A C T A P A L A E O N T O L O G I C A P O L O N I C A
Vol. 25 1980 No. 3—3

HSIEN HO TSIEN

ECOLOGY, EVOLUTION, DISTRIBUTION AND POPULATION OF *HEXAGONARIA* IN WESTERN EUROPE

TSIEN, H. H.: Ecology, evolution, distribution and population of *Hexagonaria* in Western Europe. Acta Palaeont. Polonica, 25, 3/4, 633—644, January 1981.

The record of *Hexagonaria* in the Lower and Middle Devonian shows that only slow rates of change occurred at these times, whereas in Frasnian time there occurred complex diversity and speciation patterns. Very rapid faunal changes and mass extinctions in corals have been observed near the boundary of Middle Devonian and Upper Devonian and at the end of *Fr 1* time. Based on the study of population variation, ecological variation and phylogenetic lineage, the complete evolutionary patterns of *Hexagonaria* can be traced in the Givetian and Frasnian. The evolutionary patterns observed in different facies demonstrate that: 1. most changes in diversity and speciation were strictly related to differences in the biology of species adapted to different or changing environments, 2. the critical factors in encouraging diversification of species appear to be a combination of ecologic conditions and paleogeographic situations, 3. some parallel evolutions were independent of environments and paleogeographic isolation but were due to time.

Key words: corals, Rugosa, evolution, population variation, ecological variation, Upper Devonian, Europe.

Hsien Ho Tsien, Laboratoire de Paléontologie, Université Catholique de Louvain, 3 Place Louis Pasteur, B-1348 Louvain-la-Neuve, Belgium. *Received: September 1979.*

INTRODUCTION

There is little agreement among coral specialists on the definition of genera. For example, *Hexagonaria lecomptei* Tsien, 1977 is assigned to *Argutastrea* by Coen-Aubert (Coen-Aubert and Lacroix, 1979). This lack of agreement is mainly due to misidentification based on only a few coral specimens sent by other geologists or found in museum collections, without analysis of population variation, ecological variation and phylogenetic lineage. The Middle Devonian and Frasnian sedimentary basin of Belgium is a small, complex but complete sedimentary basin which contains a highly fossiliferous complex of carbonates and shales. The basin is small enough for the lateral and vertical distribution of rugose corals to be easily studied. It is also so geologically complex (containing a wide spectrum of rock types) and continuous, that ecological variations and evolutionary stages of *Hexagonaria* can be shown in detail. *Hexagonaria* is very abundant both in reef complexes of basinal facies and in reef complexes of stable platform facies. Indeed it occurs almost throughout the rock sequence in a continuous succession. Aided by some supplementary information from FRG, northern and western France, Pyrénées and Spain, *Hexagonaria* of western Europe provides a most satisfactory example of lineage studies. Therefore, some of the disagreements on generic concepts will probably vanish gradually.

This paper also represents an attempt to gain some insight into evolution through the study of *Hexagonaria* Gürich, 1896 in Western Europe.

STRATIGRAPHY

Mailleux's stratigraphic scheme (Mailleux et Demanet 1929) is a traditional European system which differes from those of other countries; the units of this system are defined indistinctly: sometimes, they are lithostratigraphic, sometimes biostratigraphic, but their designation is chronostratigraphic (Tsien 1972, 1977*a*). Besides, this stratigraphic scheme is not suitable for coral facies and reef phenomena. As an example, the *F 2h, F 2i, F 2j,* and *F 3* do not fit coral facies and zones and reef phenomena; coral facies and zonation and reef problems become very confused and difficult. The corals from the *F 2h* and lower part of the *F 2i* are entirely different from those of the upper part of the *F 2i* and *F 2j*; corals and reefs are well developed in the *F 3* of the Philippeville region. Therefore new informal chronozones are here proposed (fig. 1). Figure 1 shows also the stratigraphic correlation of the Devonian sequence in Belgium with other localities in the FRG and USA and the coral-bearing facies and the relationships among the different sedimentary facies.

Eifelian is not a synonym of Couvinian, because the lower boundary of the Couvinian is not the same as the lower boundary of the Eifelian. The lower boundary of the Couvinian is at the base of the Bure Formation which corresponds very closely to the lower boundary of the *patulus* Zone (Weddige 1977).

PALEOECOLOGY OF *HEXAGONARIA*

Hexagonaria is particularly sensitive to environmental conditions. Its pattern of distribution parallels that of the rock facies (Tsien 1977*a*: fig. 2) and such characteristics as shape, form of the calice, presence or lack of a calicular platform, presence or lack of a calicular boss between dissepimentarium and tabularium, etc. are strongly influenced by the environ-

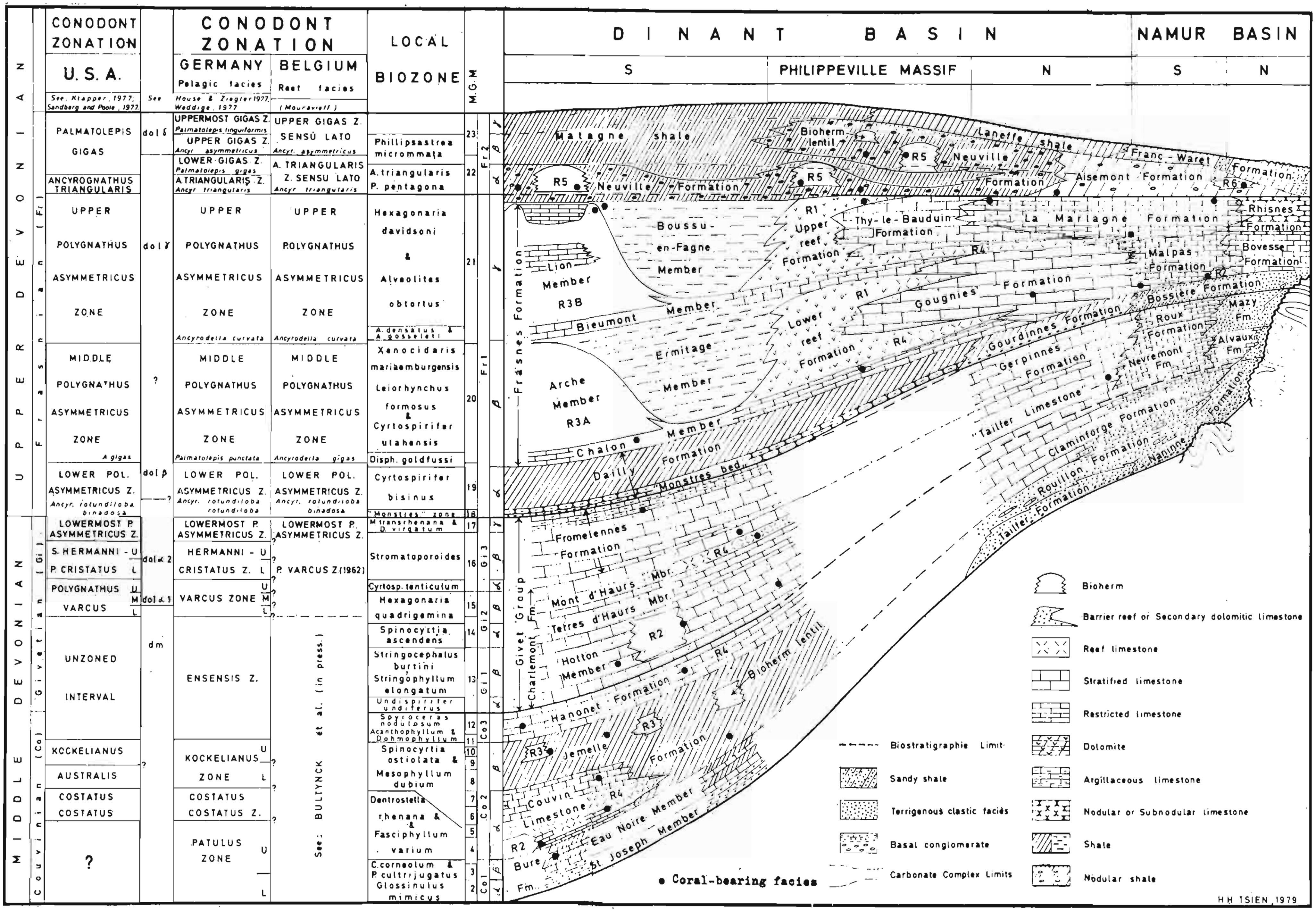

Fig. 1. Relationships of the different sedimentary facies and the stratigraphic correlation of Devonian sequence in Belgium with other localities in FRG and the USA.

Table 1. The different coral assemblages in different facies and in different ages.

		MOBILE PLATFORM CONDITION (Basinal Condition)		Shelf Margin Reef Facies	STABLE PLATFORM CONDITION				
		Biohermal Complex Facies			Open Sea Platform Carbonate Facies			Restricted Platform Carbonate Facies	
	MGM	Reef Facies	Peri-reef Facies	Barrier Reef	Assemblage 1	Assemblage 2	Assemblage 3	Assemblage 1	Assemblage 2
Fr2	22								
Frlγ	21	*H. hexagona* *H. davidsoni* *H. mae* *H. buxutiensis* *H. gamboni* *H. marmini* + numerous other organisms	*H. davidsoni* *H. mae* *H. buxutiensis* *H. gamboni* + numerous other organisms	*H. davidsoni* *H. mae* *H. hexagona*	*H. davidsoni* *H. fewata* new gen.	*H. hexagona* *H. marmini* *H. lecomptei*	*H. hexagona* *H. bracobanda*	*H. lecomptei* *H. fewata*	*H. marmini* *H. hexagona*
		H. hexagona *H. davidsoni* *H. marmini*		*H. davidsoni* *H. marmini*	*H. davidsoni* *H. marmini*				*H. hexagona*
Frlβ	20	*H. hexagona* *H. marmini* *H. davidsoni*			*H. hexagona* *H. davidsoni* *H. marmini*				*H. hexagona*
Frlα	19 18								

ment. In general, *Hexagonaria* has a thin disk-like form, with a large flat calicular platform, in open marine, shallow water conditions. It has a globular colony shape, with a relatively deep calicular pit with a pronounced rim around it and a large calicular platform, in the reef facies. *Hexagonaria* species, generally with thick disk-like form and/or with globular colony shape, have also a flat calicular platform but a rather deep calicular pit in open marine deeper or calm conditions. In the restricted facies they have a deep funnel-shaped calice (Tsien 1974). *Hexagonaria davidsoni* (Edwards et Haime, 1851), *H. hexagona* (Goldfuss, 1826) and *H. lecomptei* show different external forms and calices in the different facies (fig. 2). Sometimes, the same colony shows a shallow calicular pit with flat calicular platform on one side and a deep calicular pit with funnel-shaped calice on the other side. It appears that the side with the shallow calicular pit was facing against the current and the side with deep calicular pit was sheltered by the calm conditions. The arrangement of dissepiments in longitudinal section and the trabecular angles are determined by the calicular forms and consequently determined by the ecological conditions. The external forms are more variable in the basinal condition and more constant in the stable platform conditions.

CORAL-BEARING FACIES

Fig. 1 (and Tsien 1977*a*: fig. 2) shows the coral-bearing formations in the Dinant and Namur basins. The facies variation and distribution patterns are quite different in the stable phases (tectonically calm periods) and in the transgressive phases. The different major facies and minor facies or beds have been briefly summarized by Tsien (1977*b*, 1977*c*, 1979). Based on the lithic faunal associations, several types of rugose coral facies with different *Hexagonaria* assemblages in different ages in the Frasnian can be recognized in the Dinant and Namur basins (table 1). Only two types of *Hexagonaria* facies, open marine platform carbonate facies and restricted marine platform carbonate facies, can be recognized in the Givetian of Belgium.

1. Open marine shale facies.

The small individual corals, *Metriophyllum* and *Nalivkinella,* are typical of the deeper part of the open shelf or of the basin.

2. Mobile platform conditions (basinal condition).

A. Reef facies.

Association of globular *Hexagonaria, Tabulophyllum,* massive and lamellar stromatoporoids, *Thamnopora* and *Stachiodes* is found in the pure limestone facies with high habitat diversity; organisms are numerous in species as well as individuals. In this case, globular *Hexagonaria* indicates shallow, agitated conditions.

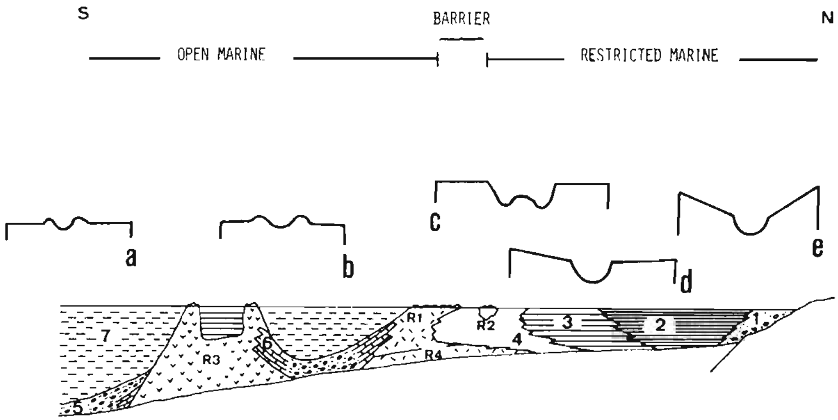

Fig. 2. Different calices in the different facies: *a* peri-reef facies, *b* reef facies, *c* open marine platform carbonate facies, *d* open marine platform, deeper water condition, *e* restricted marine platform carbonate facies.

B. Peri-reef facies.

Argillaceous limestones and nodular shales with tabular *Hexagonaria*, lamellar or dendroid *Alveolites*, flat *Atrypa* and *Gypidula.* In this case, *Hexagonaria* has a large calicular platform which seems to indicate open marine conditions.

3. Barrier reef facies.

Coarsely crystalline dolomite facies are generally interpreted as barrier reefs (Tsien 1977*b*). *Hexagonaria* associations have been found in the lower part and uppermost part of the reef facies.

4. Stable platform carbonate facies.

A. Open marine platform carbonate facies.

Argillaceous limestone facies with rather simple habitat structure. Organisms are numerous as individuals but belong to few species. Three assemblages have been found (table 1). *Hexagonaria,* generally with globular colony shapes, has relatively deep calices.

B. Restricted marine platform carbonate facies.

Hexagonaria has a deep funnel-shaped calice. Rugose corals are generally ecologically restricted, therefore they are usually thought to have no great biostratigraphic value. This, however, is not true. The evolution of the Givetian and Frasnian rugose corals was very rapid, so that they can provide useful coral zonations from Couvinian to Upper Frasnian in Belgium and northern France. Tsien (1977*a*: table 2) showed the coral inventory presently recognized in the Middle Devonian and Frasnian of Belgium. 69 Frasnian species and 56 Givetian species have been found; but only 66 Frasnian species and 36 Givetian species which are modified from table 1 of Tsien (1968) are listed in the table. One new genus and 3 new species mentioned in this paper are described by Groessens and

Tsien (1980). The rugose coral fauna of the Frasnian beds differs radically from that of the Givetian. *Hexagonaria, Disphyllum,* and *Phacellophyllum* are common in the Givetian and Frasnian; but the Givetian forms are different from that of the Frasnian.

EVOLUTION OF *HEXAGONARIA*

European *Hexagonaria* as a whole first appeared in the early Devonian rocks of the Armorican Massif of western France (Barrois 1889). Three species have been found in this region from the Siegenian and Emsian

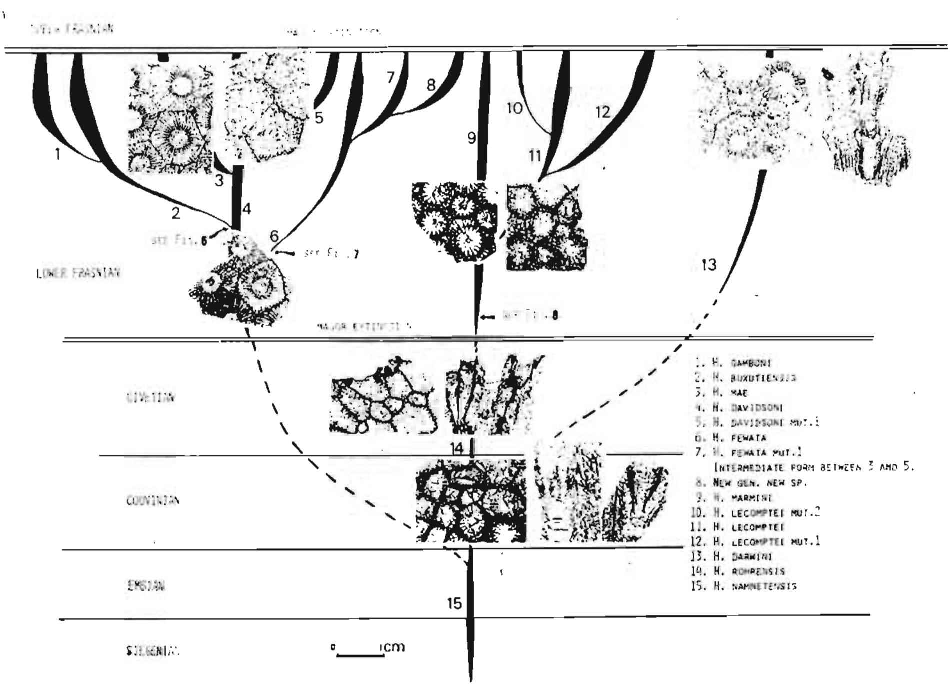

Fig. 3. The evolution of *Hexagonaria namnetensis* group.

rocks. They are described by Sorauf (1969). *Hexagonaria namnetensis* and *H. venetensis* appear related to *H. davidsoni* and *H. quadrigemina* lineages respectively (fig. 3 and fig. 4). *H.* cf. *longiseptata* is very close to *H. longiseptata.* The record of *Hexagonaria* in the Lower and Middle Devonian shows that only slow rates of change occurred at these times, whereas in Frasnian time complex diversity and speciation patterns occurred. Very rapidal faunal changes and mass extinctions in corals have been observed near the boundary of Middle Devonian and Upper Devonian and at the end of *Fr 1* time. One Couvinian species and six Givetian species have been described from the Middle Devonian of Belgium (Tsien 1977*a*: table 2). Only two coral facies, open marine and restricted marine plat-

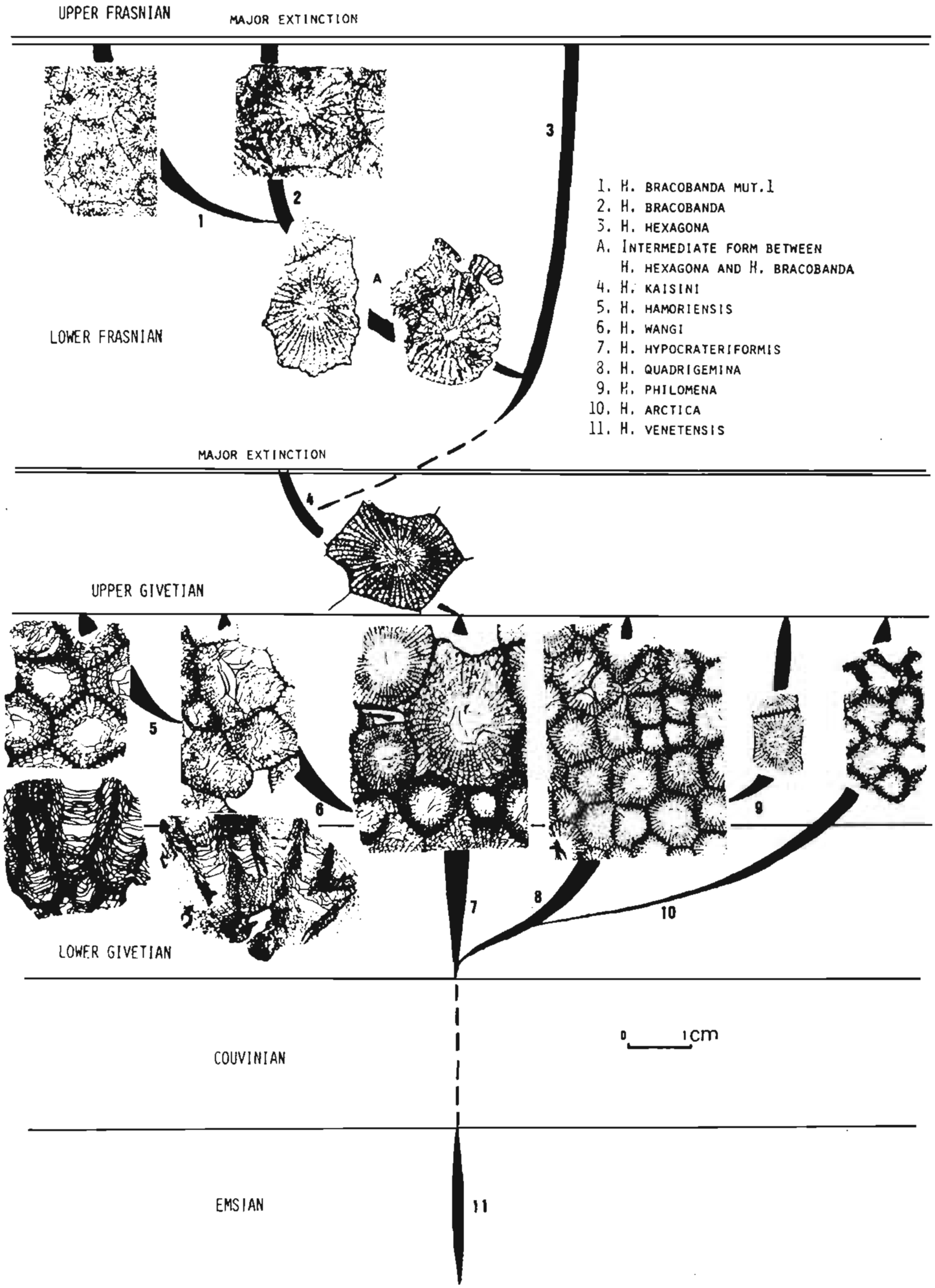

Fig. 4. The evolution of *Hexagonaria venetensis* group.

form carbonate facies, have been found in the Givetian. The study of population variation, ecological variation and phylogenetic lineage shows that most *Hexagonaria* species appear related to the *H. hypocrateriformis* — *H. quadrigemina* groups. During Early Frasnian time, the rate of subsidence in the southern part of the Dinant Basin was different from that of its northern flank. Whereas the southern area was a subsiding basin, the northern area was a relatively stable shelf. Very complex reef formations with high habitat diversity were developed in the subsiding basin contemporaneously with the formation of carbonate complexes on the relatively stable shelf.

In basinal conditions with high habitat diversity, the corals are numerous in species as well as individuals, while in the stable environment of the stable platform conditions, the corals are numerous as individuals but belong to few species. The geologic distribution of rugose corals of western Europe has been summarized in various publications (Sorauf 1967; 1969; Thien 1968, 1977*a*, 1977*b*; Joseph and Tsien 1975, 1977*b*; Brice *et al.* 1977; Scrutton 1968; Glinski 1955; Birenheide 1969).

Figures 3—7 summarize the evolutionary pattern of *Hexagonaria* during Devonian time. The sampling is complete and multiple in six *Hexagonaria* assemblages of the eight facies in the *Gi 2* and *Fr 1* periods. But gaps in sampling due to the discontinuous nature of the fossil record exist in *Co 2, Gi 1, Gi 3, Fr 1α* and *Fr 1β* periods. This difficulty is lessened by the rather simple speciation and diversity in *Co 2, Gi 1, Gi 3, Fr 1α* and *Fr 1β* times. Therefore, the complete evolutionary patterns and variations in the structure of the coral skeleton from youth to maturity can be easily traced and studied in the two and four different *Hexagonaria* assemblages of *Gi2* and *Fr 1* times. Intermediate forms have been found in each lineage.

1. Mobile platform conditions (basinal conditions).

Facies 1 (Reef facies).

This facies is a pure limestone facies with high habitat diversity. Fig. 5 summarizes the evolutionary pattern of *Hexagonaria* in the bioherm complexes under basinal conditions from the beginning of *Fr 1* time to the mass extinction at the end of *Fr 1* time. Six species of *Hexagonaria* have been found in this facies along with numerous other organisms. Only three of the species have been found in the lower part of the *Fr 1* zone. *H. mae* Tsien, 1977 (large calice with long minor septa) and *H. buxutiensis* Tsien, 1977 (small calice with short minor septa) are clearly derived from *H. davidsoni* (Edwards et Haime, 1851) (large calice with short minor septa). *H. gamboni* Tsien, 1977 (small calice with long minor septa) is derived from *H. buxutiensis*. *H. davidsoni* — *M. mae* and *H. buxutiensis* — *H. gamboni* lineages show parallel evolutionary changes.

Both *H. mae* and *H. gamboni* show large peripheral dissepiments and the degeneration of septa in the peripheral part at the end of *Fr 1* time.

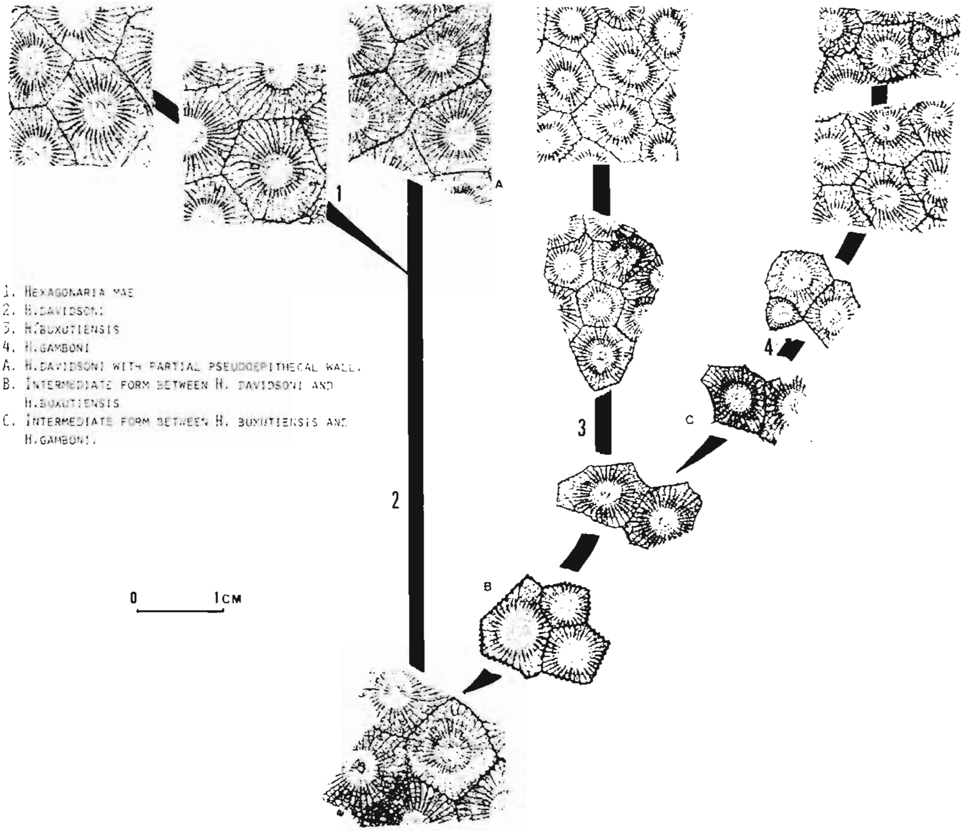

Fig. 5. The evolutionary pattern of *Hexagonaria* in the reef complexes of the mobile platform condition.

In the late stage of evolutionary pattern of *Hexagonaria* at the end of *Fr 1* time, almost all specimens of *Hexagonaria* show the degeneration of septa in the peripheral part and the development of large peripheral dissepiments. These phenomena are more evident on the stable platform among the *H. davidsoni* — *H. fewata* — gen. n., sp. n. group (fig. 6).

Facies 2 (Peri-reef facies).

Hexagonaria in this facies shows the same evolutionary pattern as in Facies 1.

2. Barrier reef facies (Shelf margin reef facies).

Only a few corals have been found. The fossil record is incomplete.

3. Stable platform carbonate facies.

A. Open marine platform carbonate facies.

Assemblage 1. — Morphological variation of *H. davidsoni*, *H. fewata* and gen. n., sp. n. shows clearly the derivation of *H. fewata* from *H. davidsoni* and the derivation of gen. n., sp. n. from *H. fewata* (fig. 6). Both *H. davidsoni* and *H. fewata* show large peripheral dissepiments near the end of *Fr 1* time. Sometimes, the septa are entirely degenerated in the

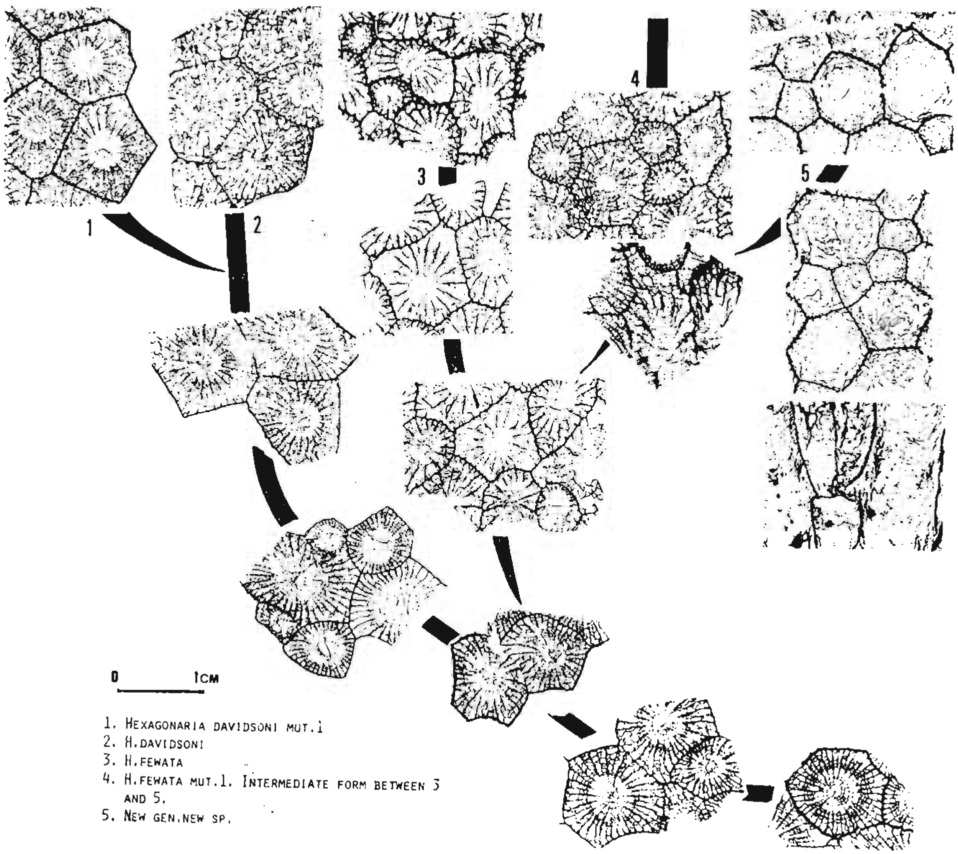

Fig. 6. The evolutionary pattern of *Hexagonaria* in the coral assemblage 1 of the stable platform carbonate facies.

peripheral part and in *H. fewata* mut. 1 the large peripheral dissepiments are so well developed that it is very difficult to distinguish it from gen. n., sp. n.

Assemblage 2. — In coral assemblage 2, the relationship between *H. marmini* (Edwards et Haime, 1851) and *H. lecomptei* is very clear (fig. 7). *H. lecomptei* shows also large peripheral dissepiments near the end of *Fr 1* time and has the same tendency as *H. davidsoni* to become smaller in size, but this tendency is more evident in the basinal conditions among the *H. davidsoni* — *H. buxutiensis* group.

Assemblage 3. — The morphological variations of *H. bracobanda* and the relationship between *H. hexagona* and this species are shown in figure 4. This species shows also the large peripheral dissepiments near the end of *Fr 1* time. This evolutionary pattern parallels those of *H. lecomptei* and *H. fewata* but is significantly independent of depositional environments.

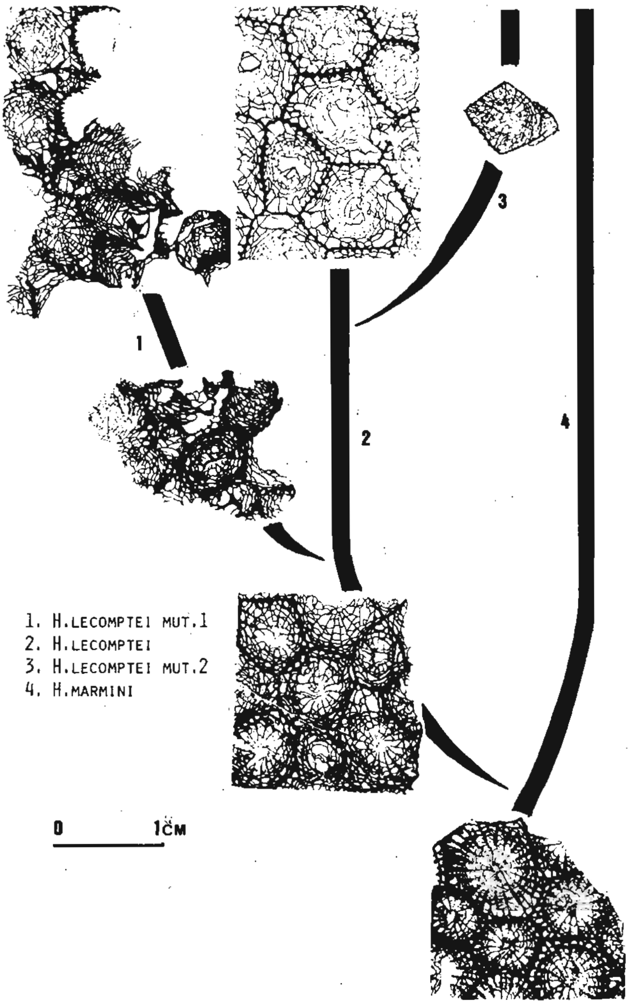

Fig. 7. The evolutionary pattern of *Hexagonaria* in the coral assemblage 2 of the stable platform carbonate facies.

B. Restricted platform carbonate facies.

Two coral assemblages have been found (table 1). The fossil record is incomplete.

DIVERSITY, SPECIATION AND EXTINCTION OF *HEXAGONARIA*

The major extinctions occurred near and at the boundary of Middle Devonian — Upper Devonian and Lower Frasnian — Upper Frasnian. Stratigraphic distribution of fossil corals (Tsien 1977*a*: table 2) illustrates clearly the changes that occurred during these two important crises in the evolution of *Hexagonaria*. It is equally true that the periods of high extinction rates in rugose corals correspond to those in other groups. In the basinal conditions, the section along the railway cut at Neuville shows the complete stratigraphic range and evolution of *Hexagonaria* and *Phillipsastrea* (Tsien 1975). In this section, the change from the *Hexagonaria* assemblage (*H. davidsoni, H. mae, H. buxutiensis* and *H. gamboni*) to the *Phillipsastrea* assemblage is abrupt. Two nodular shale beds in normal succession show the same lithologic characteristics. But one is very rich in *Hexagonaria* while the second bed and the beds thereafter contain abundant *Phillipsastrea*. On the stable platform, the section of abandoned quarry at Engis shows exactly the same phenomena; but the *Hexagonaria* assemblage (*H. lecomptei* mut. 1, *H. lecomptei* mut. 2, *H. lecomptei* and *H. marmini*) and the *Phillipsastrea* assemblage (*P. pentagona, P. goldfussi*) show also the evolutionary pattern of the stable platform conditions (fig. 7).

Several cases of speciation are observed in the carbonate complexes. Some of them are found to coincide with changing benthic conditions (facies 1 and 2). In these facies, slight environmental changes could influence the competition between species, thereby encouraging the diversification of species. Some other cases of speciation are caused by geographic isolation (inner stable platform condition). Consequently, the critical factors encouraging the diversification of species seem to be the combination of ecologic conditions and paleogeographic situation. Evolutionary changes occur during or immediately after speciation events. Important faunal changes are generally associated with widespread transgressions or regressions. Lineage studies demonstrate both progressive and abrupt species transition. Evolution of some species is the result of changing environmental conditions. In other species, evolution is independent of environmental conditions but is due to time (parallelism of some *Hexagonaria* evolution).

Acknowledgements. — I gratefully acknowledge financial support from the National Foundation for Scientific Research.

REFERENCES

BARROIS, C. 1889. Faune du Calcaire d'Erbray. — *Mém. Soc. Géol. Nord*, **3**, 1—348.

BIRENHEIDE, R. 1969. Typen Mittel- und Ober-devonischer Rugosa aus der Sammlung Goldfuss. — *Senckenberg. lethaea*, **50**, 1, 37—55.

BRICE, D., BIGEY, F., MISTIAEN, B., PONCET, J. et ROHART, J.-C. 1977. Les organismes constructeurs (Algues, Stromatopores, Rugueux, Tabulés, Bryozoaires) dans le Dévonien de Ferques (Boulonnais — France). Associations — Répartition stratigraphiques. 2nd Intern. Symp. Corals and Fossil Coral Reefs, Paris 1975. — *Mém. B. R. G. M.*, **89**, 136—151.

COEN-AUBERT, M. et LACROIX, D. 1979. Le Frasnien dans la partie orientale du bord sud du Synclinorium de Namur. — *Ann. Soc. Géol. Belgique*, **101**, 269—279.

GLINSKI, A. 1955. Cerioide Columnariidae (Tetracoralla) aus dem Eifium der Eifel und des Bergischen Landes. — *Senckenberg. lethaea*, **36**, 1/2, 73—114.

GROESSENS, E. et TSIEN, H. H. 1980. Le Frasnien du Sondage de Feluy. — (in preparation).

JOSEPH, J. et TSIEN, H. H. 1975. Calcaires Mésodévoniens et leurs faunes de Tétracoralliaires en haute Vallée d'Ossau (Pyrénées-Atlantiques). — *Bull. Soc. Hist. Natur. Toulouse*, **111**, 1—2, 179—203.

— et — 1977*a*. Les Pyrénées dans la paléogéographie dévonienne. Nouveaux jalons fournis par les Tétracoralliaires. 2nd Intern. Symp. Coral and Fossil Coral Reefs, Paris 1975. — *Mém. B. R. G. M.*, **89**, 112—115.

— et — 1977*b*. Rugosa du Couvinien et du Givetien des Pyrénées Béarnaises: affinités avec les faunes d'Europe occidentale. — *Mém. Soc. Géol. Nord.*, **97**, 45—48.

MAILLIEUX, E et DEMANET, F. 1929. L'échelle stratigraphique des terrains primaires de la Belgiques. — *Bull. Soc. Belgique, Géol.*, **38** (1928), 124—131.

SCRUTTON, C. T. 1968. Colonial Phillipsastraeidae from the Devonian of South-east Devon, England. — *Bull. Brit. Mus. (Nat. Hist.), Geol.*, **15**, 5, 183—281.

SORAUF, J. E. 1967. Massive Devonian Rugosa of Belgium. — *Pap. Univ. Kansas Paleont., Inst.*, **16**, 14 p.

— 1979. Lower Devonian Hexagonaria (Rugosa) from the Armorican Massif of Western France. — *Palaeontology*, **12**, 2, 178—188.

TSIEN, H. H. 1968. Distribution of Rugose corals in the Middle and Upper Devonian (Frasnian) Reef complex of Belgium. — Intern. Symp. Devonian System, Calgary 1967, **2**, 273—293.

— 1972. Middle Devonian and Frasnian stratigraphy of Belgium. Conseil Géol., Com. Nat. Strat., Doc. no 7, 1—25.

—1977. Paleoecology of Middle Devonian and Frasnian in Belgium. — Intern. Symp., Namur, 1974, publ. **12**, 53 pp.

— 1977*a*. The sequence and distribution of Frasnian Rugose coral faunas in Belgium. 2nd Intern. Symp. Corals and Fossil Coral Reefs, Paris 1975. — *Mém. B. R. G. M.*, **89**, 203—220.

— 1977*b*. Morphology and development of Devonian reefs and reef complexes in Belgium. — Proc. 3rd Intern. Coral Reef Symp., Miami, 191—200.

— 1977*c*. L'activité récifale au cours du Dévonien Moyen et du Frasnien en Europe occidentale et ses particularités en Belgique. — *Soc. Géol. Nord*, **97**, 57—66.

— 1977*d*. Rugosa massifs du Dévonien de la Belgique. — *Mém. Inst. Géol. Univ. Louvain*, **29**, 197—229.

— 1979. Paleoecology of algal-bearing facies in the Devonian (Couvinian to Frasnian) reef complexes of Belgium. — *Palaeogeog., Palaeoclim., Palaeoecol.*, **27**, 103—127.

WEDIGGE, K. 1977. Die Conodonten der Eifel-Stufe im Typusgebiet und in benachbarten Faziesgebieten. — *Senckenberg. lethaea*, **58**, 4/5, 271—419.