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Tullypothyridina, new late Givetian rhynchonellid (brachiopod) genus

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Abstract

A new genus, *Tullypothyridina*, type species *T. venustula* (HALL, 1867), is described from the late Givetian of central New York, Pennsylvania, eastern Kentucky, and probably eastern Iowa. The type species of the related genus *Hypothyridina* BUCKMAN, 1906, *H. cuboides* (SOWERBY, 1840), the name of which was originally and subsequently given to the American species, is discussed. The taxonomic definition of this late Givetian species from South Devon, its stratigraphic position, and its paleogeographic significance are examined. The type species of the genus *Glosshypothyridina* RZHONSNITSKAYA, 1978, *G. procuboides* (KAYSER, 1871), is also scrutinized; this late Eifelian species from the Eifel region has been considered as closely allied, when not identical, to both the American and English species.

Key-words: Hypothyridinidae, *Tullypothyridina*, rhynchonellids, brachiopods, late Givetian, North America.

Résumé

L'auteur fonde un nouveau genre, *Tullypothyridina*, avec *T. venustula* (HALL, 1867) du Givetien supérieur du New York central, de Pennsylvanie, du Kentucky oriental et probablement de l'Iowa oriental comme espèce-type. L'espèce-type du genre apparenté *Hypothyridina* BUCKMAN, 1906, *H. cuboides* (SOWERBY, 1840), dont le nom fut donné à l'origine, et après, à l'espèce américaine, est l'objet d'une discussion relative à la définition taxinomique de cette espèce du Givetien supérieur du Devon méridional, sa position stratigraphique et sa signification paléogéographique. L'espèce-type du genre *Glosshypothyridina* RZHONSNITSKAYA, 1978, *G. procuboides* (KAYSER, 1871), est aussi examinée; cette espèce de l'Eifelien supérieur de l'Eifel a été considérée comme une espèce étroitement liée, voire identique, aux espèces anglaise et américaine.

Mots-clefs: Hypothyridinidae, *Tullypothyridina*, Rhynchonellides, Brachiopodes, Givetien supérieur, Amérique du Nord.

Introduction

VANUXEM (1842, pp. 163-167) was the first to mention the New York species, but did not describe it, because he considered it identical to PHILLIPS's (1841, pp. 84, 148) *Terebratula cuboides* from South Devon: "This [*Cuboidal atrypa*] is an English name, given to a fossil by Mr. Phillips, which, from the figure and description conjoined, shows identity with that of the Tully limestone" (p. 164). VANUXEM was impressed by the similarity of the specimen he figured (1842, fig. 41.No.1 = antero-ventral, lateral and posterior views) with the one figured by PHILLIPS (1841, pl. 34, fig. 150 = anterior view). It was an excellent observation, because PHILLIPS's figured specimen is a good representative of one of the various forms from South Devon grouped under the name "*cuboides*". The specimen described by SOWERBY (1840, explanation of pl. 56, fig. 24 = anterior and dorsal views) shows but a faint resemblance to the one figured by VANUXEM. This is important, because SOWERBY is the founder of the species, of which this specimen is the holotype. This original confusion led to conflicting systematic, stratigraphic, and palaeogeographic interpretations that still survive. So did the mention by SOWERBY of the presence of the species "also in the Eifel" without further indication.

The opinion that the New York and South Devon species (and sometimes other homonym European species) were identical prevailed from 1842 until 1938 (see synonymy) and was emphasized by de VERNEUIL [1847, pp. 646-647, 660, 669-670, 679, 697-698, table; see also the translation and comments on this paper by HALL (1848, pp. 176-177, 359-360, 369; 1849, table, p. 219, p. 229)]. Still, at the same time HALL (1843, pp. 215, 216), who gave the first, and very short, description of the species as *Atrypa cuboides*?, started questioning this identity and observed that the American species had less costae than the South Devon species (6 to 8 in the sulcus as against 15), and the top of the tongue located lower; de VERNEUIL (1847, p. 698) made a similar observation when stating that the New York species had 6 costae in the sulcus, while the European one had 8 to 11.

HALL (1843, p. 215) gave the following verdicts: "It seems scarcily possible that this shell can be different from the English specimens", "In other respects there is a precise correspondence". Brushing aside his past (1843) wavering, HALL (1867, pp. 346-348, pl. 54A, figs. 24-43) recognized the New York species to be independent; he called it *Rhynchonella venustula*, and gave the first elaborate and abundantly illustrated description of its external and internal characters.

Some eminent American and European scientists (see synonymy) defended opposite views as illustrated by three examples: "Auch in Nordamerica fehlt sie [*R. cuboides*] nicht (*venustula* HALL)" (KAYSER, 1883, p. 79), "There is little doubt but that *Rhynchonella intermedia*, *R. Emmonsi* and *R. venustula* are varieties of *R. cuboides* of the Devonian of Europe, and when the opportunity offers to illustrate a series of specimens I

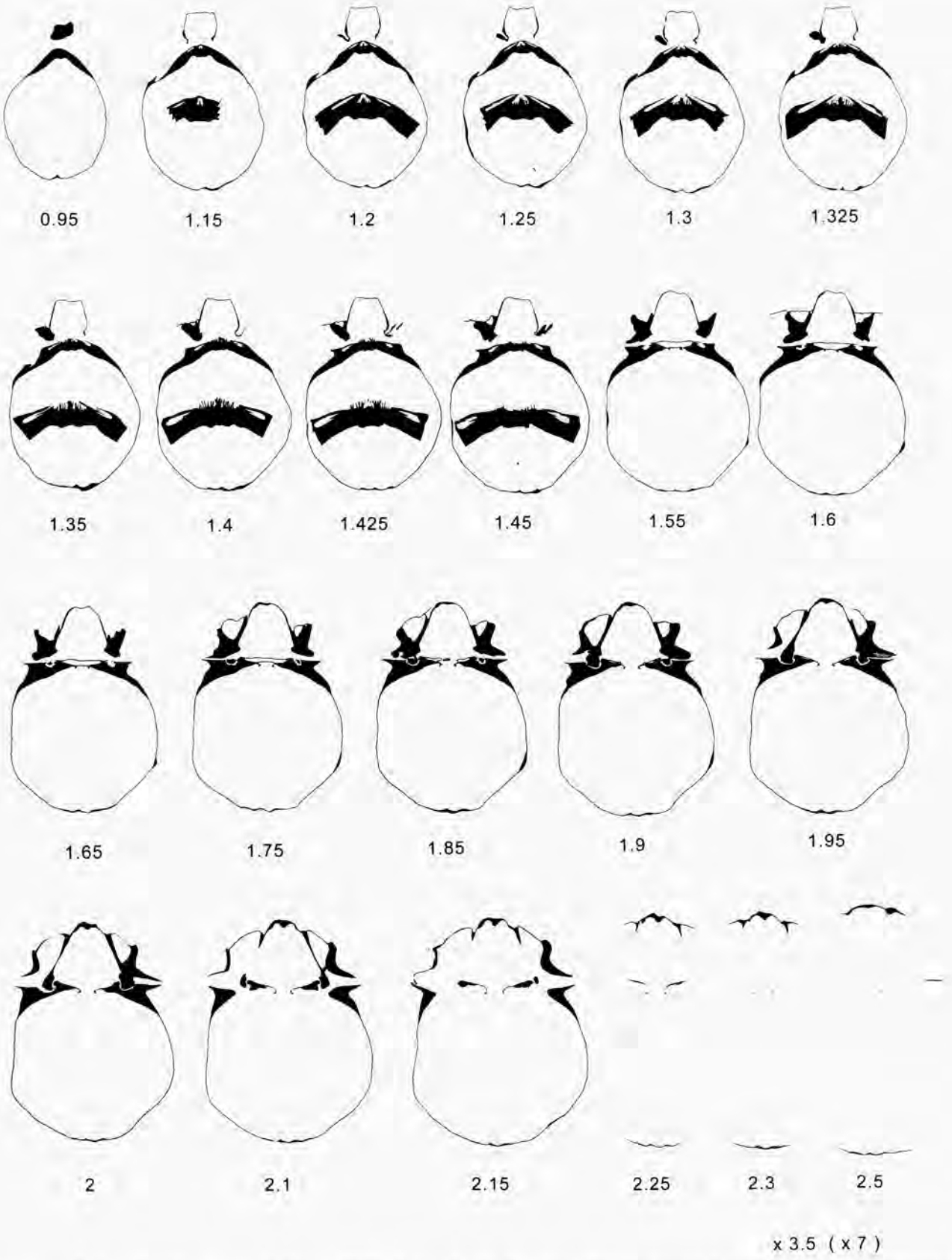

Figure 1 — *Tullypothyridina venustula* (HALL, 1867). Camera lucida drawings of transverse serial sections; figures are distances in mm forward of the dorsal umbo. Topotype H, IRScNB a11978. Measurements: length = 20.6 mm; width = 24.4 mm; thickness = 20.2 mm. The cardinal process is enlarged (x7) in sections 2 to 10 in order to reveal its details. The socle of the cardinal process is not blackened between sections 11 and 17 in order to show its progressive disappearance and its relationship to the hinge plate and the crural bases.

think this can be readily be shown. Many American species now under local names will ultimately be placed with species described from Europe, and the reverse will also be true when American species have priority'' (WALCOTT, 1884, p. 157), ''*R. venustula* is by common consent allied to *R. cuboides* of Europe'' (WILLIAMS, 1890, p. 493), ''*R. venustula*, which only an expert could separate from some specimens of the European *R. cuboides*'' (WILLIAMS, 1891, p. A142).

HALL changed his previous position first indirectly via CLARKE (1885b, p. 385), who wrote that HALL considered *Rhynchonella venustula* as ''eine Varietät des britischen Typus der *R. cuboides*'', and then directly in HALL & CLARKE (1893, p. 200), who consider *R. venustula* as a ''variant of the well-known horizon-marker, *R.* (*Atrypa*) *cuboides*, Sowerby'', and the same authors (1894, p. 244) ''*Hypothyridina venustula*, Hall. (= *Rhynchonella cuboides*, Sowerby)''.

Hypothyridinidae RZHONSNITSKAYA, 1956
Tullypothyridina n. gen.

DERIVATIO NOMINIS

The name is an arbitrary combination of Tully and the last five syllables of *Hypothyridina*.

TYPE SPECIES

Rhynchonella venustula HALL, 1867.

DIAGNOSTIC FEATURES

Medium-sized, exceptionally large-sized. Cuboidal. Dorsal valve high. Very shallow sulcus and very low fold starting near the beaks. Cardinal commissure sticking out. Hinge line narrow. Maximum thickness of shell either at front or slightly posterior to it. Very wide and slightly variable apical angle. Sulcus generally narrow. Anterior part (= tongue) of sulcus at right angle to its posterior part. Tongue high, rectangular, slightly recurved posteriorly in its upper part. Ventral interarea short. Lower half of dorsal flanks vertical or almost vertical. Costae very low, starting at the beaks. Median costae commonly divided. Lateral costae narrower than median costae, rarely divided. Furrows very narrow. Median grooves on the anterior part of the ventral median and dorsal lateral costae; costae tending to become flat in this part of the shell. Number of median costae usually moderate, number of lateral costae high. Parietal costae present. Slender dental plates and cardinal process present. Very slender crura composed of two parts. Septum and septalium absent.

SPECIES ASSIGNED TO THE GENUS

In addition to the type species, the contemporaneous species, *Rhynchonella intermedia* BARRIS, 1879, from eastern Iowa also belongs to the genus. This rare species was found in the Corniferous Formation, or, as we know now, in the Solon Member (lowest member of the Little Cedar Formation), corresponding, in terms of the conodont succession, to the Middle and Upper *Polygnathus varcus* Zones. The type material is housed in the Putnam Museum in Davenport, Iowa. In 1981 the author found four specimens of the type series, three of them accompanied by a label. All labels mention Cook's quarry as the locality. Cook's quarry, then located at the gates of Davenport near the Mississippi River, has disappeared. With the exception of the smaller size, none of the differences from *Rhynchonella venustula* mentioned by BARRIS (1879, p. 286), some repeated by STAINBROOK (1942a, p. 613), could be confirmed on specimens of similar size of the New York species; STAINBROOK (1942a, pp. 612, 613) gave a full description of the species and established a new variety (*magniventra*). In particular, the number of costae on the fold of the four specimens examined is 7, 9, 9, and 11, and the number of lateral costae 17, 18, 23, and 25. The author of the present paper is inclined to follow WELLER (1909, pp. 265, 266), who stated that *R. intermedia* was apparently ''specifically identical with the New York species [as *Hypothyris cuboides*]''. The specimen figured by BARRIS (1879, pl. 11, figs. 5-7) is here designated as the lectotype of the Iowan species; it is not a holotype as stated by STAINBROOK (1942a, p. 613).

It is probable that representatives of the genus are present in South Devon and in other parts of western Europe, e.g. *Terebratula cuboides* figured by PHILLIPS (1841, pl. 34, fig. 150).

DESCRIPTION

Remarks

COOPER & WILLIAMS (1935, p. 841) ''placed the specific range of costae on the tongue at three to fourteen'', but wrote that they ''would restrict the name *venustula* '' to adult shells containing ''from six to eight costae'' in the sulcus. They stated in other words that ''the variation in number of costae [five to eight] on the tongue of *Hypothyridina* [in the Laurens Member]'' was ''approximately in the range of *H. venustula* sensu stricto''. This is the position also adopted by the present author. The four figured specimens (Pl. 1, Figs. 6-25) fall into this category. See further details in the paragraph dealing with the ''Varieties'' of the species.

Medium-sized, exceptionally large-sized. Outline cuboidal. Strongly dorsibiconvex. Contour subrounded to subelliptical (narrow major axis) in ventral and dorsal views. Contour of dorsal valve a high half-ellipse or half-circle in cardinal profile, contour of ventral valve a half-lens. Sulcus and fold starting near the beaks. Anterior, lateral and cardinal commissures sharp, and only slightly, sometimes almost not, undulated by the costae. Lateral parts of the anterior commissure at right angle to the lateral commissures. Lateral commissures located low and passing to the cardinal commissure by a more or less pronounced and dorsally oriented bend. Cardinal commissure sticking out as a result of the postero-lateral margins being markedly concave near the commissure. Hinge line narrow, considerably shorter than maximum width of shell, which is located about mid-valve length.

Ventral valve shallow, sometimes evenly and slightly convex, but generally the umbonal region is convex while flanks become progressively slightly concave, exception-

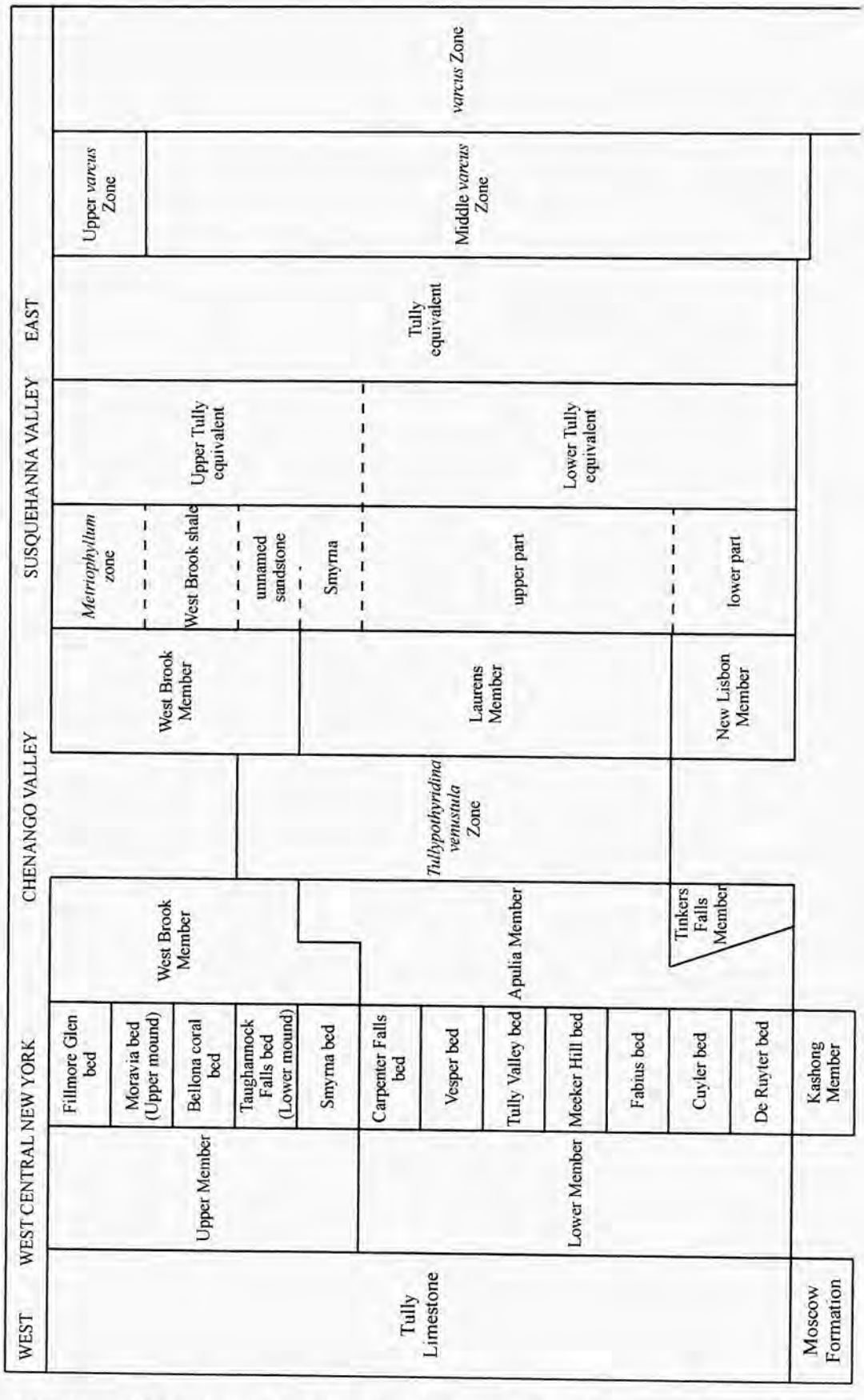

Figure 2 — Subdivisions of the late Givetian Tully Limestone. Columns 4 and 6 = subdivisions of COOPER & WILLIAMS (1935), and columns 1-3, 7-9 = subdivisions of HECKEL (1973). Columns 10 and 11 = conodont zonation of ZIEGLER *et al.* (1976) and KLAPPER (1981a,b). Modified from HECKEL (1973, fig. 4, p. 10).

ally flat, towards the postero-lateral margins. Sulcus well marked, very shallow, generally narrow, starting imperceptibly, widening and deepening slowly towards the front. Maximum width of sulcus reached at the junction of the lateral and anterior commissures and is maintained through the whole of the height of the tongue that starts there as a result of a bend at right angle of the sulcus. Width of sulcus at front variable, but generally moderate. Bottom of sulcus flat to slightly convex. Tongue high, rectangular, and clearly delineated. Upper part of tongue – sometimes as much as two-thirds its height – slightly recurved posteriorly; in this part the sulcus is either extremely shallow or on a level with the parallel borders of the tongue. Top of tongue slightly (generally) to moderately convex, exceptionally flat, located posterior to maximum shell length. Beak small, erect to slightly incurved, coming close to dorsal valve because of inflated dorsal umbonal region. Interarea low, short, separated from flanks by sharp beak ridges.

Dorsal valve high and gibbous. Umbonal region strongly inflated, extending beyond ventral umbonal region. Flanks curving abruptly, almost vertical or vertical in their lower half. Fold very low. Top of fold slightly to moderately convex. Beak strongly incurved. Top of valve either at front or slightly posterior to it.

Costae well marked, very low, flat-rounded, starting at the beaks. Furrows very narrow. Median costae moderately wide, commonly divided, and regular in their anterior half, because most of divisions occur in the posterior part of the unrolled length of both valves. Lateral costae narrow to moderately wide, rarely divided, regular, narrower than median costae. Ventral median costae and dorsal lateral costae tending to become flat near the commissure. Faint (very shallow and narrow) median grooves run on one to two anterior fifths of unrolled length of the median ventral and the lateral dorsal costae. Grooves are related to the growth of spine-like projections located near the anterior commissure (top of tongue) of the dorsal valve and near the lateral commissures of the ventral valve; spine-like projections are best observed as pits on internal moulds. WESTBROEK (1967, fig. 68, p. 61, fig. 69, p. 62 as *Hypothyridina cuboides*; neither age nor locality given) suggested a model for the position and growth of the marginal spines; this model could apply here. Grooves of one valve are opposite the furrows of the other valve. Number of median costae variable, usually moderate. Numerous lateral costae. Either one or two parietal costae present on one or both flanks of the sulcus and fold; they do not reach the commissure.

Length, width and height only slightly different as implied by the cuboidal outline of the shell. Unrolled length of the ventral valve great for the same reason, and also on account of the very shallow sulcus. Maximum width of shell occurs at a point located around mid-length. Top of ventral valve located one quarter to about half-length anterior to the ventral beak. Top of dorsal valve, and thus maximum thickness of shell, either at front or slightly posterior to it. Very wide and slightly variable apical angle and angle of the cardinal commissure.

Dental plates slender and strongly convergent. Umbonal cavities wide. Teeth stout, short, entering the dental sockets vertically in serial transverse sections. Strong and short cardinal process composed, in its upper part, of a strong central lamella, and six to seven slender lamellae on both sides. The central lamella divides anteriorly in thinner lamellae. All lamellae disappear rapidly anteriorly, but the socle of the cardinal process continues before fading out progressively. Dental sockets shallow. Lateral parts of the divided hinge plate thick, passing to very slender, short, and elongated crural bases, which are strongly curved dorsally. Crura short, narrow, thin, lamellar, and remaining close to each other. Septum and septalium absent. Ventral muscular field oval and strongly impressed; its width is around 30 per cent the width of the shell, and its length around 45 per cent of the length. Dorsal muscular field "narrow, elongate and extremely obscure" according to HALL & CLARKE (1893, p. 201). Genital and vascular markings of the ventral valve are often seen on moulds. The impressions of the ventral valve are shown here (Pl. 1, figs. 36, 40) and have been illustrated by HALL (1867, pl. 54A, figs. 35, 36), HALL & CLARKE (1893, pl. 60, figs. 53-55; 1894, pl. 44, fig. 13), and by COOPER & WILLIAMS (1935, pl. 57, figs. 8, 19).

COMPARISONS

Comparison of *Tullypothyridina* n. gen. with the genera *Glosshypothyridina* RZHONSNITSKAYA, 1978 and *Hypothyridina* BUCKMAN, 1906 cannot be attempted without dealing with the systematic and stratigraphic problems, past and present, connected with their type species. These problems are intricate and require some explanation.

Comparisons with Glosshypothyridina

Some misconceptions concerning *G. procuboides* (KAYSER, 1871), the type species of the genus originally described from the Eifel region and Belgium, are discussed here. KAYSER (1871) does not mention any precise locality, but Gees (Gerolsteiner Mulde) and Schönecken (Prümer Mulde) may be considered as such, because these localities are those of *Terebratula cuboides* described by SCHNUR (1853, p. 239) and put into synonymy by KAYSER (1871, pp. 513, 514). Anyhow, we know that the species is present in the southern Eifelian (Ahrdorfer, Gerolsteiner, Hillesheimer, Prümer, and Rohrer) "Mulden".

The stratigraphic range of the species, as given by KAYSER (1871, p. 514), is: "Im obersten Theile der Calceola-Schichten und besonders in der Crinoiden-Schicht [in the Eifel region]", "auch in den Calceola-Schichten Belgiens", i.e. late Eifelian nowadays. SCHNUR (1853) and KAYSER (1871) both insisted on the scarcity of the species.

The lectotype (here designated), the only specimen figured by KAYSER (1871, pl. 9, figs. 3a,b = anterior and lateral views), is probably part of a private collection in Trier or Bonn, and is not available for examination; therefore, SCHNUR's figure (1853, pl. 24, figs. 4a-c) is a welcome complement to the illustration of the species.

This short introduction brings us to the next problem: the extension of the stratigraphic range of *Glosshypothyridina procuboides* to the late Givetian in Bergisches Land, Lahnmulde, Sauerland, and South Devon. As a result of an excursion lead by Ussher in 1888, KAYSER (1889, pp. 184-185, 186) recorded the

presence of *Rhynchonella procuboides* in the "oberen Horizont der *Calceola*-Stufe" (late Eifelian) of Hope's Nose east of Torquay and in the "Stringocephalenkalk" (Givetian) near Torquay and Lummaton, and *R. cuboides* in Frasnian rocks at Chudleigh and Saltern Cove near Torquay. In considering the late Eifelian *Rhynchonella procuboides* from the Eifel region and Belgium as occurring in the Givetian (late Givetian nowadays) from South Devon, KAYSER, its author, considerably extended the stratigraphic range of the species. Following KAYSER's lead, various authors mentioned or described *R. procuboides* in rocks of late Givetian age in Germany (Bergisches Land, Lahnmulde, and Sauerland), e.g. HOLZAPFEL (1895, pp. 278-279, table, p. 315, pp. 327, 336, 351, table, p. 355, pp. 366, 376, pl. 18, figs. 5, 5a-c); LEIDHOLD (1928, pp. 42, 45-46); TORLEY (1934, pp. 72, 78, 80, 83, 86-87, 134, 135, table, p. 137, pl. 4, figs. 49a,b, 50a,b, 51a,b, 52a,b, 53a,b, 54a,b, 55a,b, 56a,b, 57a,b). In South Devon ELLIOTT (1961, p. 258) duplicated KAYSER's (1889) discovery of *R. procuboides* in the late Givetian Lummaton limestones, and concluded, as WHIDBORNE (1893, p. 135) already did, that *Hypothyridina cuboides* had to be the name for it; he also stressed its close analogy to *Hypothyris procuboides* described by TORLEY (1934) from the late Givetian Massenkalk of Sauerland and the Lahnmulde. In so doing, ELLIOTT not only accepted the identity of the late Eifelian German species and the late Givetian English one, but also did not consider the possibility, mentioned below, that more than one taxon could be present in those limestones under the same name (*cuboides*). The above mentioned scientists, including KAYSER, went ahead comparing the alleged late Givetian representatives of *Rhynchonella procuboides* to alleged Frasnian representatives of *Hypothyridina cuboides* from various regions of western Europe, but not to the late Givetian South Devon holotype of that species. In other words a (probably) incorrectly identified *Rhynchonella procuboides* was compared with an unmistakably incorrectly identified *Hypothyridina cuboides*. This has been common practice when valid taxa were supposed to be compared to *H. cuboides*. KAYSER himself (1871, p. 514; 1883, pp. 79, 90, 99, 101, 102), when pointing out the differences between the late Eifelian species he established, *Rhynchonella procuboides*, and *R. cuboides*, only included alleged Frasnian representatives of the latter species from Belgium, Harz Mountains (Iberg), Sauerland and Silesia in his comparison.

Analogies between *R.* (or *Hypothyridina*) *venustula* and *R.* (or *H.*) *procuboides* seen by the following authors have also to be reinterpreted, because comparisons anteriorly were made to German (chiefly Sauerlandian) and South Devon alleged late Givetian representatives of the late Eifelian species from the Eifel region: HOLZAPFEL (1895, p. 278 as *Rhynchonella*), COOPER & WILLIAMS (1935, p. 823 as *Hypothyridina*), and COOPER (1967, p. 704 as *Hypothyridina*). HOLZAPFEL even went so far as to consider the possibility of *Rhynchonella procuboides* being a junior synonym of *R. venustula*.

The age of various massive limestones around Torquay and Plymouth in South Devon was long a source of debate. The core of the argument that prevailed for many years has been the coexistence or association of *Hypothyridina cuboides* and *Stringocephalus* DEFRANCE *in* de BLAINVILLE, 1825 (sometimes *S. burtini*) in what has been called the Lummaton fauna from the Lummaton, Barton and Woolborough quarries: see DAVIDSON (1865, pp. 65-66, pl. 2, fig. 6, pl. 13, figs. 16-19, 21; 1882, pp. 19, 46, pl. 2, fig. 18, pl. 3, fig. 2); WHIDBORNE (1893, pp. 97, 134); USSHER (1890, pp. 503-504; 1903, pp. 7, 60-61, 65, 103; 1907, p. 73; 1913, pp. 14-15); JUKES-BROWNE (1906, pp. 296, 299, 300); SHANNON (1928, p. 113); LLOYD (1933, pp. 43, 76); ELLIOTT (1961, pp. 256, 257); HOUSE (1963, p. 6; 1971, p. 80); SCRUTTON (1978, p. 39). Although the Lummaton fauna, the Lummaton Shell Bed or the Shell Bed are often mentioned in the literature, it is obvious that there is a main (or Main) Lummaton Shell Bed as indicated by HOUSE (1963, p. 1, p. 6) or Shell Beds as mentioned, as a possibility, by HOUSE (*in* HOUSE & SELWOOD 1966, p. 57), and by SCRUTTON (1978, p. 40); the latter author recognizes a Lummaton Shell Beds Member. The thickness of these beds is not given and they are sometimes described as lenses. The Lummaton fauna obtained and described by WHIDBORNE (1893) comes according to JUKES-BROWNE (1906, p. 299) from "a weathered patch of grey rock [grey shelly limestone]" at the top of one of the quarries operated at that time.

Another point that has been commonly overlooked is that the Lummaton Shell Bed, no matter its definition "forms but a small part [of the Lummaton limestones]" as rightly stated by ELLIOTT (1961, pp. 256, 258), who appropriately adds that a "revision of the Lummaton-Barton fauna and the occurrence of its species in the quarries, so far as can be ascertained, is desirable".

As far as the present paper is concerned, the controversy has been artificial all along, because the presence of representatives of the genus *Stringocephalus* should have been enough to indicate a certain Givetian age. Therefore, *Hypothyridina cuboides*, found in the same rocks, should have been considered evidently as a Givetian species that has very little in common with the various Frasnian species bearing the same name.

The late Givetian age of the Lummaton Shell Bed is now clearly established by the identification of the *Maenioceras terebratum* goniatite Zone by HOUSE (1963, pp. 1, 5, 6; 1971, p. 80; 1977, p. 20), and of the Middle and Upper *Polygnathus varcus* conodont Zones by SCRUTTON (1978, p. 40).

But major problems remain, the first one being that the single specimen (the holotype) figured and described by SOWERBY (in SEDGWICK & MURCHISON, 1840, pl. 56, fig. 24) is not part of the Lummaton fauna; it came from the Plymouth Limestone about 40 km apart. Was then WHIDBORNE (1893, pp. 134, 135 as *Wilsonia cuboides*) right when he claimed that the "Lummaton shell" was "undoubtedly the true *Rhynchonella cuboides*"? Some species introduced during the 19th century by British palaeontologists (J. de C. Sowerby, Phillips, Davidson, and Whidborne) are still without an acceptable generic assignment, while others, such as *Atrypa crenulata* J. de C. SOWERBY,1840 or *Atrypa impleta* J. de C. SOWERBY,1840, were incorrectly lumped together with *Rhynchonella cuboides* (e.g. WHIDBORNE,1893, p. 135 considered the two species as "shapes of *R. cuboides*"). It is enough to have a look at DAVIDSON's figures (1865, pl. 13, figs. 16-21) to conclude that more than one taxon is included in his conception of *R. cuboides*. Closer to us the specimen of *Hypothyridina cuboides* figured in the 4th edition of the British Palaeozoic Fossils (1996, pl. 34, fig. 5) is very different from the holotype of the species. For the time being we are almost (the reservation is due to the problem connected with the holotype) certain that *Hypothyridina cuboides* is part of the fauna. The author does not feel confident – too much information is lacking, especially concerning the internal characters of the taxa under consideration – that the late Eifelian species *Glosshypothyridina procuboides* from the Eifel region and Belgium, and the genus itself, are present in the late Givetian Lummaton fauna (see above). Other examples exist of late Eifelian rhynchonellid species from the Eifel region incorrectly reported in the late Givetian Massenkalk from Sauerland and the Lahnmulde; *Isopoma brachyptyctum* (SCHNUR, 1853) is one of them. It is also not excluded that

Tullypothyridina n. gen. could be represented in the fauna. In no case should sight be lost of the fact that d'ORBIGNY (1850, p. 93) gave the name *Atrypa subcuboides* to the South Devon species erroneously identified as *Terebratula cuboides* by PHILLIPS (1841, p. 84, pl. 34, fig. 150). This name is available.

For reasons given above, the following comparison with *Glosshypothyridina* is based only on its type species, the late Eifelian *G. procuboides* from the Eifel area. Due to lack of satisfactory information on their internal characters, the author cannot consider as definite the assignment to the genus of the following two small species from the Kuznetsk Basin: *G. batschatensis* (RZHONSNITSKAYA, 1968b) from the late Zlichovian and early and middle Eifelian, and *G. vulgaris* (RZHONSNITSKAYA, 1968b) from the late Eifelian.

Glosshypothyridina and *Tullypothyridina* n. gen. exhibit some similar features: medium size; dorsibiconvex, the dorsal valve being considerably deeper than the ventral valve; the contour of dorsal and ventral valve in cardinal profile; the lateral parts of the anterior commissure at right angle to the lateral commissures; the lateral commissures located quite ventrally; the cardinal commissure sticking out as a result of the postero-lateral margins being markedly concave near the commissure; the sulcus and fold well marked, starting imperceptibly; the sulcus very shallow; the fold very low; the high, rectangular, and clearly delineated tongue; the borders of tongue parallel; the upper part of tongue slightly curved posteriorly; the top of tongue slightly (generally) to moderately convex, exceptionally flat, located posterior to maximum length of shell; the dorsal flanks curving abruptly, almost vertical to vertical in their lower half; the top of shell at front or slightly posterior to it; costae well marked, very low, rounded; lateral costae narrower than median costae; ventral median costae and dorsal lateral costae, with median grooves in their anterior part, tending to become flat near the commissure; the presence of parietal costae.

Many characters make *Glosshypothyridina* distinct from *Tullypothyridina* n. gen.: the smaller thickness; the transversely elongated outline, because as a rule width is clearly exceeding length; the subelliptical (long major axis) to subpentagonal contour in ventral and dorsal views; sulcus and fold starting at some distance from the beaks; the commissure more undulated by the costae; the anterior extremity of fold sharply bent towards the commissure with, and as a consequence, a strong convexity of this extremity, and the location of the central part of the anterior commissure always below the top of the shell (due to this marginal bend the median costae are cut in such a way that they seem to be divided); a longer hinge line; a shallower ventral valve which is slightly convex or flat with the exception of the umbonal region which is moderately convex; a sulcus widening more rapidly towards the front, wider at front, and with an usually slightly deeper central part; a longer interarea; a dorsal umbonal region rarely inflated and, consequently, extending exceptionally beyond the ventral umbonal region; the simple and narrower costae starting at some distance from the beaks; a slightly different distribution of costae (ten to fourteen median costae, fifteen to twenty-four lateral costae); wider furrows and grooves.

Internal characters of *Glosshypothyridina procuboides* are insufficiently known to allow a valid comparison with those of *Tullypothyridina venustula*. Serial transverse sections given by SCHMIDT (1941, pl. 7, figs. 19a-e as *Hypothyridina procuboides*; in SCHMIDT & MCLAREN 1965, figs. 442, 2a-d, p. H570 as *H. procuboides*) are contradictory, because the serial transverse sections published in 1965 show a kind of septum and septalium not seen in the sections published in 1941, and about which she wrote (p. H569) that they were "scarcely discernible". These sections have been incorporated in the new Treatise by SAVAGE (2002, fig. 766, 1c-j, p. 1129). Dental plates are thin in both species, but in *Glosshypothyridina procuboides* umbonal cavities are wider and deeper, dental plates are not convergent, the cardinal process is more massive, and teeth enter the dental sockets latero-dorsally.

Comparisons with Hypothyridina

Problems related to the genus *Hypothyridina* are both multiple and complex.

It has come into usage to consider *Hypothyridina cuboides* SOWERBY, 1840 as a well-established species, and, consequently, *Hypothyridina* BUCKMAN, 1906, of which it is the type species, as a well-established genus. Reality is quite different. *Hypothyridina* and *H. cuboides* are poorly known.

In order to understand the type species of *Hypothyridina* it is necessary to check the type series, which is restricted to a single specimen, the holotype. This specimen was considered as lost for a long time. ELLIOTT (1961, p. 258) wrote: "Sowerby's figured type (1840, pl. 56, fig. 24), probably selected as a large and distinctive specimen rather than as an average one, as was then the custom, cannot be recognised amongst the relevant material in the Geological Survey Museum". The author of the present paper "discovered" the specimen in the Sedgwick Museum of Cambridge University, where it is deposited under its original name, *Atrypa cuboides*, and given the number H4007 (Pl. 1, figs. 1-5). The specimen comes from the Plymouth Limestone of Plymouth, southern Devon, England. It is assumed that it was collected by the Rev.R.Hennah (see SEDGWICK & MURCHISON, 1840, pp. 692, 703). Photographs of the specimen are given in the present paper (Pl. 1, Figs. 1-5) in order to complement the two wood-cuts of SOWERBY (1840, pl. 56, fig. 24 = anterior and dorsal views) reproduced a few times in the literature: WILLIAMS (1890, pl. 13, figs. 1, 5), LLOYD (1933, pl. 3, fig. 10), SCHMIDT & MCLAREN [1965, fig. 443 (2a,b), p. H570], SIEGFRIED (in KAEVER *et al.*, 1980, pl. 21, figs. 5a,b, p. 147), and SAVAGE (2002, fig. 765, 1a,b, p. 1128).

Despite an extensive search, the author found only two specimens that showed some similarity to the holotype: one from Woolborough quarry figured by DAVIDSON (1865, pl. 13, figs. 16, 16a,b), the other from Lummaton quarries figured by WHIDBORNE (1893, pl. 10, figs. 6, 6a = enlarged specimen). Similarity lies in the large number of median costae (larger than in the holotype), the high tongue, and the very shallow sulcus, but the holotype is smaller, narrower (l/w = 1.05 against 0.78 and 0.70), and has a wider sulcus restricting the width of the ventral flanks. Two other specimens from Plymouth and Torquay referred to by MCCOY (1855, pp. 381-382 numbered H3871 and H3872 from the Sedgwick Museum) show the same similarities and differences, but they are almost twice the size of the holotype.

It is also necessary to give a good definition of *Hypothyridina*. This will remain impossible as long as the problems related to its type species remain unsolved. A proper description was never published, although the genus gives its name to a family. There is no original description and subsequent descriptions refer to one or various taxa *assumed* to belong to it; the type species is unavoidably mentioned, but the single specimen on which the species rests is almost never included in the description or alluded to.

BUCKMAN (1906, p. 324) proposed the name *Hypothyridina* as a substitute for the *Hypothyris* as used by PHILLIPS (1841) and KING (1846, 1850); the latter genus had to be rejected chiefly

for nomenclatorial reasons. The full quotation of BUCKMAN's original text is as follows: "Genus HYPOTHYRIDINA, nom. nov. Genotype *Atrypa cuboides*, Sowerby, = *Hypothyris*, King, Hall & Clarke, Schuchert et al.(non Phillips)". What did the authors BUCKMAN refers to by name actually write? KING (1846, pp. 27, 28, 29, 31, 32-35; 1850, pp. 21, 110-117, 119) included in *Hypothyris* numerous taxa related to one another only by their hypothyrid character (acute apex + subapical foramen), which he considered, as PHILLIPS (1841, p. 45) already did, as the major diagnostic characteristic of the genus. HALL & CLARKE (1893, pp. 200-202; 1894, p. 828) described external and internal characters supposed to be present in a range of species assigned to *Hypothyridina*, but did not specify in which of these species the internal characters were observed. SCHUCHERT (1897, p. 233) simply did not give any description.

If it is easily acceptable that the illustrated holotype of *Hypothyridina cuboides* was unavailable for serial sectioning, it is more difficult to understand that serial transverse sections were never made in any of the numerous "*H. cuboides*" incorrectly identified as such all over the world or in *Tullypothyridina venustula*, all of them represented by a great number of specimens. In the 1965 Treatise, the age of the type species of *Hypothyridina* is given (p. H569) as "probably Upper Devonian", and SCHMIDT [in SCHMIDT & MCLAREN, 1965, figs. 442 (1a,b, 2a-d), p. H570] illustrated the supposed internal characters of the genus by poor serial transverse sections made in two specimens: one Middle Devonian specimen from the Eifel area identified as *H. procuboides* (KAYSER) (4 sections), and two young Upper Devonian specimens from the Dillmulde identified as *H.* sp. cf. *H. impleta* (SOWERBY) (2 sections). The former shows a septum, the latter not. These sections have been included in the new Treatise by SAVAGE (2002, fig. 765, 1f-g, p. 1128 as *H.* sp. cf. *H. impleta*, fig. 766, 1g-j, p. 1129 as *Glosshypothyridina procuboides*). As it is to be expected, if a genus is only defined by a few characters that have not been checked in its type species, and of which some or most are to be found in a few genera, it becomes a catch-all-name. This is the case of *Hypothyridina*.

For all reasons just mentioned no reliable comparison is possible between *Tullypothyridina* n. gen. and *Hypothyridina*. However, it is worthwhile to compare the external characters of *Tullypothyridina venustula* and the holotype of *Hypothyridina cuboides*. They have many characters in common, e.g. medium size; cuboidal outline; cardinal commissure sticking out; narrow hinge line; shallow ventral valve and high dorsal valve; very shallow sulcus and very low fold; high rectangular tongue; upper part of tongue slightly recurved posteriorly; short ventral interarea; strongly inflated dorsal umbonal region, extending beyond ventral umbonal region; vertical dorsal flanks in their lower half; well marked, very low and rounded costae; very narrow furrows; commonly divided median costae; numerous lateral costae (21); presence of parietal costae (1-2/?-?); maximum width of shell occurring about mid-length (47 per cent of shell length anterior to ventral beak). The holotype of *H. cuboides* differs from *Tullypothyridina venustula* by a longitudinally oval outline; sulcus and fold starting further away from the beaks; a relatively wider sulcus; narrower median costae; lateral costae not narrower than median costae; ventral median and dorsal lateral costae not tending to become flat near the commissure; a higher number of median costae (14); an angle of the cardinal commissure (126°) smaller than in average specimens of *T. venustula*); different ratios [l/w: 1.05, t/w: 1.02, t/l: 0.98 as against 0.85 to 0.98, 0.80 to 1.01 (mostly 0.80 to 0.94), and 0.82 to 1.05 (mostly 0.94 to 0.96) respectively]. The following characters could not be compared on account of the state of preservation of the specimen: beginning of costae, and presence or absence of median grooves.

The species to which this single matchless specimen gave its name, although never reassessed, was successful in more than one way: (1) it invaded many regions of the world and the world literature immediately after its establishment (two years after for New York); (2) it influenced various stratigraphic correlations and palaeogeographic reconstructions based on the Frasnian "couches à *cuboides*" or "Cuboides-Schichten" concept; (3) it became the type species of the genus *Hypothyridina*, which has been declared one of the cosmopolitan genera of the Frasnian fauna [or merely a cosmopolitan genus (e.g. SAVAGE, 2002, p. 1127)], and to which a notable number of species of variable age have been assigned; and (4) the genus in turn was designated the type genus of the family Hypothyridinidae in which 24 genera have been definitively or provisionally included. It will remain a mystery why *H. cuboides* was found almost over the all world and generally considered to be of Frasnian age. May be this is due to the magic of the cuboidal shape? Did COOPER (in COOPER *et al.*, 1942, p. 1765) not write: "rotund form and square front make the genus [*Hypothyridina*] easy to recognize, but the identification of species is difficult"?

Tullypothyridina venustula (HALL, 1867)

	1842	Cuboidal atrypa (A. cuboides) - VANUXEM, fig. 41.No.1, p. 163;
	1842	*Cuboidal atrypa*, Cuboidal atrypa - VANUXEM, pp. 164, 165, 166;
	1842	*cuboides*, cuboides - VANUXEM, p. 164;
	1842	Cuboid atrypa - VANUXEM, p. 165;
	1843	Atrypa cuboides?, *Atrypa cuboides*? - HALL, pp. 215, 216, fig. 92.1 (= fig. 41. No.1, p. 163 in VANUXEM, 1842), fig. 93.1;
e.p.	1846	Hypothyris cuboides - KING, p. 28;
	1847	*Terebratula cuboides* Sow. - de VERNEUIL, p. 660;
e.p.	1847	*Terebratula cuboides* Sow. - de VERNEUIL, p. 679, table, pp. 697-698;
	1848	*Terebratula cuboides* - NAUMANN, p. 393;
e.p.	1848	*Terebratula cuboides* - de VERNEUIL (English translation with annotations by HALL), p. 369;
e.p.	1849	*Terebratula cuboides* - de VERNEUIL (English translation with annotations by HALL), p. 219, table;
e.p.	1850	*Atrypa subcuboides*, d'Orb., 1847 - d'ORBIGNY, p. 93, n° 884;
e.p.	1853	*Terebratula cuboides* SOWERBY sp. - GEINITZ, p. 56;
e.p.	1853	*Atrypa subcuboides* d'Orb. - DE RYCKHOLT, p. 8;
	1856	*Rhynchonella cuboïdes* - SANDBERGER & SANDBERGER, p. 507, t.27;
e.p.	1860	*Rhynchonella cuboides* Sow. - d'EICHWALD, p. 762;
	1862	*Rhynchonella cuboides* - NAUMANN, p. 398;
v*	1867	*Rhynchonella venustula* - HALL, pp. 346-348, pl. 54A, figs. 24-43 [figs. 34-39 will be considered by COOPER & WILLIAMS 1935 as a variety (*robusta*)];
	1867	*Rhynchonella subcuboides* - MEEK, p. 94;
	1877	*Rhynchonella venusta* Hall - HALL & WHITFIELD, p. 247;
	1879	*Rhynconella* (sic) *venustula*, Hall - BARRIS, pp. 285- 286;

1880 *Rhynchonella venustula* HALL (*Atrypa cuboides* SOW.) - ROEMER, p. 50;
1880 *Rhynchonella venustula* HALL (*Rhynchonella cuboides*) - ROEMER, p. 51;
1880 *Rhynchonella cuboides* - ROEMER, table, p. 53;
1883 *Rhynchonella venustula* HALL - KAYSER, p. 79;
1884 *Rhynchonella venustula*, Hall - WRIGHT, p. 203;
1884 *Rhynchonella venustula* Hall - WALCOTT, pp. 154, 157;
1885a *Rhynchonella venustula* Hall - CLARKE, p. 60;
1885b *Rhynchonella venustula* HALL - CLARKE, p. 385;
1887 *Rhynchonella venustula* - WILLIAMS, pp. 18, 24, table, p. 27;
1887 *Rhynchonella cuboides* - FRECH, table 2;
1887 *Rhynchonella venusta* (= *cuboides*) - GOSSELET, p. 261;
1889 *Rhynchonella venustula* - MILLER, p. 61;
1889 *Rhynchonella venustula*, Hall - LESLEY, pp. 886, 903-904, figs. 8a, 92.1 (= fig. 41.No.1, p. 163 in VANUXEM, 1842 and figs. 92.1, p. 215, 93.1, p. 216 in HALL, 1843);
1889 *Rhynchonella* (*Stenoschisma*) *venustula* - LESLEY, p. 893;
e.p. 1890 *Rhynchonella venustula* - WILLIAMS, p. 36;
1890 *Rhynchonella venustula*, Hall - WILLIAMS, pp. 490, 492, 493, 494, table, p. 497, pl. 13, figs. 4, 8, 14, 23, 24, 27-29, 31-34;
1891 *Rhynchonella venustula* - WILLIAMS, pp. A142, A143;
1891 *Rhynchonella cuboides* - CLARKE, p. 104;
1891 *Rhynchonella venustula* (= *cuboides*) - KAYSER, p. 96;
1891 *Rhynchonella venustula* - WHITEAVES, p. 232;
e.p. 1891 *Rhynchonella cuboides* (*venustula*) - WHITEAVES, p. 251;
e.p. 1891 *Rhynchonella venustula* (*cuboides*) - WHITEAVES, p. 252;
1893 *Rhynchonella venustula*, Hall - WHIDBORNE, pp. 135, 136;
1893 *Rhynchonella venustula*, Hall - HALL & CLARKE, p. 200;
v* 1893 *Hypothyris venustula*, Hall (= *Rhynchonella cuboides*, Sowerby) - HALL & CLARKE, pl. 60, figs. 49-55 (figs. 49, 50, 52, 55 = pl. 54A, figs. 39, 43, 37, 36 in HALL, 1867);
v* 1894 *Hypothyris venustula*, Hall (= *Rhynchonella cuboides* Sowerby.) - HALL & CLARKE, p. 244, pl. 44, figs. 10-13 (figs. 10-12 = pl. 54A, figs. 39, 43, 37 in HALL, 1867 = pl. 60, figs. 49, 50, 52 in HALL & CLARKE, 1893; fig. 13 = pl. 60, fig. 53 in HALL & CLARKE, 1893);
1895 *Rhynchonella venustula* HALL - HOLZAPFEL, p. 278;
1897 *Rhynchonella cuboides* (= *venustula* HALL) - FRECH, p. 210;
1897 *Rhynchonella cuboides* - FRECH, table 19;
1901 *Rhynchonella cuboides* SOW. resp. *venustula* HALL - DREVERMANN, p. 155;
1901 *Hypothyris cuboides* - CLARKE, p. 135;
1903 *Hypothyris cuboides* Sowerby - LOOMIS, p. 892;
1903 *Hypothyris cuboides* Sowerby - CLELAND, p. 42;
1904 *Rhynchonella cuboides* - CLARKE & LUTHER, pp. 25, 56;
1904 *Hypothyris cuboides* - CLARKE & LUTHER, pp. 25, 56;
1904 *Hypothyris cuboides* Sowerby (sp.) - CLARKE & LUTHER, p. 56;
1904 *Rhynchonella venustula* - CLARKE & LUTHER, p. 56;
e.p. 1904 *Hypothyris cuboides* - CLARKE, p. 382;
1905 *Hypothyris cuboides* - CLARKE & LUTHER, p. 50;
non 1905 Hypothyris cuboides *Sowerby* - CLARKE, p. 64;
1905 *Hypothyris cuboides* - KINDLE in WILLIAMS & KINDLE, p. 70;
e.p. 1908 *Rhynchonella venustula* = *cuboides* - KAYSER, p. 173;
1909 *Hypothyris cuboides* - WELLER, pp. 262, 265;
e.p. 1909 *Hypothyris cuboides* - GRABAU & SHIMER, figs. 366a-d, p. 294 [figs. 366a-d = pl. 54A, figs. 37-39, 42 in HALL, 1867 as *Rhynchonella venustula*; figs. 366a,c = pl. 10, figs. 52, 49 in HALL & CLARKE, 1893 as *Hypothyridina venustula* (*Rhynchonella cuboides*) = pl. 44, figs. 12, 10 in HALL & CLARKE, 1894 as *Hypothyridina venustula* (= *Rhynchonella cuboides*];
1909 *Hypothyris cuboides* (Sowerby) - GRABAU & SHIMER, p. 295;
e.p. 1910 *Hypothyridina cuboides* - SCHUCHERT, p. 542;
1911 *Rhynchonella venustula* HALL - GORTANI, pp. 186, 188;
non 1912 *Rhynchonella cuboides* SOW. var. *venustula* HALL - KLÄHN, p. 32, table, p. 37;
e.p. 1913 *Hypothyris cuboides* - SWARTZ *et al.*, p. 27;
e.p. 1913 *Rhynchonella venustula-cuboides* - PROSSER *et al.*, p. 31;
1913 *Rhynchonella cuboides* - CLARKE & SWARTZ, p. 594;
non 1915 *Rhynchonella* (*Hypothyris*) *cuboides* Sow., var. *venustula* Hall - NALIVKIN, p. 1837;
1915 *Rhynchonella venustula* Hall - NALIVKIN, p. 1838;
non 1915 *Rhynchonella venustula* - NALIVKIN, p. 1838;
non 1916 *Rhynchonella cuboides* var. *venustula* HALL - FRECH, p. 223;
1917 *Hypothyris cuboides* - GRABAU, p. 948;
1917 varietal form of the European *Hypothyris cuboides* (Sowerby) - GRABAU, p. 957;
1917 *Hypothyris venustula* Hall - GRABAU, pp. 957-958;
e.p. 1926 *Hypothyris cuboides* - WEDEKIND, pp. 221, 224;
1928 *Hypothyris venustula* Hall - LEIDHOLD, p. 44, footnote 2;
1929 *Hypothyris cuboides* - SAVAGE, pp. 112, 249;
1930 *Hypothyridina venustula* (Hall) [*H. cuboides*] - COOPER, p. 121;
non 1930 *Hypothyris venustula* Hall. - NALIVKIN, pp. 3, 4, 74-75 *pro parte*, pp. 75, 76, table, p. 153, pp. 169, 184, table, p. 204, p. 219, pl. 4, figs. 25a-d;
1930 *Hypothyris venustula* Hall - NALIVKIN, pp. 74-75 *pro parte*;
1930 *Hypothyris cuboides* - SAVAGE, pp. 17, 18;
1930 *Hypothyris* cf. *cuboides* - SAVAGE, p. 17;
1930 *Hypothyris cuboides* - KINDLE in SAVAGE, p. 18;
1930 *Hypothyris cuboides* (Sowerby)? - SAVAGE, p. 79;
1930 cf. *Hypothyris cuboides* - SAVAGE, p. 142;
1931 *Hypothyris cuboides* (*Hypothyridina venustula*) - GOLDRING, p. 358 *pro parte*, pp. 396, 415, figs. 56H, I, p. 413;
1931 *Hypothyris cuboides* - SAVAGE & SUTTON, p. 445;
1931 *Hypothyridina venustula* - GRABAU, table 36, p. 132, p. 133;
1932 *Hypothyridina* (*Hypothyris*) *cuboides* - von ENGELN, pp. 42, 49, 62;
1932 *Hypothyridina venustula* (Hall) (H. cuboides) - TRAINER, pp. 6, 10;

1932 *Hypothyridina venustula* (Hall) - TRAINER, pp. 7, 8, 10;
non 1933 *Rhynchonella venustula* Hall - NALIVKIN, pp. 208, 209;
1933 *Hypothyridina cuboides* - HUDDLE, p. 304;
1933 *Hypothyridina venustula* - COOPER, p. 540;
1934 *Hypothyridina venustula* - WILLARD, pp. 58, 61;
1934 *Hypothyridina venustula* (Sowerby) - WILLARD, pp. 60, 61;
1935 *Hypothyridina venustula* (Hall) - SMITH, appendix, p. 110;
1935 *Hypothyridina venustula* - CHADWICK, p. 309;
1935a *Hypothyridina venustula* (Hall) - WILLARD, p. 93, figs. 1a-c, p. 94, pp. 95, 96;
? 1935a related to a multicostate variety of *Hypothyridina venustula* - WILLARD, p. 96;
1935b *Hypothyridina venustula* (Hall) - WILLARD, pp. 39, 41;
1935c *Hypothyridina venustula* (Hall) - WILLARD, pp. 1203, 1211;
1935 *Hypothyridina venustula* (Hall) - COOPER & WILLIAMS, p. 795, pl. 56, figs. 2, 3, pp. 800, 801, fig. 3 (= p. 803), pp. 806, 811, 812, 813, 815, 823, 838, 839, 841, list, p. 856, pl. 57, figs. 8, 15;
? 1935 *Hypothyridina venustula* var. - COOPER & WILLIAMS, pl. 56, fig. 1, pp. 810, 812, 823;
v*? 1935 *Hypothyridina venustula robusta* Cooper and Williams, n. var. - COOPER & WILLIAMS, p. 841, list, p. 856, pl. 57, figs. 13, 19;
v*? 1935 *Hypothyridina venustula multicostata* Cooper and Williams, n. var. - COOPER & WILLIAMS, p. 841, list, p. 856, pl. 57, figs. 17, 20;
1935 *Hypothyridina venustula* sensu stricto - COOPER & WILLIAMS, p. 841;
1936 *Hypothyridina venustula* Hall - MAILLIEUX, p. 22;
1937 *Hypothyridina venustula* (Hall) - WILLARD, p. 1245, table 1, p. 1247, p. 1250, pl. 2, figs. 17, 18, 20-22;
non 1938 *Hypothyris venustula* Hall (= *Rhynchonella cuboides* Sow.) - NALIVKIN, pp. 80, 85, pl. 2, fig. 6;
non 1938 *Hypothyris cuboides* Sow. (= *venustula* Hall) - NALIVKIN, p. 81;
non 1938 *Rhynchonella cuboides* (*Hypothyris venustula* Hall) - NALIVKIN, p. 82;
non 1938 *Hypothyris cuboides* Sow. (= *H. venustula* Hall) - NALIVKIN, p. 82;
non 1938 *Hypothyris venustula* - NALIVKIN, p. 83;
1939 *Hypothyridina venustula* (Hall) - WILLARD, pp. 135, 207, 208, 214, 225, 228, table 25, p. 229, pp. 231, 312, 315, 322;
1942 *Hypothyridina venustula* - COOPER in COOPER *et al.*, pp. 1761, 1765, 1786-1787, 1787;
1942a *Rhynchonella venustula* Hall - STAINBROOK, p. 612;
1942a *Hypothyridina venustula* - STAINBROOK, p. 613;
1944 *Hypothyridina venustula* (Hall) - WARREN, p. 114;
1945 *Hypothyridina venustula* - STAINBROOK, p. 10;
1946 *Hypothyridina venustula* (Hall) - CAMPBELL, pp. 861, 863, 864;
non 1947 *Hypothyridina venustula* Hall - NALIVKIN, pp. 17, 27, 31;
1949 *Hypothyridina venustula* - STEVENSON & SKINNER, pp. 30, 31, 33;
non 1953 *Hypothyridina wenustula* (Hall) - RZHONSNITSKAYA, p. 181;
1955 *Hypothyridina venustula* (Hall) - IVANIYA & KRAEVSKAYA, pp. 263, 264;
1956 *Hypothyridina venustula* (Hall.) - BUBLICHENKO, p. 102;
1957 *Hypothyridina venustula* - WILLARD, p. 2303;
non 1957 *Hypothyridina venustula* Hall.- KOMAR, p. 37;
1959 *Hypothyridina venustula* - VEEVERS, pp. 101, 104;
1959 *Hypothyridina venustula* s.s. - VEEVERS, p. 104;
1959 *Hypothyridina venustula robusta* Cooper & Williams 1935 - VEEVERS, p. 104;
1960 *Hypothyridina venustula* Hall - LYASHENKO & TIKHOMIROV, p. 4;
non 1961 *Hypothyridina venustula* Hall. - GORZHEVSKIY & MURATOV, table 1, p. 93;
1963 *Hypothyridina venustula* - FRAKES, p. 189;
1963 *Hypothyridina venustula* - ELLISON, p. 207;
1964 *Hypothyridina venestula* - CHUTE & BROWER, p. 108;
1964 *Hypothyridina venustula* (Hall) - NORRIS in MCLAREN & NORRIS, p. 50;
1964 *Hypothyridina venustula* - RICKARD, Chart Series, No. 4;
1967 *Hypothyridina venustula* (Hall) - COOPER, pp. 702, 704;
1967 *Hypothiridina venustula* - OLIVER *et al.*, fig. 17, p. 1033;
non 1967 *Hypothyridina venustula* Hall - KOMAR, table 3, p. 59, table 5, p. 60;
1968a *Hypothyridina venustula* (Hall) - RZHONSNITSKAYA, p. 261, table 14;
1969 *Hypothyridina venustula* - JOHNSON & FRIEDMAN, pp. 455, 457;
1969 *Hypothyridina venustula* - OLIVER *et al.*, chart;
1969 *Hypothyridina venustula* (Hall) - HECKEL, p. 13;
1970 *Hypothyridina venustula* (Hall) - COOPER, pl. 1, figs. 7, 8 (= pl. 57, fig. 15 *in* COOPER & WILLIAMS, 1935);
non 1973 *Hypothyridina venustula* Hall - BUBLICHENKO & AVROV, p. 70;
1973 *Hypothyridina venustula* Hall - RZHONSNITSKAYA, p. 224;
1973 *Hypothyridina venustula* (Hall) - HECKEL, fig. 4 (= p. 11), pp. 13, 70, 107, appendix B, pp. 193, 194, 195, 196, 197, 198, 202, appendix C, p. 207, appendix C5a, p. 216;
? 1973 *Hypothyridina venustula robusta* - HECKEL, appendix C5a, p. 216;
? 1973 *Hypothyridina venustula multiplicata* - HECKEL, appendix C5a, p. 216;
1974 *Hypothyridina venustula* Hall - BUBLICHENKO, p. 12, table 3 (= p. 20) *pro parte*, pp. 70, 71 *pro parte*, 75, 76;
non 1974 *Hypothyridina venustula* Hall - BUBLICHENKO, p. 16;
non 1974 *Hypothyridina venustula* (Hall), 1867 - BUBLICHENKO, table 3 (= p. 20) *pro parte*, pp. 70-71, pl. 8, figs. 7a,b,v,g;
? 1974 *Hypothyridina venustula multicosta* Cooper et Williams - BUBLICHENKO, p. 70;
non 1975 *Hypothyridina venustula* (Hall) - MENNER & SIDYACHENKO, p. 179;
1975 *Hypothyridina venustula* - RICKARD, pl. 3;
1978 *Hypothyridina venustula* - DE WITT & COLTON, p. A4;
1979 *Hypothyridina venustula* - NORRIS, p. A235, fig. 6, p. A239;

1981 *Hypothyridina venustula* (Hall) - DUTRO, fig. 1 (= p. 69), p. 76, fig. 6 (= p. 77);
1981 *Hypothyridina venustula* - KLAPPER, p. 41;
1982 *Hypothyridina venustula* (Hall, 1867) - COOPER & DUTRO, p. 74;
1984 *Rhynchonella venstula* Hall - XU & YAO, p. 558;
1985 *Hypothyridina venustula* - RICKARD, p. 228;
1985 *Rhynchonella venustula* - KIRCHGASSER *et al.*, p. 245;
1985 *Hypothyridina venustula* - KIRCHGASSER *et al.*, p. 246, table 7, p. 248, pp. 249, 253;
1992 *Hypothyridina venustula* HALL 1867 - SARTENAER & HARTUNG, p. 51;
1994 *Hypothyridina venustula* - LINSLEY, pp. 75, 100, pl. 81 (= p. 186), figs. 19-40 [figs. 21 (= 32)- 24, 26-31, 33-40 = pl. 54A, figs. 39, 43, 30, 31, 37, 34, 35, 32, 33, 38, 26-29, 40, 41, 24, 25 in HALL, 1867; figs. 19, 20, 21 (= 32), 22, 25, 26 = pl. 60, figs. 53, 54, 49-52 in HALL & CLARKE, 1893; figs. 20, 21 (= 32), 22, 26 = pl. 44, figs. 13, 10-12 in HALL & CLARKE, 1894; figs. 21 (= 32), 26, 38 = figs. 366 c,a,b in GRABAU & SHIMER, 1909 as *Hypothyris cuboides*];
non 1994 *Hypothyridina venustula* (Hall) - KOZLOV & DUBATOLOV, p. 29;
1996 *Hypothyridina* cf. *H. cuboides* - BRETT *et al.*, fig. 1, pp. 4-5;
1997 *Hypothyridina venustula* (Hall) - HECKEL, pp. 79, 88.

TYPES

Among the syntypes the specimen figured by HALL (1867, pl. 54A, fig. 42) and by GRABAU & SHIMER (1909, fig. 366d, p. 294 as *Hypothyris cuboides*) is here designated as the lectotype.

Measurements of seven topotypes (A-H; catalogue numbers IRScNB a11971-11977) are given in the present paper (Table 1); four of them (A,C,D,E) have been photographed (Plate 1). An eighth specimen (H; catalogue number IRScNB a 11978) has been sectioned (Text-fig. 1). Localities of topotypes A,C,D,E are indicated in the explanation of Plate 1. Topotypes B,F,G,H come from the same locality as topotypes C,E.

DESCRIPTION

Remark

The only descriptions in the literature are those of HALL (1843, pp. 215, 216 as *Atrypa cuboides*?; 1867, pp. 346-348) in New York and WILLARD (1937, p. 1250) in Pennsylvania. Scraps of descriptions may be found in various publications, e.g. CLARKE (1885b, p. 385 as *Rhynchonella cuboides*), HOLZAPFEL (1895, p. 278 as *R. cuboides*), WILLARD (1935a, pp. 95-96), and COOPER & WILLIAMS (1935, p. 841).

This refers only to specific characters in need of further elaboration.

Width of sulcus at front varying between 55 and 70 per cent (most of the values between 55 and 66 per cent) of

in mm	Topotype A	Topotype B	Topotype C	Topotype D	Topotype E	Topotype F	Topotype G	Holotype *H.v.m.* USNM 89867	Cotype *H.v.r.* USNM 89863
l	22.8	(22.4)	21.6	19.7	19.5	17.6	16	20.5	20.7
w	26.9	25.5	22.1	20.5	22.8	(19.6)	18.2	23.1	22.2
lpv unrolled	39.5	(45)	37.5	39.5	38	34	27.5	38.5	38
t	21.6	23.1	20.2	20.7	18.6	16.5	15.2	19.7	20.8
tpv	6.1	5.3	7.4	4.5	6.4	5.7	5.2	6	6.4
tbv	15.5	17.8	12.8	16.2	12.2	10.8	10	13.7	14.4
l/w	0.85	(0.88)	0.98	0.96	0.86	(0.90)	0.88	0.89	0.93
t/w	0.80	0.91	0.91	1.01	0.82	(0.84)	0.84	0.85	0.94
t/l	0.95	(1.03)	0.94	1.05	0.82	0.94	0.95	0.96	1
apical angle	132°	?	115°	?	138°	134°	136°	137°	135°
angle of the cardinal commissure	142°	?	(117°)	?	147°	140°	?	147°	139°

Table 1 — Measurements (in mm) based on 9 specimens; figures in parentheses are reasonable estimates on damaged specimens. Abbreviations used: l = length; w = width; t = thickness; pv = ventral valve; bv = dorsal valve. *H.v.m.= Hypothyridina venustula multicostata*. *H.v.r. = H. venustula robusta*.

the shell width; 77 per cent is the width of sulcus of COOPER and WILLIAMS's (1935) figured specimen of the variety *multicostata* (Pl. 1, Figs. 26-30). Top of tongue located at a point between 7 and 33 per cent posterior to maximum shell length. Length of ventral interarea around one third of the shell width. According to COOPER & WILLIAMS (1935, p. 841), who studied "many hundred specimens", the number of median costae varies between 3 and 14 (see also the introductory remarks to the description of the new genus). The number of lateral costae varies between 13 and 19. Width of median costae at front varies from 1 to 1.5 mm.

Measurements of nine specimens, of which six have been photographed, are given on Table 1. Columns 1 to 5, 8, 9 refer to adult specimens [column 1 to the largest specimen at the author's disposal; columns 8 and 9 to COOPER & WILLIAMS's (1935) varieties *multicostata* and *rotunda* respectively], columns 6 and 7 to ephebic specimens.

Although length, width and thickness are only slightly different, width is the greatest dimension, while thickness is only exceptionally greater than length. Thickness of dorsal valve varying between 63 and 79 per cent of the shell thickness. Maximum thickness of ventral valve located at a point varying between 29 and 47 per cent of the shell length anterior to the ventral beak. Maximum width occurs at a point between 41 and 58 per cent (most of the values varying between 46 and 55 per cent) of the shell length anterior to the ventral beak. Apical angle varying generally between 133° and 140°, the angle of the cardinal commissure between 140° and 147°; specimen of column 3 on Table 1 is an exception.

Transverse serial sections of one specimen (topotype H, IRScNB a 11978) are shown in Text-figure 1; they are the first sections ever made in a specimen of *Tullypothyridina venustula*.

DISCUSSION OF SYNONYMY

Although rather complete, the synonymy list is by no means exhaustive, chiefly because the species is very often mentioned in the Tully Formation under its generic name alone. The list shows that the confusion of the New York species with the South Devon species, of which it was sometimes considered as a mere variety, lasted until 1938. WILLIAMS (1890, p. 494) and HALL & CLARKE (1893, p. 200) even referred to *Rhynchonella venustula* as the American "type" or "representative" of the European species. Outside of North America the species has been erroneously mentioned (sometimes as a variety) in rocks of Frasnian age in Germany (Aachen region), Kazakhstan, Russia (Altai Mountains, Arctic region, Urals, Siberia), and Uzbekistan, these citations are placed in negative synonymy. "e.p. " in front of some references means that they include also, but not only, the New York species.

For explanation of the question marks see, on pages 42-43, "Varieties" of *Tullypothyridina venustula*.

COMPARISONS

For comparisons with *Tullypothyridina? intermedia* see Species attributed to the genus (page 31).

STRATIGRAPHICAL RANGE, GEOGRAPHICAL DISTRIBUTION, AND INTERNATIONAL CORRELATIONS

Assignment of the Tully Limestone to the Frasnian

Although the specific identity of *Tullypothyridina venustula* and its late Givetian age are clearly established, a few words have to be written on the misconceptions that influenced the early history of the species: (1) the incorrect identification (*cuboides* instead of *venustula*); (2) the early Frasnian age given to the Tully Limestone of central New York instead of a late Givetian one; (3) the correlation of this Tully Limestone with Frasnian beds (Cuboides-Schichten, horizon, zone, stage, fauna, Kalk; Iberger Kalk; etc...) of various parts of the world [generally with western Europe (from France in the west to the Ural Mountains in the east), sometimes with China, Siberia, Iran, and Iowa], this implying the acceptance in all these regions of one and the same species, *Hypothyridina cuboides*, which is represented by a single specimen (the holotype) of late Givetian age in its type area in South Devon.

The story started with VANUXEM (1842, p. 164), who wrote that the "precise position which the *cuboides* [Atrypa cuboides is one of his identifications of the New York species (see Synonymy)] holds in New-York, will soon determine the position of its kindred one in England" (see further details in the Introduction).

As mentioned in the introduction (see also Species assigned to the genus), VANUXEM considered the New York species and the South Devon species called *Terebratula cuboides* by PHILLIPS (1841) as identical, and belonging most probably to *Tullypothyridina* n. gen., and certainly not to the genus *Hypothyridina* with type species *H. cuboides* (SOWERBY, 1840).

After VANUXEM only the SANDBERGERS (1856, p. 507) were close to reality in stating that the Tully limestone containing *Rhynchonella cuboïdes* J. SOW. sp. was equivalent ("belonged") to the Stringocephalenkalk. Other scientists brushed the late Givetian species aside for one or two of the reasons mentioned above or for all of them, and adopted as a yard-stick for *Hypothyridina cuboides* various Frasnian species from western Europe to which this name was unduly given. These are:

HALL (1843, pp. 215-216); de VERNEUIL [1847, pp. 646-647, 660, 669-670, 679, 697-698, table; see also the translation and coments on this paper by HALL (1848, pp. 176-177, 359-360, 369; 1849, table, pp. 219, 229); see further details in the Introduction]; CLARKE (1885a, p. 60; 1885b, p. 385; 1901, p. 135); WILLIAMS [in FRAZER (translated into French by G. DEWALQUE), 1888, p. 12; 1889, p. 22; 1890, pp. 481, 482, 484, 485, 489, 492, 494, 496, 498-499 (the least that can be written of this publication, based on an erroneous conception of relative contemporaneity (= homotaxy), was clearly expressed by COOPER (in COOPER *et al.* 1942, p. 1786): "In discussing the Tully fauna H.S.Williams neither considered nor understood the entire fauna"]; 1891, pp. A141-A143, A145); WHITEAVES (1891, pp. 251-252); KAYSER (1891, p. 96, table, p. 98; 1908, table, p. 171, p. 173, table, p. 179); HALL & CLARKE (1893, explanation of plate 60; 1894, p. 244, explanation of plate 44; see further details in the Introduction); FRECH (1897, p. 210, table 19); LOOMIS (1903, p. 892); CLELAND (1903, p. 42); CLARKE (1904, p. 382); CLARKE & LUTHER (1904, pp. 25, 56; 1905, p. 50); WELLER (1909, pp. 262, 263, 265-266, 268); SCHUCHERT (1910, table, p. 541, p. 542); ULRICH (1911, correlation chart 2); PROSSER *et al.* (1913, p. 31); SWARTZ *et al.* (1913, p. 27); CLARKE & SWARTZ (1913, p. 594); GRABAU (1917, pp. 945, 947, 949, 956, 957-958); WEDEKIND (1926, pp. 221, 224); SAVAGE (1929, pp. 112, 149; 1930, p. 142); COOPER (1930, pp. 121-122); GOLDRING (1931, pp. 358, 396,

415); TRAINER (1932, p. 8); von ENGELN (1932, pp. 42, 48-49, 62); WILLARD [1934, p. 57; 1935a, p. 93; 1935b, pp. 39, 41, 42, 44; 1935c, p. 1217 (credence withheld on account of "the evident disagreement among recent students of New York Devonian stratigraphy"); 1937, pp. 1239, 1244, 1246, 1253; 1939, pp. 207, 208; 1957, p. 2303); COOPER & WILLIAMS (1935, p. 783); MAILLIEUX (1936, p. 22); STAINBROOK (1942a, p. 604; 1942b, p. 889; 1945, pp. 1, 9, 10-11; 1948, pp. 788, 789); BRINKMANN (1948, table between p. 70 and p. 71); LYASHENKO & TIKHOMIROV [1960, p. 4; *Hypothyridina venustula* and *H. calva* are considered as vicarious species, but the latter is mentioned in various uppermost Lower Frasnian formations (Ust'yarega in South Timan, Sargaevo in the Volga-Urals region, and Khvorostan in the Russian Platform); HOUSE [1962, pp. 255-256 with some reservations, pp. 263-264, table 3, p. 265, pp. 272-273 in West Brook Member, 273 with some reservation, p. 274 in Apulia Member (probably); 1965, fig. 1, p. 82, p. 83; 1967, p. 1065 in West Brook Member, p. 1067; 1973, pp. 4, 8); 1975, pp. 271, 273, table 2, p. 274; 1982, pp. 449-459; for the publications here mentioned, it must be borne in mind that HOUSE kept arguing that the base of the Tully Formation, the "Assise de Fromelennes", and the *lunulicosta* Zone should be considered as the base of the Frasnian]; FRAKES (1963, pp. 183, 188); CHUTE & BROWER (1964, p. 108, appendix, p. 126); RICKARD (1964, chart; 1985, p. 228 *pro parte*); SCHMIDT (in SCHMIDT & MCLAREN 1965, p. H569); JOHNSON & FRIEDMAN (1969, pp. 451, 452); SELLECK & HALL (1977, p. B-8, 22).

Assignment of the Tully Limestone to the Givetian

"Although the Tully fauna is now regarded as Upper Devonian, the predominant Hamilton elements would suggest an earlier age"; this sentence written by COOPER & WILLIAMS (1935, p. 824) set the pace for a drastic shift in what had been the North American position for almost fifty years with regard to the age of the Tully Limestone. The same year CHADWICK (1935, p. 309) also made some reservations on the Frasnian age of the Tully Limestone in writing among other things that the "paleontologic claim for Upper Devonian age of the Tully limestone rests, therefore, upon the single species, *Hypothyridina cuboides*, and on its identification with the European *H. cuboides*". This reversal of thinking was echoed by WELLS (1940, pp. 502, 503-504), and formalized by COOPER (*in* COOPER *et al.* 1942, pp. 1733, 1740, 1750, 1765, 1786-1789, chart N° 4; 1944, pp. 217-218).

This was not the end of the controversy. As will be gathered from the post-1942 references given above, although a few rallied to the prevailing opinion (see below), some scientists kept on maintaining that the Tully Limestone was of early Frasnian age, and anyhow that any "modification" had to be approved by an international decision. Therefore, COOPER (1967, pp. 701, 703-704, 706, 707, 708) found himself constrained to restate his opinion in strong words: "a particular group of animals [goniatites] has been regarded as having higher value in age assignment and correlation than any other" (p. 701). A similar wording was used by COOPER & GRANT (1973, pp. 364-365). Is this the reason why HECKEL (1973, p. 5) chose to brush aside, as he already did in 1969, the problem of the age of this limestone? After a last wavering by RICKARD (1975, pl. 3, p. 9), who left the placing of the Givetian/Frasnian boundary as querried, the following references indicate that the late Givetian age of the Tully Limestone was not questioned any more:

OLIVER *et al.* (1967, fig. 4, pp. 1006-1007, p. 1020, fig. 17, p. 1033, p. 1034; conflicting views are put clearly; 1969, chart); OLIVER (1967, p. 734, fig. 1, p. 735, p. 743); RZHONSNITSKAYA (1968a, table 15, pp. 258-259, p. 261, table 14; conflicting views are reported, but comparison is attempted with beds of early Frasnian age in the USSR; 1973, p. 224; the author sides with the consensus on the late Givetian age of the Tully Formation, but keeps on comparing its fauna with the one of the early Frasnian beds from the Urals); NORRIS [1979; "the problem of the boundary between the Middle and Upper Devonian" is declared "as yet unresolved" (p. A235), but the Tully is incorporated in the late Givetian (Taghanic) on fig. 6 (= p. A239); readers must take into account that the manuscript was submitted in 1969)]; RICKARD (1985, p. 228 *pro parte*); KIRCHGASSER *et al.* (1985, table 7, p. 248); HOUSE & KIRCHGASSER (1993, p. 283; see remark above on HOUSE's position regarding the base of the Frasnian).

During the same period results of conodont investigations, confirming the late Givetian age of the Tully Formation, started to be published: KLAPPER & ZIEGLER (1967, fig. 1, p. 71, pp. 72, 79); ORR & KLAPPER (1968, p. 1066, fig. 1, p. 1067, pp. 1067-1068); ORR (1971, fig. 4, p. 10, pp. 13, 18); KLAPPER *et al.* (1971, fig. 2, p. 294, p. 297, fig. 3, p. 298); ZIEGLER *et al.* (1976, p. 110, fig. 1, p. 111, pp. 113, 114, 116, tables 1, 2, p. 117, table 3, p. 118, table 4, p. 119); KLAPPER (1981a, pp. 61-63, fig. 2, p. 62).

The debate was thus closed, and the International Subcommission on the Devonian System decided in 1982 to consider the base of the Lower *Mesotaxis asymmetrica* Zone as the base of the Frasnian, i.e. where the Givetian/Frasnian boundary was historically placed. This decision was ratified during the 26th International Congress of Geology (Moscow, 1984).

Range of Tullypothyridina venustula in the Tully Formation of central New York

In central New York the Tully Formation extends as a limestone unit for nearly 100 miles along outcrop from Canandaigua Lake to Chenango Valley; it reaches its maximum thickness of 30 to 35 feet at its type section north-east of Tully in Onondaga County. The numerous localities where *Tullypothyridina venustula* has been collected may be found in the publications on New York mentioned in the References, VANUXEM (1842), COOPER & WILLIAMS (1935), and HECKEL (1973) being the most relevant.

The Tully Formation was subdivided into three parts by COOPER & WILLIAMS (1935). The middle subdivision was called the Apulia Member from the westernmost extension of the formation (Canandaigua Lake) to the Unadilla Valley [the upper subdivision being in this area the West Brook Member, and the lower one the Tinkers Falls Member, which is only locally (Owasco Valley to Otselic Valley) developed]. In the easternmost extension of the formation, i.e. from the Unadilla Valley to Schenevus, the middle subdivision was called the Laurens Member [the upper subdivision being in this area also the West Brook Member and the lower one (from Unadilla Valley to Otego Valley) the New Lisbon Member]. HECKEL (1973, p. 12), arguing that COOPER & WILLIAMS's (1935) members were biostratigraphic units, replaced them by rock-stratigraphic ones. He subdivided the Tully Limestone in west-central New York into a Lower and an Upper Member, the Lower Member being subdivided into seven beds (from base to top: De Ruyter, Cuyler, Fabius, Meeker Hill, Tully Valley, Vesper, and Carpenter Falls), and the Upper Member into five beds (from base to top: Smyrna, Taughannock Falls, Bellona, Moravia, and Fillmore Glen); the Lower and Upper Members were already proposed by HECKEL (1969, fig. 2, p. 4, p. 5). The Lower Member plus the lowermost bed (Smyrna bed) of the

Upper Member correspond to COOPER & WILLIAMS's (1935) Apulia Member, and the other beds of the Upper Member to their West Brook Member.

To the east (Otsego County) HECKEL subdivided what he called the Tully equivalent into a Lower Tully and an Upper Tully equivalent, the Lower Tully equivalent being in turn subdivided into a lower and an upper part, and the Upper Tully equivalent into four subdivisions (from base to top: Smyrna, unnamed sandstone, West Brook shale, *Metriophyllum* zone of the Unadilla Formation). The upper part, plus eventually the Smyrna bed, correspond to COOPER & WILLIAMS's (1935) Laurens Member, the other subdivisions of the Upper Tully equivalent to the West Brook Member. At Borodino, between Skaneateles and Otisco Lakes, HECKEL (1973) recognized an Upper Member [of the Tully Formation] mound complex (already introduced in 1969, fig. 2, p. 4); he subdivided it into a lower and an upper mound considered as lateral equivalents of the Taughannock Falls and the Moravia beds respectively. According to HECKEL (1973, pp. 13, 20, 22-23, 27, 35, 57, 85, 87, 91, 145, 155, 193, 194, 195, 198, 202, 204, appendix C5a, p. 216) *Hypothyridina venustula* is found in the Lower Member of the Tully Limestone (abundant in several zones), the Lower Tully equivalent, the De Ruyter (common to the west, rare to the east), Fabius (locally abundant), Tully Valley (rare), Carpenter Falls (locally abundant), Smyrna (locally common), Taughannock Falls (rare in west) beds, lower mound (rare), and upper mound (questionable and rare). This corresponds closely with COOPER & WILLIAMS's (1935, p. 795, pl. 56, figs. 1-3, pp. 800, 801, 806, 810, 811, 812, 815, 841, list, p. 856, pp. 861, 862) and COOPER's (1967, pp. 702, 703) observations; they found *H. venustula* in abundance in the Apulia and Laurens Members, and very rarely in the West Brook Member.

Thus, the species is rare and questionable above the Taughannock Falls bed and its lateral equivalent, the lower mound, and in the upper mound; it is absent in the highest bed (Fillmore Glen) of the Upper Member of the Tully Formation.

ZIEGLER *et al.* (1976, p. 110, fig. 1, p. 111, pp. 113, 114, 116) and KLAPPER (1981a, pp. 61-63, fig. 2, p. 62) consider the Tully Formation as corresponding to the upper part of the Middle *Polygnathus varcus* Zone (the zone starts with the limestone bed at the top of the Kashong Member of the underlying Moscow Formation), which extends to the Moravia bed, and to the Upper *P. varcus* Zone extending from the upper part of the Moravia bed to the top of the Fillmore Glen bed. According to the information given above, *Tullypothyridina venustula* is absent in the highest part of the Tully Formation, and its range in terms of the conodont zonation is as follows: upper part of the Middle *Polygnathus varcus* Zone, and possibly the lower part of the Upper *P. varcus* Zone.

Presence of Tullypothyridina venustula outside of New York

T. venustula has been mentioned for a long time in Pennsylvania (WILLARD 1934, 1935a, 1935b, 1935c, 1937, 1939, 1957; COOPER *in* COOPER *et al.*, 1942; STEVENSON & SKINNER 1949; ELLISON 1963; FRAKES 1963; HECKEL 1969, 1973; see Synonymy) in beds correlated with the Tully Formation of central New York. The Tully Formation of Pennsylvania is shalier and is known from outcrops in south-west, west-central, central, and east-central parts of the State as well a from bore-holes in its northern and western parts. Depending on the location of outcrops WILLARD (1934, p. 61; 1935a, pp. 93, 96; 1935b, pp. 41, 42; 1937, pp. 1244, 1245, 1250; 1939, pp. 135, 208, 214, 235) suggested correlations with the Apulia, Laurens, Tinkers Falls, and West Brook Members of the Tully Formation of central New York.

In the Estill and Powell Counties of east-central Kentucky SAVAGE (1929, pp. 112, 249; 1930, pp. 17-19, 78-79, 142; *in* SAVAGE & SUTTON 1931, p. 445 as *Hypothyris cuboides*, identified by E.M. Kindle) recognized the species in the Duffin layer (i.e. the basal layer of the New Albany shale) and in other hard layers interbedded with the black shale in the lower part of the New Albany shale; he correlated these beds with the Tully Formation of central New York. This finding was confirmed by HUDDLE (1933, p. 304 as *Hypothyridina cuboides*), COOPER (in COOPER *et al.* 1942, pp. 1761, 1787-1788; 1944, pp. 217-218; 1957, p. 270; 1967, p. 704 as *H. venustula* and *Hypothyridina*), HECKEL (1973, p. 67 as *Hypothyridina*), and CAMPBELL (1946, fig. 4, p. 860, pp. 861, 862, 863, 864, 867, 868, 902, pls.1, 2 as *H. venustula* and *Hypothyridina*).

The Tullypothyridina venustula Zone

One or more *H. venustula* and/or *Hypothyridina* zones (exceptionally called assemblage zones) have now and then been mentioned in a loose way in the literature. A single zone has been considered as equivalent either to the Tully Limestone or to its middle part or to one of its members (Apulia Member). Sometimes the word "zone" has been used to indicate the presence of the species or the genus in one bed (e.g. Carpenter Falls bed). In one case three *Hypothyridina* zones have been recognized in the Laurens member near New Lisbon (COOPER & WILLIAMS, 1935, pp. 810-811, pl. 56, fig. 2).

The *Tullypothyridina venustula* Zone is considered in the present paper as a range zone.

"Varieties" of *Tullypothyridina venustula*

COOPER & WILLIAMS (1935, p. 841, list, p. 856, pl. 57, figs. 13, 17, 19, 20) formally established two varieties, *Hypothyridina venustula multicostata* (Pl. 1, Figs. 26-30) and *H. venustula robusta* (Pl. 1, Figs. 31-35, 40) found in the Apulia Member of the Tully Formation, and considered as "end products of the variation observed". These varieties, which nowadays have to be considered as subspecies, are more completely illustrated in the present paper (Pl. 1, Figs. 26-35). These authors (1935, p. 841), who did not accept a "specific separation", stated that the "most useful character" for assessing the variation of the species "proved to be the costation of the tongue and sulcus". According to COOPER & WILLIAMS (1935, p. 841, explanation of plates, pp. 861-862), *H. venustula multicostata*, which has an "exceedingly wide tongue, bearing from nine to fourteen costae", "seems to be confined to western New York", notably near Ovid, while *H. venustula robusta*, "which is most abundant at Tinkers Falls, Fabius, Cuyler, and vicinity", is an "usually robust variety" "characterized by three to six large costae on the tongue", and "a very narrow tongue and a consequent drawing of the antero-median angles of the shell toward the mid-line". These two varieties were not the only ones COOPER & WILLIAMS (1935, p. 823) grouped under "*H. venustula* , and varieties"; they mentioned two other varieties (p. 810, p. 812, pl. 56, fig. 1 as *H. venustula* var.) in the Laurens Member of the Tully Formation at 1½ miles east of New Lisbon, and 1½ miles northeast of Laurens. One of these unnamed varieties is probably the "multicostate eastern [Otsego County] New York variety" from the Laurens Member to which, according to WILLARD (1935a, p. 96), the specimens of *H. venustula* from central Pennsylvania (South Danville) are "most closely related".

According to HECKEL (1973, appendix C5a, p. 216), *Hypothyridina venustula multicostata* (called *multiplicata* by mis-

take) "often dominates in the higher and western parts of the Lower Tully, and is the only form of this species seen in the Upper Tully", while *H. venustula robusta* "is dominant and essentially restricted to the zone in the basal layer of the eastern part of the Fabius bed".

Are these two varieties (now subspecies), which have a restricted range in the geographically separated areas in which they are found, entering the variability of *H. venustula* or not? They are opposed by COOPER & WILLIAMS (1935, p. 841) and by HECKEL (1973, appendix C5a, p. 216) to an "*H. venustula* sensu stricto" and a "normal form" respectively. Although COOPER & WILLIAMS's (1935, p. 841) reluctance to accept specific separation was based on the investigation of many hundreds of specimens, their examination was carried out on the collection taken as a whole, and not bed by bed. The status of the unnammed varieties needs also to be assessed. Until such information becomes available, the author prefers to adopt a conservative attitude and includes *H. venustula multicostata* and *H. venustula robusta* in the synonymy of the species with a question mark.

Conclusions

It is necessary to try to escape the dilemna due to the poor definition and the misconception of the species *Hypothyridina cuboides*, the genus *Hypothyridina*, and the family Hypothyridinidae.

The purpose of this paper is to clear the way for further investigations. Collections from the Dinant Basin are at present under examination. In using the expression "*H. cuboides*", the author (1977, p. 67) indicated clearly his reluctance to accept the presence of the South Devon species in the Frasnian of Belgium. It is evident that most "*H. cuboides*" of the literature, which some authors, e.g. SCHMIDT (1941, p. 27), ELLIOTT (1961, p. 258), and DROT (1971, p. 78), distinguished as *H. cuboides* auct., belong neither to the species nor to the genus. They will have to be assigned to a few new genera and species, and not to a single genus as suggested by ELLIOTT (1961, p. 258), who wrote that "*H. cuboides* auct. from the Upper Devonian needs a new name". SCHMIDT (1941, p. 27) assessed the situation correctly when she stated that "*H. cuboides* auct. scheint selber keine einheitliche Art zu sein, sondern mehrere zu trennende Formen zu enthalten". Prior to the establishment of the new genera, large collections will have to be examined afresh, in particular in the areas where the "couches à *cuboides*" or "Cuboides-Schichten" concept prevailed, i.e. Belgium and France (Dinant Basin), Germany (Aachen region, Eifel), Poland, and Urals.

Lectotypes have been selected in the present paper for *Glosshypothyridina procuboides* (KAYSER, 1871) (p. 33), *Tullypothyridina intermedia* (BARRIS, 1879) (p. 31), and *T. venustula* (HALL, 1867) (p. 39).

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Explanation of Plate 1

All figures are natual size

Figs. 1-5 — *Atrypa cuboides* SOWERBY, 1840. Holotype, H4007, Sedgwick Museum, Cambridge University, England (= pl. 56, fig. 24 in SOWERBY, 1840). Plymouth, southern Devon. Plymouth Limestone. Collector: Rev. R. Hennah. Ventral, dorsal, anterior, posterior, and lateral views. Costal formula: $\frac{14}{14}; \frac{1-2}{?-?}; \frac{21}{?}$.

Figs. 6-10 — *Tullypothyridina venustula* (HALL, 1867). Topotype A, IRScNB a11971. Tinkers Falls Labrador Valley, central New York. Tully Formation, Apulia Member. Collector: P. Sartenaer, 1959. Ventral, dorsal, anterior, posterior, and lateral views. Costal formula: $\frac{8}{7}; \frac{1-1}{1-1}; \frac{17}{18}$.

Figs. 11-15 — *Tullypothyridina venustula* (HALL, 1867). Topotype E, IRScNB a11975. June's quarry, type locality of the Tully Limestone, central New York. Tully Formation, Apulia Member. Collector: P. Sartenaer, 1959. Ventral, dorsal, anterior, posterior, and lateral views. Costal formula: $\frac{8}{8}; \frac{1-2}{1-1}; \frac{18}{19}$.

Figs. 16-20 — *Tullypothyridina venustula* (HALL, 1867). Topotype C, IRScNB a11973. Same locality and collector. Ventral, dorsal, anterior, posterior, and lateral views. Costal formula: $\frac{7}{6}; \frac{2-2}{2-1}; \frac{16}{17}$.

Figs. 21-25 — *Tullypothyridina venustula* (HALL, 1867). Topotype D, IRScNB a11974. Bucktail Falls, Otisco Valley, central New York. Tully Formation, Tinkers Falls Member. Collector: P. Sartenaer, 1959. Ventral, dorsal, anterior, posterior, and lateral views. Costal formula: $\frac{8}{9}; \frac{2-1}{2-1}; \frac{16}{17}$.

Figs. 26-30 — *Hypothyridina venustula multicostata* COOPER & WILLIAMS, 1935. Holotype, USNM (United States National Museum) 89867 (= pl. 57, figs. 17, 20 in COOPER & WILLIAMS, 1935). Chamberlin's Quarry, 1½ miles north-northeast of Ovid, central New York. Tully Formation, Apulia Member. Collectors: G.A. Cooper & J.S. Williams, 1933. Ventral, dorsal, anterior, posterior, and lateral views. Costal formula: $\frac{15}{14}; \frac{0-1}{0-1}; \frac{18}{19}$.

Figs. 31-35 — *Hypothyridina venustula robusta* COOPER & WILLIAMS, 1935. Cotype, USNM 89863 (= pl. 57, fig. 13 in COOPER & WILLIAMS, 1935). 2½ miles south of Fabius, central New York. Tully Formation, Apulia Member. Collectors: G.A. Cooper & J.S. Williams, 1933. Ventral, dorsal, anterior, posterior, and lateral views. Costal formula: $\frac{6}{5}; \frac{1-1}{1-1}; \frac{13}{14}$.

Figs. 36-39 — *Hypothyris venustula* HALL, 1867 (= *Rhynchonella cuboides*, SOWERBY). Topotype, Pal.Col. 12426, Department of Geology, Field Museum of Natural History, Chicago (specimen previously housed in the Walker Museum) (= pl. 60, fig. 54 in HALL & CLARKE, 1893). Ovid, central New York. Tully Limestone. Collector: J. Hall. Ventral, dorsal, anterior, and lateral views.

Fig. 40 — *Hypothyridina venustula robusta* COOPER & WILLIAMS, 1935. Cotype, USNM 89863a (= pl. 57, fig. 19 in COOPER & WILLIAMS, 1935). Same locality and collectors as for cotype USNM 89863. Ventral view.

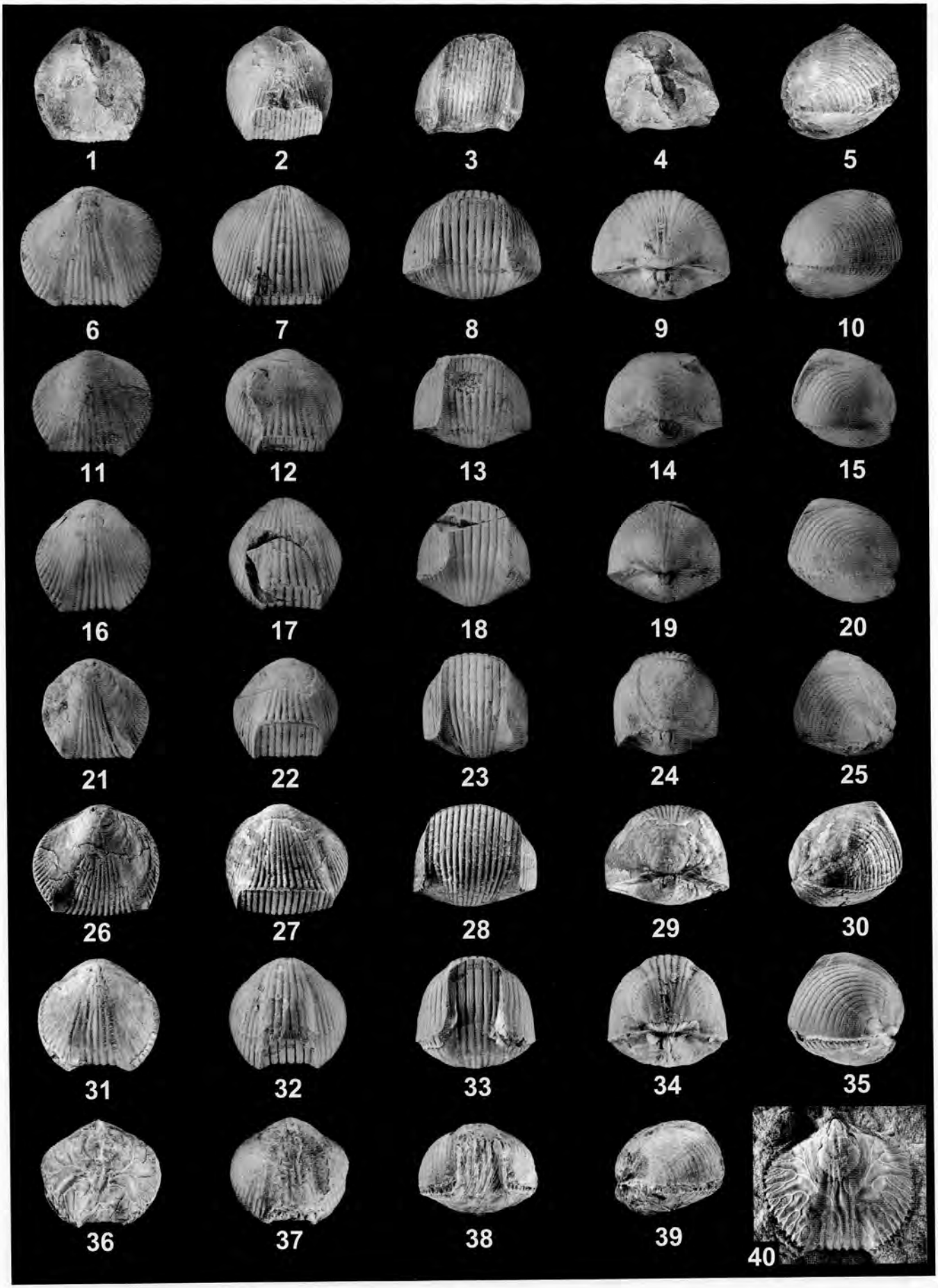
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PLATE 1