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The late Maastrichtian cancellothyridid brachiopod *Terebratulina chrysalis* (Von Schlotheim, 1813) from the type Maastrichtian (southern Limburg, the Netherlands) and elsewhere in Europe*

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Abstract

A complete growth series of *Terebratulina chrysalis* (Von Schlotheim, 1813) collected from its type area near Maastricht (the Netherlands) is described and illustrated, with fully adult and gerontic specimens included so as to increase current knowledge of this taxon. Most specimens collected from other European outcrops are juveniles which are similar to juveniles from the type area near Maastricht. However, adults collected from the latter area and those from lower Maastrichtian white chalk deposits in northern Europe are quite different. These differences can be explained by palaeoenvironmental conditions and taphonomic processes.

Keywords: Brachiopoda, Cancellothyridoidea, *Terebratulina*, Cretaceous, Europe, intraspecific variability

Introduction

In 1802-1804(?), Faujas de Saint-Fond illustrated a cancellothyridid brachiopod (pl. 26, fig. 9) collected from the St Pietersberg area, south of Maastricht, although he did not propose any name for it. He compared this specimen to a species represented in 'fig. 6a, b and c, planche 241 de l'Encyclopédie' (= 'Encyclopédie ou Dictionnaire Raisonné des Sciences, des Arts et des Métiers of Diderot & d'Alembert', published between 1751 and 1765, with eleven volumes of plates published between 1762 and 1772). Faujas's original figures are reproduced herein (see Fig. 1). In view of the fact that Faujas did not follow Linnaean binomial nomenclature, Von Schlotheim (1813, p. 113) later erected the species *Terebratulites chrysalis*, referring to both of Faujas's illustrations (i.e., pl. 26, figs 7 and 9), despite the fact that these illustrations clearly represent very different and distinctive brachiopods. The genus *Terebratulina* was erected in 1847 by d'Orbigny, who unfortunately confused *Terebratulina chrysalis* with *T. striata* Wahlenberg, 1821, a Campanian species from southern Sweden. Further confusion was added later by Davidson (1852), who synonymised *Terebratulina chrysalis* with *Terebratulina striata*, *T. striatula* (Mantell, 1822) and *T. defrancii* (Brongniart, 1822).

However, Von Buch (1835) restricted the name *'Terebratula chrysalis'* to Faujas's pl. 26, fig. 9, and this point of view was followed by Roemer (1841, p. 40, no. 22) and by Von Hagenow (1842, p. 538, no. 9). Wind (1953, p. 79) designated 'lectotype' the specimen illustrated in Faujas's pl. 26, fig. 9,while Steinich (1965, pp. 53, 66) presented this figure as the original illustration for *T. chrysalis*. Simon (2007) demonstrated that the specimen illustrated in Faujas's pl. 26, fig. 7 was not a *T. chrysalis*, but a representative of the genus *Gisilina* Steinich, 1963, for which he introduced the name, *G. souparti*.

Since 1813, *T. chrysalis* has been one of the most widely cited Maastrichtian brachiopod in the literature. Steinich (1965, p. 53) presented an exhaustive list of synonyms with a critical analysis which resolved most of the existing confusion between the various species of *Terebratulina* from the chalk. Simon (1998, p. 200) and Simon (2000, p. 140) completed this synonymy list for works published after 1965. Outside the type area (i.e., the neighbourhood of Maastricht), this cancellothyridid has been recognised in many European countries and it constitutes a conspicuous element of the Maastrichtian invertebrate fauna. This is the case in the chalk of Rügen, northeast Germany (Steinich, 1965), in the Aachen area, western Germany (Keutgen,

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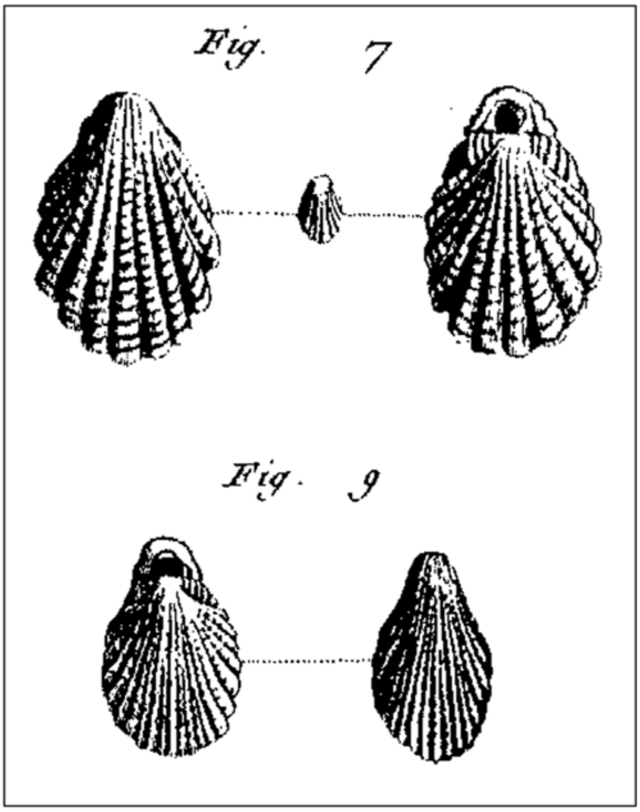

Fig. 1. Reproduction of Faujas's figures 7 and 9 in plate 26 of the Histoire Naturelle de la Montagne Saint-Pierre de Maestricht, *fig. 9 being the original reference to* Terebratulina chrysalis *(Von Schlotheim, 1813). The specimen illustrated in fig. 7 is not* T. chrysalis *but belongs to* Gisilina souparti *Simon, 2007.*

1996) and in Maastrichtian deposits of Denmark (Surlyk, 1972, 1982, 1984; Johansen, 1987, 1989a, b). *Terebratulina chrysalis* has also been recorded from Norfolk, southeast England (Johansen & Surlyk, 1990), southern Belgium (Simon, 1998), Poland (Popiel-Barczyk, 1968; Bitner & Pisera, 1979) and Russia (Katz, 1974). Late Campanian examples of *T. chrysalis* have described by Simon (2000) from the Chalk of Trivières at Cuesmes, province of Hainaut (southern Belgium). This material might well represent the oldest occurrence of the species.

Although there are numerous descriptions and illustrations of *T. chrysalis* from various European localities, material from the type area so far illustrated is only that by Faujas (1802-1804?, pl. 26, fig. 9). Obviously, this unique shell is neither a fully adult specimen nor an early juvenile (see Fig. 1). A poor illustration such as this one precludes proper assessment of specific morphological variation as well as comparisons with other European material. The complete developmental cycle of the species is poorly known, because the fully adult growth stages, commonly found in the type area, have not been illustrated previously. Here, for the first time, specimens collected from the Meerssen Member in the Maastricht area are described; these illustrate a complete growth series.

To a very wide European distribution, this species adds an astonishing ability to colonise different types of habitats. The material from the type area is from coarse-grained, highly fossiliferous, late Maastrichtian biocalcarenites (Meerssen Member) with rich (sub)tropical faunas typical of the euphotic zone (Jagt, 1999). This shallow environment with a relatively high hydrodynamic regime was under the influence of waves and storms. On the other hand, the material from Rügen studied by Steinich (1965) originates from a white chalk ooze typical of a deeper and quieter setting. If the material collected at both localities belongs to a single taxon, i.e. *T. chrysalis*, the different environmental responses illustrated by the morphology of this brachiopod are important. That is why such are highlighted in the present study. Material collected from the type area is compared to specimens from the white chalk in Rügen, as well as with material from the Kunrade Limestone facies (Maastricht Formation), which offer an opportunity to study a different late Maastrichtian population. This helps to understand the clear differences observed between adults from various lithologies.

Material and methods

Fossils collected by Faujas and his assistants were sent to Paris where they are preserved at the Muséum national d'Histoire naturelle. Part of the vertebrate collection is on display. However, the invertebrate collections appear largely to have been lost (J.-M. Pacaud, pers. comm., 2004). For this reason, Faujas's originals and the 'lectotype' designated by Wind (1953, p. 79) in particular was not available for the present study. However, as pointed out by Simon (2007, p. 132), illustrations of plate 26 were drawn with precision.

Faujas's material stems from part of the St Pietersberg near Maastricht which has now been excavated at the ENCI-Heidelberg Cement Group quarry; it was collected from subterranean galleries in which only the Nekum Member and the lower portion of the overlying Meerssen Member (Maastricht Formation; upper Maastrichtian) were accessible. For a detailed discussion of lithostratigraphic units, facies interpretation and biozonation, reference is made to Jagt (1999, pp. 27-31), who also provided a map of the various quarries in southern Limburg (the Netherlands). The former Blom quarry (Berg en Terblijt, east of Maastricht), indicated in that map, is of particular importance. Collections held at the Natuurhistorisch Museum Maastricht (NHMM), contain numerous samples from the Meerssen Member with specimens of *T. chrysalis*. A lot in the L. Blezer Collection (NHMM BL 0357), from the former Blom quarry (Meerssen Member, subunit IV f-4) comprises 150 individuals of *T. chrysalis*, documenting all growth stages from early juveniles to very large adult and gerontic specimens. Another sample in the same collection (NHMM BL 039) offered twenty-two specimens of large, adult *T. chrysalis*. From this collection some specimens, in a perfect state of preservation, are illustrated here. Several

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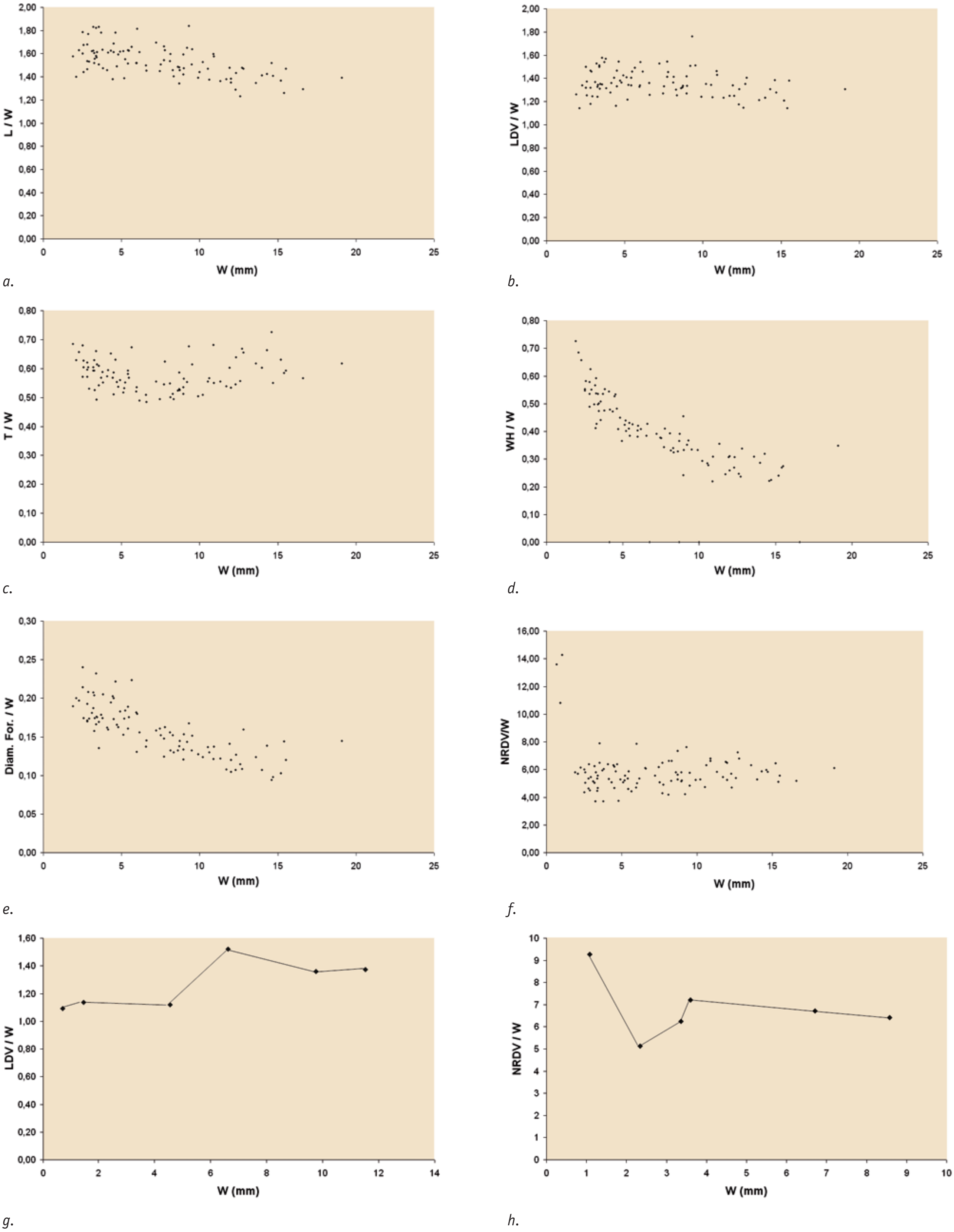

Fig. 2. Scatter diagram for Terebratulina chrysalis *(Von Schlotheim, 1813) from the Meerssen Member (Maastricht Formation, late Maastrichtian) at the former Blom quarry, Berg en Terblijt (southern Limburg, the Netherlands). L: length (mm); W: width (mm); LDV: length of dorsal valve (mm); T: thickness (mm); WH: length of hinge line (mm); Diam. For.: diameter of foramen (mm); NRDV: number of costae on dorsal valve. Relationships between a. ratios L/W and width; b. LDV/W and width; c. T/W and width; d. WH/W and width; e. Diam. For/W and width; f. NRDV/W and width; g. Relationships between ratio LDV/W and width observed in one specimen during growth; h. Relationships between ratio NRDV/W and width observed in one specimen during growth.*

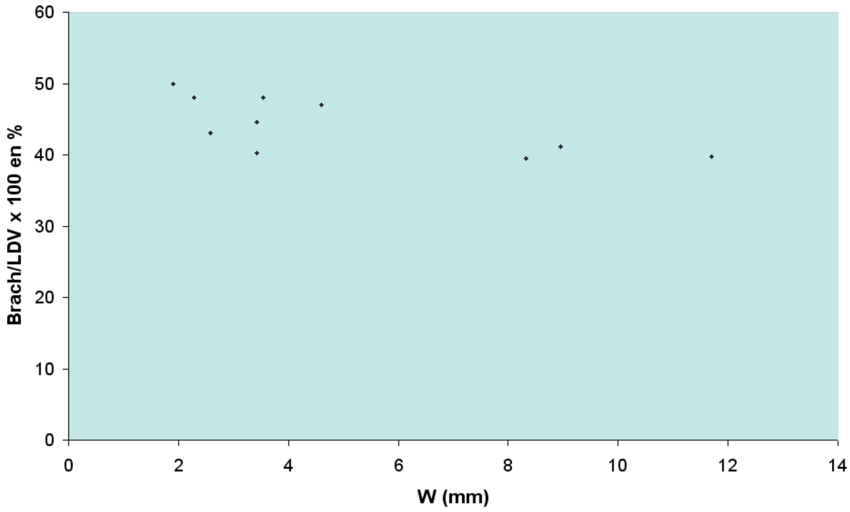

Fig. 3. Scatter diagram for Terebratulina chrysalis *(Von Schlotheim, 1813) from the Meerssen Member (Maastricht Formation, late Maastrichtian) at the former Blom quarry, Berg en Terblijt (southern Limburg, the Netherlands). Relationships between the relative length of the brachidium (length of the brachidium/length of the dorsal valve x100 in %) and the width of the shell (W in mm).*

ultra-juvenile specimens are known from the Meerssen Member at the ENCI-HeidelbergCement Group quarry; these document the earliest growth stages. In view of the fact that this material is similar to the specimen available to Faujas , it is here used for the description of specimens from the type area of the taxon.

For comparison, 147 specimens of *T. chrysalis* in the H. Senden Collection, from the Kunrade Limestone facies in the Kunrade area (southern Limburg, the Netherlands), have also been studied. This material, deposited at NHMM, provides another complete population, including all age classes. The Kunrade Limestone facies is considered to be of late Maastrichtian age (Kennedy, 1987, p. 159) and Felder & Bless (1989) confirmed the presence of the key index belemnitellid coleoid *Belemnitella junior* Nowak, 1913. The specimens of *T. chrysalis* studied in the present note probably represent ecozone V as proposed by Felder & Bless (1989), which would match the base of the Emael Member in the Maastricht area (Jagt, 1999, p. 18). An early Maastrichtian specimen of *T. chrysalis* from the white chalk facies in Rügen is also used for comparison.

Specimens used in the present study were cleaned in an ultrasonic bath; small individuals were then studied in SEM, while larger-sized shells were photographed after having been coated with ammonium chloride. Suprafamilial classification follows Williams et al. (1996) and hierarchy within the superfamily Cancellothyridoidea Thomson, 1926 follows Lee et al. (2006, pp. H2145-2151).

Systematic palaeontology

Order Terebratulida Waagen, 1883
Suborder Terebratulidina Waagen, 1883
Superfamily Cancellothyridoidea Thomson, 1926
Family Cancellothyrididae Thomson, 1926
Subfamily Cancellothyridinae Thomson, 1926
Genus Terebratulina *d'Orbigny, 1847*

Type species
Anomia retusa Linnaeus, 1758.

Terebratulina chrysalis *(Von Schlotheim, 1813)*

Figs 1-3, 4A-I, 5A-T, 6A-P, 7A-P, 8A-S, 9A-Z, AA-CC.

Emended diagnosis
Medium-sized, generally ventribiconvex *Terebratulina* with an oval, teardrop to subpentagonal outline with greatest width slightly anterior to mid-shell. Lateral sides of shell rounded. Both valves with numerous costae, increasing by intercalation, carrying knobs, better developed on the posterior part of the ventral valve, less so on the anterior parts of both valves. Interspaces very fine. Anterior commissure rectimarginate in juveniles, becoming uniplicate in large adults or gerontic specimens. Beak not attrite, short, truncate, suberect with incomplete submesothyrid foramen. Posterior part of beak rounded, not pointed. Beak ridges strong. Interarea very sharply delimited, with strong tuberculation on its ventral sides. Dorsal valve with ears clearly developed, ornamented with parallel, knobbed ridges. Ears relatively large in juveniles reducing in size during growth. Hinge line wide in juveniles becoming much shorter in adult or gerontic specimens. Brachidium made of a complete ring, rather narrow in juveniles but developing into a wider, finer ring with a strongly arched transverse band in adult representatives.

Locus typicus
St Pietersberg subterranean galleries, now excavated at the ENCI-HeidelbergCement Group quarry, Maastricht, southern Limburg, the Netherlands.

Stratum typicum
Lower portion of the Meerssen Member (Maastricht Formation, late Maastrichtian; *Belemnitella junior* and *Belemnella* (*Neobelemnella*) *kazimirovensis* coleoid zones).

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Description

External characters

The adult shell is oval-subpentagonal in outline (Fig. 5A-D), with its maximum width situated just at mid-length (Fig. 5A) or just anterior to mid-length (Fig. 5B-D). This outline is also seen in juveniles with a width of 2 mm. However, juveniles are more oval and early juveniles have a more subtriangular outline (Fig. 4A).

The length/width (L/W) and length of dorsal valve/width (LDV/W) ratios vary during growth (Figs 2, 3), increasing rapidly to a value between 1.4 and 1.8 for a shell width around 5 mm and then they decrease regularly until the adult stage of growth. This means that the length of the shell increases rapidly during early ontogeny. Later, the process of shell development is reversed and shell width increases more rapidly than the length until the adult stage of growth.

The shell is relatively thick with a thickness/width ratio situated between 0.5 and 0.7 (Fig. 2c). Juveniles are often dorsibiconvex (Fig. 5E, G, I, R-T), sometimes equally convex (Fig. 5F, H). Shell becomes biconvex during growth and large adults can have a ventribiconvex shell (Fig. 5N, O).

The ears are clearly developed on the dorsal valve and they are quite large in juveniles. At young stages of growth the hinge angle is very large allowing a wide development of the ears. The ears are ornamented with parallel ridges each bearing each one or two strong tubercles or knobs. The ears are relatively less expressed in adult shells; they become narrower as the hinge angle decreases during growth (Fig. 5A-D).

The anterior commissure is rectimarginate in juveniles and during young stages of growth (Fig. 5R-T). Adult shells exhibit a uniplicate anterior commissure (Fig. 5P, Q) due to a low sulcus on the anterior part of the ventral valve.

The ornament of the costae is made of strong tubercles or knobs placed along the whole length of the costae in juveniles (Figs 4B, C; 6A, C). The size of these knobs decreases during growth. In young shells the posterior part of the ventral valve is always better preserved and exhibits stronger intact tubercles on the costae. The anterior part of the ventral valve is ornamented with smaller knobs that are often eroded (Fig. 6D, E). Sometimes they are absent in the anterior part of the shell and smooth costae are not rare (Figs 4F; 6C, D). Adults have costae with small knobs but they remain better developed in the umbonal area (Fig. 6F, G).

Costae development starts when the shell reaches a width of 0.5 mm (Fig. 4A). Ten costae are immediately produced at the first stage of growth and this number remains constant until a shell width of around 2 mm is reached (Fig. 4B). At a width of 2.5 mm, the number of costae increases rapidly and regularly until the adult stage of growth. This is illustrated in Fig. 2F. The number of costae on the dorsal valve/width (NRDV/W) ratio is relatively high for juveniles and it falls rapidly. For shells wider than 2.5 mm, the value of this ratio (between 4.0 and 8.0) is more or less constant until adult stage of growth. New costae arise by intercalation. The number of costae is identical for the ventral and dorsal valve in juveniles. However, the number of costae is much higher on the ventral valve in adult representatives. The ratio number of costae on dorsal valve/number of costae on ventral valve ranges between 87/110 and 117/140. As the number of costae increases rapidly during growth, the interspaces between costae become progressively narrower (Fig. 6F, G).

Terebratulina chrysalis is typically a species which exhibits a very large number of costae at the adult stage of growth. Several growth lines are observed. They are not very strong and their number is quite variable.

The hinge line is relatively large in juveniles and the hinge angle is quite wide. During growth, the hinge line becomes reduced and narrower and the hinge angle decreases. The variation of the length of hinge line/width (WH/W) ratio is especially strong during growth (Fig. 2D) and this morphological character is the most influenced by the growth process. This variation is associated with a reduction of the ear surfaces.

The beak is short, suberect and truncate in lateral view. It is not attrite. Beak ridges are sharply constructed in juveniles and young specimens. The foramen is hypothyrid in early juveniles, becoming submesothyrid in juveniles and young specimens (Fig. 5E-J). In adults the beak ridges are still clearly visible but the foramen is mesothyrid (Fig. 5K-O). The beak is pinched as its lateral parts are deeply curved and sharply delimited by the beak ridges and the interarea. In juveniles, these lateral parts are ornamented with two rows of knobs (costellae). The number of knobbed rows increases regularly during growth (Figs 5E-J; 7E, F) and it can reach a value as high as 14 in large adults (Fig. 5L), but this number is quite variable (Fig. 5M) and it is not a reliably distinctive specific character.

The foramen is incomplete, limited by disjunct small triangular deltidial plates. Deltidial plates are small, triangular. They are sharply raised from the interarea and their extremities are then folded horizontally. In dorsal view the foramen is subtriangular in early juveniles but it becomes rapidly subcircular to circular during growth. The diameter of the foramen is relatively larger in juveniles and is progressively reduced during growth as illustrated by the variation of the diameter of foramen/width ratio (Diam. For./W in Fig. 2E). The interarea is extremely limited.

Internal characters

A pedicle collar is developed in the ventral valve. The hinge is not very strong, with relatively low outer and inner socket ridges. Teeth are without denticulum, elongated and pointed and they are placed in shallow sockets.

The cardinal process has a semi-circular outline and is well developed in the dorsal valve (Fig. 8D, H). It consists of a ventrally depressed, thickened structure placed between the posterior parts of the inner socket ridges. The myophore is

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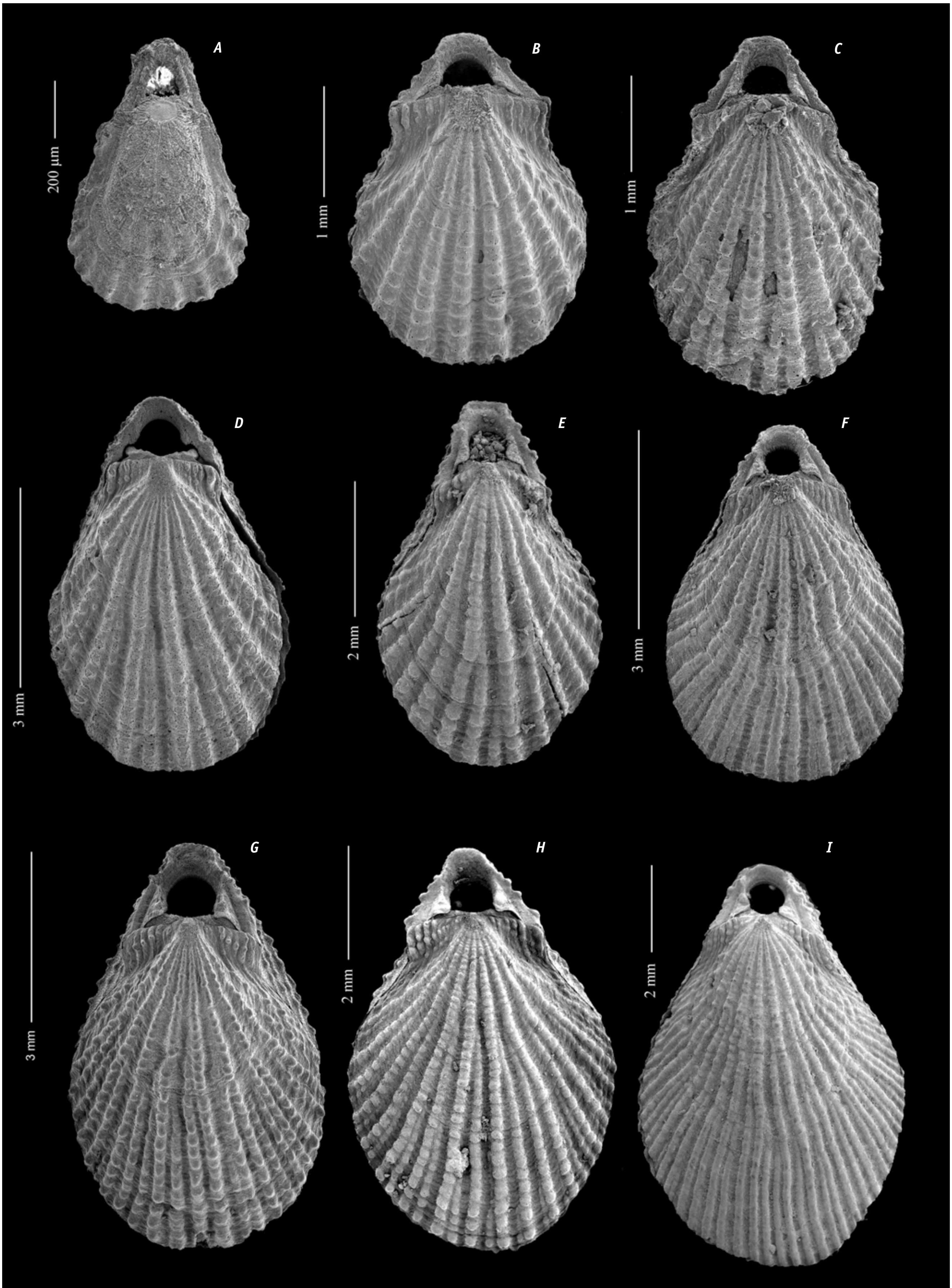

Fig. 4

Fig, 4. Terebratulina chrysalis *(Von Schlotheim, 1813) from the Meerssen Member (Maastricht Formation, late Maastrichtian) at the ENCI-HeidelbergCement Group quarry, Maastricht, southern Limburg, the Netherlands. A – early juvenile specimen (NHMM 2010 031) with a subtriangular outline; primary costae are at the beginning of their formation (width 0.64 mm). B-I – growth series from subunit IVf-4, Meerssen Member, at the former Blom quarry, Berg en Terblijt, southern Limburg, the Netherlands (all in the L. Blezer Collection, NHMM), seen in dorsal view. B – Juvenile specimen (NHMM BL 0357-43) with an elliptical outline; the initial set of primary complete costae is present (width 2.1 mm), C – Juvenile specimen (NHMM BL 0357-55), slightly larger with new intercalated costae (width 2.6 mm); D – Larger juvenile specimen (NHMM BL 0357-45; width 3.5 mm); E – Other juvenile specimen of similar size (NHMM BL 0357-91; width 3.4 mm); F – Young growth stage showing a strong increase in number of costae (NHMM BL 0357-44; width 3.6 mm); G – Larger specimen with strong increase in number of costae (NHMM BL0357-46; width 4.6 mm); H – A slightly larger growth stage (NHMM BL 0357-92; width 6.7 mm); I – The number of costae can be variable; this specimen has a similar size (width 6.6 mm,) but exhibits many more costae (NHMM BL 0357-16).*

strong. The brachidium develops rapidly in juveniles. At a width of 1.9 mm, the crural processes are already fused and the descending branches of the loop are connected by the transverse band. This builds a complete ring which is, at this stage, subtriangular in anterior view (Fig. 7D). There are no outer hinge plates and the crural bases are fused with the inner socket ridges. At a width of 2.3 mm, the ring becomes more subtrapezoidal in anterior view (Fig. 7E) and the transverse band becomes ventrally arched. During growth, the ring appears more tubular in ventral view (Fig. 7I, specimen of 4.3 mm width). Simultaneously, the transverse band becomes more arched (Fig. 7L). Noteworthy is the fact that the relative width of the ring, when seen in anterior view, is variable. This is illustrated in Fig. 7P for a specimen with a width of 4.6 mm. At this stage of growth, the ring is more subrectangular to oval in anterior view. When the adult stage is reached, the tube-like structure of the loop is transformed into a narrower ring and the transverse band is progressively more arched ventrally (Fig. 8A-D, I-K).

The length of the brachidium, compared to the length of the dorsal valve, tends to be reduced during growth (Fig. 3). In early juveniles the length of the brachidium represents 50 per cent of the length of the dorsal valve. In adults or gerontic specimens, it is as short as 38 per cent. As usual in representatives of the genus *Terebratulina*, *T. chrysalis* developed a very strong spicular skeleton which is occasionally well preserved. In some cases even the brachia of the lophophore are preserved in living position. An example is given here in Fig. 7G, H.

Comparison with material from Rügen, northeast Germany

Generally, specimens of *T. chrysalis* illustrated from different European countries are juveniles or very young specimens which match the description of juveniles given here. For instance, this is the case for material illustrated by Katz (1974, pl. 84, fig. 8), Bitner & Pisera (1979, pl. 3, figs 12-15), Johansen (1987, pl. 4, figs 1-3) and Johansen & Surlyk (1990, pl. 3, figs 1, 4, 5). Fully adult specimens are rarely presented. One example is given in Johansen & Surlyk (1990, pl. 3, figs 2, 3).

However, Steinich (1965, pp. 53-66) published a very complete study on 1500 specimens of *T. chrysalis* from the lower Maastrichtian white chalk of Rügen. Most specimens studied were juveniles, but a complete growth series was described and illustrated (Steinich, 1965, pls 8, 9). Steinich based his identification of *T. chrysalis* on the small specimen illustrated in Faujas's pl. 26, fig. 9. Amongst the specimens illustrated by Steinich (1965), a fully adult is presented in pl. 8, fig. 1a-d. This specimen, similar to those presented by Johansen & Surlyk (1990, pl. 3, figs 2, 3), appears quite different from the fully-grown specimens from the type area illustrated here. A comparison between the type material and specimens from other localities is thus called for.

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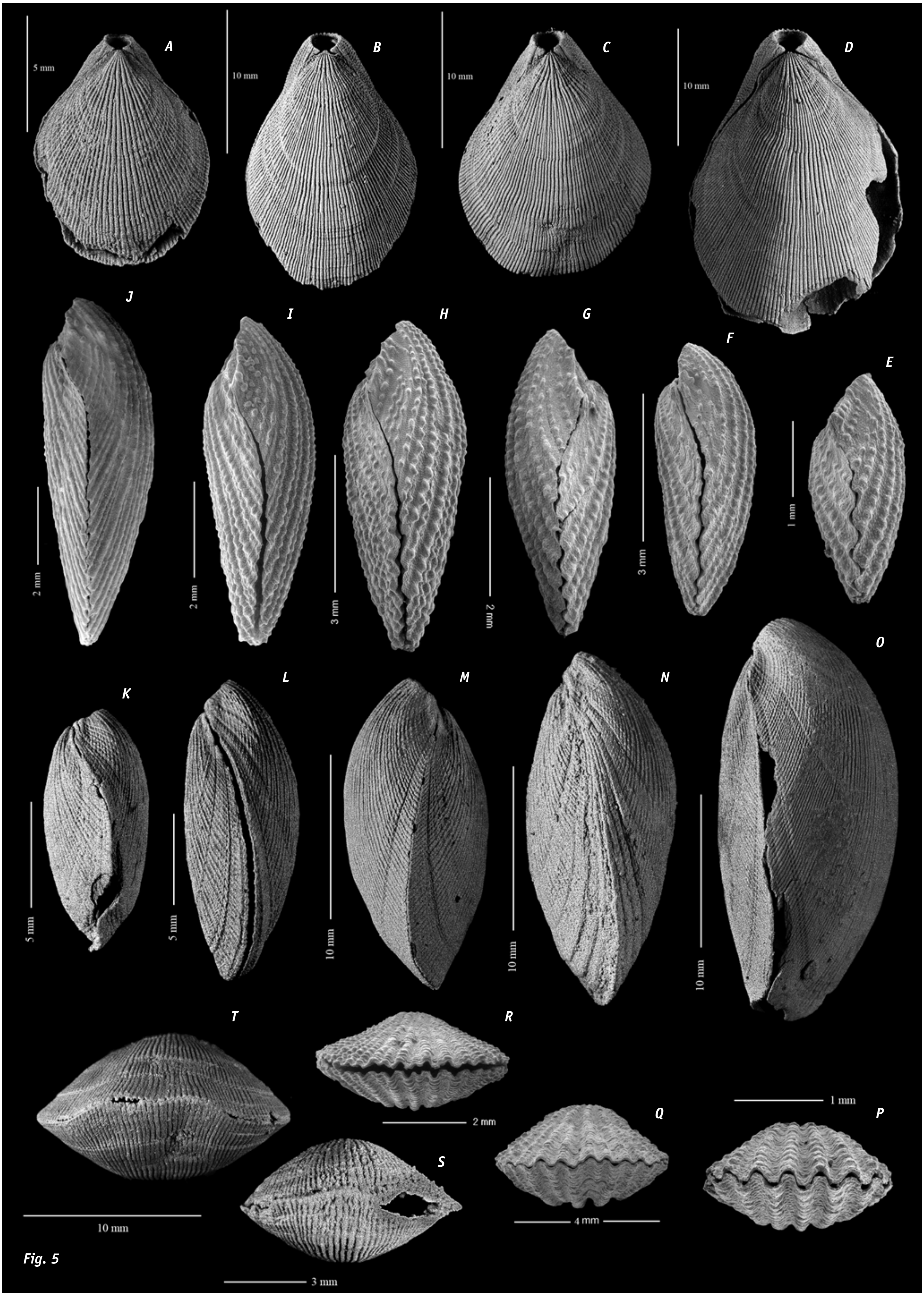

A
5 mm
B
10 mm
C
10 mm
D
10 mm
J
2 mm
I
2 mm
H
3 mm
G
2 mm
F
3 mm
E
1 mm
K
5 mm
L
5 mm
M
10 mm
N
10 mm
O
10 mm
T
10 mm
R
2 mm
S
3 mm
Q
4 mm
P
1 mm

Fig. 5

Fig. 5. Terebratulina chrysalis *(Von Schlotheim, 1813) from subunit IVf-4, Meerssen Member, at the former Blom quarry, Berg en Terblijt, southern Limburg, the Netherlands. All material contained in the L. Blezer Collection (NHMM). A-D – Growth series with all specimens seen in dorsal view; A – Early adult specimen (NHMM BL 039-10), the number of costae on the dorsal valve reaching 98, and the hinge line being relatively reduced (width 8.7 mm); B – Adult specimen (NHMM BL 039-04; width 12.9 mm); C – Larger fully adult specimen (NHMM BL 039-09) with a dorsal valve ornamented with 130 costae; ears are relatively small and the hinge angle is shorter compared with specimens illustrated in Fig. 4 (width 15.4 mm); D – The largest adult specimen observed in the present study with a dorsal valve ornamented with 180 costae (width 19.2 mm); E-O. Growth series with all specimens observed in lateral view; shells are slightly dorsibiconvex in juveniles, becoming biconvex during growth and ventribiconvex in gerontic specimens. The lateral parts of the beak are strongly curved. The beak is not attrite at any growth stage; E – NHMM BL 0357-43 (width 2.1 mm); F – NHMM BL 0357-45 (width 3.5 mm); G – NHMM BL 0357-91 (width 3.4 mm); H – NHMM BL 0357-46 (width 4.6 mm); I – NHMM BL 0357-92 (width 6.7 mm); J – NHMM BL 0357-16 (width 6.6 mm); K – NHMM BL 039-10 (width 8.7 mm); L – NHMM BL 039-04 (width 12.9 mm); M – NHMM BL 039-09 (width 15.4 mm); N – NHMM BL 039-01 (width 16.6 mm); O – NHMM BL 039-07 (width 19.2 mm); P-T – Growth series with all specimens observed in anterior view. The anterior commissure is rectimarginate in juveniles, but becomes uniplicate in adult and gerontic specimens. The variability of the valve convexity is also seen; P – NHMM BL 0357-43 (width 2.1 mm); Q – NHMM BL 0357-44 (width 3.6 mm); R – NHMM BL 0357-92 (width 6.7 mm); S – NHMM BL 039-10 (width 8.7 mm); T – NHMM BL 039-09 (width 15.4 mm).*

The ontogenetic succession is an important taxonomic character in the genus *Terebratulina*. This succession of growth stages can help distinguish different species. The early growth stages observed in material from the type area are very similar to those observed in the material from Rügen. A direct comparison of our specimen illustrated in Fig. 4B and the one in Steinich (1965, pl. 9, fig. 9a) confirms this. Another young specimen (width 3.8 mm) from Rügen is illustrated here in Fig. 8L-S. It can be compared with specimens of similar size from Maastricht, here illustrated in Fig. 4D, E. Specimen in Fig. 4D has a beak structure and ear development identical to that in the specimen from Rügen. The structure of the deltidial plates and interarea are also identical in the specimen illustrated in Fig. 4E and in that from Rügen (Fig. 8L-S). The costae developed at early growth stages are also identical for both. The same conclusion can be drawn from a comparison between the posterior structures of the ventral valve. The lateral parts of the beak and the strong tuberculation of external limit of the interarea are identical in the material from both areas (Fig. 6M, N; 8P, Q). The only noticeable distinction is that the costae in specimens from Rügen remain finer during later growth. As a result of this, the interspaces are larger in later growth stages. However, this character can be directly linked to palaeoenvironmental differences. In a deeper and quieter environment, the development of costae and their ornament are weaker than in those from increased hydrodynamic settings.

A comparison of the brachidia offers another striking similarity. The loop is subtriangular in early juveniles, but more subquadrangular and tube-like at later growth stages in both populations. The variation of the morphological parameters is similar (see Steinich, 1965, figs 44-60) and the absolute range of values identical. However, it should be noted that the maximum size of Rügen specimens is much less than those from the type area. The largest adult shell from Rügen attains a length of 15.5 mm. In the type area, shells with a length of 25 mm are not exceptional; they are perfectly preserved and not compressed.

Adult specimens from Rügen (Steinich, 1965, pl. 8, fig. 1a-c) as well as those from the white chalk of Rørdal, Denmark (Johansen & Surlyk, 1990, pl. 3, figs 2, 3) are rather small (13.2 and 6.1 mm, respectively) and compressed, making comparisons difficult. However, following our observations and measurements, small- and medium-sized shells from Rügen and the Maastricht type area must be assigned to the same species. Deviations observed for adult specimens at both localities are explained by differences in palaeoenvironmental conditions and taphonomic processes. Observations on material from Kunrade (Kunrade Limestone facies) can also yield clues for understanding the shell variation observed between adult specimens from white chalk facies and specimens from the type area.

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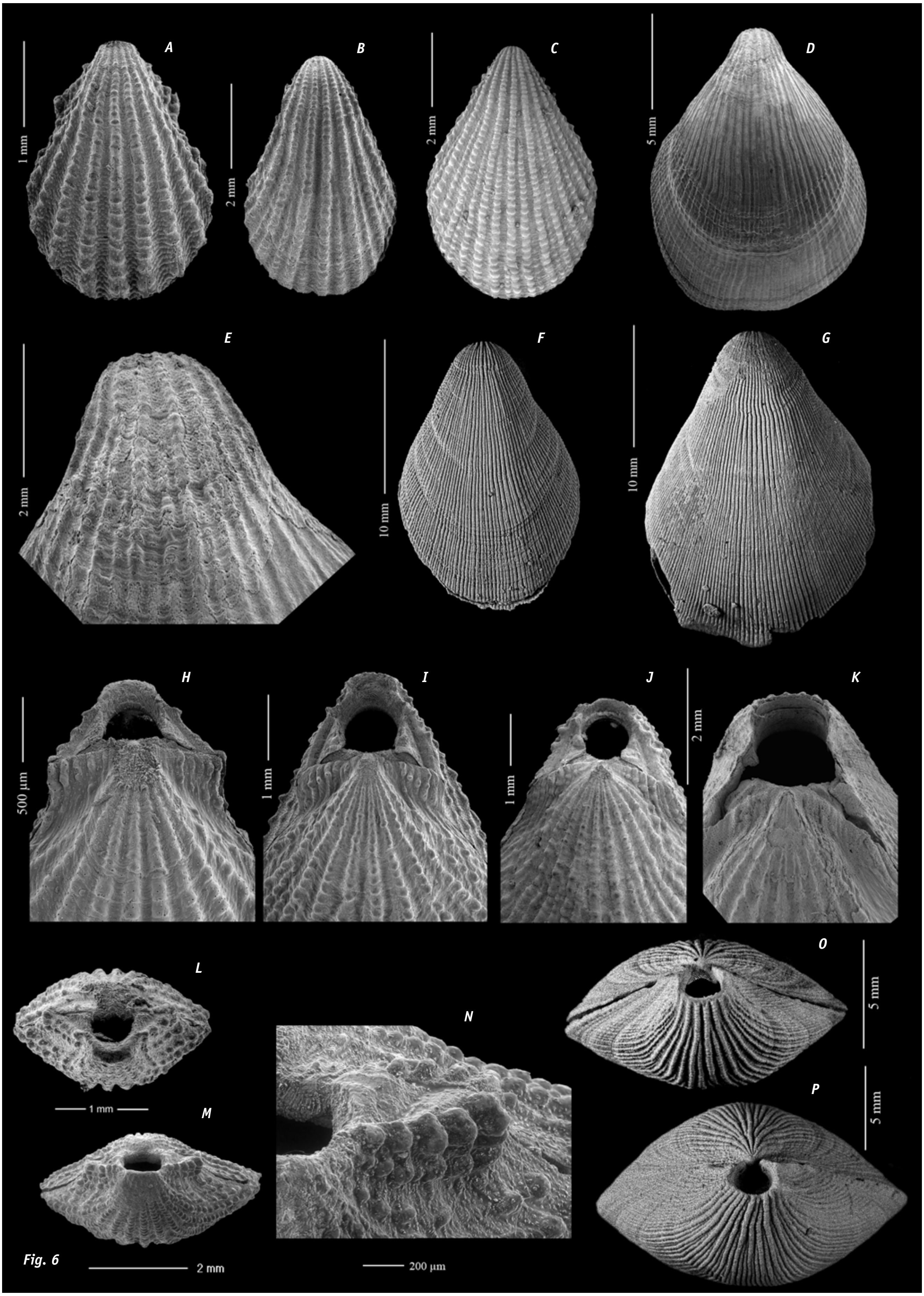
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Fig. 6

Fig. 6. Terebratulina chrysalis *(Von Schlotheim, 1813) from subunit IVf-4, Meerssen Member, at the former Blom quarry, Berg en Terblijt, southern Limburg, the Netherlands. All material in the L. Blezer Collection, NHMM. A-G – Growth series with all specimens observed in ventral view; the important increase in number of costae during growth is illustrated. The ornament made of stronger knobs present on the posterior part of the beak is pointed out. Noteworthy is the rounded outline of the tip of the beak; A – NHMM BL 0357-43 (width 2.3 mm); B – NHMM BL 0357-45 (width 3.5 mm); C – NHMM BL 0357-92 (width 6.7 mm); D – NHMM BL 0357-68 (width 11.7 mm); this specimen has costae with weak ornament. Costae are partially smooth, partially ornamented with poorly developed knobs. However, on the posterior part of the beak the costae are ornamented with stronger knobs; E – NHMM BL 0357-68 (width 11.7 mm); detail of the ornament of the umbo; F – NHMM BL 039-04 (width 12.8 mm); G – NHMM BL 039-07 (width 19.2 mm); H-K – Growth series illustrated by detailed views of the beak in dorsal view. The reduction of the hinge line and ears through growth is seen; ornament of the ears consists of several knobbed ridges. The foramen is incomplete and subcircular; H – NHMM BL 0357-43 (width 2.3 mm); I – NHMM BL 0357-46 (width 4.6 mm); J – NHMM BL 0357-16 (width 6.6 mm); K – NHMM BL 0357-68 (width 11.7 mm); L-P – Growth series with all specimens presented in posterior view. The curved lateral parts of the beak are easily seen in this position; L – NHMM BL 0357-43 (width 2.3 mm); M-N – NHMM BL 0357-92 (width 6.7 mm), general posterior view and detailed posterior view to show the palintrope structure and the heavy tuberculation of the external limit of the interarea, respectively; O – NHMM BL 039-04 (width 12.8 mm); P – NHMM BL 039-07 (width 19.2 mm).*

Comparison with material from Kunrade, southeast Netherlands

Abundant material of *T. chrysalis* from the Kunrade Limestone facies is consistent with the description of material from the Meerssen Member in the type area of the species. The Senden Collection studied here offers a unique opportunity to observe numerous specimens of all growth stages. The specimens illustrated in Fig. 9A-Q are clearly identical to those from the Meerssen Member here shown in Fig. 4D-G.

Many adults or gerontic specimens (15) are also contained in the Senden Collection. They are identical to adults from the Meerssen Member in the Blezer Collection. However, some adult specimens from Kunrade present a distorted outline, due to compression which can shift the original position of the dorsal and ventral valves. This is seen in the specimen illustrated in Fig. 9R-V. The general outline is preserved in this case and the valves are displaced due to pressure on the hinge (arrows; see Fig. 9U).

Compression can also act dorso-ventrally. The shell is therefore flattened on both dorsal and ventral sides and thus looks similar to adult shells from Rügen (Steinich, 1965, pl. 8, fig. 1a-c) or Rørdal, Denmark (Johansen & Surlyk, 1990, pl. 3, figs 2, 3).

Two examples are given in Fig. 9W-Z, AA-CC), the one in Fig. 9AA-CC being a relatively small adult representative (length 10.8 mm, width 7.8 mm and thickness 3.7 mm). The compression acted on the whole shell, but more strongly on its anterior part. The shell spread out in all directions and became slightly pyriform. Worthy of note is the difference observed in the relative width of the interspaces between costae. On the posterior part of this shell the interspaces are narrow and much wider in the anterior part of the shell due to deformation. Such larger interspaces are observed also in material from Rügen and Rørdal. The second specimen (Fig. 9W-Z) is larger (length 20.8 mm, width 15.3 mm and thickness 7.2 mm). The compression of this shell affected the anterior part of the shell but it was still stronger on the ventral side. Here also the width of the interspaces between costae is slightly increased by the compression of the anterior part of the shell. With such a compression mode, the shell becomes very similar to adult shells from Rügen (lower Maastrichtian white chalk). When comparing these fully adult specimens, here illustrated in Fig. 9R-Z), the strong distortion through taphonomic changes in time becomes apparent.

Conclusions

For the first time, representatives of *Terebratulina chrysalis* from the type area of the species (Meerssen Member) have been studied in detail and illustrated. A complete growth series is now available, enabling a documentation of the entire ontogenetic process. Fully adult and gerontic specimens are also noted; in fact, such adult material is seen for the first time

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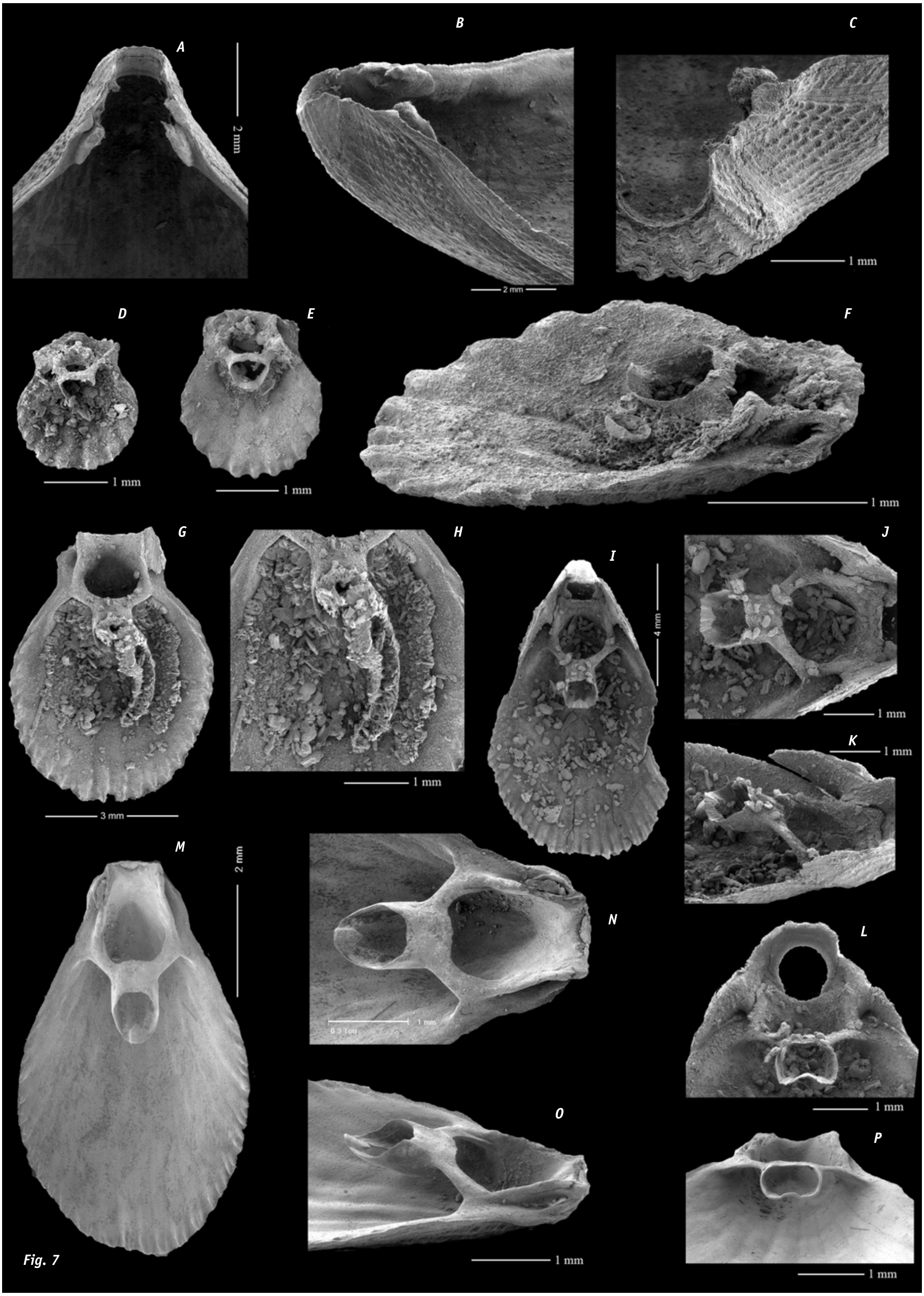
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Fig. 7

Fig. 7. Terebratulina chrysalis *(Von Schlotheim, 1813) from subunit IVf-4, Meerssen Member, at the former Blom quarry, Berg en Terblijt, southern Limburg, the Netherlands. All material in the L. Blezer Collection, NHMM. A-C – Detailed observation of the posterior part of an adult ventral valve. A – NHMM 0357-68, in dorsal view (width 11.7 mm); posterior part of a disarticulated ventral valve. The pedicle collar is exposed. The left deltidial plate and the left tooth can be observed; B – NHMM 0357-68, in oblique lateral view (width 11.7 mm), the curved lateral part of the beak is exposed with its ornament consisting of nine tuberculate costellae. The number of costellae depends of the age but is a variable character; C – NHMM 0357-68, in oblique posterior view (width 11.7 mm); the curvature of the lateral part of the beak is pointed out; D-P – Growth series for the development of the brachidium. D – Early juvenile specimen (NHMM BL 0357-25), in ventral view (width 1.9 mm), crural bases are fused to socket ridges and the crural processes are already fused together to form a ring-like loop which has a subtriangular outline. E-F – Early juvenile specimen (NHMM BL 0357-44; width 2.3 mm), in ventral view (the suture of the crural processes is clearly visible and the ring is still subtriangular in outline. The transverse band is narrow and very slightly arched) and oblique lateral view, respectively, the slightly arched structure of the transverse band is well visible. The length of the brachidium represents, at this stage of growth, nearly 50 per cent of the length of the dorsal valve; G-H – Juvenile specimen (NHMM BL 0357-46; width 3.5 mm); dorsal valve in ventral view exposing the brachidium with one intact spiculated brachium, in general ventral view and detailed view of the spiculated brachium, respectively; I-L – Juvenile specimen (NHMM BL 0357-47), exposing a complete brachidium (width 3.5 mm), in general view of the dorsal valve in ventral view, complete loop in ventral view, the ring formed by the fusion of the crural processes is tube-like. The cardinal process is already strongly developed; oblique lateral view showing the slightly arched transverse band, and anterior view of the ring becoming, at this stage of growth, more subquadrangular, respectively; M-P – NHMM BL 0357-15, exposing a complete brachidium (width 4.6 mm), dorsal valve in ventral view (M), detail of the brachidium in ventral view. The relative length of the brachidium reaches 46 per cent of the length of the dorsal valve. The ring formed by the fusion of the crural processes is tube-like (N), oblique lateral view of the brachidium showing the arched transverse band (O), anterior view of the ring which is ovate-subquadrangular at this stage of growth (P).*

which results in a better knowledge of specific variation. Previously, most of the material collected in different European countries comprised juvenile or very young specimens only. Except for Kunrade, fully adult shells, such as the ones collected from the Maastricht area, have never been found before, let alone documented.

The juvenile and young specimens from the Maastricht area and from all other published European localities have identical morphological characters and are clearly representatives of *T. chrysalis*. However, a great difference is observed between the outline of adults from the Maastricht area and those from the lower Maastrichtian white chalk in northeast Germany and Denmark. At first glance, these lots could be regarded as two distinct species. However, it should be not that different settings (quiet vs high hydrodynamic palaeoenvironments) may have an impact on the development of certain characters. A coastal, high-energy setting would have promoted the development of strongly knobbed costae whereas a deeper, quieter environment would have favoured more delicate and fine ornament.

Moreover, the study of late Maastrichtian material from the Kunrade Limestone facies in southern Limburg (the Netherlands) has offered an opportunity to understand how compression processes through time might have affected the general outline of the shell. Specimens of adult *T. chrysalis* identical to those found in the Meerssen Member were observed in association with several distorted specimens having similar outlines to those originating from Rügen or Rørdal. Thus, early Maastrichtian material from different European white chalk outcrops should also be identified as small, compressed representatives of *T. chrysalis*.

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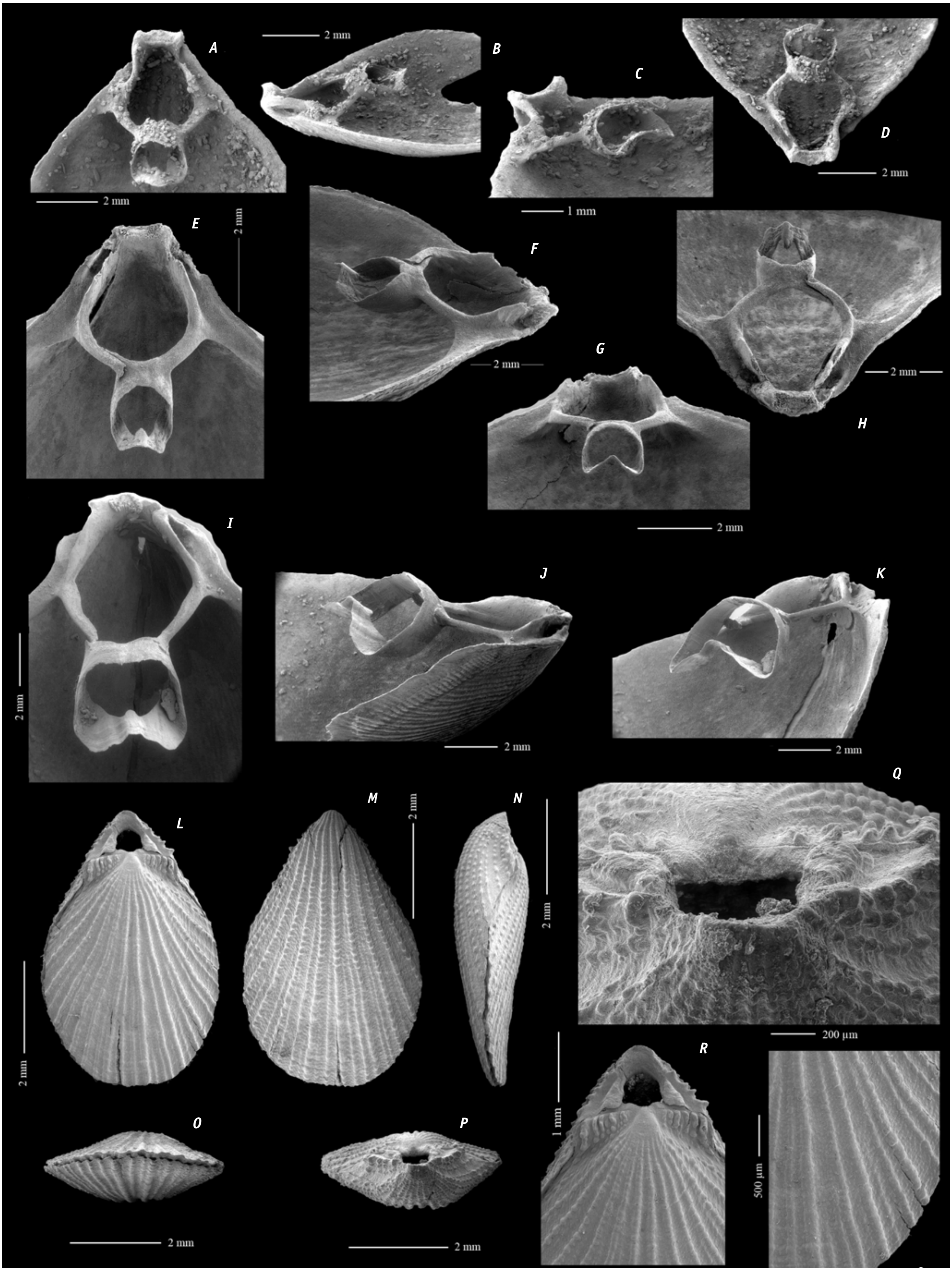

Fig. 8

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Fig. 8. Terebratulina chrysalis *(Von Schlotheim, 1813) from subunit IVf-4, Meerssen Member, at the former Blom quarry, Berg en Terblijt, southern Limburg, the Netherlands. All material in the L. Blezer Collection, NHMM. A-K. Growth series for the development of the brachidium; A-D – Young adult specimen (NHMM BL 0357-38) exposing a complete brachidium (width 8.9 mm), complete loop in ventral view (A); brachidium in oblique lateral view; the transverse band is more arched (B), oblique antero-lateral view showing the transverse band and the outline of the ring (C), brachidium in oblique posterior view; cardinal process and sockets are clearly visible (D); E-H – Adult specimen (NHMM BL 0357-68) exposing a complete brachidium (width 11.7 mm), complete loop in ventral view. The ring is less 'tube like' as it becomes narrower (E), oblique lateral view of the brachidium with its more strongly arched transverse band (F), anterior view of the ring with its strongly arched transverse band (G), oblique posterior view of the brachidium. Cardinal process and socket ridges are well exposed (H). I-K – Fully adult specimen (NHMM BL 039-07) exposing a complete brachidium (width 19.2 mm), complete loop in ventral view. The ring is now very narrow; the 'tube-like' structure is not observed at this stage of growth (I), oblique lateral view of the brachidium with its fairly arched transverse band (J), oblique antero-lateral view of the brachidium which shows the semicircular aspect of the ring which is the latest growth stage observed (K). L-S –* Terebratulina chrysalis *(Von Schlotheim, 1813) from Rügen, lower Maastrichtian white chalk (NHMM 2010 032; width 3.9 mm), dorsal view (L), ventral view (M), lateral view (N), anterior view (O), posterior view (P), details of posterior (Q) and dorsal views (R) and detail of ornament (S). The curved lateral parts of the beak and the strong knobbed ornament of the external limit of the interarea are clearly visible (Q), detail of the beak in dorsal view. The deltidial plates are identical to those observed for the material collected from the Maastricht area. The ears are ornamented with similar knobbed parallel ridges (R), detailed dorsal view of the costae which are much finer with wider interspaces. This is an adaptation to a deeper and quieter environment (S).*

Fig. 9 (next page). Growth series for Terebratulina chrysalis *(Von Schlotheim, 1813) collected at Kunrade (southern Limburg, the Netherlands) from the Kunrade Limestone facies (ecozone V, equivalent to basal Emael Member, Maastricht Formation, late Maastrichtian). All material from the H. Senden Collection, NHMM, and illustrated in dorsal, ventral, lateral, anterior and posterior views. A-E. Early juvenile specimen (NHMM 2010 033), width 2.4 mm; this individual was about to increase the number of costae, closely similar in size and outline to the specimen illustrated in Fig. 4C. F-L – Slightly larger juvenile specimen (NHMM 2010 034), width 3.0 mm, the similarity with material from the Maastricht type area being obvious. The detailed view of the beak (Fig. K) in dorsal view shows deltidial plates are disjunct and clearly visible. The ears are quite large and ornamented with knobbed parallel ridges. The oblique posterior view (Fig. L) illustrates the structure of the palintrope. The external limit of the interarea is ornamented with strong knobs. M-Q – Young adult stage of growth (NHMM 2010 035), width 6.8 mm. The strongly increased number of costae is typical of the species. R-V. Large, fully adult specimen (NHMM 2010 036), width 17.8 mm. This representative suffered from uneven compression on its dorsal and ventral valve (see arrows). The two valves are therefore disjoined in the commissural plane. The hinge resisted this movement. However, the general outline of the valves does not appear altered. This specimen has a sulcus developed on both valves, an uncommon morphology amongst specimens from Kunrade or from Blom and Terblijt, where most adult specimens have only one ventral sulcus or even no sulcus at all. W-Z. Fully adult specimen (NHMM 2010 037), width 15.3 mm. This specimen suffered strong compression dorso-ventrally and the shell spread out. It now resembles specimens from the white chalk from Rügen and Rørdal. Note that the interspaces between costae are wider in the compressed parts of the shell. AA-CC – Smaller specimen (NHMM 2010 038), width 7.8 mm. This shell suffered dorso-ventral compression, distorting the shell which exhibits a very similar outline to adult specimens from the white chalk (e.g., Rügen).*

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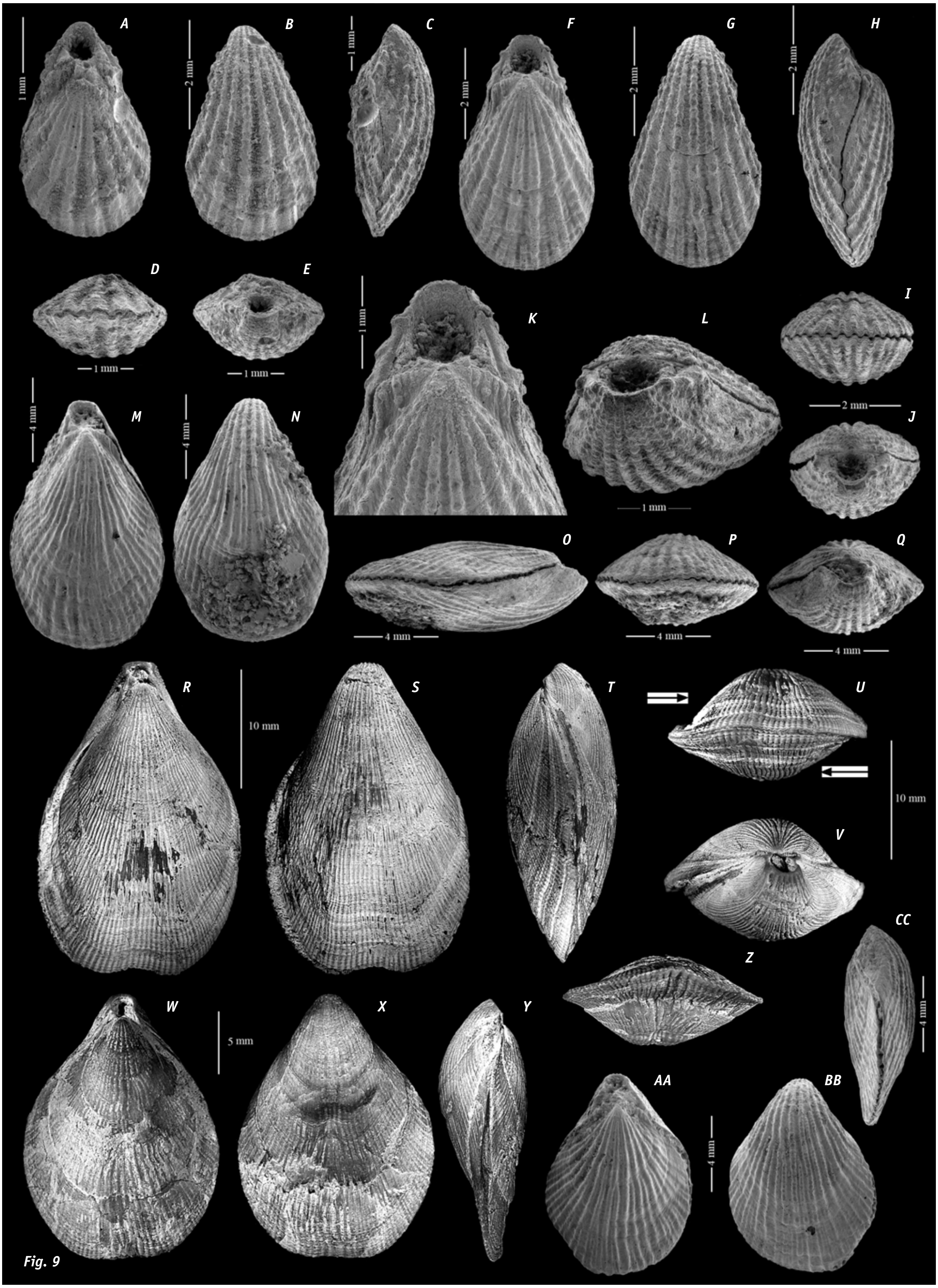

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