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THE ORIGIN AND EVOLUTION OF THE MIDDLE DINANTIAN CONODONT GENERA *DOLIOGNATHUS*, *DOLLYMAE*, *SCALIOGNATHUS*, AND *STAUROGNATHUS*, AND RELATED FORMS (*)

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(2 figures dans le texte et une planche)

RÉSUMÉ

Le Dinantien moyen se caractérise, en de nombreux endroits de la Terre, par la présence de divers genres de conodonte : *Doliognathus* Branson et Mehl, *Dollymae* Hass, *Scaliognathus* Branson et Mehl, *Staurognathus* Branson et Mehl et *Bactrognathus* Branson et Mehl. L'origine et l'évolution de ces différents genres sont retracées à partir d'exemples provenant du Tournaisien supérieur de la Belgique. De nouvelles faunes provenant de la Carrière Lambert, du Rocher Bayard et du Rocher du Bastion sont citées et figurées. Une comparaison est faite avec d'autres parties du globe.

ABSTRACT

Spathognathodus bultyncki Groessens evolved from *Prioniodina prelaevipostica* Rhodes, Austin, and Druce and gave rise to *Dollymae bouckaerti* Groessens. The genus *Scaliognathus* Branson and Mehl developed from *D. bouckaerti* by closure of the basal cavity. *Doliognathus* Branson and Mehl developed from either *S. bultyncki* or *Scaliognathus*. *Dollymae* sp. A Voges evolved from *Pelekysgnathus* sp. A Voges. The New Genus B of Groessens also evolved from *Pelekysgnathus* sp. A. New Genus B was the forerunner of the genus *Staurognathus* Branson and Mehl. The origin of these distinctive conodonts is shown from examples found in the Tournaisian Tn3c rocks of Belgium. New faunas from the Rocher Bayard and from the section between the quarry Lambert and the Rocher du Bastion are mentioned. The conodont sequence described is compared with those from other areas of the world.

Middle Dinantian rocks in many parts of the world are characterised by the presence of the distinctive conodont genera *Doliognathus* Branson and Mehl, *Dollymae* Hass, *Scaliognathus* Branson and Mehl and *Staurognathus* Branson and Mehl. The genus *Dcliognathus* has been recovered from Belgium (Groessens 1971a, 1971b), Britain (Matthews 1969a), Germany (Voges 1959), North America (Branson and Mehl 1941, Burton 1964, Hass 1959, Thompson 1967, Thompson and Fellows 1969), and Spain (Higgins et al 1964, Marks and Wensink 1970). The genus *Dollymae* was found in Belgium (Groessens 1971a), Germany (Voges 1959), and North America (Hass 1959). *Scaliognathus* is known from Austria (Flügel and Ziegler 1957, Schulze 1968), Belgium (Groessens 1971a, Conil, Lys and Mauvier 1964, Conil et al. 1967, Conil et

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al. 1969), Britain (Matthews 1969a, 1969b, Morris 1969), Czechoslovakia (Zikmundová 1967), France (Pelhate-Peron 1967), Germany (Bischoff 1957, Voges 1959), Ireland (Hill 1971), Italy (Manzoni 1965), North Africa (Remack-Petitot 1960), North America (Branson and Mehl 1941, Burton 1964, Hass 1959, Thompson 1967, Thompson and Fellows 1969), and Spain (Boogaert 1967, Budinger 1965, Higgins et al. 1964, Marks and Wensink 1970). *Staurognathus* is known from Belgium (Conil et al. 1969, Groessens 1971a), and from North America (Branson and Mehl 1941, Hass 1959, Thompson 1967 and Thompson and Fellows 1969).

These characteristic genera appear suddenly, but their phylogeny has never been traced, nor described. Austin (in press) suggested that a form described as *Bactrognathus perplanus* by Mehl and Thomas (1947) could have given rise to these genera. New faunas from Belgium (Groessens (1971a) enable the phylogeny of these genera to be traced and refute the suggestion of Austin.

Prioniodina prelaevipostica Rhodes, Austin, and Druce is typical of the upper Tn3b of Belgium. Transitional stages to the from of the genus *Dollymae* are known from a number of sequences in Belgium (Groessens 1971a). *Prioniodina prelaevipostica* is a small form characterised by a prominent main denticle, a large basal cavity and an anterior and posterior blade. Younger beds in Belgium are characterised by forms which show a reduction in the size and number of denticles on the posterior process. The main denticle increases in size as does the basal cavity. The cavity also extends further towards the anterior extremity of the unit. Eventually, the form *S. bultyncki* Groessens is produced. *S. bultyncki* is similar in lateral view to *Bactrognathus perplanus* Mehl and Thomas and to the genus *Pelekysgnathus* Thomas. The genus *Bactrognathus* is distinguished by the flexed nature of the unit. *S. bultyncki* is caracterised by the presence of a large, posteriorly projecting main denticle at the posterior extremity of the unit and by a single row of nodes on the anterior blade. The basal cavity is also quite large. *S. bultyncki* has been listed as *B. perplanus* by Conil et al. (1969) and by Morris (1969). Futher development sees the formation of lateral projections at the posterior extremity of the unit. The basal cavity extends along the length of the unit and to the termination of the lateral projections. The lateral projections continue to develop until in the most advanced stage (*Dollymae bouckaerti* Groessens) the lateral projections are at least half the length of the anterior process. Later development sees an increase in the complexity of the nodes on the lateral processes. The genus *Scaliognathus* Branson and Mehl probably developed from *D. bouckaerti* by a closing of the basal cavity. Transitional specimens are known. Forms of *S. anchoralis* could also have developed directly from other forms of *Prioniodina*.

The genus *Doliognathus* Branson and Mehl appears to have evolved from *S. bultyncki* by the development of a projection on only one side of the unit. The development of *Doliognathus* took place parallel to the development of *Dollymae*. *Doliognathus* could also have evolved from *Scaliognathus* by the loss of one of the lateral processes.

The similarity in lateral view between *S. bultyncki* and *Bactrognathus perplanus* has been mentioned above. It is suggested that the genus *Bactrognathus* could also have evolved from *S. bultyncki*.

Pelekysgnathus sp. A of Voges is similar in appearance to *S. bultyncki*, but has a double row of nodes on the anterior part of the unit. Illustrations of *Dollymae* sp. A (Voges 1959) show a double row of nodes the anterior platform. It is suggested that *Dollymae* sp. A of Voges evolved from *Pelekysgnathus* sp. A Voges during Tournaisian Tn3c *Dollymae* sp. A in turn giving rise to *Dollymae hassi* Voges.

New Genus B of Groessens could also have evolved from *Pelekysgnathus* sp. A. This form which appears in rocks of Tournaisian Tn3c age was the forerunner of *Staurognathus* Branson and Mehl. The latter developed by the formation of lateral processes, in a manner similar to the development of *Scaliognathus* from *S. bultyncki*.

This new interpretation of the evolution of the distinctive Middle Dinantian conodonts (Text-fig. 1) has led to a review of the existing knowledge of the Middle

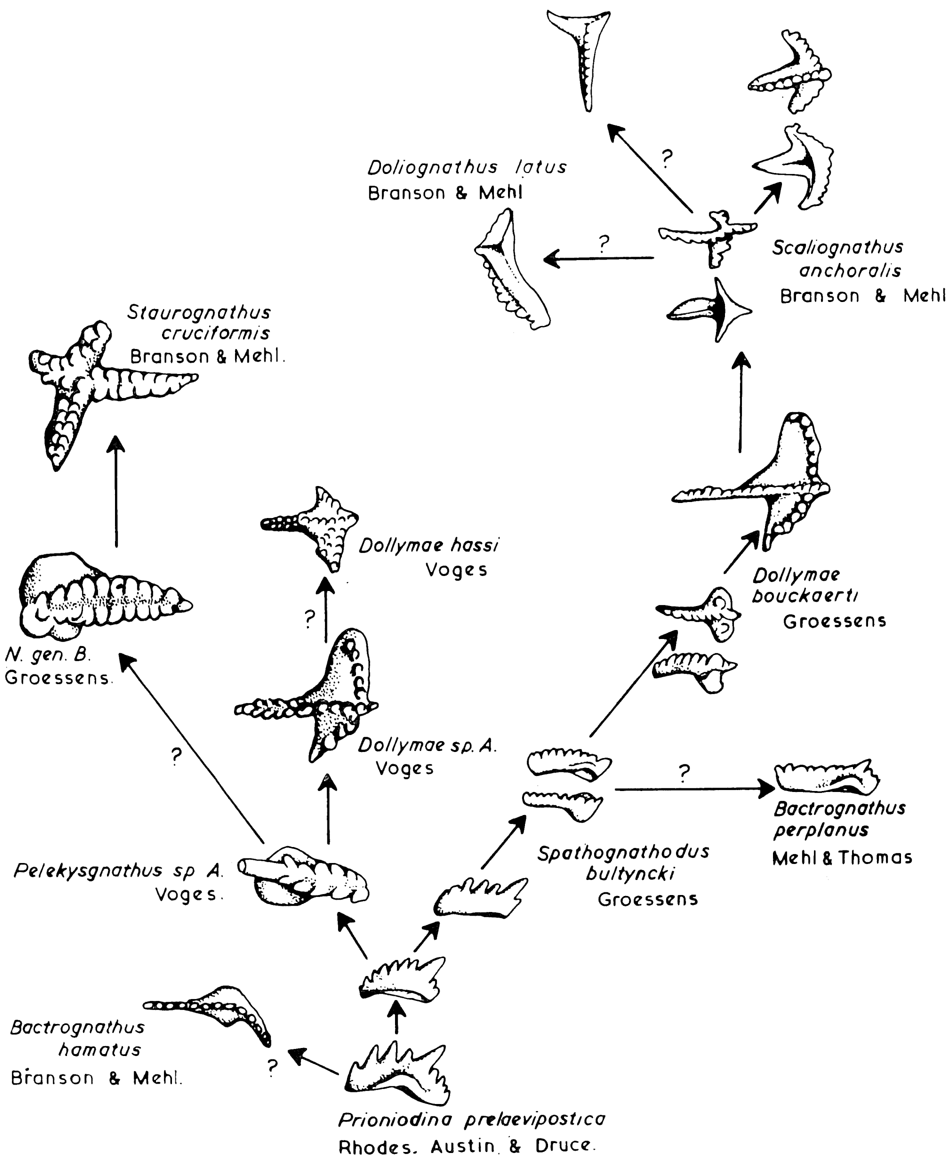

Fig. 1. — Chart to show the origin and evolution of the Middle Dinantian conodont genera *Doliognathus*, *Dollymae*, *Scaliognathus*, and *Staurognathus*, and related forms.

Dinantian and in particular Upper Tournaisian conodont faunas of Belgium and the stratigraphy of the rocks which contain them (Groessens 1971a).

Groessens (1971a log 3) indicated that *S. bultyncki* appeared in the Tn3b stratotype section of the Carrière Scouffleny in the top part of $Tn3c_1$. It therefore appears higher stratigraphically in the section than *Pericyclus princeps* and *Muensteroceras complanatum* (see Conil et al. 1971, chart facing p. 18). *P. princeps* and *M. complanatum* in their type areas are older than *Scaliognathus anchoralis*.

Conil et al. (1969) listed conodonts from three sections. Two of these sections Dinant 9 (Old Lime Kiln quarry, South of the bend on the road to Ciney) and Dinant 5 (site of the Rocher Bayard at Dinant) contained *S. bultyncki* (*B. perplanus* of the 1969 paper). The upper part of the Old Lime Kiln Quarry section (Dinant 9) is better correlated with the Tn3c rather than with the upper part of the Tn3a (Conil et al. 1969 Table 1).

The rocks of the Rocher Bayard (Dinant 5 section) have been processed and prolific faunas have been recovered. The following species are present.

Dollymae bouckaerti Groessens
Gnathodus antetexanus Rexroad and Scott
Gnathodus delicatus Branson and Mehl
Gnathodus punctatus (Cooper)
Polygnathus communis carinus Hass
Pseudopolygnathus longiposticus (Brason and Mehl)
Pseudopolygnathus triangulus pinnatus Voges
Scaliognathus anchoralis Branson and Mehl
New Genus B Groessens

This fauna correlates with level 100/0 of the Route de Salet section (Groessens 1971a p. 10, 11 and log 6). Section Dinant 37 (at Dinant, St. Paul Suburb, Lambert Quarry and Bastion rock) is a stratotype for the V1a and the presence of *S. anchoralis* and *Hindeodella segaformis* Bischoff in bed 37/202 (Conil et al 1960 Table 1) represents an anomaly, as elsewhere in Belgium at Salet, Walcourt, Modave and Freyr (Text-fig. 2) these species have been found in rocks of Tn3c age. The section Dinant 37 has been reprocessed and bed 202 did not yield the association *S. anchoralis* and *H. segaformis*. These forms however, were recorded from bed 37/122 in the section (see also Groessen's 1971a log 8). This suggests that the record of *S. anchoralis* and *H. segaformis* in bed 202 (Conil et al. 1969) was either an example of reworking, because at this level in the section there are small reworked fragments of limestone of reef facies, or as suggested by Groessens (1971a p. 13) the sample was contaminated during preparation.

Comparison with other regions

Spathognathodus bultyncki occurs in the C_1 beds of the Castletown district of Ireland (Chabot 1971 oral communication). Hill (1971 oral communication) has found *Dollymae bouckaerti* in the lower part of the Waulsortian bank complex in County Limerick, Ireland, in beds which Shephard-Thorn (1963) assigned to the C_1 sub-zone. *Scaliognathus anchoralis* was also reported by Hill (1971) from the lower part of the reef in County Limerick. Morris (1969) reported the presence of *S. bultyncki* (*B. perplanus*) from the Weaver beds of the South Pennines. *Scaliognathus anchoralis* also occurred at the same horizon. Thus the reef of County Limerick and part of the Weaver beds of the South Pennines are of Tournaisian age.

Matthews (1969) reported *Scaliognathus* and *Doliognathus* from the Viverdon Chert Formation of Cornwall. It is not possible to determine the precise age of this fauna because the fauna is reworked, as evidenced by the presence of *Siphonodella* (Branson and Mehl), which is no younger than basal Tn3a in Belgium and of *Palmatolepis* Ulrich and Bassler, which is a Devonian genus.

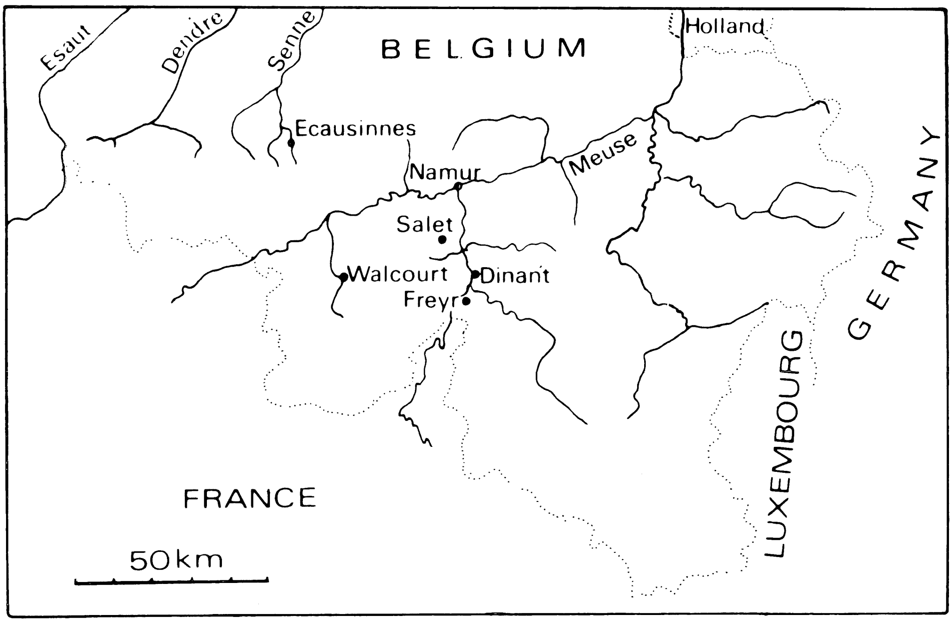

Fig. 2. — Locality Map.

Prioniodina prelaevipostica is a characteristic species of the Avonian Z_2 subzone in Britain. The overlying Laminosa Dolomite yields few conodonts (Rhodes, Austin and Druce 1969). The presence of the gnus *Mestognathus* Bischoff in the upper part of the Laminosa Dolomite suggests, that the *anchoralis* Zone should occur in the lower part of the Laminosa Dolomite as it occurs immediately below the first appearance of *Mestognathus* in Belgium. *Mestognathus* in Belguim first appears at the base of the Viséan. The presence of *Mestognathus* in the Upper part of the Laminosa Dolomite of the Avon Gorge suggests that the upper part of the Laminosa Dolomite is of Viséan age.

In Germany, Bischoff (1957) recorded *Scaliognathus* and Voges (1959) recorded *Scaliognathus, Doliognathus* and *Dollymae.* Voges noted that *Dollymae* first appeared in the German sequence after the first appearance of *Scaliognathus.* This conflicts with the evidence from Belgium. Care has to be taken with these German faunas as reworking is common (Krebs 1963).

In Spain, Higgins et al (1964) and Marks and Wensink (1970) noted the presence of *Scaliognathus* and *Doliognathus* in their faunas. The genus *Doliognathus* was, however, lacking from the faunas described by Boogaert (1967) and Budinger (1965). The genus *Dollymae* has not been recorded from Spain. Only the genus *Scaliognathus* has been recorded from Austria, Czechoslovakia, France, Italy and North Africa. None of the genera *Doliognathus Dollymae, Scaliognathus* and *Staurognathus* have been found to date in Australia or Asia.

PLATE 1

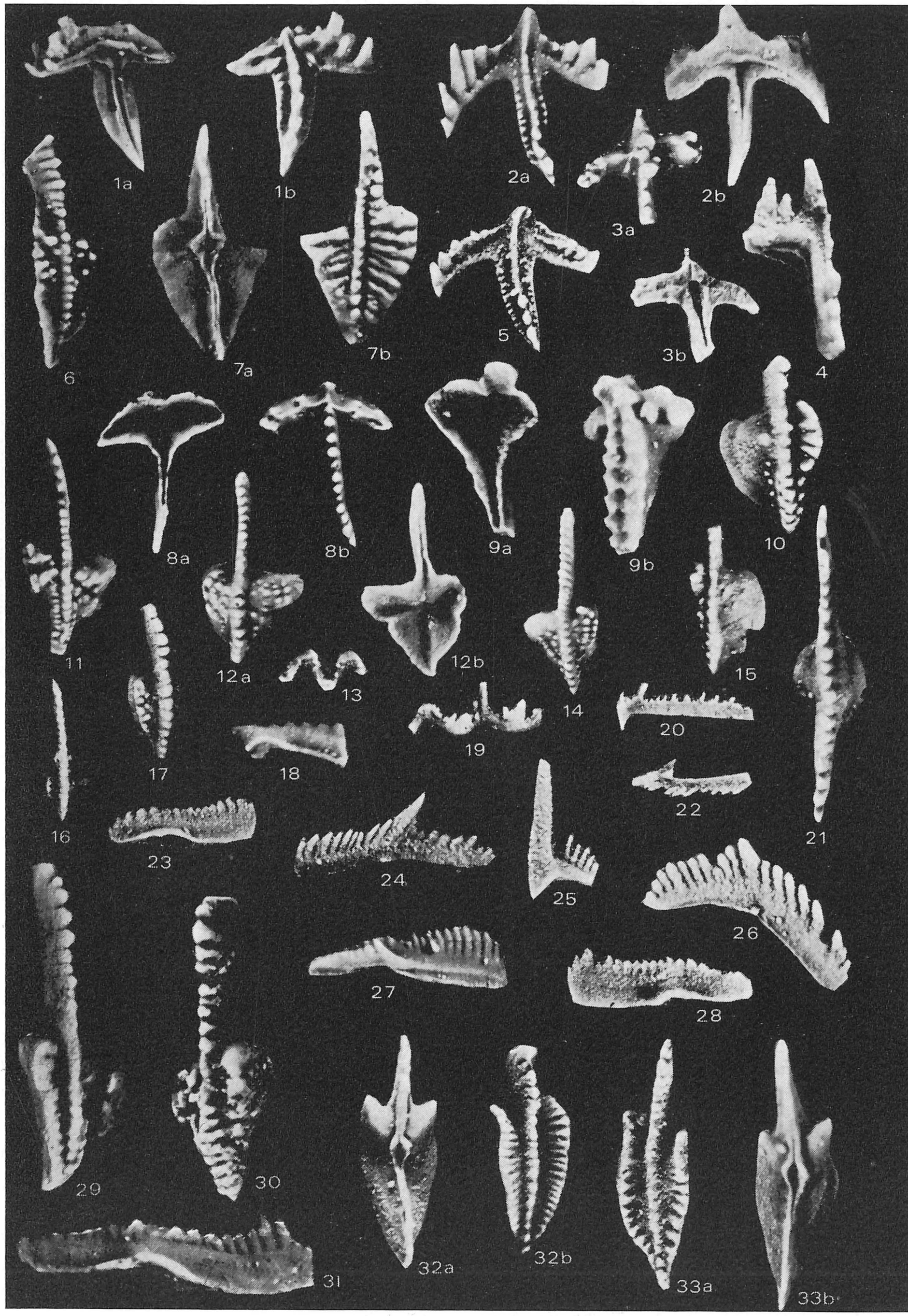
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PLATE 1

(all magnifications × 30)

Figs. 1a, b. — *Scaliognathus anchoralis* Branson and Mehl. 1a Aboral view. 1b Oral view specimen 5/3145/31. Rocher Bayard Bed 45.

Figs. 2a, b. — *Scaliognathus anchoralis* Branson and Mehl. 2b Aboral view, specimen 37/122/30, Dinant 37, Bed 122.

Figs. 3a, b. — *Dollymae bouckaerti* Groessens — *Scaliognathus anchoralis* Branson and Mehl transition. 3a Oral view. 3b aboral view Specimen 5/45/32. Rocher Bayard Bed 45.

Fig. 4. — *Prioniodina* sp. Oral view Specimen M/10/30. Modave 10 Bed 18.

Fig. 5. — *Scaliognathus anchoralis* Branson and Mehl. Oral view Specimen 100/30 45/30. Route de Salet Bed 45.

Fig. 6. — *Polygnathus communis carinus* Hass. Oral view Specimen 5/46/1. Rocher Bayard Bed 46.

Figs. 7a, b. — *Pseudopolygnathus triangulus pinnatus* Voges. 7a Aboral View. 7b Oral vieuw specimen 5/45/33. Rocher Bayard Bed 45.

Figs. 8a, b. — *Dollymae bouckaerti* Groessens. 8a Aboral View. 8b Oral view specimen 5/45/34. Rocgher Bayard Bed 45.

Figs. 9a, b. — New genus B Groessens — *Staurognathus* Branson and transition. 9a Aboral View. 9b Oral view specimen 5/45/35. Rocher Bayard Bed 45.

Fig. 10. — *Gnathodus semiglaber* Bischoff. Oral view specimen 100/181/1. Route de Salet Beds 181-196.

Fig. 11. — *Gnathodus punctatus* (Cooper) Oral view specimen 5/45/36. Rocher Bayard Bed 45.

Figs. 12a, b. — *Gnathodus delicatus* Branson and Mehl. 12a Oral view. 12b Abora) view specimen 5/45/37. Rocher Bayard Bed 45.

Fig. 13. — *Hindeodella segaformis* Bischoff. Oral view Specimen 37/122/30. Dinant 37. Bed 122.

Fig. 14. — *Gnathodus delicatus* Branson and Mehl. Oral view specimen 5/45/38. Rocher Bayard Bed 45.

Fig. 15. — *Gnathodus semiglaber* Bischoff. Oral view specimen 100/181/2. Route de Salet Beds 181-196.

Fig. 16. — *Gnathodus antetexanus* Rexroad and Scott. Oral view specimen 100/45/40. Route de Salet Bed 45.

Fig. 17. — *Gnathodus symmutatus homopunctatus* (Ziegler). Oral view specimen 100/181/3. Route de Salet Beds 181-196.

Fig. 18. — *Spathognathodus bultyncki* Groessens. Lateral view specimen 5/46/2. Rocher Bayard Bed 46.

Fig. 19. — *Hindeodella segaformis* Bischoff. Lateral view specimen 100/45/41. Route de Salet Bed 45.

Fig. 20. — *Hindeodella subtilis* Ulrich and Bassler. Lateral view specimen 100/45/42. Route de Salet Bed 45.

Figs. 21, 31. — *Spathognathodus crassidentatus* (Branson and Mehl). 21. Oral view. 31. Lateral view specimen 100/45/43. Route de Salet Bed 45.

Fig. 22. — *Neoprioniodus* sp. Lateral view specimen 100/45/44.Route de Salet Bed 45.

Fig. 23. — *Spathognathodus pulcher* Branson and Mehl. Lateral view specimen 100/45/45. Route de Salet Bed 45.

Fig. 24. — *Ozarkodina* cf *delicatula* (Stauffer and Plummer). Lateral view specimen 100/45/46. Route de Salet B3d 45.

Fig. 25. — *Neoprioniodus barbatus* (Branson and Mehl). Lateral view specimen 100/45/47. Route de Salet Bed 45.

Fig. 26. — *Ozarkodina macra* Branson and Mehl. Lateral view specimen 100/45/48. Route de Salet Bed 45.

Fig. 27. — *Polygnathus communis* Branson and Mehl. Lateral view specimen 5/45/39. Rocher Bayard Bed 45.

Fig. 28. — *Spathognathodus pulcher* Branson and Mehl. Lateral view specimen 100/45/49. Route de Salet Bed 45.

Fig. 29. — *Gnathodus semiglaber* Bischoff. Oral view specimen 100/181/8. Route de Salet Beds 181-196.

Fig. 30. — *Gnathodus semiglaber* Bischoff. Oral view specimen 100/181/9. Route de Salet Beds 181-196.

Figs. 32a, b. — *Polygnathus inornatus* Branson and Mehl. 32a Aboral view. 32b Oral view specimen 100/181/10. Route de Salet Beds 181-196.

Figs. 33a, b. — *Pseudopolygnathus longiposticus* Branson and Mehl. 33a Oral view. 33b Aboral view specimen 100/181/11. Route de Salet Bed 45.

Hass (1959) reported the genera *Dollymae* and *Bactrognathus* from the *Gnathodus punctatus* Zone of the Chappel Limestone and the genera *Bactrognathus, Doliognathus, Scaliognathus* and *Staurognathus* from the overlying *Bactrognathus communis* Zone at the top of the Chappel Limestone. Thus in Texas the order of appearance of *Dollymae* and *Scaliognathus* is the same as that in Belgium.

Dollymae has not been reported to date from other areas in North America. This genus is stratigraphically restricted in Belgium and it may be that more detailed sampling in other regions of North America will lead to the discovery of *Dollymae*. However, many areas have already been subjected to detailed sampling and the genus has still not been found. *Dollymae* may be absent from these areas because of local discontinuities.

Bactrognathus is present in Missouri in the Fern Glen Limestone of earliest Osage age (Mehl and Thomas 1947), Branson and Mehl (1941) stated that *Doliognathus, Scaliognathus* and the first of the typical bactrognathids appear in southwestern Missouri in a thin shale, which overlies the Fern Glen Limestone and is the local representative of the Pierson Limestone. Branson and Mehl (1941) also reported specimens of *Bactrognathus, Doliognathus* and *Staurognathus* from the basal beds of the so-called Sycamore Limestone of Pontotoc County, Oklahoma. Cooper (1948) reported the presence of *Bactrognathus, Doliognathus* and *Staurognathus* in the limy shale that overlies the Welden Limestone in Oklahoma. Cooper (1938) also found *Bactrognathus* and *Doliognathus* in the shale above the Rockford Limestone in Indiana. Burton (1964) reported the following sequence of appearances from the Lake Valley Formation of New Mexico : — first *Bactrognathus*, then *Doliognathus* and *Staurognathus* together, followed by *Scaliognathus*.

Thompson (1967) studied the Lower Osagean rocks of southwestern Missouri. He found *Doliognathus* from the middle of the *Bactrognathus-Pseudopolygnathus multistriatus* assemblage zone into the *Bactrognathus distortus — Gnathodus cuneiformis* assemblage zone. The genus *Staurognathus* was confined to the upper part of the *Pseudopolygnathus multistriatus* subzone of the *Bactrognathus — P. multistriatus* assemblage zone. *Scaliognathus* ranged in southwestern Missouri through the *Doliognathus latus* subzone of the *Bactrognathus — Pseudopolygnathus multistriatus* assemblage zone and the *Bactrognathus distortus* subzone of the *B. distortus-Gnathodus cuneiformis* assemblage zone. Thompson and Fellows (1969) who redefined the base of the Osagean to coincide with the first appearance of *Polygnathus communis carinus* Hass, restated the distribution of the genera *Doliognathus, Scaliognathus* and *Staurognathus* in southwestern Missouri and adjacent areas.

CONCLUSION

Documentation of the evolution of characteristic Middle Dinantian genera as outlined in this paper refines the stratigraphy of Tournaisian rocks in Belgium. It also aids correlation of rocks present in other areas of the world with the Belgian stratotypes. The conodont fauna recovered from the Rocher Bayard listed, and illustrated in the accompanying plate confirms that this reference section is younger than was previously thought.

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