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Taxonomy, evolutionary History and Distribution of the middle to late Famennian Wocklumeriina (Ammonoidea, Clymeniida)

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With 12 figures, 5 plates and 4 tables

Abstract

Old collections, new records, and data from global literature are used for taxonomic revisions and for a new reconstruction of the evolutionary history of the triangularly coiled clymenids, the Wocklumeriaceae, and their ancestors. *Epiwocklumeria applanata* is first reported from the topmost Wocklum Limestone at Hasselbachtal and Drewer, and this supports the distinction of an *applanata* Subzone just prior to the global Hangenberg Event which wiped out the whole group. The Wocklumeriaceae and Glatziellidae record of the famous Oberrödinghausen Railway Cut and of other Rhenish sections is revised. The Maïder of Southern Morocco has yielded first *Parawocklumeria patens, paprothae, Wocklumeria sphaeroides plana, Kielcensia ingeniens* n. sp., and *Synwocklumeria mapesi* n. sp. *Parawocklumeria distributa* Czarnocki forms the type-species of *Tardewocklumeria* n. gen. Lecto- and neotypes for several taxa are designated. The variability and paedomorphic patterns of *Wo. sphaeroides* are discussed. The Wocklumeriaceae represent the terminal Famennian (Upper Devonian VI-C/D) radiation of a long-ranging lineage which evolved in parallel to other clymenid groups. They are characterized by sutural features and by longidomic and very slowly expanding whorls. The polyphyletic traditional Gonioclymeniina are divided into the suborder Wocklumeriina (with Wocklumeriaceae, Glatziellaceae n.superfam. and Biloclymeniaceae) and into the Gonioclymeniaceae of the Clymeniina. *Gyroclymenia* Czarnocki is regarded as a junior synonym of *Pleuroclymenia* Schindewolf which, however, does not include the '*Pleuro.*' *americana* and *eurylobica* groups. *Pleuroclymenia* represents the ancestral form of the Wocklumeriina and also the phylogenetical link with *Platyclymenia (Varioclymenia)* of the Clymeniaceae. The Gonioclymeniaceae had their roots in advanced Platyclymeniidae.

Key words: Ammonoidea, Clymeniida, Upper Devonian, Famennian, Hangenberg Event, Taxonomy, Phylogeny, Palaeobiogeography.

Zusammenfassung

Alte Aufsammlungen, Neunachweise und globale Literaturdaten werden für taxonomische Revisionen und für eine neue Rekonstruktion der Evolution der Dreiecksclymenien (Wocklumeriaceae) und ihrer Vorfahren benutzt. *Epiwocklumeria applanata* wird zum ersten Mal im Hasselbachtal und bei Drewer nachgewiesen, und diese Funde bestätigen die Abtrennung einer *applanata*-Subzone im unmittelbar Liegenden des Hangenberg-Event, welcher zum Aussterben der gesamten Gruppe führte. Die Verbreitung von Wocklumeriaceae und Glatziellidae im klassischen Profil des Bahneinschnittes bei Oberrödinghausen und an anderen Fundorten im Rheinischen Schiefergebirge wird revidiert. Der Maïder in Süd-Marokko lieferte erstmalig *Parawocklumeria patens, paprothae, Wocklumeria sphaeroides plana, Kielcensia ingeniens* n. sp. und *Synwocklumeria mapesi* n. sp. *Parawocklumeria distributa* Czarnocki bildet die Typus-Art von *Tardewocklumeria* n.gen. Weiterhin werden die Variabilität und paedomorphe Erscheinungen bei *Wo. sphaeroides* diskutiert. Die Wocklumeriaceae repräsentieren im höchsten Famennium (UD VI-C/D) die Radiationsphase einer langlebigen phylogenetischen Linie, die sich parallel zu anderen Clymenien entwickelte. Sie ist durch Suturmerkmale und lange Wohnkammern bei niedrigmündigen Gehäusen charakterisiert. Die als polyphyletisch erkannten Gonioclymeniina werden in die Wocklumeriina (mit Wocklumeriaceae, Glatziellaceae n.superfam. und Biloclymeniaceae) und in die Gonioclymeniaceae der Clymeniina geteilt. *Gyroclymenia* Czarnocki ist ein jüngeres Synonym von *Pleuroclymenia* Schindewolf, umfasst jedoch nicht die ‚*Pleuro.*' *americana*- und ‚*Pleuro.*' *eurylobica*-Artgruppen. Die Gattung ist die ursprünglichste Form der Wocklumeriina und stellt gleichzeitig das Bindeglied zu *Platyclymenia (Varioclymenia)* der Clymeniaceae dar. Die Gonioclymeniaceae wurzeln in fortgeschrittenen Platyclymeniidae.

Schlüsselwörter: Ammonoidea, Clymeniida, Oberdevon, Famennian, Hangenberg Event, Taxonomie, Phylogenie, Palaeobiogeographie.

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Introduction

In one of his most famous and classical papers, Schindewolf (1937) has both investigated the detailed ammonoid biostratigraphy of the German Wocklum-Stufe or Wocklum Limestone (terminal Famennian, Upper Devonian [=UD] VI) and the evolution of triangularly coiled clymenids which represent the most bizarre group of Devonian ammonoids. Since then, a wealth of new data has become available concerning the biostratigraphy (reviews in Becker 1988, 1996; Korn 1993, Korn et al. 1994) and paleobiogeography (Becker 1993a) of ammonoids around the Devonian-Carboniferous boundary. Triangularly coiled clymenids belonging to the Wocklumeriaceae have been described or mentioned from 20 sedimentary basins of five continents (Fig. 1: Europe, Asia, North Africa, North America, South America) giving an almost pantropical distribution in warm-water cratonic shelf areas. A detailed overview of the global record of Wocklumeriaceae genera and species is compiled in Table 1 (for complete references see later text). The list includes new regional records as well as new species. Several members of *Kielcensia, Triaclymenia, Tardewocklumeria* n. gen. and *Synwocklumeria* appear to have been endemic. The richest and most diverse faunas come from Germany (Rhenish Massif and Thuringia), Poland, the Urals, and South China. Clearly, there was not a single evolutionary centre, as former phylogenetic reconstructions based on German-Polish taxa only (Schindewolf 1937, Korn 1995a, b) might suggest. For the present review and revision, more than 1500 Wocklumeriaceae specimens have been studied.

In the evolutionary model developed by Schindewolf (1937), triangular coiling was invented iteratively in three independent latest Famennian clymenid lineages: in *Soliclymenia* (Hexaclymeniidae), in the Parawocklumeriidae, and in the Wocklumeriidae. Bogoslovskiy (1981) and Czarnocki (1989), however, later described intermediate forms between parawocklumeriids and wocklumeriids. Korn (1992a, 1995a, b) emphasized their phylogenetic significance and correctly outlined briefly the evolutionary transition between the two families which form a single natural systematic unit, the Wocklumeriaceae. This superfamily is characterized by the following combination of apomorphies: (1) triangularly coiled early to adult stages, (2) weak to strong constrictions in straight whorl parts, and (3) subdivision (or later complete reduction) of both dorsal and ventral lobes.

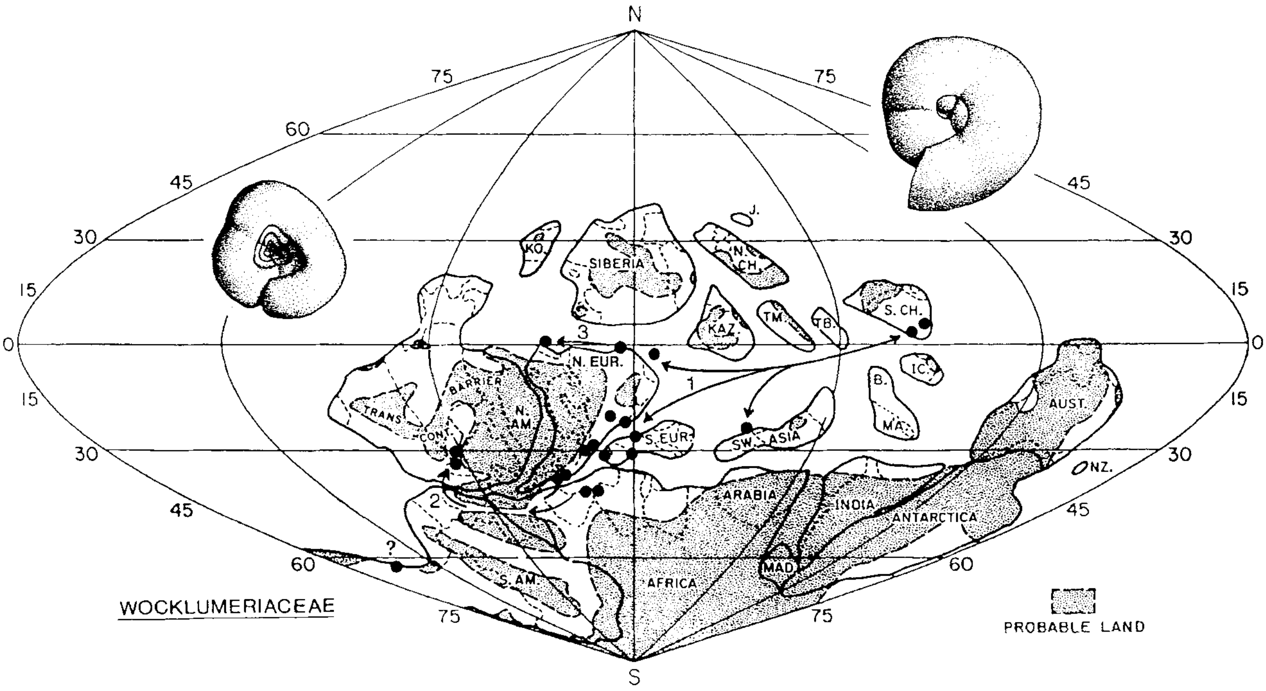

Fig. 1. Global distribution of late Famennian (UD VI-C/D) Wocklumeriaceae showing three routes of potential faunal exchange: **1.** along the Prototethys; **2.** from North Africa to W of the Appalachians; **3.** along the western Ural seaway. The occurence on the Chilenia Terrane (see Breitkreuz 1986) is still questionable. Abbreviations: **KO.**, Kolyma (NE Siberia), **N.** and **S. CH.**, North and South China, **IC.**, Indochina (Vietnam, Kambodia, Laos); **B.**, Burma (Myanmar); **MA.**: Malyasia; **J.**, Japan; **TB.**, Tibet; **TM.**, Tarim Plate; **Kaz.**, Kazackstan; **Aust.**, Australia; **NZ.**, New Zealand; **N.** and **S. EUR.**, Northern and Southern Europe; **N.** and **S. AM.**, North and South America; **MAD.**, Madagascar

As already said, Korn (1995a, b) used only species of the Rhenish Slate Mountains in his phylogenetic reconstruction and, therefore, his model is incomplete and simplified. The long-known sudden and synchronous appearance of parawocklumeriids and later the cryptogenic entry of *Wocklumeria* in German sections strongly suggests an influence of migrational events on the known spatial and stratigraphic distribution of members of the group. However, it is strange that the entry of such taxa is not correlated with any obvious lithofacies change. Distribution control by subtle ecological factors is further indicated by peak frequencies of specific species in distinctive beds of rather uniform successions (see *Parawocklumeria* Bed = Bed 98–99N at Hasselbachtal, Becker 1996). There is no reason to assume that speciation mostly took place in Germany. Morphologically intermediate species and endemic end-members of lineages are now known from eastern Europe, Asia, North Africa and North America. Based on taxonomic revisions and new systematic descriptions, an attempt is made here to include all these in a new reconstruction of the evolutionary history of the group. It is clear that this can only be a state-of-the-art model which has to be completed and updated when more, in some cases better preserved and precisely dated material of rare and new taxa is found. The two new species described herein are based on single specimens and they show how obviously incomplete our knowledge still is.

Questions have been raised (compare systematics in Schindewolf 1937 with Korn 1992b) concerning the origin of the Wocklumeriaceae and their relationships with other clymenid groups. Morphological comparisons and taxonomic concepts of related groups will therefore be reviewed. This is aided by some new material of Hexaclymeniidae and certain Platyclymeniidae. A new taxonomic positioning of the Wocklumeriaceae, based on new phylogenetic models, requires a far-reaching revision of traditional clymenid higher-level systematics. This is aided by a new understanding of the ancestry of gonioclymenids and their relatives which, following Korn (1992b), requires the dissolution of the traditional suborder Gonioclymeniina.

Abbreviations and definitions: **dm**, diameter; **wh**, whorl height; **ah**, apertural height; **ww**, whorl widths; **uw**, umbilical width. **A**, adventitious lobes; **E**, external or ventral lobes; **I**, internal or dorsal lobes; **L**, lateral lobes; **U**, umbilical lobes; a double point in sutural formulas mark the umbilical seam. Longidomic, body chamber longer than one whorl; mesodomic, body chamber between $^3/_4$ and one whorl, brevidomic, body chamber between $^1/_2$ and $^3/_4$ whorl. For late Famennian ammonoid zonation and abbreviations see Becker (1993b, 1996) and Korn (1999). ***Wo.***, *Wocklumeria;* ***Epiwo.***, *Epiwocklumeria;* ***Synwo.***, *Synwocklumeria;* ***K.***, *Kielcensia;* ***Parawo.***, *Parawocklumeria;* ***Tardewo.***, *Tardewocklumeria*; ***Tria.***, *Triaclymenia;* ***Kampto.***, *Kamptoclymenia;* ***Pleuro.***, *Pleuroclymenia;* ***Progonio.***, *Progonioclymenia;* ***Hexa.***, *Hexaclymenia;* ***Glat.***, *Glatziella*; ***Post.***, *Postglatziella;* ***Platy.***, *Platyclymenia;* ***Vario.***, *Varioclymenia;* ***Trocho.***, *Trochoclymenia;* ***Uralo.***, *Uraloclymenia;* ***Nod.***, *Nodosoclymenia.* An * in synonymy lists marks the introduction of taxa, a + refers to records or description of new material.

Institutional abbreviations: **MB**.- and **Oc**-numbers refer to material deposited in the Museum für Naturkunde (**MfN**); **GPIG** specimens are housed in the Geological Institute of Göttingen University; **Z**-numbers refer to the collection of the Bundesanstalt für Geowissenschaften and Rohstoffe (**BGR**) in Berlin-Spandau.

Material and localities

Fig. 2

Hasselbachtal

A revision and correlation of the Hasselbachtal Auxiliary Stratotype succession has been published by the author (Becker 1996) and other details were published in Becker et al. (1984), Becker (1988) and Luppold et al. (1994). It has been emphasized that further collecting is likely to fill current record gaps of longer ranging species and to add first records of further species. This was proven by new fieldwork in 1996 to 1998 which produced, amongst others, the first *Epiwocklumeria applanata* Wedekind (MB.C.2701) from the topmost part (upper 14 cm, Bed 113aN) of the Wocklum Limestone.

All collections of Becker (1996) and new material were available for this study. Additional specimens of *Wo. sphaeroides sphaeroides* (Richter), including many juveniles, were found loose (MB.C.2723.1–18) or came from Beds 100N (MB.C.2720), 106/108N (MB.C.2721.1–2), 113N (MB.C.2703, 2718–2719), 113aN (MB.C.2710.1–4), 113cN (MB.C.2710.5–7) and 114N (MB.C.2722.1–2). Three new specimens

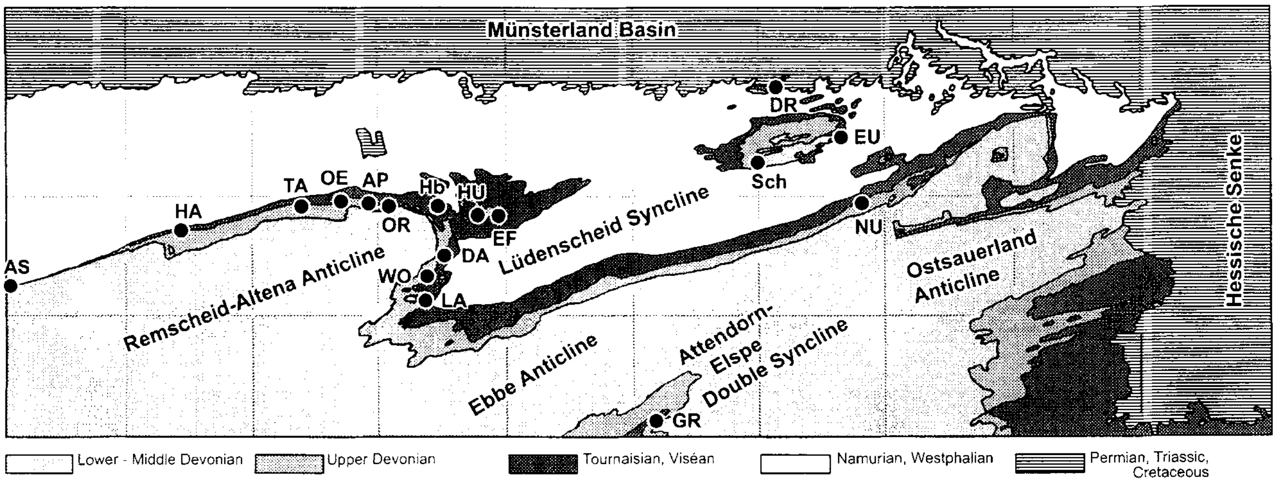

Fig. 2. Geographic position of all known Wocklumeriaceae-localities in the northern part of the Rhenish Slate Mountains. Abbreviations: **AS,** Aske, E of Hagen; **HA,** Hasselbachtal, N of Hohenlimburg; **TA,** Tannenkopf, N of Iserlohn (Seiler area); **OE,** Oese, E of Hemer-Becke and Höcklingsen; **AP,** Apricke; **OR,** Oberrödinghausen railway cut and road section; **Hb,** Hangenberg, NE of Eisborn; **HU,** Humberg, S of Ainghausen; **EF,** Effenberg and Müssenberg, NW and N of Hachen; **DA,** Dasberg near Hövel or Wettmarsen; **WO,** Burg or Borkewehr near Wocklum; **LA,** Langenholthausen/Trachtenberg; **Sch,** old shooting ground near the Bilstein Cave; **DR,** Provincial Quarry Drewer; **EU,** Eulenspiegel; **NU,** Nuttlar; **GR,** Grimminghausen. Geological overview taken from Luppold et al. (1994: fig. 1)

(MB.C.2704.1–3) of *Wo. sphaeroides plana* Schindewolf were found loose, others (MB.C.2702.1–3) came from Bed 113aN.

Oese

Since Denckmann (1901), the Oese section at the B7 road between Hemer and Menden (sheet 4512 Menden, Fig. 2) has been known as an important Devonian-Carboniferous locality and it has been illustrated by Luppold et al. (1994). However, the ammonoid sequence has not been investigated in much detail and only preliminary data concerning the Wocklum Limestone have been given by Becker et al. (1993). The topmost 35 cm yielded *Wo. sphaeroides sphaeroides* (e.g., MB.C.2724–2725 = Oc 1705 and 1774, MB.C.2726), *Wo. sphaeroides plana* (MB.C.2727 = Oc 1756), and *Parawo. paradoxa* (e.g., MB.C.1713–1716 = Oc 1713, 1766, 1709, 1727). *Epiwocklumeria* has not yet been found and only few *Parawocklumeria* but no kamptoclymenids or *Triaclymenia* were collected so far from lower down (UD VI-C) in the sequence.

Oberrödinghausen

The Oberrödinghausen Railway Cut has been famous since Schindewolf's (1937) pioneer study. A. Denckmann collected at the turn of the century wocklumeriids in the Hönne area but his poor fragments (MB.C.1782.1–3, leg. 1901) were not identified. Schmidt (1924) first recorded *Wo. sphaeroides* (MB.C.1800.1–13, MB.C.2205 = *Wo. sphaeroides plana*) and *Wo. distorta*. Schindewolf (1937) claimed that the latter in fact belong to *Parawo. paradoxa*. This is confirmed by examination of Schmidt's collection (MB.C.1793.1–7), including a figured original (Schmidt 1924: pl. 6, figs ?14, 15; MB.C.1727). Since the latter specimen was misoriented, Schmidt illustrated a ventral lobe rather than a ventral saddle. Schmidt (1924) also misidentified some juvenile *Wo. sphaeroides* as parawocklumeriids (det. *Wo. distorta*, MB.C.1794.1–2).

Schindewolf's extensive collections of Wocklumeriaceae and glatziellids is available and inventory numbers are given here. However, the holotypes of *Wo. sphaeroides plana, Wo. sphaeroides aperta* Schindewolf, *Kamptoclymenia endogona* Schindewolf, *Kampto. trigona* Schindewolf, *Triaclymenia triangularis* Schindewolf, *Postglatziella carinata* Schindewolf, as well as all illustrated *Epiwocklumeria* and other figured specimens have been lost in the Berlin collection. Fortunately, neotypes for most taxa can be selected from paratypes. Revision of the large parawocklumeriid collection showed that Schindewolf did not distinguish forms with practically closed *(Parawo. paradoxa)* or small, triangularly open umbilicus (*Parawo. paprothae* Korn in Clausen et al. 1989a). Poorly preserved involute morphotypes of *paprothae* and *paradoxa* are indistinguishable and a perfect separation of both taxa probably has not been achieved. In large samples from the *sphaeroides* Zone, typical (clearly umbilicate) *paprothae* morphotypes are easy to segregate from *paradoxa* (see Pl. 4). Some rather involute specimens identified by Schindewolf as *Parawo. distorta* are better also regarded as open umbilicate morphotypes of *Parawo. paprothae*. Since sutures are not preserved in most specimens assigned to *distorta*, affinities with other convolute triangular clymenids (e.g., *Synwocklumeria*) known from elsewhere are theoretically possible. The railway cut record, including small recent collections, is as follows (Fig. 3; former Schindewolf identifications are given in brackets):

Bed 1 (33–35 cm)	*Wo. sphaeroides sphaeroides* (MB.C.912, original of Pl. 2, Fig. 1, intermediate to *plana*; MB.C.1718.1–33, ?MB.C.1718.34–45, MB.C.2214.1–74, MB.C.2218.1–5, MB.C.2219.1–2) *Wo. sphaeroides plana* (MB.C.1721.1–4, including the neotype, ?MB.C.1721.5, MB.C.2215.1–2, MB.C.2216.1–30, MB.C.2217.1–5) *Wo. sphaeroides aperta* (MB.C.2220.1–4) *Wo. sphaeroides* ssp. juv. (MB.C.1–480) *Epiwo. applanata* (MB.C.2221.1–6) *Parawo. paradoxa* (MB.C.2715.1–292, 1740.1–11, 1741.1–2) *Parawo. paprothae* (MB.C.1699.1–10, umbilicate, det. *paradoxa*)
Bed 1 (9.5–14 cm below top)	*Wo. sphaeroides* cf. *sphaeroides* (MB.C. 1742.1–2) *Parawo.* cf. *Parawo. paradoxa* (MB.C.1743)
Bed 1 (14–17 cm below top)	*Parawo. paradoxa* (MB.C.1744)
Bed 2 (18–20 cm)	*Wo. sphaeroides sphaeroides* (MB.C.1722–1-4) *Parawo. paradoxa* (MB.C.2716.1–3, juveniles; MB.C.1726.1–5, specimens with sculpture; MB.C.1746.1–48) *Parawo. paprothae* (MB.C.1747, umbilicate, det. *paradoxa*)
Bed 2 (lower ca. 10 cm)	*Wo. sphaeroides* juv. (MB.C.1745)
Bed 3 (13 cm)	*Wo. sphaeroides sphaeroides* (MB.C.1783.1–7) *Wo. sphaeroides plana* (MB.C.1784.1–2) *Wo. sphaeroides aperta* (lost) *Mimimitoceras trizonatum* Korn juv. (MB.C.1785.1–2, with open umbilicus, det. *Wocklumeria*) *Parawo. paradoxa* (MB.C.1786.1–24) *Parawo. paprothae* (MB.C.1787.2–16, det. *paradoxa*, mostly involute intermediates to *paradoxa*, MB.C.1787.1 typical and with wider umbilicus) *Parawo. paradoxa* vel *paprothae* (MB.C.1788.1–26) *Postglatziella carinata* (MB.C.2200.1–36, including the neotype)
Bed 4 (13 cm)	*Wo. sphaeroides plana* (MB.C.1749.1–4, det. cf. *sphaeroides* and sp.; 1749.4 perhaps intermediate to *aperta*) *Parawo. paradoxa* (MB.C.1820.1–9) *Parawo. paprothae* (MB.C.1822.1–8, involute morphotypes, MB.C.1822.6–8, umbilicate morphotypes) *Parawo. paradoxa* vel *paprothae* (MB.C.1821.1–21) *Post. carinata* (MB.C.2201)
Bed 5 (20–23 cm)	*Wo. sphaeroides* ssp. (squashed, MB.C.1755) *Parawo. paradoxa* (MB.C.1789.1–20) *Parawo. paprothae* (MB.C.1790.1–3, det. *paradoxa*) *Parawo. paradoxa* vel *paprothae* (MB.C.1791.1–23) *Postglatziella* sp. juv. (MB.C.2222.1–2)
Bed 6 (13–15 cm)	*Parawo. paradoxa* (MB.C.1795.1–3) *Parawo. paradoxa* vel *paprothae* (MB.C.1811.1–3) *Parawo. paprothae* (MB.C.1796.1–2, det. *paradoxa*; MB.C.1810.1–2, very involute morphotypes) *Glatziella glaucopis* Schindewolf (MB.C.554.6.1–10)
Bed 7 (18–20 cm)	*Parawo. paprothae* (MB.C.1808.1–22, very involute morphotypes; MB.C.1765, det. *distorta*, with wider umbilicus) *Parawo. ?paprothae* (MB.C.1809.1–24) *Parawocklumeria* sp. indet. (MB.C.1775, det. *?paradoxa*) *Parawo. distorta* (MB.C.1764.1–13, 1764.9 with healed shell fractures, 1764.10 with wrinkle layer, 1764.11 transitional to *patens*) *Parawo. patens* Schindewolf (MB.C.1757) *Tria. triangularis* (lost) *Kampto. trigona* (MB.C.1750.1–3) *Kampto. endogona* (MB.C.1813.1–13, including the neotype) *Glat. glaucopis* (MB.C.554.7.1–8)
Bed 8 (15 cm)	*Parawo. paprothae* (MB.C.1760.1–13, det. *paradoxa*; MB.C.1761.1–2, very involute morphotypes, det. *paradoxa*; MB.C.1766, det. *distorta*, with beautiful wrinkle layer, ?MB.C.1819.1–12) *Parawo. distorta* (MB.C.1767.1–2, ?MB.C.1814.1–4, e.p. det. *paradoxa*) *Parawo. patens* (MB.C.1758)

	Parawocklumeria sp. (MB.C.1818, det. *paradoxa*, pathologically with two A-lobes) *Tria. triangularis* (MB.C.1816) *Kampto. trigona* (MB.C. 1751, the neotype) *Kampto. endogona* (MB.C.1812.1–2) *Glat. glaucopis* (MB.C.554.8.1)
Bed 9 (17 cm)	*Parawo. paprothae* (MB.C.2224.1–19, det. *paradoxa*, mostly poorly preserved small specimens) *Parawo. distorta* (MB.C.1768.1–2, rather involute; MB.C.1768.3, rather evolute, intermediate to *patens*) *Parawo. patens* (MB.C.1759; MB.C.1769, det. *distorta*) *Tria. triangularis* (MB.C.1817) *Kampto. ?trivaricata* Schindewolf (lost) *Kampto. endogona* (MB.C.2223) *Glat. glaucopis* (MB.C.554.9.1–5)
Bed 10 (20–22 cm)	*Parawo.* cf. *Parawo. paprothae* (MB.C.1752, det. *paradoxa*) *Parawocklumeria* sp. indet. (with wrinkle layer, det. *paradoxa*, MB.C.1753) *Mimimitoceras liratum* juv. (Schmidt) (MB.C.1754, det. *paradoxa*) *Parawo. distorta* (MB.C. 1770) *Tria. triangularis* (MB.C.1815, neotype) ?*Triaclymenia* sp. (see Schindewolf 1937: p. 91, lost) *Glat. glaucopis* (MB.C.554.10.1) *Glat. minervae* (Renz) (MB.C.2202.1–3, only fragments)
Bed 15	*Glatziella ?silesiaca* juv. (MB.C.2225, det. cf. *tricincta*, but unribbed)
Bed ?	*Wo. sphaeroides sphaeroides* (MB.C.2203.1–11) *Wo. sphaeroides plana* (MB.C.2204.1–3)

The revision of Schindewolf's collection allows a refinement of taxon ranges and of the Oberrödinghausen zonation (Fig. 3). The *paradoxa* Zone (UD VI-C) can be divided into a lower *paprothae* (Luppold et al. 1994) or *endogona* (VI-C_1: Beds 10–7) and an upper *paradoxa* Subzone (VI-C_2: Bed 6, perhaps lower parts of Bed 5). The *sphaeroides* Zone (UD VI-D_1) starts lower than previously thought within Bed 5. The massive main part of Bed 2 probably correlates with Bed 109N at Hasselbachtal, and *Parawo. paprothae* ranges into the overlying Bed 1 of the *applanata* Subzone (VI-D_2).

Further specimens of *Wo. sphaeroides* come from the Road Section nearby (see Luppold et al. 1994) which is overgrown at present. A juvenile (MB.C.1728 = Oc 1688) shows that sutural elements are fully developed very early in ontogeny (at less than 3.5 mm dm).

Burg or Borkewehr near Wocklum

The type section for the Wocklum Limestone and Wocklum-Stufe near Wocklum (topographic sheet 4613 Balve) is rather insufficiently studied. It yielded Wedekind's (1914, 1918) partly lost types of *Epiwo. applanata*, *Wo. denckmanni*, and *Parawo. paradoxa*. A section log and some conodont data were given by Luppold et al. (1994). Available material includes *Wo. sphaeroides sphaeroides* (MB.C.1725, leg. Wedekind, lectotype of *Wo. denckmanni*; ?MB.C.1778.1–4, leg. Schmidt in 1920; MB.C.1798, det. *Wo. distorta*, leg. Schmidt in 1920; MB.C.1724.1–3, collection of Lange from 1923; MB.C.1780, leg. Schindewolf in 1924: thin section, MB.C.2226, leg. Schindewolf in 1924), *Wo. sphaeroides plana* (MB.C.2227.1–2, leg. Schindewolf in 1924), *Parawo. paradoxa* (lectotype GPIG 389–100, ?syntypes GPIG 265–267; MB.C.1797.1–2, leg. Schmidt in 1920; MB.C.1776.1–6, leg. Schindewolf in 1924), *Parawo. paprothae* (GPIG 389–78a, syntype of *Parawo. paradoxa*, original of Wedekind 1918: pl. 19, fig. 17; MB.C.1777.1–2, leg. Schindewolf in 1924), and *Parawocklumeria* sp. (MB.C.1779, det. *Wo. sphaeroides*, leg. Schmidt). Lange's (1929) material of *Parawo. paradoxa* has not been traced in Berlin. Currently there are no specimens of *Epiwo. applanata* from the type locality available and Wedekind's original is lost.

Drewer

In the last decade, the Devonian-Carboniferous boundary beds of the famous Drewer Quarry have been intensively re-studied by Korn et al. (1994). Earlier, Schindewolf (1926, 1937) reported that *Wo. sphaeroides* ranges into the Hangenberg Shale (UD VI-E). The former Prussian Geological Survey collection in the Museum für Naturkunde includes a distorted *Wo. sphaeroides plana* (MB.C.1748), leg. by Schindewolf, and a *Wo. sphaeroides* cf. *aperta* (MB.C.1781, det. ?*sphaeroides*), leg. by Schmidt in 1922 (see notes in Schmidt 1927). New *Wocklumeria* records come from Becker (1988: 199, MB.C.1683)

Table 1

Geographical distribution of all currently known members of the Wocklumeriaceae. Abbreviations: **C**, Chile; **In**, Indiana; **O**, Oklahoma; **R**, Rhenish Massif; **T**, Thuringia; **D**, Devon; **Co**, Cornwall; **A**, Armorican Massif; **M**, Montagne Noire; **Ta**, Tafilalt and Maïder, Southern Morocco; **Al**; Southern Algeria (Saoura Valley); **Ca**, Carnic Alps; **H**, Holy Cross Mountains, Poland; **Si**, Silesia, Southern Poland; **U**, Southern Urals; **P**, Polar Urals; **Ba**, Bashciria; **Cc**, Caucasus; **G**, Guangxi, Southern China; **Gz**, Guizhou, Southern China. Signs: + record, × record under different taxonomy, ? questionable record.

taxon	C	In	O	R	T	D	Co	A	M	Ta	Al	Ca	H	Si	U	Po	Ba	Cc	G	Gz
Kamptoclymenia				+	+							+	+	+						+
– *endogona*				+										+						
– *trigona*												+	?	+						
– *trivaricata*														+						
– *endogonoides*																				+
– aff. *endogona*													+							
Triaclymenia				+									+	+						
– *triangularis*				+									?							
– *primaeva*													+							
? *subtriangularis*														+						
Parawocklumeria				+	+	+	+			+		+	+	+	+					+
– *patens*				+	+					+				+						
– *paprothae*				+	?					+		+	x		x					
– *paradoxa*				+	+	x	+					+		+	x					+
– *distorta*				+	+	?	+					+	+	+	+					?
? n. sp.							+													
Tardewocklumeria													+		+					
– *distributa*													+							
– *perplexa*															+					
Synwocklumeria							+			+			+		+	+	+	+		
– *angustilobata*													+							
– *mapesi* n. sp.										+										
– *kiensis*															+			+		
– *bashcirica*																	+			
– *heterolobata*													+							
– *dunhevedensis*							+						x							
– sp.																+				
Epiwocklumeria		?		+									+							
– *applanata*				+									+							
– ?sp.		+																		
Kielcensia			+							+			+							
– *ingeniens* n. sp.										+										
– *b. bohdanoviczi*													+							
– *b. inaequilobata*													+							
– *b. pusilla*													+							
– n. sp.			+																	
Wocklumeria	?			+	+		+	+	+	+	+	+	+		+				+	+
– *s. plana*				+	+		+			+	+		+							
– *s. sphaeroides*				+	+		+	+	?	+	+	+	+		+				+	+
– *s. aperta*				+	+						+		+							
	C	In	O	R	T	D	Co	A	M	Ta	Al	Ca	H	Si	U	Po	Ba	Cc	G	Gz

and Korn (1988) but the youngest occurence is in nodules sitting in dark grey shale right below the true Hangenberg Black shale marking the global mass extinction level (topmost UD VI-D; Bed 4 of Korn 1988; Bed 16a of Clausen et al. 1989b; Bed WA/93 of Korn et al. 1994). An *Epiwo. applanata* (MB.C.2229) found in May 1998 in WA/93 gives evidence that the last nodules belong in the *applanata* Subzone (UD VI-D_2). Poorly preserved other Wocklumeriaceae sampled in 1996/98 consist of *Wo.* cf. *Wo. sphaeroides plana* (MB.C.1738.1) and *Wo. sphaeroides sphaeroides* (MB.C.1738.2) from Bed WA/93, and of *Parawo. paradoxa* from WA/91b (MB.C.1739.1–2). According to Schmidt (1924: 151, det. ?*Wo. distorta*), the latter species ranges also into the "lower part of Hangenberg Shale" (= Bed 93). Korn et al. (1994) did not include the taxon in their list of common species of the *sphaeroides* Zone at Drewer. Three specimens (MB.C.1799.1–3) leg. by Schmidt in 1921 are unidentifiable ?*Parawocklumeria*.

Other localities in the northern Rhenish Massif

see Fig. 2

A number of other Wocklum Limestone localities formed the basis for the studies around the Devonian-Caroniferous boundary by Schmidt (1924). Clymenids were deposited in the former collection of the Prussian Geological Survey and are now in the Museum für Naturkunde. There are, for example, a *Parawocklumeria* sp. (det. *Wo. denckmanni*) from Dasberg (sheet Balve, MB.C.1774, leg. Schmidt in 1920; compare Lange 1929: 31) and faunas from N of Riemke (sheet Iserlohn, leg. Paeckelmann in 1920): *Glat. ?glaucopis* (MB.C.2208), *Parawocklumeria* sp. (MB.C.2209, det. *distorta*). The topmost Wocklum Limestone from between Apricke and Riemke has yielded to Schmidt (leg. 1921) *Wo. sphaeroides sphaeroides* (MB.C.2210.1–4) and *Parawo. paradoxa* (MB.C.2211.1–2). As early as 1900, A. Denckmann has collected *Wo. sphaeroides sphaeroides* (MB.C.2212.1–4) from a brook cut N of Apricke. A brief description of the Apricke succession was given in Luppold et al. (1994).

Becker (1997a) has briefly reviewed the occurence of *Wo. sphaeroides plana* at Aske NW of Hagen (sheet 4610 Hagen), the westernmost wocklumeriid locality in the Rhenish Massif (Paeckelmann 1932). Schindewolf (1926: 114, 1937) mentioned the occurence of *Parawocklumeria* sp. and *Cymaclymenia* sp. (MB.C.2717) from the Seiler area, W of the Tannenkopf near Iserlohn (sheet 4612 Iserlohn). The parawocklumeriid (MB.C.2712) is a negative that cannot be identified with more precision.

Schindewolf (1937: 41) also recorded the *Wocklumeria*-Stufe at the Humberg near Ainghausen (sheet 4613 Balve). This is based on collections from 1935 which include *Wo. sphaeroides sphaeroides* (MB.C.1771.1–5) and *Parawo. paradoxa* (MB.C.1804). Another locality was created during excavations for a water pipeline in the forest 350 m SW of Stiepel (northern border of sheet Balve). The outcrop yielded *Parawo. paprothae* (MB.C.1772.1–2, one specimen with 29 mm dm) and *Parawo.* cf. *Parawo. paradoxa* (MB.C.1773.1–2). From Langeloh near Langenholthausen (leg. Paeckelmann), there are *Wo. sphaeroides* ssp. (MB.C.1801) and *Parawo. para-*

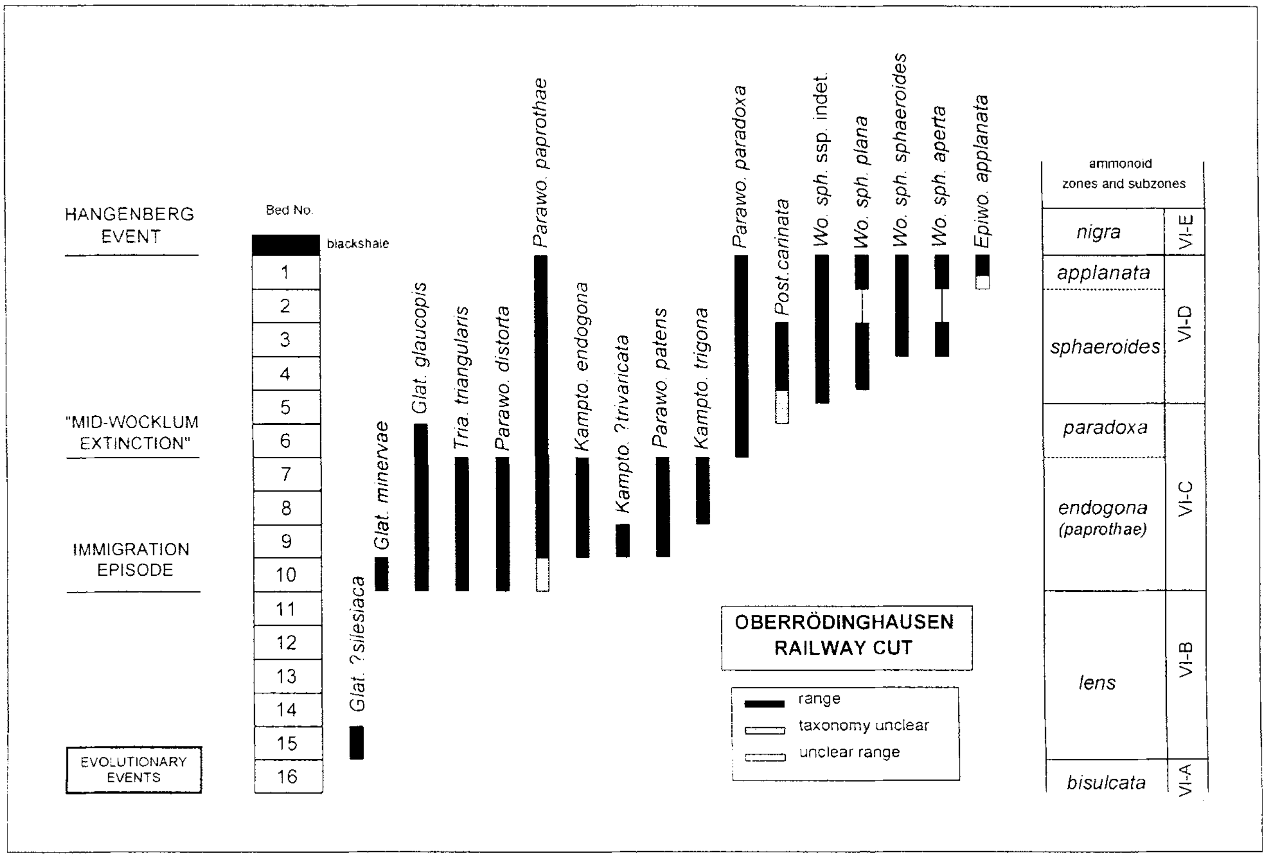

Fig. 3. Ranges of Wocklumeriaceae and Glatziellidae in the Oberrödinghausen railway cut section, based on a revision of the collections of Schindewolf (1937) in the Museum für Naturkunde. For lithological details see the log in Luppold et al. (1994). The sudden disappearance of open umbilicate taxa indicates a distinctive "Mid-Wocklum Extinction" well below the global Hangenberg Event marked by the spread of blackshales

doxa (MB.C.1802). Two additional *Wo. sphaeroides* (MB.C.1803.1–2) were found by Henke near Langenholthausen.

Other authors have reported *Parawocklumeria* and *Wocklumeria* from additional localities (Fig. 2) but material was not available for this study: Höcklingsen (? = Oese), Hangenberg, Effenberg, Müssenberg, Trachtenberg, Bilstein, Eulenspiegel, N of Nuttlar. References are given in the review of the distribution of individual taxa.

Kellerwald

A. Denckmann collected in 1895 from dense red micrites at the Hauern near Bad Wildungen (labelled as "Adorf Limestone") a *Parawo. paradoxa* (MB.C.2709) which, however, was assigned by Schmidt (1924) to *Wo. distorta*. A correct identification of the same specimen was given by Schindewolf (1937: 44). Schmidt (1933) reported also *Wo. sphaeroides* (det. *Wo. denckmanni*) from Braunau but material has not survived in Berlin.

Thuringia

The Schleiz region (Berga Anticline) yielded so far only few Wocklumeriaceae. These are *Parawo. patens?* of Müller (1956) (MB.C.2713), a *Parawo. distorta* (MB.C.552) described by Weyer (1981) from the Geipel Quarry (section now destroyed), and *Wo. sphaeroides* from the Kahlleite-East Quarry (Bartzsch et al. 1995, section currently covered). Bartzsch & Weyer (1980, 1982) described and illustrated *Wo. sphaeroides* (with all three subspecies) and *Parawo. paradoxa* from the Saalfeld area. *Kamptoclymenia* does also occur in the region (oral comm. D. Weyer 1998), and the *paradoxa* material probably includes *Parawo. paprothae*. For this study, material deposited in the collection of the Bundesanstalt für Geowissenschaften (BGR) in Berlin-Spandau was examined in detail. It includes two of Richter's (1848) syntypes of *Wo. sphaeroides* (X4895–96), 77 specimens of *Wo. sphaeroides sphaeroides* from Fischersdorf-West (Z542–605, collection Barzsch 1962, det. Schindewolf, material of Pfeiffer 1954; Z526; Z23.1–2, leg. Gründel; Z670.1–2, det. *Wo. plana*), six specimens of *Wo. sphaeroides plana* from Fischerdorf-West (Z671.1–2 to Z673.1–2), six specimens of *Wo. sphaeroides sphaeroides* from Fischersdorf-East (Z667.1–2, Z668.1–4), a *Wo. sphaeroides sphaeroides* from Gleitsch (Bed 10, No. 2339), *Wo. sphaeroides sphaeroides* from a road outcrop W of Fischersdorf (Bed 10, 2338.1–12, 2340.1–5), and a *Wo. sphaeroides plana* (2337.1) from the latter locality. This rather large suite allows a good insight into the morphological variability of Thuringian *Wocklumeria*. The regionally youngest *Wo. sphaeroides* (Beds 32.8 to 32.10, MB.C.2172–73) were recently described from shales right below the Hangenberg event layer by Bartzsch et al. (1998).

Dzikowiec (Ebersdorf)

The rich terminal Famennian ammonoid faunas from Dzikowiec in Silesia have been described by Schindewolf (1937), and later by Lewowicki (1959). The Ebersdorf collection of the former Prussian Geological Survey mostly burnt during the 2nd World War and there are only some blackened remains in the MfN of a former significant assemblage. Preserved are the juvenile *Kampto. trigona* illustrated by Schindewolf (MB.C.2711) and a *Parawo.* cf. *paradoxa* (MB.C.2228). Unfortunately, the holotype of *Soliclymenia solarioides* (Münster) is lost. The holotype of *Glat. tricincta* Schindewolf (X5673), *Glat.* cf. *tricincta* (Schindewolf 1937: pl. 3, fig. 2, X5671), and the holotype of *Glat. diensti* Schindewolf (X5675) are deposited in the BGR collection at Spandau (see Pl. 2).

Tafilalt and Maïder, Southern Morocco

The Fezzou area of the Maïder, southern Morocco (see map in Becker 1995) is famous for its well-preserved haematitic and calcareous Famennian ammonoids but a detailed description of faunas and sections has only just began. Already Hollard & Jacquemont (1956: footnote on p. 23) and Hollard (1963) listed the presence of questionable (cf.) *Wocklumeria* at the Jebel Aguelmous. This is confirmed by new specimens collected near Fezzou by the author (MB.C.2707–2708) and by V. Ebbighausen (MB.C.3066). They belong to untypically small-sized morphotypes of both *Wo. sphaeroides sphaeroides* and *sphaeroides plana*. Similar specimens have been illustrated by Petter (1960) from the Saoura Valley (Marhouma) of southern Algeria. The best succession along the Aguelmous is exposed S of M'bidia (Lambida) where limestone nodules from just below the reddish weathering Hangenberg blackshale have yielded small to median-sized *Wo. sphaeroides* ssp. (MB.C.3064.1–4). A part of the specimens shows intensive overgrowths by bryozoa and tabulate corals on both sides of the shell. Several meters below, in a unit with *Balvia (Kenseyoceras) lens* Korn, a single *Parawo. patens* has been discovered by J. Bockwinkel (Leverkusen). In the southern Maïder, at Mrakib (see Becker et al. 1999 and Korn 1999), a relative small *Wo. sphaeroides sphaeroides* was found by R. Feist.

A haematitic *Parawo. paprothae* (leg. Ebbighausen, Eb-C19 = MB.C.) from the Fezzou area (Loc. 54) represents the first record of a second species of the genus from the Maïder. Weyer (1995) pointed out, that the cephalopod limestone succession at the Djebel Erfoud of the Tafilalt (see map in Becker 1993a) ranges also into the *Parawo. paradoxa* Zone, and this was recently confirmed by a *Parawo. paradoxa* illustrated by Korn (1999).

Oklahoma

Over (1992) mentioned the presence of wocklumeriids in the terminal Devonian parts of the Woodford Shale of Oklahoma. These specimens belong to a new species of *Kielcensia* with two and a half evolute and triangular whorls without constrictions which follow involute early stages. A detailed description will be published in cooperation with American colleagues.

Comment on the terminal Devonian ammonoid zonation

The Hasselbachtal and Drewer *Epiwocklumeria* end doubts (Becker 1996) whether an *applanata* Subzone (UD VI-D_2; see Korn 1993, Luppold et al. 1994: table 2) can be recognized in the upper part of the *sphaeroides* Zone (= Upper *paradoxa* Zone). Previously, the species has been found in succession only at Oberrödinghausen; the holotype came from the Borkewehr near Wocklum. As discussed below, *Epiwo. dunhevedensis* Selwood may be better placed in *Synwocklumeria*. It cannot be used to recognize the typical *Epiwocklumeria* level in Cornwall. Unfortunately, no precise data are available whether the Kowala fauna of Czarnocki (1989) with *Epiwo. applanata, Wo. sphaeroides, Parawocklumeria distorta* (Tietze) and *Kielcensia* came from a single unit (see comment by Dzik 1991). It indicates, however, that the *applanata* level is not only useful on a regional scale but also for interbasinal correlation. *Epiwo. applanata* and perhaps *Cymaclymenia evoluta* (see Korn et al. 1994) are the only ammonoids that first appear in strata just below the Hangenberg mass extinction level at the base of the Hangenberg blackshale (Fig. 3). Although rather rare, *applanata* thus characterizes an important last phase in clymenid evolution which, following the concept of Schindewolf (1937), seems useful to be separated at subzonal level.

Evolution and distribution of the Wocklumeriaceae

General aspects

The reconstruction of the evolution of triangular clymenids suffers from endemic distributions and cryptogenic sudden and ca. simultaneous appearances of taxa with different level of morphological specialisation (Korn 1995a). The lack of visible sutures in many specimens may prevent the recognition of the true spatial and time distribution of some species. Another problem is the common large intraspecific variability in longidomic, bottom-dwelling (demersal or suprabenthic) ammonoids. Low selective pressure in niches that did not require rapid lateral swimming or which were not affected by high water agitation resulted in poor or unfixed streamlining (highly variable whorl and umbilical width). Typical goniatite examples are cheiloceratids (Becker 1993a) and *Prolobites delphinus* Sandberger & Sandberger. The latter not only has variable conchs but also differently shaped sutures in individuals (compare Bogoslovskiy 1969: fig. 51). Excessive shell variabilities have not been observed in primitive members of the Wocklumeriaceae *(Kamptoclymenia, Triaclymenia)* but apply to *Parawo. paradoxa* and *Wo. sphaeroides*, and this has to be taken into account in taxonomic concepts. Sutural variabilities in *Prolobites delphinus* alter the shape and size of saddles and lobes but not the general pattern and sutural formula. Much less variation is found in the complexly lobed *Wo. sphaeroides* (compare diagrams in Schindewolf 1937, Bogoslovskiy 1981, Czarnocki 1989, and Becker 1996). In Wocklumeriaceae with less developed lobes and saddles (see *Parawo. laevigata* Bogoslovskiy 1981: fig. 50; large Schindewolf collection), there are variations of the shape and amplitude of elements and common sutural asymmetries but the overall sutural pattern remains stable. An exception is a *Parawocklumeria* from Bed 8 at Oberrödinghausen (MB.C.1818) with three shallow flank lobes on one side of the distorted shell which may be a pathological phenomenon. Unfortunately, the other side of the asymmetric specimen is not well-preserved.

Generally, it is believed that at least larger sutural details were always functional in the whole group and ontogenetic changes provide, as in all other Palaeozoic ammonoids, insights into the evolutionary history. The gradual transformation from simple-lobed early forms to the stratigraphically younger more and more elaborate sutures of Wocklumeriidae shows that septal shapes were determined by selection pressure. Sutural complication is seen as an evolutionary strategy to increase the surface and capacity of intra-cameral organic sheets allowing faster pumping of cameral liquids and greater vertical mobility. In taxa living close to the substrate, this perhaps aided escape movements.

The revision and reconstruction of the evolutionary history is based on morphological comparison of all known Wocklumeriaceae taxa in combination with known time ranges (stratophenetic analyses and interpretation of morphological series). It has to be viewed as state-of-the-art model. Since the spatial distribution of most Wocklumeriaceae was strongly influenced by rapid migrational effects (Figs 1 and 3) in the palaeotropics (and subtropics), there is no strong emphasis on aspects of the paleobiogeographical history. The developed evolutionary model is characterized by parallel and iterative changes in whorl involution and sutural simplification or complication. In accordance with Korn (1995a, b), five phylogenetic trends can be identified from records which provide a framework for interpretation:

1) Older clymenids lack triangular stages and early Wocklumeriaceae (partly) have only short early ontogenetic triangular stages – derived and younger taxa all have expanded triangular stages in ontogeny. This heterochronic trend was reversed only in additional (hypermorphic) mature stages of some youngest taxa.
2) Ancestors and early Wocklumeriaceae are (extremely) evolute – derived and later forms are increasingly involute. Again, a reversal of this rule is only observed in additional (hypermorphic) stages of some youngest species.
3) Older taxa and early ontogenetic stages have simple sutures with few elements (six lobes) – most derived and younger taxa have more complex sutures (up to ten lobes).
4) Ancestors and early taxa have rounded and rather shallow lobes – most derived and later taxa developed deep (lingulate) or even pointed lobes.
5) Some early taxa have keels at maturity – derived and younger forms show no traces of a keel or of ventrolateral furrows.

The shell and suture ontogeny normally reflects the phylogeny of ammonoids. Shell features in Wocklumeriaceae, however, were introduced at various stages giving examples of palingenesis (peramorphosis), paedomorphosis and of proterogenesis (as defined by Schindewolf 1925).

Evolutionary history and distribution of Parawocklumeriidae

Kamptoclymenia Schindewolf, 1937

The Parawocklumeriidae comprise all clymenids with triangularly coiled ontogenetic stages which have no lobes in median position both on the venter or dorsally. *Kamptoclymenia* is regarded as the initial member of the Wocklumeriaceae since it is among the oldest of the superfamily (UD VI-C_1, Fig. 4) and because of very short triangular stages and due to morphological characters which are present in stratigraphically older (potentially ancestral) clymenids: extreme evolution, mature keels, simply rounded lobes. The sutural formula for the genus is E/2A:I/2 (Fig. 5a, b).

In morphological terms, the extremely evolute *Kampto. endogona* Schindewolf with short, early ontogenetic triangular stage and moderately depressed whorl cross-section from the *endogona* Subzone (= *paprothae* Subzone) appears to be the starting point for the incredibly successful evolution of the Wocklumeriaceae (Figs 6a, 7). The species is known from Germany (Schindewolf 1937: Oberrödinghausen, Korn 1993: Müssenberg) and Poland (Dzikowiec: *Phenacoceras ?paradoxum* Frech, 1902, non Münster; Kowala, Holy Cross Mountains: aff. *endogona* Czarnocki, 1989).

Kamptoclymenia n.sp. of Becker (1988) is very poorly preserved and probably does not belong to the genus (Becker 1996). Evolute shell form and sutures resemble *Trochoclymenia*; the only specimen came from just below the *Balvia (Kenseyoceras) lens* Zone which roughly correlates with the age of that genus in Silesia. Close to *Kampto. endogona* is *Kampto. endogonoides*

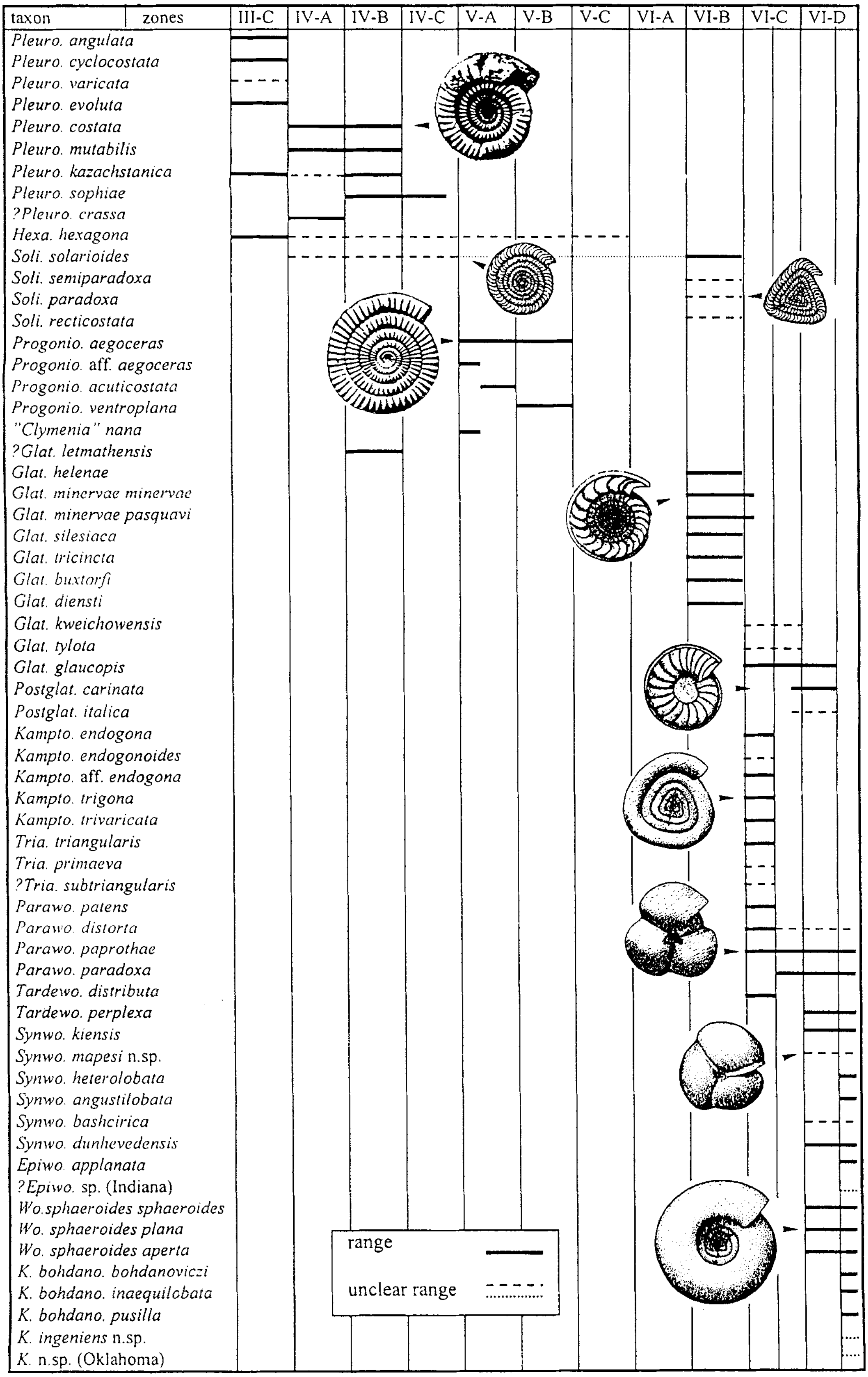

Fig. 4. Known stratigraphical ranges of all valid Wocklumeriaceae and Glatziellaceae n. superfam. Described species not recognized are as follows: *Gyro. rotundata* Czarnocki (= *Pleuro. costata*), *Platy. (Vario.) kazachstanica simplex* Kind (= *Pleuro. kasachstanica*), *Glat. multicostata* Sun & Shen (= *Glat. minervae minervae*), *Parawo. laevigata* Selwood (= *Parawo. paradoxa*), *Parawo. laevigata obesa* Selwood (= *Parawo. paradoxa*), *Kielcensia mirabilis* Czarnocki (? = *Synwo. dunhevedensis*), *Wo. denckmanni* Wedekind (= *Wo. sphaeroides sphaeroides*)

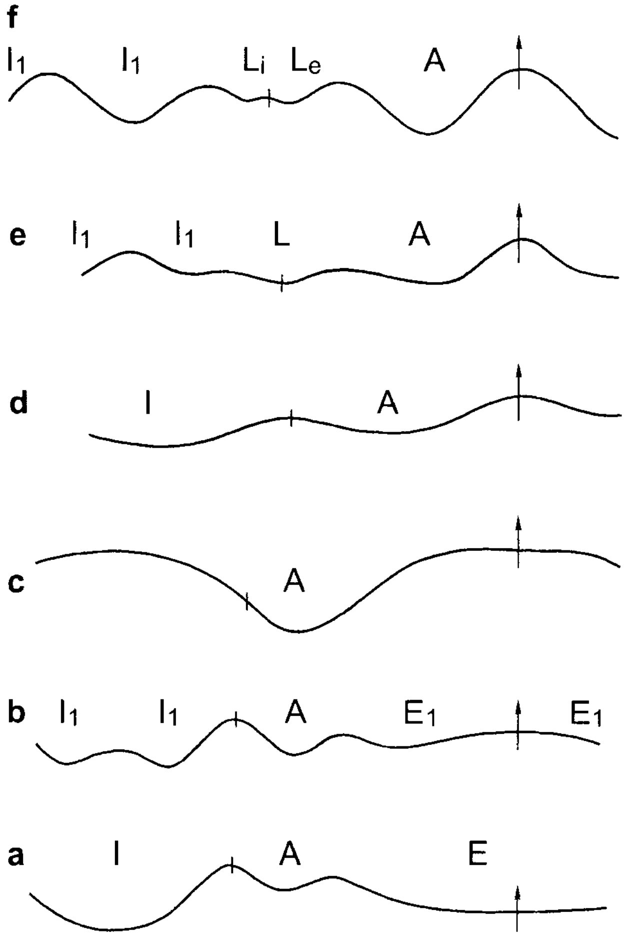

Fig. 5. Published sutural ontogenies in various genera of the Parawocklumeriidae; **a,** *Kamptoclymenia endogona* (after Schindewolf 1937: fig. 20a), juvenile stage; **b,** *Kamptoclymenia endogona* (after Schindewolf 1937: fig. 20b), adult stage; **c,** *Triaclymenia triangularis* (after Schindewolf, 1937: fig. 22), adult stage; **d,** *Parawo. paradoxa* (after Czarnocki 1989: pl. XLIII, fig. 2a), very early stage; **e,** *Parawo. paradoxa* (after Czarnocki 1989: pl. XLIII, fig. 2b), juvenile stage; **f,** *Parawo. paradoxa* (after Czarnocki 1989: pl. XLIII, fig. 2c), adult stage

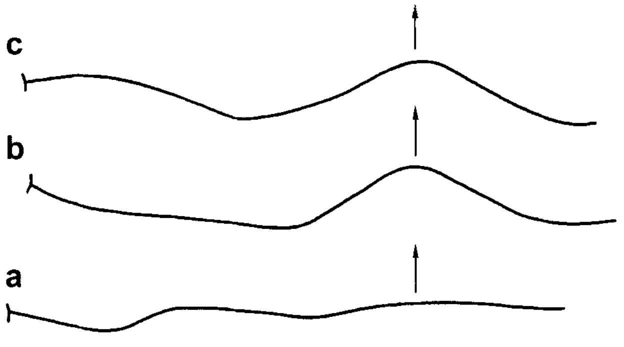

Fig. 6. Sutures in *Kamptoclymenia* and *Parawocklumeria* specimens. **a,** *Kampto. endogona*, neotype, MB.C.1813.1, Oberrödinghausen Railway Cut, Bed 7, at ca. 13 mm dm (2.7 mm wh); **b, c,** Juvenile *Parawo. paprothae*, MB.C.3061, from the Fezzou area, Maïder, at 5.8 mm dm/3.3 mm wh (a), and at 6.3 mm dm/3.6 mm wh (b). Sutures resemble early stages in *Parawo. paradoxa* as illustrated by Czarnocki (1989)

Ruan from the terminal Devonian of South China (Guizhou: Wangyou; Ruan 1981). It has the broader whorls seen in *Kampto. trigona* Schindewolf which again extended the triangular juvenile stage (Fig. 7). This pattern is characteristic of the proterogenetic mode of evolution as described by Schindewolf (1925, 1937) but reduction of maximal shell size from ca. 26 mm in *Kampto. endogona* to 15–20 mm in *Kampto. trigona* supports the idea of Korn (1995b) that this includes neotenic developments after a new feature (triangular whorls) was abruptly introduced in earliest post-embryonic stages. Greater shell involution, a second important phylogenetic trend, was observed by Schindewolf (1937: 90) in a single specimen which he still included in *Kampto. trigona*. The species occurs in the *endogona* Subzone of the Rhenish Massif (Schindewolf 1937: Oberrödinghausen, Korn 1993: Müssenberg), perhaps in the Carnic Alps (photo shown by D. Korn) and Poland (Schindewolf 1937: Dzikowiec, ?Kowala: *Tria.* cf. *Tria. triangularis* Czarnocki, 1989, only pl. XI, fig. 14,). *Kampto. trivaricata* Schindewolf from the *endogona* Subzone of Dzikowiec (*Aganides paradoxus* Frech, 1904, non Münster) and perhaps also from Oberrödinghausen (Schindewolf 1937) is the most advanced kamptoclymenid (Korn 1992a, b) in which triangular coiling extended into the adult, keeled stage, and involution has proceeded as well (Fig. 7).

Triaclymenia Schindewolf, 1937

It is an open problem, whether *Triaclymenia* represents an evolutionary side-branch (left out in Korn 1995b: fig. 12.4) or an intermediate between *Kamptoclymenia* and *Parawocklumeria* as suggested by Schindewolf (1937). In adult *Kamptoclymenia*, the adventitious lobe on the flanks is deeper and more prominent than the divided ventral lobe (Schindewolf, 1937: figs 20–21; see Figs 5b, 6a). *Tria. triangularis* Schindewolf from the *endogona* Subzone of Oberrödinghausen is almost as evolute as *Kampto. trivaricata* (Fig. 7) but it is significantly more compressed. There is a deep flank lobe, by comparison most likely the A-lobe, but both ventral and dorsal lobes, present in all other related and groups, are completely reduced (Schindewolf, 1937: fig. 22; re-illustrated in Figure 5c). This leaves a pair of A-lobes next to a very elevated and prominent ventral saddle. Outer sutures are similar in the somewhat more involute *Tria. primaeva* Czarnocki from Kowala (probably *endogona* Subzone) which may be regarded as a descendent (Fig. 7), suggesting a triaclymenid lineage in parallel with the main evolution of triangular clymenids. However, the absence of dorsal lobes is not yet proven in *primaeva*, and more material may rule out possible affinities with open umbilicate parawocklumeriids. Specimens figured by Czarnocki (1989) as *Tria.* cf. *Tria. triangularis* may all or mostly not belong to the genus. The keeled *Aganides subtriangularis* Frech from Dzikowiec (Fig. 7) is perhaps close to *Tria. primaeva* but lacks adult constrictions. Due to the lack of sutures, the systematic position cannot be clarified but the subtriangular coiling at late stages leaves the possibility that the species represents an early branch of *Kampto. trigona* that became more involute. Generally, *Triaclymenia* is still a rather poorly known genus.

Parawocklumeria Schindewolf, 1926

In typical *Parawocklumeria*, the lobe next to the ventral saddle is the most prominent one (Figs 5d–f, 6b–c). Schindewolf (1937) regarded it as an equivalent of the flank lobe of *Triaclymenia* which has migrated towards the venter since new lobes were introduced around the umbilicus. The sutural ontogeny of *Parawo. paradoxa* illustrated by Czarnocki (1989: pl. XLIII, fig. 2a–c; re-illustrated in Figure 1d–f) both supports and contradicts Schindewolf's idea of a *Triaclymenia-Parawocklumeria* link. It shows an early ontogenetic flank lobe bordering a simple ventral saddle (as in *Triaclymenia*) that migrates slightly to the venter and becomes deep and prominent. On the dorsal side, however, a shallow dorsal lobe as in *Kamptoclymenia* is present which is subdivided subsequently by a mid-dorsal saddle. At the umbilical seam, a lateral lobe appears at the same time (Figs 5e, 6c) which is later divided by a small saddle. The shallow lobes around the umbilicus may disappear or melt with the main flank lobe in deeply constricted whorl segments (Fig. 6b). The sutural ontogeny of *Parawocklumeria* suggests that it branched off from *Kamptoclymenia* in parallel with *Triaclymenia*. In the *Parawocklumeria* branch, the dorsal lobe was kept whilst it was completely reduced in *Triaclymenia*. The sutural formula of *Parawocklumeria* is interpreted to be $A(L_c{:}L_i)I/2$.

The moderately evolute (uw 0.33–0.42% dm) and adult keeled *Parawo. patens* Schindewolf (Fig. 7) from the *endogona* Subzone (UD VI-C_1) of Poland (Schindewolf 1937: Dzikowiec) and Germany (Schindewolf 1937: ?Oberrödinghausen; Müller 1956: ?Geipel Quarry, MB.C.2713, Pl. 4: 11, 12; Korn 1993: Effenberg) is regarded as the most primitive member of the genus (see also Korn 1995b). It resembles and was probably derived by early ontogenetic sutural changes from the more evolute *Kampto. trivaricata*. *Tria. triangularis* can be seen as a more compressed sister species. Very typical for *patens* is the subtriangularly shaped and high ventral saddle. If sutures are not visible, uncertainties may remain concerning the correct identification of evolute and convolute triangular clymenids. This explains why Schindewolf (1937) added a query to *patens* material from Oberrödinghausen. New collections from *endogona* Subzone equivalents of the Maïder suggest that the species occurs also in southern Morocco.

The convolute (uw 0.2–0.33% dm) *Parawo. distorta* (Fig. 7) may be regarded as an intermediate between *patens* and the more involute parawocklumeriids that have lost their mature keel traces due to neoteny. However, all available illustrations of *distorta* sutures (Schindewolf 1937: fig. 26, Bogoslovskiy 1981: fig. 49, Ruan 1981: fig. 82a, b, Czarnocki 1989: pl. XLIII, fig. 6b) show a ventral saddle which differs in its broad flattening and in the occasional presence of an incipient shallow median ventral lobe significantly from the subtriangular saddles found in other species of the genus. *Parawo. distorta* is regarded as the evolutionary starting point for a new lineage characterized by the re-introduction of median ventral lobes which is the main apomorphy of the Wocklumeriidae. At present there is insufficient knowledge of intraspecific variability of *Parawo. distorta* and sutures have not been illustrated for the type of Tietze (1871). Schindewolf (1937) re-figured the holotype but did not show its sutures. Possibly there are two convolute parawocklumeriids with different (triangular or flattened) ventral saddles which lead to different descendant groups (*Parawo. paprothae* and *Tardewocklumeria* n.gen.) but at present this remains speculation. Forms assigned to *Parawo. distorta* have been reported from the Rhenish Massif (Schindewolf 1937: Oberrödinghausen, Clausen et al. 1979: Bilstein Cave), Thuringia (Weyer 1972, 1981: Geipel Quarry, MB.C.552), Silesia (Tietze 1871), the Holy Cross Mountains (Czarnocki 1989: Kowala), Cornwall (Selwood 1960: Oldtree Lodge), the Carnic Alps (Gaertner 1931: Großer Pal), and Southern Urals (Bogoslovskiy 1981). Specimens illustrated by Ruan (1981) have rather narrow umbilici. The same

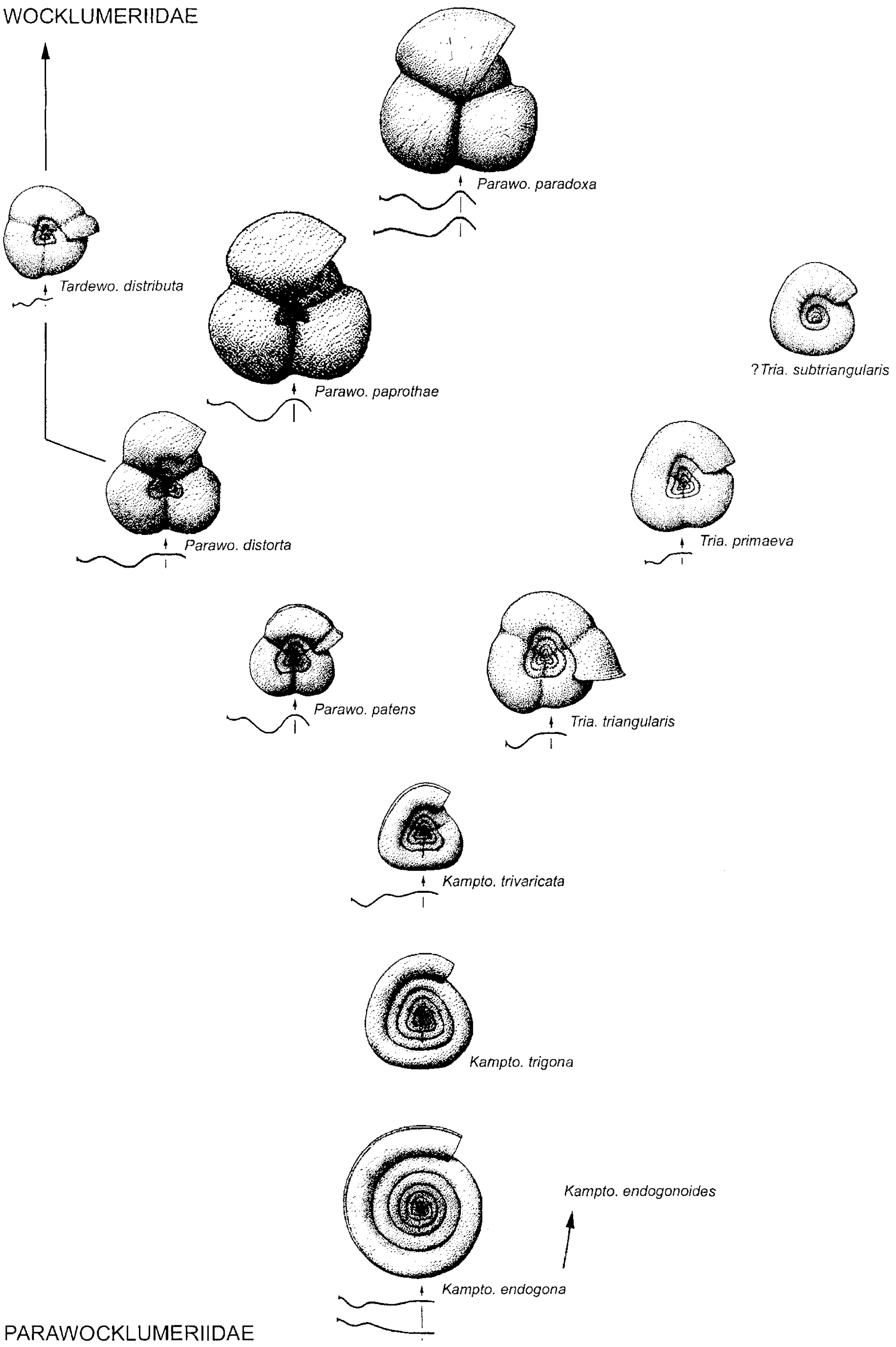

Fig. 7. Morphological series illustrating the reconstructed phylogeny of the Parawocklumeriidae. All illustrations are in identical magnification (ca. × 0.75) in order to show size effects of paedomorphic trends. The introduction of triangular coiling in early stages of *Kampto. endogona* and its subsequent extension into adult stages is a typical example of proterogenesis as defined by Schindewolf (1925, 1937)

applies to a specimen from Chudleigh, South Devon (House & Butcher 1973) which was illustrated in Selwood et al. (1984). The Chinese and Devon forms perhaps belong to *Parawo. paprothae*.

The Oberrödinghausen *distorta* material of Schindewolf (1937), and probably also the Geipel specimens, came from the *endogona* Subzone. Czarnocki (1989) reported *distorta* in association with riphaeoclymenids (under the names *Liroclymenia* and *Dimeroclymenia*) not only from (?the lower part of) the *paradoxa* Zone (UD VI-C_1) but also together with *Wocklumeria*, *Epiwocklumeria* and *Kielcensia*. This suggests a longer range (UD VI-D) than in the classical German sections. The largest known, somewhat questionable *distorta* (MB.C.1814) reaches slightly more than 20 mm dm.

The main parawocklumeriid morphological sequence continues (Fig. 7) with the involute but still somewhat open umbilicate *Parawo. paprothae*. It has been reported from the Rhenish Massif (Clausen et al. 1989a: Müssenberg, *endogona* Subzone; Becker 1996: Hasselbachtal, late *paradoxa* Subzone to early *sphaeroides* Subzone) and the Carnic Alps (Korn 1992a: Grüne Schneid, probably *endogona* Subzone). A record from Southern Morocco is added here. As mentioned above, the species is also still present as a minor faunal element in the *Epiwo. applanata* Subzone of Oberrödinghausen. A subtriangular, high, *patens*-type ventral saddle was illustrated by Becker (1996: pl. 2, fig. 12; see also fig. 7). Judging from illustrations in Bogoslovskiy (1981), it seems possible that some material identified as *Parawo. laevigata* Selwood from the southern Urals in fact belongs to *Parawo. paprothae* (e.g., Bogoslovskiy 1981: No. 2688/142, pl. XVI, fig. 10). The same applies to a *Parawocklumeria* sp. and a *Parawo. paradoxa* from Kowala figured by Czarnocki (1989: pl. XI, fig. 15, pl. XII, fig. 4). The probable presence of *paprothae* in Thuringia still needs documentation.

Clausen et al. (1989a) illustrated the relative variable size of the umbilicus in *paprothae* and it seems difficult to distinguish advanced involute *paprothae* morphotypes from *Parawo. paradoxa*. There is clearly a gradual transition from *paprothae*, starting in UD VI-C_1, to *paradoxa* which enters in UD VI-C_2. In the definition of Korn, *paprothae* still includes all very involute forms with narrow triangular slits on the umbilical wall (Clausen et al. 1989a: pl. 4, figs 7, 8, 10, 12) whilst *paradoxa* has a very small and more rounded umbilical opening (Clausen et al. 1989a: pl. 4, figs 15, 17) which is larger on internal moulds. This difference is not visible in many imperfectly preserved specimens. The stratigraphical overlap of the two forms in UD VI-C_2 and VI-D at Hasselbachtal and Oberrödinghausen proves that they are not parts of a simple chronomorphocline and taxonomic distinction is warranted, but perhaps only at subspecies level. *Parawo. paradoxa* is one of the most common triangular clymenids and reached relatively large sizes (MB.C.1713 from Oese: 27 mm dm; MB.C.1772.1 from Stiepel: 29 mm dm). More or less equally large *Parawo. paprothae* occur at Oberrödinghausen (e.g., MB.C.1699.1–2). This supports the idea (compare Korn 1995b) of a hypermorphic trend in advanced parawocklumeriids. Records of *Parawo. paradoxa* come from the following localities: Rhenish Massif (Wedekind 1918: Burg near Wocklum; Schmidt 1922, det. *Wo. distorta*, Bilstein; Schmidt 1924, det. *Wo. distorta*, Oberrödinghausen, Apricke, Höcklingsen, Dasberg, Drewer, Ense = Hauern, Müssenberg; Paeckelmann 1924, det. *Wo. distorta*, Effenberg, see also Korn & Luppold 1987; Schindewolf 1937: Langenaubach; Becker et al. 1984: Hasselbachtal; Paproth et al. 1986 and Becker et al. 1993: Oese), Thuringia (Pfeiffer 1954: Bohlen, Bartzsch & Weyer 1980: Fischersdorf-East), Carnic Alps (Korn 1992b: Grüne Schneid), Holy Cross Mountains (Czarnocki 1989: Miedzianka, *Parawocklumeria* sp. from Kowala), Silesia (Schindewolf 1937: Dzikowiec), Southern Urals (Bogoslovskiy 1981, det. *Parawo. laevigata*, Kia), southern Morocco (Korn 1999: Djebel Erfoud), Guizhou, South China (Sun 1964: Taihua; Sun & Shen 1965: Wangyou, Laowapu; Sheng 1985: Muhua; Sheng in Ji et al. 1989: Dapoushang).

Parawocklumeria laevigata Selwood from SW England (Selwood 1960: Stourscombe, South Cornwall; House 1963: Chudleigh, South Devon) has been put into synonymy of *Parawo. paradoxa* by Korn (in Clausen et al. 1989a) although it differs from other members of the genus in its much simpler sutures which lack a lobe at the umbilicus (Selwood 1960: fig. 4A, non *Parawo. laevigata* in Bogoslovskiy 1981). The very low median saddle is very unlike that in *Triaclymenia* but strongly resembles the juvenile suture of *Parawo. paradoxa* illustrated by Czarnocki (1989). The new haematitic *Parawo. paprothae* (MB.C.3061, Pl. 4: 7, 8) from Fezzou shows that outer sutures may be influenced by the strong and deep constrictions. One suture running at the bottom of a constriction (Fig. 6b) lacks the

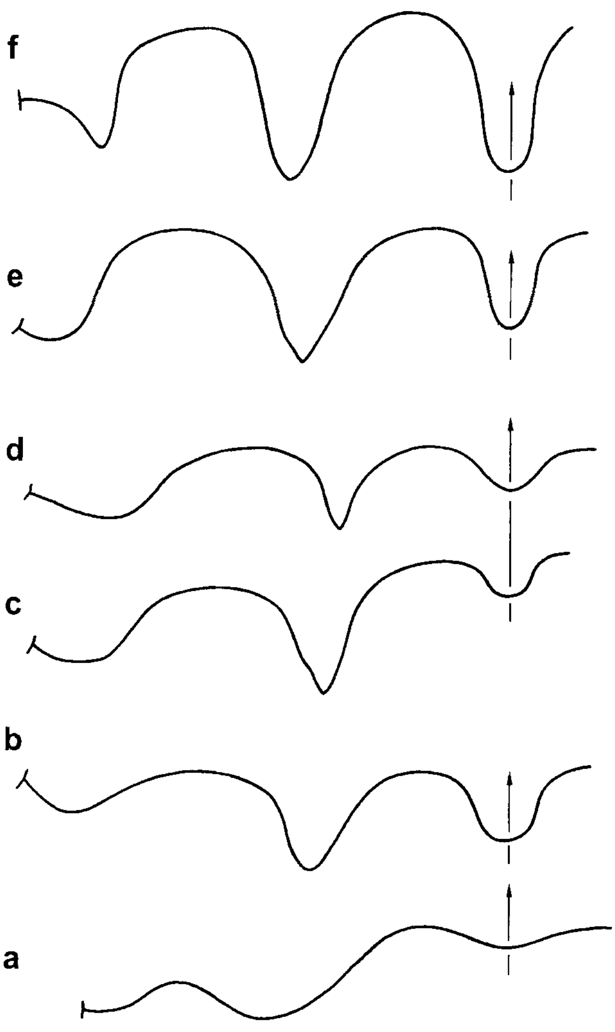

Fig. 8. Sutures of various Wocklumeriidae. **a,** *Tardewocklumeria distributa* (after Czarnocki 1989: pl. XLIII, fig. 6c); **b,** *Synwocklumeria mapesi* n.sp., MB.C.2706, holotype, at 5.5 mm wh (ca. 12 mm dm); **c,** *Kielcensia ingeniens* n.sp., MB.C. 2705, holotype, at 7.5. wh (ca. 14 mm dm); **d,** *Kielcensia ingeniens* n.sp., holotype, same size = other side of specimen, reversed for comparison to show sutural variability; **e,** *Wocklumeria sphaeroides plana*, small early rotund morphotype, MB.C.3066 (leg. V. Ebbighausen), at 3.5 mm wh (ca. 11 mm dm); **f,** *Wocklumeria sphaeroides sphaeroides*, normal-sized (triangular) morphotype, MB.C.912, at ca. 6 mm wh (ca. 15 mm dm)

low saddle separating A- and L-lobe and therefore is very close to the one illustrated in *laevigata*. For this reason, the latter is not seen as an advanced *Triaclymenia* with closed umbilicus but, as suggested by Clausen et al. (1989a), is placed as an intraspecific variant in *Parawo. paradoxa*. Support comes from the stratigraphical age: the Stourscombe Beds can confidently be dated as *paradoxa* Subzone since their lower faunal division (see Selwood 1960) has no evolute Parawocklumeriidae or Glatziellidae but the marker goniatites (Becker 1996) *Balvia (Kenseyoceras) nucleus* and *Balvia (Mayneoceras) biformis* which enter at the base of UD $VI\text{-}C_2$. *Parawo. laevigata* var. *obesa* Selwood is also regarded as a junior synonym of *Parawo. paradoxa* in which there is considerable variability of whorl thickness.

Another strange parawocklumeriid with very small umbilicus from the *paradoxa* Subzone of Cornwall has been decribed by Selwood (1960) in open nomenclature (*Parawocklumeria* sp.). Its suture, with very broad saddle occupying all of the flank and small A-lobes bordering a low and weakly developed median saddle, is not comparable with any other involute and triangular form. Current knowledge does not suggest it to be an extreme variant of *paradoxa* but more material is needed to decide whether it represent a new species.

Evolutionary history and distribution of Wocklumeriidae

Fig. 9

Tardewocklumeria n. gen.

The main apomorphy of the Wocklumeriidae is the presence of median ventral lobes (Fig. 8) which are formed by a shallow to deep and narrow septal fold at the venter. As outlined above, the Wocklumeriidae probably started as a side-branch from *Parawo. distorta* (Fig. 7). *Tardewo. distributa* (Czarnocki) from the *paradoxa* Zone (probably *endogona* Subzone) of Kowala (Figs 8, 9) shares the convolute coiling and a broad flank lobe with *distorta*, but has a well-developed, widely rounded ventral lobe (Czarnocki 1989: pl. XLIII, fig. 6c, refigured here in Figure 8a). Dorsal sutures have not been described but it is possible that the genus does not yet possess the second I-lobe of all more advanced Wocklumeriidae. According to current interpretation, a lineage of *Parawocklumeria*-like forms with wide ventral lobes continued to a very involute end-member, *Tardewo. perplexa* (Bogoslovskiy) which has kept the apomorphic wide and shallow ventral lobe. The species was found associated with *Wocklumeria* in the Kia Section of the southern Urals. As in parawocklumeriids and in juvenile *Synwo. kiense* (Bogoslovskiy 1981: fig. 26a), *Tardewo. perplexa* has a relative widely rounded flank lobe. The inner flank saddle, however, is rather wide as in *Synwo. mapesi* n. sp. or as in *Epiwocklumeria*. The alternative, that *perplexa* descended from involute *Synwocklumeria* by secondary (paedomorphic) sutural simplification cannot be ruled out completely.

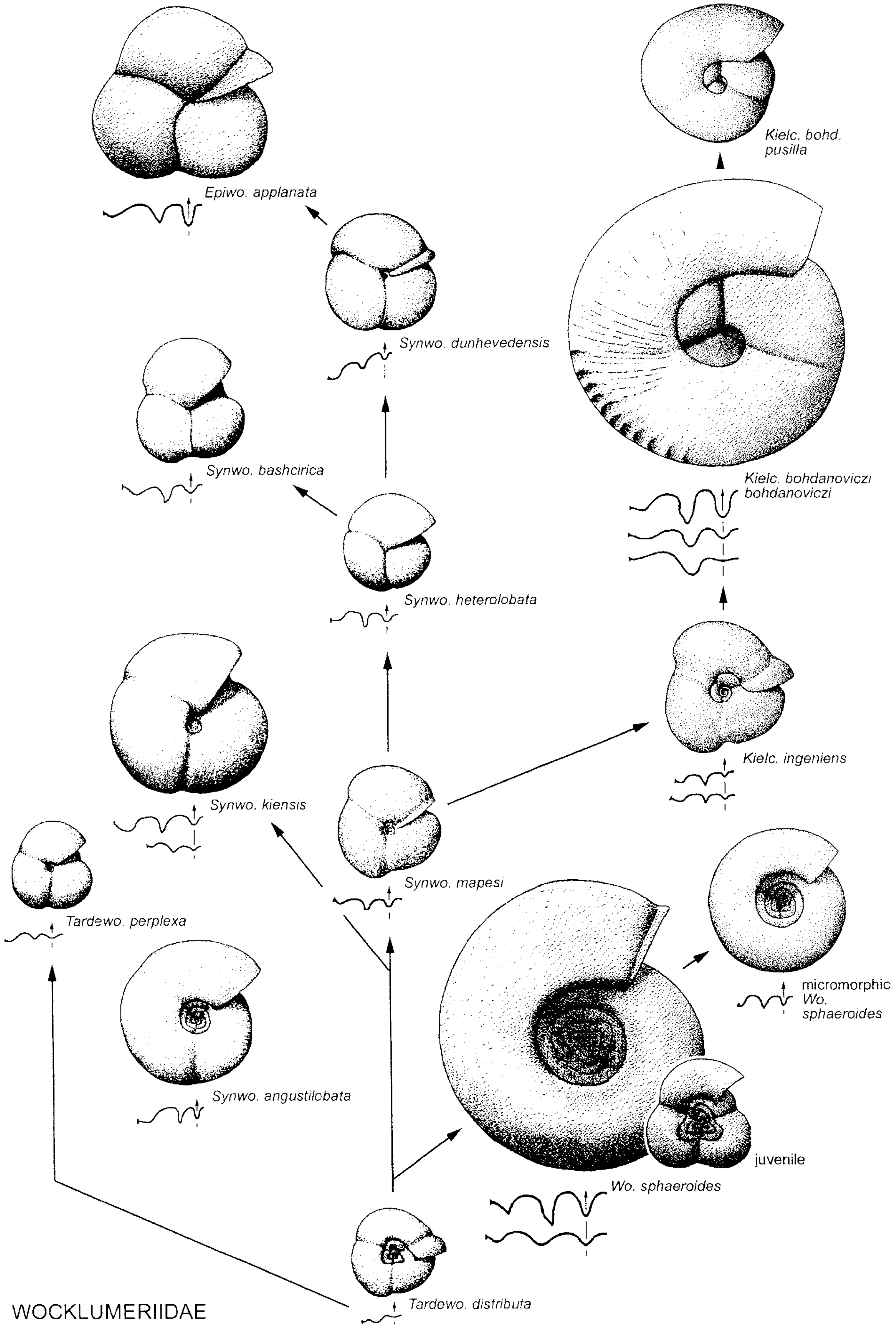

Fig. 9. Morphological series illustrating the reconstructed phylogeny of the Wocklumeriidae. All illustrated specimens in identical magnification (× 0.85)

Synwocklumeria Librovich, 1957

Synwocklumeria differs from *Tardewocklumeria* n.gen. by the narrow, deep and lingulate to pointed flank lobes, broad and higher inner flank saddle, and by the narrow, small, rounded ventral lobes (Figs 8b, 9). The sutural formula is the same as in all descendent Wocklumeriidae: $EAL_c : L_iI_1I_2$. *Epiwocklumeria* is distinguished only by its parallel, pointed and very deep ventral lobe and by complete involution (Fig. 9). For this reason, some authors (e.g., Weyer 1981) placed *Synwocklumeria* in synonymy of *Epiwocklumeria*. The taxonomic position of *Tardewocklumeria* is not touched by this discussion. Czarnocki (1989) described from Kowala of the Holy Cross Mountains a range of new wocklumeriids assigned to the new genus *Kielcensia*. Typical forms around its type (sub)species have involute early stages which abruptly turn into evolute adult whorls. *Kielcensia* is here restricted to those biform taxa showing the marked change in shell ontogeny. Other species such as *K. angustilobata, K. mirabilis*, and *K. heterolobata* have triangular, involute shells throughout their known ontogeny and are currently better placed in *Synwocklumeria*.

An ancestral, still convolute synwocklumeriid would look similar to early stages of *Wo. sphaeroides*. Such a form (Fig. 9) with still rounded subumbilical lobes and deep lingulate A-lobes has been desribed by Czarnocki (1989) as *K. angustilobata*. It is well possible that *angustilobata* is an ancestral representative of *Synwocklumeria* but substantiation is needed that the species does not develop mature *Wocklumeria* stages. *Synwo. mapesi* n. sp. from Morocco (Figs 8b, 9) with small open umbilicus (as in *Tardewo. perplexa*) is the next member in the morphological sequence of the genus. The adventitious flank lobe is still lingulate and the dorsolateral saddle rather wide. *Synwo. kiensis* Bogoslovskiy from the *sphaeroides* Zone of Kia (Ural) and the Caucasus (Chegodaev & Puporev 1979) is rather similar in shell form but the A-lobe is pointed and the lateral saddle rather narrow. The Asian species reaches rather large size (28 mm) and this may be regarded as a hypermorphic evolutionary trend in comparison with *mapesi* n. sp. *Synwo. bashcirica* Librovich from the western slope area of the Urals (Bashkiria) essentially has the same sutures but the flank lobe is inflexed towards the umbilicus which almost closes in adult stages (Fig. 9). These specialisations mark it as an evolutionary sidebranch. Poorly preserved *Synwocklumeria* have also been reported from the Kozhim area of the northern Timan/Polar Urals (Chermnykh et al. 1988; Nemirovskaya et al. 1993).

Epiwockumeria dunhevedensis Selwood from the *sphaeroides* Zone of Cornwall (Fig. 9) is moderately compressed and completely involute but has strongly prorsiradiate sutures with a still rather small and narrow ventral lobe. Therefore, the species is better included in *Synwocklumeria*. *K. mirabilis* Czarnocki is probably identical with *Synwo. dunhevedensis*, or at least very close to it. Another completely involute species is *Synwo. heterolobata* Czarnocki which is said to have very deep and narrow lingulate A-lobes. Morphologically, it is intermediate between *Synwo. mapesi* n. sp. and *Synwo. dunhevedensis* (Fig. 9). However, future studies of larger collections may prove sutural variability in synwocklumeriids, and there is perhaps just one variable species with closed umbilicus.

Epiwocklumeria Schindewolf, 1937

Epiwocklmeria applanata Wedekind (Fig. 9) is seen as an end-member of the *Synwocklumeria* lineage, characterized by gradual sutural complication, closure of the umbilicus and by the increase in total size. It is mostly distinguished by the further deepening of the ventral lobe, widening of the inner flank-saddle and by strong shell compression. With a maximum diameter of 30–35 mm (Czarnocki 1989), *applanata* is a larger species than the possibly ancestral *Synwo. dunhevedensis* or related completely involute species. Obviously there was iterative hypermorphosis in the Wocklumeriidae (Fig. 9). *Epiwo. applanata* defines the *applanata* Subzone of the Rhenish Massif (Wedekind 1918: Burg; Schindewolf 1937: Oberrödinghausen; new Hasselbachtal and Drewer records, Pl. 4: 13–16) and occurs as well in the Holy Cross Mountains (Czarnocki 1989). The genus possibly is also present in North America. The specimen described by House et al. (1986) from Rockford (Indiana) differs from juvenile *Mimimitoceras* by deeper constrictions which do not weaken across the venter. Since the ventral lobe was not observed, the specimen might also represent an involute *Synwocklumeria*.

Kielcensia Czarnocki, 1989

The type of *Kielcensia*, *K. bohdanoviczi bohdanoviczi*, is characterized by slighty open umbilicate to involute triangular early to median stages which abruptly turn into adult, normally coiled and convolute whorls which reach almost 50 mm in diameter (Fig. 9). Shallow constrictions are still present in the first part of the evolute stage but disappear completely at maturity. It seems that an additional ontogenetic stage was added by hypermorphosis to *Synwocklumeria*-type median stages (see Korn 1995b). Adult sutures are as in *Synwocklumeria* in *K. bohdanoviczi inaequilobata* but have a narrower and deeper ventral lobe in the typical subspecies: the subumbilical lateral lobe remains wide and rounded. An interesting member of the *Kielcensia*-branch is represented by *K. bohdanoviczi pusilla*. It reaches only 25 mm in size (Fig. 9) but though possesses a convolute, normally coiled whorl added to small, very involute and triangular early stages. *K. bohdanoviczi pusilla* may have evolved from *bohdanoviczi bohdanoviczi* or in parallel to it, by the re-onset of neoteny which operated at median stages, and which resulted in the suppression of parts of the triangularly coiled whorls. In morphological terms, *K. ingeniens* n. sp. (Figs 8c, d, 9) from southern Morocco is intermediate between *Synwo. mapesi* n. sp. and advanced *Kielcensia*. Early stages have a small open umbilicus and the change to subevolute but still triangular adult whorls occurs at relatively small size and not as abrupt as in some Polish *Kielcensia* specimens. The new species may represent the starting point for a parallel lineage within the genus since a second new form from Oklahoma is hypermorphic as *K. bohdanoviczi bohdanoviczi* but has strongly triangular evolute mature whorls without constrictions.

Wocklumeria Wedekind, 1918

Wocklumeria is interpreted as an earlier second sidebranch from the main Wocklumeriidae lineage from *Tardewocklumeria* to *Epiwocklumeria* which is characterized by corresponding closure of the umbilicus and increasing sutural complication (Fig. 9). *Wocklumeria* has widely open umbilicate and triangular early stages similar as in *Parawo. patens* and *Parawo. distorta*. This suggests an origin in convolute synwocklumeriids. As said above, detection of the direct ancestor is hampered by the fact that it would be distinguished from true wocklumeriids only by the lack of their normally coiled adult whorls and probably would be identified as *Wocklumeria* juveniles. In this circumstance, it is suspicious that faunas from Guizhou have so far only yielded juvenile and triangular specimens, but no normally coiled wocklumeriids.

Selwood (1960) conducted some statistical investigation of wocklumeriids and found no strict distinction between the three species recognized by Schindewolf (1937). Arbitrarily, all three taxa are distinguished at subspecies level (see taxonomic chapter). Adult *Wo. sphaeroides* (= *denckmanni* Wedekind) reach more than 45 mm in diameter which is significantly more than the 28 mm in the largest known *Synwocklumeria*. The assumption of a hypermorphic evolutionary lineage iteratively to *Kielcensia* (compare Korn 1995b) seems well justified. However, only a part of youngest *Wocklumeria* populations is large-sized and in various regions there are, as in *Kielcensia*, micromorphic specimens reaching only 20 to 25 mm maximum size. Not adult but median triangular stages seem to have been lost, giving a very special type of intraspecific paedomorphic development (neoteny in a wide sense). This is supported in micromorphic specimens by widely rounded subumbilical lobes (Fig. 8e) as in *Synwocklumeria* whilst typical *Wo. sphaeroides* have narrow L_e-lobes at the same size (Fig. 8f). Further details are given in the taxonomic section.

Wocklumeria sphaeroides is a very abundant clymenid at many German localities: Rhenish Massif (Wedekind 1914: Burg = Borkewehr near Wocklum, det. *Wo. denckmanni*; Wedekind 1918: N of Nuttlar, det. *Wo. denckmanni*; Schmidt 1924: Hasselbachtal, Apricke, Oberrödinghausen, Dasberg, Trachtenberg; Schindewolf 1926: Drewer; Gallwitz 1927: Höcklingsen; Schmidt 1927 and Clausen et al. 1979: Bilstein Valley; Paeckelmann 1932: Aske; Schmidt 1933: Braunau, Kellerwald; Weber 1934: Grimminghausen; Korn 1981: Müssenberg; Paproth et al. 1986 and Becker et al. 1993: Oese; Luppold et al. 1994: Hangenberg, Eulenspiegel), Thuringia (Pfeiffer 1954: Bohlen, *Wo. sphaeroides sphaeroides* and *sphaeroides plana*; Schindewolf 1937: Leutenberg, Probstzella Railway Station; Bartzsch & Weyer 1980, 1982: Fischersdorf-East, with all three subspecies, Fischersdorf-West, Gleitsch Railway Cut, Mühltal near Obernitz; Bartzsch et al. 1995: Kahlleite-East). Further records are from Cornwall (Selwood 1960: Stourscombe Quarries, ?Overwood Farm; Whiteley 1981: ?Viverdon Down Trenches), the Armorican Massif (Peneau 1929: St. Juliens-de-Vouvantes), perhaps the Montagne Noire (Flajs & Feist 1988: La Serre, det. *Wocklumeria* sp.; Korn 1993: Col de Puech de la Suque), southern Morocco (Hollard

& Jacquemont 1956: Jebel Aguelmous, cf. *Wocklumeria*, confirmed by new material, leg. S.Z. Aboussalam; Korn 1999: Mrakib; new record from Fezzou), Southern Algeria (Petter 1954, 1960: all three subspecies at Marhouma), the Carnic Alps (Korn 1992a: Grüne Schneid), the Holy Cross Mountains (Czarnocki 1989: Miedzianka, Kowala), the Urals (Bogoslovskiy 1981: Kia), Guangxi (Yu et al. 1987 and Ruan 1988: Nanbiancun; Gong et al. 1985: ?Zaisha), and Guizhou (Sun 1964: Taihua = Daihua; Sun & Shen 1965: Laowapu, Wangyou). Breitkreuz (1986) reported a wocklumeriid from Chile but so far only field observations have been made and the fate of material is unclear (oral. comm. H. Bahlburg, Münster).

Origin of the Wocklumeriaceae and systematic relationships

The Hexaclymeniidae as possible ancestors of the Wocklumeriaceae

Since the times of Schindewolf (1937), no direct ancestor of Wocklumeriaceae has been recovered from strata just below their earliest occurrences in the upper Wocklum-Stufe anywhere in the world. The ancestry of the superfamily, therefore, has to be inferred from morphological comparison and from the identification of common characters (synplesiomorphies) with other, older clymenid groups. The evolutionary history has to be deduced from ontogenies and the successive appearance of morphological innovations in time.

Comparison of Wocklumeriaceae and Hexaclymeniidae

The sutural ontogeny of the most primitive member of the superfamily, *Kampto. endogona*, shows (Fig. 5a) that ventral and median saddles are not yet present in juveniles. The juvenile sutural formula is simply EA:I. This is basically the pattern found in all genera of the Hexaclymeniidae (Fig. 10e).

The species identification of triangular clymenids is often complicated by the lack of visible sutures. This simply reflects the fact, well-known also from longitudinal sections (e.g., Schindewolf 1937, Czarnocki 1989), that the body chambers reaches much more than a full whorl. In convolute to involute taxa it covers all or most parts of the phragmocone. Already Trueman (1941) outlined the fundamental significance of the body chamber length for shell orientation and paleoecology. During life, the aperture of all Wocklumeriaceae was oriented downwards to the substrate (see examples in Fig. 1) which suggests bottom-feading and demersal (suprabenthonic) lifestyle. Such autecological interpretation is supported by the common reduction of the lateral (ocular) sinus of the growth lines and aperture which is seen as a measure for the protection of the soft-body against benthic predators such as various arthropods.

Schindewolf's idea of phylogenetic relationships between wocklumeriids, parawocklumeriids and Hexaclymeniidae is supported by the long

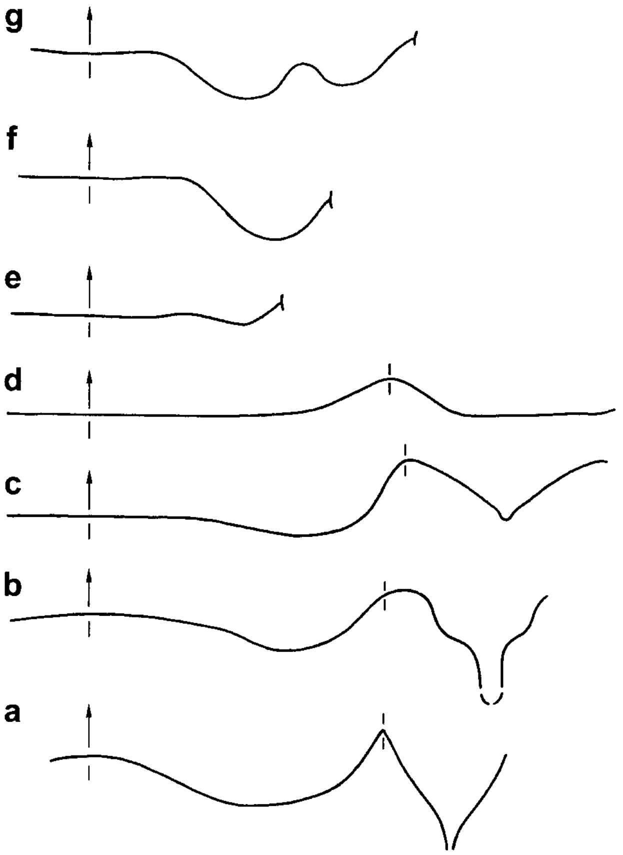

Fig. 10. Sutures of depressed Platyclymeniidae, various Hexaclymeniidae and of *Trochoclymenia*. **a,** *Platyclymenia (Varioclymenia) pompeckji*, after Perna (1914: text-fig. 72), UD III-C; **b,** *Platyclymenia (Varioclymenia) pompeckji*, MB.C.1729 (= Oc 575), Nie Brickwork Quarry, Bed 7 (*delphinus* Zone, UD III-C), at 7 mm wh (ca. 30 mm dm); **c,** '*Pleuroclymenia*' *americana*, MB.C.1734.1, Threefork Shale, Montana, UD IV-A, leg. RTB in 1987, at ca. 5 mm wh; **d,** *Pleuroclymenia costata*, topotype of '*Platy. crassissima*', MB.C.1266, Kirchhofen, *annulata* Zone (UD IV-A), at ca. 17.5 mm dm (ca. 6 mm wh); **e,** *Hexaclymenia hexagona*, MB.C.1805.2, Enkeberg, *delphinus* Zone (UD III-C), at 3.5 mm wh (ca. 13 mm dm); **f,** '*Clymenia*' *nana*, MB.C.3062, Jebel Aguelmous, Maïder, leg. V. Ebbighausen, UD V-A, at 10.5 mm dm; **g,** *Trochoclymenia wysogorskii*, MB.C.3065, original of Schindewolf (1937: 24), Ebersdorf (Dzikowiec), at 25 mm dm (5 mm wh)

body chambers of the latter [see, e.g., median section of *Progonioclymenia acuticostata* (Münster) in Bogoslovkiy 1981], by the long septal necks both in the Parawocklumeriidae and in genera of the Hexaclymeniidae (Schindewolf 1937, Bogoslovskiy 1976), and by the typical shell form with broad, depressed, very slowly expanding whorls. Of course, there is a strict functional relationship between body chamber length and low whorl expansion rate. Neutral buoyancy required for a functional hydrostatic apparatus gives upper limits for the ratio between body chamber and phragmocone volumes. Throughout growths, there has to be a balance between body + shell weight and the positive buoyancy of gas chambers. Broad whorl profiles, however, can be formed independently from changes in expansion rates by co-variation between whorl and umbilical width (Becker 1993a, Checa et al. 1996).

It has been questioned (Korn 1992b) whether the Hexaclymeniidae, defined by their EA:I sutures, form a valid systematic group at all. Ventral lobes of clymenids have to be seen in conjunction with the trend to develop flat and tabulate venters (Schindewolf 1937; Korn 1992b; e.g., in *Stenoclymenia* and *Pricella*). Septal folds ("true lobes") may be distinguished from shallow and rounded lobes ("pseudolobes" sensu Schindewolf 1937: 54) created by the intersection of the curved septum by a flat outer shell wall. If "pseudolobes" (and therefore shell form) characterize a lineage, sharing perhaps in addition other conch features, this, of course, can be used as synapomorphy in taxonomic definitions. Korn's (1992b) dissolution of the Hexaclymeniidae is rejected here. His placing of hexaclymeniid genera in three different and unrelated families is in conflict with suture and shell characteristics. In addition, within the family, morphological and stratigraphical intermediates between genera are known whilst an iterative origin of members is not supported by intermediates to clymenids of other families. *Hexaclymenia* differs, for example, from all Cyrtoclymeniidae by their very short septal necks, shorter body chambers and by the different shape of the dorsal lobes in the latter. *Progonioclymenia* superficially resembles ribbed and evolute Platyclymeniidae but these are mostly brevidomic, compressed, and have very deep, narrow and parallel dorsal lobes. Relationships with certain intermediate mesodomic and depressed platyclymenids will be discussed later. *Soliclymenia* is very similar to *Progonioclymenia* (Weyer 1981, Price & Korn 1989) and is perhaps an ancestor of the Glatziellidae, but still lacks their apomorphies: the divided ventral lobe (Fig. 11b) and the pronounced keel. Therefore, it cannot be placed in the Glatziellidae.

The ventral lobe of some Hexaclymeniidae also cannot be explained by their cross-sections alone. *Soliclymenia* displays a shallow ventral lobe despite a gently curved and not tabulate venter (e.g., Bogoslovskiy 1981: fig. 5d) whilst '*Pleuroclymenia*' *americana* (Raymond) and *Platyclymenia pompeckji* Wedekind with similar wide and flatly rounded venter have low ventral saddles instead of a wide lobe (Miller 1938, Perna 1914; see Fig. 10a–c). Due to the lack of appropriately preserved material, septal faces have not yet been studied in most Hexaclymeniidae but it has to be remembered that the radius of septal curvature is as important as the cross-section for the course of sutures.

Gyroclymenia Czarnocki, 1989 and *Pleuroclymenia* Schindewolf, 1934

The three-ribbed hexaclymeniid genera discussed above cover stratigraphically the Famennian III to VI (Fig. 4) but are too dissimilar to be close relatives of the smooth and constricted *Kamptoclymenia*. Czarnocki (1989) added *Gyroclymenia* as a fourth genus. It embraces a range of evolute, strongly to weakly ribbed species with characteristic ventral constrictions, wide dorsal lobe, shallow rounded lateral lobe, and broad and shallow ventral lobes which is sometimes not seperated from the flank lobe (Fig. 10e). Representatives of this group occur not only in Poland but also widely in the UD III-C to IV-B of the Rhenish Massif (e.g., Kattensiepen, Warstein region; MB.C.1732 from the Nie Brickwork Quarry, northern Sauerland; specimens from the Hauern, Kellerwald, MB.C.1806.1–6; see Pls 1, 2). All species of the genus are longidomic.

The so far unfigured holotype of *Pleuro. crassissima* (Schindewolf 1955; = *Platy. crassa* Schindewolf, 1923a, non *Platy. quenstedti* var. *crassa* Schindewolf, 1923a; Marburg University collection, No. 3154) is ribbed until late stages (ca. 37 mm dm) and also has characteristic deep constrictions as well as very wide and shallow ventral lobes. *Gyroclymenia* clearly is a subjective junior synonym of *Pleuroclymenia*. A Berlin topotype (MB.C.1266) from the *annulata* Zone of Kirchhofen near Weilburg (southern Rhenish Massif) turned out to be congeneric with *Gyroclymenia*

Table 2
Dimensions of various *Pleuroclymenia* species.

species/specimen.	dm	uw	wh	ah	ww	uw%	ww%	ah%	wh/ww
kasachstanica									
MB.C.1731	29.5	13.8	8.8	6.7	11.1	46.8	37.6	22.7	0.8
MB.C.1731	23.2	11	6.9		10.3	47.4	44.4		0.67
costata									
Marburg 3154	ca. 37	16.3	12.2		16.6	44.1	44.9		0.73
MB.C.1266	19	8.7	5.8	4.5	10.4	45.8	54.7	23.7	0.56
MB.C.1266	15	6.6	4.7	3.8	8	44	53.3	25.3	0.59
MB.C.1266	11.5	5.3	3.3		ca. 6.8	46.1	ca. 59		ca. 0.5
MB.C.1806.3	9.1	4	2.8		5	44	61.5		0.56
MB.C.1806.5	7	3	2.3		4	42.9	57.1		0.58
MB.C.1806.6	5.8	2.6	1.8		3.6	44.8	62.1		0.5
cyclocostata									
MB.C.1732	41	21.6	10.7	ca. 8.5	14.4	52.7	35.1	ca. 20.7	0.74
MB.C.1732	33.8	17.8	8.9		ca. 13	52.7	ca. 38.5		ca. 0.7
mutabilis									
MB.C.1807.1	16.8	7.3	5	4	8	43.5	47.6	23.8	0.63
MB.C.1807.2	16.2	8.2	4.3		8	50.6	49.4		0.54
MB.C.1807.3	14	5.7	4.7		6	40.7	42.9		0.78

as well. The specimen has been discussed and synonymized with *crassissima* by Schindewolf (1924: 100) himself. As outlined by Lange (1929), the topotype is also identical with ?*Cycloclymenia costata* Lange which becomes an older subjective synonym. The valid identification of the *Pleuroclymenia* type species, therefore, is *Pleuro. costata* (Lange). Unfortunately, Lange's type of *costata* could not be traced in the remains of his collection in the Museum für Naturkunde and in the Geological Institute of Hamburg University (oral. comm. W. Weitschat 1998).

A purchased topotype (?syntype, MB.C.1731) confirms that *Platyclymenia kasakhstanica* Kind, 1944 from the Mugodzhar Mountains possesses the typical ventral constrictions and long body chamber of *Gyroclymenia*. This species, interestingly, is completely smooth apart from earliest whorls. *Platy. Quenstedti* var. *crassa* Schindewolf (1923a) may represent another smooth species with broad, kidney-shaped cross-section, but it has never been illustrated and, therefore its generic assignment is open. *Pleuro. sophiae* (Czarnocki) also lacks ribs but is more involute than *kasachstanica*. Smooth pleuroclymenids may belong to the so far undocumented lineage leading to *Kamptoclymenia* but in terms of time (Fig. 12) and morphology there is still a rather wide gap between both.

Homoeomorphs and ancestors of *Pleuroclymenia*

The revision of *Pleuroclymenia* as member of the Hexaclymeniidae in the future requires a generic re-assigment of the mesodomic *Pleuro. americana* Group which lacks constrictions and which has shallow dorsal lobes but low ventral saddles (see Schindewolf 1934 and Miller 1938; topotypes MB.C.1734.1–3, leg. RTB 1987; collection of the University of Iowa City: SU I 12277 etc.). Other species assigned to *Pleuroclymenia*, such as *Pleuro. eurylobica* Petersen and *Pleuro. ohioense* House et al., as well as *Clymenia lagowiensis* Sobolev, *Platy. (Platy.) inflata* Czarnocki and *Cyrtoclymenia enkebergensis* var. *crassa* Petter (non *crassa* Wedekind), represent a thick-whorled and subinvolute side-branch of unrelated *Protactoclymenia* (Cyrtoclymeniidae) with concavoconvex growth lines. According to shell morphology (wide umbilication, ribbing, broad, depressed whorls, mesodomic body chamber) and stratigraphical range (UD III-C, *Prolobites delphinus* Zone), the ribbed *Platy. pompeckji* Group was the phylogenetic link (Fig. 12) between *Pleuroclymenia* and the brevidomic Platyclymeniidae (Clymeniina, Clymeniaceae). The *pompeckji* Group is characterized by rather deep dorsal lobes as in typical *Platyclymenia* (Fig. 10a, b). *Platy. pompeckji* was designated by Matern (1931) as the type-species of *Varioclymenia* Wedekind which was followed by Nalivkina (1953). The taxon is used here as a subgenus of *Platyclymenia* lacking parabolic ribs and with whorls that are as wide as or wider than high at median to adult stages. In this definition, *Platy. (Varioclymenia)* includes a range of taxa from the *Prolobites delphinus* Zone (UD III-C) of Germany (see Pl. 1: 1–7), the Urals and of the Mugodzhar Mountains:

- *Clymenia annulata* var. *correcta* Perna, 1914 (probably = *Cl. placida*)
- *Clymenia brevicostata* Münster, 1842 (e.g., MB.C.1735, Pl. 1: 5–6 und MB.C.1763, leg. Paeckelmann, from Enkeberg, Beds 8 and 9 – type material should be at Bayreuth)
- *Platyclymenia (Varioclymenia) callimorpha* Lange, 1929 (probably a subspecies of *cycloptera*)
- *Clymenia cycloptera* Wedekind, 1908 [House 1970 re-illustrated Wedekind's original of plate 43, fig. 11 as holotype. However, Wedekind had reported two specimens and did not select a type. Hence, the twice figured specimen has to be called lectotype.]
- *Platyclymenia humilis* Schindewolf, 1934 (= *brevicosta* Wedekind, 1908, nom. vad.; e.g., MB.C.1736, Pl. 1: 7, see Becker 1985: fig. 3a, Nie Brickwork Quarry)
- *Clymenia placida* Perna, 1914
- *Clymenia* (*Varioclymenia*) *pompeckii* Wedekind, 1908 (nom. corr.: *pompeckji*, e.g., MB.C.1729, Pl. 1:1, 2, and MB.C.1737 = Oc 575 from the *delphinus* Zone of the Nie Brickwork Quarry; MB.C.1730, leg. RTB 1985, from Enkeberg, see Pl. 1: 3, 4)
- *Platyclymenia* (*Varioclymenia*) *pompeckji* var. *decora* Kind, 1944 (probably a subspecies or morphotype of *brevicostata* Münster)
- *Platyclymenia* (*Varioclymenia*) *pompeckji* var. *kasakstanica* Nalivkina, 1953 (non *Vario. kasachstanica* Kind, 1944; invalid homonym; probably a subspecies or morphotype of *brevicostata* Münster)
- *Platyclymenia* (*Varioclymenia*) *pompeckji* var. *senilis* Lange, 1929 (subspecies of *cycloptera*)
- *Platyclymenia* (*Varioclymenia*) *transita* Kind, 1944 (probably identical with *callimorpha*)

There is clearly taxonomic oversplitting in *Varioclymenia* and the study of larger populations will show which of the names should be kept. The genus is perhaps also rarely present in unpublished collections from Southern Morocco. Since a platyclymenid-type dorsal lobe has only been illustrated in *Platy.* (*Vario.*) *pompeckji* (Perna 1914, re-illustrated in Figure 10a), it cannot be ruled that some of the listed forms belong to the '*Pleuro.*' *americana* Group with shallow dorsal lobes. A *pompeckji* fragment from the Nie Brickwork Quarry (MB.C.1737 = Oc 575, Fig. 10b) shows dorsal sutures with moderately wide, pointed and deep lobes, which are, related to the broad concave whorl part, not quite as narrow as in *Platyclymenia* (*Platyclymenia*).

Evolution of the Hexaclymeniidae

At a very early stage in clymenid evolution (early *Prol. delphinus* Zone, UD III-C), slowly expanding varioclymenids which still have tornoceratid-type dorsal lobes, depressed whorl profile and increased body chamber length obviously gave rise to the oldest and ribbed pleuroclymenids (Figs 10, 12). These developed constrictions as an adaptive measure to protect the vulnerable soft parts against benthic predators behind a more rigid apertural margin. At the same time, dorsal lobes became shallow and incipient ventral lobes formed. The youngest *Pleuroclymenia* are known from the *Protoxyclymenia dunkeri* Zone (UD IV-B) of the Rhenish Massif (Becker 1997a) and from similar levels of the Holy Cross Mountains (Czarnocki 1989) and of the famous Kia Section in the southern Urals (Bogoslovskiy in Simakov et al. 1983; see Fig. 4). The oldest and moderately small (max. 23 mm dm) *Soliclymenia* entered probably at about this time in the Urals (Bogoslovskiy 1981) and perhaps in the Carnic Alps (Price & Korn 1989). The morphological step from evolute and ribbed *Pleuro. evoluta* (Czarnocki) to extremely evolute soliclymenids with deeper ventral lobes was rather small. Members of the pleuroclymenid ancestor group, especially *Platy.* (*Vario.*) *humilis* (e.g., MB.C.1736, see Pl. 1: 7), developed iteratively similar conches as in *Soliclymenia*.

From the oldest and still poorly documented soliclymenids of the higher part of UD IV it was only another small step to large-sized (up to 50 mm dm) and more compressed *Progonioclymenia* of UD V-A/B (Figs 4, 12), characterized by a rimmed, flat or grooved venter. Species of *Progonioclymenia* differ from each other in the shape of the venter, their ornament, and by the development of ventrolateral spines in the type-species (Schindewolf 1937, Price & Korn 1989). A fragmentary assemblage from Ballberg near Hövel (MB.C.1756.1–21, Bed 3, leg. Schindewolf in 1931), which also yielded the neotype of *Progonio. acuticostata* (Münster), shows that there is more intraspecific variability than previously recognized. Ribbing varies from recti- to prorsiradiate and from straight to slightly concave. The same applies to collections from the Kellerwald (leg. Denckmann in 1893–1897: MB.C.3063.1–2, 3068.1–2, 3069, leg. Schwalm in 1902: MB.C.3070.1–3). Ribs disappear at a marginal spiral rim (Pl. 2: 9, 10) and the ventral furrow appears late in ontogeny (Pl. 2: 8). Spines have not been observed and early whorls are smooth. Currently, the more common Rhenish form is assigned to *Progonio. aegoceras* (sensu Price & Korn 1989). *Soliclymenia* and *Progonioclymenia* have roughly the same geographical distribution as *Pleuroclymenia* but both do occur in the Carnic Alps.

Soliclymenia must have survived during the Famennian V in some region to give rise by some paedomorphic change (Korn 1995a, b) to smaller-sized (max ca. 17 mm dm) species of the lower Wocklum-Stufe (Fig. 12). In this youngest hexaclymenid lineage, triangular coiling (*Soli.*

paradoxa) developed as an iteration to the Wocklumeriaceae (Fig. 4). Homoeomorphism occurs in completely unrelated groups. Triangular coiling re-appeared, as an example, again in much later Carboniferous goniatites (Croneis 1930). Though, it is rather common that identical selective processes lead to similar morphological features in genetically close taxa, a phenomenon described as mosaic evolution. Therefore, the invention of triangular whorls in advanced soliclymenids, rather than in any other clymenid group, seems to support (but, of course, does not prove) relations between Hexaclymeniidae and Wocklumeriaceae.

Hexaclymenia hexagona (Wedekind) is thought to represent an early smooth to slightly ribbed, keeled side-branch from *Pleuroclymenia* (Fig. 12) with unusual spiral striae that are obviously only visible on well-preserved specimens. Adult whorls expand somewhat faster than in other members of the family (Pl. 2: 5, 6). Wedekind (1908) reported six specimens and did not select a type. Therefore, his original of plate 43, figs 7, 7a, should not be called holotype (House 1970, with re-illustration) but lectotype. This, so far, monotypic genus ranged from the *delphinus* Zone (UD III-C) perhaps into younger strata (Renz 1914; Schmidt 1924: "oberer Clymenienkalk", ?UD V; Sanz-Lopez et. al. 1999: well above *Annulata* Event, UD IV-B). As other members of the family, it is known from Germany, Poland, and Russia. Specimens leg. by Lotz & Denckmann in 1900 (MB.C.1805.1–6) show that the ventral lobe is much shallower than illustrated in Schindewolf (1923b). In MB.C.1805.3 (Fig. 10e), a wide and flat ventral lobe is almost continuous with the shallow flank lobe, resembling sutures in some *Pleuroclymenia* (Fig. 10d) and in small *Kamptoclymenia* (Fig. 5a). A deep ventral lobe was only artificially produced by grinding too strongly. The new observations may explain why Perna (1914: fig. 74) has not shown any ventral lobe at all in a Ural specimen. According to Perna, the dorsal lobe is relative wide as in other Hexaclymeniidae.

Keeled clymenids (MB.C.1733 = Oc 488, MB.C.1734 = Oc 770) assigned to *Hexa. hexagona* from the lower part of the *delphinus* Zone of the Nie Brickwork Quarry (Becker 1985) differ in their strong shell compression and weak radial ornament on the lower flank. Sutures are not preserved but both specimens are more likely to belong to the poorly known *Genuclymenia guembeli* (Wedekind).

Origin of the Wocklumeriaceae

Known smooth pleuroclymenids are not evolute enough to include a possible direct ancestor of *Kamptoclymenia*. However, there is a long overlooked small-sized clymenid from UD V which is more similar in showing marked constrictions, and a flattened venter with very shallow ventral lobes (Fig. 10f): *Clymenia nana* Münster. As suggested by D. Korn (in press), the species has to be placed in a new genus. It occurs in Germany as well as in the Carnic Alps (D. Korn, written comm.) and rarely in the Tafilalt and Maïder of southern Morocco (e.g., MB.C.3062, leg. V. Ebbighausen, Pl. 3: 1, 2). At the Jebel Aguelmous and in the southern Tafilalt (Jebel Ouaoufilal), the typical level is very low in the Dasberg Stufe (regional *Endosiphonites muensteri* Zone, Becker et al. 1999). Kamptoclymenids have wider whorls than *'Clymenia' nana* as well as shallower flank lobes (Fig. 6a), but at present the latter is a candidate for phylogenetical relationships (see Fig. 12).

Another rather enigmatic genus with very similar, extremely evolute and smooth shell from the lower *Wocklumeria* Stufe is *Trochoclymenia*. The genus occurs rarely in Silesia but, as mentioned above, a single similar, poorly preserved and roughly contemporaneous specimen has been described by Becker (1988) from Hasselbachtal. The older (lower UD V, not IV) North African *Trocho. ornata* Petter (lectotype here designated as original to her plate III, fig. 7) is a close relative of *Endosiphonites muensteri* and not related to *Trocho. wysogorskii* (Frech). The latter has two rounded flank lobes as in *Kamptoclymenia*, but the outer, not the inner flank lobe is deeper (Fig. 10g). According to Schindewolf, the probably lost holotype has a deep dorsal lobe as in the Platyclymeniidae. Furthermore, constrictions are lacking. Preparation of a second specimen from Dzikowiec (MB.C.3065) described by Schindewolf (1937: 24) showed that sutures are similar to Frech's type and Schindewolf's suture illustration (his figure 3) is regarded as doubtful. *Trochoclymenia* reaches more than 50 mm dm which is larger than both *'Clymenia' nana* and *Kampto. endogona*. With respect to the shell form and to the long gap between other Platyclymeniidae and *Trochoclymenia*, it is possible that *Trochoclymenia* was derived from *'Clymenia' nana* and that it represents a parallel group to *Kamptoclymenia* with extra umbilical lobes. Unfortunately, available specimens (Berlin, third topotype of Czarnocki

1989) do not show dorsal sutures and no final judgement is currently possible. Lewowicki (1959) failed to re-collect the species at the type locality. It should be noted, however, that the earliest whorls in Czarnocki's specimen appear to be somewhat polygonally coiled.

Systematic relationships of the Wocklumeriaceae

Glatziellaceae n. superfam.

(nom. transl. herewith from Schindewolf 1928)

Soliclymenia may have given rise to evolute and ribbed glatziellids which share the slowly expanding and longidomic whorls but which developed pronounced keels and which divided the ventral lobe at late ontogenetic stages (Fig. 11a, b). Becker (1997a), however, described a much earlier (UD IV-B) smooth glatziellid which is here assigned with a query to the genus. The spiral rim bordering the venter of *Progonioclymenia* (Pl. 2: 9, 10) also can be interpreted as an incipient keel. At present, the origin of Glatziellidae is not yet clarified. The group developed iteratively the same outer sutures as the smooth kamptoclymenids (compare Fig. 5b with 11b) but the dorsal lobe remained undivided (Schindewolf 1937). Advanced glatziellids became narrow umbilicate and goniatite-like (*Glat. glaucopis* Renz, *Postglatziella*; Fig. 4) which parallels evolutionary trends in the sister taxon Wocklumeriaceae. *Sinoglatziella* has been placed in synonymy with *Glatziella* (Becker 1997a). *Glat. glaucopis* reaches larger sizes than other members of the group (Becker 1997a) which can be seen as yet another iterative hypermorphic trend in the Wocklum Stufe. Longidomic Hexaclymeniidae and descendent glatziellids can be combined in a systematic unit with wide and simple dorsal lobe and lacking constricted, triangularly coiled ontogenetic stages (compare Weyer 1981: 9). For priority reasons of existing family-level taxa, this new superfamily is named as Glatziellaceae n. superfam.

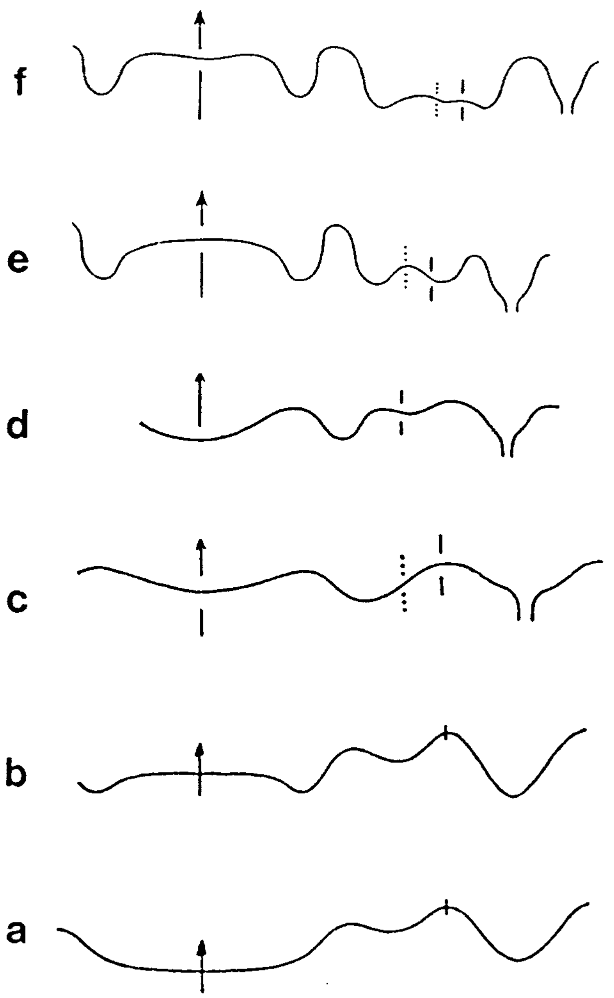

Fig. 11. Sutures of Glatziellidae and Biloclymeniaceae, illustrating the iterative formation of wide ventral saddles in both families. **a,** *Glatziella helenae* (Glatziellidae, after Schindewolf 1937: fig. 15a), juvenile stage; **b,** *Glatziella helenae* (Glatziellidae, after Schindewolf 1937: fig. 15b), adult stage; **c,** *Uraloclymenia volkovi* (Pachyclymeniidae, after Bogoslovskiy 1981: fig. 13b) at 18 mm dm (6.7 mm wh); **d,** *Pachyclymenia intermedia* (Pachyclymeniidae, after Bogoslovskiy 1981: fig. 15a), at ca. 30 mm dm; **e,** *Kiaclymenia semiplicata* (Biloclymeniidae, after Bogoslovskiy 1981: fig. 18c), at ca. 10 mm wh; **f,** *Biloclymenia aktubensis* (Biloclymeniidae, after Bogoslovskiy 1981: fig. 19b), at ca. 24 mm dm (12 mm wh)

Gonioclymeniina Schindewolf, 1923a, Sellaclymeniaceae Schindewolf, 1923a, and Gonioclymeniaceae Hyatt, 1884

In traditional clymenid systematics, the suborder Gonioclymeniina (nom. transl. from Gonioclymeniaceae of Schindewolf 1923a by Ruzhencev 1957) embraced all forms with ventral lobe. Bogoslovskiy (1981), House (1981), and Bogoslovskaya et al. (1990) followed Schindewolf's (1937, 1955) phylogenetic concepts and recognized the superfamilies Sellaclymeniaceae (including the Hexaclymeniidae and Wocklumeriidae; supposedly without adventitious lobes), Gonioclymeniaceae (with A-lobes) and Parawocklumeriaceae. Korn (1992a) and Becker & Kullmann (1996) recognized the significance of intermediate triangular clymenids between Parawocklumeriidae and Wocklumeriidae, and consequently combined both families in a superfamily Wocklumeriaceae. The family level taxon Wocklumeriidae has "page priority" to Parawocklumeriidae in Schindewolf (1937).

Without discussion, Korn (1992a) also eliminated the distinction between the (remaining) Sellaclymeniaceae and Gonioclymeniaceae which is followed here. It has to be emphasized that all clymenids posses an adventitious mid-flank lobe which they inherited from their tornoceratid ancestors (House 1970, Becker & Kullmann 1996). Sutural simplification resulted in the reduction of the lateral lobe at the umbilicus and in the shortening of the outer subumbilical saddle as it is known iteratively in tornoceratid groups such as *Planitornoceras* (Becker 1995). This trend led to most simple-lobed forms such as *Cyrtoclymenia* and *Platyclymenia* but their primitive septal shape is a derived character. Sutural patterns in ammonoids generally followed strict genetical programs. Although the shape of the single mid-flank lobe in many clymenids is (secondarily) to a large extent controlled by cross-section (Westermann 1975, Korn 1992a), the "pseudolobe" or flank part of any clymenid septum was still secreted as in tornoceratids by the "adventitious part" of the epithelium. Subsequent returns from "pseudolobes" to shallow "true" mid-flank lobes probably involved the re-activation of episodically supressed genetical data. The clymenid mid-flank lobe always should be called A-lobe but it seems useful to mark if there are "true" septal folds. The probably heterochronic re-appearance of shallow lobes in umbilical position (e.g., in *Parawocklumeria*; Fig. 5e) similarly can be interpreted as a return of lateral lobes by mid-ontogenetic unblocking of disused genom parts.

Origin of the Gonioclymeniaceae

Czarnocki (1989) described from the Holy Cross Mountains the genus *Nodosoclymenia* which combines in species such as *Nod. pseudobiimpressa* Czarnocki simple platyclymeniid sutures with gonioclymeniid growth ornament which is almost straight and rectiradiate or prorsiradiate on the flanks. Evolute and moderately fast expanding

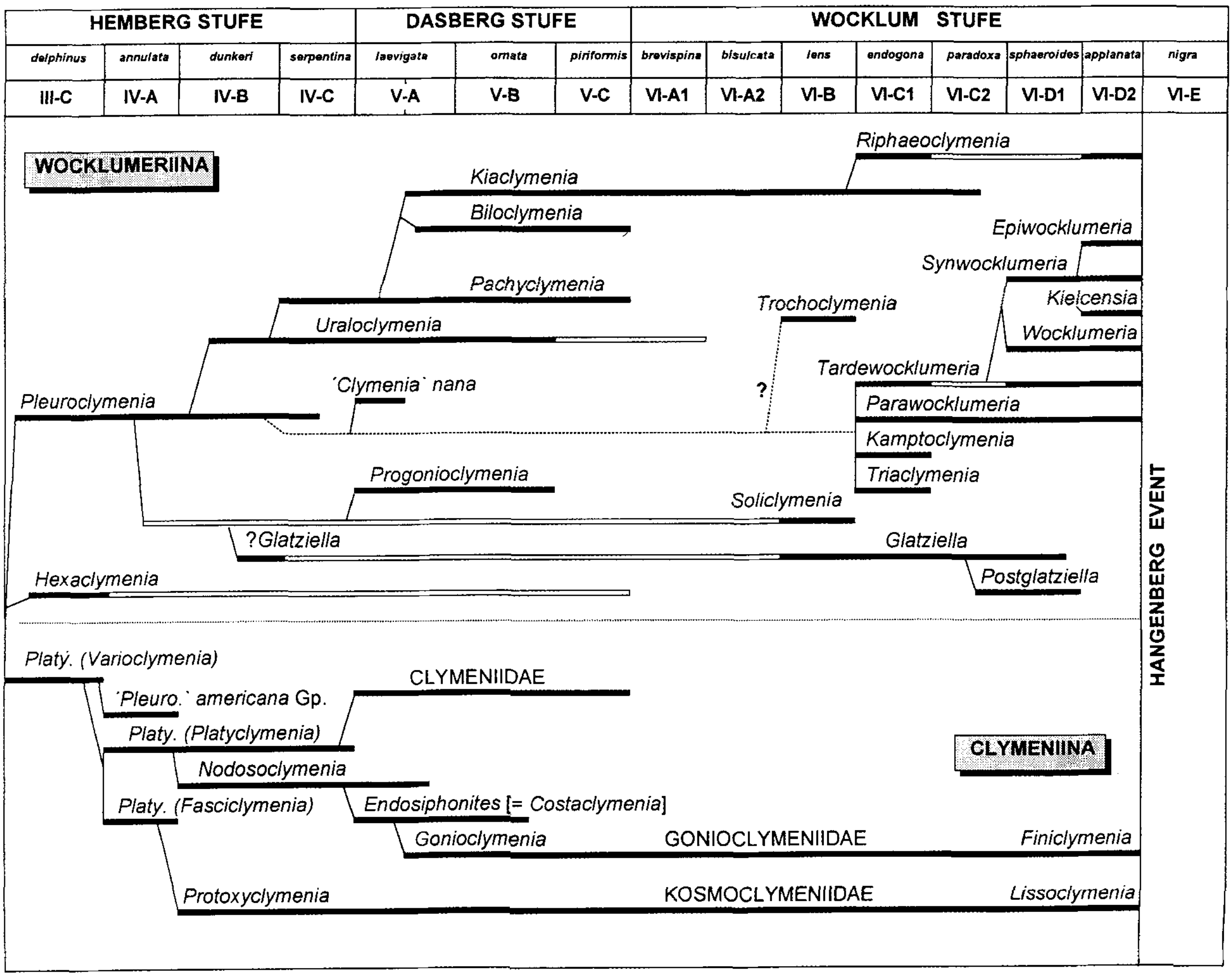

Fig. 12. Stratigraphical ranges and supposed phylogenetical relationships within middle to late Famennian genera of the Wocklumeriina and of selected Clymeniina groups (Clymeniaceae: Platyclymeniidae, Clymeniidae, Kosmoclymeniidae; Gonioclymeniaceae: Costaclymeniidae, Gonioclymeniidae)

whorls, short body chambers, narrow, deep dorsal lobes and trends towards large size are also common in both groups. *Nodosoclymenia* preceded the oldest Gonioclymeniaceae (*Costaclymenia* Schindewolf, a junior synonym of *Endosiphonites* Ansted) immediately in the late Hemberg Stufe and, as noted by Dzik (1991) and Becker & Kullmann (1996), has to be seen as the phylogenetic link between Platyclymeniidae (Clymeniaceae) and Gonioclymeniaceae (Fig. 12). There are no intermediate forms between Hexaclymeniidae and Costaclymeniidae to support Schindewolf's (1937, 1949) phylogenetic views. *Nodosoclymenia* occurs not only in Poland, but also in the Rhenish Massif (e.g., fragments from UD IV-B of the Nie Brickwork Quarry). Earliest Costaclymeniidae such as *Endosiph. muensteri* Ansted (= *limatus* Czarnocki) have very shallow ventral lobes. Ventral "pseudolobes" developed in several other Clymeniaceae (Platyclymeniidae: *Stenoclymenia*, Cyrtoclymeniidae: *Pricella*, Cymaclymeniidae: *Kazakhoclymenia*) independently. Narrow "true" ventral lobes are characteristic of the Sellaclymeniidae and Gonioclymeniidae which both were derived from the Costaclymeniidae (see Schindewolf 1949 and Weyer 1981).

The traditional Gonioclymeniina are clearly polyphyletic and have to be broken down into the monophyletic Gonioclymeniaceae (= Sellaclymeniaceae) as descendents of the Clymeniaceae on one side, and into the Wocklumeriaceae and Glatziellacea on the other side. Both groups evolved in parallel since the earliest time of clymenid evolution and represent two natural larger groups which should be recognized at suborder level. The Clymeniina Wedekind, 1914 (= Platyclymeniina Schindewolf, 1923b) combine the brevidomic/mesodomic Cyrtoclymeniaceae (convolute), Clymeniaceae (evolute) and Gonioclymeniaceae (evolute, always with lateral and ventral lobes). The **Wocklumeriina** embrace all primarily longidomic lineages with originally wide and shallow and subsequently often divided dorsal and ventral lobe.

Biloclymeniaceae Bogoslovskiy 1955 (nom. transl. by Becker, 1997b)

Bogoslovskiy (1977, 1981) investigated the phylogeny of the Miroclymeniidae Schindewolf (1924) which then included the *Uraloclymenia-Pachyclymenia* lineage as well as the enigmatic *Miroclymenia*. Korn (1981) placed the latter in synonymy with *Cymaclymenia*. The Miroclymeniidae consequently became a younger synonym of the Cymaclymeniidae Hyatt. The main content of the former Miroclymeniidae was later placed by Korn (1992b) in his new family Pachyclymeniidae. The latter and the descendent Biloclymeniidae are united here in the superfamily Biloclymeniaceae. They are characterized by mostly relative involute, compressed, moderately fast expanding whorls, biconvex growth lines, wide ventral lobes which may become divided (Figs 11c–f), and by body chambers of about one whorl in length. The group represents a very characteristic evolutionary branch which cannot be confused with other clymenids although the shell-form of some taxa may resemble cymaclymenids with thick whorls. Bogoslovskiy (1977, 1981) followed Schindewolf's (1937) idea of phylogenetic links with the Hexaclymeniidae. This is not only supported by ventral lobes of early members as in some Hexaclymeniidae (compare *Uraloclymenia* and *Pleuroclymenia*, *Glatziella* and *Kiaclymenia*; see Bogoslovskiy 1981 and Figs 10, 11) but also by the long septal necks found in *Pachyclymenia, Kiaclymenia* and *Biloclymenia* (Schindewolf 1937, Bogoslovskiy 1976).

The Biloclymeniaceae were most likely derived from unribbed pleuroclymenids and are placed in the Wocklumeriina. All *Pleuroclymenia* and several Pachyclymeniidae (e.g., *Borkowia kozlowskii* Czarnocki; here placed in *Uraloclymenia*, most *Pachyclymenia*) have characteristic internal shell thickenings (mould constrictions). The mostly convolute and compressed whorl cross-section gives a clear distinction of Biloclymeniaceae from Hexaclymeniidae but primitive species such as *Uralo. kazakhstanica* Bogoslovskiy and *Uralo. lateumbilicata* Bogoslovskiy are morphologically intermediate to smooth forms such as *Pleuro. kasachstanica* (Pl. 1: 8, 9). The stratigraphical age and Asian distribution of smooth pleuroclymenids (UD III-C) and early Pachyclymeniidae is in good accordance with close affinities. Differences in growth line ornament may be the result of the change to a more pelagic lifestyle. The Biloclymeniaceae differ from the Glatziellaceae in their somewhat shorter body chamber and more compressed, faster expanding whorl-profile (sometimes only of late stages). The keeled *Riphaeoclymenia* (Bogoslovskiy 1981 = *Dimeroclymenia* and *Liroclymenia* of Czarnocki 1989) however, is a larger-sized homoemorph of evolute glatziellids which indicates a morphological reversal in a late phylogenetical branch of the group. The Biloclymeniaceae are distinguished from the Wocklumeriaceae by the lack of triangular ontogenetic stages and by the undivided dorsal lobe.

Taxonomy

Suborder Wocklumeriina Becker 1997b

Diagnosis (emended from Becker 1997b): Extremely evolute to completely involute, smooth or ribbed, whorl section mostly depressed; body chamber originally longidomic, mesodomic in some derived groups; suture primarily with shallow and wide dorsal lobe, adventitious flank lobe and wide ventral lobe, advanced forms with narrow, subdivided or reduced dorsal and ventral lobes; lateral and umbilical lobes re-appear around the umbilicus in some groups; septal necks long to extremely long (holochoanitic).

Included superfamilies: Glatziellaceae Schindewolf, 1928, Biloclymeniaceae Bogoslovskiy, 1955, and Wocklumeriaceae Schindewolf, 1937. In advanced members of Glatziellaceae only the ventral lobe became more complex, in advanced Biloclymeniaceae the ventral lobe was divided and umbilical lobes were added, and in the Wocklumeriaceae there were changes both in the ventral and dorsal lobe.

Remarks: The Clymeniina differ in their brevidomic to mesodomic conchs which increase faster in whorl height and which are mostly compressed. There are no primary wide and shallow ventral lobes. The dorsal lobe is deep and narrow. Derived and broad-whorled Clymeniina may have a wider dorsal lobe but usually there is a small median (siphuncular) truncation left (see *'Pleuro.' eurylobica* Petersen 1975: pl. 7, fig. 5). Data on septal necks in Clymeniina are still rather insufficient but some taxa have very short, others long necks (Bogoslovskiy 1976, Drushchits et al. 1976).

Stratigraphical range: Middle Hemberg (*Prolobites delphinus* Zone, UD III-C) to upper Wocklum Stufe (*Epiwo. applanata* Subzone, UD VI-D_2).

Glatziellaceae Schindewolf, 1928 (nom. transl.)

Diagnosis: Extremely evolute to involute, smooth or ribbed, body chamber longidomic (longer than one whorl), whorls slowly expanding and with low apertures. Sutures with simple and wide dorsal lobe, adventitious flank lobe and wide ventral lobe which may be subdivided by median saddles and secondary ventral lobes. Sutural formulas: $EA:I - (E_1-E_1)A:I - E_2E_1AI - (E_2-E_2)E_1AI$.

Included families: Hexaclymeniidae Lange, 1929 and Glatziellidae, Schindewolf 1928. Weyer (1981) preferred to recognize both groups only at subfamily level. *Trochoclymenia* possibly belongs here as well. If this can be proven, it should form the base for a third family with umbilical lobes.

Stratigraphical range: Middle Hemberg (*Prolobites delphinus* Zone, UD III-C) to upper Wocklum-Stufe (*Wo. sphaeroides* Subzone, UD VI-D_1).

Geographical distribution: Germany (Rhenish Massif, Thuringia, Franconia, Harz Mountains), Carnic Alps (Austria/northern Italy), Great Britain (Devon, Cornwall), Poland (Holy Cross Mts., Silesia, Carpathian Foreland, Lublin Basin), Morocco, Russia (Urals), Kazakhstan (Mugodzhar Mts.), South China (Guizhou).

Family Hexaclymeniidae Lange, 1929

Diagnosis (emended from Lange, 1929): Small to medium-sized, evolute to extremely evolute, smooth or ribbed, often with internal shell thickenings (mould constrictions), venter rounded, flat, bicarinate or slightly keeled; dorsal and ventral lobes simple, wide and rounded. Sutural formula: EL:I.

Included genera: *Pleuroclymenia* Schindewolf, 1934, *Gyroclymenia* Czarnocki, 1989 (= *Pleuroclymenia*), *Hexaclymenia* Lange, 1929, *Progonioclymenia* Schindewolf, 1937, *Soliclymenia* Schindewolf, 1937, Gen. nov. (*Clymenia nana* Group).

Stratigraphical range: Middle Hemberg (*Prolobites delphinus* Zone, UD III-C) to lower Wocklum Stufe (*Balvia* (*Kenseyoceras*) *lens* Zone, UD VI-B).

Geographical distribution: Rhenish Massif, Harz Mts., Franconia, Maïder, ?Devon (?*Pleuroclymenia* in House 1959), Carnic Alps, Holy Cross Mts., Silesia, Urals, Mugodzhar Mts. Records from North America, Asia and Australia are lacking so far. Thus, the family may have been restricted to the western part of the Protothetys and to the Ural ocean.

Pleuroclymenia costata (Lange, 1929)

Fig. 10d, Pl. 1: 11–14

*+ 1921 *Platyclymenia crassa* Schindewolf: 162 [nom. nud., non *quenstedti* var. *crassa* nom. nud.]

*	1922	*Platyclymenia* (*Varioclymenia*) *brevicostata* Kegel: 39 [fide Schindewolf 1924]
+	1923b	*Platyclymenia crassa* Schindewolf: 458–459, fig. 19c [non *Platy. quenstedti* var. *crassa* = ?*Pleuro. crassa*]
*	1924	*Platyclymenia crassa* Schindewolf: 100
*+	1929	?*Cycloclymenia costata* Lange: 24, 63, pl. 2, fig. 14
*? e.p.	1929	*Platyclymenia* (*Varioclymenia*) *brevicosta* Lange: 20 [only *annulata* Zone record]
	1931	*Platyclymenia crassa crassa* Matern: 102 [non *quenstedti crassoides* = *crassa*]
v	1934	*Platyclymenia* (*Pleuroclymenia*) *crassa* Schindewolf: 343
*?	1936	*Platyclymenia* (*Pleuroclymenia*) aff. *crassa* Paeckelmann: 31
*?	1938	*Platyclymenia* (*Pleuroclymenia*) *crassa* Paeckelmann: 25
+	1955	*Platyclymenia* (*Pleuroclymenia*) *crassissima* Schindewolf: 428 [nom. nov.]
+	1956	*Platyclymenia* (*Pleuroclymenia*) *crassima* Müller: 69 [nom. vad.]
*+	1989	*Gyroclymenia rotundata* Czarnocki: 32, pl. I, figs 17, 17a, pl. II, figs 8, 8a, pl. XXXIX, fig. 3b, pl. XL, fig. 2a, b

Types: The illustrated specimen of Lange (1929) from the *annulata* Zone (UD IV-A) of the Beul, here designated as lectotype, has been misplaced and may be lost. It is possible that syntypes are preserved in the collection at Hamburg University. The holotype of *Pleuro. crassissima* from the *annulata* Zone of Kirschhofen is No. 3154 in the Schindewolf collection at Marburg. Figures of it have been made available by J. Price/M.R. House and D. Korn.

Description: In the holotype of *Pleuro. crassissima*, inner whorls have marked straight, somewhat rursiradiate ribs which become finer on the last whorl and which are, from ca. 30 mm dm on, restricted to the inner flanks. There are several mould constrictions and the venter is broadly rounded. The Berlin topotype of the same species (MB.C.1266, Pl. 1: 10–12) is preserved in dark grey to brownish limestone. The last whorl has been eroded on one side and shows five concave constrictions which are restricted to the venter. There are slightly more than thirty rounded, straight, rursiradiate ribs on the last whorl which terminate at the flank shoulders and on the lower part of the deep and rounded umbilical wall. The maximum whorl width lies in the ribbed middle part of the flanks. Early whorls have a more depressed cross-section than later ones. Sutures show a high saddle at the umbilical seam from where they deflect backwards in gentle curvature (Fig. 10d). A very wide and flattened E-lobe is not really separated from the widely curved adventitious flank lobe. Similar sutures were illustrated by Czarnocki (1989) for his *Gyro. angulata* and juvenile *Gyro. cyclocostata*.

Five specimens from the Hauern give insights into the variability of the species and show fine, lirate, densely spaced (> 10 per mm) convex growth lines. Ribs are sometimes slightly concave on the flanks. For dimensions see Table 2. In MB.C.1806.4, the wrinkle layer, consisting of rectiradiate, rarely branching wrinkles, covers the hair keel of the preceeding whorl. MB.C.1806.2 has a healed shell fracture as it can be expected from longidomic bottom-dwellers.

Remarks: There is certainly taxonomic oversplitting in *Pleuroclymenia*. Large collections are needed to decide which taxa should be kept and which should be put into synonymy or should only be recognized at subspecies level. Schindewolf's holotype and Lange's lectotype are slightly more involute than the Berlin topotype of *Pleuro. crassissima*. *Pleuro. varicata* (Sobolev) is even more involute (uw <40% dm) and more compressed. The latter is also true for *Pleuro. angulata* (Czarnocki), *Pleuro. cyclocostata* (Czarnocki), and the very evolute *Pleuro. evoluta* (Czarnocki). *Pleuro. rotundata* (Czarnocki) has similar shell parameters as *costata* and is regarded as a junior subjective synonym. *Pleuro. kasachstanica*, *Pleuro. mutabilis* (Czarnocki) and *Pleuro. sophiae* (Czarnocki) loose the ribbing during different ontogenetic phases.

Stratigraphical range: *Annulata* Zone (UD IV-A) of the Rhenish Massif to *Protoxyclymenia* Zone (UD IV-B) of the Holy Cross Mountains (Besówka) and of the Kia section (Bogoslovskiy in Simakov et al. 1983).

Pleuroclymenia kasachstanica Kind, 1944

Pl. 1: 8, 9

*+	1944	*Platyclymenia* (*Varioclymenia*) *kasachstanica* Kind: 160–161, 166, pl. 1, figs 16–17
*?	1944	*Platyclymenia* (*Varioclymenia*) *kasachstanica* var. *simplex* Kind: 161, 166

Material: A purchased single topotype (?syntype, MB.C.1731, Pl. 1: 8, 9).

Description: The specimen is well-preserved and complete. The preserved part of the body chamber is longer than one whorl. Coarse recrystallisation prevents a clear recognition of complete sutures but undoubtedly there is a relative high saddle at the umbilical seam followed by a gently curved flank lobe that grades into a straight or only slightly undulose part across the outer flanks and venter. Dense straight, slightly rursiradiate flank ribbing (ca. 25–30 ribs per whorl) is present until 6 mm dm. Last undulose ribs disappear at ca. 8 mm dm. Smooth adult whorls have few and shallow constrictions which are restricted to the flatly rounded venter. The whorl cross-section is subrectangular with maximum flank width on the mid-flank. For dimensions see Table 2.

Remarks: *Pleuro. mutabilis* is a related species with rather variable conch parameters (uw and wd) that still has subdued dense ribs at median stages. *Uralo. lateumbilicata* Bogoslovskiy (1977) is more involute, thicker, and has well-developed A- and E-lobes.

Stratigraphical range: *Delphinus* Zone (UD III-C) of Kasakhstan. Bogoslovskiy (in Simakov et al. 1983) quotes the species also from strata with *Protoxyclymenia* (UD IV-B) at Kia.

Pleuroclymenia cyclocostata (Czarnocki, 1989)

Pl. 2: 3, 4

*	1972	*Gyroclymenia cyclostata* Pajchlowa: 100 [nom. nud.]
+	1989	*Gyroclymenia cyclocostata* Czarnocki: 13, 23, 33, pl. I, figs 1–5, 9, 12–13, 16, pl. XXXIX, figs 1b, 2a, 2b, pl. XL, fig. 5
*v	1992	*Gyroclymenia cyclocostata* Becker: 12

Description: MB.C.1732 (Pl. 2: 3, 4) is an internal mould which has been eroded on one side. Only about the last two whorls are preserved. The cross-section is subrectangular with flattened, rounded venter and weakly rounded flanks. The body chamber occupies more than the last whorl (ca. 380°). The latter displays 32 distinctive straight ribs which terminate at the ventrolateral shoulders. The venter has four marked constrictions with rather deep median sinus. Ribs and constrictions do not overlap. The last septum shows a high saddle at the umbilical seam and a wide and rounded A-lobe on the ribbed flank. Ventral parts are not visible. For dimensions see Table 2.

Remarks: In terms of umbilical widths (ca. 53% dm) and wh/ww ratio (0.69 to 0.74), the Sauerland specimen is somewhat intermediate between *Pleuro. cyclocostata* and *Pleuro. evoluta. Pleuro. angulata* (uw = 42–44% dm) and *Pleuro. varicata* (uw < 40% dm) are also compressed but much more involute.

Stratigraphical range: *Delphinus* Zone (UD III-C) of the Rhenish Massif and Holy Cross Mountains (Ostrówka, ?Kielce).

Pleuroclymenia mutabilis (Czarnocki, 1989)

Pl. 2: 1, 2

*+	1989	*Gyroclymenia mutabilis* Czarnocki: 23, 33, pl. II, figs 2, 4, 6, 10, pl. XXXIX, fig. 3d, pl. XL, fig. 4a, b

Description: Three specimens from the Hauern near Braunau (Kellerwald) conform to the species as illustrated by Czarnocki (1989). The cross-section is broad kidney-shaped with well-rounded venter. Ventral constrictions are seen in MB.C.1807.2 (Pl. 2: 1, 2). The ribbing weakens between 10 and 15 mm dm and is rather dense (25 to 35 ribs per whorl). A suture is poorly visible on MB.C.1807.1 and has a high saddle at the umbilical seam and a rounded flank lobe extending straight to the venter, similar as shown by Czarnocki in *Pleuro. angulata.* Growth lines are very fine (up to 13/mm), lirate and straight to convex on the flanks. A wide ventral sinus is developed. MB.C.1762, det. *Platy.* (*Pleuro.*) *crassa*, from Burg (Rösenbeck Syncline, sheet 4518 Madfeld) resembles the Kellerwald specimens but is rather poorly preserved.

Stratigraphical range: *Annulata* Zone (UD IV-A) of the Rhenish Massif and UD IV-B of the Holy Cross Mountains (Besówka, Kielce).

Superfamily Wocklumeriaceae Schindewolf, 1937 (emend.)

Diagnosis: Evolute to completely involute (umbilicus closed), smooth, early ontogenetic stages triangularly coiled with regular constrictions, adult stages triangular or normally coiled, body chamber very longidomic (much more than one whorl), sutures with divided or completely reduced dorsal and ventral lobes. Sutural formulas: $(E_1{-}E_1)A{:}(I_1{-}I_1) - A - AL_e{:}L_i(I_1{-}I_1) - EAL_e{:}L_iI_1I_2$.

Included families: Parawocklumeriidae Schindewolf, 1937 and Wocklumeriidae Schindewolf, 1937.

Stratigraphic range: Upper Wocklum-Stufe (*endogona* Subzone, UD VI-C_1, to *applanata* Subzone, VI-D_2).

Geographical distribution: See Table 1.

Family Parawocklumeriidae Schindewolf, 1937

Kamptoclymenia endogona Schindewolf, 1937

Figs 5a–b, 6a, 7, Pl. 3: 3, 4

*	1902	*Phenacoceras ? paradoxum* Frech: 63, pl. 3, fig. 5 [fide Schindewolf 1937]

*+v	1937	*Kamptoclymenia endogona* Schindewolf: 88–89, text-figs 20, 24, pl. 3, figs 8–15
	1950	*Kamptoclymenia endogona* Schindewolf: 262, text-fig. 226h
*	1959	*Kamptoclymenia endogona* Lewowicki: 78, 81, 100, 109, pl. I, fig. 5
aff.	1989	*Kamptoclymenia* aff. *endogona* Czarnocki: 41–42, pl. III, fig. 7
*	1993	*Kamptoclymenia endogona* Korn: fig. 3

Type: Schindewolf's holotype from Bed 8 at Oberrödinghausen is lost, and MB.C.1813.1 from Bed 7, the only more or less complete larger paratype, is designated as neotype. The specimen is probably the original of Schindewolf's text-fig. 20b.

Description: The neotype has at ca. 10 mm dm a distinctive concave constriction on the gently curved venter. Sutures show that the saddle between E- and A-lobes is mostly not as well-developed as in Schindewolf's illustration. The median saddle is very low giving only a slight difference to *Pleuroclymenia* sutures (Fig. 6a). Early whorls are not well-preserved in the neotype but triangular coiling is visible in juvenile paratypes such as MB.C.1813.2–3. Shell measurements of syntypes (Table 3) show that extreme conch evolution (uw > 60% dm) develops rather late in ontogeny (dm > 10 mm). Shell compression increases during growths and wh/ww ratios rise from around 0.5 to 0.8.

Remarks: *Kampto. endogonoides* differs only by more depressed whorl profile at median ontogenetic stages. *Kampto. trigona* has extended triangular stages and also thicker whorls.

Stratigraphical range: Lower to upper part of *endogona* Subzone (UD VI-C_1).

Kamptoclymenia trigona Schindewolf, 1937

Fig. 7, Pl. 3: 5, 6

*+v	1937	*Kamptoclymenia trigona* Schindewolf: 89–90, pl. 3, figs 16–18
	1950	*Kamptoclymenia trigona* Schindewolf: 262, text-fig. 226i
*?	1989	*Triaclymenia* cf. *triangularis* Czarnocki: pl. XI, fig. 14 [only]
*	1993	*Kamptoclymenia trigona* Korn: fig. 3

Type: Schindewolf's holotype from Bed 8 at Oberrödinghausen has been lost. A second specimen from Bed 8, MB.C.1751, the largest complete paratype, is here designated as neotype.

Remarks: Schindewolf has given a good description of his species. Widely spaced shallow to distinctive constrictions with marked sinus are, as in *Pleuroclymenia*, restricted to the venter (MB.C.750.1–2). They are slightly eroded on the neotype. None of the available specimens shows sutures. Shell parameters of some specimens are given in Table 3. As in *Kampto. endogona*, adult whorls become more evolute (uw reaches up to 2/3 of dm) and their wh/ww ratios finally exceed 0.5.

Stratigraphic range: Lower (Korn 1993) to upper (Schindewolf 1937) part of *endogona* Subzone (UD VI-C_1).

Triaclymenia triangularis Schindewolf, 1937

Figs 5c, 7, Pl. 3: 7, 8, 15

*+v	1937	*Triaclymenia triangularis* Schindewolf: 91, text.-fig. 22, pl. 3, figs 3, ?4
	1950	*Triaclymenia triangularis* Schindewolf: 262, text-fig. 226l
?non	1989	*Triaclymenia* cf. *triangularis* Czarnocki: 42, pl. XI, figs 1, 6, 14 [fig. 14 = ?*Kampto. trigona*, figs 1 and 6 ?= convolute species such as *Tria. primaeva*, *Parawo. distorta* or *Tardewo. distributa*]

Types: Schindewolf's holotype from Bed 10 at Oberrödinghausen has been lost. A second, relatively large but rather poorly preserved paratype from Bed 10 (MB.C.1815, Pl. 3: 7, 8) is designated as neotype. It is the only specimen that shows sutures and is the original of Schindewolf's text-figure 22.

Remarks: The compressed, evolute (uw = 40–50% dm) shell form, with adult wh/ww ratios of 0.8 or more, allows easy distinction from *Kampto. varicata* and *Parawo. patens*, even if sutures are not preserved. MB.C.1817 is an adult whorl fragment showing subtriangular cross-section (Pl. 3: 15) and the formation of an incipient keel. Its growth lines have a very shallow flank sinus, a very low and short ventrolateral salient and a small, diverging ventral sinus.

Stratigraphical range: Lower to Upper part of *endogona* Subzone (UD VI-C_1).

Parawocklumeria paradoxa (Wedekind, 1918)

Figs 5d–f, 7, Pl. 4: 5, 6

+*	1916	*Wocklumeria paradoxa* Schindewolf: 36 [nom. nud.]
+v c.p.	1918	*Wocklumeria paradoxa* Wedekind: 172–173, pl. XIX, fig. 16 [non fig. 17 = *Parawo. paprothae*]
*	1921	*Wocklumeria distorta* Schmidt: 290
*v e.p.	1924	*Wocklumeria distorta* Schmidt: 121, pl. 6, figs 14–15 [e.p. = *Wo. sphaeroides* juv.]
*	1924	*Wocklumeria distorta* Paeckelmann: 85
	1926	*Parawocklumeria paradoxa* Schindewolf: 114, footnote 7
*	1929	*Wocklumeria paradoxa* Lange: 30, 31

*v e.p. 1937 *Parawocklumeria paradoxa* Schindewolf: 15, 16, 17, 21, 22, 27, 3043, 4495–96, text-fig. 23, pl. 4, figs 11–16 [e.p. = *paprothae*]
1950 *Parawocklumeria paradoxa* Schindewolf: 260, 262, text-fig. 225, 226n
* 1954 *Parawocklumeria paradoxa* Pfeiffer: 58
+* 1960 *Parawocklumeria laevigata* Selwood: 156, 167–168, 169, text-fig. 4A, pl. 27, figs 16–20
+* 1960 *Parawocklumeria laevigata* var. *obesa* Selwood: 156, 169, text-fig. 4B, pl. 28, figs 1–2
1960 *Parawocklumeria paradoxa* Müller: 145, text-fig. 1991-m
* 1964 *Parawocklumeria paradoxa* Sun: pl. 1, fig. 3
* 1965 *Parawocklumeria paradoxa* Sun & Shen: 36, 37, 39, 66–67, text-fig. 23, pl. I, figs 11–12
1979 *Parawocklumeria paradoxa* Weyer: 99
* 1979 *Parawocklumeria paradoxa* Clausen et al.: 59
* 1980 *Parawocklumeria paradoxa* Bartzsch & Weyer: 39
* 1981 *Parawocklumeria paradoxa* Korn: tab. 1
*e.p. 1981 *Parawocklumeria laevigata* Bogoslovskiy: 107–109, pl. XVI, figs 6–10 [e.p. probably = *paprothae*]
* 1981 *Parawocklumeria paradoxa* Ruan: 114–115, text-fig. 81, pl. 28, figs 17–25, 37–38
1982 *Parawocklumeria paradoxa* Bartzsch & Weyer: text-fig. 14.2
1983 *Parawocklumeria laevigata* Simakov et al.: tab. 2
*v 1984 *Parawocklumeria paradoxa* Becker et al.: 189
* 1985 *Parawocklumeria paradoxa* Sheng: 89–90, pl. 11, figs 5–8
1985 *Parawocklumeria paradoxa* Gong et al.: 26
*v 1986 *Parawocklumeria paradoxa* Paproth et al.: 4, 21
1987 *Parawocklumeria paradoxa* Korn & Luppold: 201
*v 1988 *Parawocklumeria paradoxa* Becker: 195, 196, 197, 198, pl. 1, fig. 7
*e.p. 1989 *Parawocklumeria paradoxa* Czarnocki: 43–44, pl. XLIII, figs 2–5, pl. XLIV, fig. 1a–d [non pl. XII, fig. 4 = ?*paprothae*]
* 1989a *Parawocklumeria paradoxa* Clausen et al.: text-fig. 3, pl. 4, figs 14–18
* 1989b *Parawocklumeria paradoxa* Clausen et al.: 176, 221
* 1989 *Parawocklumeria paradoxa* Sheng in Ji et al.: 118–119, pl. 32, figs 1a–4b
* 1992a *Parawocklumeria paradoxa* Korn: 9, text-fig. 3, Pl. 1, figs 1–2
v e.p. 1993 *Parawpcklumeria paradoxa* Becker et al.: 23, 25, 38, 50, 51, 52, 56 [old Schindewolf records e.p. = *paprothae*]
1993 *Parawocklumeria paradoxa* Korn: figs 3, 8
* 1994 *Parawocklumeria paradoxa* Luppold et al.: 21, 34
1994 *Parawocklumeria paradoxa* Korn et al.: 116
1995a *Parawocklumeria paradoxa* Korn: 162, text-figs 3, 5
1995b *Parawocklumeria paradoxa* Korn: figs 12.2, 12.4
*v 1996 *Parawocklumeria paradoxa* Becker: 22, 23, 24, pl. 2, fig. 8
* 1998 *Parawocklumeria paradoxa* Bartzsch et al.: 44
* 1999 *Parawocklumeria paradoxa* Korn: 153, text-fig. 3, pl. 3, fig. 2

Type: In the Göttingen collection five syntypes are preserved, including the original of Wedekind's pl. XIX, fig. 17 (GPIG 389–78a) which shows a typical suture on a polished part of an earlier whorl. Preparation of the umbilical region,

Table 3
Dimensions of various Parawocklumeriidae.

species/specimen	dm	uw	wh	ww	uw%	ww%	wh/ww
Kampto. endogona							
lost holotype	25.8	15.7	5.5	7	60.9	27.1	0.79
neotype MB.C.1813.1	12.3	7.7	2.8	4.7	62.6	38.2	0.6
MB.C.1813.2	7	3.9	1.75	3.1	55.7	44.3	0.56
MB.C.1813.3	6.3	3.7	1.4	2.8	58.7	44.4	0.5
MB.C.1812.2	4	2.1	1	2.2	52.5	55	0.45
Kampto. endogonoides							
holotype 33544	10.5	5.8	2.3	5.1	55.2	48.6	0.45
Kampto. trigona							
lost holotype	15	9.3	3	6.3	62	42	0.48
neotype MB.C.1751	12.2	8	2.5	4.7	65.6	38.5	0.53
neotype MB.C.1751	9	6	1.75	3.8	66.7	42.2	0.46
MB.C.1750.2	9	5	2.2	4.5	55.6	50	0.49
MB.C.1750.3	5.9	3.3	1.3	3.2	55.9	54.2	0.41
MB.C.1750.3	3.6	1.9	0.9	2.2	52.8	61.1	0.41
Tria. triangularis							
neotype MB.C.1815	18	9	5	6	50	33.3	0.83
lost holotype	16	6.5	ca. 6	ca. 7.5	40.6	46.9	ca. 0.8
MB.C.1816	9.3	4.3	3.1	4.2	46.2	45.2	0.74
Tria. primaeva							
holotype 502	19	5	5	8	26.3	26.3	0.63
Parawo. paradoxa							
lectotype GPIG 389–100	21.8	1.7	11.3	12	7.8	55	0.94

unfortunately, proved the presence of a rather wide and triangular umbilicus (Pl. 4: 3, 4) as in *Parawo. paprothae*. In order to preserve the latter taxon, established subsequently without knowledge of the *paradoxa* type series, a second, formerly unillustrated syntype, GPIG 389–100 (Pl. 4: 5–6), is designated as lectotype. The specimen is a rather complete, median-sized internal mould with a moderately large and round umbilical opening.

Remarks: As discussed above, the distinction between *paradoxa* and *paprothae* is not easy, especially in poorly preserved material. Internal moulds tend to have a wider umbilicus than specimens with preserved shell. It is the shape of the umbilical opening, not the relative umbilical width, that separates involute *paprothae* morphotypes from *paradoxa*. For this reason, the single Maïder parawocklumeriid (MB.C.3061, Pl. 4: 7, 8) has been assigned to *Parawo. paprothae* rather than to *paradoxa*. Sutures of both taxa are identical. The relative whorl thickness varies considerably but strong compression as in *Epiwo. applanata* is normally not found. The latter species differ also in the convex course of constrictions and in the even smaller umbilicus; all characters allow a clear distinction of specimens lacking sutures. Shell homoeomorphy is more significant between *Parawo. paradoxa*, *Synwo. dunhevedensis*, and *Synwo. heterolobata*.

Stratigraphical range: *Paradoxa* Subzone (UD VI-C_2) to the top of the *applanata* Subzone (UD VI-D_2).

Family Wocklumeriidae Schindewolf, 1937

Tardewocklumeria n. gen.

Figs 7, 8a, 9

e.p.	1972	*Mesowocklumeria* (Czarnocki) Pajchlowa: 101 [nomen nudum: e.p. = *Parawocklumeria*, e.p. = *Triaclymenia*]
v	1981	*Synwocklumeria* (?) Bogoslovskiy: 74
e.p.	1989	*Parawocklumeria* Czarnocki: 43 Type species: *Parawocklumeria distributa* Czarnocki, 1989.

Type species: *Parawocklumeria distributa* Czarnocki, 1989.

Derivation of name: From lat. tardus = little, weak; due to its ancestral position in the Wocklumeriidae.

Diagnosis: Triangularly coiled throughout ontogeny and with strong constrictions, umbilicus small to moderately wide, sutures with rounded and wide median ventral lobe, rounded flank lobe (first ventral lobe) and small rounded subumbilical lobe. Sutural formula: $EAL_{(c)}: ?L_i(?I_1-I_1)$.

Included species: Type species and *Synwocklumeria* (?) *perplexa* Bogoslovskiy, 1981.

Remarks: Bogoslovskiy's types have been examined in Moscow and nothing needs to be added to his descriptions. The new genus is distinguished from similarly coiled parawocklumerids by its wide and distinctive ventral lobe. *Synwocklumeria* is characterized by narrow lingulate to pointed mid-flank lobes and narrower, small ventral lobes. *Tardewocklumeria* n.gen probably is not just an intermediate phylogenetic stage between open-umbilicate Parawocklumeriidae and Wocklumeriidae but, based on the time difference of the two species included, it may represent a sidebranching lineage with closing umbilicus that reached (according to Bogoslovskiy in Simakov et al. 1983) in parallel with *Parawocklumeria* and *Synwocklumeria* the latest Wocklumian *Wo. sphaeroides* Zone.

Pajchlowa (1972) published determinations of J. Czarnocki in faunal lists and this included taxa which were not recognized subsequently in the posthumous monography of Czarnocki (1989). Various open umbilicate triangular clymenids *(patens, primaeva, distorta, distributa)* were combined in the nomen nudum *Mesowocklumeria*. Other taxa such as *Kielcensia bohdanowiczi minima*, *Sphaerowocklumeria parva* (= *parra* nom. vad.), *Sphaero. nuciformis*, *Wo. accessa* and *Wo. globulosa* remained uncommented and undescribed until now. It is not clear whether these names refer to material subsequently regarded as conspecific with other forms or whether the Polish faunas include additional Wocklumeriaceae which were left out in Czarnocki (1989).

Unfortunately, the dorsal lobes of *Tardewocklumeria* are still unknown. This leaves the two possibilities that the internal median saddle was or was not yet divided by a second I-lobe. Since outer sutures in the type-species are still rather reminiscent of *Parawocklumeria*, it is inferred that the same applies to dorsal parts.

Stratigraphical range: *Parawo. paradoxa* Zone (Kowala, Czarnocki 1989) to *Wo. sphaeroides* Zone (Kia Section, Simakov et al. 1983).

Synwocklumeria mapesi n. sp.

Figs 8b, 9, Pl. 4: 11, 12

Type: MB.C.2706, purchased at Erfoud and presented in 1997 by Prof. Royal Mapes, Athens, Ohio. The holotype is the only available specimen although various localities around the Jebel

Aguelmous have been collected by the author in company with M. R. House (Southampton), V. Ebbinghausen (Odenthal), P. Bockwinkel (Leverkusen), S. Z. Aboussalam (MfN), D. Weyer (Magdeburg), R. Mapes, and others.

Type level and locality: Maïder, latest Famennian, most likely UD VI-C/D. The holotype was purchased together with other ammonoids that are typical for the Fezzou area. In the Erfoud region, haematitic UD VI faunas are only known from around the Jebel Aguelmous.

Diagnosis: A rather involute species of *Synwocklumeria* with broad dorsolateral saddle and narrow, rounded A-lobe.

Description: The holotype is a well preserved haematitic internal mould showing the last three septa and traces of healed dorsolateral shell damages. The conch is strongly tripartite, with deep constrictions, and resembles *Parawo. paprothae* (see Pl. 4). The umbilicus is small but open, the cross-section subcircular with curved flanks and venter. Dimensions are given in Table 4.

Remarks: The new species resembles *Synwo. kiensis* but differs by details of the suture, especially by the rounded A-lobes, and by the rather wide and asymmetric inner flank saddle. *Synwo. dunhevedensis* and *Synwo. heterolobata* have a practically closed umbilicus, *Synwo. angustilobata* has a tongue-shaped A-lobe and is more convolute. *Synwo. bashcirica* is distinguished by its asymmetric and pointed midflank lobe.

Kielcensia ingeniens n. sp.

Figs 8c–d, 9, Pl. 4: 9, 10

Type: Holotype MB.C.2705, the only available specimen, purchased in Erfoud and presented by Prof. R. Mapes.

Type level and locality: Maïder, latest Famennian, most likely UD VI-C/D (see comments under *Synwo. mapesi* n.sp.).

Derivation of name: Due to the supposed ancestral position in the genus.

Diagnosis: A *Kielcensia* species with v-shaped adventitious lobe and narrow umbilicus of early stages that opens rapidly whilst coiling remains strongly tripartite.

Description: The holotype is a well-preserved haematitic mould with remains of the body chamber occupying about 2/3 of the last whorl. The whorl cross-section is subcircular with rounded flanks and venter. The shell is strongly tripartite throughout ontogeny. The umbilicus opens during the last preserved whorl rapidly from ca. 10% dm to 25% dm and the umbilical opening forms a rather rounded ellipsoid. The conch shape resembles *Parawo. paprothae* up to ca. 14 mm dm, and *Parawo. distorta* subsequently. Sutures show some variability but all have a pointed, narrow to moderately wide, v-shaped A-lobe, a rounded, subumbilical lateral lobe, and a relatively small, rounded ventral lobe.

Remarks: The new species differs from all forms of *K. bohdanoviczi* by the shape of the A-lobe and by the rapid opening of the umbilical spiral while the shell remains strongly constricted and tripartite. *K. ingeniens* n.sp. is morphologically intermediate between *Synwocklumeria* and *K. bohdanoviczi*. A second new *Kielcensia* from Oklahoma (Becker et al. in prep.) differs by unconstricted strongly triangular adult whorls.

Wocklumeria sphaeroides sphaeroides (Richter, 1848)

Figs 8e–f, 9, Pl. 5: 1–10

*+v	1848	*Goniatites sphaeroides* Richter: 34, pl. 4, figs 113–115
v	1862	*Goniatites sphaeroides* Gümbel: 311, 322
	1864	*Goniatites sphaeroides* Richter: 614
*	1914	*Wocklumeria Denckmanni* Wedekind: 10 [nom. nud.]
v	1916	*Wocklumeria Denckmanni* Schindewolf: 36 [nom. nud.]
*+v	1918	*Wocklumeria Denckmanni* Wedekind: 172, pl. XIX, figs 18–21
	1921	*Gattendorfia sphaeroides* Schindewolf: 168
	1923b	*Wocklumeria Denckmanni* Schindewolf: 396
*v e.p.	1924	*Wocklumeria sphaeroides* Schmidt: 121, pl. 6, figs 16–17 [e.p. = *Parawocklumeria* sp. or *sphaeroides plana*]
*v e.p.	1924	*Wocklumeria distorta* Schmidt: 121
	1924	*Wocklumeria sphaeroides* Schindewolf: 106–108, fig. 1b
	1924	*Wocklumeria Denckmanni* Schindewolf: 106–108, fig. 1c
	1926	*Wocklumeria Denckmanni* Schindewolf: 97, fig. 1b
*v e.p.	1927	*Wocklumeria sphaeroides* Schmidt: 9, 10 [e.p. = cf. *aperta*]
*	1927	*Wocklumeria sphaeroides* Gallwitz: 497
*	1929	*Wocklumeria sphaeroides* Peneau: 189, pl. 12, fig. 3a–c
	1929	*Wocklumeria denckmanni* Lange: 30, 31
v non	1932	*Wocklumeria sphaeroides* Paeckelmann: 96 [fide Becker 1997 = *sphaeroides plana*]
*	1933	*Wocklumeria denckmanni* Schmidt: 6
?*	1934	*Wocklumeria* sp. Weber: 544, 545
*	1937	*Wocklumeria sphaeroides* Schindewolf: 15, 28, 35, 41, 42, 43, 44, 45, 69–70, text-fig.12, pl. 1, figs 12–15, pl. 2, figs 1–3
	1938	*Epiwocklumeria sphaeroides* Paeckelmann: 28

	1950	*Wocklumeria sphaeroides* Schindewolf: 262: text-fig. 226f
v	1952	*Wocklumeria sphaeroides* Schindewolf: 286
*v	1954	*Wocklumeria sphaeroides* Pfeiffer: 58, pl. VIII, figs 5–6
*	1956	*Wocklumeria* Hollard & Jaquemont: 23 (footnote)
* e.p.	1960	*Wocklumeria sphaeroides* Selwood: 159–161, pl. 26, figs 3–5 [e.p. = *sphaeroides plana* and *sphaeroides aperta*]
*	1960	*Wocklumeria sphaeroides* Petter: 19–20, text.-fig. G–G1, pl. II, figs 7, 8, 11
*	1960	*Wocklumeria sphaeroides* Müller: 148, text-fig. 199g–h, text-fig. 201A,b, text-fig. 201B
cf.	1963	cf. *Wocklumeria* sp. Hollard: Tab. 1
*	1964	*Wocklumeria sphaeroides* Sun: 807, pl. I, figs 1–2
	1965	*Wocklumeria sphaeroides* Sun & Shen: 36, 37, 3946–47, pl. I, figs 5–10
	1966	*Wocklumeria sphaeroides* Babin: 381
?	1970	*Wocklumeria?* sp. Hollard: 924
*	1979	*Wocklumeria sphaeroides* Clausen et al.: 59
*	1979	*Wocklumeria sphaeroides* Weyer: 99, pl. 1, fig. 4
*v e.p.	1980	*Wocklumeria sphaeroides* Bartzsch & Weyer: 35, 37, fig. 21, 3 [non fig. 2a, b = *sphaeroides plana*]
*	1981	*Wocklumeria sphaeroides* Korn: tab. 1
*	1981	*Wocklumeria sphaeroides* Ruan: 6, 111, pl. 28, figs 9–16
*	1981	*Wocklumeria sphaeroides* Bogoslovskiy: 69, pl. VII, figs 5–6
*?	1981	?*Wocklumeria* sp. Whiteley: 189
*	1982	*Wocklumeria sphaeroides* Bartzsch & Weyer: 33
	1982	*Wocklumeria sphaeroides* Paproth & Streel: 40, 45, text-fig. 17, tab. 6
	1983	*Wocklumeria sphaeroides* Simakov et al.: tab. 2
	1984	*Wocklumeria sphaeroides* Korn in Clausen & Leuteritz: 50
*v	1984	*Wocklumeria sphaeroides* Becker et al.: 189
v	1985	*Wocklumeria sphaeroides* Becker: 33
?*	1985	*Wocklumeria* sp. Gong et al.: 11
*v	1986	*Wocklumeria sphaeroides* Paproth et al.: 4, fig. 19
	1986	*Wocklumeria sphaeroides* Bartzsch & Weyer: 149, pl. II, fig. 7
*	1987	*Wocklumeria* sp. Yu et al.: pl. 1, figs 5–6
?*	1988	*Wocklumeria* sp. Flajs & Feist: 55, text-fig. 5
*v	1988	*Wocklumeria sphaeroides* Becker: 198, 199, text-fig. 3, pl. 1, figs 5–6
*	1988	*Wocklumeria sphaeroides* Korn: 215, text-fig. 1
	1988	*Wocklumeria sphaeroides* Ruan: 256, pl. 65, fig. 2a, b
*	1989	*Wocklumeria sphaeroides* Czarnocki: 26, 28, 30, 39, pl. IX, figs 11–12, 14, pl. X, figs 4–8, 12–17, pl. XLI, fig. 8, pl. XLII, figs 2–6
	1989a	*Wocklumeria sphaeroides* Clausen et al.: 358, fig. 3
	1989b	*Wocklumeria sphaeroides* Clausen et al.: 175
?	1991	*Wocklumeria* sp. Paproth et al.: fig. 6
*	1991	*Wocklumeria sphaeroides* Korn: 557, fig. 2
*v	1993	*Wocklumeria sphaeroides* Becker et al.: 23, 31, 38, 50, 55, text-figs 18, 24, 46
*	1993	*Wocklumeria sphaeroides* Korn: 582, 585, figs 3, 5
*?	1993	*Wocklumeria* sp. Korn: fig. 9
*	1994	*Wocklumeria sphaeroides* Luppold et al.: 16–17, 21, 23, 29, 35, ?41
*	1994	*Wocklumeria sphaeroides* Korn et al.: 116, 122–123, text-figs 5–6, 16d, 21
*	1995	*Wocklumeria sphaeroides* Bartzsch et al.: 24
	1995a	*Wocklumeria sphaeroides* Korn: 162, text-fig. 6
*v	1996	*Wocklumeria sphaeroides* Becker: 23, 24, text-figs 2, 3a
*v	1998	*Wocklumeria sphaeroides* Bartzsch et al.: 44, 45, text-figs 3.3–3.4
*	1999	*Wocklumeria sphaeroides* Korn: 153, pl. 3, fig. 3

Types: BGR X4895 (Pl. 5: 1, 2) is selected here as the lectotype of *Wo. sphaeroides.* This median-sized Richter (1848) syntype is tectonically somewhat distorted and does not show sutures but agrees well with his plate IV, figures 113 and 114. A second syntype (BGR X4896) is even stronger distorted but shows a mature single constriction at rather small size (ca. 28 mm dm). Wedekind's types of *Wo. denckmanni* have been lost in the collection of Göttingen University. MB.C.1725 from the Wocklum type locality, leg. by Wedekind and deposited in Berlin, is regarded as another syntype and designated here as lectotype (Pl. 5: 5, 6).

Remarks: Large collections from the Rhenish Massif and from Thuringia give insights into the intraspecific variability of *Wo. sphaeroides.* Selwood (1960) plotted shell parameters (umbilication, relative whorl widths) and found no clear distinction between the three *Wocklumeria* species recognized by Schindewolf (1937). In the present study, Schindewolf's taxa are kept arbitrarily at subspecies level to allow easy characterisation of shell form of specimens. *Wo. sphaeroides aperta* is a rather rare morphotype, and *Wo. sphaeroides plana* is not as abundant as the typical subspecies at German localities. All three forms, however, have identical time ranges within the *sphaeroides* Zone.

Wocklumeriids from North Africa are mostly much smaller-sized than European populations. Originally (Becker 1997b) it was thought that they represent a new micromorphic species or subspecies. The maximum size of wocklumeriids correlates strongly with the size at which the morphological transformation from constricted triangular to normal rotund coiling takes place. Rhenish *Wo. sphaeroides* (all subspecies) frequently reach between 30 and 48 mm dm and specimens may still be constricted at 25 to 28 mm dm (*sphaeroides sphaeroides*: MB.C.1720 and MB.C.2218.1–5, *sphaeroides plana*: MB.C.1721.4 and MB.C.2217.1–5). An inter-

Table 4
Dimensions of some Wocklumeriidae.

species/specimen	dm	uw	wh	ww	uw%	ww%	wh/ww
Synwo. mapesi n.sp.							
holotype MB.C.2706	16.5	2	6.7	10.4	12.1	63	0.64
Kielcensia ingeniens n.sp.							
holotype MB.C.2705	16.3	3	6.6	9.8	18.4	60.1	0.67
holotype MB.C.2705	ca. 13.5	1.5	ca. 6.5	ca. 9	ca. 11	ca. 67	0.72
Wo. sphaeroides sphaeroides							
lectotype X4895	ca. 30	9.2	9.5	17.7	ca. 30	ca. 60	0.54
lectotype *Wo. denckmanni*	34.5	10.4	13.5	ca. 23	30.1	66.7	0.59
Wo. sphaeroides plana							
neotype MB.C.1721.1	ca. 41	15	14	17	ca. 36.5	ca. 41.5	0.82
paratype MB.C.1721.3	37.3	12	12.7	19	32.2	50.9	0.67
Wo. sphaeroides aperta							
neotype MB.C.2220.1	33.8	17	7.2	22.3	50.3	66	0.32
Epiwo. applanata							
MB.C.2701	27.5	0	14	10.4	0	44.1	1.17
MB.C.2229	20	0	11	ca. 8	0	ca. 40	ca. 1.35
MB.C.2221.2	13.6	0	7	6	0	51.5	1.35

mediate morphotype between *sphaeroides sphaeroides* and *sphaeroides plana* from Hasselbachtal (Beds 106–113N, MB.C.3067, Pl. 5: 9, 10) has a last concave constriction as late as at 31 mm dm. At Oberrödinghausen, *Wo. sphaeroides* from the lower part (Beds 5 to 3) of UD VI-D reach only 30 to 33 mm dm; bigger specimens were exclusively collected from Beds 1 and 2. This suggests a morphological gradient in time, a hypermorphic trend within the zone, caused by the addition of whorls during median (triangular) ontogenetic stages. Uniform facies conditions speak against an alternative interpretation as ecophenotypical change. Since the species is much more abundant towards the top of its zone (peak abundance in the *applanata* Subzone: more than 650 specimens in the Berlin collection), the lack of large morphotypes at older levels may perhaps be based on a sampling artefact. However, Hasselbachtal collections gave a similar size trend with specimens bigger than 37 mm dm found (so far) first in Bed Ha 103bN (MB.C.2703). Other large-sized *Wo. sphaeroides* have been found at the top of the Wocklum Limestone at Oese (MB.C.2724 = Oc 1705), Drewer (MB.C.1683, 1748: 45 mm dm) and at Borkewehr (MB.C.2227.1: 47 mm dm).

The smallest fully rotund (last whorl unconstricted and not subtriangular) *Wo. sphaeroides sphaeroides* from the Rhenish Massif are between 21.5 (MB.C.1718.2) and 24 mm in diameter (MB.C.2219.1) and come from Bed 1 at Oberrödinghausen. Such morphotypes are rather rare. There is an even smaller rotund *Wo. sphaeroides plana* (MB.C.2215.1: at 20 mm dm) from the same bed. Similar forms have not yet been found in the lower part of the *sphaeroides* Zone, neither at Oberrödinghausen, nor at Hasselbachtal. Therefore, it seems that there was a heterochronic trend towards a size dimorphism in the species which, as in *Kielcensia*, could be expressed taxonomically.

A large Thuringian population from around Fischersdorf does not show the Rhenish pattern. Large morphotypes of *Wo. sphaeroides sphaeroides* are much rarer (BGR Z568: 45 mm dm, Z584: 40 mm dm) but there are more early rotund specimens such as BD 523 with only 12.5 mm dm. Another early rotund specimen (Z7559) is illustrated on Plate 5 (Figs 7 and 8). The lectotype (Pl. 5: 1, 2) with ca. 30 mm dm is rather typical fore the Saalfeld area. Small normally coiled *sphaeroides plana* occur as well (BGR Z673.2: ca. 21 mm). At Fezzou and Lambidia in the Maïder, triangular coiling may disappear both in *Wo. sphaeroides sphaeroides* (MB.C.3066) and in *sphaeroides plana* (MB.C.2707, Pl. 5: 17, 18; MB.C.2708) before 15 mm dm. The largest adults (MB.C.3064.1–2) of the region reach ca. 30 mm dm. Petter (1960) illustrated from Southern Algeria both small, early rotund *sphaeroides plana* and larger (max. 35 mm dm) *sphaeroides sphaeroides*. This shows that normal-sized wocklumeriids did spread to North Africa but very large-sized morphotypes (> 40 mm dm) are not yet documented.

A very large specimen (49 mm dm) showing the typical terminal umbilical widening and single mature apertural constriction was illustrated by Selwood (1960) from Cornwall. Small-sized morphotypes, by contrast, have not been mentioned. From the Urals only normal-sized (up to 35 mm dm) *Wo. sphaeroides* have been described so far (Bogoslovskiy 1981). Czarnocki (1989) illustrated from Poland normal to moderately large-sized (max. 40 mm dm) material. From Guizhou, only juvenile and triangularly coiled *Wo. sphaeroides* have been described so far (Sun & Shen 1965, Ruan 1981). As mentioned above, this leaves the possibility that they belong to a synwocklumeriid ancestor. From Guangxi (Ruan 1988) there is only a poorly preserved specimen.

In summary, Selwood's (1960) observation of extreme intraspecific shell variability is fully confirmed. Small early rotund, normal-sized and very large (late triangular) morphotypes, however, show distinctive differences in stratigraphical and spatial distribution. This indicates continuing heterochronic developments but intermediates (mostly from Thuringia) suggest that speciation had not been completed before the abrupt global extinction at the peak of distribution, caused by the sudden anxoxic pulse of the global Hangenberg Event (Fig. 12).

Stratigraphical range: *Wo. sphaeroides* to *Epiwo. applanata* Subzones (UD VI-D$_1$ to VI-D$_2$).

***Wocklumeria sphaeroides plana* Schindewolf, 1937**

Pl. 5: 13–18

*v	1932	*Wocklumeria sphaeroides* Paeckelmann: 96 [fide Becker 1997]
*+v	1937	*Wocklumeria plana* Schindewolf: 70–71, pl. 2, figs 4–6
*	1954	*Wocklumeria plana* Pfeiffer: 58, pl. VIII, fig. 7
*	1954	*Wocklumeria plana* Petter: 12. 1960 *Wocklumeria plana* Petter: 20, text-fig. 2F, pl. II, figs 6, 9, 11–13
*	1960	*Wocklumeria plana* Müller: text-fig. 201A.a
*e.p.	1960	*Wocklumeria sphaeroides* Selwood: 159–161
*?e.p.	1963	cf. *Wocklumeria* sp. Hollard: tab. 1
?e.p.	1967	*Wocklumeria*? sp. Hollard: 924
*	1979	*Wocklumeria plana* Clausen et al.: 59
*	1980	*Wocklumeria plana* Bartzsch & Weyer: 37
* e.p.	1980	*Wocklumeria sphaeroides* Bartzsch & Weyer: fig. 2a, b
*	1984	*Wocklumeria plana* Korn in Clausen & Leuteritz: 50
*v	1986	*Wocklumeria plana* Paproth et al.: 4
	1986	*Wocklumeria plana* Bartzsch & Weyer: 149
	1989b	*Wocklumeria plana* Clausen et al.: 175
v	1993	*Wocklumeria plana* Becker et al.: 31, text-fig. 19
*v	1996	*Wocklumeria sphaeroides plana* Becker: 24, text-fig. 3b
v	1997	*Wocklumeria sphaeroides plana* Becker: 33–34

Type: Schindewolf's holotype has been lost. A moderately preserved large (max. dm > 40 mm) paratype from Bed 1 of Oberrödinghausen (MB.C.1721.1, Pl. 5: 13–14) which shows sutures is here designated as neotype.

Remarks: As outlined above, *Wo. plana* probably represents only an intraspecific morphological variant of *sphaeroides*. This is supported by very similar stratigraphical and spatial distribution as well as by identical patterns of size distributions. BGR Z581 (Bartzsch Collection) is an exceptional specimen with four rather than three constrictions on the last whorl. MB.C.2707 (Pl. 5: 17–18) from Fezzou shows a mature shallow constriction already at 20 mm dm. The largest specimen with 48 mm dm is MB.C.2216.1 from Oberrödinghausen (Bed 1).

***Wocklumeria sphaeroides aperta* Schindewolf, 1937**

Pl. 5: 11, 12

*+	1937	*Wocklumeria aperta* Schindewolf: 71–72, text-fig. 14, pl. 2, figs 7–9
	1950	*Wocklumeria aperta* Schindewolf: 262, text-fig. 226e
*	1954	*Wocklumeria aperta* Petter: 12
e.p.	1960	*Wocklumeria sphaeroides* Selwood: 159–161
*	1980	*Wocklumeria aperta* Bartzsch & Weyer: 37
	1982	*Wocklumeria aperta* Bartzsch & Weyer: fig. 12
*	1989	*Wocklumeria aperta* Czarnocki: 39–40, pl. IX, fig. 15, pl. X, fig. 11
*	1993	*Wocklumeria aperta* Becker et al.: 38
*	1996	*Wocklumeria sphaeroides aperta* Becker: 23, 24

Type: Schindewolf's holotype and all other figured specimens have been lost. Four preserved paratypes are all rather poorly preserved and the most typical fragmentary specimen, neotype MB.C.2220.1, is not suitable for photographic illustration. The characteristic dimensions are given in Table 4.

Remarks: *Wo sphaeroides aperta* is rather rare and is not yet known as micromorphic morphotype. Petter (1954) mentioned the form from Algeria but did not describe it subsequently (Petter 1960). Selwood (1960) found in his Cornwall population intermediates but no specimens that fully fit the definition of the subspecies.

Stratigraphical range: *Sphaeroides* Subzone (Hasselbachtal, ?Oberrödinghausen) to *applanata* Subzone (e.g., Oberrödinghausen, Oese).

Epiwocklumeria applanata (Wedekind, 1918)

Fig. 9, Pl. 4: 13–16

*+	1918	*Wocklumeria paradoxa* var. *applanata* Wedekind: 173, pl. 19, fig. 15.
*	1929	*Wocklumeria applanata* Lange: 30
*	1937	*Epiwocklumeria applanata* Schindewolf: 73, text-fig. 13, pl. 2, figs 10–12
	1960	*Epiwoclumeria applanata* Müller: 148, text-fig. 199i–k
*	1989	*Epiwocklumeria applanata* Czarnocki: 28, 40, pl. X, figs 1–3, 9–10; pl. XLV, fig. 5

Type: The holotype (monotype) of Wedekind (1918) from Wocklum has been lost in the collection at Göttingen. Currently, there is no trace of topotypes collected later by Lange (1929). The new Hasselbachtal specimen (MB.C.2701, Pl. 4: 15–16) showing the suture is the best currently available German representative of the species and genus and a potential neotype. MB.C.2221.1 is the original to Schindewolf's (1937) text-figure 13 and displays inner sutures.

Description: In every aspect the new Hasselbachtal and Drewer (MB.C.2229, Pl. 4: 13–14) specimens conform with those figured by Wedekind, Schindewolf and Czarnocki. It seems that there was little intraspecific variation in the compressed whorl form and in the course of the suture. This proves that large intraspecific conch variability does not apply to all advanced Wocklumeriaceae.

Stratigraphical range: Latest Wocklumian, *Epiwo. applanata* Subzone (UD VI-D$_2$).

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Plate 1. **1–2**, *Platyclymenia (Varioclymenia) pompeckji* Wedekind, MB.C.1729, Nie Brickwork Quarry, NE section, lower part of UD III-C, lateral and adoral views, showing straight ribbing and the typical flat venter, × 1.5. **3–4**, *Platyclymenia (Varioclymenia) pompeckji* Wedekind, MB.C.1730, topotype, Enkeberg, UD III-C, leg. RTB in 1985, lateral and adoral views, specimen showing the mature reduction and change in ribbing as well as a strange trumpet-like terminal apertural widening with coarse growth ornament, × 1. **5–6**, *Platyclymenia* (*Varioclymenia*) *brevicostata* (Münster), MB.C.1735, Enkeberg, Bed 9, leg. Paeckelmann in 1925 (det. *Platy.* cf. *pompeckji*), UD III-C, lateral and adoral views, showing straight ribbing and the convex venter, × 2. **7**, *Platyclymenia* (*Varioclymenia*) *humilis* Schindewolf, MB.C.1736 (see Becker 1985: fig. 3a), Nie Brickwork Quarry, old, now burried section, Bed 9, middle part of UD III-C, lateral view, showing concave ribbing similar as in *Soliclymenia*, × 3. **8–9**, *Pleuroclymenia kasachstanica* (Kind), MB.C.1731, purchased topotype (perhaps even a syntype), western Mugodzhar Mts, UD III-C, lateral and adoral views, showing the early loss of ribs and a typical ventral mould constriction, × 1.5. **10–12**, *Pleuroclymenia costata* (Lange), MB.C.1266, Kirschhofen near Weilburg, topotype of *Pleuro. crassissima* Schindewolf, UD IV-A, lateral view, × 2.5, showing rursiradiate ribbing; ventral view, × 2.5, showing ventral termination of ribs and mould constrictions; adoral view after removal of the last half whorl, × 3. **13–14**, *Pleuroclymenia costata* (Lange), MB.C.1806.1, small fragmentary specimen from the Hauern near Braunau, Kellerwald, leg. Schindewolf in 1931, UD IV-A, lateral and ventral views, showing details of the ornament, × 3

Plate 2. **1–2**, *Pleuroclymenia mutabilis* (Czarnocki), MB.C.1807.2, Hauern near Braunau, UD IV-A, leg. Schindewolf in 1931, lateral and ventral views, showing the gradual disappearance of ribbing and ventral ornament with a shallow sinus of growth lines, × 2.5. **3–4**, *Pleuroclymenia cyclocostata* (Czarnocki), MB.C.1732, large specimen, Nie Brickwork Quarry, old section (Becker 1985), Bed 14, top part of UD III-C, lateral and adoral views, × 1.5. **5–6**, *Hexaclymenia hexagona* (Wedekind), MB.C.1805.1, topotype, Enkeberg, leg. Lotz & Denckmann, UD III-C, lateral and ventral views, showing growth ornament and the typical whorl form. **7–8**, *Progonioclymenia aegoceras* (Frech), MB.C.3068.1, Ense near Wildungen, Kellerwald, leg. Denckmann in 1893, UD V, lateral and ventral views, showing the strong and straight ribbing of mature whorls, × 1.5. **9–10**, *Progonioclymenia aegoceras* (Frech), MB.C.3063.1, Hauern near Wildungen, Kellerwald, leg. Denckmann in 1897, UD V, lateral and oblique view, showing the marginal rim terminating straight ribs (the lack of ornament of inner whorls is based on erosion), × 3.5. **11–12**, *Glatziella tricincta* Schindewolf, BGR Spandau, X5673, holotype (see Schindewolf 1937: pl. 3, fig. 1a, b), Quarry at Ebersdorf (now Dzikowiec), UD VI-B, lateral and ventral views, showing strong ribbing and the marginal double furrow, × 4. **13–14**, *Glatziella minervae* (Renz), MB.C.2202.1, fragmentary specimen, Oberrödinghausen Railway Cut, Bed 10 (see Schindewolf 1937: 17), UD VI-C$_1$, lateral view, showing strong flank ribs and deep spiral furrows, × 4; ventral views, showing concave ribs terminating at the furrows and the very broad, keeled venter, × 3. **15–16**, *Glatziella diensti* Renz, BGR Spandau X6575, holotype (see Schindewolf 1937: pl. 3, fig. 3, text-figs 17, 18), cut at median plane, Quarry at Ebersdorf (now Dzikowiec), UD VI-B, lateral and ventral views, resembling *Glat. minervae*, but venter not as broad

Plate 3. **1–2**, *'Clymenia' nana* Münster, MB.C. 3062, Jebel Aguelmous at Lambidia (Loc. 123), Maïder, leg. V. Ebbighausen, UD V-A, lateral and ventral views, showing extremely evolute and smooth coiling and marked ventral constrictions, × 3. **3–4**, *Kamptoclymenia endogona* Schindewolf, MB.C.1813.1, neotype, Oberrödinghausen Railway Cut, Bed 7, leg. Schindewolf in 1934, upper part of UD VI-C$_1$, lateral, × 3, and ventral views, × 4. **5–6**, *Kamptoclymenia trigona* Schindewolf, MB.C.1751, neotype, Oberrödinghausen Railway Cut, Bed 8, leg. Schindewolf in 1934, upper part of UD VI-C$_1$, lateral and ventral views, showing the extremely evolute and depressed whorl form, × 4. **7–8**, *Triaclymenia triangularis* Schindewolf, MB.C.1815, the poorly preserved neotype, Oberrödinghausen Railway Cut, Bed 10, leg. Schindewolf in 1934, lower part of UD VI-C$_1$, lateral and ventral views, showing the typical, compressed cross-section, × 2.5. **9–10**, *Parawocklumeria patens* Schindewolf, MB.C.1757, Oberrödinghausen Railway Cut, Bed 7, leg. by Schindewolf in 1933 (see Schindewolf 1937: 16, 94), upper part of UD VI-C$_1$, lateral and ventral views, × 4. **11–12**, *Parawocklumeria patens* Schindewolf, MB.C.2713, original of Müller (1956: pl. 2, fig. 27), Geipel Quarry, Bed 17, Thuringia, UD VI-C$_1$, lateral and adoral views, × 4. **13–14**, *Parawocklumeria ?patens* Schindewolf, MB.C.1769, Oberrödinghausen Railway Cut, Bed 9, see Schindewolf (1937: 16, 94), lower part of UD VI-C$_1$, lateral and ventral views, × 4. **15**, *Triaclymenia triangularis* Schindewolf, MB.C.1817, paratype of Schindewolf (1937: 91), Oberrödinghausen Railway Cut, Bed 9, leg. Schindewolf in 1934, lower part of UD VI-C$_1$, ventral view, showing mature subtriangular cross-section and shallow sinus of growth ornament. **16–17**, *Parawocklumeria distorta* (Tietze), MB.C.1768.3, Oberrödinghausen Railway Cut, Bed 9, leg. Schindewolf in 1930–32 (see Schindewolf 1937: 16, 95), lower part of UD VI-C$_1$, lateral, × 3, and adoral views, × 2, showing shell form that resembles juvenile *Wo. sphaeroides*

Plate 4. **1–2**, *Parawocklumeria paprothae* Korn, MB.C.2714.2, Oberrödinghausen Railway Cut, Bed 1, leg. Schindewolf, UD VI-D$_2$, lateral and adoral views, showing a relative wide umbilicus, × 1.5. **3–4**, *Parawocklumeria paprothae* Korn, GPIG 389-78a, somewhat corroded specimen, syntype of *Parawo. paradoxa* Wedekind (1918: pl. 19, fig. 17), Burg near Wocklum, UD VI-D, lateral view, showing a rather wide umbilicus, and ventral view, × 2. **5–6**, *Parawocklumeria paradoxa*, GPIG 389-100, lectotype, previously unfigured syntype of Wedekind (1918), Burg near Wocklum, UD VI-D, lateral view, showing small rounded umbilicus of internal mould, × 2. **7–8**, *Parawocklumeria paprothae* Korn, MB.C.3061, leg. V. Ebbighausen, Fezzou, Maïder, UD VI-C/D, lateral and adoral views, showing typical sutures with rounded ventral saddle, crowding of last septa despite small size, and a small but markedly triangular umbilical opening, × 5. **9–10**, *Kielcensia ingeniens* n. sp., MB.C.2705, holotype, purchased specimen from the Maïder, UD VI-?D, lateral and ventral views, showing sutures and the rapid opening of the umbilicus during the last preserved whorl, × 3. **11–12**, *Synwocklumeria mapesi* n. sp., MB.C.2706, holotype, purchased specimen from the Maïder, UD VI-?D, lateral and adoral views, showing the small open umbilicus and sutures, × 3. **13–14**, *Epiwocklumeria applanata* (Wedekind), MB.C.2229, Provincial Quarry at Drewer, Section WA, Bed 93, leg. RTB 1998, UD VI-D$_2$, lateral and adoral views, showing typical convex constrictions and compressed cross-section, × 2.5. **15–16**, *Epiwocklumeria applanata* (Wedekind), MB.C.2701, Hasselbachtal, Bed 113aN, leg. RTB 1997, UD VI-D$_2$, lateral and ventral views, × 2

Plate 5. *Wocklumeria sphaeroides* div. ssp. **1–2**, *Wo. sphaeroides sphaeroides* (Richter), BGR Spandau, X4895, lectotype (typical morphotype), original of Richter (1848: 34, pl. 4, figs 113–114), Bohlen near Saalfeld, Thuringia, UD VI-D, lateral and ventral views, showing broad whorl profile and relative small umbilicus, × 1.5. **3–4**, *Wo. sphaeroides sphaeroides* (Richter), MB.C.912, triangular stage of typical morphotype, original of Schindewolf (1937: pl. 2, fig. 1), Oberrödinghausen Railway Cut, Bed 1, leg. Schindewolf in 1926, UD VI-D$_2$, lateral and adoral views, × 2.5. **5–6**, *Wo. sphaeroides sphaeroides* (Richter), MB.C.1725, previously unillustrated syntype and lectotype of *Wo. denckmanni* Wedekind, Burg near Wocklum, UD VI-D, lateral and adoral views, showing broad whorls and moderately wide umbilicus, × 1.5. **7–8**, *Wo. sphaeroides sphaeroides* (Richter), BGR Spandau, Z559, micromorphic and earl rotund morphotype, Fischersdorf W near Saalfeld, Thuringia, leg. K.

Bartzsch, UD VI-D, lateral and ventral views, × 2.5. **9–10**, Intermediate between *Wo. sphaeroides sphaeroides* and *sphaeroides plana*, MB.C.3067, late triangular morphotype, Hasselbachtal, Beds 106-113N, leg. RTB 1999, UD VI-D, lateral and adoral views, × 1.5. **11–12**, *Wo. sphaeroides aperta* Schindewolf, MB.C.1631 (= Oc 1984), original of Becker (1996), Hasselbachtal, Bed 94N, lower part of UD VI-D_1, lateral and adoral views, showing rather wide umbilicus and broad, extremely depressed cross-section, × 1.5. **13–14**, *Wo. sphaeroides plana* Schindewolf, MB.C.1721.1, neotype (syntype of Schindewolf 1937: 15, 70, 71), large-sized morphotype, Oberrödinghausen Railway Cut, Bed 1, UD VI-D_2, lateral and adoral views, showing umbilicus that opens suddenly on the last half whorl, and the rather compressed cross-section, × 1.5. **15–16**, *Wo. sphaeroides plana* Schindewolf, MB.C.2704.1, normal, triangular juvenile, Hasselbachtal, Bed 113aN, lower part of UD VI-D_2, lateral and adoral views, × 2. **17–18**, *Wo. sphaeroides plana* Schindewolf, MB.C.2707, micromorphic, early rotund morphotype, Fezzou, Maïder, leg. RTB in 1985, UD VI-D, lateral and adoral views, × 2

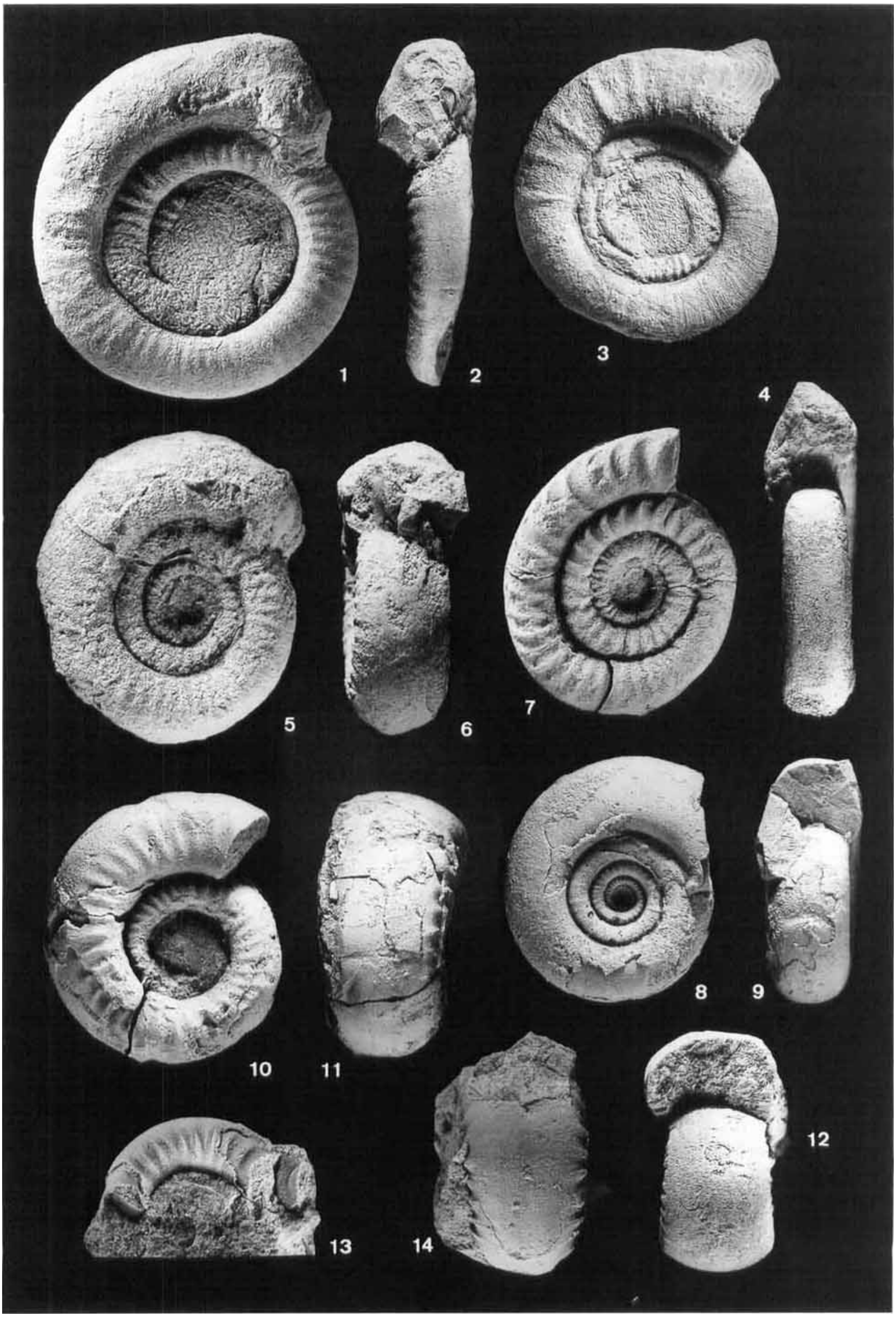


Plate 1

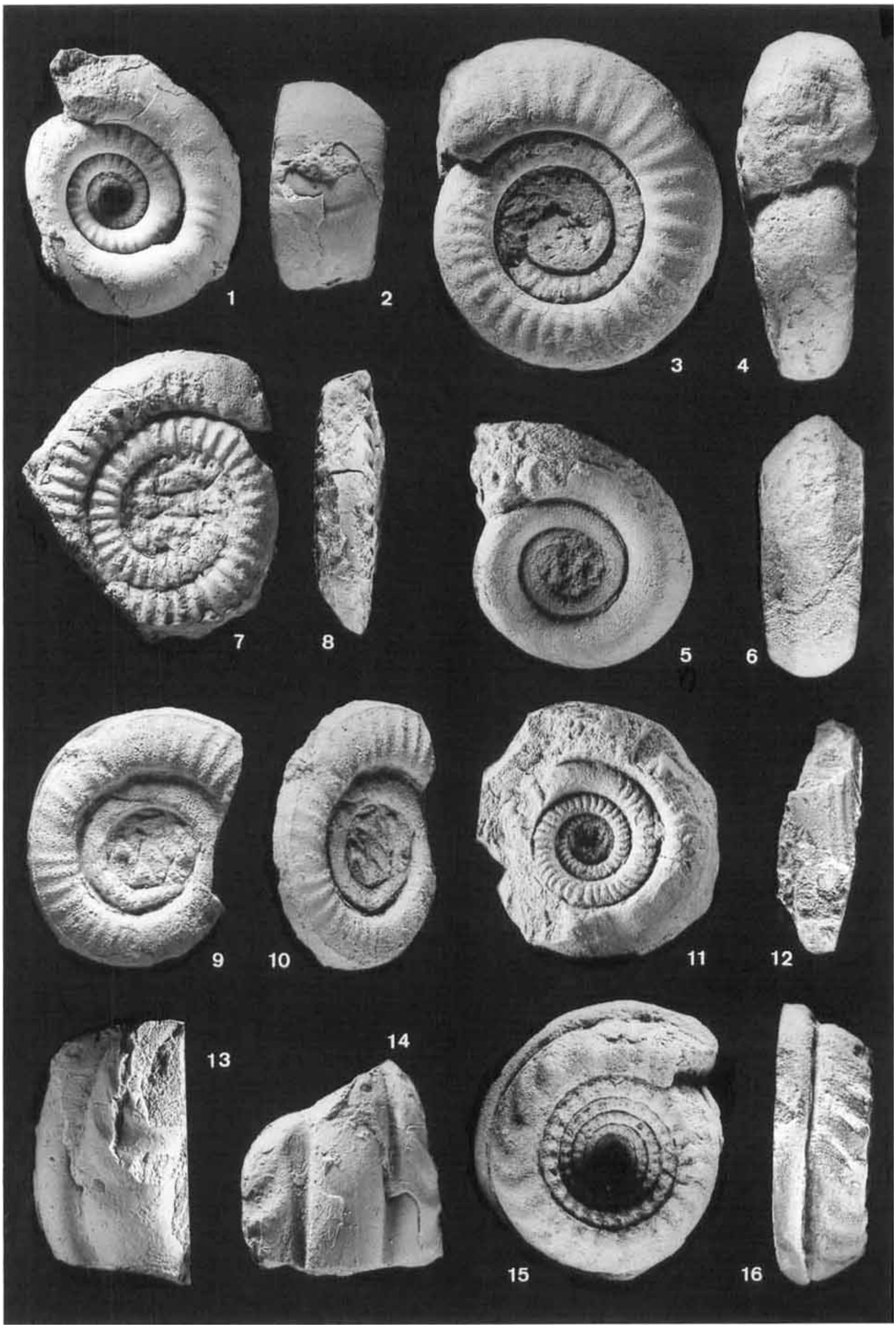
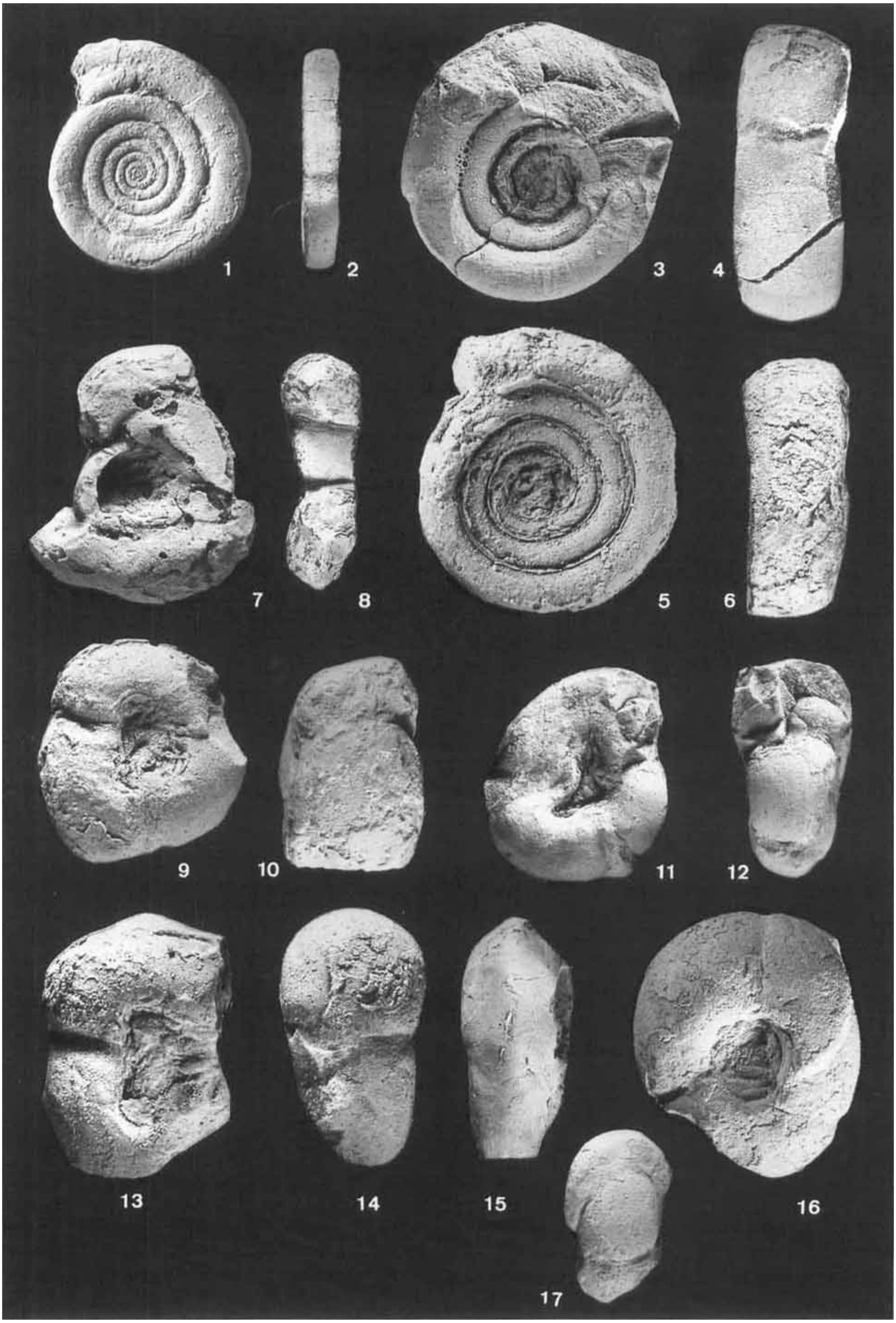


Plate 2



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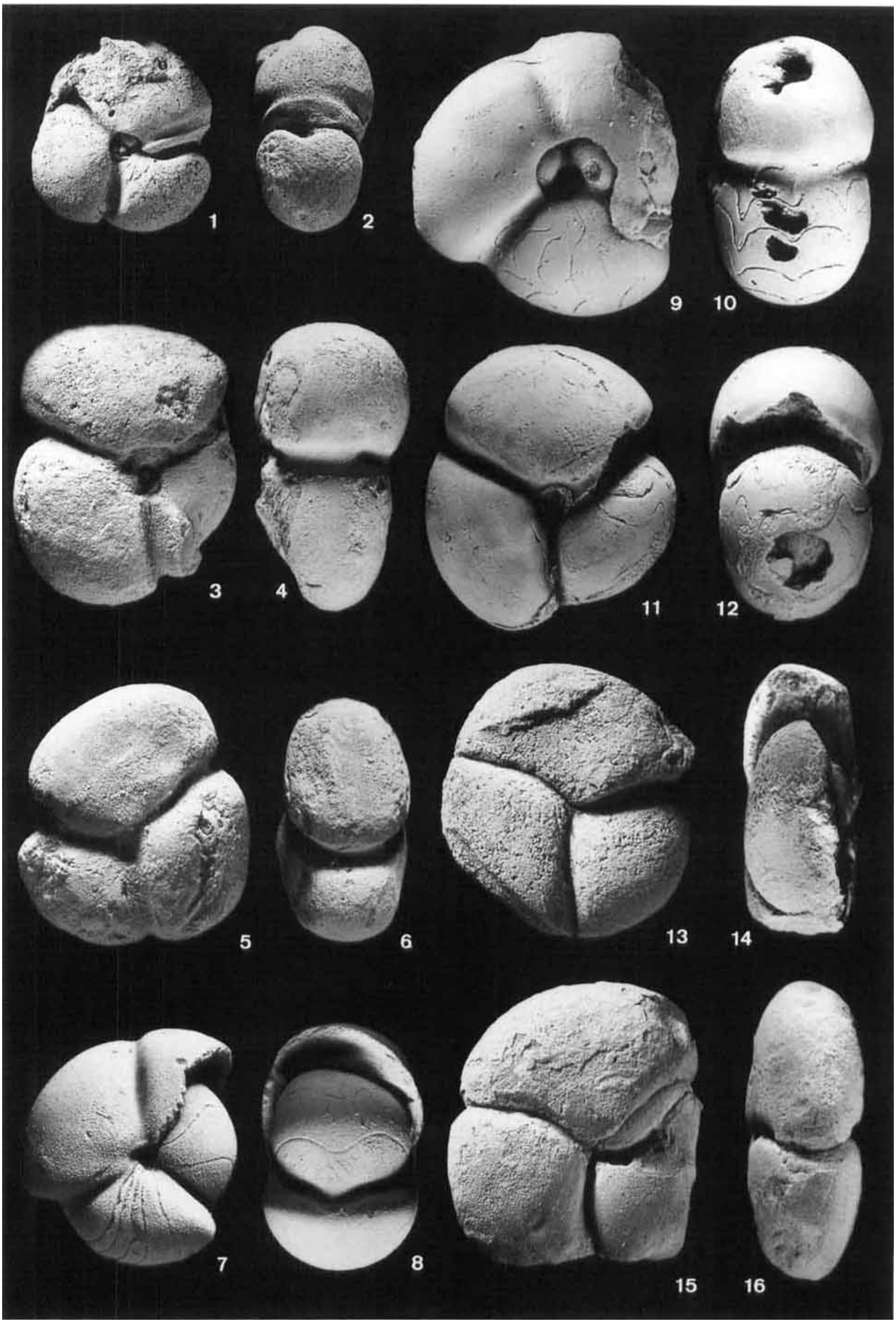

Plate 4

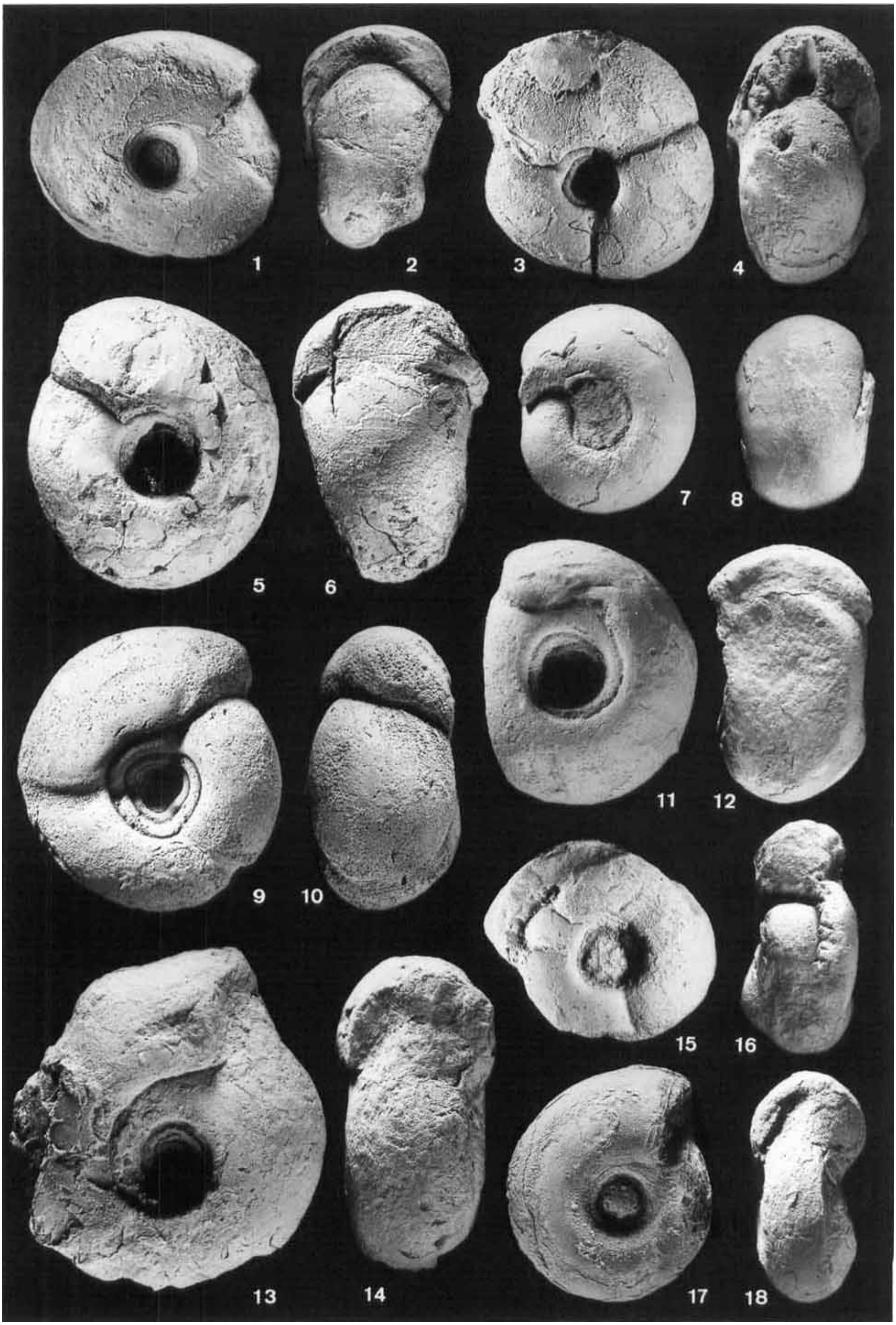

Plate 5