

Brachiopod-bivalve assemblages of the Middle Triassic Terebratula Beds, Upper Silesia, Poland

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Five types of brachiopod-bivalve assemblages occur in Terebratula Beds and in the lower part of the Karchowice Beds (Middle Triassic, Muschelkalk) from the Strzelce Opolskie Quarry (Upper Silesia). These are: (1) Brachiopod Coquina Assemblage dominated by the terebratulid brachiopod *Coenothyris vulgaris*; (2) Crumpled/Wavy Limestone Assemblage including bivalves and brachiopods; (3) Bivalve Coquina Assemblage dominated by pseudocorbulid bivalves; (4) Hardground Assemblage dominated by the brachiopod *Tetractinella trigonella*; and (5) Crinoid Limestone Assemblage dominated by crinoid columnals and the brachiopod *Punctospirella fragilis*. The distribution of the assemblages correlates with the eustatically-controlled lithological variation in the carbonate-dominated sequence of the Upper Silesian Muschelkalk. The brachiopod coquinas are parautochthonous remnants of terebratulid banks which thrived during the high bioproductivity but low oxygen conditions. Those conditions were caused by the biogenic influx generated from the terrains flooded during the Middle Triassic transgression. During the regressive phase, that resulted in the gradual decrease in bioproductivity and parallel increase in oxygen levels, the terebratulid banks were replaced by pseudocorbulid banks. With the further regression – and thus, the further increase in oxygen level – pseudocorbulid banks were replaced by the assemblages indicative of well-oxygenated oligotrophic environments (Hardground and Crinoid Limestone Assemblages). The observed changes in the faunal composition reflect mainly differences in metabolism and feeding strategy among dominant taxa.

Key words: Paleoecology, benthic assemblages, brachiopods, bivalves, Muschelkalk, Triassic, Upper Silesia, Poland.

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Introduction

The Terebratula Beds in the Muschelkalk (Middle Triassic) sequence of Upper Silesia (Figs 1, 2) have been known for their rich fossil content for a long time (Terebratula–Encrinurus beds of Eck 1863, 1865). The first monographic treatment of the fossils

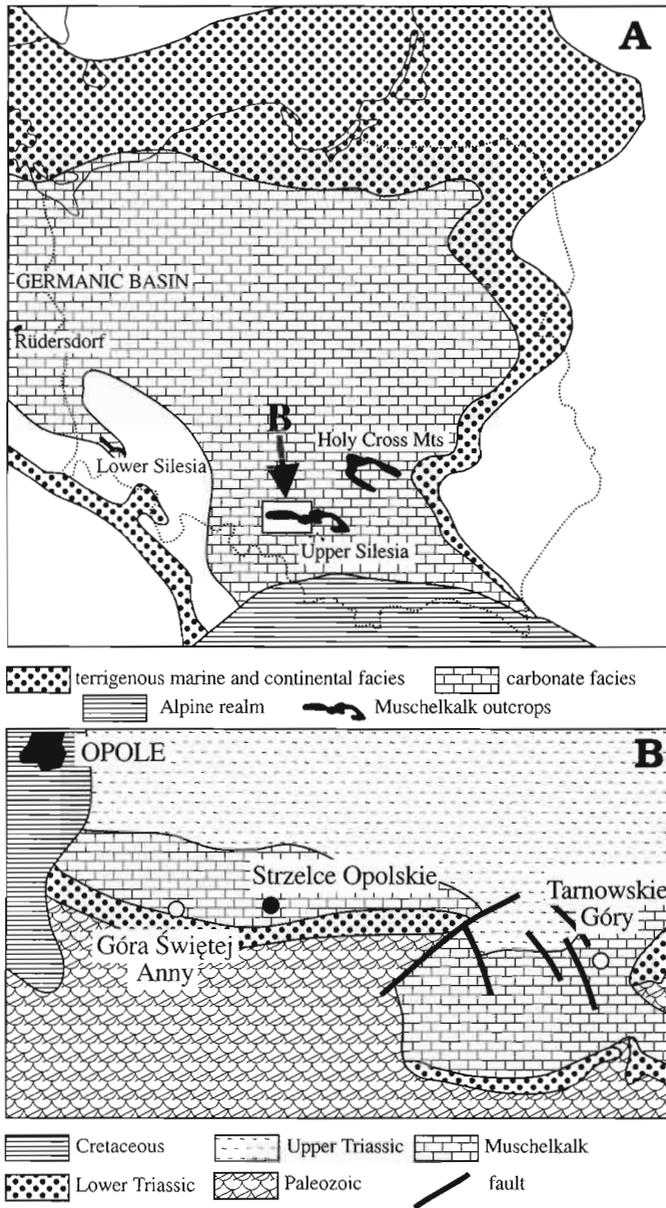


Fig. 1 A. Middle Triassic paleogeography of Poland. Modified after Dzik & Trammer (1980). B. Geological sketch map of the western part of Upper Silesia. Modified after Bodzioch (1993).

occurring in this unit was published by Assmann (1937, 1944). He established also a lithostratigraphic scheme which remains valid for this area to this day (Fig. 2). Subsequently, paleontological investigations supplied information about conodonts (Zawidzka 1975), foraminifers (Gaździcki *et al.* 1975), and echinoderms (Hagdorn & Głuchowski 1995). Brachiopods were described by Usnarska-Talerzak (1988, 1990).

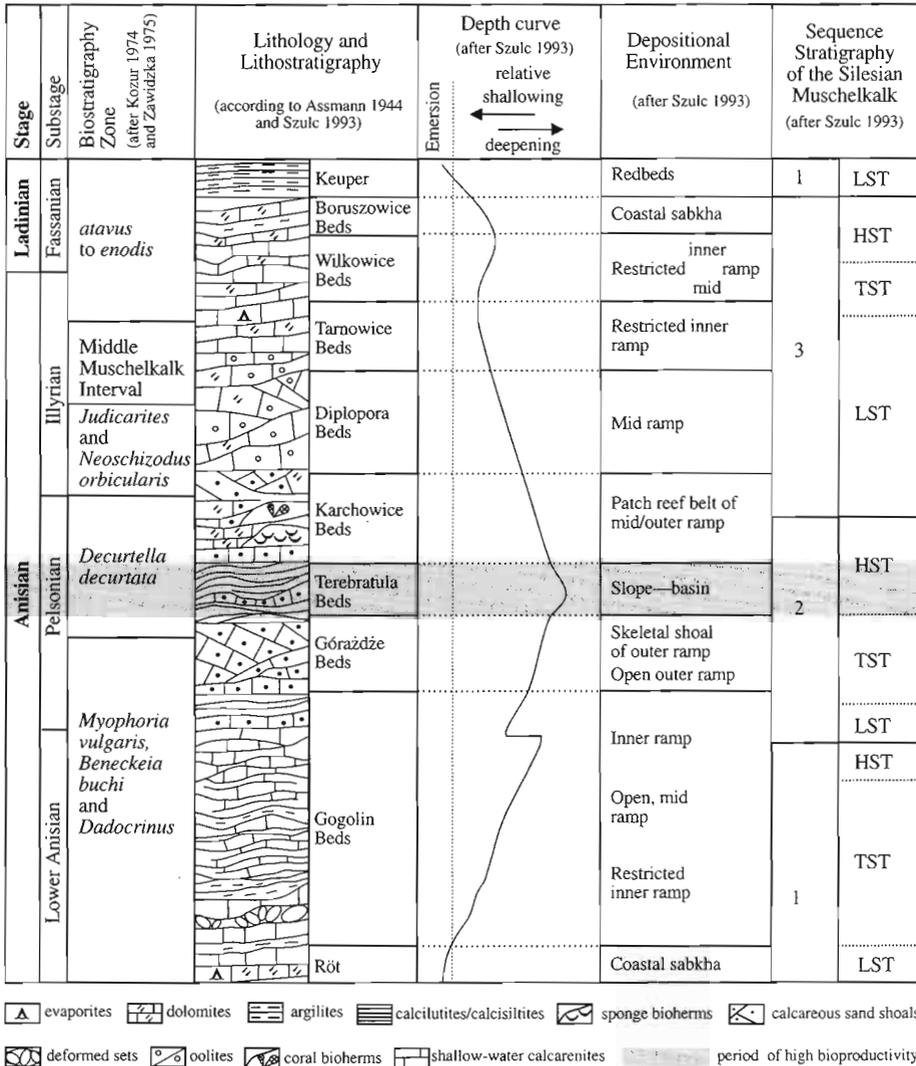


Fig. 2. Stratigraphy and evolution of the Silesian Muschelkalk Basin. After Szulc (1993) and Hagdorn & Giuchowski (1993).

Of special interest, due to their mass appearance, are the terebratulids, particularly *Coenothyris vulgaris* (Schlotheim, 1820) (Małkowski 1975; Usnarska-Talerzak 1988; Trammer *et al.* 1996). According to sedimentological investigations (Dzuleński & Kubicz 1975; Bodzioch 1985; Szulc 1993; Niedźwiedzki 1993), terebratulid coquinas were catastrophic in origin; an effect of storms and/or tectonic events. In contrast, little has been published on paleoecology of the fossil assemblages represented in the Terebratula Beds. This paper, based on the field observations and quantitative data from the Strzelce Opolskie Quarry, aims at a detailed paleoecological analysis of brachiopod and bivalve dominated assemblages of the Terebratula Beds.

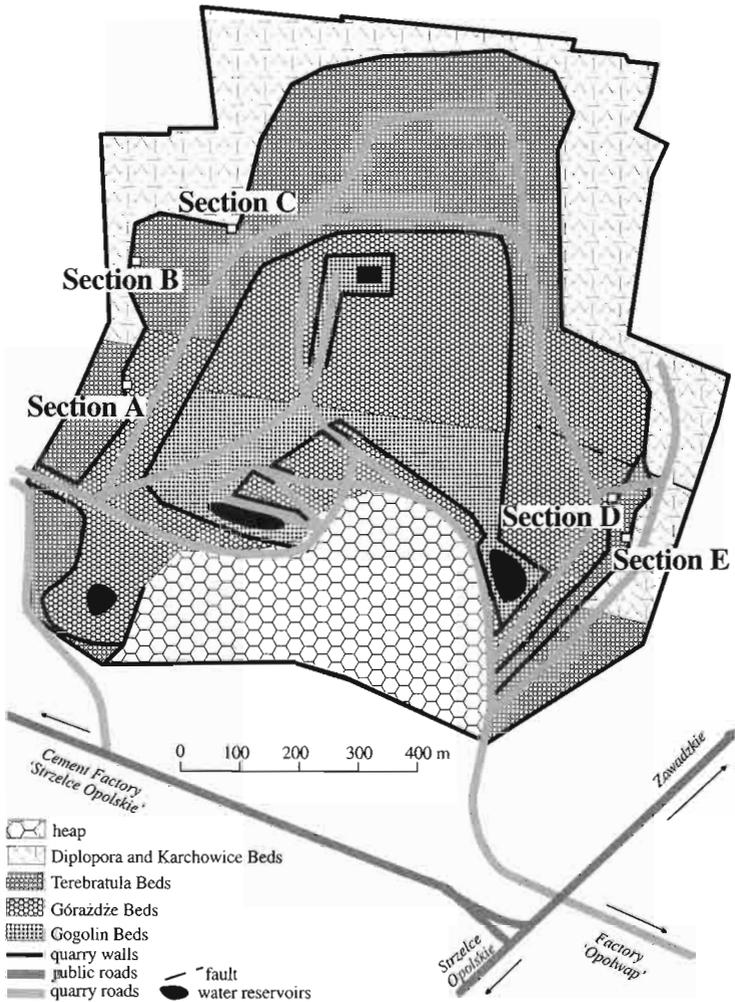


Fig. 3. Geological sketch map of the Strzelce Opolskie Quarry showing location of the sections (see also Figs 4–9).

General setting and methods

The Strzelce Opolskie Quarry provides one of the best exposures of the Muschelkalk deposits in Upper Silesia (Fig. 1). Paleogeographically, this is the southern margin of the Germanic Basin. The Muschelkalk Sea was connected with the Tethys Ocean to the south. According to Szulc (1993), the Terebratula Beds represent the maximum transgression event in the Silesian part of the Muschelkalk Basin (Fig. 2).

In the first step of my analysis, I divided the section into distinct, environmentally-dependent lithologic units and determined taxonomic composition of their fossil content. In the second step, I conducted the taphonomic and quantitative analyses of

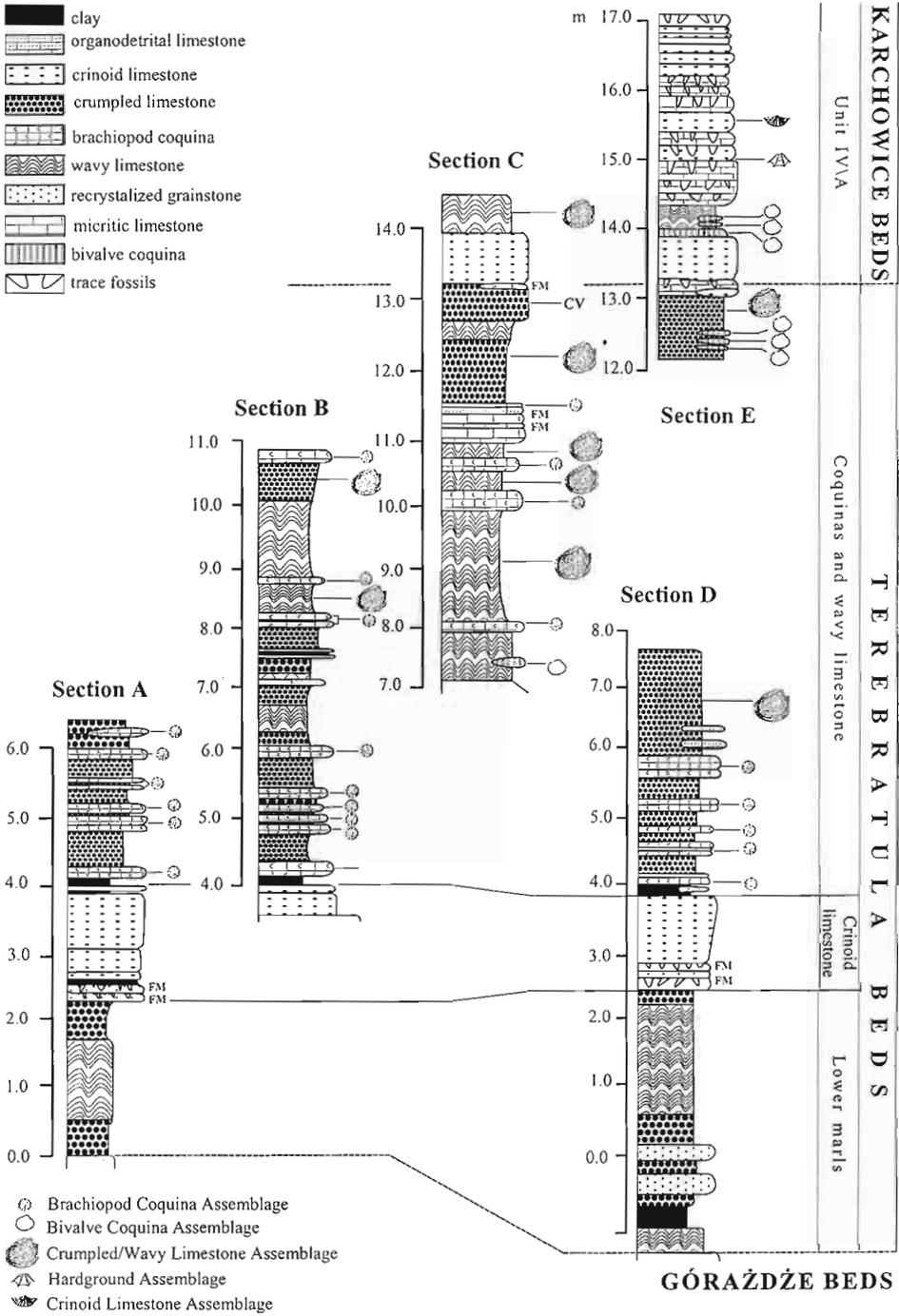


Fig. 4. Five measured sections from the Strzelce Opolskie Quarry and the stratigraphic distribution of the fossil assemblages. Abbreviations: FM – firmground, CV – bed with unusually well preserved specimens of *Coenothyris vulgaris* (Schlotheim, 1820).

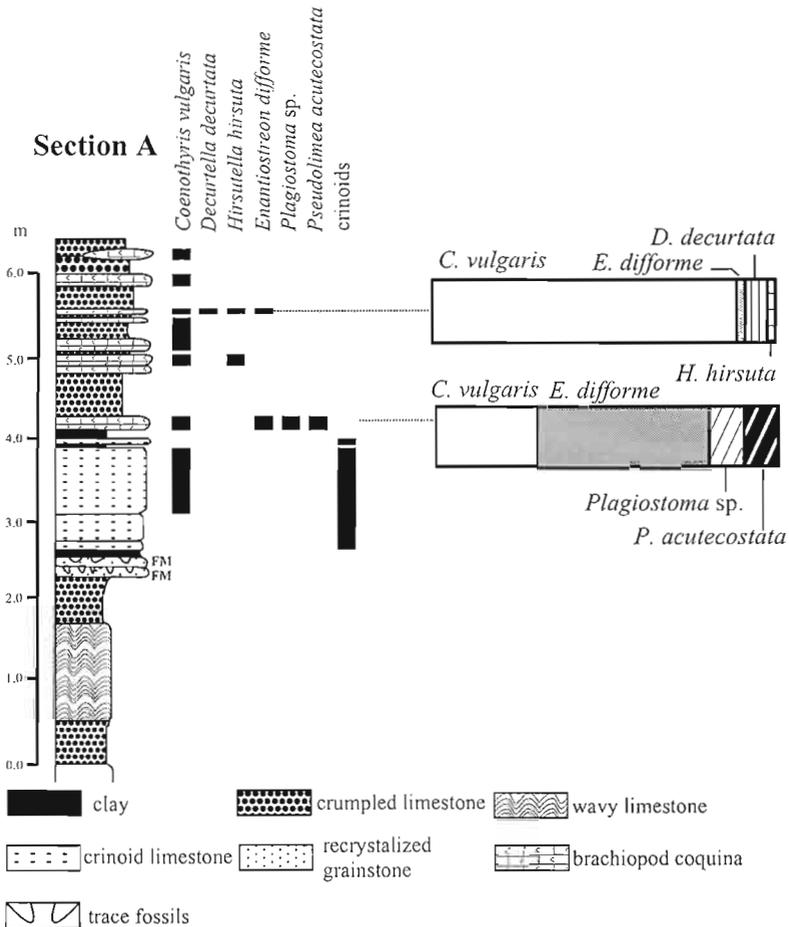


Fig. 5. Section A of the Strzelce Opolskie Quarry and stratigraphic ranges of the most characteristic fossils. Bars show relative abundance of calcitic brachiopod and bivalve shells on the bedding planes. A, B. Brachiopod coquina assemblages.

the fossils in each unit and distinguished fossil assemblages. Finally, I offered paleoecological and paleoenvironmental interpretation for those assemblages.

I obtained data for paleoecologic analysis by counting specimens in the field, primarily on bedding planes. In addition, to estimate biovolume (as an approximation for biomass), I measured area covered by each specimen (*cf.* Fürsich & Werner 1991). Because the taxonomic composition of autochthonous and parautochthonous shell beds does not differ from the composition of the much more heavily time-averaged, multiple-event shell beds, the latter have not been excluded from the analysis. As long as environmental parameters were constant, time-averaging influenced only the total abundance of specimens but not necessarily the relative proportion of species or the taxonomic diversity (Fürsich & Aberhan 1990).

The recurring faunistic associations are referred to here as 'assemblages'. This neutral term implies purely descriptive status of the units. Depending on their tapho-

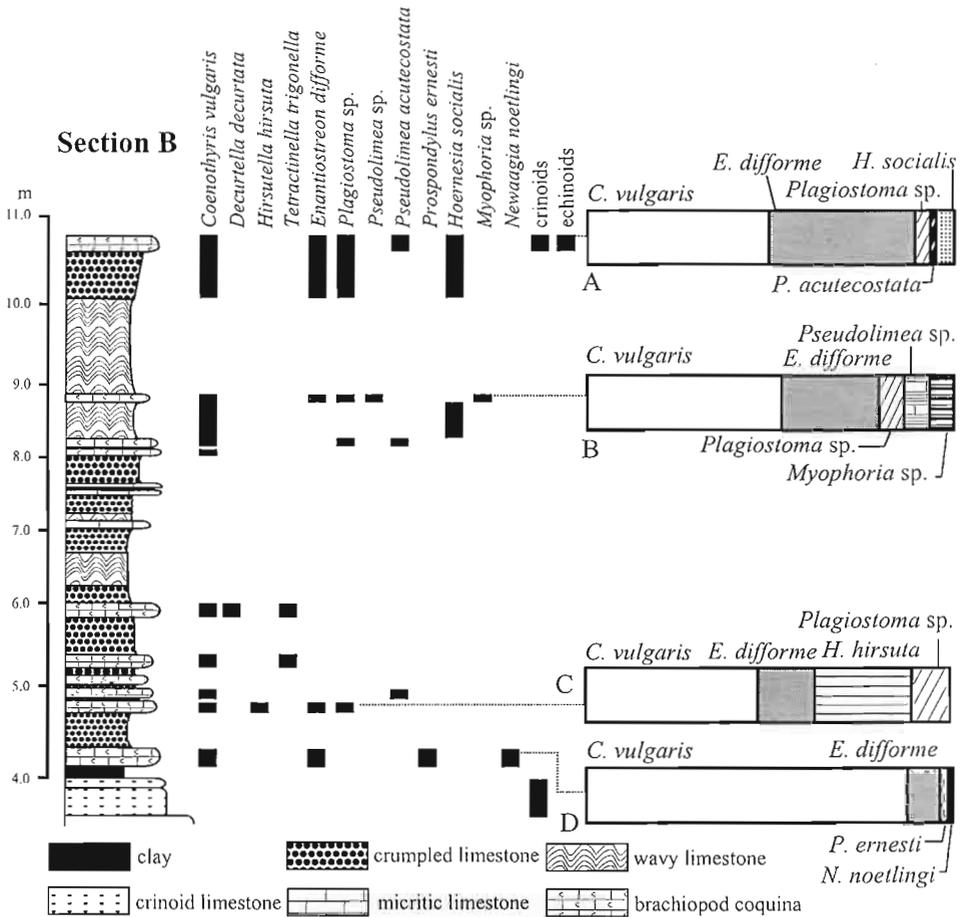


Fig. 6. Section B of the Strzelce Opolskie Quarry and stratigraphic ranges of the most characteristic fossils. Bars show relative abundance of calcitic brachiopod and bivalve shells on the bedding planes. A–D. Brachiopod coquina assemblages.

nomie history and their temporal resolution, the fossil assemblages can be interpreted ecologically to various extent and with various confidence (e.g., Hoffman 1979, 1982a, b; Kidwell & Bosence 1991).

Lithologic Units

The paleoecologic analysis is based on five sections from the Strzelce Opolskie Quarry (Fig. 3). The five sections cover the entire span of the Terebratula Beds and the lowermost part of the Karchowice Beds (Figs 4–9). Following Kotlicki & Radek (1975), I subdivided the Terebratula Beds into three units. The fourth sampled unit is the lowermost part of the Karchowice Beds (Fig. 4) as defined by Bodzioch (1990). The four units can be briefly summarized as follows:

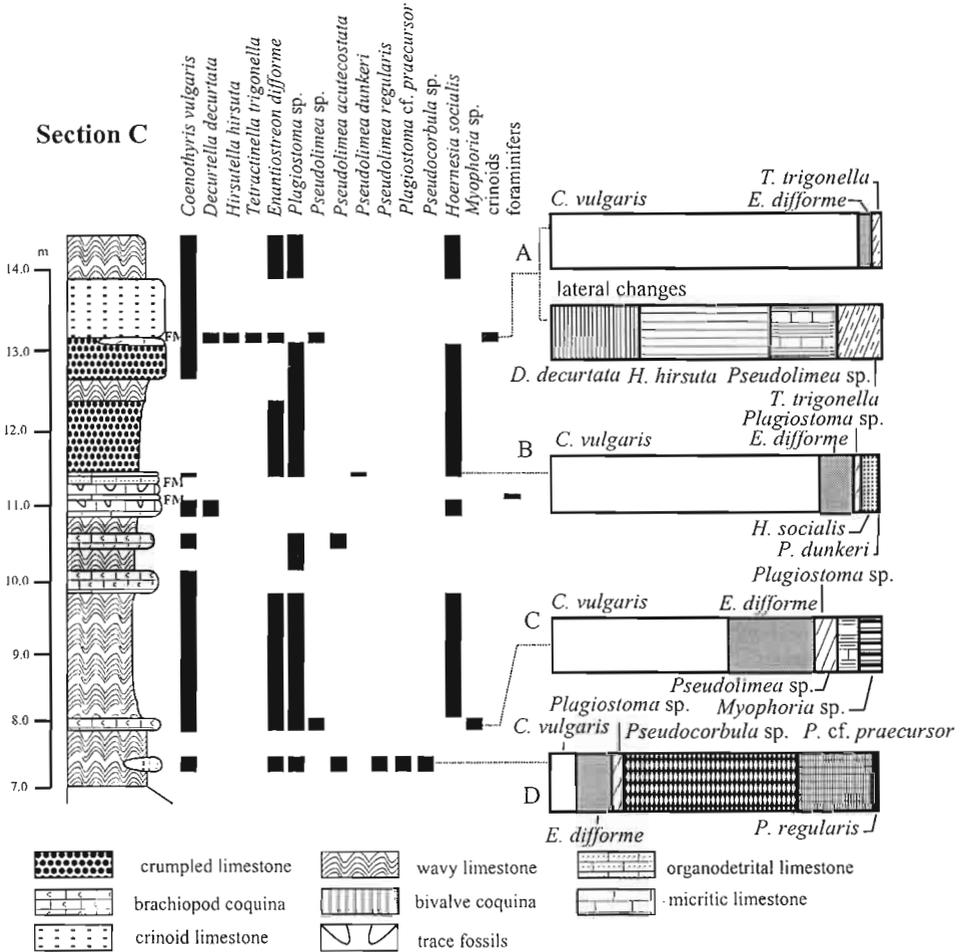


Fig. 7. Section C of the Strzelce Opolskie Quarry and stratigraphic ranges of the most characteristic fossils. Bars show relative abundance of calcitic brachiopod and bivalve shells on the bedding planes. **A–C.** Brachiopod coquina assemblages. **D.** Bivalve coquina assemblage.

Lower marls. — Crumpled and wavy limestones dominate in this unit. Shelly fossils are practically absent. Only in one place badly preserved tiny bivalves have been observed (maybe *Pseudocorbula* sp.). In the upper part of the unit, in a layer of crumpled limestone, a specimen of ammonite has been collected. This specimen is very similar to *Acrochordiceras* cf. *ippeni* (Arthaber, 1880) described by Dzik (1990); the latter probably came from the same stratum.

Crinoid limestone. — Two firmgrounds occur in the lower part of this unit. The middle and upper parts are composed of thick calcarenitic beds. Dominant skeletal components change upward from mixed skeletal debris in the lower part, through crinoid columnals in the middle part, to terebratulid shell debris in the upper part. This is consistent with observations of Szulc (1991, 1993), who also interpreted this thick calcarenitic layer as tsunamite.

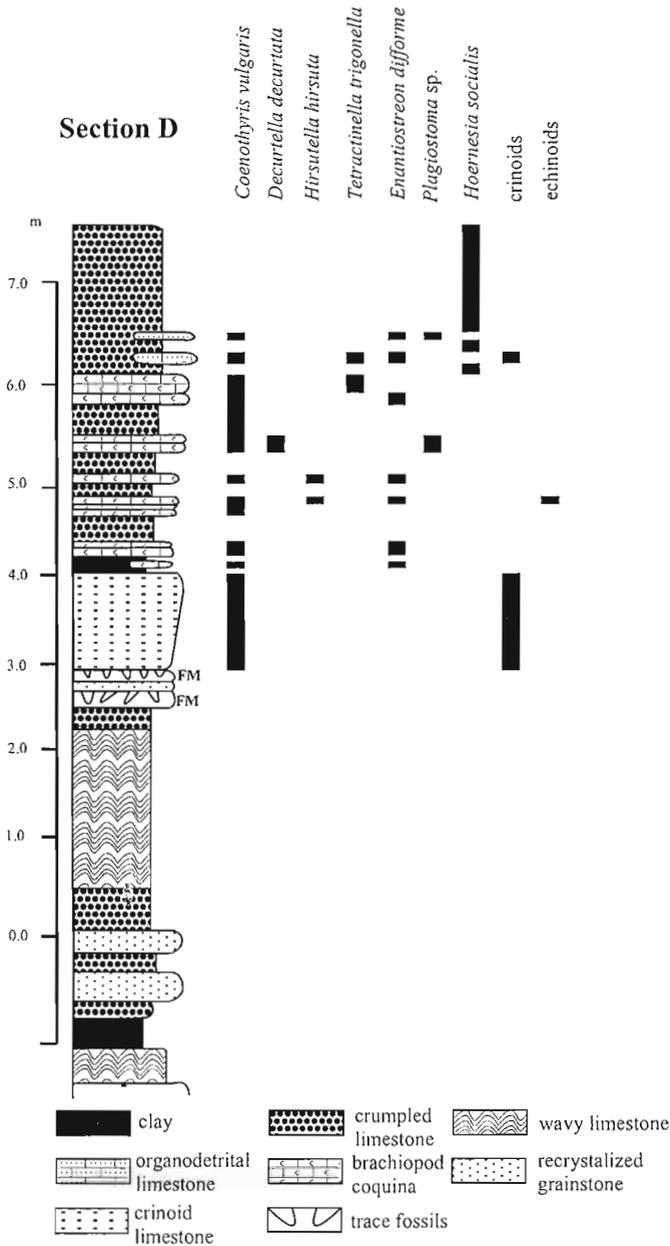


Fig. 8. Section D of the Strzelce Opolskie Quarry and stratigraphic ranges of the most characteristic fossils.

Coquinas and wavy limestone. — Four lithological types have been distinguished:

(a) Brachiopod coquina. Up to 30 cm thick coquina layers, separated by crumpled and wavy limestone, occur in the whole unit (Fig. 4). They commonly consist of the

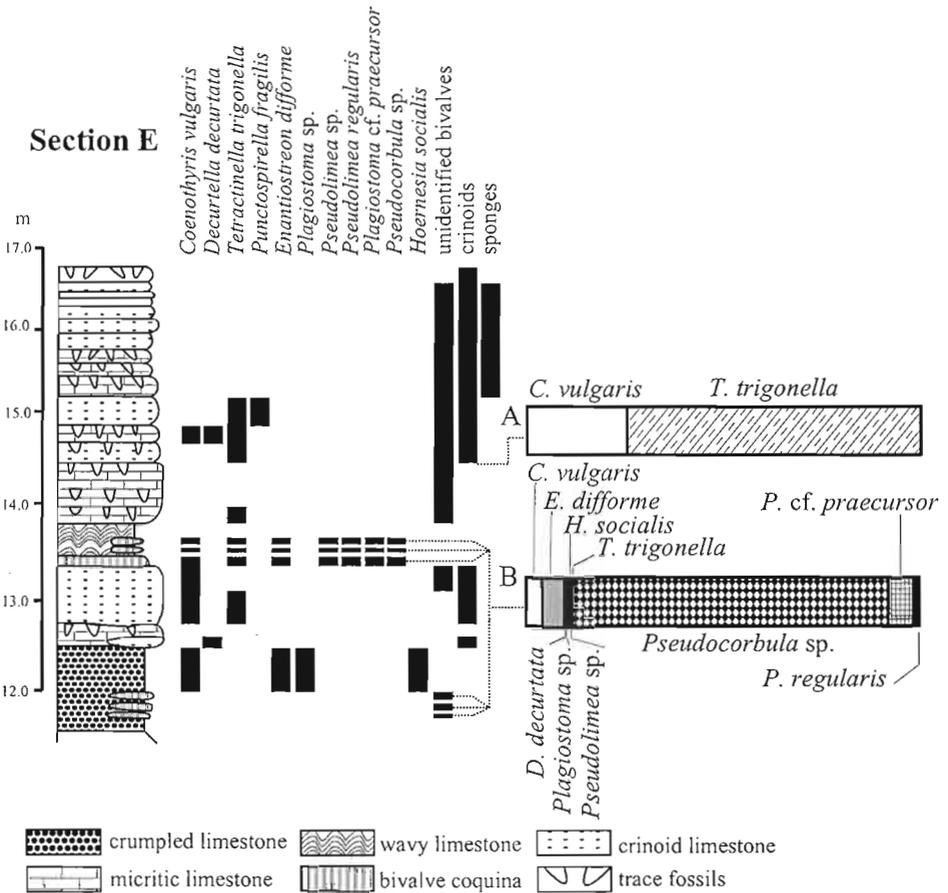


Fig. 9. Section E of the Strzelce Opolskie Quarry and stratigraphic ranges of the most characteristic fossils. Bars show relative abundance of calcitic brachiopod and bivalve shells on the bedding planes. **A.** Hard-ground assemblage. **B.** Bivalve coquina assemblage.

mixture of brachiopod and bivalve shells (articulated and disarticulated), shell fragments, crinoid columnals and echinoid spines.

(b) Crumpled and wavy limestone. Limestone beds which exhibit deformational structures varying from wavy bedding and gentle undulations, to structures intricately crumpled and fragmented (for more details see Bogacz *et al.* 1968). Fossils are uncommon but their number increases upward.

(c) Bivalve coquina. This lithology appears in the uppermost part of the unit as thin shell beds composed of closely packed internal molds of small articulated bivalves.

(d) Organodetrital limestone with foraminifers. Numerous benthic foraminifers, chiefly *Glomospira densa* (Pantič, 1965), are the main component of this limestone. The thin section analysis suggests that this is a microfacies analogous to that described by Głazek *et al.* (1973).

Unit IV/A of the Karchowice Beds sensu Bodzioch (1990). — Crinoid and micritic limestones (pelmicrite according to Bodzioch 1990) dominate in this unit. *C. vulgaris* and

E. difforme, which are typical of the Terebratula Beds, disappear. I identified sponges *Silesiaspongia rimosa* Piserá & Bodzioch, 1991, as well as brachiopods *Punctospirella fragilis* (Schlotheim, 1814) and *Tetractinella trigonella* (Schlotheim, 1820). Very numerous are columnals of crinoids and, in places, shells of unidentified bivalves. Hardgrounds with a rich assemblage of trace fossils are well developed on the micritic limestone bedding planes (see Bodzioch 1994 for description).

Description and interpretation of the fossil assemblages

Brachiopod Coquina Assemblage. — 38 bedding planes with 1598 specimens were classified as brachiopod coquinas. I identified fifteen species of bivalves and brachiopods (Fig. 10). Two species, *Coenothyris vulgaris* (Schlotheim, 1820) and *Enantiostreon difforme* (Schlotheim, 1823) make up nearly 90% of fauna. The two species are dominated by large, most likely adult, individuals. Rhynchonellids *Decurtella decurtella* (Girard, 1843) and spiriferids *Hirsutella hirsuta* (Alberti, 1865) are also characteristic of the Brachiopod Coquina Assemblage (Fig. 11B, C). In places other fossils appear including: *Plagiostoma* cf. *striatum* (Schlotheim, 1823), *Pseudolimea acutecostata* (Assmann, 1937), *Pseudolimea* sp., *Hoernesia socialis* (Schlotheim, 1823), *Prospodylus comtus* (Goldfuss, 1826) and *Prospodylus ernesti* Assmann, 1937, and ?*Leptochondria* sp. Columnals of crinoids and spines of the echinoid *Triadotiaris grandaeva* (Alberti, 1834) occur sparsely.

I distinguished two main types of coquinas. The coquinas of the first type are composed of articulated shells of brachiopods and epifaunal bivalves, often preserved in life position. The valves are fragmented only rarely, signs of abrasion and bioerosion are rare, but encrustation is present. Thus, these coquinas are regarded as autochthonous. It is hard to find them in the quarry wall, but they can be observed on the loose blocks on the quarry floor (four bedding planes; Fig. 11A). The coquinas of the second type consist of closely packed, commonly disarticulated, low to highly fragmented valves, and exhibit a sharp erosive base. These non-autochthonous shell beds are, according to Bodzioch (1985), single or composite tempestites (one-event and multiple-event beds *sensu* Aigner *et al.* 1978). Both types of coquinas show similar taxonomic composition.

Almost all animals in the Brachiopod Coquina Assemblage represent sessile epibenthic organisms. Few exceptions include the semi-infaunal bivalve *Hoernesia socialis* and the vagile epibenthic echinoid *Triadotiaris grandaeva*. The most numerous brachiopod *Coenothyris vulgaris* has a large pedicle foramen which suggests that it lived attached to the substrate with its pedicle (for detailed description of attachment scars see Małkowski 1975). These brachiopods could have formed clusters with many individuals sequentially attached to one another, as can be observed among some Recent brachiopods (e.g., Thayer 1975). Among other common organisms of the brachiopod coquinas, the bivalve *Enantiostreon difforme*, that lived cemented to the substrate (Nolte 1989; Ockert 1993; Bodzioch 1994; Fig. 11A), is also numerous. Crinoids and *Newaagia noettingi* (Frech, 1909), that also lived cemented to the substrate, are also present. Abundant occurrence of *E. difforme* strongly suggests the presence of hard substrate. The absence of fully infaunal organisms further corroborates that interpretation. In sum, the faunal composition of the assemblage

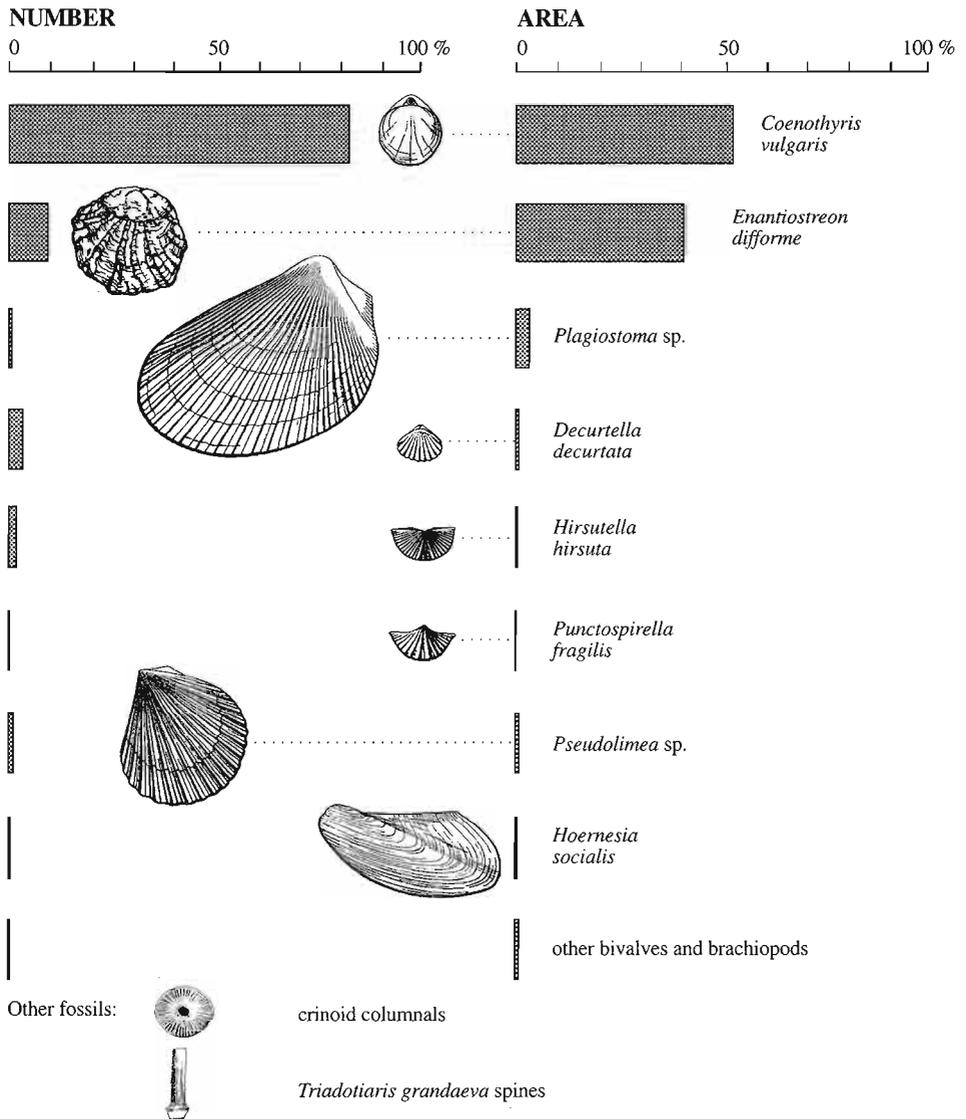


Fig. 10. Relative abundance of species in the Brachiopod Coquina Assemblage estimated by number of specimens (left chart) and surface covered by them on the bedding plane (right chart); based on data from all examined bedding planes. Shell drawings used in this and other diagrams taken from Schmidt (1928) and Hagdorn & Gluchowski (1995).

suggests that the substrate inhabited by it was at least firmed. This prevented infaunal organisms from entering the habitat and allowed, in turn, for the development of terebratulid banks. According to Bodzioch (1985), the origin of these banks was similar to that of the terebratulid banks from the Upper Muschelkalk of Germany (Aigner *et al.* 1978; Hagdorn & Mundlos 1982).

The Brachiopod Coquina Assemblage, with numerous large terebratulids and oyster-like terquemids *Enantiostreon* seems analogous to the oyster bank assemblages

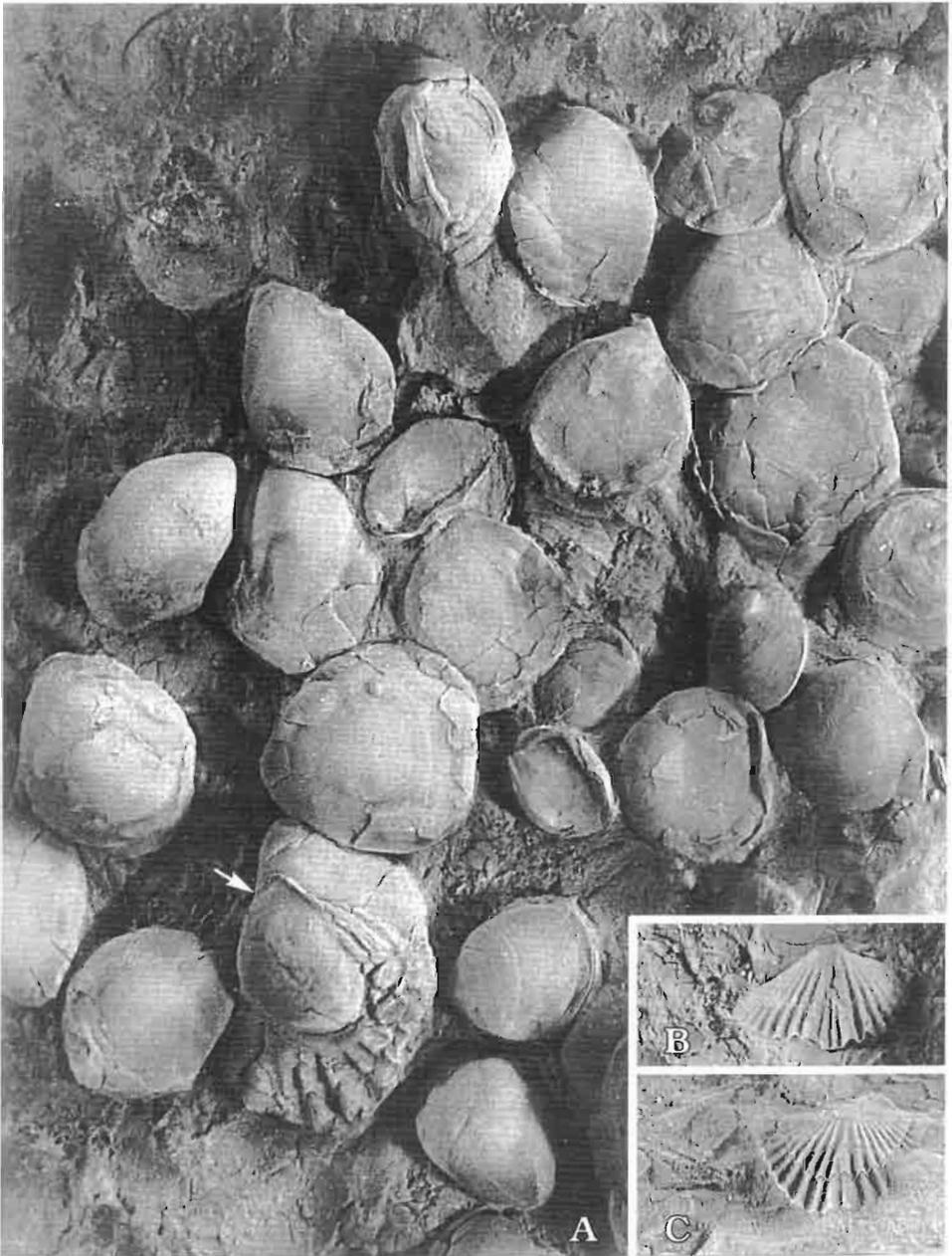


Fig. 11. Brachiopod Coquina Assemblage. A. Bedding plane with autochthonous association of the brachiopod *Coenothyris vulgaris* (Schlotheim, 1820) and the bivalve *Enantiostreon difforme* (Schlotheim, 1823). The white arrow indicates the *Enantiostreon difforme* specimen attached to the brachiopod *Coenothyris vulgaris*. Note that the bivalve shell is shaped according to the brachiopod's morphology; $\times 1.2$. B, C. Ventral and dorsal valves of the brachiopod *Hirsutella hirsuta* (Alberti, 1865) from the brachiopod coquina fossil assemblages; $\times 2$.

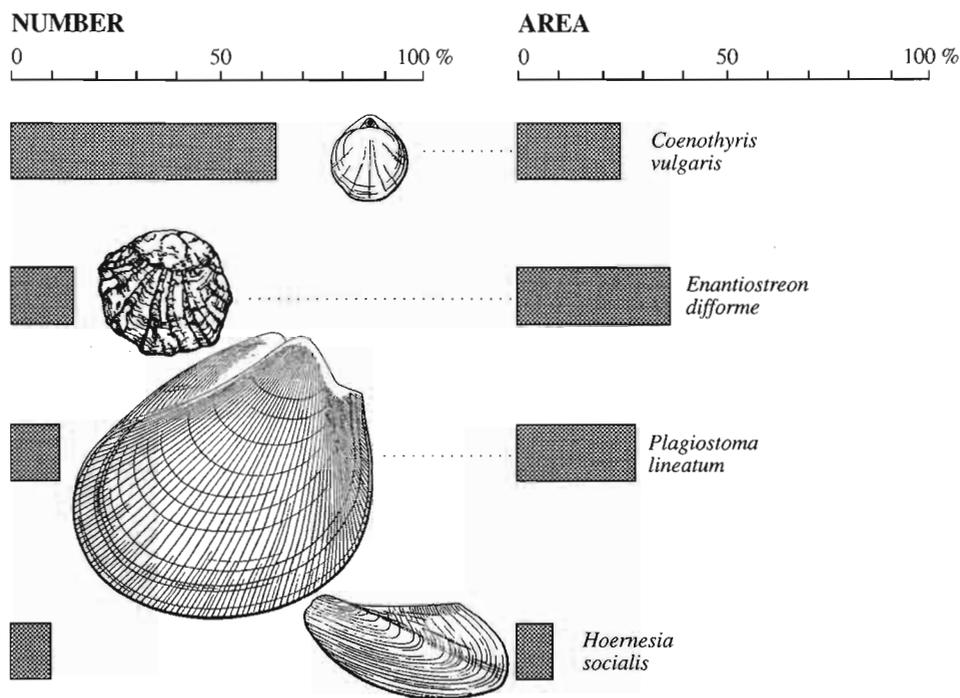


Fig. 12. Relative abundance of species in the Crumpled/Wavy Limestone Assemblage estimated by number of specimens (left chart) and surface covered by them on the bedding plane (right chart); based on data from all examined bedding planes.

from the early Kimmeridgian of Poland, where the oyster *Actinostreon gregareum* (J. Sowerby, 1816) and the terebratulid *Epithyris subsella* (Leymerie, 1846) predominate (Dzik 1979). The zeilleriid brachiopods were rare in the early Kimmeridgian oyster assemblage (Dzik 1979) and in the Anisian brachiopod coquinas (cf. Usnarska-Talerzak 1990). These assemblages were both most likely characterized by eutrophic conditions (Machalski 1993; this paper). The zeilleriids seem rather to be typical of oligotrophic environments e.g., in the early Kimmeridgian oolite assemblage (Dzik 1979) and the Anisian sponge bioherms (cf. Assmann 1937; Bodzioch 1994).

Crumpled/Wavy Limestone Assemblage. — This type of assemblage is represented by 110 specimens on three large bedding planes. Three species of bivalves (*E. difforme*, *P. cf. lineatum*, *H. socialis*) and one brachiopod species (*C. vulgaris*) are present. *C. vulgaris* prevails in number (Fig. 12), whereas *E. difforme* and *P. lineatum* prevail in covered area. Fossils are highly dispersed within the limestone. Large number of fossils have been observed near contact of the crumpled and wavy limestones with coquinas. The most typical species of this assemblage is the large bivalve *P. cf. lineatum*, often preserved in life position (see Seilacher 1954).

This type of assemblage has been observed within the crumpled limestone and also in the wavy limestone. According to Bodzioch (1985) and Niedźwiedzki (1992), the crumpling of limestone in the Strzelce Opolskie Quarry was produced by infaunal organisms. Indeed, traces of activity of soft-bodied infauna are common in those beds.



Fig. 13. Bedding plane with bivalve coquina assemblage including *Pseudocorbula* sp., *Enantiostreon difforme* (Schlotheim, 1823), and *Plagiostoma* cf. *praecursor* (Quenstedt, 1856); $\times 1.5$.

Such activity surely enhanced instability and a density stratification effect. The trace fossils found here (*Planolites* and *Palaeophycus* according to Szulc 1993) are compressed and smeared what is indicative of soupy or soft bottom conditions (compare Ekdale 1985). It is noteworthy, that the *C. vulgaris* samples analyzed by Małkowski (1975) surely came from the crumpled limestones (particularly from CV bed – see Fig. 4) where the brachiopods are preserved very well: with complete valves and often even with their original color pattern. The unconsolidated bottom forced the brachiopods to utilize other shells (also of the same species) as a hard substrate. The semi-infaunal bakevelliid *Hoernesia socialis*, that lived in soft-substrate habitats (McGhee 1978), is more common here than in any other type of the assemblage.

Bivalve Coquina Assemblage. — Nine bedding planes with 697 specimens represent this type of assemblage, which includes ten species of bivalves and brachiopods. The small bivalve *Pseudocorbula* sp. is the dominant species (80% in number, 47% in area; Fig. 14). Abundant are also other bivalves: *Plagiostoma* cf. *praecursor* (Quenstedt, 1856) (5% in number, 15% in area) and small individuals of *E. difforme* (5% in number, 15% in area). Only one brachiopod species, *C. vulgaris*, is numerous (3% in number, 10% in area). Less common are *H. socialis*, *Plagiostoma* sp. and *Pseudolimea regularis* (Alberti, 1864).

Bivalve coquinas occur as thin beds (up to few centimetres thick) or pavements. *Pseudocorbula* sp. is represented by internal molds (Fig. 15B, C) densely packed and chaotically oriented on the bedding planes (Fig. 13, 15A). Valves, before their dissolution, were articulated and closed. Such a mode of preservation of infaunal, thin-

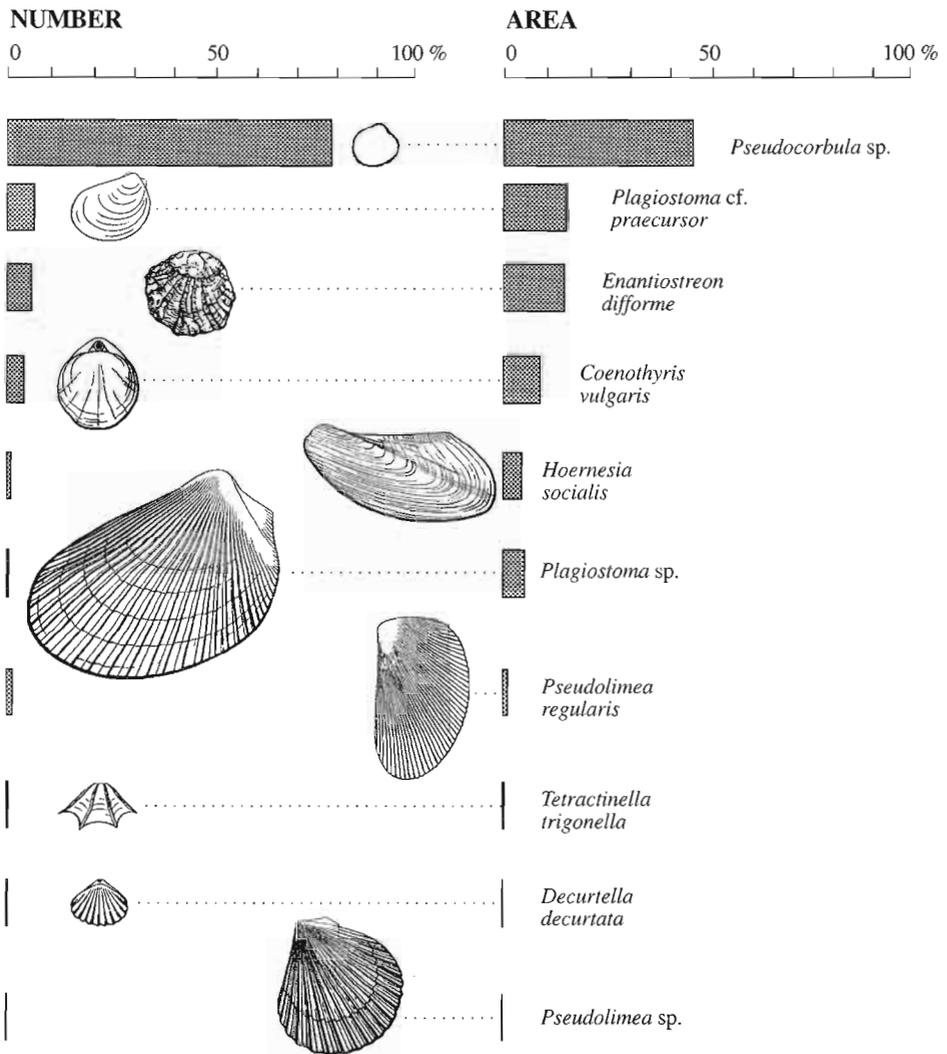
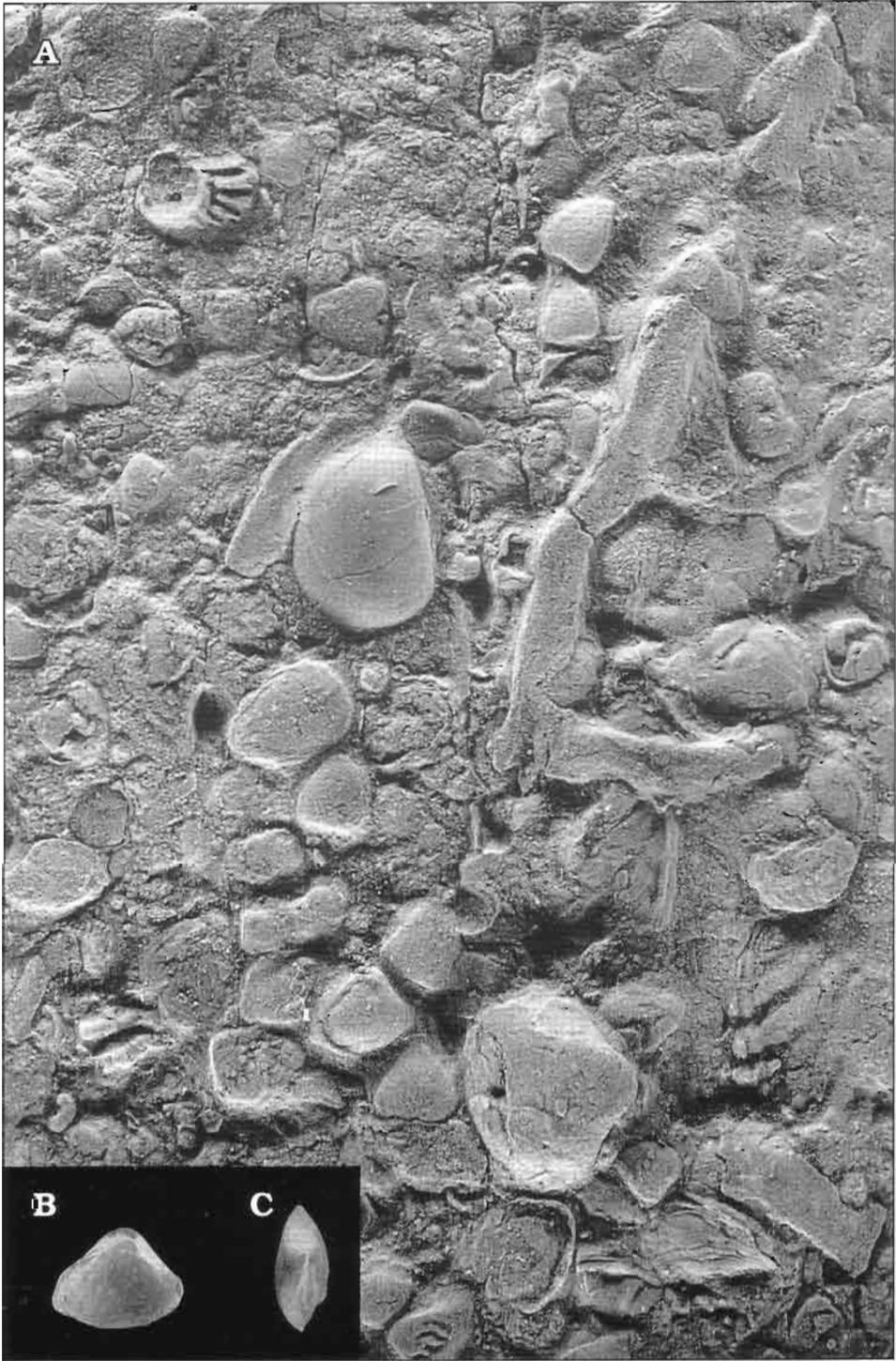


Fig. 14. Relative abundance of species in the Bivalve Coquina Assemblage estimated by number of specimens (left chart) and surface covered by them on the bedding plane (right chart); based on data from all examined bedding planes.

shelled bivalves suggests that this assemblage is predominantly parautochthonous (similar to storm wave concentrations described by Fürsich & Oschmann 1993).

The Bivalve Coquina Assemblage was dominated by the burrowing infaunal bivalves, *Pseudocorbula* sp., and *P. cf. praecursor*. Epibenthic species were much less numerous. Only the ubiquitous *C. vulgaris* and *E. difforme* are common. However, the

Fig. 15. Bivalve Coquina Assemblage. **A.** Bedding plane with *Pseudocorbula* sp., *Plagiostoma praecursor* (Quenstedt, 1856), and small specimens of *Enantiostreon difforme* (Schlotheim, 1823); $\times 1.7$. **B, C.** Internal molds of *Pseudocorbula* sp.; $\times 1.8$.



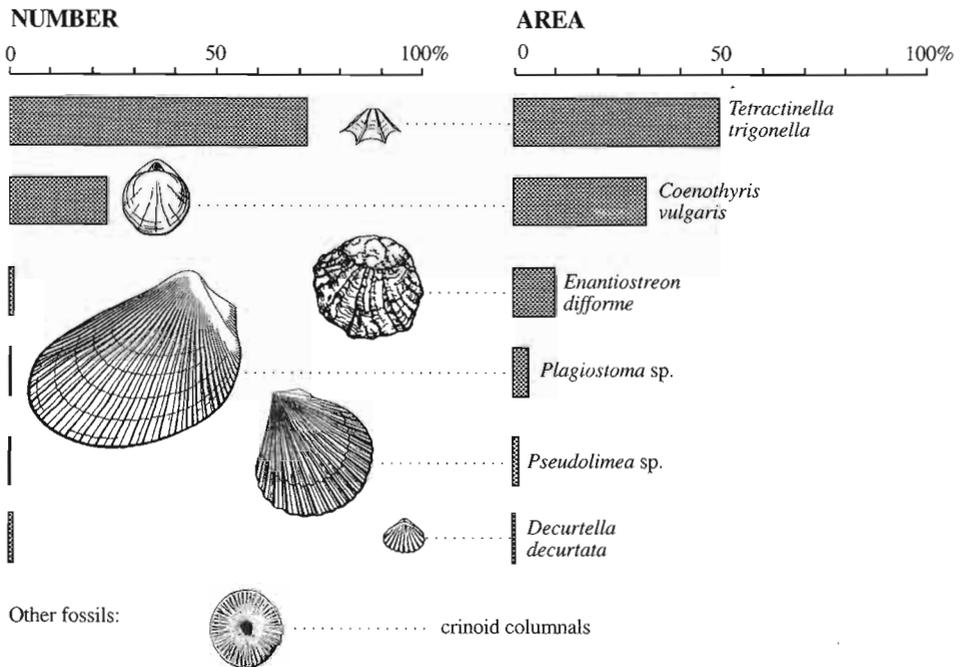


Fig. 16. Relative abundance of species in the Hardground Assemblage estimated by number of specimens (left chart) and surface covered by them on the bedding plane (right chart); based on data from all examined bedding planes.

individuals of *E. difforme* found here are much smaller than those found in the Brachiopod Coquina Assemblage. It is possible that there was too little hard substrate for epibenthic organisms. Most likely, there was at least a thin layer of unlithified sediment that made it possible for a shallow-burrowing infauna to colonize the substrate. The mass occurrence of parautochthonous pseudocorbulid shells (Figs 13, 15A) and their morphology suggest that these bivalves built banks similar to those made by corbulid bivalves in the Jurassic (Oschmann 1988a, b; Wignall 1990), Tertiary, and Recent (Lewy & Samtleben 1979).

Hardground Assemblage. — Except one case (Fig. 4), the assemblages representing this type have been found only in the loose blocks scattered on the quarry floor. The most common fossil is *T. trigonella* (70% in number, 50% in area; Fig. 16). Relatively common is also *C. vulgaris*. Considerably less common are *E. difforme*, *Plagiostoma* sp., *Pseudolimea* sp., and *D. decurtata*. The brachiopod *T. trigonella* appears often in small patches of about ten individuals of similar age (Fig. 17). Most of the shells have joint valves, with the pedicle foramen directed toward the substrate. Thus, the Hardground Assemblage is dominated by *in situ* preserved specimens. In addition, *T. trigonella* occurs abundantly, usually exceeding 50 individuals per square meter, in thin layers of fine and well-sorted organodetrital limestone that cap the hardground surfaces. Such layers have been observed in the unit IV/A of the Karchowice Beds. The individuals of *T. trigonella* have also been observed in the fill of the hardground hollows.

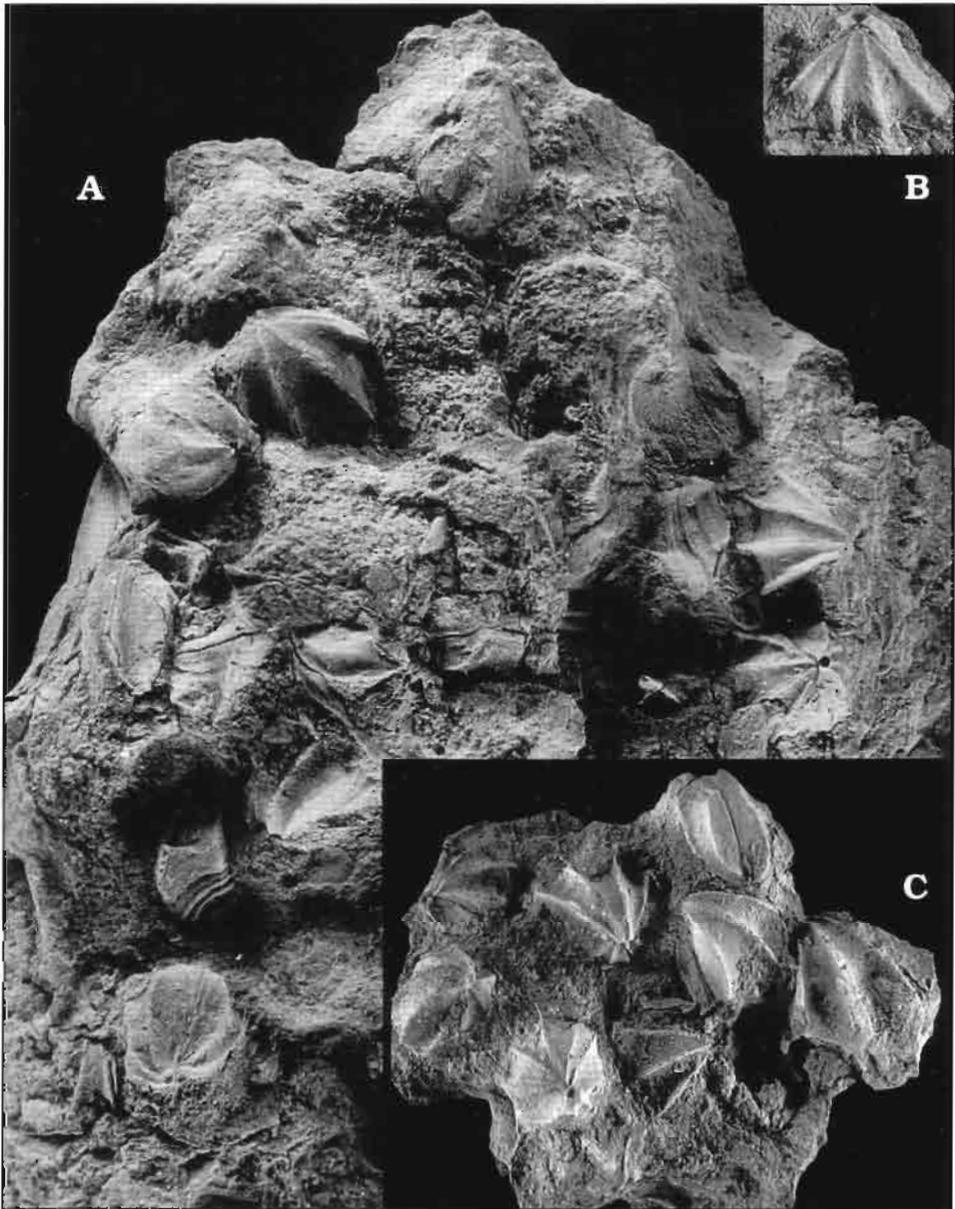


Fig. 17. Hardground Assemblage. A, C. Bedding planes with *Tetractinella trigonella* (Schlotheim, 1820); A $\times 1.5$, C $\times 1.3$. B. Unusual specimen of *T. trigonella* with five ribs; $\times 2$.

The Hardground Assemblage is dominated by the brachiopod *Tetractinella trigonella*. Its mass appearance is always associated with the hardground surfaces. The occurrence of individuals of similar size in patches and with the pedicle foramen oriented toward the substrate suggests that they had short strong pedicles and the brooding of the larvae had been restricted (similarly to some Recent brachiopods – Thayer 1975, 1977; Valentine &

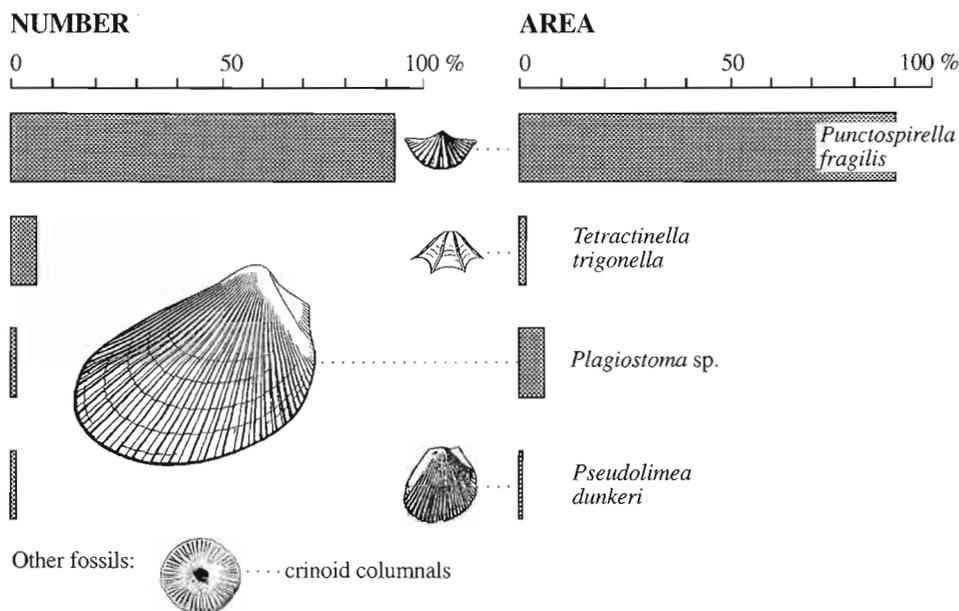


Fig. 18. Relative abundance of species in the Crinoid Limestone Assemblage estimated by number of specimens (left chart) and surface covered by them on the bedding plane (right chart).

Jablonski 1983). This athyrid brachiopod collected its food in detritus-sorting currents associated with the formation of the hardground. Special adaptations to such environments – expressed in hydrodynamically optimized shape of the shell, strong attachment to the substrate and ‘early warning’ protection (Rudwick 1965) – efficiently eliminated competitors that collected food in a similar way. The sparse occurrence of the cementing bivalve *E. difforme* despite the favorable substrate, suggests that some other factors played important role in controlling distribution of this species.

Crinoid Limestone Assemblage. — I have found only one bedding surface of reasonable size that represents this assemblage (Fig. 19). The assemblage occurs as the discrete laminae of disarticulated brachiopod and bivalve shells within the crinoid limestone of the Karchowice Beds, and is similar to *Tetractinella/Encrinurus* association described by Bodzioch (1994). The main component of the limestone are crinoid columns. Among shelly fossils, *P. fragilis* dominates (90% in number as well as in area; Fig. 18). *T. trigonella* appears in small number. Bivalves are rare, represented by *Plagiostoma* sp. and *Pseudolimea dunkeri* (Assmann, 1937). Bodzioch (1994) observed that individuals of *P. fragilis* attached themselves to other skeletons (sponges and large bivalves such as *Plagiostoma* or *Pleuronectites*). I have found only disarticulated valves that must have been transported some distance. Thus, their primary relation to the substrate cannot be established.

Detailed description of the Karchowice Beds was made by Bodzioch (1994). He found sponge-coral-echinoderm bioherms in the middle and upper parts of this unit (which were not analyzed by myself), and he described 43 bivalve and brachiopod species, fifteen gastropod species and many species of sponges and corals from the Karchowice Beds.

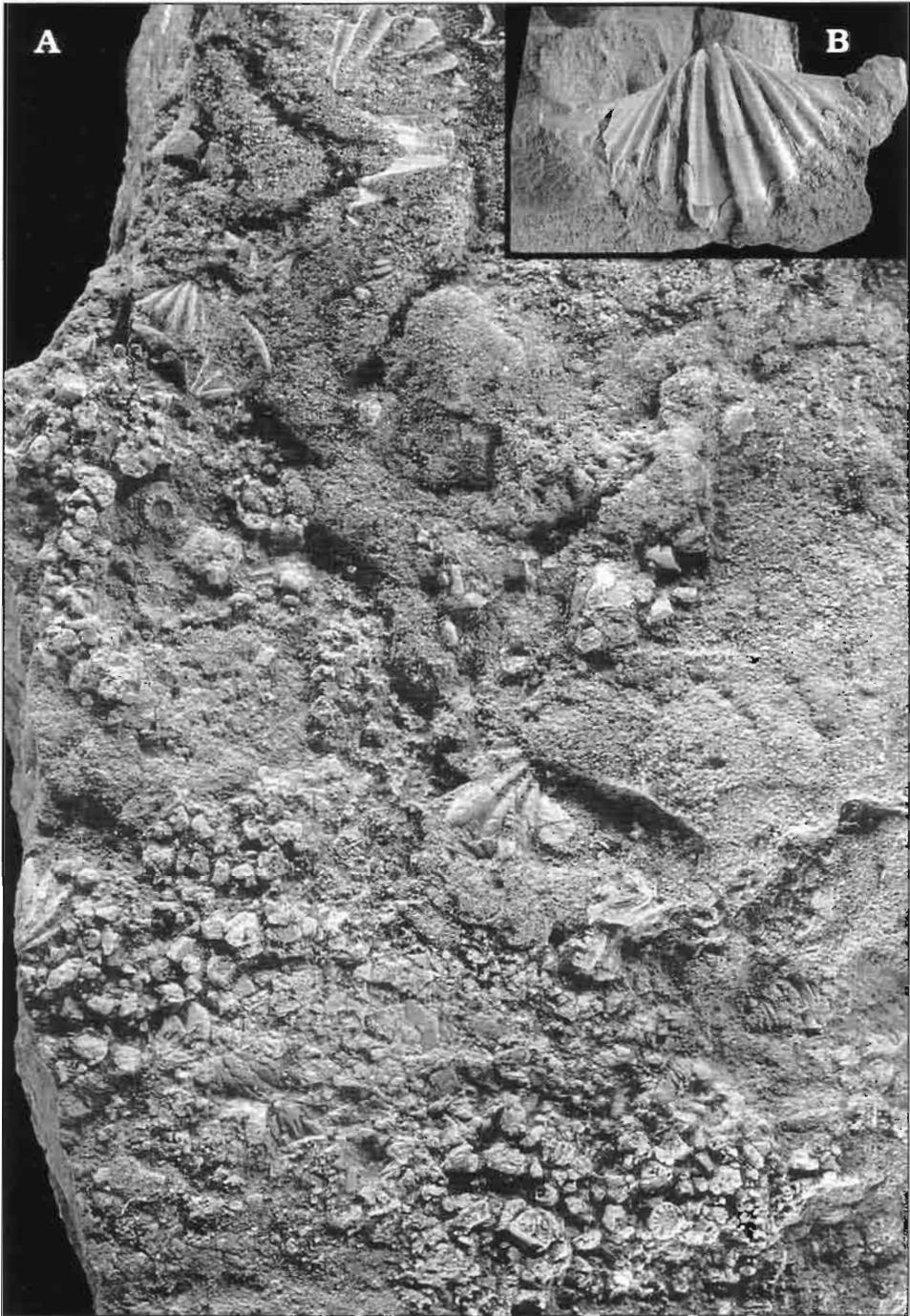


Fig. 19. Crinoid Limestone Assemblage. A. Bedding plane with *Punctospirella fragilis* (Schlotheim, 1814), *Tetractinella trigonella* (Schlotheim, 1820), and crinoid columns; $\times 1.6$. B. Ventral valve of *P. fragilis*; $\times 1.5$.

Factors controlling distribution of Triassic shelly organisms

Numerous factors may control distribution of Recent and fossil assemblages including salinity, temperature, climate, substrate, light, and depth of a basin. I would like to concentrate on two of them, i.e., oxygen content and supply of nutrients, because they seem to be main factors controlling the vertical distribution of the fossil assemblages during the sedimentation of the Terebratula Beds. In addition, sedimentation rate may have played an important role in the case of the Brachiopod Coquina Assemblage and Crumpled/Wavy Limestone Assemblage.

The benthic assemblages described above show features of variable oxygen supply. Following the classical classification scheme of Rhoads & Morse (1971; see also Byers 1977; Savrda *et al.* 1984; Tyson & Pearson 1991; Etter 1995), the environments of the Terebratula Beds may be arranged according to increase of the oxygen level during their sedimentation:

1. Anaerobic biofacies: no shelly fauna and laminated sediment (crumpled and wavy limestone of the lower marls' unit).

2. Dysaerobic biofacies: no shelly fauna and bioturbated sediment (firmgrounds of the unit of the crinoid limestone and part of wavy and crumpled limestones from the coquinas and wavy limestone unit).

3. Aerobic biofacies: shelly fauna and bioturbated sediment. Benthic assemblages in this biofacies may have been arranged according to increase of oxygen level: (a) Brachiopod Coquina Assemblage and Crumpled/Wavy Limestone Assemblage (they probably differ in sedimentation rate); (b) Bivalve Coquina Assemblage; (c) Hardground Assemblage, Crinoid Limestone Assemblage, and sponge-coral-echinoderm bioherms of the Karchowice Beds.

The sponge-coral-echinoderm bioherms of the Karchowice Beds may also be classified under point 3(c).

The anaerobic conditions during the sedimentation of the Terebratula Beds were previously suggested by Dżułyński & Kubicz (1975) and Szulc (1991, 1993). It seems likely that the oxygen deficient conditions were caused by a high bioproductivity of the basin in which sediments of the Terebratula Beds were formed. The dependence of brachiopods on colloidal and dissolved organic matter makes them abundant mainly in high productivity zones (McCammon 1969). In contrast, suspension-feeding bivalves (all bivalves found in the Terebratula Beds), feed on phytoplankton and suspended organic particles (e.g., Cox 1969; Steele-Petrović 1979; Rhodes & Thayer 1991) and can flourish also in ecosystems with lower productivity levels.

Increased productivity is caused by high supply of nutrients to planktonic organisms. These are mainly phosphates and nitrates carried out either from deeper ocean regions by upwellings and/or from the land interior by rivers. In such zones of increased productivity, insufficient supply of oxygen that hampers development of the benthic organisms is commonly (but not always) observed (Demaison & Moore 1980). Similar anoxic phenomena were identified in the Paleozoic (Bowen *et al.* 1974; Thayer 1974) as well as in the Mesozoic (Rhoads *et al.* 1972; Demaison & Moore 1980; Oschmann 1988a, b; Wignall 1990, 1994; Etter 1995). These events are frequently associated with marine transgressions (Demaison & Moore 1980).

Brachiopods, particularly those having punctae (such as *Coenothyris vulgaris*), are better adapted to the poor oxygen environments than many other marine organisms. It is usually regarded that bivalve mollusks overtook the ecologic niches occupied earlier by the brachiopods, now a relic group (Steele-Petrović 1979; but see also Gould & Calloway 1980; Boucot 1986; Rosenzweig & McCord 1991). In some present-day environments, however, in particular those with decreased or variable oxygen content and sufficiently developed hard substrate, brachiopods continue to dominate over bivalves. This is the case, for example, in the British Columbia fjords (Tunnicliffe & Wilson 1988). Their advantages in such environments include: (1) low metabolic rates, 10 to 50% of the oxygen uptake of comparable gastropod and bivalve molluscs held in similar conditions (Curry *et al.* 1989); (2) the possibility to close their valves for long periods of time (Shumway 1982); and (3) easy conversion to anaerobic metabolism (Hammen 1977) or decreasing metabolic rates and respiration by the punctae (Shumway 1982; Thayer 1986; but see Reindl *et al.* 1995). Punctae are also sites of the storage of metabolites (Curry *et al.* 1989).

The Terebratula Beds were deposited during the maximum transgression of the early Middle Triassic sea (Szulc 1993; Fig. 2). Transgressions may result in biogenic influx from newly flooded terrains. The biogenic influx, in turn, increases biogenic productivity, but may also cause oxygen depletion in marine environments (Demaison & Moore 1980).

In the early Middle Triassic eustatic regression phase, a distinct shallowing took place (Szulc 1991). Biogenic influx ceased, reducing the high primary biologic production and, as a result, the oxygen conditions improved. In that period, a better oxygenation of the soft muddy bottom allowed for the development of the pseudocorbulid banks. Corbulid associations from the English and French Kimmeridgian have been attributed to similar episodic conditions (Oschmann 1988a, b; Wignall 1990). The increase in oxygen content and decrease in bioproductivity both continued with the regression, whereas sedimentation shifted from marly to limy. Hardgrounds then developed with a mass occurrence of *Tetractinella trigonella*. That brachiopod was probably adapted to lower productivity of ecosystem, similarly to its Jurassic homeomorph — *Cheirothyris fleuriauxa* (d'Orbigny, 1850), which lived in the coral reef environments (*cf.* Malinowska 1965; Barczyk 1969; Wiśniewska-Żelichowska 1971). After the stabilization of the low sea level and low productivity, as well as the increase in oxygen content, the sponge-coral-echinoderm bioherms with numerous and diversified fauna developed (Bodzioch 1989, 1991, 1994; Pisera & Bodzioch 1991).

Conclusions

The brachiopod-bivalve assemblages in the Middle Triassic Terebratula Beds from the Strzelce Opolskie Quarry, indicate profound changes in biological productivity of the marine ecosystem. They were probably evoked by a phosphate influx from land areas newly flooded during the Early Middle Triassic transgression. The high primary bioproduction caused oxygen deficiency. In poorly oxygenated and nutrient rich waters, the brachiopod *Coenothyris vulgaris* characterized by a low metabolic activity dominated. In transitional conditions, the small shallow-burrowing bivalve *Pseudocor-*

bula sp. occurred, while in well-oxygenated, oligotrophic waters crinoids and the brachiopod *Tetractinella trigonella* were dominant.

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Zespoły ramienionogowo-mażowe ze środkowotriasowych warstw terebratulowych Dolnego Śląska

ANDRZEJ KAIM

Streszczenie

W środkowotriasowych warstwach terebratulowych i w dolnej części warstw karchowickich w kamieniołomie w Strzelcach Opolskich wyróżniono pięć typów zespołów ramienionogowo-mażowych: (1) zespół muszłowców ramienionogowych, zdominowany przez *Coenothyris vulgaris*; (2) zespół wapieni gruzłowych i falistych, zawierający małże i ramienionogi; (3) zespół muszłowców małżowych, zdominowany przez pseudokorbulidy; (4) zespół twardego dna, w którym najliczniejszy jest ramienionóg *Tetractinella trigonella*; i (5) zespół wapienia krynoidowego, złożony ze szczątków liliowców i skorupek ramienionoga *Punctospirella fragilis*. Występowanie wymienionych zespołów skamieniałości w badanym profilu jest skorelowane z eustatycznie kontrolowanymi zmianami litologicznymi w węglanowej sekwencji wapienia muszłowego na Górnym Śląsku. Muszłowce ramienionogowe są parautochtonicznymi pozostałościami ławic terebratulowych, które obficie występowały w warunkach wysokiej bioproduktywności i niskiej zawartości tlenu. Takie warunki były prawdopodobnie spowodowane przez napływ składników odżywczych z obszarów zalanych podczas transgresji środkowego triasu. Faza regresywna spowodowała stopniowe zmniejszanie produktywności biologicznej i polepszanie warunków tlenowych. Ławice terebratulowe zostały zastąpione przez ławice pseudokorbulowe. W trakcie postępującej regresji pojawiły się zespoły wskazujące na dobrze natlenione środowiska oligotroficzne (zespół twardego dna i zespół wapienia krynoidowego). Zaobserwowane zmiany faunistyczne odzwierciedlają różnice w metabolizmie i sposobie odżywiania dominujących gatunków.