. alternatus* and *I. cornutus* (E. HOULLEBERGHS, unpublished).
Icriodus form species are frequent in Belgian Famennian conodont faunas, since they are representative of icriodid and polygnathid-icriodid conodont biofacies, which occupied the nearshore, intertidal to shallow subtidal shelf environments (DREESEN & THOREZ, 1980).

Although not very useful for international correlation purposes, Famennian Icriodids are very helpful in studying the paleogeographical evolution of sedimentary basins, especially when shallow to very shallow marine environments are expected.
Moreover, when the index conodonts are lacking (such as *Palmatolepis, Polygnathus* or *Bispathodus*), Icriodids may represent complementary guides for the intervals studied (such as the *velifer, styriacus* ? , and *costatus* Zones) in the Belgian Famennian.

2.- THE *ICRIODUS* BIOFACIES CONCEPT .

KREBS (1959) and MULLER (1962) considered *Icriodus* as a near-reef conodont form with benthonic affinities.

SEDDON (1970) distinguished a near-reef *Icriodus* Biofacies, as opposed to a *Palmatolepis* Biofacies of the basin itself, in the Upper-Devonian of the Canning Basin, Australia.

SEDDON & SWEET (1971) proposed a general ecologic model for conodonts, suggesting that the conodonts were segregated by vertical stratification. According to this model, conodonts of the *Icriodus* Biofacies were confined to a zone near the ocean surface, where as the *Palmatolepis* Biofacies occupied deeper zones.

DRUCE (1970, 1973) preferred a lateral differentiation model : the *Icriodus* fauna inhabited shallow water, where as the *Palmatolepis* fauna preferred deeper water. He stated further (DRUCE, 1976) that : "... even though the *Icriodus* Biofacies may have been able to occupy the upper water niche of the ocean it preferred to live in near-coastal regions ... ".

SANDBERG (1976) demonstrated lateral differences in conodont associations from a given zonal interval (Upper *styriacus* Zone) in the Late Upper-Devonian of the Rocky Mountains, U.S.A. He distinguished five conodont biofacies which are related to five major facies, ranging from continental rise to offshore bank and lagoon. He stated that : "... the closely related platform genera *Icriodus* and *Pelekysgnathus* occur only from the continental shelf shoreward and hence are considered to be indicators of shallow water deposition. They did not live in the shallowest depth zone, however, because they are not ubiquitous. They must have lived at rather shallow depth and have been affected by bottom conditions, because they become scarce in moderately deep water on the continental shelf and have not been found in deeper water on the continental slope".

In this interval, the *Icriodus* form species occur in the polygnathid-icriodid and less commonly in the palmatolepid-polygnathid and polygnathid-pelekysgnathid biofacies (SANDBERG, 1976 ; SANDBERG & ZIEGLER, 1979).

According to WEDDIGE & ZIEGLER (1976, *Icriodus* preferred turbulent and nearshore water, where as *Polygnathus* mainly dominated in deeper, more offshore, less agitated water (type Eifelian, Middle-Devonian of W-Germany).

SCHUMACHER (1976) finally, described *Icriodus*-dominated faunas from shallow subtidal facies

from late Givetian - early Frasnian boundary beds of Central Missouri, U.S.A.

3.- DISTRIBUTION OF ICRIODIDS IN THE BELGIAN FAMENNIAN AND THEIR PALEOECOLOGICAL SIGNIFICANCE

In the Famennian type area of the Dinant tectonic basin (Ourthe Valley, Famenne area), mega-environments are differentiated on the paleoshelf, which characterize a regressive megasequence (THOREZ, 1973-77). The lateral and vertical distribution pattern of the platform conodont associations (biofacies) is directly or indirectly controlled by the migration of the different lithofacies in the studied sedimentary basin (DREESEN & THOREZ, 1980). The presence moreover of mixed conodont biofacies is attributed to sedimentological mechanisms such as tidal currents, storm wave action and débris-flow.

We found the highest frequencies of Icriodids in sediments deposited on tidal flat areas (shallow subtidal to intertidal) and in the neighbourhood of local shoals and reef-like bio-accumulations (crinoidal mud mounds).

The Lower Famennian sediments (deposited during the *triangularis* and *crepida* Zones) are chiefly composed of nodular shales with a diversified brachiopod fauna. The calcareous horizons yield an almost exclusive palmatolepid conodont biofacies, except for the lowermost Famennian strata (Lower ? - Middle *triangularis* Zone) in which an outburst of Icriodids can be observed (up to more than 50 o/o of the conodont fauna). At the same time, and especially at the southeastern border of the Dinant Synclinorium, a temporary increase of sandy intercalations in the otherwise homogenous shale deposits is noticed (DUSAR, 1976).
This outburst of Icriodids near the Frasnian/Famennian boundary has been observed in all parts of the Dinant and Vesdre Basins and results obviously from some widespread tectonic (?) disturbances, which brought a sudden and temporary influx of Icriodid conodont elements (DUSAR, 1980).

Another hypothesis may be advanced to explain this striking "boom" of Icriodids at the Frasnian-Famennian stage boundary : the presence of Upper Frasnian bioherms ("F2j") at shallow depths, could have influenced the topography of the Lower Famennian seabottom : above those bioherms temporary shoals could have existed and could have been prolific for an icriodid conodont biofacies in a normally offshore shelf environment.

In this zonal interval the " *Icriodus alternatus* - group" reaches its maximum. Different morphological trends are observed (see below) as well as a phylomorphogenetical lineage between *I. alternatus* and *I. cornutus* (fig. 1).
The most obvious morphological characteristics for this group are a regular denticulation pattern and a weakly developed cusp. Specimens formerly attributed to *I. nodosus* (HUDDLE) probably represent broad specimens of *I. alternatus* with an extremely expanded basal cavity exhibiting spur and sinus ; they are now considered as a particular morphotype of *I. alternatus.*

The presence of a deep, wide and asymmetrical basal cavity finally, has been considered as an adaptation to relatively quiet, more offshore (?) marine environments (DREESEN, 1978).

From the Upper *triangularis* Zone to the uppermost *crepida* Zone (perhaps including the lowermost rhomboidea Zone ?), we observe an almost exclusive palmatolepid conodont biofacies, with no or only very few Icriodids. The sediments deposited during this interval represent the most offshore fully marine deposits of the Belgian Famennian ; goniatites (Cheiloceratids) have also been found in the same zonal interval.

A second morphological group of Icriodids, the "*Icriodus cornutus-costatus* group", appears at the base of the Upper Famennian (base of the *rhomboidea* Zone, according to BOUCKAERT, STREEL & THOREZ, 1968) (fig. 2).
The different members of this group are characterized by the presence of a pronounced cusp, an irregular denticulation pattern, and a relatively small basal cavity. Some Icriodids moreover, with an irregular or even bizarre denticulation pattern, are exclusively found in some particular sedimentary environments of the Upper-Famennian (DREESEN, 1978).
Icriodus cornutus chojnicensis MATYJA seems to be characteristic of the surroundings of reef-like crinoidal mud mounds, at the top of the Esneux Formation and the base of the Souverain-Pré Formation. These *Icriodus* form species, which are normally confined to a polygnathid-icriodid conodont biofacies, are frequently removed by (storm) wave action to the neighbouring "fore reef" and "back reef" subtidal environments, which are normally inhabited by a palmatolepid-polygnathid conodont biofacies.

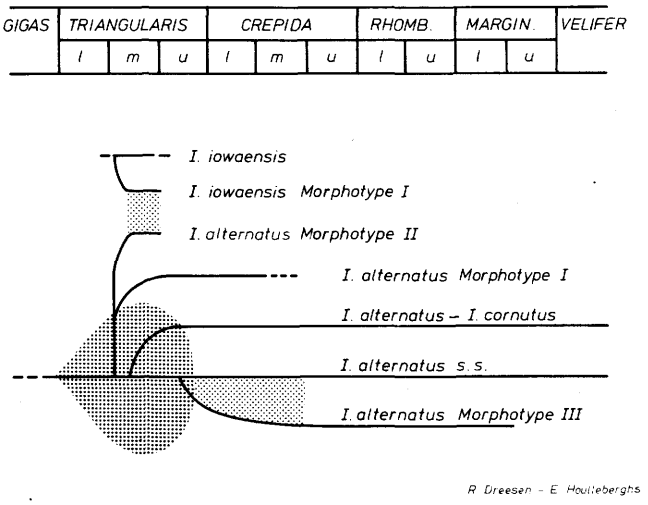

Figure 1.

Phylomorphogenetical relations within the I. alternatus stock. (shaded areas = fields of transition)

Icriodus cornutus pectinatus n. subsp. is a rather small icriodid form with ridgelike or crestlike transversally fused denticles ; it is frequently found in thin-bedded lenticular or nodular limestones of the Comblain-la-Tour Formation, which was deposited in intertidal to shallow subtidal marine environments during the Lower *velifer* Zone.

Coarse-grained organoclastic limestone lenses within quartzitic sandstone-beds at the base of the Montfort Formation (dispalying "ball-and-pillow" structures) yield a particular icriodid form : *Icriodus costatus bultyncki* n. subsp., associated to pelekysgnathids, polygnathids of the *P. semicostatus*-group and asymmetrical "shallow water" conodont forms such as *Scaphignathus* and *Pandorinellina cf. insita* (Lower-Middle *velifer* Zones).

Both singular icriodid forms became mixed either with elements of a palmatolepid-polygnathid biofacies (Comblain-la-Tour Formation), or with elements of a polygnathid-pelekysgnathid or even a clydagnathid ? biofacies (Montfort Formation), through the mechanism of tidal currents or tidal inlets, connecting fore-barrier and backbarrier or tidal lagoonal environments (DREESEN & THOREZ, 1980).

No conodonts have yet been recorded from the *styriacus*-Zone in Belgium ; during this time interval, unfavourable facies occured for the conodont animal, such as evaporitic, tidal lagoonal and alluvio-lagoonal environments (THOREZ, 1969-77).

The youngest Upper-Famennian deposits, the so-called "Strunian" beds, are characterized by the subspecies *I. costatus dusari* n. subsp. and *I. costatus darbyensis* KLAPPER ; these forms represent typical icriodid elements of the mixed polygnathid-icriodid and bispathodid-pseudopolygnathid conodont biofacies, which inhabited tidal flat environments, announcing thenew transgression at the base of the Lower Carboniferous.

Within the basins studied and within a specific zonal interval, some differences between the Icriodid distribution of different sections may also be related to depositional environment : so it is worth noting that the transition from *I. alternatus* to *I. cornutus* within the *P. triangularis*-Zone, took place earlier at the north-eastern border of the Dinant Basin (Hamoir region) than at its southern borders (Senzeille region) (E. HOULLEBERGHS 1980, in press).

In the same way the icriodid populations composition during the Lower *marginifera*-Zone, in the Vesdre Basin, is different with regard to the shelf subenvironment : we recorded almost exclusively specimens of *I. cornutus chojnicensis* in the nearshore Verviers-Trooz area, whereas *I. alternatus* s.s. is still present in the more offshore sediments of the Aachen area (Stolberg-Hahn area ; KASIG, DREESEN & BOUCKAERT, 1979).

4.- PHYLOMORPHOGENETIC RELATIONS WITHIN THE FAMMENNIAN *ICRIODUS*-STOCKS

The *Icriodus alternatus*-stock comprises different morphotypes and numerous transitional forms (see further) (fig. 1). *Icriodus cornutus* SANNEMANN evolved from *Icriodus alternatus* BRANSON & MEHL during the Middle and Upper *triangularis*-Zones, by a progressive narrowing of the basal cavity and a progressive downcurving of the posterior aboral surface. Typical specimens of *Icriodus cornutus cornutus* are lacking because of the scarcity of Icriodids during the *crepida*- and lowermost *rhomboidea*-Zones : during this zonal interval a palmatolepid conodont biofacies was present, excluding any nearshore conodont form. *Icriodus iowaensis* YOUNGQUIST & PETERSON evolved from *Icriodus alternatus* BRANSON & MEHL by widening of the basal cavity and by a progressive chevron-like arrangement of the denticles on its platform ; this form has only been recorded from the Middle *triangularis*-Zone to the base of the Upper *triangularis*-Zone. Within the *Icriodus cornutus*-stock different subspecies are erected, based on differences of

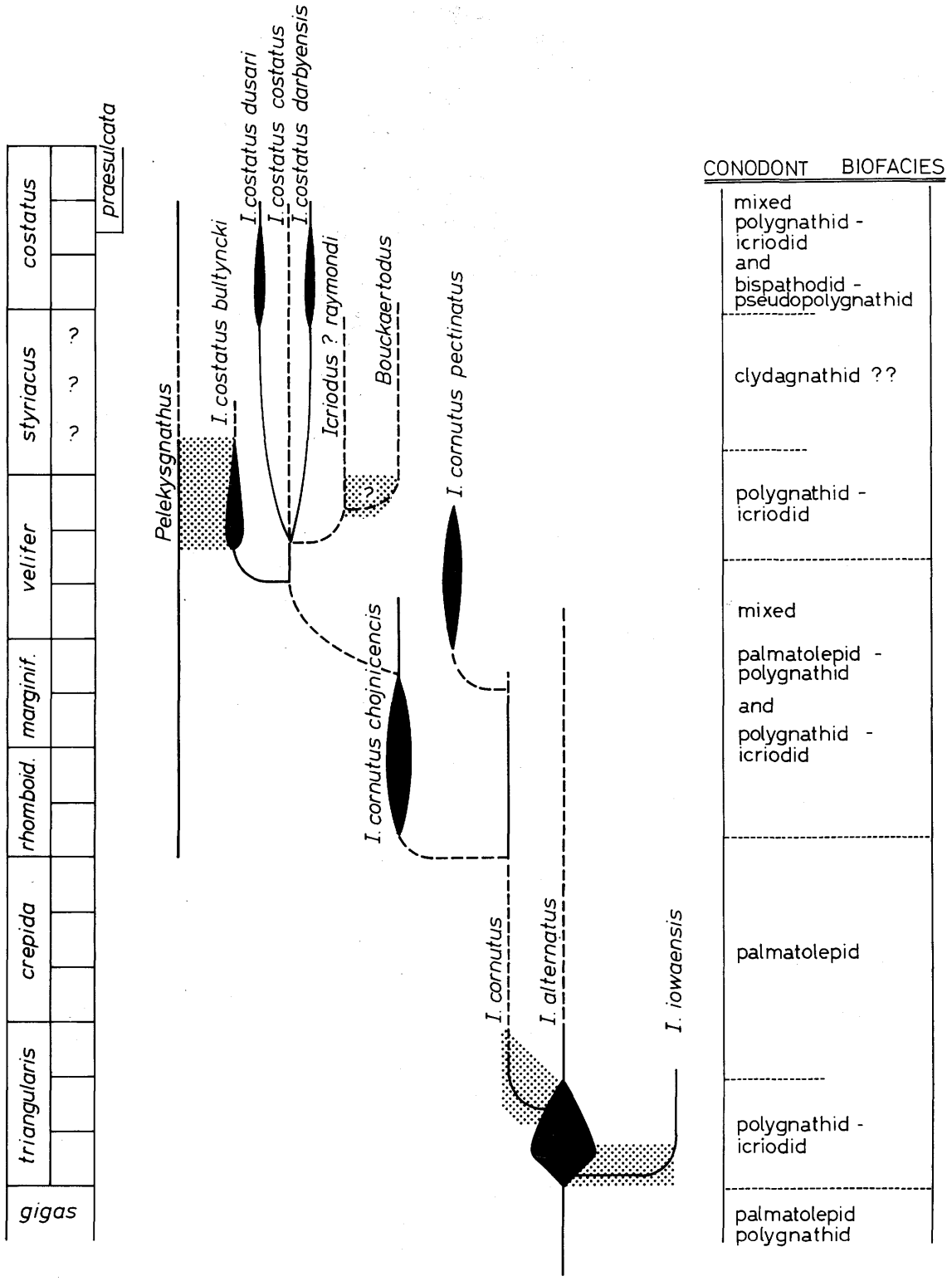

Figure 2.- Phylomorphogenetical evolution of Icriodus during the Famennian Stage in Belgium. (shaded areas = fields of transition)
R. DREESEN & E. HOULLEBERGHS, 1980

their denticulation pattern and stratigraphical range . Transitional forms to *Pelekysgnathus* may be observed, especially within the subspecies *Icriodus cornutus chojnicensis* MATYJA ; these specimens are characterized by the presence of only one distinct row of denticles and a few adventive denticles.
The *Icriodus cornutus*-stock gave rise to the *Icriodus costatus*-stock by a progressive arching of the longitudinal axis of the unit.
Within this latter stock intraspecific morphological variability resulted in the recognition of four subspecies (fig. 2).

Confusion arose when two different morphological forms were illustrated in the second volume of the Catalogue of Conodonts (1975) under the name of *Icriodus costatus* (THOMAS).
As the majority of the specimens illustrated in the literature, identified as *Icriodus costatus,* is quite different from the original holotype of THOMAS (1949), we decided to reserve the name *Icriodus costatus costatus* for all specimens similar or analogous to the original holotype.
Icriodus darbyensis, a junior synonym of *Icriodus costatus,* introduced by KLAPPER in 1958, is now retained for a subspecies of *I. costatus,* bearing three transversally connected rows of not-alternating denticles.
Icriodus costatus dusari n. subsp. differs from *I. costatus darbyensis* KLAPPER in having slightly alternating denticles and in missing these cross ridges.
Mature specimens of *Icriodus costatus darbyensis* in our Belgian material, displaying a relatively broad asymmetrical platform, show some affinities with *Icriodus ? raymondi* SANDBERG & ZIEGLER ; they differ however in the shape of their basal cavities and profiles. *Icriodus costatus bultyncki* n. subsp. is very close to the nominate subspecies, but differs from it in its characteristic reticulate platform ornament. The specimens of *Pelekysgnathus darbyensis* (KLAPPER) illustrated by ETHINGTON, FURNISH and WINGERT (1961) are now identified as *I. costatus bultyncki ;* in that case this new subspecies, which is restricted to the higher parts of the *velifer*-Zone in Belgium, would range as high as the *costatus*-Zone.
Transitional forms between *I, costatus bultyncki* and *Pelekysgnathus* are quite frequent ; this morphological feature which occurs at different stratigraphical levels within the Famennian and between different form-subspecies, may be considered as a facies-related homeomorphic development of icriodid conodont elements.

5.- SYSTEMATICS

Family Icriodontidae MULLER & MULLER, 1957
Genus Icriodus BRANSON & MEHL, 1938.

Icriodus alternatus BRANSON & MEHL, 1934 - s.s.
Pl. III : 6-8 ; Pl. IV : 1-4 and 6

Synonymy :

1934 *Icriodus alternatus* n. sp. - BRANSON & MEHL p. 225-226, pl. 13 : 4-6.

1959 *Icriodus alternatus* BRANSON & MEHL - HELMS p. 642, pl. 1 : 1 ; pl. 4 : 7.

1962 *Icriodus alternatus* BRANSON & MEHL, ZIEGLER p. 51-52.

1966 *Icriodus alternatus* BRANSON & MEHL, ANDERSON, p. 405, pl. 52 : 11-12.

1966 *Icriodus alternatus* BRANSON & MEHL, GLENISTER & KLAPPER, p. 804.

1971 *Icriodus alternatus* BRANSON & MEHL, SZULCZEWSKI, p. 21.

1975 *Icriodus alternatus* BRANSON & MEHL, DRUCE p. 105, pl. 29 : 1-4.

1975 *Icriodus alternatus* BRANSON & MEHL, KLAPPER in Catalogue of Conodonts ; vol. 2, p. 69-70, pl. of Icr. 3 : 5-6.

Diagnosis

A species of the formgenus *Icriodus* characterized by a narrow platform, on which the elongated middle row denticles alternate with the sharp, hornlike lateral row denticles.
The basal cavity is small, more or less symmetrical and droplike.

Description

The platform is small, about five times as large as wide. The middle row denticles which are small and ellipical, alternate with those of the two lateral rows. These lateral row denticles, which are well developed, equidimensional and hornlike, stand isolated on the surface or on the margins of the narrow platform. Posteriorly, the cusp and an other denticle of the middle row are aligned with each other and extend behind the last lateral row denticles.

The anterior platformtip consists of a more or less triangular knob. This knob is followed by a second middle row denticle which is situated on the posterior half of the distance between knob and the next lateral row denticles. Going furtheron posteriorly on the platform, the middle row denticle is placing itself, more and more equidistantional between the lateral row denticles. The margins of the interior part of the basal cavity run parallel with those of the platform. In the second half of the unit the cavity margin is broadening and shows a more or less symmetrical, droplike outline.

Remarks

A certain morphological variability has been observed. Typical specimens of *I. alternatus s.s.* are found in the Famennian-shales at the S. and S.E. border of the Dinant Basin. In samples of the Aachen area, specimens of *I. alternatus s.s.* were found with a less robust appearence. In those icriodids, the middle row denticles are characterised by a very strong elongated form. The lateral row denticles stand more isolated on the margin of a narrow platform, due to their higher and sharper outline. The margin of the basal cavity starts also broadening more posteriorly than in the typical specimens of *I. alternatus s.s.* Within the fauna collected from the new outcrop of the "Schistes de Senzeilles" near the village of Senzeilles, it was possible to prove the evolutionary trend form *Icriodus alternatus* BRANSON & MEHL, 1934 - s.s. to *Icriodus cornutus* SANNEMANN - 1955, already mentioned by GLENISTER & KLAPPER (1966). The evolution starts with the form *I. alternatus* s.s. In a first stage the cusp becomes higher, and more accentuated than the other denticles. In a next stage the higher and bigger cusp is sligthly inclining posteriorly, so that in plan view the cusp extends the margin of the basal cavity. Almost simultaneously the cusp and the last but one posterior denticle are becoming fused. In a third stage the anterior denticles of the lateral rows become gradually more inclined on the platform margins. The cusp fuses with that middle row denticle and reaches a more hornlike aspect. At the same moment the margin starts downcurving to a maximum of about 45°.

Occurence

In Belgium, *I. alternatus* s.s. is found in the Famennian-shales of the S. and SE. border of the Dinant Basin.

In the Famennian-shales of the Aachen-area, *I. alternatus* s.s. is the most frequent icriodid conodont form.

Range

I. alternatus s.s. occurs, in Belgium, from the middle *triangularis*-Zone (top of the upper *gigas*-Zone ?) to the lower *crepida*-Zone (base of the middle *crepida*-Zone).

In the Aachen-area, they range as high as the *velifer*-Zone (?).

Icriodus alternatus BRANSON & MEHL, 1934 - Morphotype I

Pl. II : 6-9 ; Pl. III : 1-5

Diagnosis

A morphotype of *Icriodus alternatus* characterised by a large basal cavity, a wide platform bearing ellipical lateral row denticles alternating with weakly developed middle row denticles.

Description

The circular, weakly developed middle row denticles alternate with those of the lateral rows. The main axes of these ellipical denticles are slightly convergating to the central part of the platform, especially in the posterior part of the unit.

The anterior platform tip consists of a more or less triangular knob. Posteriorly, the cusp and the last lateral row denticle, which extend behind the last couiple of denticles, are aligned with the inner lateral row.

The basal cavity, quickly broadening, may present a weakly developed spure and sinus.

Remarks

I. alternatus Morphotype I differs from *I. alternatus* s.s. by the alignement of the posteriormost denticles and by the outline of the basal cavity.

This morphotype of *I. alternatus* differs from *I. alternatus* Morphotype II by its more rounded lateral row denticles in the former and the more pronounced convergation-pattern of these denticles in the latter.

Occurence

Icriodus alternatus Morphotype I has been found in the basal part of the Famennian-shales Formation of the S. and SE. border of the Dinant Basin.

Range

Icriodus alternatus Morphotype I occurs in the middle *triangularis*-Zone to the lower (middle ?) *crepida*-zone in Belgium.

Icriodus alternatus BRANSON & MEHL, 1934
Morphotype II
Pl. II : 1-5

Diagnosis

A morphotype of *I. alternatus* characterized by a wide basal cavity and a large platform. The middle row denticles are rounded and alternate with those of the lateral rows. The latter have a ridgelike, elongated form, and their main axes show some convergency to the median denticle row.

Description

The middle row denticles are alternating with the elongated lateral row denticles. The main axes of these ridgelike denticles, especially those of the posterior half of the unit, show a pronounced convergency-pattern to the center of the large platform. The posterior end of the platform consists of a well developed cusp, preceded by a denticle, which is aligned to the inner lateral row.

The basal cavity is well developed, and its posterior part is characterized by the presence of a spur and sinus.

Remarks

We consider this morphotype of *I. alternatus* as a transitional form between *I. alternatus* BRANSON & MEHL, 1934 - s.s. and *I. iowaensis* YOUNGQUIST & PETERSON, 1947.

Occurence

I. alternatus Morphotype II has been found in the basal part of the "Schistes de Senzeilles" in the Senzeilles-outcrop (lowermost part of the Famenne-Shales Formations).

Range

I. alternatus Morphotype II occurs within the middle *triangularis*-Zone.

Icriodus alternatus BRANSON & MEHL, 1934
Morphotype III
Pl. IV : 7

Diagnosis

A tiny morphotype of *I. alternatus* showing a small, asymmetrical basal cavity and a narrow platform. The median row denticles are elongated, where as the lateral ones are conical.

Description

The lateral row denticles, are well developed and slightly dipping towards the median row. The elongated middle row denticles alternate with those of the lateral rows.
The median row is connected to the cusp by a weakly developed denticle. The platform is narrow.

The basal cavity has a semicircular posterior end and displays in some cases of a weak sinus.

Occurence

Rare in the Famenne-Shales Formation of the SE and S border of the Dinant Basin.
A high frequency is found in the "Esneux-Schichten" of the Aachen area.

Range

I. alternatus Morphotype III occurs in Belgium from the middle (lower ?) *triangularis*-Zone up to *crepida*-Zone.
In the Aachen area it ranges up to the *velifer*(?)-Zone.

Icriodus iowaensis YOUNGQUIST & PETERSON, 1947
Pl. I : 1-3

Synonymy

1938 *Icriodus expansus* n. sp. BRANSON & MEHL, p. 150-161, pl. 26 : 18-19.

1947 *Icriodus iowaensis* n. sp., YOUNGQUIST & PETERSON, p. 247, pl. 37 : 22-24, 27-29.

1947 *Icriodus circularis* n. sp., YOUNGQUIST & PETERSON, p. 246, pl. 37 : 15.

1947 *Icriodus incrassatus* n. sp., YOUNGQUIST & PETERSON, p. 247, pl. 37 : 2, 25.

1947 *Icriodus spicatus* n. sp., YOUNGQUIST & PETERSON, p. 248, pl. 37 : 8-9.

1966 *Icriodus iowaensis* YOUNGQUIST & PETERSON, ANDERSON ; p. 406, pl. 52 : 8, 9, 13, 17-21.

Diagnosis

A species of *Icriodus* in which the median row denticles are fused into an irregular longitudinal ridge, all ridgelike, lateral row denticles are connected to wich.

The biconvex basal cavity is large.

Description

Cross ridges connect the lateral row denticles to the medium row denticles, which results into an irregular, chevron-like denticulation pattern. A discontinuous median ridge runs over the whole platform length.
In plan view, a triangular cusp extends the rounded posterior margin of the basal cavity. This cavity is large, biconvex and often asymmetrical.

Remarks

According to SZULCZEWSKI (1971), the transversal ridges are connecting conspicuously lateral and median denticles rows, only in the anterior part of the unit.
In our specimens, we observed those ridges in the posterior part of the conodont. In some cases, the platform ornamentation is different as the median ridge is not extending to the anterior platform tip. In that case we observe an irregular ridgelike pattern in the posterior part and a chevron-like denticulation in the anterior half of the platform.

Occurence

Some rare specimens of *I. iowaensis* are found in the Famenne-Shales of the Vesdre-area.

Range

I. iowaensis occurs from the middle *triangularis*-Zone to the upper *triangularis*-Zone.

Icriodus iowaensis YOUNGQUIST & PETERSON, 1947 - Morphotype I

Pl. I : 4-8

Synonymy

1971 *Icriodus iowaensis* YOUNGQUIST & PETERSON, SZULCZEWSKI, p. 22.

Diagnosis

A morphotype of *I, iowaensis* characterized by a platform on which only the anterior part bears transversal ridges. The middle row denticles are not present or only weakly developed. The basal cavity is wide.

Description

The denticles of the anterior part of the wide platform fuse into transversal or chevron-like ridges. The main axes of the ellipical denticles of the central part of the lateral row show a slightly convergency pattern to the medial depression. This depression is caused by the absence or the very weakly development of the middle row denticles.
A normally developed cusp is situated in the extension of that median depression.

The basal cavity is wide.

Remarks

Some specimens of *I. iowaensis* Morphotype I are intermediate between *I. alternatus* BRANSON & MEHL, 1934 - Morphotype II and *I. iowaensis*.
The specimens of *I. iowaensis* as described by SZULCZEWSKI (1971) fits our description. They are characterized by a platform of which only the anterior end shows some ridges, by the absence of the middle row denticles, and by the lack of a prominent cusp.

Occurence

I. iowaensis Morphotype I is found in the "Schistes de Senzeilles" (the basal part of the Famenne-Shales Formations).

Range

I. iowaensis Morphotype I has only been recorded from the middle *triangularis*-Zone to the base of the upper *triangularis*-Zone.

Icriodus cornutus SANNEMANN, 1955

Icriodus cornutus cornutus SANNEMANN, 1955

Synonymy

1955 *Icriodus cornutus* n. sp. SANNEMANN, p. 130, pl. 4 : 19-21.

1956 *I. cornutus* SANNEMANN-BISCHOFF, pl. 10 : 42.

1966 *I. cornutus* SANNEMANN-GLENISTER & KLAPPER, pl. 95 : 2-3.

1967 *I. cornutus* SANNEMANN-WOLSKA, pl. 2 : 5.

1969 *I. cornutus* SANNEMANN-OLIVIERI, pl. 14 : 4-5.

1971 *I. cornutus* SANNEMANN-SZULCZEWSKI, pl. 7: 3.

1975 *I. cornutus* SANNEMANN-KLAPPER in Catalogue of Conodonts, vol. II, p. 101-102, pl. 8 : 6.

1976 *I. cornutus cornutus* SANNEMANN-DREESEN, unpublished Ph. D. thesis, part II, pl. VI : 1-3.

Original diagnosis

A species of *Icriodus*, characterized by a "postero-oral" oriented thornlike cusp on the posterior end of the unit.

Description

In upper view slender and narrow, with three rows of enticles. The exterior denticles are cone-shaped and well developed, those of the margin row mostly hardly indicated. "... in lateral view, the oral and aboral side are parallel to each other, except for the posterior third, where the aboral margin inclines over 45°, subsequently at right angles to the posterior end of the cusp" (SANNEMANN, 1955).

Remarks

According to MOUND (1968) the inclination of the cusp at the end of the median row is responsible for the typical bending of the aboral margin. The median row denticles alternate with those of the lateral rows, as in *I. alternatus* BRANSON & MEHL. The platform is laterally not declined but progresses symmetrically to the longitudinal axis. The exterior-row denticles face each other at right angles and may show transversal elongation.
According to KLAPPER (1975) *I. cornutus* is a rather small species and its main characteristic is the pronounced posterior cusp.

Range

From the upper part of the Middle *triangularis*-Zone to the upper part (?) of the *marginifera*-Zone in Belgium.

Icriodus cornutus chojnicensis MATYJA, 1972

Pl. V : 1-14

Synonymy

1972 *Icriodus schojnicensis* n. sp. MATYJA, p. 475, pl. 4 : 1-4.

1974 *I. chojnicensis* MATYJA-MATYJA, pl. 6 : 1a-b.

1976 *I. cornutus chojnicensis* MATYJA-DREESEN, unpublished. Ph. D. thesis, part II, pl. 5 : 1-13.

Original diagnosis

(personnal communication of H. MATYJA, 1975 : english translation of the original diagnosis in Polish of MATYJA, 1972) : "a species of *Icriodus* with a short platform. Basal profile downarched posteriorly. Basal cavity drop-like. The denticles arranged irregularly. The quantity of denticles of the lateral rows variable, but always less than those of the median row. The denticles are high, conical, sharply terminated. The posterior denticle is raised much higher than the other ones. In some specimens the posterior lateral denticles may disappear".

New diagnosis

A subspecies of *Icriodus cornutus* SANNEMANN, with a short platform and an irregular denticulation pattern ; the number of the lateral row denticles is always less than that of the median row.

Description

In our specimens the rather small and isolated denticles of the median row, are often either partially fused into elongated nodes or completely fused into a weakly undulous longitudinal ridge . The lateral-row denticles on the other hand, are strongly developed, they are extremely pointed in some specimens and mostly randomly inserted. Their number is always less than or at most equal to that of the median row. The aboral margin progresses undulously in lateral view, the inclination of the posterior basal margin is not always as pronounced as in the nominate subspecies.

Range

Marginifera-Zone to the Lower *velifer*-Zone in Belgium ; MATYJA (1972-1974) recorded the same stratigraphical range.

Icriodus cornutus pectinatus n. subsp.

Pl. VI : 1-12

Synonymy

1976 *Icriodus cornutus pectinatus* n. subsp. DREESEN, unpublished Ph. D. thesis, part II, p. 11-12, pl. V : 14-21.

Derivatio nominis

Pecten = little crest ; because of the crestlike fused denticles.

Locus typicus : Pessoux, Pl. Ciney 167 E, nº 3106.

Stratum typicum

Pessoux nº 10 : arenaceous shales and psammites with nodular and lenticular organoclastic limestones ; base of the Comblain-la-Tour Formation.

Holotype : Plate VI : 3.

Material : 50 specimens.

Diagnosis

A narrow and often thiny subspecies of *I. cornutus* SANNEMANN, with bridgelike of crestlike transversally fused denticles on an extremely narrow platform.

Description

In upper view rectilinear, in lateral view the posterior part is slightly to distinctly inclined. The posterior inclination of the pronounced cusp is responsible for the abrupt bending of the posterior margin (as in the nominate subspecies).
On the anterior platform (anterior half to 2/3 of the platform) the denticles are fused in typical short and high, transversal crests. In the posterior part, the denticles are mostly isolated and aligned with the cusp. It is interesting to note the progressive decrease of the number of (fused) denticles, from front to back : at first three, then two and at last only one (being the continuation of the cusp). The number of crests is function of the total length of the conodont. Basal cavity as in the nominate subspecies.

Remarks

This new subspecies differs from the nominate subspecies by the presence of transversal crests and by lacking alternating denticles.

Range

This new form-subspecies is restricted to the lower part of the *velifer*-Zone (top of the Souverain-Pré Formation ; very frequent in the Comblain-la-Tour Formation).

Icriodus costatus (THOMAS, 1949)

Icriodus costatus costatus (THOMAS, 1949)

Synonymy

1949 *Pelekysgnathus costata* n. sp. THOMAS, pl. 2 : 9.

1975 *Icriodus costatus* (THOMAS)-KLAPPER in Catalogue of Conodonts, vol. II, p. 103, *Icriodus*-plate 2 : 2a, b.

Diagnosis

(After KLAPPER, 1966) : the nominate subspecies of *I. costatus*, strongly inclined and declined, with a very pronounced posterior cusp, well isolated with respect to the other denticles. The unit may be curved at both extremeties. The lateral-row denticles are parallel to the median-row denticles and are connected by transversal ridges. The shallow basal cavity is largest in the posterior part.

Remarks

Icriodus costatus probably evolved from *I. cornutus* which it resembles. The main difference between *I. costatus* and *I. cornutus* is the more pronounced cusp and the stronger degree of inclination in the former. According to ETHINGTON *et al.* (1961) *I. costatus* (THOMAS) is an intermediate form between *Icriodus* and *Pelekysgnathus.*
In the Belgium material several transitional forms between both genera may be found, especially between *I. costatus bultyncki* n. subsp. and *Pelekysgnatus* (pelekysgnathid forms with one or more adventive denticles). According to ANDERSON (1966) some double-rowed *Icriodus* forms are also transitional to *Pelekysgnathus inclinatus* THOMAS.

Range

Upper *marginifera*-Zone (?) to *costatus*-Zone.

Icriodus costatus bultyncki n. subsp.

Pl. VII : 1-14

Synonymy

1961 *Pelekysgnathus darbyensis* (KLAPPER)-ETHINGTON, FURNISH & WINGERT, pl. 90 : 16-17.

1976 *Icriodus costatus bultyncki* n. subsp. DREESEN unpublished Ph. D. thesis, vol. II, p. 13-14, pl. V : 22-30.

1979 *Icriodus costatus* (THOMAS)-SANDBERG & ZIEGLER, pl. 6 : 12-13.

Derivatio nominis

Gratefully dedicated to Prof. Dr. P. BULTYNCK, Lab. of Paleontology, Kath. Univ. Leuven, Belgium.

Locus typicus : Hamoir, 158 W nº 44 (= Ham 182-1).

Stratum typicum

Small lenticular crinoidal limestone bed, at the top of a pseudonodular sandstone bed ; base of the Montfort Formation.

Holotype : Plate VII : 9.

Material : 35 specimens.

Diagnosis

A subspecies of *Icriodus costatus,* characterized by a very irregular or obsolete denticulation, which consists of different shallow and irregular depressions and rises.

Description

The very pronounced and gently declined triangular cusp is very conspicuous and bears a ridge on its oral surface. The unit is both moderately to strongly inclined and declined. The platform is rather broad and ornamented with a very precarious reticulate pattern of depressions and rises. Typical teeth are mostly missing ; at most one can observe three mutually connected longitudinal ridges ; these connections delimit the typical depressions. Some forms are transitional to *Pelekysgnathus* (double-rowed forms, one-rowed forms with adventive denticles). The shallow basal cavity is analogous to that of the nominate subspecies.
Some species of *I. costatus bultyncki* become strongly asymmetrical by irregular connecting of the different ridges.

Range

In Belgium, until yet, exclusively found in the barrier-sandstones facies of the Montfort Formation, upper half of the *velifer*-Zone. The specimens illustrated by SANDBERG & ZIEGLER (1979) come from the Middle- and Upper *styriacus*-Zones of Colorado and Utah (U.S.) ETHINGTON *et al.* (1961) illustrated specimens which are found in conodont faunas indicating the *costatus*-Zone.

Icriodus costatus darbyensis KLAPPER
Pl. VIII : 1-3

Synonymy

1958 *Icriodus darbyensis* n. sp. -KLAPPER, pl. 141 : 9, 11, 12.

1975 *Icriodus costatus* (THOMAS, 1949), -KLAPPER, *Icriodus*- plate 2 : 1a, b ; p. 79 Cat. Conodonts, vol. II.

1976 *Icriodus costatus* (THOMAS, 1949) -DREESEN, DUSAR & GROESSENS, pl. 9 : 1, 4 ; pl. 11 : 1, 3-6.

Diagnosis

A subspecies of *Icriodus costatus,* with a relatively broad platform bearing three non-equivalent denticle-rows, which are connected to each other by transversal ridges.

Description

The cusp is as pronounced as in the other subspecies of *I. costatus.* The lateral- and median-row denticles are not alternating. The median-row denticles are mostly only weakly developed and they are connected to the late ral-row denticles by transversal ridges.
The platform outline is often asymmetrical by the stronger development of one of the lateral-row denticles. In that case the cross ridges are not always straight or continuous. The unit is not to only slightly arched.

Remarks

Initially, we considered *I. costatus darbyensis* and *I. costatus dusari* n. subsp. as two different Morphotypes of a new subspecies of *Icriodus costatus* (THOMAS).
After our discussion with Dr. C. SANDBERG and Dr. G. KLAPPER on the taxonomic problems within the *I. costatus*-stock, during the Vienna meeting of August 1980 (E.C.O.S. II), we decided to use the name of *I. darbyensis* KLAPPER for one of those morphotypes. (KLAPPER introduced *I. darbyensis* in 1958 as a new species, but considered it in 1966 as a junior

synonym of *I. costatus* (THOMAS).

Range

Lower and Middle (?) *costatus*-Zone in Belgium ; KLAPPER (1958) recorded it form the *costatus*-Zone.

Icriodus costatus dusari n. subsp.

Pl. VIII : 4-12

Synonymy

1966 *Icriodus costatus* (THOMAS)-ANDERSON, pl. 52 : 1-6, 10.

1975 *Icriodus costatus* (THOMAS)-DREESEN, DUSAR & GROESSENS, pl. 9 : 2, 3, 5-8 ; pl. 10 : 2, 5-7 (fig. 2 = holotype).

1976 *Icriodus costatus* (THOMAS)-BOUCKAERT & DUSAR, pl. 4 : 8-9.

Derivatio nominis

Dedicated to our friend and collegue Michiel DUSAR, Geological Survey of Belgium, Brussels.

Locus typicus

Yves-Gomezée road section ; Pl. Walcourt 137 E nº 569.

Stratum typicum

YG 14c : thin bed of sandy organoclastic coarse limestone within a rhythmic succession of compact sandstones, calcareous sandstones, marls and shales.

Material : more than 100 specimens.

Diagnosis

A subspecies of *Icriodus costatus* with a relatively broad but only slightly arched platform, bearing three distinct rows of conical denticles, which are not connected to each other by cross ridges.

Description

A prominent cusp distinctly sets off from the rest of the platform, and is connected to it by a discrete denticle, of the median row. The platform bears three distinct equivalent denticle rows being aligned with each other.

The median- and lateral-row denticles are slightly alternating. The denticles of the median row are often connected to each other and become finally fused into a low longitudinal ridge (see DREESEN, DUSAR & GROESSENS, 1975; Pl. 10 : 5, 7 ; Pl. 11 : 2). The posterior margin of the narrow and shallow basal cavity is still visible in upper view.

I. costatus dusari differs from *I. costatus darbyensis* by the alternation of its denticles and by the absence of cross ridges. It is also different from *Icriodus ? raymondi* SANDBERG & ZIEGLER by the shape of platform and profile.

Range

Typical icriodid conodont element of the *costatus*-Zone in Belgium ; perhaps already in the upper part of the *velifer*-Zone.

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The repository for all illustrated specimens is the Lab. Micropaleontology, Section Historical Geology of the Inst. Earth Sciences, K.U. Leuven, Belgium

PLATE I

Icriodus iowaensis YOUNGQUIST & PETERSON, 1947

1. Verviers VRG-28-14, C 1438, 60 x.
2. Verviers VRG-28-24, C 1439, 120 x.
3. Senzeilles 1, C 1440, 125 x.

Icriodus iowaensis Y. & P., 1947, Morphotype I

4. Senzeilles 3, C 1441, 60 x.
5. Senzeilles 3, C 1442, 125 x.
6. Senzeilles 3, C 1443, 125 x.
7. Senzeilles 3, C 1444, 125 x.
8. Senzeilles 7, C 1445, 125 x.

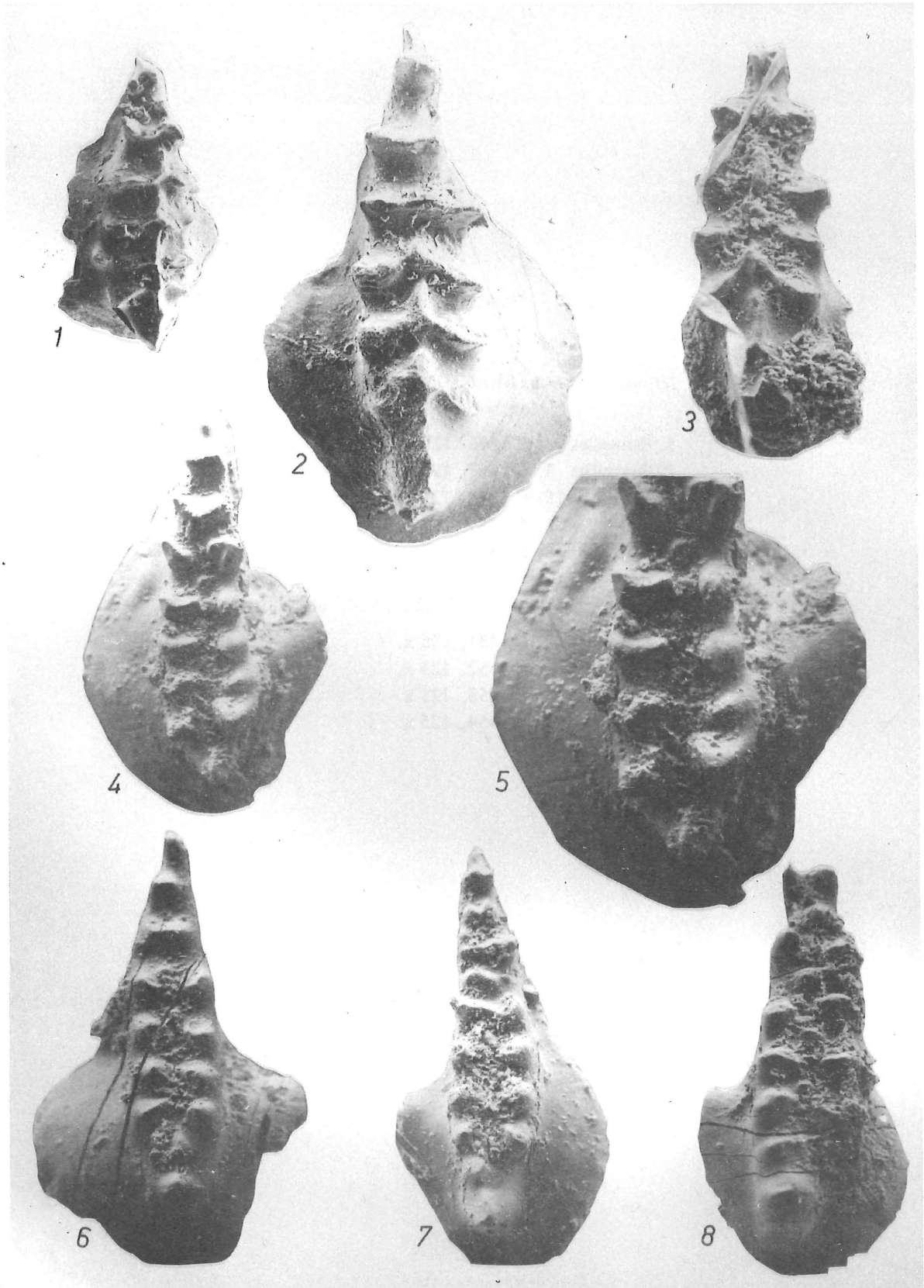
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PLATE II

Icriodus alternatus BRANSON & MEHL, 1934,
Morphotype II

1. Senzeilles 3, C 1446, 125 x.
2. Senzeilles 3, C 1447, 125 x.
3. Senzeilles 15, C 1448, 125 x.
4. Senzeilles 1, C 1449, 125 x.
5. Senzeilles 18, C 1450, 125 x.

Icriodus alternatus Br. & M., 1934, Morphotype I

6. Senzeilles 3, C 1451, 125 x.
7. Senzeilles 3, C 1452, 125 x.
8. Senzeilles 3, C 1453, 125 x.
9. Senzeilles 4, C 1454, 125 x.

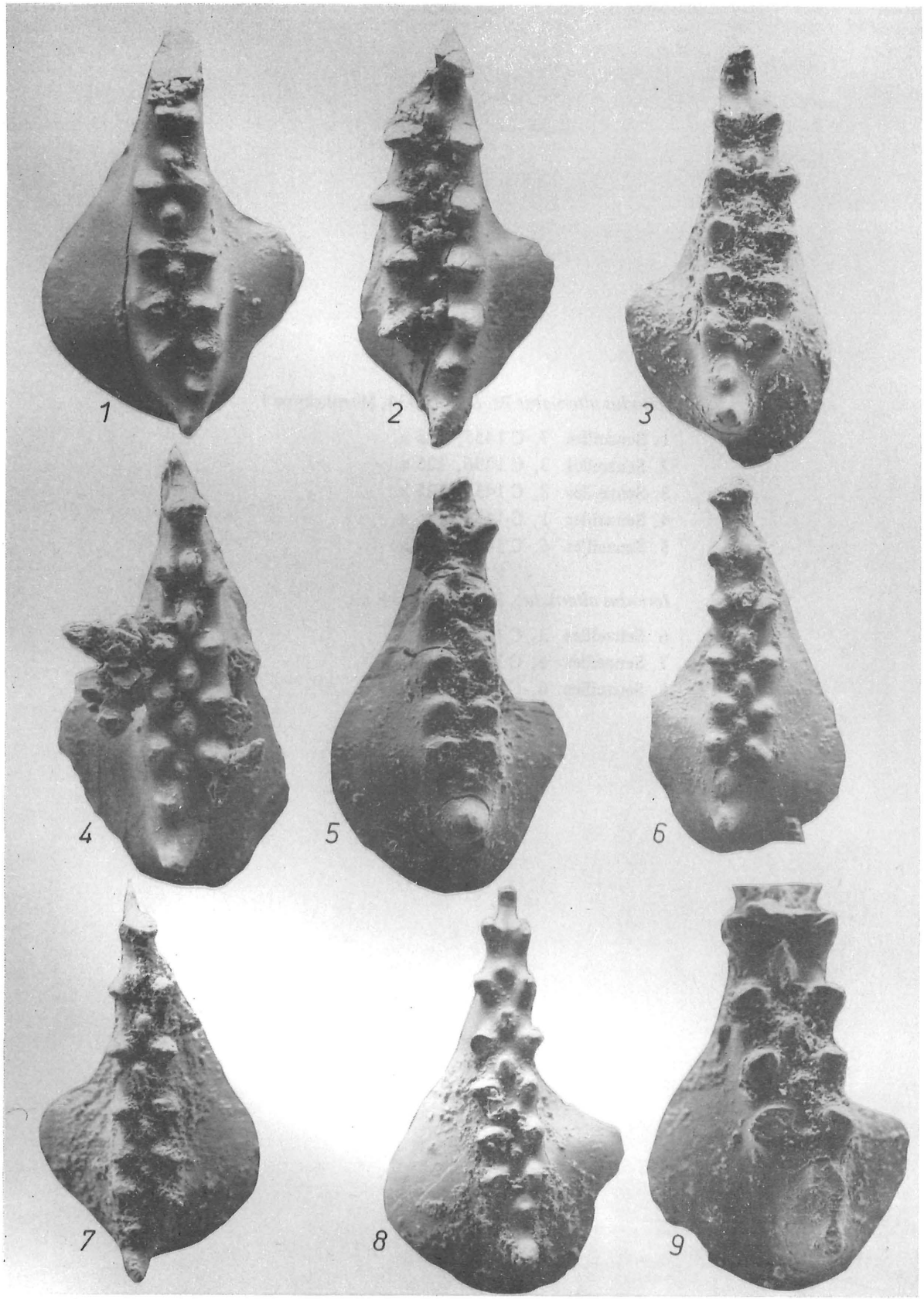
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PLATE III

Icriodus alternatus Br. & M., 1934, Morphotype I

1. Senzeilles 7, C 1455, 125 x.
2. Senzeilles 3, C 1456, 125 x.
3. Senzeilles 3, C 1457, 125 x.
4. Senzeilles 1, C 1458, 125 x.
5. Senzeilles 6, C 1459, 125 x.

Icriodus alternatus Br. & M., 1934, s.s.

6. Senzeilles 3, C 1460, 125 x.
7. Senzeilles 6, C 1461, 240 x.
8. Senzeilles 6, C 1462, 240 x.

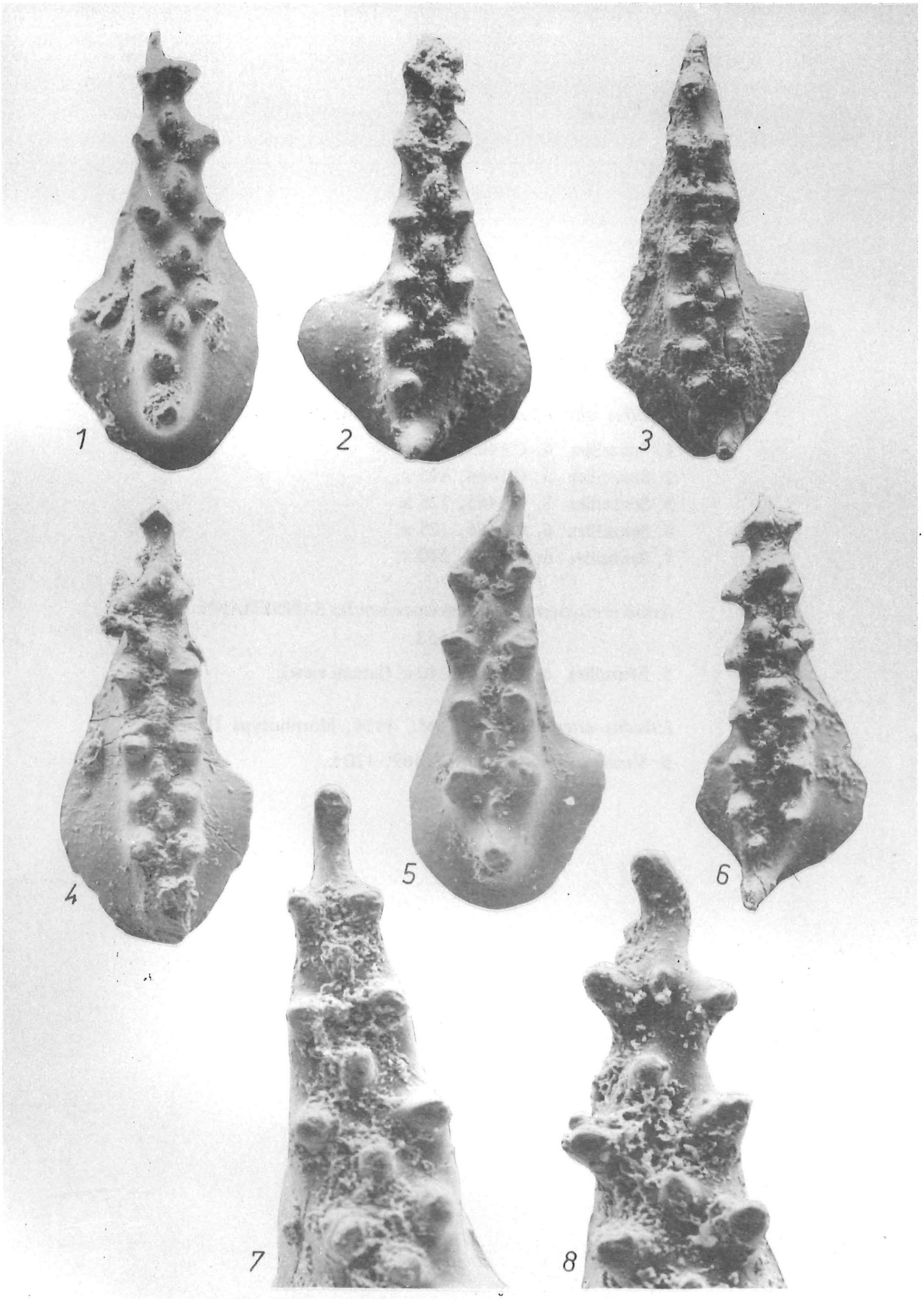
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PLATE IV

Icriodus alternatus BRANSON & MEHL, 1934, s.s.

1. Senzeilles 4, C 1463, 240 x.
2. Senzeilles 3, C 1464, 125 x.
3. Senzeilles 3, C 1465, 125 x.
4. Senzeilles 6, C 1466, 125 x.
7. Senzeilles 6, C 1467, 240 x.

Icriodus alternatus - - - *Icriodus cornutus* SANNEMANN 1953

5. Senzeilles 6, C 1468, 240 x. (lateral view).

Icriodus alternatus Br. & M., 1934, Morphotype III

6. Verviers VRG-30-3a, C 1469, 120 x.

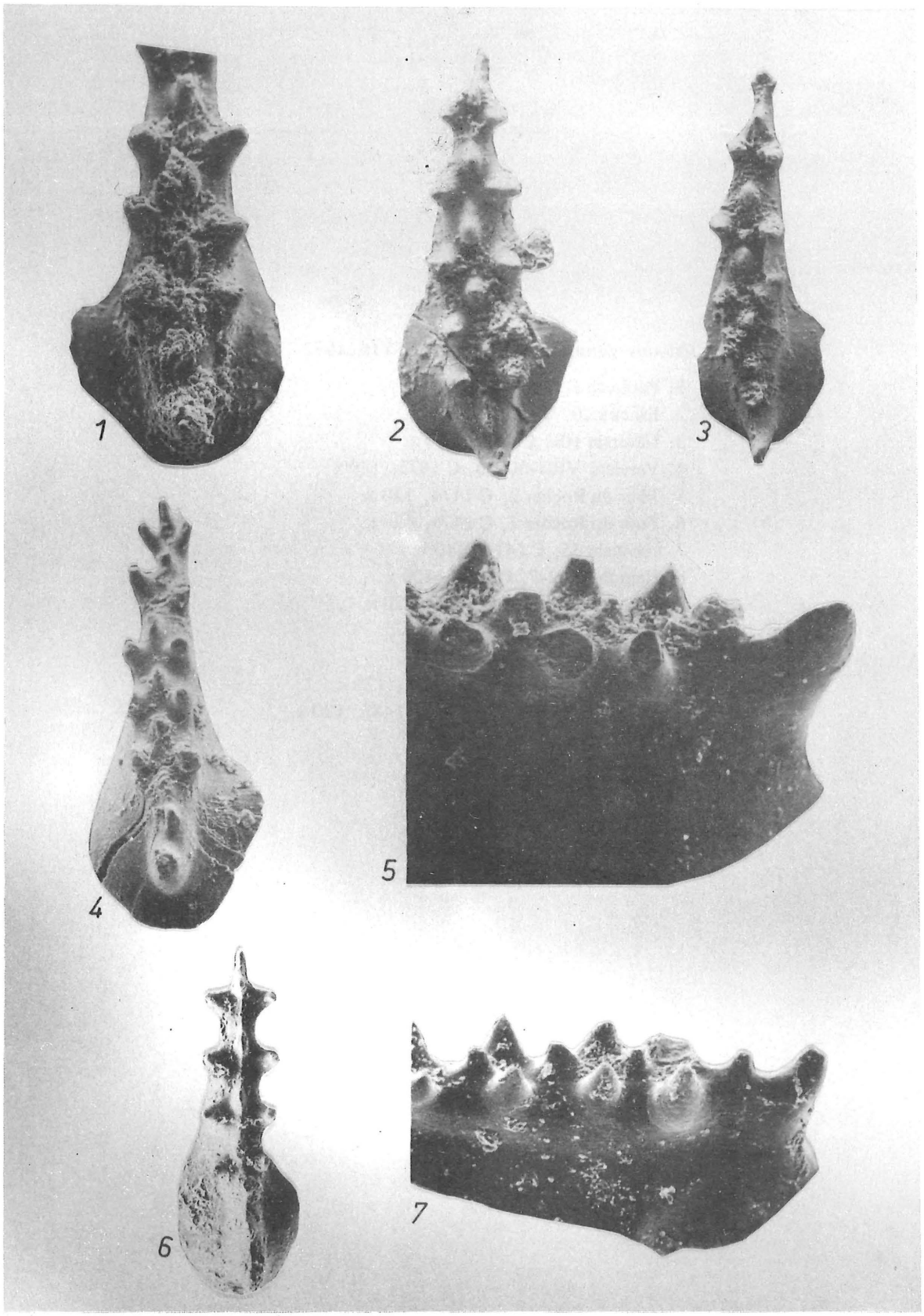
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PLATE V

Icriodus cornutus chojnicensis MATYJA, 1972

1. Poulseur 1, C 1470, 120 x.
2. Esneux 20, C 1471, 120 x.
3. Haversin 10a, C 1472, 120 x.
4. Verviers VRG-30-3b, C 1473, 120 x.
5. Tour du Rocher 2, C 1474, 120 x.
6. Tour du Rocher 2, C 1475, 120 x.
7. Haversin 35, C 1476, 240 x.
8. Hamoir 1002-7, C 1477, 120 x.
9. Tour du Rocher 2, C 1478, 120 x.
10. Haversin 3, C 1478, 120 x.
11. Haversin, 35, C 1480, 120 x.
12. Aye-Tige de Hogne 1, C 1481, 120 x.
13. Borehole A 200 : 42,20 m, C 1482, 120 x.
14. Haversin 10, C 1483, 60 x.

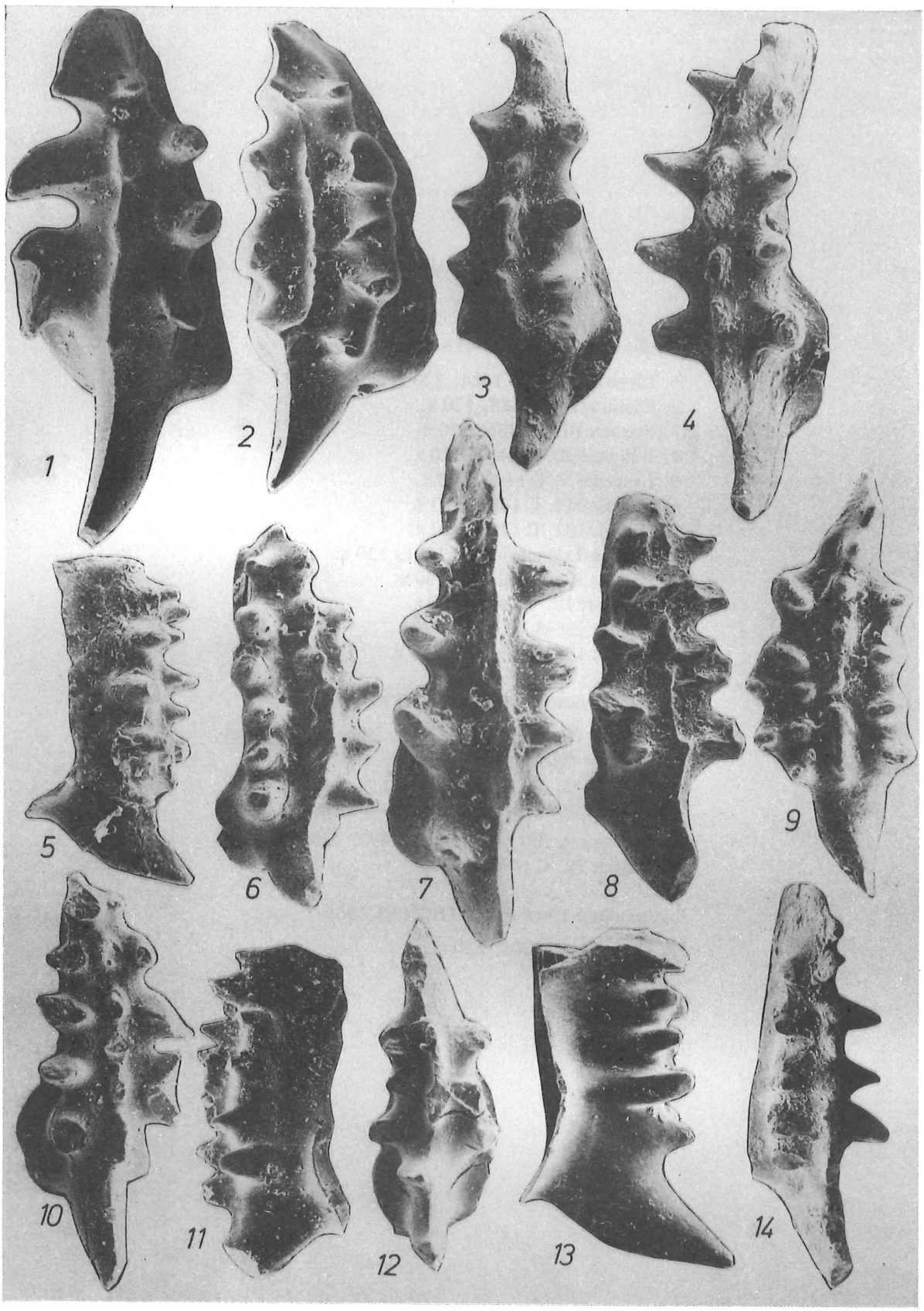
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PLATE VI

Icriodus cornutus pectinatus n. subsp.

1. Hamoir 194-3, C 1484, 120 x.
2. Custinne 8, C 1485, 120 x.
3. Pessoux 10, C 1486, 120 x.
4. Walcourt 20, C 1487, 120 x.
5. Landelies 5, C 1488, 120 x.
6. Hamoir 942, C 1489, 120 x.
7. Hamoir 182, C 1490, 120 x.
8. Achène-Leignon 1-3, C 1491, 120 x.
9. Hamoir 1015', C 1492, 120 x.
10. Walcourt 17, C 1493, 240 x.
11. Hamoir 194-3, C 1494, 120 x.
12. Hamoir 194-3, C 1495, 120 x.

Icriodus cornutus chojnicensis MATYJA, 1972

14. Esneux 20, C 1496, 120 x, lateral view, transitional to *Pelekysgnathus ?*

Icriodus costatus (THOMAS) - - *Pelekysgnathus*

13. Borehole A 200 : 42,40 m, C 1497, 120 x.
16. Esneux 20, C 1498, 120 x.

Pelekysgnathus inclinatus ? THOMAS, 1969

15. Dison 42, C 2000, 120 x.

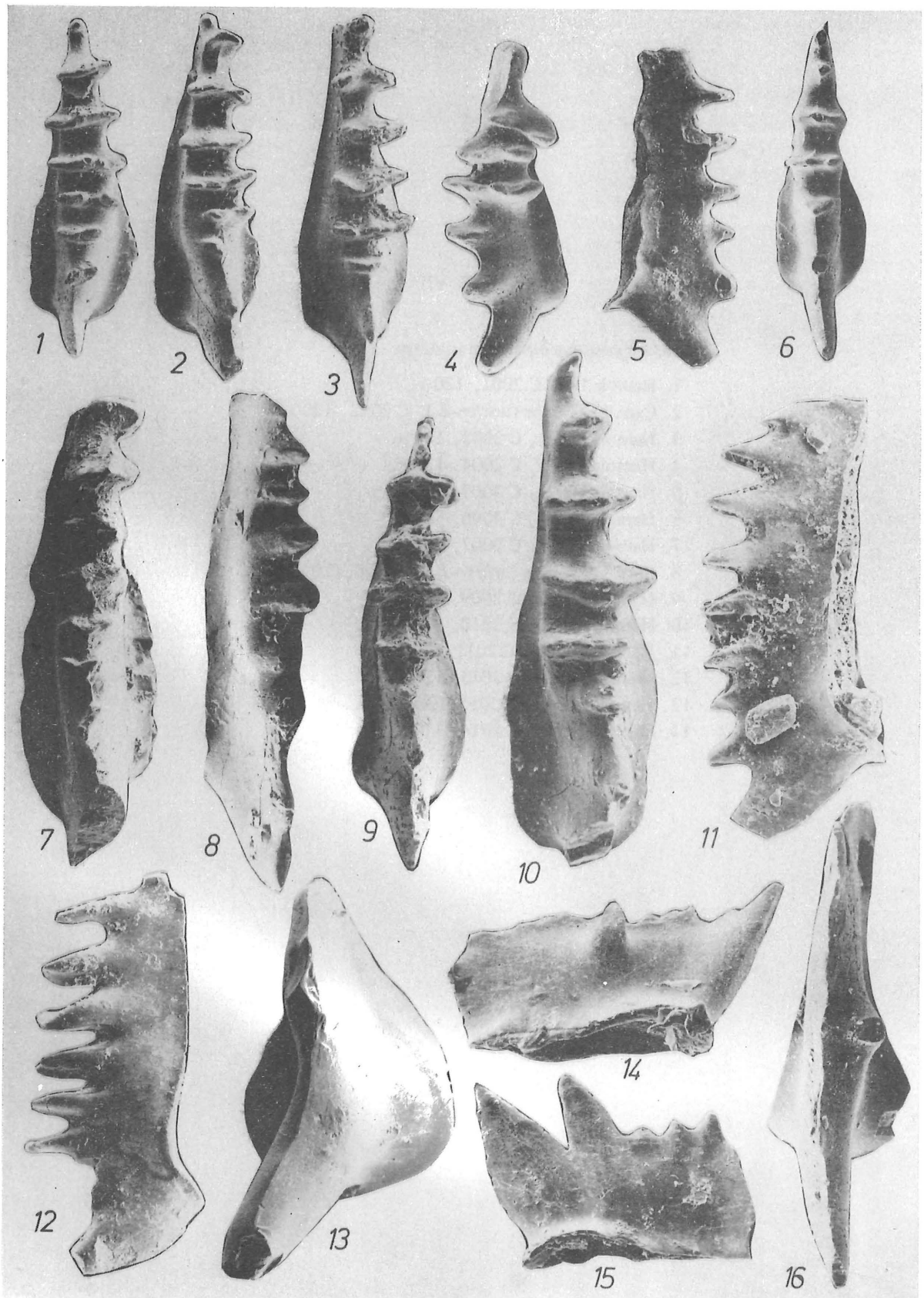
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PLATE VII

Icriodus costatus bultyncki n. subsp.

1. Hamoir 182, C 2001, 120 x.
2. Carr. La Gombe (*velifer*-Z.), C 2002, 120 x.
3. Hamoir 182-1, C 2003, 120 x.
4. Hamoir 1002a, C 2004, 120 x.
5. Hamoir 1002a, C 2005, 120 x.
6. Hamoir 182-1, C 2006, 60 x.
7. Hamoir 182b , C 2007, 120 x.
8. Carr. La Gombe (*velifer*-Z.), C 2008, 120 x.
9. Hamoir 182-1, C 2009, 120 x.
10. Hamoir 194-8, C 2010, 120 x.
11. Hamoir 1002-7, C 2011, 120 x.
12. Hamoir 182 , C 2013, 120 x.
13. Hamoir 808.12, C 2013, 120 x.
14. Hamoir 182.1, C 2014, 120 x.

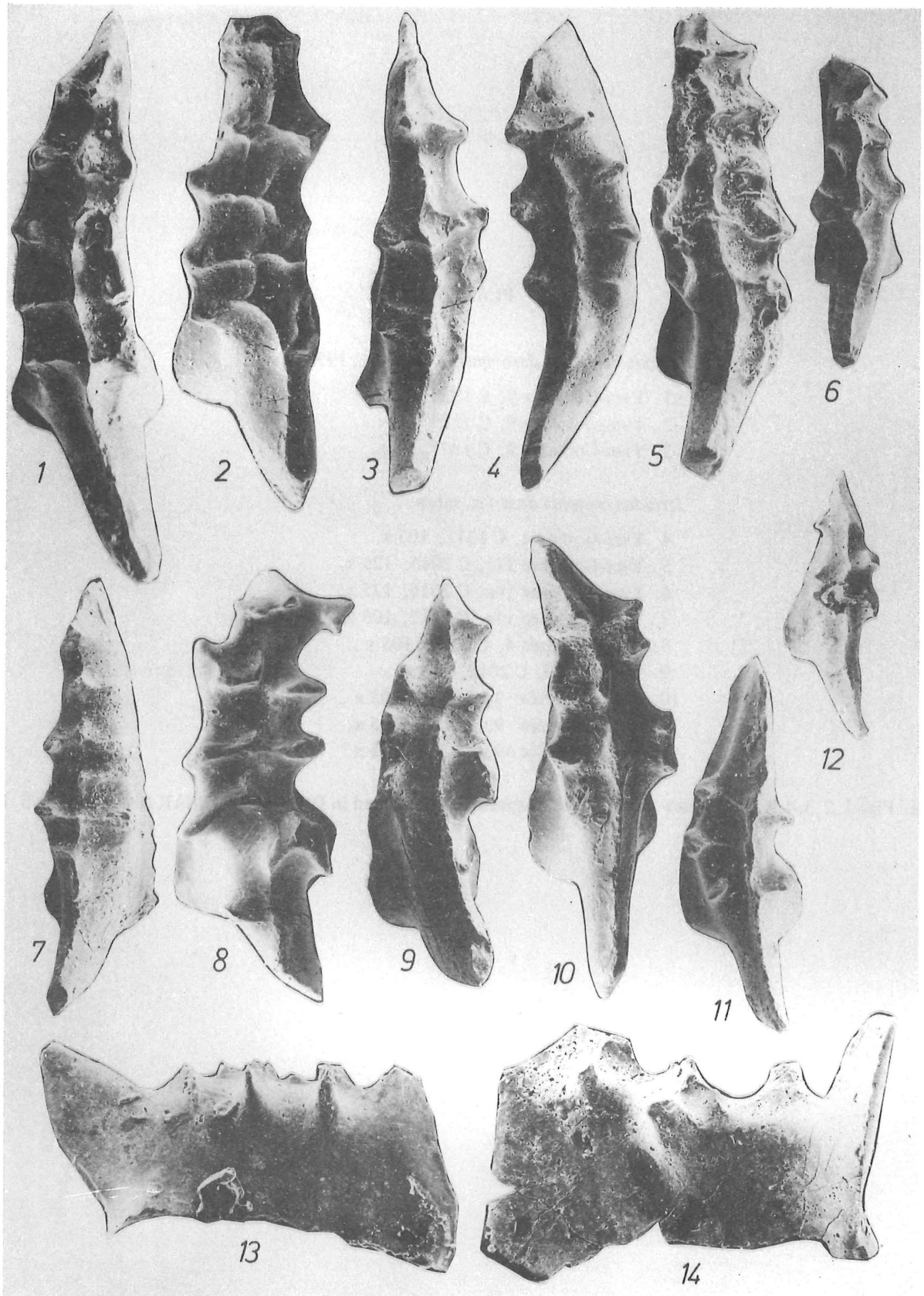
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PLATE VIII

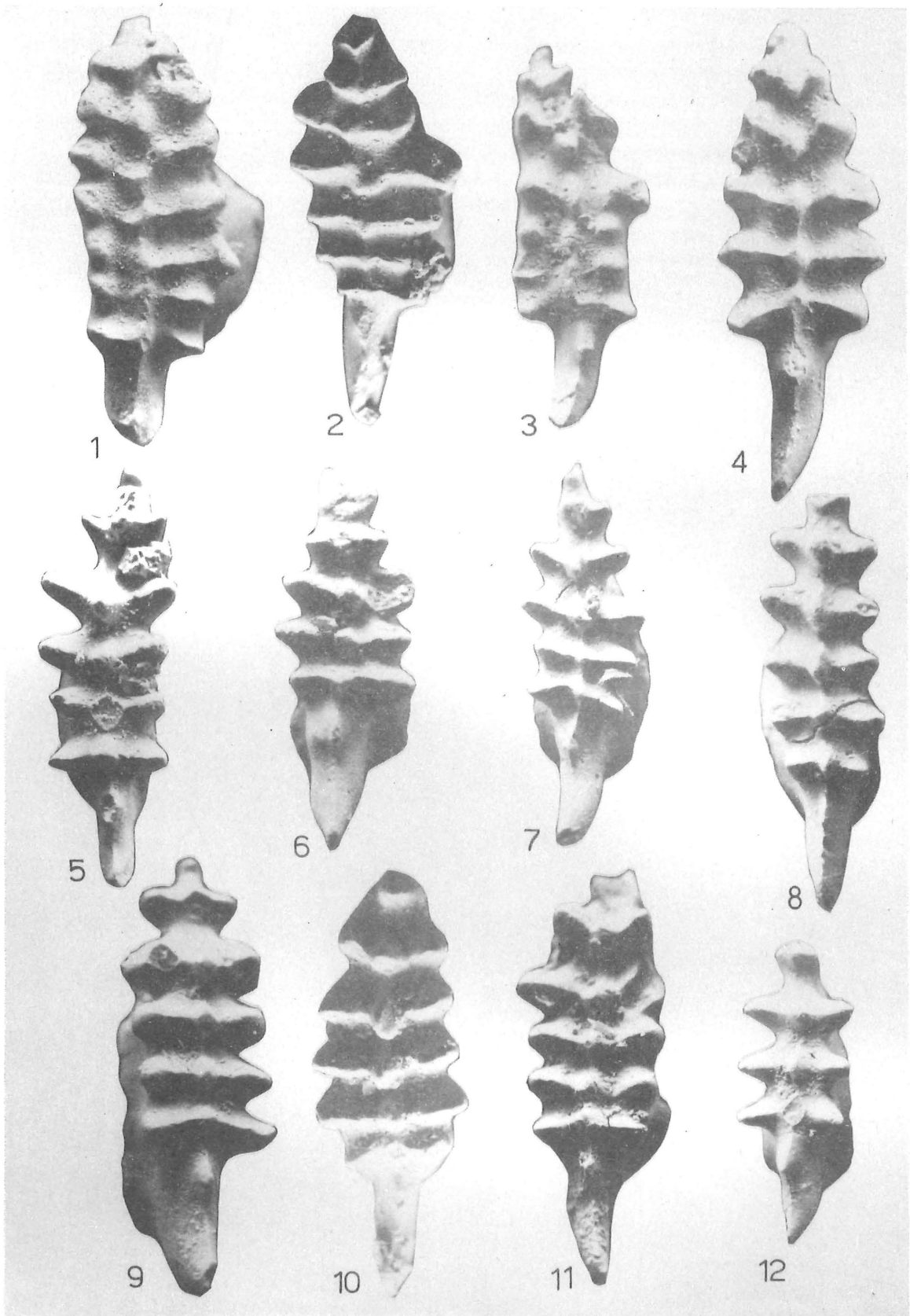
Icriodus costatus darbyensis KLAPPER, 1958

1. Yves-Gomezée 9, C 1323, 75 x.
2. Yves-Gomezée 9, C 1325, 75 x.
3. Yves-Gomezée 9, C 1327, 75 x.

Icriodus costatus dusari n. subsp.

4. Yves-Gomezée, C 1311, 105 x.
5. Yves-Gomezée 14c, C 2015, 125 x.
6. Yves-Gomezée 14a, C 2016, 125 x.
7. Yves-Gomezée 14a, C 2017, 105 x.
8. Yves-Gomezée 4, C 1320, 105 x.
9. Walcourt 10, C 2018, 125 x.
10. Yves-Gomezée 9, C 1319, 105 x.
11. Yves-Gomezée 9, C 2019, 105 x.
12. Yves-Gomezée 10, C 1316, 105 x.

Note : Figs 1,2,3,4,8,10,12 : new photographs of specimens illustrated in DREESEN, DUSAR & GROESSENS, 1975.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