

Fig. 223. Stratigraphic distribution of species of the Cyrtoclymeniidae, Hexaclymeniidae, Glatziellidae, and Wocklumeridae in the Polish Famennian. Position of samples not included in Figs. 2 and 3 on the geochronological scale is hypothetical.

SUCCESSION OF THE FAMENNIAN AMMONOID FAUNAS IN POLAND

The fossil record of the ammonoid faunal dynamics is much more complete in the Famennian of the Holy Cross Mountains than in the Frasnian of the same area (Dzik 2002). Still, it remains highly punctuated and incomplete. Even in the most fossiliferous localities (Jabłonna, Łagów), cephalopod conchs occur only in few horizons. Their stratigraphic relationship is usually hard to determine because the strata were accessible to exploitation for a limited time and most of the material collected by myself is derived from the scree of exposures no longer accessible. Even in cases of the bed-by-bed collecting by previous authors (Sobolew 1912; Czarnocki 1989), the original descriptions and most of the specimens were lost as a result of historical turbulencies in this part of Europe. The review of the evolution of ammonoid faunas presented below has to be thus taken with caution, as based on limited evidence and tentative stratigraphic attribution of many findings.

Biogeographic affinities. — Perhaps the most surprising aspect of the Holy Cross Mountains Famennian ammonoid assemblages is their rather remote similarity to those from the Rhenish Slate Mountains in Germany. Polish assemblages are generally more diverse, as acutely shown by comparison of the species contents of the *Platyclymenia annulata* Zone fossil assemblages from Ostrówka (Czarnocki 1989) with the classic Kattensiepen, quantitatively studied by Korn (2002), or Enkenberg (Korn 2004a). Perhaps the most striking is the apparent lack of *P. annulata* in Poland! This has not only faunistic but also biostratigraphic implications. It turns out that geographic and ecologic ranges of the Famennian ammonoids were rather restricted, as compared with conodonts. The pattern of change in the studied area does not need to be the same as in western Europe. Therefore the process should be seen also in its geographic dimension.

A similar distinction characterizes also the southern Urals Famennian, as can be estimated on the basis of Perna (1914) and numerous papers by Bogoslovsky (e.g., 1960, 1981). Despite its location on the opposite, western *versus* eastern, side of the East European Platform, the South Urals faunas seem more alike than those from the Rhenish Massif. This is well exemplified by the protornoceratid and earliest clymenias assemblages, apparently having an eastern provenance.

Changes at the Frasnian–Famennian boundary. — The question of the nature of the Frasnian–Famennian transition in the Holy Cross Mountains has been already discussed by myself (2002) and little

new evidence emerged since that time in respect to ammonoids (although a lot of new data has been published on other faunal groups and the local stratigraphy: Racki and House 2002; Baliński *et al.* 2002). Similarly as in, e.g., Timan (Becker *et al.* 2000), the only tornoceratid ammonoid lineage that reaches the end of the Frasnian in the area is *Linguatornoceras*. The lack of well-defined evolutionary novelties (apomorphies) in the conch of this tornoceratid and its earliest Famennian successors makes identification of the exact ancestry and the course of evolution difficult. It remains thus to be convincingly shown whether all the post-Frasnian goniatites diversified from a single survivor or, as suggested by Becker (1993a) at least two separate lineages crossed the boundary. Most probably, the underived morphology is a reflection of their opportunistic ecology. No doubt, however, that tremendous shifts in the geographic distribution of ammonoid species at the boundary was connected with environmental changes, as it was the case also with conodonts. It is thus unlikely that the change from ancestors to successors can be traced in any single section representing the Devonian equatorial environment.

Famennian faunas. — The stratigraphically oldest occurrence of the Famennian goniatites in the Holy Cross Mountains is the now not accessible cephalopod layer at Karczówka (Gürich 1896, 1901) with mass occurrence of probably *Tornoceras typum*. Mature macroconchs of this species in somewhat younger strata at Jabłonna and Janczyce reach 12 cm of the conch diameter and it was the largest ammonoid of its time. A local outshoot of the lineage initiated a fast evolutionary change towards the oxyconic conch shape. This is probably the most convincing case of the phyletic evolution among the Devonian ammonoids, best recognized at Janczyce (Makowski 1991), but apparent also at Jabłonna and Kowala.

While *Tornoceras* evolved so directionally, the fossil goniatite assemblage was enriched with the first member of the *Polonoceras* lineage and a few sympatric species of the cheiloceratids. All these lineages entered as immigrants from an unknown source region with no signs of any evolutionary change at place. The best fossil record of their diversity is from the mid *K. crepida* Zone, with few findings from strata of younger age until the late *C. quadratinodosa* Zone. Then, a very rich assemblage of the protornoceratids, cheiloceratids, dimeroceratids, and early sporadoceratids emerges, together with the black shale and limestone facies, at Kowala and Łagów, the latter being the subject of the large monograph by Sobolew (1914a). The faunas of the *C. quadratinodosa* and *C. marginifera* are different in that underived tornoceratids were replaced by more advanced posttornoceratids as a result of another wave of immigrants. The largest ammonoid of the *C. quadratinodosa* was the dimeroceratid *Dimeroceras cf. petterae* Petersen, 1975, whereas in the *C. marginifera* Zone time it was the posttornoceratid *Maeneceras lagoviense* Gürich, 1896, both reaching about 11 cm in their conchs diameter.

The high diversity of fossil assemblages continued to the early *P. trachytera* zones, but with a dramatic change in its composition meanwhile. The cheiloceratids disappeared completely, only a few dimeroceratids survived, and sporadoceratids reduced their diversity. A number of clymenias entered the area. They co-occurred for some time with their close phylogenetic and ecological relatives, the protornoceratids.

These are clymenias that dominate all the younger assemblages. In the late *P. trachytera* Zone they are supplemented, apart of the ubiquitous *Sporadoceras varicatum*, by the prolobitids, represented probably by two long-ranging but ecologically sensitive lineages. In the *L. styriacus* Zone, large clymeniids emerged for the first time, with *Clymenia laevigata* (Münster, 1839) reaching 15 cm in diameter. The largest Famennian ammonoid was probably *Gonioclymenia speciosa* (Münster, 1832) of 30 cm diameter.

The *Prionoceras* clade, rooted in underived cheiloceratids, increased gradually its importance during the late Famennian, near its end being the dominant goniatites, associated with the morphologically conservative *Cymaclymenia*, evolute *Kosmoclymenia*, and aberrant involute wocklumeriid clymenias. More or less the same assemblage occurs in the Sudetes, different only in including several species of the minute prionoceratid *Balvia*, elsewhere known from the Rhenish Slate Mountains (Korn 1994) and England (Selwood 1960). The roots of all the post-Devonian ammonoids were within the prionoceratids (Korn *et al.* 2003).

EVOLUTION OF THE FAMENNIAN AMMONOIDS

Although little changed in the morphology of the adult conch of the earliest Famennian tornoceratids prior to their diversification into the main clades, their larval conch (referred to as such because of reasons

explained at the beginning of the ammonoid part of this work) underwent a profound transformation. The change was comparable with that during formation of the tightly coiled ammonoid larval conch in the Mid Devonian (e.g., Klofak *et al.* 1999). The larval conch was clearly demarcated, from both the spherical embryonic protoconch and the differently ornamented teleoconch, and bore 2–3 septa already in the Silurian ancestors of the ammonoids (Dzik 1981) and in bactritids (Doguzhaeva 2002). Its tight coiling was actually the only substantial modification until the origin of the tornoceratids. Near the origin of the clade in the Givetian, the first larval septum developed a deep concavity, which made tornoceratids different from all other ammonoids (Ruzhentcev 1962; Bogoslovsky 1969). As speculated above, this could have been a result of delayed secretion of the septal tissue in respect to the camerol liquid.

A limited evidence from the Holy Cross Mountains (Fig. 140) suggests that during the early Famennian this tendency was reversed and the tornoceratid ancestor of the clymenias had the first septum of underived morphology. Whether this happened prior to derivation of the cheiloceratid lineage, or the cheiloceratids originated from a Frasnian ancestor lacking the bulbous first septum, has to be shown.

GONIATITES

According to House and Price (1985) at least five lineages of the tornoceratids crossed the Frasnian–Famennian. Even if this undervalues the change, data from regions outside the equatorial Devonian has to be obtained before the monophyly of all the post-Frasnian ammonoids is accepted. Anyway, morphologic similarities among the earliest Famennian tornoceratids and cheiloceratids from the Holy Cross Mountains are so close that their origin from the single lineage of *Tornoceras typum* cannot be excluded. From the earliest Famennian *K. triangularis* Zone only poorly preserved juvenile specimens probably representing this species are known to me. In the *P. crepida* Zone mature *Tornoceras* conchs show bimodal size frequency distribution, interpreted by Makowski (1991) as the evidence of sexual dimorphism. That this was truly the case is supported by a similar size differences in the lineage of the oxyconic tornoceratids, but the supposed macroconchs are there two times smaller in diameter. At present it cannot be excluded that actually two generalized species of *Tornoceras* occur in the early Famennian of the Holy cross Mountains, different only in mature conch size. The small-size species gave rise to the local phyletic lineage of tornoceratids with acute conch venter (Fig. 224).

Oxyconic tornoceratids. — The change from the roundedly discoidal *Tornoceras typum* to the oxyconic *T. sublentiforme* was probably a case of fast phyletic evolution (Makowski 1991) restricted to the Holy Cross Mountains. It has its counterpart in the probably coeval Rhenish lineage of *Oxytornoceras* (Becker 1993a). Acute whorls developed several times also in other unrelated ammonoids known from the Holy Cross Mountains. Apparently, a selection pressure on developing this kind of conch geometry was frequently released and a response to it from developmental mechanisms was easy and fast. As a result the origin of most such short-living lineages is cryptic, having little chance to be recorded in strata.

The ancestral lineage of *T. typum* continued its occurrence in the area and it is not clear how the genetic isolation allowing the divergent evolutionary change developed.

Protornoceratid conch geometry. — The early tornoceratids had a virtually closed umbilicus throughout their ontogeny, with exception of the larval stage. Frequently a callus developed (Fig. 141A). The first tornoceratid with open (although still narrow) umbilicus emerges from the fossil record in the Holy Cross Mountains area very early, almost together with *T. typum* (Fig. 159) and it may have Frasnian roots. The virtual lack of goniatite fossils immediately above the Frasnian and during the whole the *K. triangularis* Zone is hardly any evidence, as throughout the whole Frasnian only three horizons with ammonoid are reported from the Holy Cross Mountains (Dzik 2002). No doubt that they occurred also in epochs without any fossil record. To be preserved, the ammonoid conchs require extraordinary sedimentary conditions, preventing degradation of aragonite (almost instantaneous covering with the sediment).

Despite the punctuated fossil record, it seems that the phyletic evolution towards the tabulate venter in the *Polonoceras* lineage took place in the area (Fig. 204). It reached the level of *P. dorsoplanum* in the late *C. quadratinodosa* zone. The enigmatic *P. sudeticum* from the latest Famennian of the Sudetes seems to be a continuation of the lineage after a great gape in the record, as suggested by the very characteristic arcuate depressions on the conch flanks and conical umbilicus slopes. It is different from the early Famennian *Polonoceras* in its rounded venter, suggesting a reversal in the evolution. The *C. marginifera* Zone was a

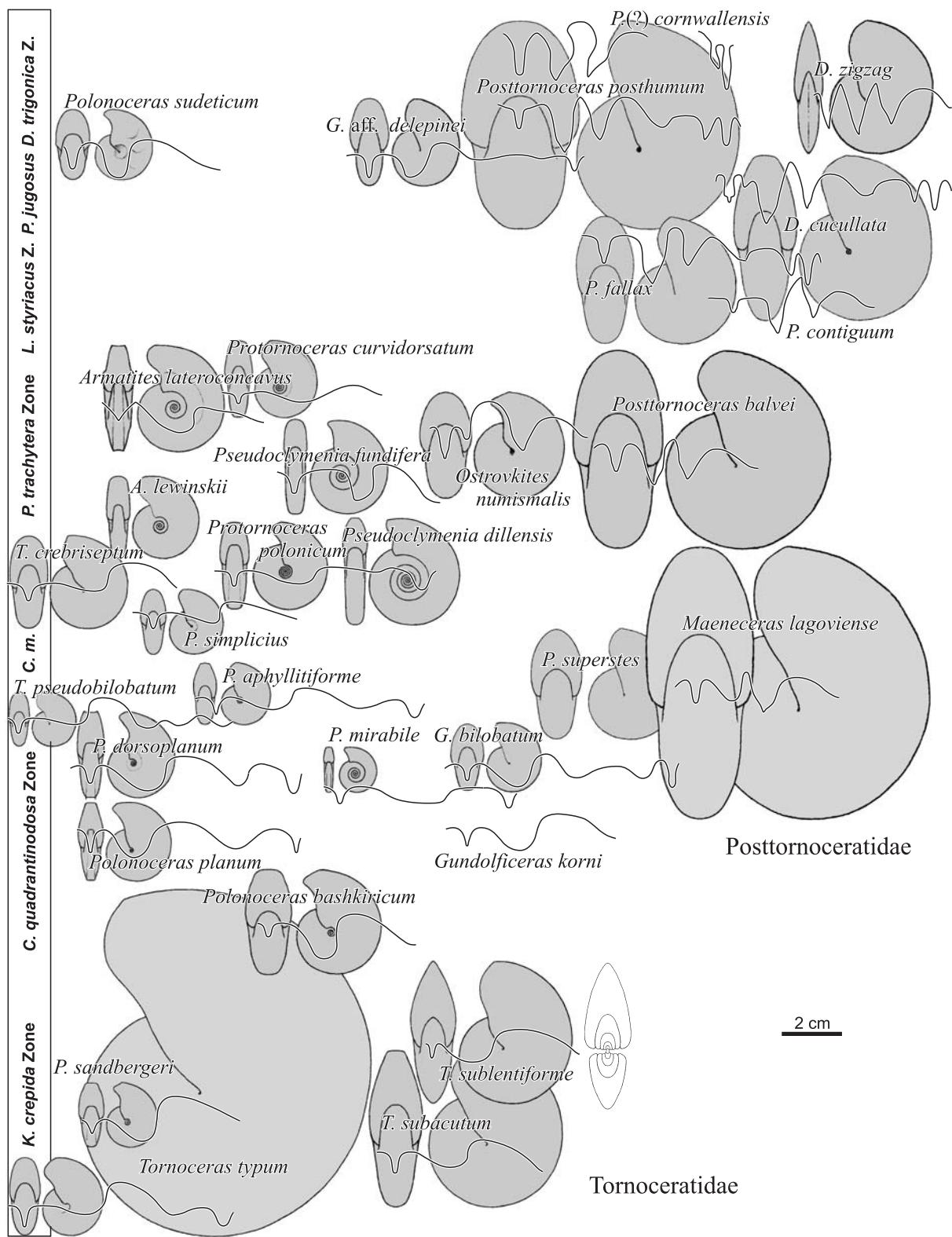


Fig. 224. Chronomorphoclines identifiable in the tornoceratid and posttornoceratid goniates in the Polish Famennian (for details of stratigraphic distribution of species see Fig. 159). Contours of probably mature specimens in scale and suture lines are given.

time of migrations and the lack of record of the lineage in this time span may be meaningful. The open umbilicate *Armatites*, which emerged in the *P. trachytera* Zone is evidently a successor of *Polonoceras* but, being known also in the Rhenish Massif (Becker 1993a), may have originated there.

A somewhat tabulate venter associated with the evoluteness of the conch developed independently in *Protornoceras*, an early offshoot of *Polonoceras*. Species of the *Polonoceras–Protornoceras* clade all had a very small mature conchs, which may be an expression of their position in the community different from that of the main lineage of the tornoceratids. There are many sympatric species of *Protornoceras*, each unusually variable in the conch morphology. Their ability to contribute new and new sympatric species to the assemblage must have been connected with their biology, but its nature remains unknown. In the most derived of the protornoceratids, the evolute *Pseudoclymenia*, an *Aturia*-like morphology of the septum developed.

Complex septa of the posttornoceratids. — The marginal concavities in the protornoceratid septa were probably of little functional meaning, as the most of the septum surface was still concave and not adapted to withstand the increased hydraulic pressure from the living chamber. The functional meaning of further undulation of the septal margin in the *Gundolficeras* lineage is also unclear, although it is represented by a virtually continuous series of morphologies in the local fossil record (Fig. 224). Whatever was its original cause, this change initiated a profound modification of the conch geometry characterizing the important branch of the posttornoceratids. In this lineage, most of the complication of the septum geometry originated near umbo.

The succession of increasing septal complexity from *Posttornoceras superstes*, through species of the genus with increasingly acute lobes of the suture, then *Discoclymenia cucullata*, and finally *D. zigzag* with acute lobes and saddles, is consistent with stratigraphic superposition of findings (Fig. 224). It is likely to be a true phyletic change but the record is too punctuated and the distribution of particular taxa to separate geographically to have a good control of migrations and evolution. A completely vaulted septum developed near the end of the lineage. The origin of the lineage remains cryptic, although *Gundolficeras* is the likely ancestor and the origin of *P. superstes* required only a further deepening of the septal undulations.

A separate lineage evolving towards similarly complicated septa is represented by *Maeneceras* that possibly replaced the *Tornoceras* in the niche of large-sized ammonoids (Fig. 224). Too little evidence has been gathered to be sure that it is rooted in *Tornoceras* and not in *Felisporadoceras*. The problem is in a rather labile apertural shapes in these Famennian goniatites. Possibly, shallow and wide auricles could reappear as a result of a reversal in the evolution of cheiloceratids.

Proterogeny in the cheiloceratid-dimeroceratid branch. — Such changes in the profile of the aperture did not occur in the early evolution of the cheiloceratid clade. It seems that after the derivation of the *Nehdenites* lineage from *Tornoceras* (this required only a reduction of the shallow apertural auricles) the shape of aperture remained rather stable until the late Famennian. Interestingly, also in the *Nehdenites* lineage a trend towards the oxyconic shape of the conch developed (Fig. 225).

There was little change in septal geometry of the cheiloceratids, until derivation of the sporadoceratids. Like in the protornoceratids, a small indentation of the suture tended to develop and the final outcome was a rather deep, pointed flank lobe. Together with various combinations of internal conch thickenings, originally parallel to aperture but in derived forms attaining quite unexpected arrangements, this help in distinguishing species. The main change was, however, in the early ontogeny of the conch and vaulting of the internal part of the septum.

The septum is balloon-shaped also in its dorsal part in *Nehdenites* and generalized *Cheiloceras*, developing at the best a minute dorsal indentation. The trifid dorsal lobe is apparently the best marker of the origin of the prionoceratid and dimeroceratid lineages (Becker 1993a) but the exact sequence of events cannot be traced at present.

The evoluteness characteristic of the larval conch expanded to a few further coils in the dimeroceratid clade. Several juvenile whorls developed a very wide, cadiconic appearance (Becker 1993a). Mature *Dimeroceras* reached large size similar to that of somewhat younger *Maeneceras* and the geologically older, large-sized *Tornoceras*, being transitional between them in the septal complexity. Despite the globose conch shape and relatively little complication of the suture, the septum of derived *Dimeroceras* was completely vaulted. This suggest an adaptation to open sea environment, allowing high hydrostatic resistance of the conch but a low investment of deficit calcium in its construction. Possibly, these three large-sized early famennian goniatites were adapted to operate at different water depths.

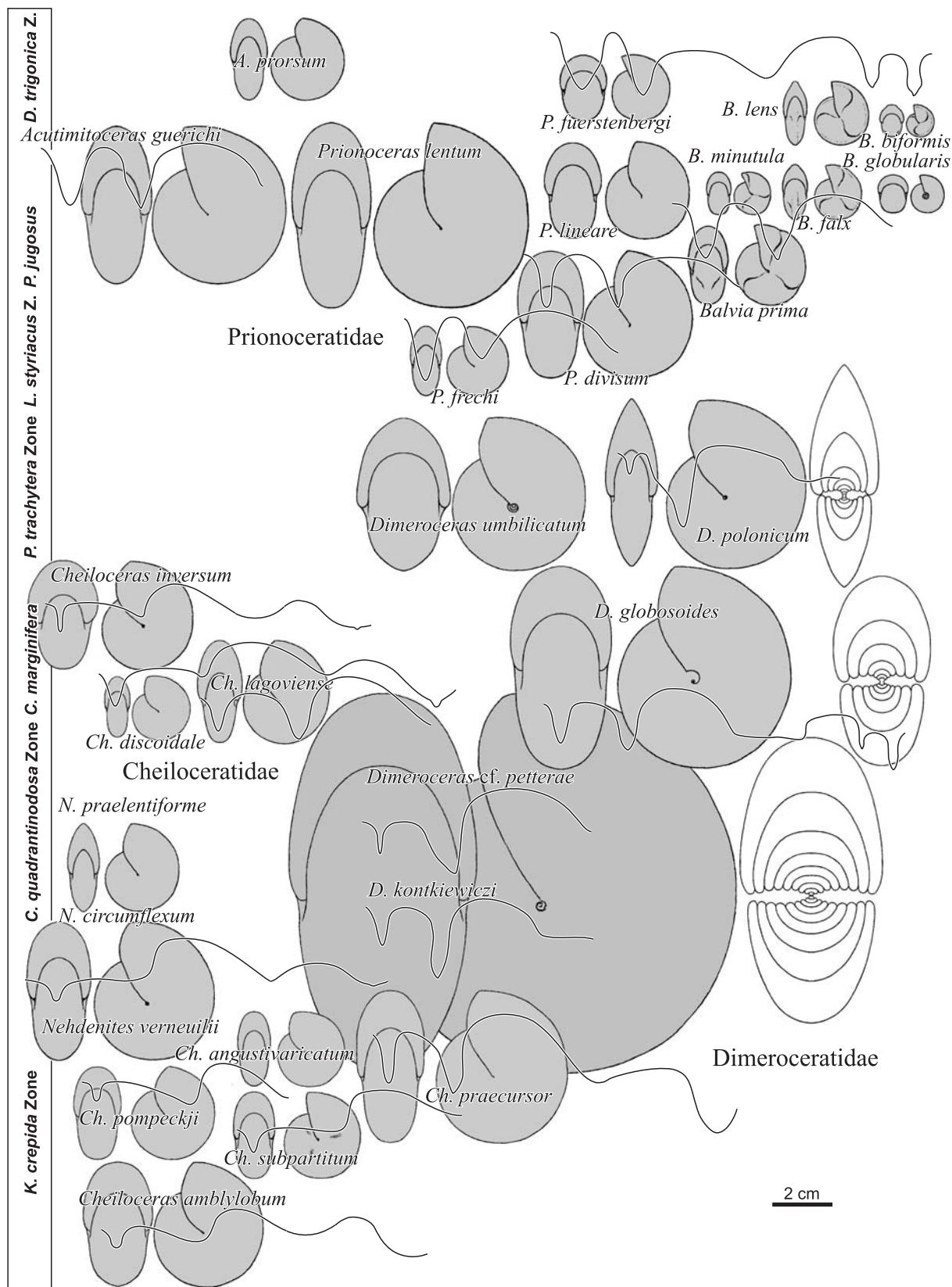


Fig. 225. Chronomorphoclines identifiable in the cheiloceratid, prionoceratid, and dimeroceratid goniatites in the Polish Famennian (for details of stratigraphic distribution of species see Fig. 181). Contours of probably mature specimens in scale and suture lines are given.

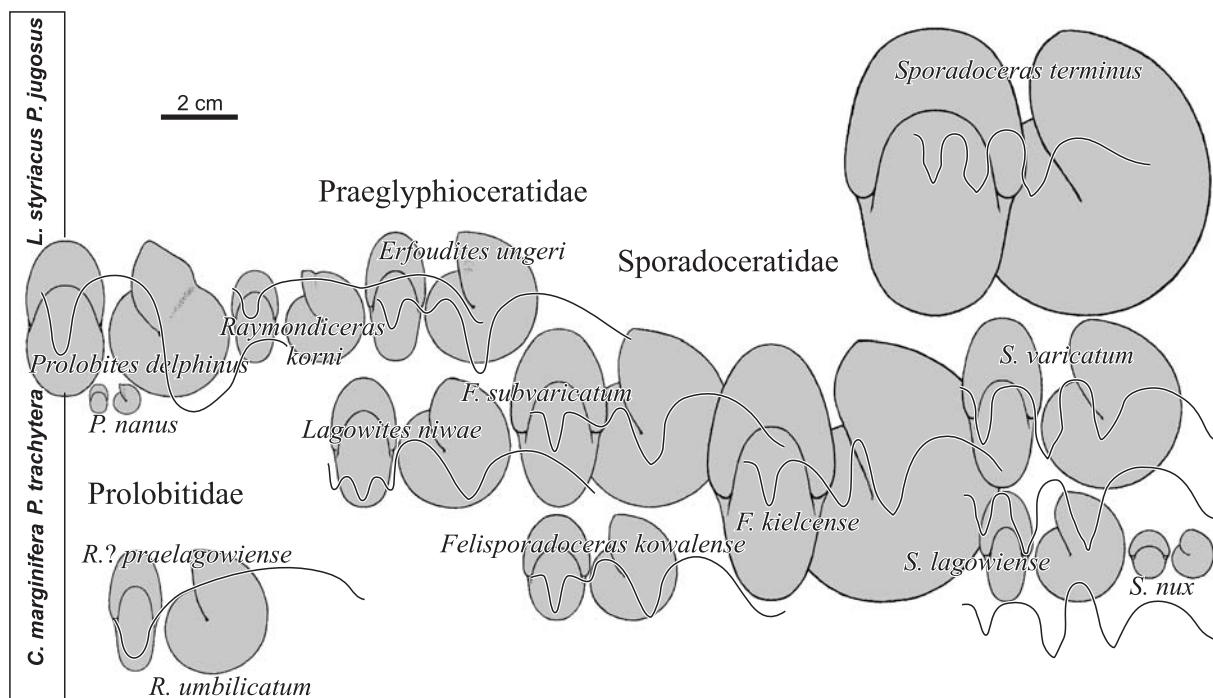


Fig. 226. Chronomorphoclines identifiable in the prolobitid, praeglyphioceratid, and sporadoceratid goniatites in the Polish Famennian (for details of stratigraphic distribution of species see Fig. 181). Contours of probably mature specimens in scale and suture lines are given.

There are many cheiloceratid species in the Holy Cross Mountains (Sobolew 1914a) but in no single case their phyletic evolution is determined. Similarly chaotic seems the distribution of *Dimeroceras* species tending to develop oxyconic conchs (*D. polonicum*). This may be a result of the punctuated fossil record.

Diminutive prionoceratids. — A profound change in the embryonic morphology, of an extent similar to that in the *Tornoceras* larvae, took place at the origin of the prionoceratids. Their conchs and septa are rather indifferent, closely resembling those of *Cheiloceras*, from which the lineage apparently emerged. Their most characteristic aspect is the barrel-like protoconch, attaining remarkable sizes as for the ammonoids (Dzik 1997, p. 109). Such protoconchs emerge in the fossil record in the Holy Cross Mountains together with the first prionoceratids. Ironically, the increase in egg size is connected there with a decrease in size of mature conch. Advanced members of the clade, numerous species of *Balvia* known from the Sudetes, are among the smallest Devonian ammonoids (Korn 1992, 1995). Although their characteristic conchs can be easily arranged in a morphocline (Fig. 225), there is no evidence of any phyletic evolution and their distribution seems controlled mostly by migration.

Near the end of the Devonian a lineage evolving towards oxyconic conchs emerged, of much importance in the Tournaisian (Korn 1994). Another prionoceratid lineage, in which the evoluteness of early stages expanded towards the mature stages, gave origin to the evolute prolecanitid ammonoids of the Carboniferous (Korn 1994).

Simplified septa and controlled ontogeny in *Prolobites*. — The morphological simplicity of the prolobitids forced Bogoslovsky (1969) to look for their ancestry among the most underived Middle Devonian agoniatitids. But this is definitely a case of secondary simplification. There seems to be a chronomorphocline connecting the simplest cheiloceratid *Nehdenites* with *Prolobites* (Fig. 226). The change was in simplification of septa connected with evolute or even cadiconic juvenile conch geometry and in a far-reaching ontogenetic regulation of mature conch features. First, the internal conch thickening was restricted to near the base of the terminal aperture, being associated there with a constriction in the living chamber. By analogy with Recent snails this may be interpreted as protective against predation. In the most derived species, the terminal aperture attained a hood-like appearance. Except for a brief time immediately before the *P. annulata* event, these goniatites were rare. Probably they occupied a rather narrow ecological niche, requiring a special and rarely occurring environment.

Complex septa of the sporadoceratids. — Unlike protornoceratids, in the series leading from *Lagowites* through *Felisporadoceras* to *Sporadoceras*, an additional complication (fluting) of the septum occurred near its venter. This is why the “tornoceratid” *Maeneceras* may be a member of this group despite auriculate aperture. Transitional morphology of the aperture in *Erfoudites* further strengthens this idea. Unlike the *Posttornoceras* lineage, sporadoceratids developed the complete vaulting of the septa rather late and only in the most globose species.

The most primitive sporadoceratid, *F. kowalense*, shows some similarity in its ventral septal geometry to that of the praeglyphioceratids (Fig. 226). This low-diversity branch of the Famennian goniatites has its homeomorph in the tornoceratid *Ostrovkites*. It was probably a short-lived side branch of the sporadoceratids of little importance to the phylogeny of the goniatites.

CLYMENIAS

There is little doubt that clymenias originated from *Protornoceras* (House 1970) and that the South Urals *Kirsoceras* is the connecting link. Yet, the exact course of the transition at the ordinal boundaries has not been determined. The protornoceratids form a whole plexus of species differing in the evoluteness of the conch and usually showing remarkable population variability. They continue their occurrence throughout the *C. quadratinidosa*, *C. marginifera*, and the early *P. trachytera* zones, probably represented by lineages evolving (and speciating?) at place. Their diversity gradually increased and the immigration of the first clymenias at the beginning of the *P. trachytera* Zone is hardly discernible in the spectrum of the ammonoid conch forms. This is only the location of the siphuncle (and replacing the ventral lobe with dorsal one) which makes the difference.

The origin of clymenias. — The first clymenias emerged in the fossil record in the Holy Cross Mountains as a remarkable number of about ten sympatric species. These were small-size ammonoids probably occupying niches in the ecosystem closely similar to those of their relative, the protornoceratids. The beginning of the *P. trachytera* Zone is marked by a sedimentary discontinuity level (Łagów) or at least a change in facies to the predominance of black shale (e.g., Kowala) and obviously a whole new biota invaded the area together with this environmental change. Perhaps the migration route was from the east (the South Urals) to

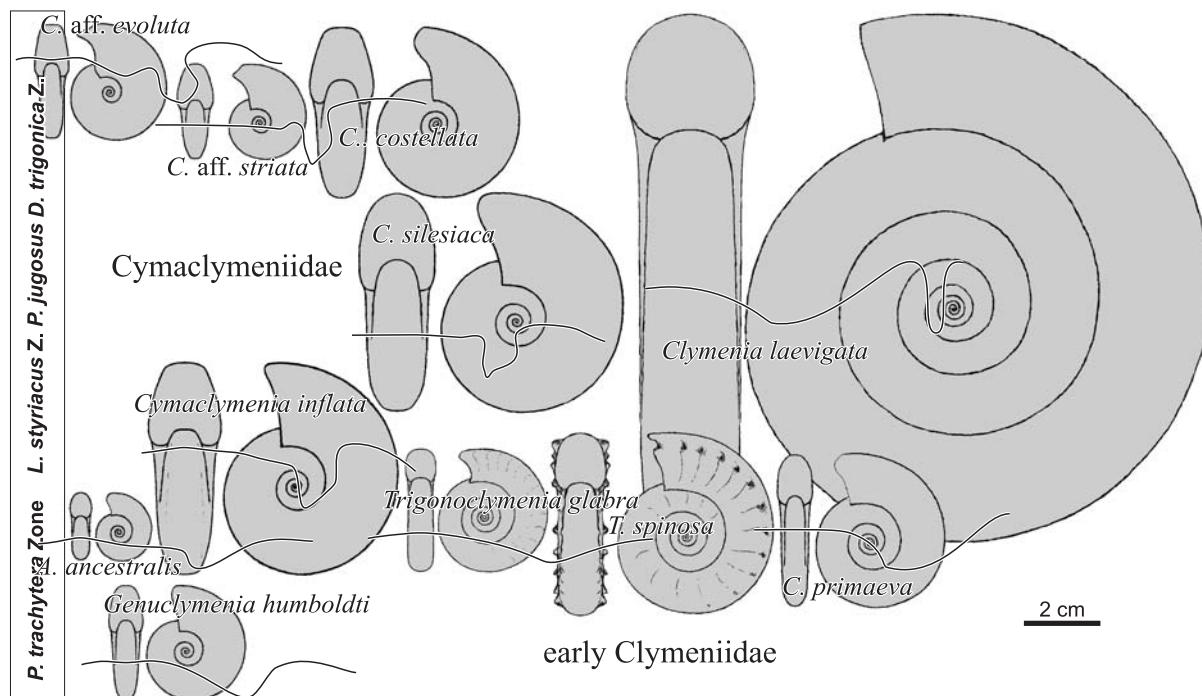


Fig. 227. Chronomorphoclines identifiable in the cymaclymeniid and early clymeniid clymenias in the Polish Famennian (for details of stratigraphic distribution of species see Fig. 196). Contours of probably mature specimens in scale and suture lines are given.

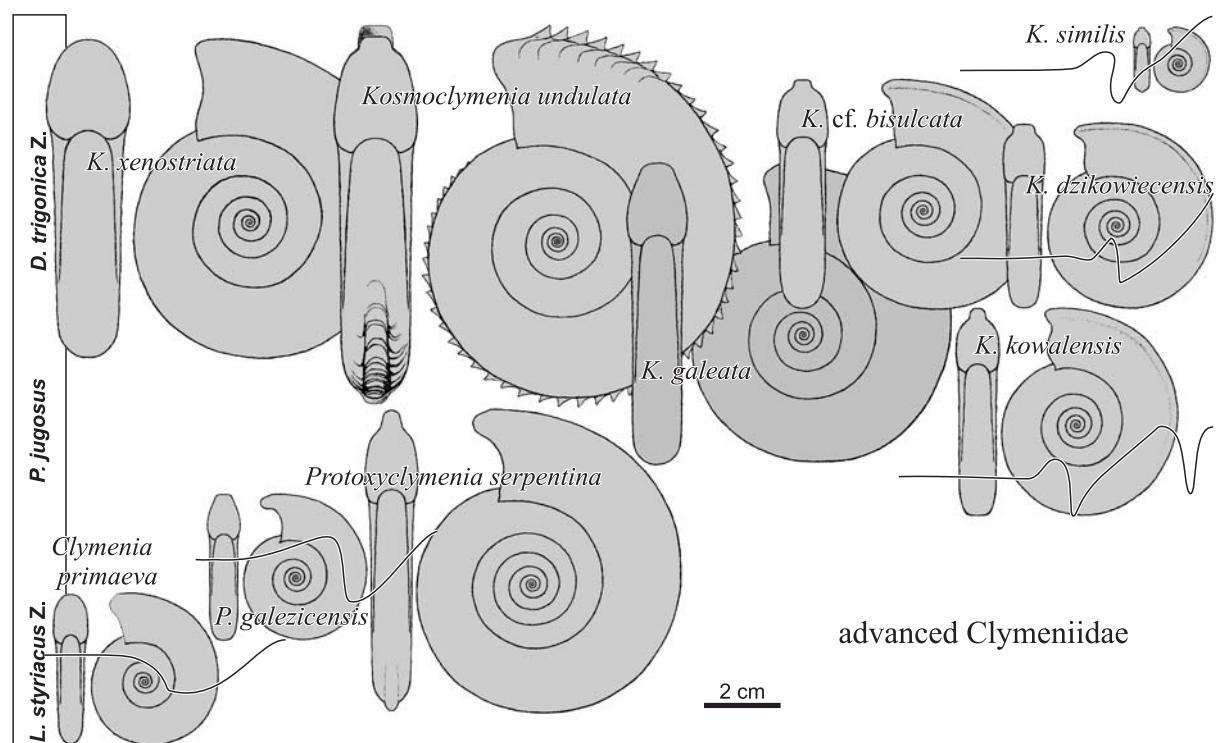


Fig. 228. Chronomorphoclines identifiable in the advanced clymeniid clymenias in the Polish Famennian (for details of stratigraphic distribution of species see Fig. 196). Contours of probably mature specimens in scale and suture lines are given.

west (the Rhenish Massif). This pattern of faunal change precludes any precise phylogenetic studies of the origin and early diversification of clymenias in the Holy Cross Mountains. The clymenias do not have any local roots there.

It seems to be of importance that among the earliest clymenias species with the conch geometry closely resembling *Protornoceras* dominate (Fig. 227). Among them there are species (of *Aktuboclymenia*) with the septal geometry of tornoceratid aspects (except for the location of siphuncle). This conch morphology has appeared highly conservative and continued their occurrence, with some minor modifications, to the end of the occurrence of the order (in the *Cymaclymenia* lineage). Paradoxically, the relatively complex suture and rather involute conchs, rather untypical for the clymenias, appear to be ancestral (plesiomorphic features).

Secondary evoluteness of the clymeniids. — Taking this point of view, the subsequent steps of the evolution was apparently simplification of the septum, which attained the balloon geometry. It can be inferred from the distribution of characters among the first Polish clymeniids, that this happened in the common ancestor of the cyrtoclymeniids (*Cyrtoclymenia*, *Pleuroclymenia*, *Platoclymenia*) and hexaclymeniids (*Praeflexiclymenia*, *Stenoclymenia*), after separation of its lineage from the ancestral cymaclymeniids (*Aktuboclymenia*). Interestingly, in the subsequent independent evolution of each of these branches, the evolute conch geometry developed. A similar increase in the spectrum of conch geometry took place earlier in the *Protornoceras* clade. In all these cases, the probable developmental mechanism of the process was an extension of the early postlarval conch geometry to later stages of the ontogeny.

Platoclymenia and *Cyrtoclymenia* were first clymenias with conch size comparable to that of the stratigraphically preceding them goniatites (Fig. 231). Even larger sizes have been achieved some time later by *Clymenia*.

Thus, from the early branch of the clymeniids with *Protornoceras*-like suture the lineage of *Trigonoclymenia* developed. This led to probably the most evolute and geometrically simple conch morphology of *Clymenia*, generally (but not quite correctly) believed to be typical of the clymenias. Despite simplified conch morphology, the septum of *Trigonoclymenia* is primitively complex. One may guess that *Kosmoclymenia* is its descendant (Fig. 228). Its septal geometry is somewhat more complex and the tendency to a periodic expansion of aperture developed further, resulting in various funnel-like structures. *Kosmoclymenia*

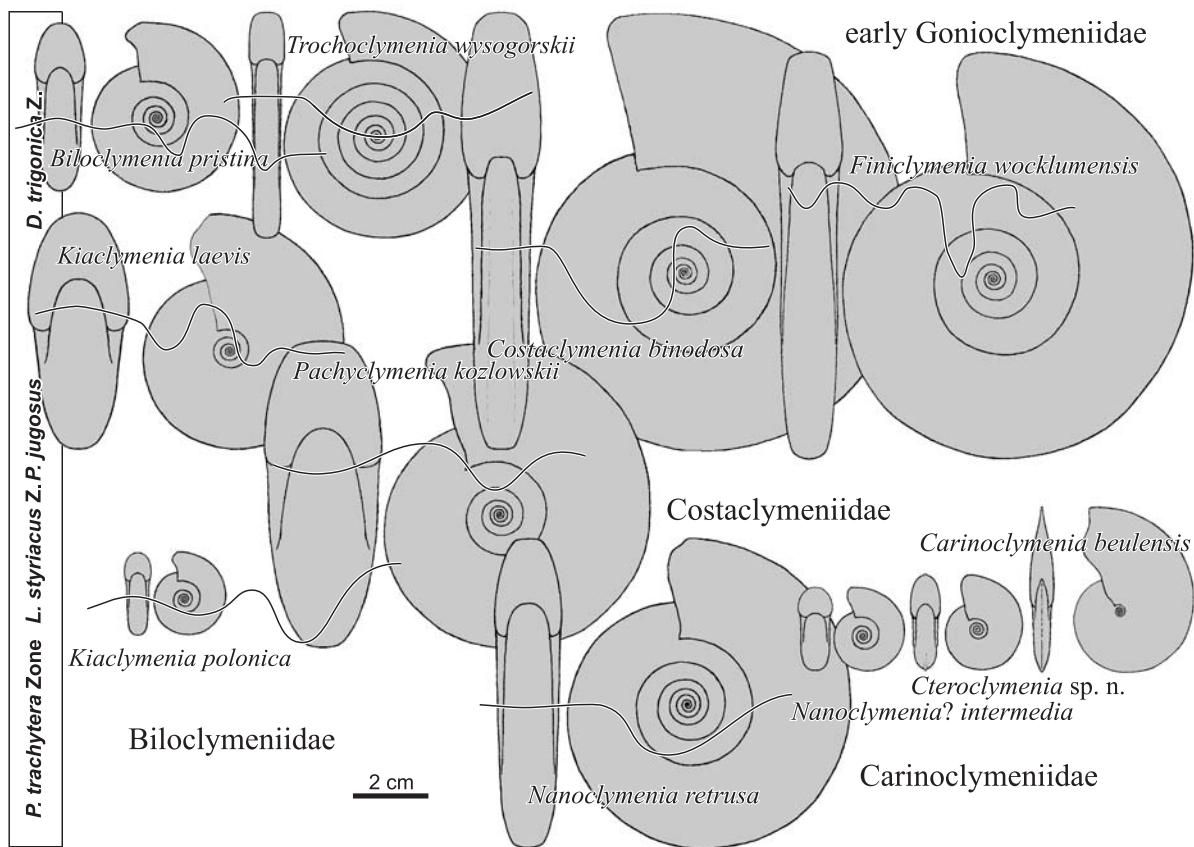


Fig. 229. Chronomorphoclines identifiable in the carinoclymeniid, biloclymeniid, costaclymeniid, and early gonioclymeniid clymenias in the Polish Famennian (for details of stratigraphic distribution of species see Fig. 218). Contours of probably mature specimens in scale and suture lines are given.

is among the most speciose genera of the clymenias. Probably the most significant aspect of its evolution is the rather advanced control of the course of ontogeny. The adult living chamber of *Kosmoclymenia* has a ventral tabulate keel, in many species with periodic apertural funnels protruding (Korn and Price 1987). The maturity was achieved at very different sizes. In some species with minute conch, the ventral keel continues throughout most of the ontogeny. Attempts to restore the course of evolution show a rather complex picture (Korn and Price 1987) and no continuous series of samples showing the phyletic evolution has been assembled until now.

Biloclymeniid septal geometry. — A highly specific mode of modification of the septal geometry was initiated in the late *P. trachytera* Zone (immediately before the *P. annulata* Event) in the lineage of *Genuclymenia*. A relationship to the geologically older *Nanoclymenia* is suggested by the transitional morphology of both the conch and suture of *Pachyclymenia*, known from significantly younger strata and probably relict. In the course of evolution, the septum attained quite a complex appearance but lobes remained smoothly sinuous until the disappearance of the lineage in the early *D. trigonica* Zone (Fig. 229).

Complex septa of the gonioclymeniids. — The tornoceratid septa and evolute conchs are shared by *Nanoclymenia* and *Costaclymenia*, the probable ancestors also of the carinoclymeniid and gonioclymeniid clades. There is a series of progressive complication of the septal geometry, proceeding in the perumbonal, ventrolateral and ventral parts of the septum, and leading to acute tips of lobes and finally of saddles (Fig. 229). *Gonioclymenia*, with its acute saddles is apparently younger geologically than the less derived *Kalloclymenia*. It was also the largest ammonoid of the Famennian. The most complex suture characterizes *Sphenoclymenia* from the *D. trigonica* Zone, but otherwise the stratigraphic distribution of morphologies does not help in deciphering the course of evolution (Fig. 230). These clymenias were apparently ecologically specific and their distribution was controlled more by changes in environment than by their evolution.

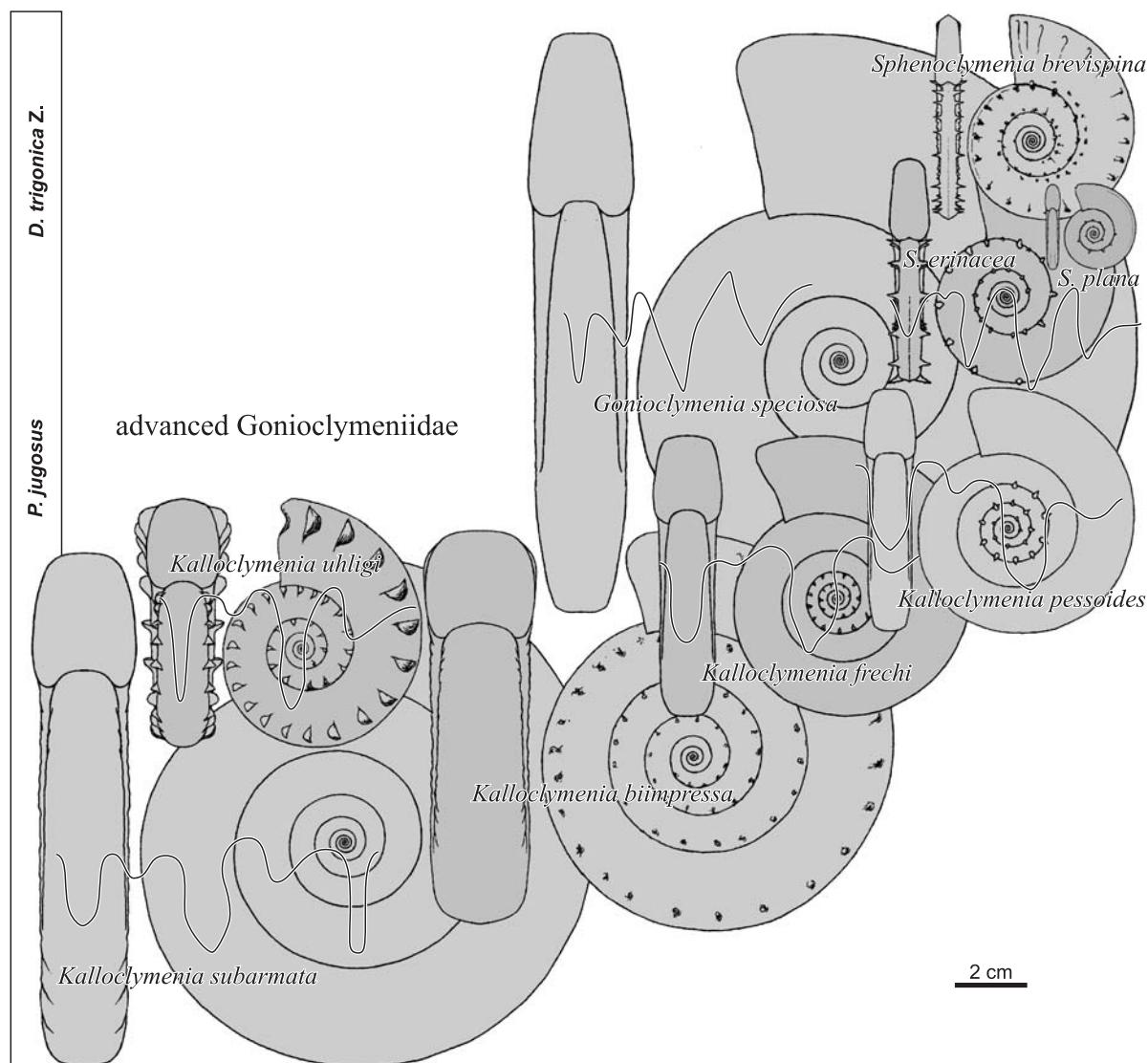


Fig. 230. Chronomorphoclines identifiable in the advanced gonioclymeniid clymenias in the Polish Famennian (for details of stratigraphic distribution of species see Fig. 218). Contours of probably mature specimens in scale and suture lines are given.

Acutely discoidal clymeniids. — Among the early clymenias with a tornoceratid septum, a tendency towards developing a discoidal conch shape, ventral ridge, and then extremely oxyconic conch was quite early initiated (Fig. 229). The succession of morphologies, with *Carinoclymenia* at the end, is consistent with stratigraphy in the Holy Cross Mountains and it is likely that the lineage evolved phyletically at the place.

Carinoclymenia was paralleled in its evolution by the unrelated conservative lineage of *Cyrtoclymenia* (Fig. 231), perhaps having something to do with more advanced in the septal geometry, geographically widespread *Falciclymenia*.

Proterogenetic lineage. — One of the most celebrated cases of the proterogenetic expansion of juvenile morphology to adult stages of the conch development in the ammonoids (Schindewolf 1937; Korn 1992, 1995; Becker 2000) can be supported and extended backward with the data from the Holy Cross Mountains. Specimens of *Soliclymenia aegoceras* from the early *P. jugosus* at Kowala (older than the minute Dzikowiec species), showing a narrow sharp-edged venter of the mature living chamber, point out towards *Stenoclymenia* as the ancestor of the lineage (Fig. 232). Even less derived member of the lineage seems to be *Praeflexiclymenia*, species of which are among the first clymenias in the Holy Cross Mountains. The evolution there was first towards simplification of septa, then increase in the conch evoluteness and tabulation of

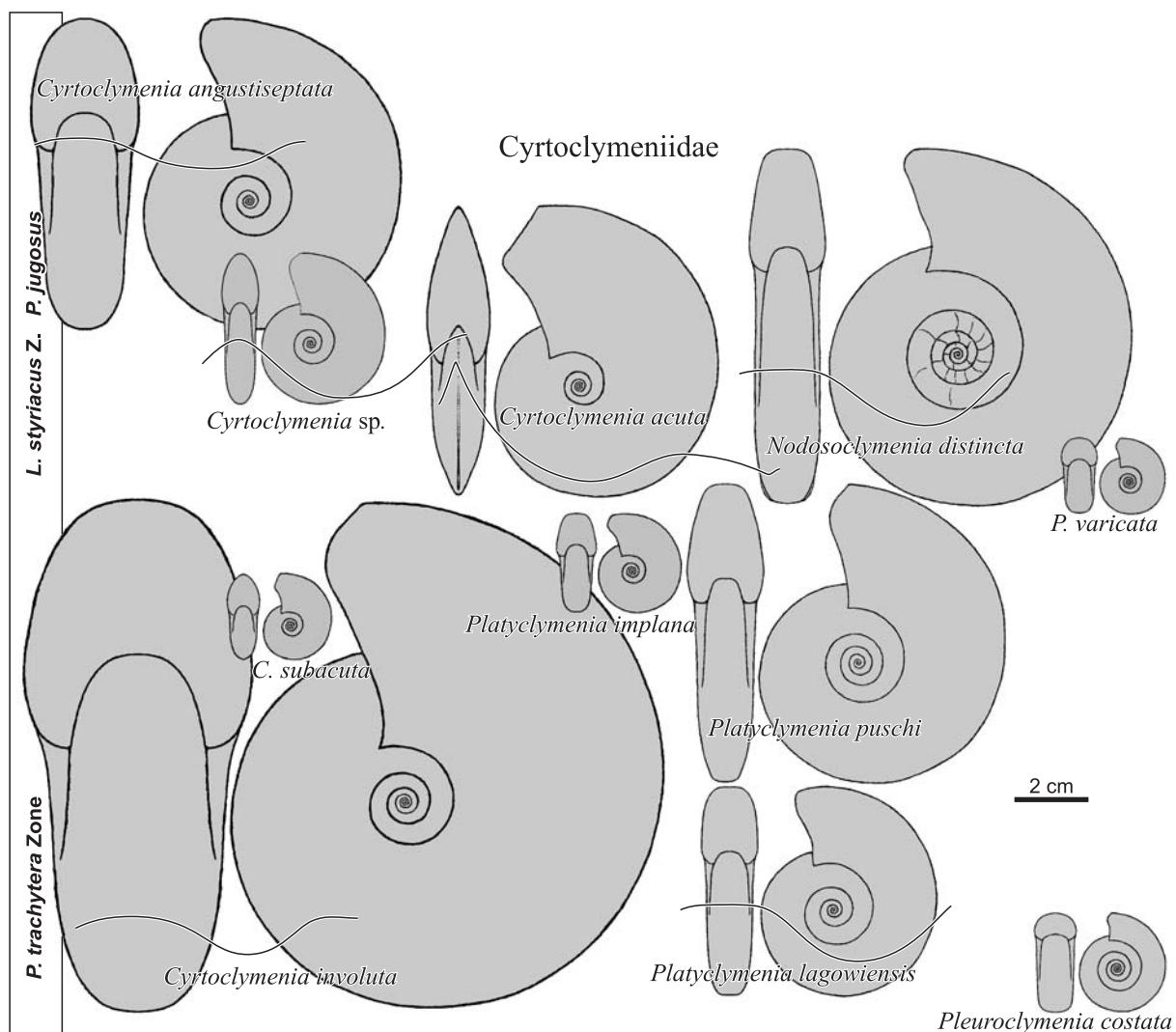


Fig. 231. Chronomorphoclines identifiable in the cyrtoclymeniid clymenias in the Polish Famennian (for details of stratigraphic distribution of species see Fig. 223). Contours of probably mature specimens in scale and suture lines are given.

the venter, and finally diminution in size and domination of ribbing on flanks of low whorls, earlier occurring only in juveniles.

Trigonal and involute wocklumeriid conchs. — This is the second case of proterogenesis and development of trigonal conch shape presented by Schindewolf (1937). The relationships within and the origin of the wocklumeriids was a matter of controversy until the subject was reopened in recent times (Korn 1992, 1995; Becker 2000). It seems now that both *Parawocklumeria* and *Epiwocklumeria* are related to *Glatziella* and have their roots in *Rhiphaeoclymenia*. The sequence of events started from formation of two ventrolateral furrows in *Rhiphaeoclymenia* inherited by its successors. In the lineage of *Glatziella* a cadiconic conch morphology developed, retaining the lateral ribbing until it was lost in *G. glaucopis*. Near the end of the Famennian the tendency to size decrease was partially reversed in the lineage of *Glatziella*, the last member of which is of medium size, typical for most of the Late Devonian ammonoids.

In the *Kamptoclymenia*–*Parawocklumeria* lineage, the ribbing disappeared, being replaced by constrictions at early ontogenetic stages, three per whorl. Mature living chamber preserved ventrolateral furrows until they were lost in *P. distorta*. Furrows are also missing in *Epiwocklumeria* and *Wocklumeria*. These latest Famennian lineages evolved divergently, developing involute oxyconic conch in *E. bohdanowiczi* (with complex ontogeny) and cadiconic conch do not showing significant ontogenetic changes in *Wocklumeria*.

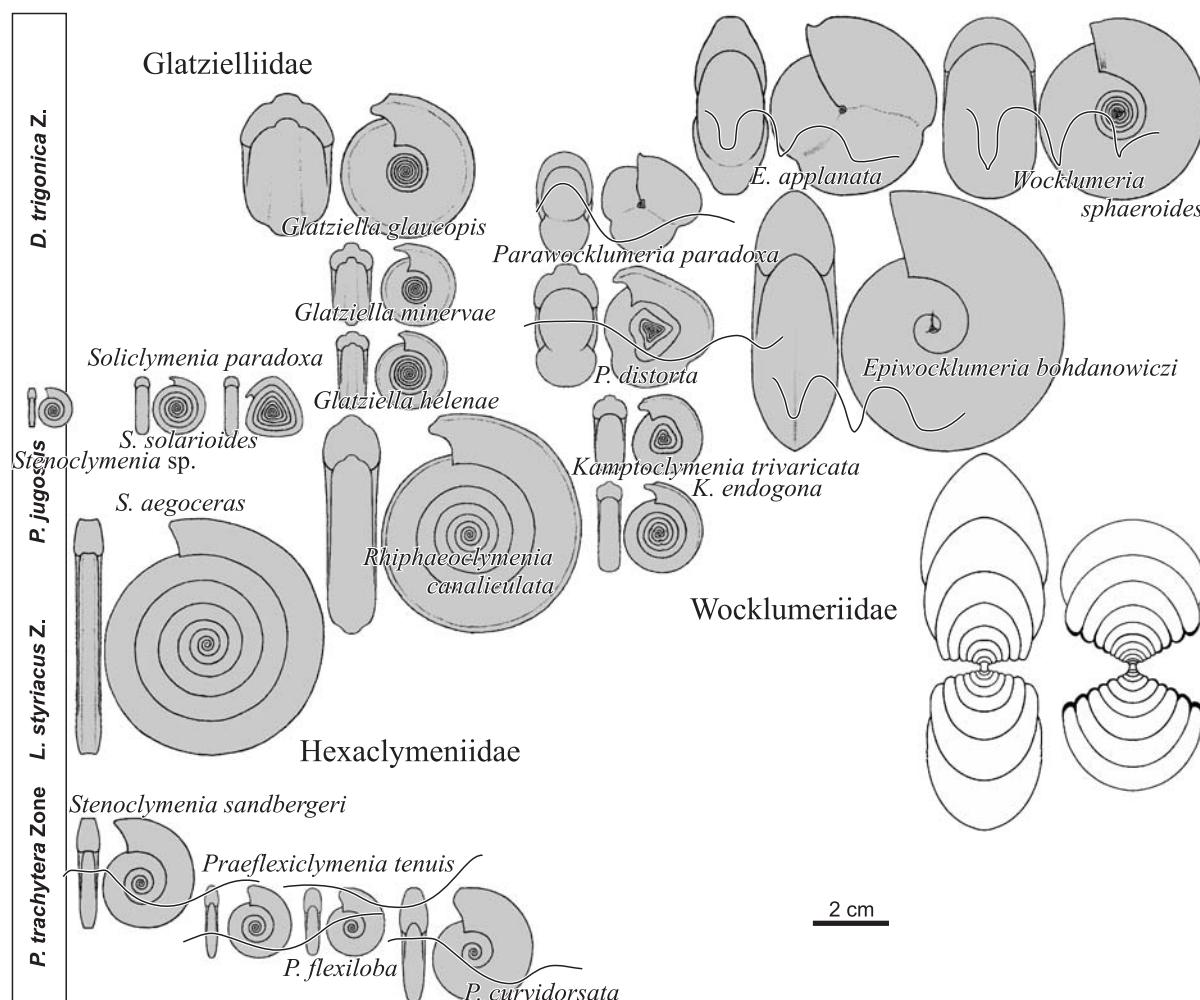


Fig. 232. Chronomorphoclines identifiable in the hexaclymeniid, glatziellid, and wocklumeriid clymenias in the Polish Famennian (for details of stratigraphic distribution of species see Fig. 223). Contours of probably mature specimens in scale and suture lines are given.

sphaeroides. The stratigraphic distribution of these clymenias in the Holy Cross Mountains and Sudetes does not help in deciphering the precise pattern of phylogeny (Fig. 232).

Even more problematic is the origin of the glatziellids and wocklumeriids. Their narrow tabulate venter and prominent juvenile whorls ribbing suggests that *Hexaclymenia* may be their ancestor. A significant time and morphologic gap separates these taxa, so much research is necessary to solve the question.

FAUNAL DYNAMICS OF OTHER FAMENNIAN PELAGIC ANIMALS

In most attempts to interpret profound changes in the Devonian living world abiotic factors tend to be invoked as the only motor of evolutionary change, frequently even of extraterrestrial nature. This is despite the at least equally obvious influence of the evolution of organisms on the environment (e.g., Algeo *et al.* 2001). No doubt that the evolutionary expansion of some ecologically important group of organisms to environments earlier not inhabited by them, or appearance of completely new modes of exploitation of the environment, had a significant influence on fates of the Devonian biota. The fossil record is awfully incomplete in respect to the main producers of biomass in the Devonian, mostly lacking any mineral skeleton and known from very few fossils from rare localities with soft-bodied organisms preservation. But even the available limited evidence provides a remarkable list of high-rank taxa that emerged and expanded in diversity during

the Devonian. Among them are the largest pelagic predators of the Famennian: the open-sea sharks, crossopterygian and ganoid fishes, concavicarid and angustidontid crustaceans, and ammonoid cephalopods. The Devonian was the time of emergence and diversification of the eumalacostracan crustaceans.

At least some of the conodonts seem to be ecological analogues of the recent chaetognaths, feeding on small crustaceans. It remains unknown which of the planktonic filter-feeding crustaceans inhabited the Famennian seas. Their weakly sclerotized body covers had little chance to fossilize. Among the planktonic crustaceans only ostracodes offer a reasonable fossil record of their faunal dynamics and evolution.

Entomozoacean ostracodes. — Faunal changes in planktonic ostracodes across the Frasnian–Famennian boundary has been described by Olempska (2002). Interestingly, the earliest Famennian assemblage of entomozoaceans has appeared to be of very low diversity with single dominant species of *Franklinella*, supplemented with rare *Nehdentalis* in higher part of the section at Płucki. This contrasts with the high diversity latest Frasnian assemblage. Pyritized entomozoid carapaces are common in black shale or limestone facies throughout the Famennian.

Concavicarid thylacocephalans and *Angustidontus*. — Phosphatized crustacean carapaces and grasping appendages are abundant on some bedding planes in the early Famennian laminated limestone at Wietrzna and Kowala. The strongly sclerotized carapaces with reticulate surface pattern up to 5 cm in length represent an unnamed species of *Concavicaris*. These were relatively large predators with large compound eyes and long but rather weakly sclerotized grasping appendages emerging from the ventral opening of the carapace, but except for carapaces nothing convincingly attributable to the concavicarids has been identified in the Holy Cross Mountains material. No doubt, however, that they were common in the pelagic environment during the Famennian playing an important role in the ecosystem.

Strongly sclerotized, secondarily phosphatized appendages and mandibles (Dzik 1980) of *Angustidontus* co-occur with concavicarids in great number throughout most of the early Famennian in the Holy Cross Mountains. These were eumalacostracans with the first postoral appendage pair transformed into a mantis-like grasping apparatus (Rolfe and Dzik 2007). Ironically, opposite to the situation in *Concavicaris*, the appendages of *Angustidontus* preserve well in the fossil record but the carapace was weakly sclerotized and no remnants of it has been found in the Holy Cross Mountains material. Although pelagic, *Angustidontus* may be related also to the stomatopods, predatory benthic crustaceans with reduced carapace, known since the Early Carboniferous. The alternately toothed grasping parts of the *Angustidontus* appendages closely resemble “hindeodella” type of conodont elements but are of an order of magnitude larger. It is likely that they fed on conodonts.

Nautiloids. — Nautiloids co-occur with ammonoids in all localities of cephalopod limestone or black shale of the Frasnian and Famennian of the Holy Cross Mountains and the Sudetes. The terminal Frasnian *linguiformis* Zone cephalopod limestone occurs in Wietrzna and Płucki. Nautiloid fossil assemblages of these sites differ dramatically, despite their age and similar conodont assemblages. In Płucki, numerous orthoconic bactritids and *Plagiostomoceras*-like orthoceratids co-occur with small-size oncoceratids probably representing an unnamed species of *Pachtoceras* (Dzik 1985). At Wietrzna, oncoceratids dominate, with large extremely breviconic undescribed form and *Lysagoraceras*-like slender conchs. The only nautiloid shared by both sites is a large orthocerati resembling the Famennian *Plagiostomoceras?* *cardiolae* (Gürich, 1896). The only locality with cephalopod limestone of the *K. triangularis* Zone is Psie Górk. The assemblage is composed almost exclusively of crushed indeterminable oncoceratids. Diverse assemblages of nautiloids has been identified in the *K. crepida* Zone at Kadzielnia and *C. marginifera* Zone at Łagów-Dule (Dzik 1985). In the latter locality also the clymeniid limestone of the *P. trachtera* Zone yielded nautiloids, but the fossils were collected from loose blocks and it is rarely possible to be confident with its exact stratigraphic location. The only reliable source of stratigraphic information on Łagów-Dule remains the study by Sobolew (1912b). Anyway, all those faunal assemblages appear to be rather different from each other but not as a result of different age, but rather of different environment. The oncoceratid nautiloids species were apparently very sensitive on the local condition. The overall spectrum of their morphologies in the Famennian is the same as in the latest Frasnian and there is hardly any reason to see termination of a substantial portion of their lineages at the Frasnian–Famennian boundary.

The mode of life of the orthoceratid and oncoceratid nautiloids, as well as their trophic preferences, remain a mystery. They were hardly efficient swimmers and even their predatory abilities may be questioned. The only unquestionable large predators of the late Devonian remain the vertebrates.

Fishes. — In the Late Devonian three groups of vertebrates are already well established in the open sea pelagic environment: ganoid fishes, sharks, and the acanthodians (e.g., Blieck *et al.* 2000; Ginter 2001). They all have Silurian roots in near-shore marine environments and in the late Silurian they rarely co-occur with conodonts in pelagic sediments. The difference in facies distribution of early vertebrates and conodonts was probably a reflection of their physiology. The conodont's kidneys, similarly to Recent myxinoids, apparently lacked renal tubuli enabling osmotic regulation of sodium content in their blood and could not enter waters of lowered salinity (Dzik 2000). This was opposite to the early agnathans and fishes easily entering brackish waters and in the Devonian (like Recent petromyzontids) expanding both to rivers and to the ocean.

The most complete record of the stratigraphic and geographic distribution of fishes is offered by acid resistant residues of limestone samples. The biological productivity of fishes was a small fraction of that of the conodonts. Only in samples from stratigraphically condensed sections, where winnowing enriched the lime mud in phosphatic debris, more than a few specimens per a few kilogram weight sample can be collected. Teeth and scales of the chondrichthyans are known from both the Frasnian and Famennian, and there is no special reason to propose any dramatic change in fish faunas at the boundary in the Holy Cross Mountains (Ginter 1992, 1995, 1999, 2000, 2002). Also placoderms, known mostly after isolated large bones show a phyletic continuity across the boundary (Ivanov and Ginter 1997). Acanthodians, known mostly after their scales, also occur on both sides of the boundary.

The Famennian fishes represent various levels in the trophic pyramid of their ecosystem. The shark *Cladoselache* from the Cleveland shale (Cleveland Member of the Ohio Shale Formation) of Ohio is known to prey on the ganoid fish *Kentuckia* (found in the stomach contents of 65% of 53 specimens; Williams 1990), but also on the crustacean *Concavicularis* (28%), and conodonts (9%). Other fishes probably were more inclined to benthic animals as their food, as suggested by coprolites from the underlying Chagrin Member of the same Formation (Hannibal *et al.* 2005). Most probably, the sharks in the Polish Famennian played a similar role as those in Ohio, as all these groups of pelagic animals are abundantly represented there in acid-resistant residues.

The characteristic feature of the early Famennian *K. triangularis* Zone fish assemblages from Karczówka and Jabłonna is the relative abundance of scales and teeth of the protoacrodontid sharks (cf., Ginter and Piechota 2004) and the acanthodians, thus a composition closely similar to the assemblage from the latest Frasnian at Miedzianka. Remnants of crossopterygian fishes are also known from the early Famennian of Karczówka (scales) and Kowala (onychodontid skull; Dzik 1992, fig. 1.6C). Interestingly, in the earliest Famennian of Dębnik near Kraków the same species of the crossopterygian *Strunius* occurs (Ginter 2002) as in the latest Frasnian of Miedzianka and Kowala. The similarity in local environment (near shore in both cases) were apparently more important than the difference in age.

The change in composition of the fish assemblages during the Famennian is mostly connected with facies changes, and only to some degree a result of evolutionary transformations. In the black limestone of the *C. marginifera* Zone at Łagów, where fish skeletal remains are relatively common, teeth of the phoebodontid sharks dominate in number over the acanthodian and ganoid fish scales. Near the *Platyclymenia annulata* Event black shale (*P. trachytera* Zone) at Kowala and limestone at Ostrówka, the ganoid? fish teeth and scales dominate associated by acanthodians, with minor contribution of shark teeth.

The general pattern of the fish distribution in the Famennian of the Holy Cross Mountains is towards reduction in their diversity (Fig. 233). This is most apparent in case of sarcopterygian fishes, known only in the earliest Famennian *P. triangularis* Zone. Chondrichthyan scales, probably partially belonging to placoderms, occur mostly in the late part of the Zone and in the *K. crepida* Zone. They disappear from the record after the *P. trachytera* Zone. The ganoid fish scales and conical minute teeth seem to be restricted to two episodes of high sea-level stand, in the *K. crepida* and *P. trachytera* zones. These were apparently open-sea pelagic species. Also acanthodians are common in most of the succession but are rare in the late Famennian. The most uniform is distribution of shark teeth. Rare teeth of advanced phoebodontid *Thrinacodus*, less derived sharks and ganoid scales occur throughout the late Famennian. They continued to the Carboniferous in the region.

Possible cause of the diversity changes. — It is generally accepted that taxonomic diversity of marine communities is a function of the heterogeneity of the environment, competition between individuals of various species, and predation pressure (Paine 1966; Connell 1975; Menge and Sutherland 1976, 1987). The pelagic environment of the Famennian Variscan Sea, located in low latitudes and opened to the ocean, the heterogeneity factor was probably of minor importance. One may thus wonder whether there were changes in predation or rather in competition that made the diversity of conodonts and ammonoids to change so dramatically (Fig. 233).

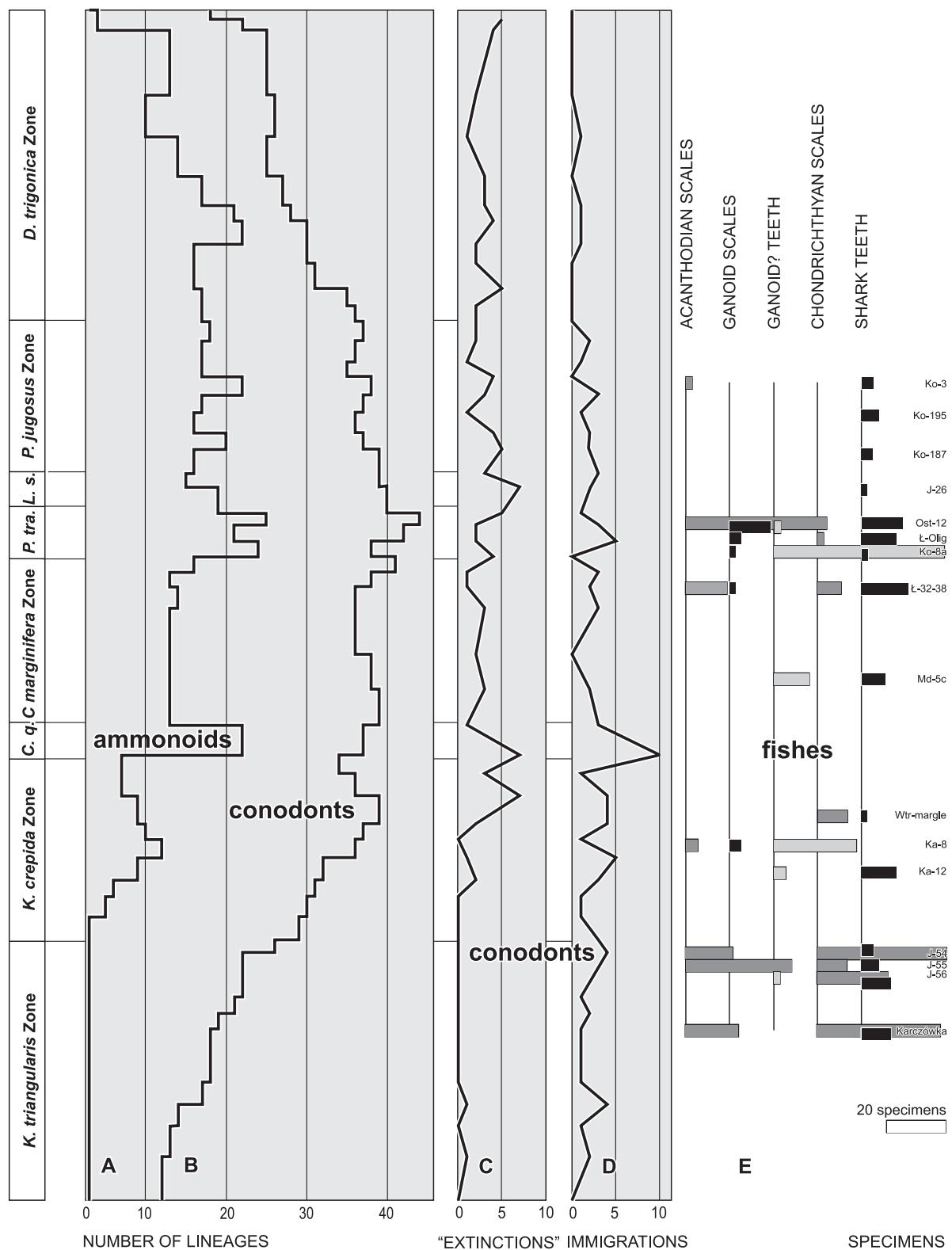


Fig. 233. Dynamics of the Famennian pelagic faunas in the Polish part of the Variscan sea. Number of lineages has been inferred from the punctuated fossils record of conodonts and ammonoids by connecting the known occurrences by hypothetical lineages. Note that the age correlation of particular sections is not precise enough to be distinguish sympatric occurrences from successive occurrences. The time segments within particular zones are arbitrary. Numbers of lineages disappearing from the record or immigrating to the area are counted for each of those units. Fish remains (ichthyoliths) are rare in most conodont samples and their number is given only for the most productive samples to show horizons with their greatest abundance and contribution of particular high-rank taxa to samples.

The conodonts were small predators with a 3–7 cm long lamprey-like bodies. They most probably occupied niches similar to those of the present-day chaetognaths and fed on small planktonic arthropods (e.g., Sweet 1988). They were almost certainly a prey to co-occurring predatory concavicarid crustaceans and possibly also to the ammonoids. Both these groups of Devonian animals had body volume at least an order of magnitude larger than the conodonts. However, in the Devonian the fishes entered pelagic environments and their contribution to fossil assemblages with conodonts and ammonoids gradually increased. It is thus tempting to check whether there was a correlation between the productivity and diversity of conodonts, ammonoids, and fishes in the course of the evolution of the Famennian ecosystem of the Variscan Sea.

The available data are unavoidably incomplete and biased, as usual in paleontology, so it would be premature to expect that a rigorous statistical work can be done based on the evidence assembled in this work. Anyway, some preliminary observations may be useful as suggestion to future research. However incomplete is the fossil record in the Famennian of the Holy Cross Mountains, it is apparent that the species diversity of conodonts dramatically, although gradually increased to reach a plateau in the *K. crepida* Zone (Fig. 233). Ammonoids show a similar pattern, but they did the same with a significant delay. They were also delayed in respect to conodonts in reducing their diversity in the late Famennian. Both groups suffered equally near the end of the Famennian, however. The pattern of distribution of skeletal elements of fishes (ichthyoliths) is completely different. The peak in their taxonomic diversity and abundance of fossils was in the earliest Famennian and there was apparently a continuity from the Frasnian, even at the species level. The dominant chondrichthyan probably gradually decreased abundance and perhaps also species diversity and only the distribution of the ganoid fishes seems correlated with eustacy, their occurrence reaching the highest level during the *K. crepida* and *P. trachytera* zones high stands of the sea level. These peaks are identifiable also in the pattern of diversity of conodonts and ammonoids, but in both cases are not so dramatic.

It can thus be hypothesized that it was probably not the predation pressure from fishes that caused conodonts and ammonoids to increase their diversity in the early Famennian. It is also unlikely that the ammonoids were the source of factors governing the distribution of taxonomic diversity of the conodonts. We have thus to return to the factor of the environment instability to explain the observed pattern of the conodont and ammonoid faunal dynamics in the Famennian of the Polish part of the Variscan Sea. However, it was probably not the instability in the ecological time terms. The source of diversity was probably provided rather by several climate and sea level changes, which forced the pelagic to change their large-scale geographic distribution (?progressive cooling and glaciation; Strel et al. 2000; Brand et al. 2004).

This could have been a factor promoting allopatric speciation and subsequent mixing of geographically distant communities. Much more research based on dense sampling in different regions of the world is necessary to identify exact sequence of events in their time and space dimensions.

CONCLUSIONS

Pelagic organisms with mineral skeleton offer the best fossil record of evolution. Among them the phosphatic teeth of conodonts are especially abundant, easy to be extracted from rock samples, and rich in information of taxonomic value. Ammonoid conchs can compete with them as a subject of evolutionary research. Although not so easily fossilizing, they attract collectors and after more than two hundred years of their professional studies by geologists and paleontologists over the whole world, one may expect that knowledge of their evolution is reasonably complete. Yet, having an opportunity to study a large collection of conodonts and ammonoids and compare it with a tremendous amount of published data I am hardly able to present a convincing picture of the evolution of pelagic biota in the Famennian of central Europe. Two aspects of the fossil record of their evolution makes this so difficult.

The first obstacle is that almost all the available evidence is restricted to the equatorial climatic zone of the Late Devonian (compare Racki 2005). As a result, the geographic dimension of their evolution remains out of reach of their students. With data from thousands of conodont samples and hundreds of localities along the equatorial zone, the evolving lineages should be traced whenever they enter the tropics. Unfortunately, taxonomic resolution seems to be too low to see all the important differences and identify affinities at sufficiently low taxonomic level. This is because virtually all the published data is on typologically defined forms of one

element type in the oral apparatus, which is composed of many elements representing usually six or seven different morphologies. The apparatus reconstructions presented in this and a few other published works help in removing this limitation. They still are too few and from not enough numerous regions to enable understanding of their evolution in time and space. Much more apparatus research is necessary to achieve this.

The second difficulty is caused by the punctuated distribution of fossiliferous strata, controlled by eustacy and changing climate, so profound in the Famennian (Johnson *et al.*, 1985, Walliser 1996; Strel *et al.* 2000). In cases when the record is complete enough to record evolution, as is the case with the palmatolepidid conodont *Tripodellus* or oxyconic goniatite *Tornoceras* lineages, its gradualistic nature is obvious. In other cases the evolution was probably of the same nature and only punctuation of the record prevents its presentation. Anyway, the sections with potentially accessible record of the phyletic evolution are rare as compared with those clearly showing geographic migrations. No doubt that migration was the most important factor controlling distribution of the equatorial Devonian faunas of pelagic organisms.

A good record of evolution appears to be more difficult to find near the paleoequator than in regions located in high paleolatitudes. No doubt that in purely physical terms the environment is less stable in high latitudes, whereas there is no special reason to believe that conditions of sedimentation differed between latitudes, in respect to possible preservation of continuous fossil record. What exactly caused this distinction remains to be determined but one may speculate, that the equatorial organisms are sensitive to even minor differences in environment, to which they immediately respond by changing their spatial distribution. It may be enough that cold deeper waters enter, or retreat from, shallow oligotrophic seas, changing either their temperature or primary productivity, to cause a dramatic rebuilding of assemblages. Perhaps what we observe in the pelagic Famennian of the Holy Cross Mountains and the Sudetes is an illustration of numerous such changes.

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Table 1. Frequencies of conodont elements in samples from the earliest Famennian of Plucki, the Holy Cross Mountains. In this and following tables elements which cannot be safely attributed to particular species on morphologic grounds are listed under generic headings. In cases when even such determination was not possible, they are attributed arbitrarily to one of species to which they may belong, as a rule to that of highest contribution to the sample.

Table 2. Frequencies of conodont elements in samples from the early Famennian of Łagów, Wietrzna, and Jabłonna, the Holy Cross Mountains.

Table 3. Frequencies of conodont elements in samples from the early Famennian of Jablonna and Lagow, the Holy Cross Mountains.

Table 4—continued																		
	J-3	J-4	J-63	J-68	J-5	J-6	J-7	J-8	J-9	J-12	J-13	J-14	J-15	J-16	L/P/ I- 2	L/ Mec		
<i>Lagoviginatus</i> <i>glaber</i>	P ₁ P ₂ S ₀ S ₁ S ₂ S ₃ M	5 4 4 2 14 2						4 6 1 2 4 1						9 12 3		1 1 5 1 1 1		
<i>P. pergraua</i>	P ₁ P ₂ S ₀ S ₁ S ₂ S ₃ M	1 2 2 1 1 1 2				2 1 1 1 1 1 1	13 13 1 1 1 1 1									3 7 1 1 1 1 1		
<i>K. quadratinodus</i> <i>sulcata</i>	P ₁ P ₂ S ₀ S ₁ S ₂ S ₃ M	137 34 1 1 4 1 2	5 13 1 1 1 2 1	14 83 7 1 2 1 1	12 112 6 1 2 2 1	189 130 4 1 1 2 1	12 8 1 1 2 2 1	130 2 1 1 1 1 1	2 1 2 1 1 1 1	4 4 2 2 2 2 1	4 4 25 25 25 25 25	4 4 2 2 2 2 1	16 16 16 16 16 16 16		1 1 1 1 1 1 1			
<i>K. regularis</i>	P ₁ P ₂ S ₀ S ₁ S ₂ S ₃ M	23 1 1 1 1 1 1	1 9 1 1 2 1 1		15 15 1 1 1 1 1			16 11 2 1 1 1 1		3 2 1 1 1 1 1								
<i>K. rupperilensis</i> <i>wolskae</i>	P ₁ P ₂ S ₀ S ₁ S ₂ S ₃ M	1 1 1 1 1 1 1																
<i>K. circularis</i>	P ₁ P ₂ S ₀ S ₁ S ₂ S ₃ M			6 1 1 1 1 1 1	25 29 3 5 5 5 1		11 29 3 5 5 5 1	47 37 2 1 1 1 1		4 2 1 1 1 1 1								
<i>K. rupperilensis</i> <i>crepida</i>	P ₁ P ₂ S ₀ S ₁ S ₂ S ₃ M	17 2 3 14 3 1 1		7 2 2 3 6 1 1	30 1 1 2 3 2 1	50 14 4 2 1 2 1	14 4 2 2 1 2 1	14 4 2 2 1 2 1	5 1 1 1 1 1 1									
<i>P. unimolarepis</i> aff. <i>sandbergi</i>	P ₁ P ₂ S ₀ S ₁ S ₂ S ₃ M	293 23 14 3 1 1 1		35 6 6 3 1 1 1														
<i>T. variabilis</i>	P ₁ P ₂ S ₀ S ₁ S ₂ S ₃ M	152 2 17 5 6 9 12	4 20 7 5 2 3 9	58 93 9 12 2 3 8	59 102 9 23 1 1 6	73 98 1 1 1 1 8	11 9 1 2 3 2 24	98 28 5 3 1 2 2	102 20 20 20 1 1 1	1 1 1 1 1 1 1	26 20 20 20 1 1 1	1 1 1 1 1 1 1	13 14 14 14 14 14 14	13 14 14 14 14 14 14	1 1 1 1 1 1 1			
<i>T. subtilis</i>	P ₁ P ₂ S ₀ S ₁ S ₂ S ₃ M	1 1 1 1 1 1 1																
<i>C. lingulifolia</i>	P ₁ P ₂ S ₀ S ₁ S ₂ S ₃ M	3 3 3 3 3 3 3																
<i>C. teminpanacea</i>	P ₁ P ₂ S ₀ S ₁ S ₂ S ₃ M																	
<i>C. prima</i>	P ₁ P ₂ S ₀ S ₁ S ₂ S ₃ M																	
<i>C. klapperi</i>	P ₁ P ₂ S ₀ S ₁ S ₂ S ₃ M																	
<i>Condilomys</i> spp.	P ₁ P ₂ S ₀ S ₁ S ₂ S ₃ M																	
Table 4. Frequencies of conodont elements in samples from the early Famennian of Jablonna, Wiertnia, and Miedzianka, the Holy Cross Mountains.																		

JABLONNA Wiertnia Miedzianka																		
	J-65	J-40	J-41	J-42	J-43	J-44	J-45	J-46	J-47	J-48	J-49	J-50	Wr- 32	Wr- 21	Wr- 33	Md- 1		
<i>Icriodus</i> <i>continuus</i>	P ₁ P ₂ -M ₁ S ₁	11 81			1								11 36	1 1	1 2	2 2		

Table 4. Frequencies of conodont elements in samples from the early Famennian of Jablonna, Wiertnia, and Miedzianka, the Holy Cross Mountains.

Table 4 – continued												Table 4 – continued																							
		J-65	J-40	J-41	J-42	J-43	J-44	J-45	J-46	J-47	J-48	J-49	J-50	Wtr-21	Wtr-32	Wtr-33	Md-1	J-65	J-40	J-41	J-42	J-43	J-44	J-45	J-46	J-47	J-48	J-49	J-50	Wtr-32	Wtr-21	Wtr-33	Md-1		
<i>Francocilia</i>	P ₁																	<i>Klapperichensis</i>	P ₁	5	2		1	2	2	1	5	1							
<i>santacrucensis</i>	P ₂																	<i>regularis</i>	P ₂	2															
<i>S₀</i>																		<i>S₂</i>		1															
<i>S₁</i>																		<i>S₄</i>		1															
<i>S₂</i>																		<i>Klapperichensis</i>	P ₁																
<i>S₃</i>																		<i>circularis</i>	P ₂																
<i>S₄</i>																		<i>S₁</i>		5	2														
<i>M</i>																		<i>S₄</i>		5	2														
<i>Francocilia</i>	P ₁	2	1	1	2	2	1	8	1	14	1	13	1	13	2	5	2			2	3	1	1	1	1	1	1	1	1	1	1				
<i>franconica</i>	P ₂	7	5	1	2	1	1	14	1	23	1	13	1	13	1	13	2			3	1	1	1	1	1	1	1	1	1	1					
<i>S₀</i>		6	1															<i>S₀</i>		1															
<i>S₁</i>		1																<i>S₁</i>		1															
<i>S₂</i>		7																<i>S₂</i>		1															
<i>S₃</i>		29	6															<i>S₃</i>		1															
<i>S₄</i>		1																<i>S₄</i>		1															
<i>M</i>		16	1															<i>M</i>		11	13	3													
<i>Melithia</i>	P ₁	2																		1	9														
<i>robustidentata</i>	P ₂																																		
<i>S₀</i>																																			
<i>S₁</i>																																			
<i>S₂</i>																																			
<i>S₃</i>																																			
<i>S₄</i>																																			
<i>M</i>		3																																	
<i>C. brevianina</i>	P ₁																																		
<i>Immagiathus</i>	P ₁	5	1	8	28	14	13	3	2	15	2	15	2	15	2	15	2			10	17	5	1												
<i>streedi</i>	P ₂																			1	4	2	1												
<i>S₀</i>		1		1	2	1	2	1	2	1	2	1	2	1	2	1	2		1	6	2	1													
<i>S₁</i>																				5	9	1													
<i>S₂</i>																				15	27	1													
<i>S₃</i>																				9	15	1													
<i>S₄</i>																				15	30	1													
<i>M</i>																				1	2	1													
<i>P. semicostatus</i>	P ₁	1																		3	12														
<i>Polygnathus</i>	P ₁	1	2																	7	10	2													
<i>procerus</i>	P ₂																			1	3	6													
<i>S₀</i>		3																		2	3	1													
<i>S₁</i>																				1	2	1													
<i>S₂</i>		2																		2	6	4													
<i>S₃</i>		1																		2	1	20													
<i>S₄</i>		1																		5	5	4													
<i>M</i>																				11	11	11													
<i>Ancyrognathus</i>	P ₁	3																																	
<i>sp. n.</i>	P ₂	2																																	
<i>S₀</i>		1																																	
<i>S₁</i>																																			
<i>S₂</i>																																			
<i>S₃</i>																																			
<i>S₄</i>																																			
<i>M</i>																																			
<i>Lagovignathus</i>	P ₁																			1	2	1													
<i>glaber</i>	P ₂																			4	4	5													
<i>S₀</i>																				1	3	2													
<i>S₁</i>																				1	1	2													
<i>S₂</i>																				16	7	2													
<i>S₃</i>																				23	2	9													
<i>S₄</i>																				1	1	6													
<i>M</i>																				16	2	9													
<i>K. quadrangularis</i>	P ₁	86	3	2	20	5	52	297	25	18	1	1	1	1	1	1	1	1	2	66	14	1													
<i>sotobata</i>	P ₂	2	9	13	37	1	2	1	1	1	1	1	1	1	1	1	1	1	2	13	9	8	2	1	1	1	1	1	1	1	1				
<i>S₀</i>																				13	37	1													
<i>S₁</i>					</td																														

Table 6. Frequencies of conodont elements in samples from the early Famennian of Kądzierznia and Łagów, the Holy Cross Mountains.

Table 6—continued									
	Md- 27	Ka- 16	Ka- 15	Ka- 14	Ka- 13	Ka- 12	Ka- 11	Ka- 10	Ka- 9
<i>Francodina</i> P ₁	4	82	23	24	21	5	3	1	1
<i>franconica</i> P ₂	2	58	12	35	30	10	7	2	1
S ₀	1	23	10	7	11	14	12	14	13
S ₁		67	14	14	14	14	14	14	14
S ₂	1	34	14	32	32	32	32	32	32
S ₃		29	12	12	12	12	12	12	12
S ₄		14	14	14	14	14	14	14	14
<i>Svetadina</i> P	1	2	7	144	14	62	63	63	63
<i>mononotosa</i> S ₁									
<i>G. dindontoides</i> S ₂	71	1							
<i>Melina</i> P ₁		4	3	1	2				
<i>kielensis</i> M		1							
<i>Melina</i> P ₁			7		8				
<i>aff. robustidentata</i> P ₂					2				
<i>M. imaria</i> P ₁			2						
<i>Polydodus</i> P ₁									
<i>confluens</i> P ₂									
S ₀									
S ₁									
S ₂									
S ₃									
M									
<i>Ctenopogonathus</i> P ₁	1	1?	1	1	2	1			
<i>brevifilumma</i> S ₀			1	1					
S ₁			3	3					
S ₂			1	1					
<i>P. volviticus</i> P ₁	209								
<i>P. pinnigerus</i> P ₁	39	1?							
<i>P. semicostatus</i> P ₁									
<i>P. kielzschiae</i> P ₂	22	148	220	217	19	143	131	23	1
<i>Polygnathus</i> P ₂	7	9	32	132	46	37	75	54	5
spp. S ₀	8	2	3	20	4	2	3	13	1
S ₁	4	1	3	12	5	4	1	1	1
S ₂	2	1	2	16	7	10	10	10	10
S ₃	17	4	14	7	57	33	16	26	26
M	6	3	4	6	40	25	7	9	43
<i>L. glaber</i> P ₁	4	1	27	5	1	1	64	6	114
<i>L. nihilobatus</i> P ₁									
<i>Lago-vigintatus</i> P ₂			3	1					
spp. S ₀			1	1					
S ₁			1	1					
S ₂			1	1					
S ₃			1	1					
M									
<i>Polydophadina</i> P ₁	4	1?	1	38	4	13	15	5	23
<i>peregrata</i> P ₂	2								
S ₀									
S ₁									
S ₂									
S ₃									
M									
<i>Ancyrognathus</i> P ₁	??								
sp. n. P ₂									
S ₀									
M									
<i>Ancyrognathus</i> P ₁									
<i>sindamina</i> P ₂									
S ₀									
S ₁									
S ₂									
M									
<i>Cteniumpunctata</i> P ₁	1?								
<i>C. punctata</i> P ₂	3	34	202	913	141	270	315		
S ₀									
M									
<i>C. pyrrha</i> P ₁									
<i>C. globina</i> P ₁									
<i>Condolepis</i> P ₂									
<i>tenuipunctata</i> S ₀									
<i>prima</i> S ₁									
<i>globra</i> S ₂									
<i>Klapfferi</i> S ₃									
M	1								

Table 6—continued									
	Md- 27	Ka- 16	Ka- 15	Ka- 14	Ka- 13	Ka- 12	Ka- 11	Ka- 10	Ka- 9
<i>K. quadratinodo-</i>									
<i>sobohata</i> P ₁									
S ₀									
S ₁									
S ₂									
S ₃									
M									
<i>Klapfferi</i> sp. P ₁									
<i>quadriplicis</i> P ₁	29								
<i>quadratinodosa</i> P ₂	8								
<i>K. arcuata?</i> P ₁	6								
<i>K. subretia</i> P ₁									
<i>Klapfferi</i> P ₁									
<i>regularis</i> P ₂									
S ₀									
S ₁									
S ₂									
S ₃									
M									
<i>Klapfferi</i> P ₁									
<i>thomboidea</i> P ₂									
S ₀									
S ₁									
S ₂									
S ₃									
M									
<i>K. termini</i> P ₁	33								
<i>K. crepida</i> P ₁									
<i>Klapfferi</i> P ₂									
<i>termini</i> P ₂									
<i>crepida</i> S ₁	1								
S ₂	2								
S ₃	3								
M	2								
<i>Palmarocepis</i> P ₁	11	8	14	58	65	5	61	26	53
<i>perforata</i> P ₂	2	2	15	1	1	1	19	10	28
S ₀									
S ₁									
S ₂									
S ₃									
M									
<i>T. variabilis</i> P ₁	4	16	131	641	142	191	177	6	1
<i>T. domenechii</i> P ₁									
<i>Tripodellus</i> P ₂									
<i>lobus</i> S ₀	6	62	10	22	17	11			
S ₁	1	8	2	2	3	2			
S ₂	1	1	20	1	7	3			
S ₃	14	14	1	1	1	3			
M	42	9	13	6	1	1			
<i>Tripodellus</i> P ₁	68								
<i>nitimus</i> P ₂	1								
S ₀									
S ₁									
S ₂									
S ₃									
M	1								
<i>C. teniumpunctata</i> P ₁	152	3	34	202	913	141	270	315	
C ₀									
C ₁									
C ₂									
M									
<i>C. pyrrha</i> P ₁									
<i>C. globina</i> P ₁									
<i>Condolepis</i> P ₂									
<i>teniumpunctata</i> S ₀	5								
<i>prima</i> S ₁									
<i>globra</i> S ₂									
<i>Klapfferi</i> S ₃									
M	1								

Table 6—continued									
	Md- 27	Ka- 16	Ka- 15	Ka- 14	Ka- 13	Ka- 12	Ka- 11	Ka- 10	Ka- 9
<i>K. quadratinodo-</i>									
<i>sobohata</i> P ₁									
S ₀									
S ₁									
S ₂									
S ₃									
M									
<i>Klapfferi</i> sp. P ₁									
<i>quadriplicis</i> P ₁	29								
<i>quadratinodosa</i> P ₂	8								
<i>K. arcuata?</i> P ₁	6								
<i>K. subretia</i> P ₁									
<i>Klapfferi</i> P ₁									
<i>regularis</i> P ₂									
S ₀									
S ₁									

Table 7. Frequencies of conodont elements in samples from the early Famennian of Karczówka, Kowala, and Wietrzna, the Holy Cross Mountains.

Table 8. Frequencies of conodont elements in samples from the early Famennian of Kowala, the Holy Cross Mountains.

Table 9. Frequencies of conodont elements in samples from the mid Famennian of Kowala and Miedzianka, the Holy Cross Mountains.

	Ko- 13	Ko- 12	Ko- 10	Ko- 18	Ko- 16?	Ko- 9a	Ko- 8b	Ko- 8a	Ko- 2c	Ko- 2a	Ko- 1c	Ko- 1b	Ko- 1a
KOWALA Miedzianka	11	10	18	15	16?	9	15	12	16	—	4	—	—
<i>J. ostioidiformis</i> P-M													
<i>J. rectus</i> P-M										1			
<i>Ierodus</i> <i>cornutus</i> P-M								21	14	26	5	47	
<i>M.?"asymmetr.</i> P-M	1	3	2	3				2	1	1	16		
<i>M. circulans</i> cf. <i>petinata</i>	P ₁ S ₀	P ₂ S ₁	S ₂										
<i>Lagoridina</i> <i>obliqua</i>	P ₁ S ₁	P ₂ S ₂											
<i>Idioprienioides</i> <i>rupius?</i>	P ₁ S ₀	P ₂ S ₁	S ₂										
<i>Gričtoundella</i> <i>difidoanalis</i> S ₁	P ₂ M												
<i>B. bohemicana</i> P	1	4	23	52				2					
<i>B. informata</i> P													
<i>B. suprema</i> P								21	21				
<i>Brammeia</i> spp.	P ₂ S ₀	1	2	7	7	7	3	1	1	14	1?	1	
<i>Apatoquithus</i> <i>pinnatus</i> S ₁	P												
<i>Vogelguthus</i> <i>unicus</i>	P ₁ S ₂	2	20	29	2	6	5	8	9	4	2		
<i>Urbaneckina</i> <i>undata</i>	P ₂ S ₁	S ₀	3	5	3	3	1	1	6	1			
<i>Planadina</i> <i>plana</i>	S ₀ M	S ₁ S ₂	2	1	1	1	1	2	2	1	3		
<i>Pandorinellina</i> <i>vulgaris</i>	P ₁ S ₀	P ₂ S ₁	S ₂	1	4	4	2	2	1	1	1	1	
<i>Metolina</i> <i>striigosa</i>	P ₁ M	P ₂ M	S ₀	S ₁	S ₂	S ₄	M	1	1	2	1	10	1
<i>Polyiododus</i> <i>lanuginosus</i>	P ₁ M	P ₂ M	S ₀	S ₁	S ₂	S ₄	M	1	1	2	1	1	
<i>Polyiododus</i> <i>triplyphyllatus</i>	P ₁ M	P ₂ M	S ₀	S ₁	S ₂	S ₄	M	10	10	4	6	2	
<i>Polyiododus</i> <i>medionodatus</i>	P ₁ P ₂	P ₂	P ₁	P ₂	P ₁	P ₂	P ₁	2	1	1	1	1	
<i>Polyorthus</i> <i>semicostatus</i>	P ₁ S ₀	P ₂ S ₁	S ₀	S ₁	S ₂	S ₄	M	1	1	1	1	1	
<i>Hemilirionta</i> <i>perplexa</i>	P ₁ S ₁	P ₂ S ₂	S ₀	S ₁	S ₂	S ₄	M	4	1	5	2	1	
<i>Neophygrinus</i> <i>communis</i>	P ₁ P ₂	P ₁ P ₂	S ₀	S ₁	S ₂	S ₄	M	1	1	1	1	1	
<i>L. bibbbatus</i>	P ₁	P ₂	S ₀	S ₁	S ₂	S ₄	M	11	5	2	9	1	
<i>L. fallax</i>	P ₁	P ₂	S ₀	S ₁	S ₂	S ₄	M	39	1	2	24	1	
<i>L. grandiosus</i>	P ₁												
<i>L. syriacus</i>	P ₁												
<i>Lagocephalus</i> spp.	P ₂ S ₀	P ₂ S ₁	S ₀	S ₁	S ₂	S ₄	M	23	3	3	15	3	
<i>P. pergyraea</i>	P ₁ S ₀	P ₂ S ₁	S ₀	S ₁	S ₂	S ₄	M	1	1	1	1	1	
<i>Klapperilpis</i> <i>rhombidea</i>	P ₁ P ₂	P ₂ S ₁	S ₀	S ₁	S ₂	S ₄	M	6	2	2	3	2	
<i>Palmatolepis</i> <i>schindewolfii</i>	P ₁ S ₀	P ₂ S ₁	S ₀	S ₁	S ₂	S ₄	M	2	1	1	1	1	
<i>P. ampla</i>	P ₁ P ₂	P ₁ P ₂	S ₀	S ₁	S ₂	S ₄	M	19	1	1	1	1	
<i>Palmatolepis</i> <i>trochrena</i>	P ₁ P ₂	P ₁ P ₂	S ₀	S ₁	S ₂	S ₄	M	11	3	2	2	1	

	Ko- 13	Ko- 12	Ko- 10	Ko- 8a	Ko- 9a	Ko- 8b	Ko- 8a	Ko- 9a	Ko- 8b	Ko- 8a	Ko- 9a	Ko- 8b	Ko- 8a	
KOWALA	11	10	18	15	16?	9	15	12	16	—	4	—	—	—
<i>M.?"asymmetr.</i> P-M	1	3	2	3				2	10	17	3	6	18	1
<i>M. circulans</i> cf. <i>petinata</i>	P ₁ S ₀	P ₂ S ₁	S ₂											
<i>B. bohemicana</i> P	1	4	23	52				2						
<i>B. informata</i> P														
<i>B. suprema</i> P								21						
<i>Brammeia</i> spp.	P ₂ S ₀	1	2	7	7	7	3	1	1	14	1?	1	1	
<i>Apatoquithus</i> <i>pinnatus</i> S ₁	P													
<i>Vogelguthus</i> <i>unicus</i>	P ₁ S ₂	2	20	29	2	6	5	8	9	4	2			
<i>Urbaneckina</i> <i>undata</i>	P ₂ S ₁	S ₀	3	5	3	3	1	1	6	1				
<i>Planadina</i> <i>plana</i>	S ₀ M	S ₁ S ₂	2	1	1	1	1	2	2	1	3			
<i>Pandorinellina</i> <i>vulgaris</i>	P ₁ S ₀	P ₂ S ₁	S ₂	1	4	4	2	2	1	1	1	1	1	

Table 10 – continued												
<i>B. bohemicana</i>	P ₁	3	1	16	9	2	16	3	2	16	26	7
<i>B. biornata</i>	P ₁											7
<i>Braunella</i>	P ₂		S ₁		1			1				7
	spp.		S ₁									29
<i>Vogelgaukus</i>	P ₁	1		1		1		1				1
	<i>brannellioides</i>	S ₂				1						1
<i>Vogelgaukus</i>	P ₁	1		1				2	4	1		1
	<i>wernerii</i>	P ₁	S ₂									1
<i>Sweetolina</i>	P ₁											6
	<i>monodonta</i>	S ₂										1
<i>Planadina</i>	S ₁₋₂											2
	<i>plana</i>	S ₁₋₂										9
<i>Pandarellina</i>	P ₁	6	2	28	23	11	2	1	12	2	4	4
	<i>vulgaris</i>	P ₂		2	2	3		1	2	6	1	1
<i>Silene</i>	S ₀								5	4	1	4
	S ₁		1	1			1		4	1	1	2
	S ₂					3			9	2	1	4
	S ₃₋₄	M ₁	2	6	6	1	1	13	4	1	3	2
<i>Melina</i>	P ₁	1	1	4	6	1	2	4	1	1	13	18
	<i>strigosa</i>	P ₂		3	2	1	4	1	20	3	6	4
<i>Innominatus</i> sp.	P ₁	1	1	1	1			6	1	2	3	1
	<i>P. pernicius</i>	P ₁							6	1	9	3
	<i>H. perplexa</i>	P ₁	5	9	5	11	3		31	3	5	10
	<i>H. marginata</i>	P ₁										2
<i>Hemimistrona</i>	P ₂			3	1	1			3	2	1	1
	spp.	S ₀										2
<i>N. communis</i>	P ₁	36	3	1								1
	<i>L. granulosus</i>	P ₁	3	4	7	2						2
	<i>L. sinuatus</i>	P ₁										8
<i>Lagovignathus</i>	P ₂			12	6	13	6	16	1			1
	spp.	S ₁										2
	S ₂		1									1
	S ₃₋₄	M ₁										2
<i>Palmatolepis</i>	P ₂	2	10	4	3	6	10	6	6	7	6	4
	<i>schiundewolfi</i>	P ₂	S ₁₋₂									1
	M ₁											25
<i>P. nigrosa</i>	P ₁	2	2	10	2	2	4	3	2	9	11	5
	<i>Tripodellus</i>	P ₁							3	10	9	29
	<i>guadilis</i>	P ₂							1	5	2	1
	S ₀								1	1	2	2
	S ₁								1	2	1	2
	S ₂								1	1	3	5
	S ₃₋₄	M ₁	1	1	1	1			1	1	1	1

Table 9 - continued												
	<i>T. minutus</i>	<i>T. tripodellus lobatus</i>	<i>T. scutellatus</i>	<i>T. donogheui</i>	<i>T. tripodellus</i> spp.	<i>C. lingulifluva</i>	<i>C. glabra</i>	<i>C. distorta</i>	<i>Condylolabis falacra</i>	<i>C. quadratinodis</i>	<i>C. influviaida</i>	<i>D. micropunctata</i>
Ko-13	Ko-12	Ko-11	Ko-10	Ko-18	Ko-15?	Ko-15	Ko-18	Ko-16?	Ko-15	Ko-9	Ko-8b	Ko-8a
M-	M-	M-	M-	M-	M-	M-	M-	M-	M-	M-	M-	M-
T. minutus	P ₁	P ₁	P ₂	P ₂	spp.	S ₁	S ₁	S ₂	S ₂	S ₃	S ₃	S ₄
Tripodellus						1	2	7	4	1	7	2
lobatus						1	2	7	4	1	7	2
T. scutellatus	P ₂	P ₂	P ₂	P ₂								
T. donogheui	P ₁	P ₁	P ₂	P ₂								
Tripodellus	P ₃	P ₃	P ₃	P ₃								
spp.	S ₁	S ₁	S ₁	S ₁								
S ₁	1	1	2	1								
S ₂	1	1	2	1								
S ₃	1	1	2	1								
S ₄	1	1	2	1								
M	1	1	2	1								
M-	M-	M-	M-	M-								
C. lingulifluva	P ₁	P ₁	P ₂	P ₂								
C. glabra	P ₁	P ₁	P ₂	P ₂								
C. distorta	P ₂	P ₂	P ₃	P ₃								
Condylolabis	P ₁	P ₁	P ₂	P ₂								
falacra	P ₂	P ₂	P ₃	P ₃								
C. quadratinodis	P ₁	P ₁	P ₂	P ₂								
C. influviaida	P ₁	P ₁	P ₂	P ₂								
Condylolabis	P ₁	P ₁	P ₂	P ₂								
marginifera	P ₂	P ₂	P ₃	P ₃								
M-	M-	M-	M-	M-								
S ₁	1	1	3	1								
S ₂	1	1	3	1								
S ₃	1	1	3	1								
S ₄	1	1	3	1								
M	1	1	3	1								
C. quadratinodis	P ₁	P ₁	P ₂	P ₂								
C. influviaida	P ₁	P ₁	P ₂	P ₂								
Condylolabis	P ₁	P ₁	P ₂	P ₂								
marginifera	P ₂	P ₂	P ₃	P ₃								
M-	M-	M-	M-	M-								
S ₁	1	1	3	1								
S ₂	1	1	3	1								
S ₃	1	1	3	1								
S ₄	1	1	3	1								
M	1	1	3	1								
D. micropunctata	P ₁	P ₁	P ₂	P ₂								
Condylolabis	P ₁	P ₁	P ₂	P ₂								
marginifera	P ₂	P ₂	P ₃	P ₃								
M-	M-	M-	M-	M-								
S ₁	1	1	3	1								
S ₂	1	1	3	1								
S ₃	1	1	3	1								
S ₄	1	1	3	1								
M	1	1	3	1								
D. micropunctata	P ₁	P ₁	P ₂	P ₂								
Condylolabis	P ₁	P ₁	P ₂	P ₂								
marginifera	P ₂	P ₂	P ₃	P ₃								
M-	M-	M-	M-	M-								
S ₁	1	1	3	1								
S ₂	1	1	3	1								
S ₃	1	1	3	1								
S ₄	1	1	3	1								
M	1	1	3	1								
C. quadratinodis	P ₁	P ₁	P ₂	P ₂								
C. influviaida	P ₁	P ₁	P ₂	P ₂								
Condylolabis	P ₁	P ₁	P ₂	P ₂								
marginifera	P ₂	P ₂	P ₃	P ₃								
M-	M-	M-	M-	M-								
S ₁	1	1	3	1								
S ₂	1	1	3	1								
S ₃	1	1	3	1								
S ₄	1	1	3	1								
M	1	1	3	1								
D. micropunctata	P ₁	P ₁	P ₂	P ₂								
Condylolabis	P ₁	P ₁	P ₂	P ₂								
marginifera	P ₂	P ₂	P ₃	P ₃								
M-	M-	M-	M-	M-								
S ₁	1	1	3	1								
S ₂	1	1	3	1								
S ₃	1	1	3	1								
S ₄	1	1	3	1								
M	1	1	3	1								
D. micropunctata	P ₁	P ₁	P ₂	P ₂								
Condylolabis	P ₁	P ₁	P ₂	P ₂								
marginifera	P ₂	P ₂	P ₃	P ₃								
M-	M-	M-	M-	M-								
S ₁	1	1	3	1								
S ₂	1	1	3	1								
S ₃	1	1	3	1								
S ₄	1	1	3	1								
M	1	1	3	1								
D. micropunctata	P ₁	P ₁	P ₂	P ₂								
Condylolabis	P ₁	P ₁	P ₂	P ₂								
marginifera	P ₂	P ₂	P ₃	P ₃								
M-	M-	M-	M-	M-								
S ₁	1	1	3	1								
S ₂	1	1	3	1								
S ₃	1	1	3	1								
S ₄	1	1	3	1								
M	1	1	3	1								
D. micropunctata	P ₁	P ₁	P ₂	P ₂								
Condylolabis	P ₁	P ₁	P ₂	P ₂								
marginifera	P ₂	P ₂	P ₃	P ₃								
M-	M-	M-	M-	M-								
S ₁	1	1	3	1								
S ₂	1	1	3	1								
S ₃	1	1	3	1								
S ₄	1	1	3	1								
M	1	1	3	1								
D. micropunctata	P ₁	P ₁	P ₂	P ₂								
Condylolabis	P ₁	P ₁	P ₂	P ₂								
marginifera	P ₂	P ₂	P ₃	P ₃								
M-	M-	M-	M-	M-								
S ₁	1	1	3	1								
S ₂	1	1	3	1								
S ₃	1	1	3	1								
S ₄	1	1	3	1								
M	1	1	3	1								
D. micropunctata	P ₁	P ₁	P ₂	P ₂								
Condylolabis	P ₁	P ₁	P ₂	P ₂								
marginifera	P ₂	P ₂	P ₃	P ₃								
M-	M-	M-	M-	M-								
S ₁	1	1	3	1								
S ₂	1	1	3	1								
S ₃	1	1	3	1								
S ₄	1	1	3	1								
M	1	1	3	1								
D. micropunctata	P ₁	P ₁	P ₂	P ₂								
Condylolabis	P ₁	P ₁	P ₂	P ₂								
marginifera	P ₂	P ₂	P ₃	P ₃								
M-	M-	M-	M-	M-								
S ₁	1	1	3	1								
S ₂	1	1	3	1								
S ₃	1	1	3	1								
S ₄	1	1	3	1								
M	1	1	3	1								
D. micropunctata	P ₁	P ₁	P ₂	P ₂								
Condylolabis	P ₁	P ₁	P ₂	P ₂								
marginifera	P ₂	P ₂	P ₃	P ₃								
M-	M-	M-	M-	M-								
S ₁	1	1	3	1								
S ₂	1	1	3	1								
S ₃	1	1	3	1								
S ₄	1	1	3	1								
M	1	1	3	1								
D. micropunctata	P ₁	P ₁	P ₂	P ₂								
Condylolabis	P ₁	P ₁	P ₂	P ₂								
marginifera	P ₂	P ₂	P ₃	P ₃								
M-	M-	M-	M-</									

Table 10. Frequencies of conodont elements in samples from the late Famennian of Kowala, the Holy Cross Mountains

Table 11. Frequencies of conodont elements in samples from the late Famennian of Kowala, the Holy Cross Mountains.

	KOWALA	Ko- 182	Ko- 183	Ko- 184	Ko- 185	Ko- 186	Ko- 187	Ko- 188	Ko- 189	Ko- 190	Ko- 191	Ko- 192	Ko- 193	Ko- 194	Ko- 195	Ko- 196	Ko- 197	Ko- 198	Ko- 199	Ko- 200	
<i>J. erectus</i>	P-M	1	3	1	1	3	3	1	4	1	21	5	21	15	98	8	3	72	14	167	3
<i>M. circularis</i>	P-M																				
<i>M. ciliopunctatus</i>	P-M																				
<i>napus</i>	P ₁ S ₀ S ₁ S ₂ S ₃ M																				
<i>G. trigonica</i>	S																				
<i>B. bohleiana</i>	P ₁	16						15	11	5	14				57		21				
<i>B. inornata</i>	P ₁							2						4		48		3	58		
<i>B. Braumehdia</i>	P ₁ spp.	2						2							11		1			2	
<i>S. S₁ M</i>	S ₁ M								1	1				1	2		1		1		
<i>A. varians</i>	S										1	3									
<i>Vogelgenitalius</i>	P ₁ braunmeiholoides	1						12	3	12	5	7	16	5	47		29	32	5	2	
<i>S. S₁ M</i>	S ₀ S ₁ S ₂ S ₃ M										2	1	1	1	1	1	5	13	8	1	
<i>Vogelgenitalius</i>	P ₁ wernerii	5									1	1	1	1	1	1	1	2	10	1	5
<i>S. S₁ M</i>	S ₀ S ₁ S ₂ S ₃ M										1	1	1	1	1	1	2	2	4	7	1
<i>Sweetadina</i>	P																				
<i>monodentata</i>	S ₁ S ₂ M																				
<i>P. planata</i>	P ₁ S ₀ S ₁ M	4																			
<i>P. vulgaris</i>	P ₁ S ₀ S ₁ M	58	1		3	15															
<i>P. Pandorinellina</i>	P ₁ S ₀ S ₁ M	4	1																		
<i>M. Melina</i>	P ₁ S ₀ S ₁ M	16	6	12	1	5	5	29	6	11	1	3	18	32	14	37					
<i>serrigosa</i>	P ₁ S ₀ S ₁ S ₂ M	2	1	1	2	1	1	11	3	1	1	5	32	14	8						

Table 12. Frequencies of conodont elements in samples from the late Famennian of Kowala, the Holy Cross Mountains.

Table 13. Frequencies of conodont elements in samples from the latest Famennian of Kowala, the Holy Cross Mountains

KOWALA	Ko-120	Ko-119	Ko-118	Ko-117	Ko-116	Ko-114	Ko-113	Ko-110	Ko-109	Ko-108	Ko-107	Ko-106	Ko-105	Ko-103	Ko-80	Ko-79	Ko-137	
<i>Dallmania^a</i>	P ₁																	
<i>M. circularis</i>	P-M ₁			2	1	15		2							1	3	1	3
<i>M. coronella</i>	P-M ₁																	
<i>Idiopriomys^b</i>	P ₁																	
<i>rufus?</i>	P ₂			1		3										1	1	
<i>S₁</i>	S ₀																	
<i>S₂</i>	S ₁																	
<i>S₃</i>	S ₂																	
<i>Brammeila</i>	P ₁																	
<i>inornata</i>	S ₁																	
<i>S₂</i>	S ₁																	
<i>M. styracosa</i>	P ₁																	
<i>P. pemphilus</i>	P ₁	1	2		2	1	16			3			1	3			3	
<i>N. communis</i>	P ₂				14	1	13	1	4			1	1		2	1		
<i>N. unicolor</i>	P ₂													6				

Table I-4 - continued										
	Ko- 102	Ko- 101	Ko- 98	Ko- 97	Ko- 93	Ko- 55	Ko- 54	Ko- 82	Md- 14	Md- 15
	P ₁ <i>wernerii</i>	P ₂	S ₀	S ₁	S ₂	S ₃	S ₄	S ₅	Md- 16	Md- 17
<i>Vogelignathus</i>									22	19
<i>monodentata</i>									8	7
<i>Sweetotina</i>									5	5
<i>Planadina</i>									7	7
<i>plana</i>	S ₀	S ₁	S ₂	S ₃	S ₄	S ₅				
<i>Pandornellina</i>										
<i>vulgaris</i>	P ₁	P ₂	S ₀	S ₁	S ₂	S ₃	S ₄	S ₅		
<i>Melitina</i>										
<i>strigosa</i>	P ₁	P ₂	S ₀	S ₁	S ₂	S ₃	S ₄	S ₅		
<i>Phyndaus</i>										
<i>tauriformis</i>	P ₁	P ₂	S ₀	S ₁	S ₂	S ₃	S ₄	S ₅		
<i>P. diversus</i>										
<i>P. senicostatus</i>	P ₁	P ₂	S ₀	S ₁	S ₂	S ₃	S ₄	S ₅		
<i>P. extratubaeus</i>	P ₁	P ₂	S ₀	S ₁	S ₂	S ₃	S ₄	S ₅		
<i>P.? exasperatus</i>	P ₁	P ₂	S ₀	S ₁	S ₂	S ₃	S ₄	S ₅		
<i>P. pennatus</i>	P ₁	P ₂	S ₀	S ₁	S ₂	S ₃	S ₄	S ₅		
<i>Polygnathus</i>										
<i>spp.</i>	S ₀	S ₁	S ₂	S ₃	S ₄	S ₅				
<i>Hemilistriona</i>										
<i>peptexa</i>	P ₁	P ₂	S ₀	S ₁	S ₂	S ₃	S ₄	S ₅		
<i>Neopolygnathus</i>										
<i>communis</i>	P ₁	P ₂	S ₀	S ₁	S ₂	S ₃	S ₄	S ₅		
<i>Lugovignathus</i>	P ₁	P ₂	S ₀	S ₁	S ₂	S ₃	S ₄	S ₅		
<i>syrnacis</i>	P ₁	P ₂	S ₀	S ₁	S ₂	S ₃	S ₄	S ₅		
<i>P. pergyraea</i>	P ₁	P ₂	S ₀	S ₁	S ₂	S ₃	S ₄	S ₅		
<i>Palmitolepis</i>	P ₁	P ₂	S ₀	S ₁	S ₂	S ₃	S ₄	S ₅		
<i>schindewolfi</i>	S ₀	S ₁	S ₂	S ₃	S ₄	S ₅				
<i>P. rugosa</i>	P ₁	P ₂	S ₀	S ₁	S ₂	S ₃	S ₄	S ₅		

Table 14. Frequencies of conodont elements in samples from the latest Famennian of Kowala and late Famennian of Miedzianka, the Holy Cross Mountains.

Table 15. Frequencies of conodont elements in samples from the mid Famennian of Lagów, the Holy Cross Mountains

Table 16. Frequencies of conodont elements in samples from the mid Famennian of Lagów and Mieczianka, Holy Cross Mountains.

Table 17. Frequencies of conodont elements in samples from the late Famennian of Ostrówka, the Holy Cross Mountains, and Gologłowy, the Sudetes.

	OSTRÓWKA Goliągów	Ost-0	Ost-1	Ost-1a	Ost-10	Ost-12	Ost-11	Ost-15	Ost-16	Ost-	Ost-	Ost-	Ost-	Ost-	Ost-	Gol-3
	Jathromodus ostroidiformis	P ₁	S ₀	S ₁	S ₂	S ₃	S ₄	M	S ₀	-7	293	-5	-2	-	2a	185
<i>Jathromodus</i> <i>erectus</i>	P ₁	S ₀	S ₁	S ₂	S ₃	S ₄	M									
<i>Latericriodus</i> <i>rarus</i> P.-M ₁	P ₁									2	99	37	1			
<i>Ichnodus</i>	P ₁									1	32	27				
<i>Peltekysanthus</i> P ₁										103						
<i>M. asymmetr.</i> P.-M ₁										74						
<i>M. circularis</i>	P ₁									178						
<i>Fluctidina</i> <i>purnelli</i>	P ₂	S ₀	S ₁	S ₂	S ₃	S ₄	M			18						
<i>Hiatopriocnoides</i> <i>rapax?</i>	P ₁	S ₀	S ₁	S ₂	S ₃	S ₄	M									
<i>B. bohemicana</i>	P ₁															
<i>B. inornata</i>	P ₁															
<i>B. suprema</i>	P ₁															
<i>B. disparilis</i>	P ₁															
<i>Bryamphela</i> spp.	P ₂	2	3	6	43	22	25	2	7	110	1	24	1	8	21	
	S ₀					3	2	1		32	3	3	2	16	5	
	S ₁					2	1	2	4	40	2	15	1	9	2	
	S ₂					19	19	9	9	127	14	5	16	13	13	
	S ₃					35	9	8	1	210	14	5	27	26	8	
	S ₄					49	15	22	1	12	241	2	18	6	8	
<i>Cinchonella</i> <i>triangularis</i>	P ₁													1		
<i>Apatognathus</i> <i>varians</i>	S ₁	S ₂	S ₃	S ₄	M									3	1	
<i>Vogeliagnathus</i> <i>brachynchloides</i>	P ₁	5	2	2	33	21	48	1	8	1	3			5	2	5
	S ₀		1	1		28	1		2	4				1		
	S ₁					3			1	6				1		
	S ₂					4			1	2				1		
	S ₃					4			2	2				1		
	S ₄					2			1	2				1		
<i>Vogeliagnathus</i> <i>werneri</i>	P ₁		1	7	251	1			2	2				1	5	
	P ₂								10							

Table 18. Frequencies of conodont elements in samples from the late Famennian of Miedzianka, the Holy Cross Mountains and Dzikowice, the Sudetes

Table 19. Frequencies of conodont elements in samples from the late Famennian of Dzikowiec, the Sudetes.

INDEX OF GENERIC AND SPECIES NAMES

Explanation to index: * — text-fig., bold — description

A

- Acutimitoceras* 14, 166, 234, **245**, 302
 - guerichi* **245**, 246*, 247*, 309*
 - prorsum* **245**, 246*, 247*, 309*
- Afrolobites* 226
- Aktuboclymenia* 255, 256, 257*, 292, 312
 - ancestralis* 257, **258**, 258*, 266*, 311*
- Alpinites* 214, 215
- Alternognathus* 17, 22*, 23*, 71, 85, 146, **147**,
 - beulensis* 29*, **148**, 150*, 184*
 - costatiformis* 151
 - pseustostrigosus* 75, 146*, 147*, **148**, 184*
 - regularis* 147, 147*, **148**, 149*, 166, 184*
- Alternognathus?*
 - sp. **148**, 151*
- Ammonites*
 - buchi* 248
 - humboldti* 248, 258
 - humboldtii* 248
 - Münsteri* 235
- Amphipora* 13
- Ancyrodella* 76, 165
 - curvata* 19
- Ancyrognathus* 108, 109, 165, 175
 - irregularis* 99
 - sinelamina* **108**, 109, 109*, 179*
 - sp. n. 29*, **109**, 109*, 179*
 - symmetricus* 108
- Ancyrolepis* 108
- Angustidontus* 317
- Antognathus* 30, 31, 32, 167*
 - mowitzaensis* 31
- Apatognathus* 56, **58**, 58*, 169
 - inversus* 67
 - klapperi* 58
 - provarians* **58**, 58*, 167*
 - varians* 58, 58*, **59**, 167*
- Araneites*
 - falcatus* 217
- Armatites* 200*, **201**
 - lateroconcavus* 200*, **201**, 216*
 - lewinskii* 200*, **201**, 216*, 307*
 - nudus* 201
 - planidorsatus* 201
- Aturia* 248, 249, 279, 308

B

- Balvia* 11, 189, **243**, 244*, 305, 310
 - biformis* **243**, 244*, 247*, 309*
 - falx* 244*, **245**, 247*, 309*
 - globularis* **245**, 247*, 309*
 - lens* 244*, **245**, 247*, 309*
 - minutula* 243, 244*, 247*, 309*
 - nucleus* 245
 - prima* **243**, 244*, 247*, 309*
- Beloceras*
 - acutodorsatum* 189
- Belodella* 15, 35
 - bilinearis* 50
- Biloboclymenia* 279, **281**
 - accessa* 281

- | | |
|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| <ul style="list-style-type: none"> <i>nebulosa</i> 281 <i>pristina</i> 280*, 281, 297*, 313* <i>Bispatherodus</i> 34, 152 <ul style="list-style-type: none"> <i>ultimus</i> 152, 156 <i>Borisiclymenia</i> <ul style="list-style-type: none"> <i>ishikayensis</i> 295 <i>Borkowia</i> 279 <i>Brancoceras</i> <ul style="list-style-type: none"> <i>lentiforme</i> 232 <i>Branmehla</i> 11, 23*, 52, 53, 56*, 71, 166, 171, 171* <ul style="list-style-type: none"> <i>bohlenana</i> 52, 53, 53*, 54, 54*, 171* <i>disparilis</i> 55, 56*, 171* <i>inornata</i> 54, 55, 55*, 99, 171* <i>suprema</i> 14, 55, 56, 56*, 171* <i>Bryantodus?</i> <ul style="list-style-type: none"> sp. 99 | <h3>C</h3> <ul style="list-style-type: none"> <i>Carinoclymenia</i> 269, 314 <ul style="list-style-type: none"> <i>beulensis</i> 268*, 269, 297*, 313* <i>Cavusgnathus</i> 27, 183 <i>Cheiloceras</i> 15, 17, 189, 219, 220*, 222*, 223*, 118, 306, 310 <ul style="list-style-type: none"> <i>amblylobum</i> 219, 220*, 224, 247*, 309* <i>angustivaricatum</i> 221, 222*, 247*, 309* cf. <i>praecursor</i> 221 <i>depressum</i> 228 <i>discoidale</i> 221, 222*, 224*, 247*, 309* <i>enkebergense</i> 144 <i>inversum</i> 189, 219, 220*, 228, 247*, 309* <i>lagoviense</i> 14, 107, 221, 223*, 224, 224*, 247*, 309* <i>longilobum</i> 224 <i>polonicum</i> 240, 246*, 247* <i>pompeckji</i> 219, 220*, 221, 247*, 309* <i>praecursor</i> 223*, 247*, 309* <i>sublagoviense</i> 224 <i>subpartitum</i> 189, 221, 222*, 247*, 309* <i>tenue</i> 218* <i>verneuili</i> 67 <i>Cladoselache</i> 318 <i>Clavohamulus</i> 35 <i>Clydagnathus</i> 146 <i>Clymenia</i> 14, 16, 52, 248, 256, 258, 279, 283, 292, 312 <ul style="list-style-type: none"> <i>aegoceras</i> 295 <i>bilobata</i> 281 <i>dunkerri</i> 259 <i>frechi</i> 248 <i>humboldti</i> 287 <i>involuta</i> 237 <i>laevigata</i> 256, 257*, 266*, 292, 305, 311* <i>nana</i> 267 <i>primaeva</i> 256, 258*, 266*, 311*, 312* <i>pseudogoniatisites</i> 206 <i>sedgwicki</i> 259 <i>spinoso</i> 255 <i>subflexuosa</i> var. <i>acuta</i> 269 <i>tenuis</i> 292 <i>wysogorskii</i> 269 <i>Compactoceras</i> 217 <i>Concavicarinis</i> 14, 15, 192, 317, 318 |
|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|

- Conchodontus* 35
Conditolepis 15, 22*, 23* 64, 132, 134, 137, **138**,
 139*, 140, 142, 144, 180, 183*
 distorta 14, 17, 18, 141*, **142**, 183*
 falcata 15, 16, 17, 22, 23*, 99, 140, **142**,
 143, 143*, 150, 183*, 231
 gilberti 17
 glabra 15, 17, 140, 140*, 141, 141*, **142**,
 143, 183*
 inflexa 144
 inflexoidea 20, **144**, 145*, 183*
 klapperi 15, 20, 127, 143, **144**, 145*, 183*
 linguiformis 165
 linguloba **138**, 139*, 183*
 lobicornis 19, 133, **138**, 139, 139*, 143, 183*
 marginifera 13, 14, 16, 17, 20, 33, 55, 142, **144**,
 145*, 183*, 305
 prima 14, 15, 16, 17, **140**, 140*, 142, 183*
 quadrantinodosa 14, 20, 102, 142, **144**, 145*,
 183*, 305
 tenuipunctata 16, 19, 110, 113, 138, **139**, 139*,
 140, 141, 143, 183*
Conditolepis (*Conditolepis*)
 inflexoidea 147
Costaclymenia 267, **269**, 271, 279, 313
 binodosa **269**, 270*, 297*, 313*
 limata 269
Crickites 186
 holzapfeli 188
Ctenopolygnathus 22*, 41, 84, 85, 88, 89, 165,
 166, 176, 176*
 angustidens 80
 brevilamina 84, 85*, 86*
 pluckiensis 176*
 rarus 23
 sp. A 84
 sp. B 84
Cteroclymenia 267
 rozmanae 267
 sp. n. **267**, 268*, 297*, 313*
Cycloclymenia
 costata **289**
Cymaclymenia 13, 248, **249**, 250*, 251, 252*,
 253*, 254, 258, 281, 305
 compressa 251
 cordata 253
 costellata **251**, 252*, 254*, 266*, 311*
 evoluta 250*
 fundilobata 252
 inflata 250*, **251**, 254*, 266*, 311*
 silesiaca 252, 252*, 253*, **254**, 254*, 266*, 311*
 sp. aff. *C. evoluta* **252**, 252*
 sp. aff. *C. striata* **251**, 252*, 266*
 sp. aff. *C. warsteinensis* 266*
 sp. n. 250*, **251**, 266*
 striata 251
 warsteinensis 251
Cyrtoclymenia 248, 281, **283**, 285*, 287, 312, 314
 acuta **283**, 304*, 315*
 angustiseptata **283**, 284*, 304*, 315*
 involuta 282*, **283**, 304*, 315*
 laxata 287
 plicata 283
 sp. **283**, 285*, 304*, 315*
 ventriosa 283
Cyrtoclymenia?
 procera **285**, 285*, 304*

D

- Dasbergina* 17, 21, 23*, 70, 71, 75, 88, 147,
 152, **158**, 163, 165, 183, 185
 brevipennata **163**, 164*, 184, 185*
 granulosa 21, 160*, **161**, 163, 185*
 kayseri 102, 109, 162*, **163**, 179*
 kowaleensis **161**, 162*, 184
 marburgensis 11, 21, **161**, 162*, 184, 185*
 micropunctata 11, 75, **159**, 159*, 185*
 sp. aff. *D. kayseri* 161, 162*, **163**, 170*
 stabilis 70, 75, 146, **158**, 158*, 159, 161, 184, 185
 trigonica 11, 13, 14, 16, 152, 156, 156*, **161**,
 161*, 162*, 184, 185*
 ziegleri 158, **163**, 164*, 184, 185*
Dianops 15
Dimeroceras 224, **228**, 230*, 232, 308, 310
 cf. *bredelarense* 232
 cf. *petterae* **230**, 230*, 247*, 305, 309*
 globosoides 228, **229**, 229*, 247*, 309*
 kontkiewiczi **228**, 228*, 247*, 309*
 lentiforme 107
 petterae 232
 polonicum 18, 231*, **232**, 309*, 310
 umbilicatum 230*, **232**, 247*, 309
Dimeroclymenia 248, 281
Dinodus 50, 51, 52, 157
 leptus 50
Discoclymenia 208, 213*, **214**
 cucullata 213*, **214**, 214*, 216*, 307*, 308
 kayseri 215
 zigzag 213*, **215**, 216*, 307*, 308
Dollymae 34
 bouckaerti 34
 sagittula 34
Dollymae?
 guizhouensis 34, 34*, 167*, 169
Drepanodina 38
 lachrymosa 38
 subcircularis 37
Drepanodus
 circularis 37
Drepanoistodus 35, 39
Dyminodina 165, 166

E

- Elictognathus* 50, 157
Elsonella
 rhenana 50
Eoasianites 187
Eokosmoclymenia 256
 subacuta 256
 transitoria 256
Eotaphrus 33
 bulynciki 34
Epiwocklumeria 16, **301**, 302, 302*, 315
 applanata 302*, **303**, 304*, 316*
 bohdanowiczii **301**, 302*, 303, 304*, 315, 316*
Erfoudites **233**, 311
 ungeri 233*, **234**, 247*, 310*
 zizensis 233
Euprioniodina
 iowaensis 99
 lateralis 99
Exotornoceras 210, 214

- F**
- Falciclymenia* 314
 - falcifera* 283
 - Falcitornoceras* 208
 - bilobatum* 197
 - falcatum* 197
 - Falcodus* 57
 - Felisporadoceras* 217, **234**, 236*, 308, 311
 - kielcense* **235**, 236*, 247*, 310*
 - kowalense* **234**, 235*, 247*, 310*, 311
 - subvaricatum* 217, **235**, 236*, 247*, 310*
 - Finiclymenia* **271**
 - wocklumensis* 271, 271*, **272**, 297*, 313*
 - Flexiclymenia*
 - fundifera* 258
 - mariae* 292, 293*
 - puschi* 248, 287
 - simosa* 249
 - staszici* 249
 - tempestiva* 249
 - Francodina* 22*, 59, **65**, 66, 66*, 69, 172
 - franconica* 59, 66*, **67**, 68, 70, 173*
 - santacrucensis* **65**, 66, 66*, 67, 173*
 - Franklinella* 317
 - Fungulodus* 30, 35
- G**
- Gattendorfia* 11, 157, 168
 - globularis* 243
 - Genuclymenia* **248**, 249, 281, 313
 - frechi* 249
 - humboldti* **248**, 249, 249*, 254*, 266*, 311*
 - Gephyroceras*
 - niedzwiedzki* 210
 - Girtyoceras* 187
 - Glatziella* 11, **299**, 315
 - diensti* 299
 - glaukopis* 298*, **299**, 304*, 315, 316*
 - helenae* 298*, **299**, 304*, 316*
 - lethmathensis* 299
 - minervae* 298*, **299**, 304*, 316*
 - tricincta* 299
 - Gnathodus*
 - kockeli* 157
 - Gomi-monomeroclymenia*
 - humboldti* 248
 - Humboldti flexilobata* 292, 293
 - humboldti genulobata* 248
 - Humboldti subacuta* 283
 - Gomi-monomeroceras (Tornoceras)*
 - dorsoplanum avaricatum* 197
 - evolutum* 206
 - kielcense* 194
 - Gomi-re-monomeroceras*
 - umbilicatooides* 206
 - umbilicatum* 206
 - Gomi-re-monomeroceras (Tornoceras)*
 - dorsatum* 203
 - flexuosum* 203
 - genulobatum planum* 203
 - planilobum* 203
 - planilobum angulatolobatum* 203
 - planilobum arcuatolobatum* 205
 - planilobum avaricatum* 203
 - simplicius rotundatum* 203, 206
 - simplicius subacutum* 196
 - simplificatum rotundatum* 203
 - simplificatum subacutum* 206
 - sinuvaricatum* 205
 - umbilicatooides* 205
- Gomi-re-protomeroceras**
 - alobatum* 206
- Gonatocyrtoceras*
 - cf. guerichi* 14
- Gondolella* 52
- Gundolficeras*
 - delepinei* 209
- Goniatiates*
 - acutolateralis* 215
 - annulatus* 287
 - ausavensis* 208
 - bifer* var. *delphinus* 226
 - binodosus* 269
 - circumflexus* 217
 - contiguus* 214
 - divisus* 240
 - Haueri* 214
 - lentiformis* 232
 - mamillifer* 228
 - maximus* 275
 - plandidorsatus* 201
 - solaroides* 295
 - speciosus* 275
 - sphaerooides* 303
 - subarmatus* 272
 - subbilobatus* 234
 - subpartitus* 219
 - uniangularis* 191
- Gonioclymenia* 243, 248, 270, 271, 275, 279, 313
 - speciosa* **275**, 277*, 297*, 305, 314*
- Gonioclymenia (Kalloclymenia)*
 - wocklumensis* 271
- Guerichia* 13, 14, 18
- Guizhoudella* 28, 49, **50**, 157, 171*
 - dinodontoides* 50, 51*, 52*, 171*
 - triangularis* **50**, 51*, 171*
- Gundolficeras* **208**, 209, 209*, 210, 214, 308
 - bilobatum* **208**, 209*, 216*, 307*
 - korni* 197, **208**, 209*, 216*, 307*
 - rotersi* 208
 - sp. n. aff. *G. delepinei* **209**, 209*
- Gyroclymenia* 287, 289
 - angulata* 289
 - cyclocostata* 289
 - evoluta* 289
 - mutabilis* 290
 - rotundata* 290
 - sophiae* 290
- H**
- Hemilistrona* **97**, 99, 102, 166, 174, 175*
 - depkei* 97
 - homoirregularis* 100*, **101**, 102, 175*
 - margaritata* 101, 101*, **102**
 - perplexa* 88*, 93, **97**, 99*, 175*
 - pulchra* 100*, **101**, 175*
 - Hexaclymenia* 292, 316
 - Hindeodella*
 - unca* 50
 - Hindeodontoides* 70
 - spiculus* 70
 - Hindeodus* 56, 169
 - scitulus* 56

I

- Icriodus* 12, 22, 22*, 23, 23*, 30, 32, 33, 35, 37, 165, 166, 169
alternatus 31*, 32, 33, 33*, 34, 166, 167*, 169
chojnicensis 23, 33
cornutus 13, 15, 32, 33, 33*, 167*, 169
costatus 33, 86
expansus 32
iowaensis 165, 169
latericrescens 31
Idiopriionodus 43, 48, 49, 166, 170*, 171
ruptus 43, 48, 48*, 170*
typus 48
uncadinoides 41, 49, 49*, 50, 170*
Imitoceras 189
acutum 245
Immognathus 84, 85, 88, 97, 157, 176, 176*
rhabdotus 87, 88*, 97
streeli 86, 87*, 176*

J

- Jablonnodus* 23*, 28, 35, 36, 37, 38, 167*, 169
erectus 39, 39*, 40, 167*, 169
oistodiformis 38, 38*, 39, 40, 167*, 169
Johnognathus 26

K

- Kosmoclymenia*
 sp. aff. *K. bisulcata* 261
trigona 301
venusta 266
Kalloclymenia 11, 14, 271, 272, 273*, 275, 276*, 313
biumpressa 273*, 274*, 275, 297*, 314*
frechi 275, 297*, 314*
glabra 272
kozhimensis 272
pessoides 275, 276*, 297*, 314*
subarmata 272, 273*, 275, 314*
uhligi 272, 273*, 297*
Kamptoclymenia 11, 300, 315
endogona 11, 300, 301, 316*
trivaricata 300, 300*, 301, 304*, 316*
Kazakhoclymenia 248
Kentuckia 318
Kiaclymenia 279, 281, 297
laevis 280*, 281, 297*, 313*
polonica 267, 279, 280*, 281, 297*, 313*
uralica 279, 281
Kielcensia 301, 302
Kirsoceras 202, 246, 311
rotundatum 246
Kladognathus 172
Klapperilepis 14, 20, 22*, 110, 111, 113, 115*, 118, 120, 132, 165, 179, 180, 180*, 181*, 182*
circularis 17, 113, 117*, 118, 180, 180*
clarki 118
crepida 12, 15, 20, 46, 110, 121*, 122, 124, 180, 180*
delicatula 17, 19, 114, 120, 120*, 180*
protorhomboidea 19, 20, 116, 116*, 180, 181*
quadratinodosolobata 17, 113, 118, 119*, 120, 140, 180*
regularis 115*, 116, 121, 181*
rhomboidea 9*, 14, 15, 16, 20, 62, 116, 116*, 180, 181*
robusta 15, 20, 121, 121*, 122, 180, 180*

- schuelkei* 14, 114, 118, 119*, 180, 180*
spathula 114, 119, 119*, 180, 180*
superlobata 138
termini 9*, 15, 16, 20, 121*, 122, 180, 180*
triangularis 19, 20, 27*, 33*, 113, 114, 114*, 115, 115*, 116, 118, 120, 122, 133, 138, 182*
ultima 12, 14, 19, 27*, 113, 113*, 114, 115, 120, 166, 179, 180, 182*
wolskiae 117*, 118, 180, 180*
Kosmoclymenia 16, 248, 253*, 255*, 259, 260, 263, 283, 305, 312, 313
ademmeri 259
bisulcata 259, 260, 312*
cf. bisulcata 266*
dzikowiecensis 262, 263*, 266*, 312*
galeata 261, 262*, 266*, 312*
kowaleensis 259, 260*, 263, 266*, 312*
parundulata 261
prima 258, 259
sedgwicki 259
similis 262, 263*, 266*, 312*
*sp. aff. *K. bisulcata** 260, 261*
undulata 260, 265*, 266, 266*, 310*
wocklumeri 265, 266
xenostriata 263, 264*, 266, 266*, 312*

L

- Lagovidina* 45, 47, 168*, 169
obliqua 42, 45, 46, 47*, 168*
Lagovignathus 22*, 23*, 102, 104, 105*, 106*, 108*, 178*, 179
bilobatus 104, 105*, 177*
bogartensis 26*
fallax 81, 104, 105, 106, 106*, 107, 177*, 179
glaber 104, 105*, 107, 177*
granulosus 17, 18, 21, 107, 108, 108*, 177*, 179
lagowiensis 21, 106*, 107, 108, 177*, 179
styriacus 13, 14, 21, 107, 108, 108*, 177*, 179
Lagovignathus?
dissimilis 28, 104, 107*, 177*, 179
Lagovilepis 179
bogartensis 12, 165, 166
Lagowites 207, 232, 311
niwae 207, 232, 233*, 310*, 247*
Latericriodus 30, 31, 169
latericrescens 31
sp. 31, 31*, 32, 167*
Latericriodus (or *Antognathus*)
rarus 31*, 32
Libodiscus 187
Ligonodina 40, 41*, 42, 44, 59, 165, 166, 168*, 169
albidens 41, 41*, 42, 168*
delicata 41
franconica 65, 67
latibasalis 43, 43*, 168*
monodentata 67
multidens 42, 42*, 47, 168*
pectinata 40, 41, 41*, 43, 168*
sudetica 43, 44*, 168*
albidens 47
Linguatornoceras 191, 191*, 305
linguum 193, 197
Liroclymenia
fundifera 299

<i>Lobotornoceras</i>	208, 209*
bicaniculatum	208
<i>Loganoclymenia</i>	248
<i>Lysagoraceras</i>	317

M

<i>Maeneceras</i>	17, 207, 215 , 216, 217, 235, 308, 311
acutolaterale	217
lagoviense	215*, 216*, 217 , 235, 305, 307*
pompeckji	217
<i>Manticoceras</i>	12, 188
<i>Manticolepis</i>	179, 180
rhenana	12, 165
winchelli	12, 165
<i>Mashkovia</i>	
silesiensis	23
<i>Mecynoceras</i>	17
<i>Mehlina</i>	11, 22*, 27, 59, 63, 71, 74 , 74*, 75, 76, 77, 77*, 78, 79, 79*, 80, 80*, 97, 99, 109, 165, 166, 172
irregularis	74, 75
kielcensis	60, 74*, 75 , 174*
lauriformis	80
lunaria	76, 77, 77*, 174*
robustidentata	63, 75 , 174*
strigosa	75, 76*, 77, 77*, 174*
sudetica	77, 77*, 174*
transita	71
<i>Mehlina?</i>	
unica	63
<i>Mesoclymenia</i>	
nalivkinae	270
<i>Mesotaxis</i>	108
<i>Mestognathus</i>	27, 183
<i>Mimimitoceras</i>	240
<i>Mitrellataxis</i>	11, 23*, 24, 28, 33*, 35 , 37, 39, 166, 169
circularis	32, 35, 36*, 37 , 167*, 169
chevronella	35, 36, 37
conoidalis	35, 36 , 36*, 37, 167*
coronella	36*, 38 , 167*
ornata	36, 36*, 37, 167*, 169
<i>Mitrellataxis?</i>	
asymmetrica	36, 36*, 37 , 167*

N

<i>Nanoclymenia</i>	267, 313
nana	267
retrusa	267 , 268*, 297*, 313*
<i>Nanoclymenia?</i>	
intermedia	267 , 268*, 297*, 313
<i>Nehdenites</i>	217 , 218*, 308, 310
circumflexus	217 , 218*, 247*, 309*
praelentiformis	218 , 218*, 247*, 309*
verneuili	12, 32, 33, 95, 120, 122, 124, 139, 217 , 218*, 219, 247*, 309*
<i>Nehdenthomis</i>	317
<i>Neopolygonathus</i>	23*, 28, 29, 90, 102 , 103*, 104, 166, 177*, 178, 179
communis	29*, 91, 101, 102 , 103, 103*, 104, 177*
purus	104
vogesi	102, 103 , 103*, 177*
<i>Neoprioniodus</i>	
postinversus	69
<i>Neospathodus</i>	52
<i>Nodosoclymenia</i>	196, 283, 287 , 289
distincta	256, 287 , 289, 289*, 304*, 315*

<i>lupata</i>	289
<i>variabilis</i>	287

O

<i>Oligophylloides</i>	18
<i>Oma-dimeroceras</i> (<i>Sporadoceras</i>)	
polonicum	235
<i>α-Oma-dimeroceras</i> (<i>Praeglyphioceras</i>)	
lagowiense	232
niwae	232
<i>α-Oma-dimeroceras</i> (<i>Sporadoceras</i>)	
subvaricatum	235
<i>Oma-monomeroceras</i> (<i>Aganides</i>)	
atavum	221
<i>Oma-monomeroceras</i> (<i>Cheiloceras</i>)	
avaricatum	219
depressum	217
discoide	217
discoideum	217
disco-transversale	221
globosum	230
globulare	219
lenticulare	217
praeglobosum	230
praepolonicum	218
sinuvaricatum	207
subpartitum lativaricatum	221
subpartitum Münst. angustivaricatum	221
tenue	218, 221
umbiliferum	230
verneuili	219
<i>Oma-re-protomeroceras</i>	
umbilicatum	226
<i>Omolonognathus</i>	
transformis	23
<i>Ornatoclymenia</i>	
<i>Ostrovkites</i>	
numismalis	207 , 207*, 216*, 307*
<i>Oxyclymenia</i>	
ornata	201
<i>Oxytornoceras</i>	
<i>Ozarkodina</i>	
homoarcuata	70, 169
	69
P	
<i>Pachtoceras</i>	317
<i>Pachyclymenia</i>	
abeli	279
kozlowskii	279 , 280*, 297*, 313*
sinuconstricta	279
<i>Palmatodella</i>	
unca	140, 141
<i>Palmatolepis</i>	
abnormis	20
abnormis sandbergi	20
aff. gracilis	127
ampla	14, 17, 20, 136*, 137 , 180, 182*
arcuata	118
clarki	118
deflectens sigmoidalis	129
delicatula postdelicatula	123
expansa	19, 21, 129, 130
glabra acuta	19
glabra glabra	16
helmsi	138
initialis	114*, 116, 131 , 131*, 133, 138, 169, 182*

- linguiformis* 12, 19, 30
marginata clarki 118
marginifera 138
marginifera utahensis 20
maxima 134
minuta wolskae 124
parva 125
perlobata 99, 131, **133**, 133*, 134*, 137, 142, 182*
perlobata helmsi 135
perlobata postera 21, 135
perlobata sigmoidea 134
postera 19
praetriangularis 115
ultima 115
quadrantinodosa inflexa 19
rugosa 9, 13, 14, 17, 21, 136*, **137**, 180, 182*
sandbergi 120, 132*, **133**, 182*, 307*
schindewolfi 19, 21, **134**, 135*, 137, 142, 150, 180, 182*
sinuosa 28
subperlobata helmsi 138
trachytera 13, 14, 18, 21, 27*, 134, 136*, **137**, 147, 180, 182*
triangularis 19, 111
variabilis 123, 124
- Palmatolepis?*
irregularis 99
- “*Palmatolepis*”
acuta 142
pectinata 142
prima 142
- Panderodella*
subrecta 54
- Panderolepsis* 138
- Pandorina*
insita 70, 71
- Pandorinellina* 23*, 59, 70, 72*, 73, 75, 146, 147, 148, 158, 166
bituberculata 73, 73*, 174*
fragilis 72*, **73**, 174*
vulgaris 70, **71**, 72*, 73, 74, 75, 158, 159, 174*, 184
- Pandorinellina?*
vogelgnathoides 59, 60, 66, **70**, 71, 71*, 172*
- Paratornoceras* 232
acutum 232
- Parawocklumeria* 242*, 300, 300*, **301**, 315
distorta 300*, **301**, 304*
distributa 301
paprothae 301
paradoxa 13, 14, 265, 298, 300* **301**, 304*, 316*
patens 301
- Pelekysgnathus* 30, 32, **33**, 34, 35, 38, 165, 166, 169
inclinatus 33, 97
planus **33**, 34*, 167*
- Pernoceras* 196
- Phoenixites* 193, 194
sulcatus 194
varicatus 194
- Pinacodus*
profundus 157
- Pinacognathus* 64, 88, 146, **157**
inornatus 88
- Pinacognathus?*
praesulcatus 88, 151*, **157**, 176*
sulcatus 88
sp. 64
- Plagiostomoceras* 317
Plagiostomoceras?
cardiolae 317
- Planadina* **70**, 171, 172
plana 59, 69*, **70**, 173*
- Planitornoceras* 201
- Planulites*
angustiseptatus 283
laevigatus 256
striatus 249
undulatus 259
- Platyclymenia* 134, 248, 255, 281, 286*, **287**, 312
annulata 14, 16, 166, 208, 226, 240, 287, 289, 304, 318
crassissima 289
implana 286*, **287**, 304*, 315*
inflata 286*
intracostata 287
involuta 137
lagowiensis **287**, 288*, 304*, 315*
laxata 287
puschi 286*, **287**, 304*, 315*
prosostriata 293
stenomphala 293
subnautilina 289
unisulcata 256
- Playfordia* 28
- Pleuroclymenia* 267, **289**, 290*, 292, 297, 312
costata **289**, 290, 290*, 304*, 315*
intermedia 267, 279
varicata **290**, 290*, 304*
- Pluckidina* **44**, 49, 165, 166, 170, 170*, 171
lagoviensis 44
lipperti **44**, 45*, 53, 170*
purnelli **44**, 46*, 170*
- Polonoceras* **197**, 198*, 199*, 208, 305, 306, 307, 308
bashkiricum **197**, 198*, 216*, 307*
dorsoplanum 198, **199**, 199*, 201, 220*, 216*, 307*
latum 203
planum 197, **198**, 198*, 216*, 307*
sandbergeri **197**, 198*
sudeticum **199**, 199*, 216*, 306, 307*
- Polygnathus* 22*, 23*, 70, **88**, 97, 166, 173, 175, 177*, 178*
aff. fallax 80, 307*
angustidiscus 84
brevilaminus 89
cf. diversus 81
communis 102, 103
depressus 91
dubius 88
extralobatus 9, 11, **94**, 94*, 95, 175, 177*
flaccida 81
gyratilineatus 109
inornatus 88
kadzielniae 95, **97**, 98*, 177*
lagowiensis 104
limbatus 91
margininvolutus 103
nodocostata 77
obliquicostatus 95
padovanii 91
pennatuloideus 81
pennatulus 88*, 176*
perbonus 37
planirostratus 91

- praecursor* 15, **89**, 89*, 90*, 91, 91*, 93,
95, 166, 177*
procerus **95**, 96*, 179, 177*
rarus 86
semicostatus 27*, **89**, 91, 92*, 95, 99, 102,
103, 178
sp. A 91
streeli 85
squalidus 95
szulczewskii 91
tuberculatus 165
vohynicus **95**, 96*, 97, 177*
webbi 86, 89, 97, 165, 166
zneapolensis 9, 11, 94*, **95**, 175, 177*
- Polygnathus?*
experplexus **93**, 93*, 177*
pennatus 88, **97**, 101
serratus 138
- Polylophodonta* 81, 108, 109, 110, 175
ovata **110**, 111*, 170*
pergyrata **110**, 112*, 179*
- Polynodosus* 22*, 23*, 76, **77**, 79, 79*, 83*, 97,
99, 104, 105, 109, 166, 173, 174*
confluens 78, **81**, 82*, 84, 110, 175, 175*
diversus 77, 78, 81, 83*, **84**, 175*
lauriformis 77, 78*, 79*, 80*, **81**, 105, 174*
nodoundatus 77, 78, **83**, 83*, 84, 175*
perplexus 78
transitus 77, 77*, 78*, **79**, 79*, 80, 81, 104, 174*
triphylattus 78, **81**, 83*, 84, 175, 175*
- Postclymenia* 254
evoluta 252
- Posttornoceras* **210**, 211*, 212*, 214, 311
aff. *contiguum* 212*, 216*
balvei **210**, 211*, 216*, 307*
contiguum 214
fallax **210**, 211*, 216*
sodalis 210
superstes **210**, 211*, 307*, 308
- Posttornoceras* (or *Xenosporadoceras*)
posthumum **210**, 212*, 214*, 307*
- Posttornoceras?*
cornwallensis 212*, **214**, 216*, 307*
- Praeflexiclymenia* **292**, 293*, 312, 314
curvidorsata 249, 291*, **292**, 293, 293*,
304*, 316*
flexilobata **292**, 293*, 304*, 316*
obliqua 292, 293
tenuis **292**, 293*, 304*, 316*
- Praeglyphioceras*
moravicus 234
- Praemeroceras* 228
- Prioniodus*
elegans 59
geminus 56
- Prionoceras* 14, 189, **240**, 241*, 242*, 243, 246*, 305
felix 234
divisum **240**, 241*, 247*
frechi **240**, 241*, 309*
fuerstenbergi 242*, **243**, 247*, 309*
lentum **243**, 247*, 309*
lineare **240**, 241*, 247*, 309*
- Progonioclymenia* 295
acuticostata 295
bogoslovskyi 295
- Prolobites* 189, 201, 203, **226**, 227*, 310
delphinus 137, **226**, 227, 227*, 237, 247*, 310*
nanus 226, **227**, 227*, 247*, 310*
- simplex* 224
- Protognathodus* 11, 14, 23*, 71, **157**, 161, 185
kockeli 10*, 21, **157**, 158*, 166, 185*, 254
- Protornoceras* 14, 196, 197, 201, 202, 202*, 203,
204*, 248, 279, 308 311, 312
aphyllitiforme **202**, 202*, 216*
bilobatiforme 203
curvidorsatum 204*, **205**, 216*, 307*
kielcense 203
kochi 196
mirabile 202, 204*, **205**, 216*, 307*
ornatum 203
polonicum 201, **203**, 204*, 216*, 307*
siemiradzkii 203
simplicius 196, 197, 202*, **203**, 208, 216*, 307*
simplificatum 201*, 202*, **203**, 216*
zuberi 203
- Protoxyclymenia* 256, **259**
galezicensis 258*, **259**, 266*, 312*
serpentina 258*, **259**, 266*, 312*
tenuissima 259
- Pseudoclymenia* 18, **206**, 206*, 259, 308
dillensis **206**, 206*, 216*, 307*
fundifera 206*, **207**, 216*, 307*
- Pseudopolygnathus* 21, 22, 23*, 37, 146, 147, 148,
152, 154, 155, 165, 166, 183
aculeatus 21, **155**, 155*, 184*
controversus 163
graulichi 88
jugosus 14, 16, 21, 143, 146, **152**, 152*,
153*, 155, 184*
ostrovkensis **152**, 154*, 155, 163, 184*
prima 152
primus 152, 154, 155
stabilis 152
ultimus 21, **156**, 156*, 183, 184*
vogesi 154
ziegleri 21, 152, **156**, 183, 184*
- R**
- Raymondiceras* 224, 225*
korni 225*, **226**, 227, 247*, 310*
umbilicatum 225*, **226**, 310*
- Raymondiceras?*
praelagowicense **225**, 225*, 310*
- Rectoclymenia* 267, 283
aff. *arietina* 267
- Rhiphaeoclymenia* 297, 299, 315
canaliculata 297, **298**, 298*, 304*, 316*
- Roinghites* 224
bottkei 226
- Roundya*
franca 67
plana 70
prava 67
- S**
- Scaliognathus*
anchoralis 13
- Scaphignathus* 23*, 146, **149**, 150, 183
leptus **151**, 151*, 184*
subserratus 148
velifer 21, 35, 147*, **150**, 151*, 184*
velifera 149
- Selwoodites* 214
- Siphonodella* 13, 19, 50, 64, 87*, 88*, 146, 157, 176
lobata 50
praesulcata 21

- Skeletognathus* 27
Soliclymenia 11, 292, 293, **295**, 297
 **295**, 295*, 304*, 314, 316*
 296*, **297**, 304*, 316*
 297
 295, **296**, 296*, 297, 304*, 316*
Spathiocaris 188
 188
 188
Spathodus
 152
 < fissilis 55
 52
 152
Spathognathodus
 breviatus 64
 59
 < werneri 64
Sphaeromanticoceras 186
Sphenoclymenia **275**, 278, 278*
 brevispina 278*, **279**, 297*, 314*
 **278**, 278*, 297*, 314*
 278*, **279**, 297*, 314*
Spinoclymenia
 256
Sporadoceras 14, 210, 211*, 214, 234, **235**,
 237, 239*, 311
 biferum 235
 **236**, 237, 237*, 247*, 310*
 < nux **237**, 239*, 240, 247*, 310*
 < orbiculare 240
 < rotundum 234
 sp. **210**, 211*
 < subbilobatum **237**
 < terminus **237**, 239*, 240, 247*, 310*
 < varicatum **237**, 238*, 247*, 305, 310*
Stenoclymenia 292, **293**, 294*, 304*, 312, 314, 316*
 < elliptica 289, 289*
 < sandbergeri 13, **293**, 294, 294*, 304*, 316*
 < stenomphala 293
Stenoclymenia?
 spp. **293**
Strunius 318
Sweetodina **67**, 67*, 70, 172
 < lagoviensis 59, 67*, **68**, 69, 70, 173*
 < monodontata 67*, **68**, 68*, 69, 173*
Synclydognathus 9*, **56**, 57*, 58, 118, 169
 < ancestralis 16, **57**, 57*, 167*
 < triramosus **57**, 57*, 167*
Syringopora 11
- T**
- Tardewocklumeria* 301
Thrinodus 318
Tornia 202, 205
Tornoceras 187, **191**, 193, 193*, 194, 196*, 197, 203,
 217, 219, 246, 305, 306, 308, 310, 321
 < acutiforme 232
 < acutum 15
 < applanatus 196
 < beulense 269
 < crebriseptum **194**, 216*
 < escoti 197
 < frechi 193
 < frechi parvum 194
 < incrassatus 193
- obliquum* 203
pseudobilobatum 196*, **197**, 216*, 307*
simplex 193
subacutum **194**, 195*, 216*, 307*
subleptiforme 15, **194**, 195*, 216*, 306, 307*
typum 188, 192*, **193**, 193*, 194, 216*,
 305, 306, 307*
- Trichognathus*
 < tumida 49
Trigonoclymenia 255, 255*, **256**, 312
 < glabra 255, 255*, **256**, 266*, 311*
 < spinescens 255*, **256**, 266*, 311*
Tripodellus 20, 22*, 23*, 28, 29, 67, 106, 118,
 122, 122*, 123, 124, 124*, 127,
 128, 129, 130*, 180, 181*, 321
 < clarki 14, 15, 19, 114, 118, 120, 122*,
 123, 123*, 124, 181*
 < donoghuei **126**, 127*, 181*
 < expansus 129
 < flexuosus 67, 122
 < gonioclymeniae 13, 19, 21, 28, 50, 127, 129,
 130, 130*, 181*
 < gracilis 9, 11, 14, 21, **129**, 130, 130*, 181*
 < lobus 46, **125**, 126*, 127, 181*
 < mancus 13, 21, **129**, 130, 130*, 181*
 < minutus 29*, 122, 124, **125**, 127, 127*,
 128, 181*
 < schleizius 28, 29*, 127, **128**, 128*, 129, 166, 181*
 < schuelkei 15
 < subgracilis 124*, **125**
 < subtilis **124**, 125*, 181*
 < tenuis 67
 < variabilis 15, 118, 123, **124**, 124*, 125, 126, 181*
Trochoclymenia 269
 < wysogorskii **269**, 295*, 297*, 313*
Truyolsoceras
 < sandbergeri 197
- U**
- Uncadina* 49*, **50**, 170*, 171
 < unca 49, 49*, **50**, 170*
Uraloclymenia 279, 281
Urbanekodina **64**, 172
 < undata 59, **64**, 64*, 172*
- V**
- Vogelgnathus* 22*, 23*, **59**, 62, 62*, 63, 63*,
 65, 66, 70, 71, 166, 171
 < arcuatus **62**, 172*
 < branmehloides **63**, 64, 172*
 < campbelli 64
 < proclinatus 59, **60**, 61*, 62, 172, 172*
 < unicus **63**, 64, 172*
 < variabilis **59**, 60*, 63, 65, 75, 172, 172*
 < werneri 63*, **64**, 172*
- W**
- Wedeckindoceras*
 < kayseri 214
Wocklumeria 11, 34, 37, 156, 300, 302, **303**, 315
 < paradoxa 301
 < paradoxa var. *applanata* 301
 < sphaeroides 11, 13, 14, **303**, 303*, 304*, 315, 316*
- Xenosporadoceras*
 < ademmeri 234