

Re-examination of the Late Emsian rhynchonellid (brachiopod) *Terebratula Daleidensis* ROEMER, 1844 from the Eifel area, and of some related species

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Abstract

The Upper Emsian *Terebratula Daleidensis* ROEMER, 1844 (now *Oligoptycherhynchus daleidensis*) from the Daleiden “MuldenGruppe”, Eifel area, is scrutinized. The ubiquity and considerable stratigraphic range gained by the species in the course of time are exposed and questioned. After examination of the lectotype, here designated, and rich existing collections, return to the original definition of this abundant species is recommended. *Rhynchonella inaurita* SANDBERGER, G. & F., 1856, commonly mistaken for *daleidensis*, is assigned to *Inaequalibellirostrum* n. gen., the type genus of Inaequalibellirostridae n. fam. The geographic distribution, the stratigraphic range, and affinities of the type species of the new genus, *I. pareti* (de VERNEUIL, 1850a) from the middle part of the Emsian of the Cantabrian Cordillera (Province of Leon) resulted, among others, in the reassessment of the genus *Stenorhynchia* BRICE, 1981, and its questionable presence in the Armorican Massif.

Keywords: *Oligoptycherhynchus daleidensis*, *Inaequalibellirostrum*, Inaequalibellirostridae, rhynchonellids, brachiopods, Emsian, Eifel area, Cantabrian Cordillera, Armorican Massif.

Résumé

L'espèce *Terebratula Daleidensis* ROEMER, 1844 (aujourd'hui *Oligoptycherhynchus daleidensis*) de l'Emsien Supérieur du groupe de synclinaux (“MuldenGruppe”) de Daleiden en Eifel est examinée en détail. Son ubiquité et son extension stratigraphique considérable acquises au cours du temps sont exposées et mises en doute. Après examen du lectotype, ici désigné, et de riches collections existantes, il est recommandé d'en revenir à la définition originelle de cette abondante espèce. *Rhynchonella inaurita* SANDBERGER, G. & F., 1856, communément confondue avec *daleidensis*, est attribuée au nouveau genre *Inaequalibellirostrum*, genre type de la nouvelle

famille Inaequalibellirostridae. La distribution géographique, l'extension stratigraphique et les affinités de l'espèce type du nouveau genre, *I. pareti* (de VERNEUIL, 1850a) de la partie moyenne de l'Emsien de la Cordillère Cantabrique (Province du Léon), sont clarifiées. Deux résultats, parmi d'autres, en sont une réévaluation du genre *Stenorhynchia* BRICE, 1981 et la mise en question de la présence de ce genre dans le Massif Armoricain.

Mots-clefs: *Oligoptycherhynchus daleidensis*, *Inaequalibellirostrum*, Inaequalibellirostridae, Rhynchonellides, Brachiopodes, Eifel, Cordillère Cantabrique, Massif Armoricain.

Introduction

Since its establishment as a characteristic species of the famous Lower Devonian locality of Daleiden (Eifel area), *Terebratula Daleidensis* ROEMER 1844 has been abundantly quoted and discussed in the German and world literature. Its considerable stratigraphic range (Upper Ludlow to Strunian, chiefly Pragian and Emsian) and its vast geographic distribution (Europe, Asia, North Africa, Canada) indicate that the name “*daleidensis*” has been unduly given to a long string of forms. A critical scrutiny of the literature shows how confusion progressively increased.

The aim of this paper is to advocate the return to the original definition of the species (text, figures, geographic and stratigraphic information) that was clear and satisfactory for that time, and to restore its lost identity and stratigraphic significance. The taxonomic status of some species that have been mistaken for or discussed in connection with *daleidensis* is examined as well.

Major problems related in the past to *daleidensis*

Terebratula Daleidensis ROEMER, 1844 versus *T. Daleidensis* SCHNUR, 1853

A problem that popped up in the literature is the difference between *Terebratula Daleidensis* described by SCHNUR [1853, p. 172, pl. 22, figs 1a-e (*Remark*: fig. 1e represents either another smaller specimen or is the ventral view of the same specimen not reproduced to scale)] and *T. Daleidensis* as originally established by ROEMER (1844, p. 65, pl. I, figs 7a-c). Although some authors, e.g. DEWALQUE (1868, p. 59; 1880, p. 67), and ROMANOWSKI (1880, p. 111), singled out a *daleidensis* attributed to SCHNUR. GOSSELET (1887, pp. 192-193, 194, 199) was the first to clearly state that one could, pending a more complete study, separate SCHNUR's *Rhynchonella Daleidensis* with $\frac{4}{3}$ median costae from ROEMER's *R. Daleidensis* with $\frac{5}{4}$ median costae.

GOSSELET went further in suggesting that SCHNUR's *R. Daleidensis* could be *Rh. inaurita* SANDBERGER, G. & F., 1856 - he also used the expression *Rh. inaurita (daleidensis)* SCHNUR. He also considered that *Rh. Daleidensis* ROEMER could be "synonyme, avec droit de prénomination" of *Rh. hexatoma* SCHNUR, 1851. In this he was in opposition with SCHNUR (1853), who did not question ROEMER's paternity of the species, and so did most palaeontologists after GOSSELET, e.g. VENYUKOV (1886, p. 108), and DREVERMANN (1904, p. 262). But the distinction survived for a long time, e.g. NALIVKIN (1930, pp. 61, 67), PAECKELMANN & SIEVERTS (1932, pp. 53, 55), NÖRING (1939, pp. 56, 57), and RZHONSNITSKAYA (1973, pp. 31-33).

What were GOSSELET's arguments?

In his description of the species, ROEMER (1844, pl. 65, pl. I, figs 7a-c) mentioned the presence of 4 costae on the fold, but figured a specimen showing 5 costae on the fold on figure 7a, and 4 costae on figure 7b, while 5 costae are drawn in the sulcus on the latter figure. For his part SCHNUR (1853, p. 172, pl. 22, figs 1a-e) considered the number of costae on the fold as varying from 4 to 6 [5 and 6 being respectively the number of costae in a rare variety, and in a stable ("beständig") smaller variety that could be a special species (*Remark*: the small variety has been described as *Xahetomus hexadaleidensis* by SARTENAER, 2009)], and illustrated a specimen carrying 4 costae on the fold. Such contradictions, also underlined by DREVERMANN (1904, p. 262) and MAILLIEUX (1931, p. 23), have brought GOSSELET (1887, pp. 193, 194) to

conclude that SCHNUR's *daleidensis* with 4 costae on the fold and 3 costae in the sulcus was different from ROEMER's *daleidensis* characterized by 5 and 4 costae, respectively.

What about the specimen figured by ROEMER (1844, pl. I, figs 7a-c)?

In April 1980, the author had the privilege to examine this specimen at the museum of the Institute of Geological Sciences of the University of Wrocław, where it is housed under the number 2054s, and in August 2006 a cast (Pl. 1, Figs 6-10) was kindly sent to him. This specimen matches ROEMER's figures by size, proportions, and number of lateral costae ($\frac{7}{8}$ and $\frac{8}{9}$), and, as such, is an acceptable representative of the species, but it has $\frac{4}{3}$ median costae and wider costae than those shown on the figures. This allows to cast doubts on its reliability, although the label joined to it, and written by ROEMER, indicates: "Devon. Daleiden in der Eifel. F. Roemer leg. 1842." Amongst the various explanations put forward for explaining these contradictions, the one proposed by DREVERMANN (1904, p. 262), who wrote that "die Abbildung ROEMERS...ist zweifellos verzeichnet", seems the most acceptable. As a matter of fact, the large available collections of toptotypical material of *daleidensis* in old collections housed in various museums, universities and scientific institutions demonstrate that more than 75% of specimens show 4 costae on the fold as indicated by ROEMER himself in his original description of the species, and 3 in the sulcus. No single specimen shows $\frac{5}{5}$ or $\frac{4}{5}$ median costae. Costae have been counted on 172 specimens (see Description of the species).

The conclusion is that $\frac{4}{3}$ is by far the usual number of median costae in the material of the species described by ROEMER (1844) as well as by SCHNUR (1853), and that GOSSELET's (1887) estimate ($\frac{5}{4}$) of this number in ROEMER's *daleidensis* is incorrect. However, GOSSELET advocated other differences for separating SCHNUR's *daleidensis* from ROEMER's *daleidensis*. According to him (pp. 192-193) the latter has a smaller size, a very deep and pointed ("pointu") sulcus, a trapezoidal tongue, and generally no parietal costae (SCHNUR's *daleidensis* show very rarely a parietal costa on each side). With the exception of a very deep sulcus, these differences are real, and SCHNUR's *daleidensis* should be considered as a separate taxon for which, as already suggested by GOSSELET (p.194), the name *inaurita*,

introduced by the SANDBERGER brothers (1856, pp. 337-338, pl. XXXIII, figs 5, 5a-c as *Rhynchonella inaurita*) is available (see below). As far as parietal costae are concerned, they have been often overlooked, and partly rightly so, because the bounding costae of the fold and the sulcus could be considered respectively as median costae that are lower than the others, and lateral costae that are higher than the others.

What about the localities of the specimens figured by ROEMER and SCHNUR?

We have seen that ROEMER's figured specimen (1844, pl. I, figs 7a-c) comes from Daleiden. This is suggested anyhow by the name given to the species. Furthermore, ROEMER (p. 65) mentioned the Daleiden Grauwacke as his main collecting site, and added that the species „ausserdem ist sie überall in der Grauwacke, namentlich auch bei Waxweiler, Braubach, Coblenz, Siegen, usw. verbreitet“ where it is „doch fast immer sehr verdrückt“. Daleiden is cited by SCHNUR only as one of the localities where he found the species (“Allenthalben in der Grauwacke, besonders häufig zu Waxweiler, Daleiden, Prüm und Daun”); therefore it is far from certain that his figures are those of one or two (see remarks above) specimen(s) from this locality.

daleidensis = livonica and daleidensis versus livonica

von KEYSERLING (1846, p. 240), BRONN (1848, pp. 1234, 1240-1241), and KAYSER (1871a, pp. 314, 316, list, p. 365; 1871b, pp. 518-520) considered *Terebratula Daleidensis* identical to *T. livonica* von BUCH, 1834 [Remark: after examination of Russian material, KAYSER (1889, p. 44) admitted that the two species were different].

QUENSTEDT's (1852, pp. 449-450, pl. 35, figs 42a-c; 1871, pp. 202-204, pl. 42, figs 57, 57a – 67 as *T. livonica*) understanding of the species is broad and obscure to say the least. Although the type locality of *T. livonica* lies near Adsel, central Latvia, QUENSTEDT (1852) described the species from “Dudley, Grauwacken der Eifel, Gothland, etc.”, illustrated it by a “Steinkern” from the “Grauwacke” of Daun (Eifel area), and considered it “ganz vom Typus der Bicorner des braunen Jura” [Remark: SARTENAER (1966, p. 3) commented on the “Bicorner”].

QUENSTEDT (1871, figs 57, 57a) gave figures of a specimen from the type area (“Mittellivland”), but, under the heading *T. Livonica*, he discussed 13 species from Daun, Dillenburg (Dill Syncline), Koněprusy (Bohemia), and Gotland, and figured specimens from the first three localities (figs 58-67). In particular, a “Böhmische”

Livonica, different from the true (“ächte”) *Livonica* is mentioned, and *T. Daleidensis* from Daun is considered completely similar (“vollständig analog”) to *T. livonica*, and not to be separated from it (“Ich trenne nicht”). It is shown in the present paper that the *daleidensis* from Daun is different from the type *daleidensis* of the Daleiden “Muldengruppe” (Eifel area).

STEININGER (1853, p. 58) thought that *T. Daleidensis* was identical with the specimen of *T. livonica* figured by de VERNEUIL in MURCHISON *et al.* (1845, pl. X, figs 3a,b), but doubted that it was identical with *T. livonica* as described by von BUCH (1834), although de VERNEUIL's specimen comes from the type locality, Adsel in central Latvia.

The SANDBERGER brothers (1856, p. 337, pl. XXXIII, figs 5, 5a-c) incorporated in *Rhynchonella inaurita* not only *Terebratula Daleidensis* and *T. livonica*, but also *T. Huotina* de VERNEUIL in MURCHISON *et al.*, 1845; after examination of specimens of *Rhynchonella livonica* from the Syas' river, von SANDBERGER (1889, p. 13) stuck to the opinion that *R. livonica* was identical to *R. inaurita* (= *R. daleidensis*). *T. livonica* expanded still further when KAYSER (1871b, pp. 518-520) and LOEWE (1913, pp. 63-65) attributed to it *T. hexatoma*, *Hemithyris Pareti* de VERNEUIL, 1850a and *Terebratula Wirtgeni* SCHNUR, 1853 in addition to the three species already included in it by the SANDBERGER brothers; KAYSER stated that *Rhynchonella livonica* “gehört zu den an meisten veränderlichen Rhynchonellen” and added that the “pugnaceenförmig *hexatoma* mit 5 scharfen Falten im Sinus...ist nichts Anderes als eine kleine Fortläuferin der *Daleidensis* [Grauwacke bei Daun und Daleiden] im Kalke”.

VENYUKOV (1886, pp. 108-109, 122-123) added *R. turanica* ROMANOWSKI, 1880 to the list of species assimilated to *R. livonica* by KAYSER.

BARROIS (1882, p. 267) expressed a finer opinion when he declared *R. daleidensis* closely related (“très voisine”) to *R. livonica*, *R. inaurita*, and *R. Pareti*, although, forty years later, BARROIS *et al.* in GOSSELET *et al.* (1922, p. 97) included *R. nymphe*, *R. daleidensis*, *R. livonica*, *R. Pareti*, *R. sub-Pareti*, and *R. sub-livonica* in a group “composé de formes intimement alliées, sinon identiques entre elles” [Remark: BARROIS *et al.* considered QUENSTEDT (1871) the author of *sub-livonica* and referred to his figures (pl. 42, figs 67, 68). QUENSTEDT mentioned only *Terebratula pseudolivonica*, which is a species of BARRANDE (1847); fig. 67 is, according to him, a “Zwischenform” between *pseudolivonica* and *Livonica*, that cannot be separated with certainty, and fig. 68 is *T. cuneata* from Gotland]. Therefore, *sub-livonica* is a misquotation.

MAURER (1896, p. 657) was less accommodating in expressing his conviction that the “forms” from the Rhenish Lower Devonian could not be considered as being the same species as *R. livonica*. Focusing on *R. daleidensis* and *R. livonica*, GÜRICH (1909, p. 146) wrote: “Da diese Arten im Unter- und Mitteldevon im Fluss sind, hält es schwer Grenzformen als besondere Arten heraus zu greifen”. In adopting a wider vision, REED (1922, p. 95), who had already (1921, p. 317) recognized “a considerable range of variation” in *R. daleidensis*, considered that *R. daleidensis*, *R. inaurita*, *R. Pareti*, *R. Partridgeae* WHIDBORNE, 1897 and *R. turanica* “should be regarded as synonyms of *R. livonica*, or at any rate not worthy of ranking above varieties”. This was the last attempt to mistake various species for the Lower Frasnian species *Ripidiorhynchus livonicus*, as the Latvian species is known nowadays; these species, of which some are discussed in the present paper, are independent taxa.

inaurita versus *daleidensis*

When the SANDBERGER brothers (1856, pp. 337-338, pl. XXXIII, figs 5, 5a-c) established *Rhynchonella inaurita*, they included in it three previously described species (*Terebratula livonica*, *T. Daleidensis*, and *T. Huotina*), and, thus, the priority should have been given to the oldest known species, *T. livonica*. At the same time, they gave to the new species a considerable stratigraphic range - Oriskany Sandstone (Pragian) to Stringocephalenkalk - and a vast geographic distribution: France (Boulonnais, Normandy), Germany (Dill Syncline, Eifel, Lahn Syncline, middle Rhine valley, Taunus), Latvia, Pennsylvania, and Russia (Central and Main Devonian Fields, Pechora, W Siberia). After examination of specimens of *Rhynchonella livonica* from the Syas' river, von SANDBERGER (1889, p. 13) dropped any doubt he had so far concerning the identity of *R. livonica* with *R. inaurita* (= *R. daleidensis*), and stated that he believed, like VENYUKOV (1886), that there was no palpable (“greifbare”) difference between the two species.

Rhynchonella inaurita has usually been considered a junior synonym of *Terebratula Daleidensis*, e.g. by KRANTZ (1857, p. 150), ROMANOWSKI (1880, p. 111), GOSSELET (1887, p. 194), MAURER (1896, p. 656), DREVERMANN (1904, p. 262), GÜRICH (1909, pl. 45, figs 6a-d), who went as far as choosing SANDBERGER'S figures (pl. XXXIII, figs 5, 5a-c) of *Rhynchonella inaurita* to illustrate *R. daleidensis*, and MAILLIEUX (1931, p. 24). DAVIDSON (1870, pp. 72, 75, 78-81, 87, pl. 5, figs 1-3; 1881, p. 341, pl. 38, fig. 21?, figs

35a,b) recognized the species in the Upper Devonian of Devonshire. This strange and false occurrence was apparently based on identification by GOSSELET. KAYSER (1871b), VENYUKOV (1886), and LOEWE (1913) assigned the species to *R. livonica* (see above). KAYSER (1878, pp. 142-143) recognized its validity, but later (1889, pp. 44-45) questioned separation of *R. inaurita* and *R. daleidensis*. BARROIS (1882, p. 267) considered *R. inaurita* as “très voisine” of *R. daleidensis*, *R. livonica*, and *R. Pareti*, and REED (1922, p. 95) took the position indicated above under the discussion of *daleidensis* versus *livonica*.

As already indicated, the author considers *inaurita* as a valid taxon, and in so doing, he falls in with GOSSELET'S (1887, p. 194) suggestion that the name *inaurita* could be given to *Terebratula Daleidensis* as described by SCHNUR (1853) if it is accepted that it is different (“si on admet cette différence”) from *T. Daleidensis* as originally described by ROEMER (1844) (see above). Of course, one will have to forget the synonymy, the stratigraphic range, and the geographic distribution proposed by the SANDBERGER brothers for the species they established.

The species is included in a new genus in the present paper.

daleidensis versus *pareti*

When establishing *Hemithyris Pareti*, de VERNEUIL (1850a, pp. 160, 162, 177) mentioned that the species was distinct from *Terebratula daleidensis* only «par la dépression qu'elle présente des deux côtés du crochet». de VERNEUIL (1850b, table, pp. 780-781, p. 785; 1866, p. 11) upheld this opinion, and added, in 1866, that there would be «peu d'inconvénients à (les) confondre». In the meantime SCHNUR (1853, p. 172) agreed that the two species were close to each other (*Remark*: SCHNUR wrote mistakenly *Pailleti* instead of *Pareti*).

As already mentioned, KAYSER (1871b, pp. 518, 520), VENYUKOV (1886, pp. 108, 123), and LOEWE (1913) incorporated *Hemithyris Pareti* in *T. livonica*, and KAYSER (1878, p. 143) confirmed that the two species were “täuschend ähnlich”. BARROIS (1882, p. 267; 1889, p. 85) also considered *Rhynchonella Daleidensis*, *R. inaurita*, *R. livonica*, and *R. Pareti* as “très voisines” [*Remark*: BARROIS *et al.* in GOSSELET *et al.* (1922, p. 97) went further in including *R. nymphe*, *R. daleidensis*, *R. livonica*, *R. Pareti*, *R. sub-Pareti*, and *R. sub-livonica* in a same group (see above)]. OEHLERT (1884, pp. 415-416) believed that *R. Pareti*, *R. subpareti*, OEHLERT 1884, and *R. cypris* d'ORBIGNY, 1847 «forment un groupe naturel avec *Rh. livonica*,

Rh. nympa, *Rh. pseudolivonica*, etc., et ne sont sans doute qu'un même type, modifié dans le temps et dans l'espace». REED's (1922, p. 96) stand on the subject has been reminded above. KAYSER (1889, p. 45) while maintaining that *R. Pareti* was "nicht verschieden" from *R. livonica*, added that the former species "schliesst sich der grossen Abänderung von Daleiden [*R. daleidensis*]...an"; DREVERMANN (1904, p. 262) and HÜFFNER (1917, p. 312) declared themselves in full agreement with KAYSER. From then on *R. Pareti* has consistently been introduced into the synonymy of *Camarotoechia daleidensis*, e.g. by MAILLIEUX (1931, pp. 20-21, 24; MAILLIEUX's synonymy is a list of citations and not a critical synonymy), COMTE (1938, pp. 58-59, 86), RENAUD (1942, pp. 98-99), LE MAÎTRE (1944, p. 48), LLOPÍS LLADÓ (1961, pp. 265-267), and SCHUMANN (1965, p. 93).

Things changed when palaeontologists started to work actively in the Cantabrian Cordillera, from where the species was first recorded, and where it is recognized as a valid taxon with a known stratigraphic range.

The species is designated in the present paper as the type species of a new genus.

daleidensis versus *hexatoma*

This problem is more important than the preceding ones, because it still persists in modern literature and hampers progress in classification and stratigraphy.

We have seen that KAYSER (1871b), VENYUKOV (1886), and LOEWE (1913) incorporated *T. hexatoma* with *T. livonica*. KAYSER (1871b, p. 520) considered *T. hexatoma* as a "Fortläuferin" of *T. Daleidensis*, from which it takes over, and reaffirmed (1889, p. 43) his opinion in writing: "Die [*Rhynchonella daleidensis*] am Rhein sehr verbreitete, durch das ganze Unterdevon hindurchgehende und auch in das Mitteldevon der Eifel (*hexatoma* SCHNUR) aufsteigende Art". GOSSELET (1887, p. 194) went further in suggesting that *R. hexatoma* and *R. Daleidensis* (not *R. Daleidensis* as described by SCHNUR 1853; see above) could be synonyms, but a few years later (in USSHER, 1890, p. 498; 1903, p. 27) he expressed himself slightly differently in writing that *R. daleidensis* was near ("voisine") to *R. hexatoma*. This was also VIËTOR's (1918, p. 439) position, who considered *R. daleidensis* as a "nahe verwandte Form" of *R. hexatoma*. In the meantime GÜRICH (1896, p. 284) made out of *Terebratula hexatoma* a variety of ROEMER's "Hauptform" (*T. daleidensis*), but MAURER (1896, p. 659) explicitly wrote that there were no transition forms between *R. daleidensis* and *R. hexatoma*. DREVERMANN (1904, p.

262) and FUCHS (in SPRIESTERSBACH & FUCHS, 1909, pp. 69-70) put an end to these wavering views in stating that *Rhynchonella hexatoma* was a "besondere Art" or "selbständige Art" as originally established by SCHNUR (1851). This should have closed the controversy, but SCHMIDT (1941) and LE MAÎTRE (1952a, b) reopened the debate.

SCHMIDT (1941, pp. 7-11) called "*daleidensis*-Gruppe" or "Gruppe der *Camarotoechia daleidensis*" a group of forms giving the impression of unity ("Eindruck der Einheitlichkeit"), although she recognized that shape was a very variable character ("die Gestalt ist innerhalb weiter Grenzen sehr wandelbar"). She focused her attention on the Lower and Middle Devonian representatives of the group, which, according to her, was distributed throughout the whole Devonian. SCHMIDT stated that *C. hexatoma* includes a number of variations ("Abweichungen"), which she treated as subgroups ("Untergruppen") or subspecies that showed transitions ("Übergänge") between them. With this in mind she described three subspecies (*C. hexatoma hexatoma*, *C. hexatoma soetenica* SCHMIDT, 1941, and *C. hexatoma wetteldorfensis* SCHMIDT, 1941) based on the number of costae and the value of the apical angle as distinctive characters. At the same time, she showed that the subspecies were not clear-cut; a particular specimen could often not be attributed to one or another of them, and that exceptional specimens were not rare. More generally, she stressed that the subgroups of the "*daleidensis*-Gruppe" had to be considered as provisional.

On top of the restrictions and approximations contained in SCHMIDT's scheme, the cumulated stratigraphic range of the subspecies, i.e. of the species, is considerable and therefore suspicious. These are an uppermost Emsian (Heisdorf Formation in the Prüm and Hillesheim Synclines) and, questionably, lowermost Eifelian (Lauch Formation in the Prüm Syncline) for *hexatoma wetteldorfensis*; lower part of lower Eifelian ["Geeser Horizont" of the Nohn Formation in the Hillesheim Syncline, not to mention a "non-characteristic specimen from the "Geeser Horizont" (upper part of the middle Eifelian Ahrdorf Formation) in the Gerolstein Syncline], and middle Eifelian "Sötenicher Schiefer" in the Sötenich Syncline (according to SCHMIDT, 1936) for *hexatoma hexatoma*; and (lower) (Lauch and Nohn formations) and middle Eifelian (Ahrdorf and Junkerberg Formations) to upper Givetian in the Blankenheim and Sötenich Synclines for *hexatoma soetenica*.

The specimen of *hexatoma wetteldorfensis* figured by SCHMIDT (1942, figs 3a-c, p. 393), and duplicated by

WERNER (1980, fig. 16, p. 17), is completely different from the holotype figured by her in 1941 (pl. 1, figs 2a,b).

The Upper Emsian species *Rhynchonella imitatrix* FUCHS in SPRIESTERSBACH & FUCHS, 1909 from the Bergisches Land and *R. (Wilsonia) dillensis* FUCHS, 1914 from the Dill Syncline are not identical to *hexatoma wetteldorfensis*, a possibility set forth by SCHMIDT (1941, p. 9); according to her, *R. imitatrix* could be a juvenile of *hexatoma wetteldorfensis*. These two remarks indicate that SCHMIDT's conception of the subspecies was unclear.

According to the author, the subspecies *hexatoma soetenica*, that covers most of this range, contains more than one taxon, a possibility already envisaged by SCHMIDT (p. 11) for the specimens from the Sötenich Syncline. Furthermore, although the subspecies is present in two synclines, all figured and sectioned specimens come from the Givetian of a restricted area (Sötenich and surroundings) in the Sötenich Syncline: holotype (pl. 1, figs 4a-c) and one paratype (pl. 1, figs 5a, b) from the "Stringocephalen-Kalk" and two paratypes (pl. 4, figs 57a, b; pl. 5, figs 5-8) from the "Stringocephalen-Schichten".

As concerns *hexatoma hexatoma*, SARTENAER (2007, p. 45) reminded that the "Geeser Horizont" near Üxheim in the Hillesheim Syncline is of early Eifelian age (lower "Nohner Schichten"), and therefore not equivalent, contrary to SCHMIDT's statement, to the "Geeser Horizont" of the Gerolstein Syncline, which is located in the upper part of the Ahrdorf Formation (middle Eifelian).

After examination of the original collections the author concludes that the external characters of the subspecies *hexatoma soetenica* and *hexatoma wetteldorfensis* differ considerably from those of *hexatoma hexatoma*, although some internal features show some analogy. They belong to two different genera, none of them being *Oligoptycherhynchus* SARTENAER, 1970, the genus to which *hexatomus* and *daleidensis* belong. Is *Cupularostrum* SARTENAER, 1961 the genus to which *Camarotoechia hexatoma soetenica* should be assigned? LARDEUX & MORZADEC (1979, p. 23 as "*Camarotoechia soetenica*") elevated the subspecies to the rank of a species that BRICE (in BRICE & MORZADEC, 1983, pp. 549-550, 553-555, pl.1, figs 1a, b, 2-7) described and attributed to *Cupularostrum*. This is an acceptable proposition for the Lower Givetian (Tibidy Formation) 40 (~) specimens from two sections near Le Faou ("Rade de Brest", "Département du Finistère", Armorican Massif), but it does not apply to the original Eifelian

material, which is difficult to tackle. The holotype (XVII 323c) is stratigraphically ("Stringocephalen-Kalk") and geographically (Sötenich) unsatisfactorily located. The largest collection of *hexatoma soetenica* comes from the middle Eifelian Ahrdorf and Junkerberg Formations in the central part of the Sötenich Syncline; it is particularly abundant in the Dalbenden horizon (third from base of the four recognized in the Junkerberg Formation) (PAULUS, 1961a, pp. 424, 427-429, 432; 1961b, pp. 32, 38; DICKFELD, 1968, unpublished thesis: "Stratigraphie und Fauna im Westteil der Sötenicher Mulde"). Dalbenden is only two kilometres to the east of Sötenich. It is surprising that SCHMIDT (1941, p. 11) mentioned as coming from the "Stringocephalen-Schichten" an old and large collection she examined in the "Landesmuseum" (Berlin), because the path Urft-Girzenberg from where this collection derives is also in Dalbenden or close to it. It is also remarkable that similar material coming from the same formation has been collected from the near-by Blankenheim (OCHS & WOLFART, 1961, pp. 23, 28, 30) and Rohr (GLINSKI, 1961, pp. 279, 281, 283) Synclines. In short, a thorough examination is needed for clarifying the stratigraphic position and range of the subspecies in its type area, and for dealing with the various taxa that have been identified as such in France ("Rade de Brest"; Lower Givetian), Germany (Sauerland; Middle Eifelian), in Libya (Fezzan; Couvinian and Givetian-Frasnian transition beds), in Mauritania [Adrar; Givetian-Frasnian boundary beds (probably Frasnian)], and in Spain (Cantabrian Cordillera; Eifelian-Givetian transition beds).

LE MAÎTRE (1952a, p. 112) stated that *C. daleidensis* presented "variations". The same year (1952b, p. 328) she called "groupe de *C. daleidensis*" "toute une série d'espèces" gathered around the species in the whole Devonian of Europe and North America. According to her, in Europe the Lower Devonian section (*C. daleidensis* and *C. nymphe*) of this group was replaced in the Middle and Upper Devonian by "toute une série de formes voisines" showing "variations" in various characters: *C. elliptica*, *C. hexatoma*, *C. hexatoma soetenica*, *C. hexatoma wetteldorfensis*, *C. triloba fornicata*, *C. ferquensis*, *C. letiensis*, *C. omaliusi*, *C. triaequalis*. LE MAÎTRE admitted presence of similar species ("espèces similaires") in the United States of America in the Lower Devonian (*C. oriskania*), and the Middle and Upper Devonian (*C. congregata*, *C. congregata* var. *parkheadensis*, *C. horsfordi*, *C. orbicularis*, and *C. prolifica*). She (LE MAÎTRE, 1952b, p. 329) also recognised in Mauritania (Adrar) three "types principaux" or "groupes", one of them

attributed to *C. hexatoma*, in mentioning that such a specific assignment was difficult on account of the “modifications qui surviennent chez une même espèce”.

With SCHMIDT (1941) and LE MAÎTRE (1952a,b) confusion reached a peak, and the “groupings” they proposed be better forgotten. Unfortunately confusion survived.

The multiplication of subspecies, varieties, variations, and transition forms cannot be regarded as an advance in our knowledge, but rather as the wavering of our understanding in the absence of a strong support.

In order to unravel this imbroglio, we have to take up the matter anew. This is what DROT (1964, pp. 182-187, figs 76-78, pl. 18, figs 8a-c, pl.19, figs 10a,b, 11a-c; 1981, pp. 46-48, figs 2a,b, p. 47, pl. 1, figs 3a-c, 4a-c, 5a-c, 6a-c) thought when she stumbled against the problem of the alleged presence of *Camarotoechia daleidensis* and *C. hexatoma* in the Moroccan pre-Sahara. She declared (1981) that the “groupe de formes” including these two species and *C. hexatoma wetteldorfensis* was in need of a “révision générale”.

Hexatoma (subspecies and varieties included) is mentioned in the literature with a Pragian to Lower Famennian stratigraphic range from the following countries: Germany (Bergisches Land, Dill Syncline, Eifel area, Harz Mountains, Hörre, Lahn Syncline, Mosel valley, middle Rhine valley, Sauerland, Taunus), Belgium, Canada, England, France, Iran, Libya, Mauritania, Morocco, Poland, Russia, Spain, and Usbekistan. Eifelian to Lower Frasnian and Upper Emsian to Lower Eifelian are the given ranges for *hexatoma soetenica* and *hexatoma wetteldorfensis*, respectively.

Most of identifications and ranges, if not all, are incorrect, with, of course, the exception of the *stratum typicum* and *locus typicus*, the Gees horizon (“Geeser Horizont”) (middle Ahrdorf Formation, lower Middle Eifelian), and the Gees-Pelm area (Gerolstein Syncline). The species, which is very rare, is also found in the lower Nohn Beds (upper Lower Eifelian) of the Hillesheim Syncline.

The Couvinian material (eleven “crushed” specimens, “most of them very flat”) from Grzegorzowice (northern Holy Cross Mountains) identified as *Camarotoechia hexatoma* by BIERNAT (1954, p. 489, table 1, pp. 490-491, pp. 509-511, pl. IV, figs 6-10) shows some analogy to the Eifelian species. It differs from it in its small thickness, and especially in its septalium partly covered with two thin plates with bifurcated extremities, a structure never encountered by the author in any other rhynchonellid.

Varieties, mutations and subspecies of *daleidensis*

Varieties (not formally named)

Many varieties of *daleidensis* have been mentioned in the literature, although seldom formally named.

The two varieties of *Terebratula Daleidensis* from the “Grauwacke” singled out by SCHNUR (1853, p. 172) have been mentioned above. One of them has been described as *Xahetomus hexadaleidensis* by SARTENAER (2009, pp. 35-37, pl.1, figs 11-60).

Other varieties, mutations, etc. have been proposed by various authors:

- variety [FUCHS, 1899, pp. 57, 78, from the Lower Emsian of the Lorelei area (Middle Rhine valley); 1911, p. 713 from the Daadener Schichten (Lower Emsian) of the Siegerland; in SPRIESTERSBACH & FUCHS, 1909, pp. 6, 70, from the Upper Emsian (“Remscheider Schichten”) of Bergisches Land; DAHMER, 1921, table, p. 198, table, p. 300, from the Upper Emsian (“Remscheider Schichten” of Bergisches Land and “Rammelsberger Schichten” and “Nessigi-Schichten” of Harz Mountains; 1932, pp. 373, 383 from the Middle Siegenian of Juseret (Neufchâteau Syncline), 1942, p. 268, fig. 29, p. 287, from the Lower Emsian of Ziegenberg (eastern Taunus)];
- variety? (DREVERMANN, 1904, p. 262, from the Siegenian of Seifen (Westerwald);
- varieties [ROMANOWSKI, 1880, p. 111, from the Devonian of Turkestan (Chatkal river valley); GÜRICH, 1909, p. 146, from the Middle Devonian; MAILLIEUX, 1936, pp.14, 87 quoting DAHMER (1932), and p. 88, two varieties not worth being described (“trop mal représentées pour être utilement décrites”) from the Upper Siegenian of Fauvillers (Neufchâteau Syncline)];
- mutations (FUCHS in SPRIESTERSBACH & FUCHS 1909, p. 70, from the Upper Emsian of the Eifel and middle Rhine valley areas);
- “Abänderungen” [KAYSER, 1889, pp. 44-45, from the Lower (“Unter-“) and Upper (“Ober-“) Emsian (“-coblenzschichten”) of Eifel area (Daun, Daleiden), includes GOSSELET’s (1887) suggestion to separate SCHNUR’s *Terebratula Daleidensis* from ROEMER’s *T. Daleidensis* (see above); DAHMER, 1921, p. 208, from the Upper Emsian (“Schalker Schichten”) of Harz Mountains];
- “Abart” [PAECKELMANN & SIEVERTS, 1932, p. 55, from Paphlagonia (Asia Minor); DAHMER, 1921, p. 278, from the Lower Emsian of the middle Rhine valley (Lorelei area) and the Upper Emsian of Harz Mountains; 1932, p. 383, from the Middle Siegenian

- of Juseret (Neufchâteau Syncline); 1942, p. 270, from the Lower Emsian of Ziegenberg (eastern Taunus)];
- “Zwischenstufe” between ROEMER’s (1844) *T. Daleidensis* and SCHNUR’s (1853) *T. hexatoma* [GÜRICH, 1896, p. 284 and SOBOLEV, 1909, p. 508, from the “Spiriferensandstein” of the northern Holy Cross Mountains (Miejska Góra)];
 - small variety [KAYSER, 1895, p. 208, pl. III, figs 1-2 from the Lower Couvinian of Pepinster, considered as a juvenile specimen of *Rhynchonella daleidensis*; DEWALQUE (*in de* PIERPONT, 1895, pp. 169, 171, 173, 174), and de DORLODOT (1901, p. 174, foot-note 1, p. 182, p. 182, foot-note 1), from the Lower Couvinian of the Vesdre Massif (Pepinster) and the southern flank of Lustin (Hestroy, Burnot) and Godinne (Rouillon) Anticlines in the Meuse river valley in the central part of the Dinant Basin].

Varieties (formally named)

The variety *Rhynchonella daleidensis gracilior* from the Lower Emsian of the Lorelei area (middle Rhine valley) was proposed by FUCHS (1899, pp. 69, 74, 84, 86, 88) and considered by him as “sehr bezeichnend für die höheren Niveaus der Hercyniaezone [“Singhofen-Schichten]”. The variety has also been mentioned: 1) from the Upper Emsian of the Bergisches Land by FUCHS *in* SPRIESTERSBACH & FUCHS [1909, pp. 6, 70 as a variety similar (“derartig”) to the variety *gracilior*; one crushed specimen], 2) from the Upper Emsian (“Kahlebergsandstein”, Giengelberger Schichten”, “Nessigi-Schichten”, “Schalker Schichten”, “Festenburg-Schichten”, and “Rammelsberger Schichten” of the Harz Mountains by DAHMER [1921, table, p. 174 possibly, p. 191, table, p. 198, pp. 206, 277-279, pl. 15, figs 18-20 (= three specimens from the “Nessigi-Schichten”), table, p. 300; 1946, p. 179]. This identification was confirmed by FUCHS *in* DAHMER, 1921, who compared it with the small Belgian variety of *daleidensis* from the Lower Couvinian of Pepinster described by KAYSER (1895, p. 208). FUCHS, however, referred to KAYSER’s pl. III, figs 1-4, that KAYSER considered as juvenile (pl. III, figs 1-2) and “normal” (pl. III, figs 3,4) forms of *daleidensis* (*Remark*: ASSELBERGHS, 1923, p. 25, pl. I, figs 4-9, attributed the specimens identified as *Camarotoechia daleidensis* by KAYSER to *C. imitatrix*); 3) from the Lower Couvinian on the southern border (Olloy area) of the Dinant Basin by MAILLIEUX (1939, p. 2 as *C. gracilior*); and 4) from the Emsian of Paphlagonia (Asia Minor) by HERITSCH & von GAERTNER (1929, pp. 191-193, pl. 1, figs 12-13), and PAECKELMANN & SIEVERTS (1932, p. 55).

MAILLIEUX (1931, pp. 23, 25 as *C. gracilior*)

contemplated the possibility that *Camarotoechia imitatrix* and *Rhynchonella daleidensis gracilior* could be synonyms.

MITTMEYER (2008, table 2, p. 142, pp. 171, 173 as *Oligoptycherhynchus daleidensis gracilior*) has given a fresh impetus to the variety in mentioning it in the middle Lower Emsian Singhofen Substage (i.e. in the lower part of the Lower Bendorf Beds), the lower part of the Spitznack Beds (lower part of the Singhofen Substage = *stratum typicum* of the variety), and in the Wambach Beds (new lithostratigraphic unit). These beds extend, according to MITTMEYER, to western Westerwald and the Mosel river region, the Taunus and eastern Hunsrück, and the southern Taunus, respectively. MITTMEYER (2008, p. 203) considers *O. prodaleidensis* n. sp. a forerunner (“Vorläufer”) of *O. daleidensis gracilior* (see below).

FUCHS’ (1899) *gracilior* is a *nomen nudum*; it has neither been described nor defined in accordance with Article 12 of the ICZN. This is also the case for DAHMER’s (1921) *gracilior*, because expressions such as “eine kleine zierliche Form von der Verwandtschaft *daleidensis*” (Kahlebergsandstein, Upper Emsian, Harz Mountains) or “eine zwerghafte Abart” (Lower Emsian, Lorelei area, middle Rhine valley) cannot be considered as descriptions or definitions; specimens of figures 18-20, plate 15, are also not an indication (Article 12c). DAHMER himself admitted (p. 278) that a closer description (“eine nähere Beschreibung”) of the variety did not exist. The name *gracilior* may be made available later with a new authorship. DAHMER submitted his collection from the Harz Mountains to FUCHS, who found it very much alike (“übereinstimmend”) *gracilior* from the middle Rhine valley. Such conformity needs to be substantiated. Furthermore all small forms with $\frac{4}{3}$ median costae cannot be put in the same basket no matter their age (early Emsian, late Emsian, and early Couvinian) and their geographic location (middle Rhine valley, Taunus, Hunsrück, Westerwald, Bergisches Land, Harz Mountains, and Dinant Basin).

For the time being, the relation of *gracilior* with the late Emsian *daleidensis* from the Daleiden “Muldenruppe” (Eifel area), and its assignment to the middle Eifelian genus *Oligoptycherhynchus* is not acceptable. MITTMEYER intended to give a description and an illustration of *gracilior* based on his large collections from the Singhofen Substage (*stratum typicum*), but could not do this in the context of the compendium on the Devonian of Germany, published in 2008.

The subspecies *O. daleidensis minor* (FUCHS)

mentioned by MITTMEYER (2008, p. 190, from the Lower Bendorf Beds is a misprint for *O. daleidensis gracilior*.

Prodaleidensis MITTMEYER, 2008

Oligoptycherhynchus prodaleidensis was mentioned by MITTMEYER (1997, p. 22) as a *nomen nudum* from the Reudelsterz Beds (upper part of the Ulmen Substage) south of Schutz near Manderscheid in the Eifel area south of the “Eifelkalkmulden”, and considered as a forerunner (“Vorläufer”) of *O. daleidensis*. MITTMEYER (2008, table 2, p. 142, pp. 163, 169, 186-190, 203, pl. 1, figs 17-18) described the species, a forerunner of *O. daleidensis gracilior*, from the same area and from Taunus and Hunsrück, with the following stratigraphic range: lower (Kaltenborn Beds) and upper (Ramersbach Beds) parts of the Middle Siegenian; lower (Nitztal Beds) and uppermost (Saxler Beds) parts of the Upper Siegenian; lower (Eckfeld and Sauerthal Beds) and upper (Lower and Upper Reudelsterz, and Kaub Beds) parts of the Lower Emsian. The description and illustration (internal moulds of one brachial valve and one ventral valve) of the species are unsatisfactory, possibly due to the publication in a compendium. It is hoped that the species will be better described and figured in the future with proper comparison with known taxa. At this stage it can be stated that the only connection of the species with *daleidensis* is the number ($\frac{4}{3}$) of median costae, and that its assignment to the genus *Oligoptycherhynchus* is erroneous.

Unnamed species and subspecies

SOLLE (1976, table, p. 22) mentioned *Oligoptycherhynchus* n. sp. aff. *daleidensis* from the lower “Gladbach-Schichten” of the lower part of the “Vallendar-Schichten” (= upper Lower Emsian) of the Olkenbach Syncline.

FUCHS (1982a, fig. 10, p. 253, p. 254 as “large growth forms of *Oligoptycherhynchus* n. sp. aff. *daleidensis*”; in FUCHS & PLUSQUELLEC 1982, p. 26 as “une nouvelle espèce voisine d’ *O. daleidensis*”) proposed a new species, never described, from the Singhofen Substage (middle Lower Emsian) and the lower and middle Vallendar Substage (upper Lower Emsian) of the Eifel area east of the “Eifelkalkmulden”; in the same area and south of the “Eifelkalkmulden” FUCHS (1989, pp. 111, 115) declared *O. daleidensis* “bezeichnend” for the Ulmen Substage (lower Lower Emsian), and singled out a “small form” from the Nasingen Beds (lower beds of the Ulmen Substage) and a “grosse Variante” (*O. sp. aff. daleidensis*) from the Neuerburg

Beds (upper beds of the Ulmen Substage). These various forms will have to find a taxonomic position, distinct from *daleidensis* as described in the present paper, if located in FUCHS’ collection housed in the “Senckenberg Forschungsinstitut und Natur Museum, Frankfurt am Main”.

WENNDORF (2001, p. 20) mentioned *O. daleidensis* subsp.? from the “Emsquarzit” (base of the lower Upper Emsian Lahnstein Substage).

Number of median costae of daleidensis used as a stratigraphic tool

ROEMER (1844) and SCHNUR (1851), the founders of *Terebratula Daleidensis* and *T. hexatoma*, respectively, considered the number of dorsal median costae, four for the former species, and six for the latter, as a distinct character. Since then, this costal numbers played a predominant part in identifying, grouping or separating species, subspecies and varieties showing evident or alleged similarities to these two species.

Two authors in particular, MAURER (1896) and SCHMIDT (1941) attributed a stratigraphic significance to the number of median costae.

MAURER (1896, pp. 656-659) stressed the point that *Rhynchonella daleidensis* was one of the most abundant species of the Lower Devonian east of the Rhine that showed extraordinary equal contour and size, and limited “Formschwankungen” at every level. He stated that specimens from the lower “Stufen” (“untere Grauwacke”, “Haliseritenschiefer”, and “Coblenzquarzit”) had $\frac{4}{3}$ median costae (with the exception of one specimen from the quartzite with $\frac{5}{4}$ median costae) and those from the upper “Stufen” (“Chondritenschiefer”, “Hohenrheiner Stufe”, and “Cultrijugatus-Stufe”) $\frac{6}{5}$ (with the exception of three specimens from the “Cultrijugatus-Stufe” with $\frac{5}{4}$ and $\frac{4}{3}$ median costae).

MAURER reminded that GOSSELET (1887) envisaged the possibility of separating SCHNUR’s (1853) *Terebratula Daleidensis* with $\frac{4}{3}$ median costae from ROEMER’s *T. Daleidensis* with $\frac{5}{4}$ median costae [Remark: GOSSELET suggested in that case that the name *inaurita* proposed by the SANDBERGER brothers (1856) could apply to the former]. In this context, according to MAURER, *Rhynchonella inaurita* and *R. daleidensis* would characterize the predominant form of the lower part and the upper part of the Lower

Devonian, respectively. Such an interpretation, in contradiction with the $\frac{6}{5}$ median costae advocated for the upper “Stufen”, is not a fair assessment of GOSSELET’s opinion (see above), because at that time by most palaeontologists the two species were considered of the same age (“Grauwacke”, “Spiriferensandstein”), and identical.

In her discussion of the *Camarotoechia daleidensis* group, ranging from the late Emsian (Wiltz Beds) to the late Givetian, SCHMIDT (1941, pp. 8, 10) separated specimens with $\frac{4}{3}$ median costae from the late Emsian (Wiltz Beds and lower part of the Wetteldorf Sandstone) from specimens with $\frac{6}{5}$ median costae from the latest Emsian (Heisdorf Beds), Eifelian, and Givetian beds [Remark: the mention by SCHMIDT of specimens with $\frac{6}{5}$ median costae in the Heisdorf Beds is due to the presence of a subspecies of *C. hexatoma*, *C. hexatoma wetteldorfensis*, that consequently allows to give a early to middle Devonian age to the species; see above]. Exceptions to this scheme are explained by SCHMIDT in the following way: isolated (“vereinzelt”) specimens from the Wiltz Beds with $\frac{6}{5}$ median costae could come from a very high horizon in these beds (Remark: these specimens are included in the species *Xahetomus hexadaleidensis*), and herald the “6-costae clothing” (“6-Rippen-Tracht”) of higher beds; the Upper Eifelian or Lower Givetian specimens of *C. hexatoma soetenica* that have $\frac{4}{3}$ median costae from near Blankenheim are otherwise nevertheless in such conformity (“Übereinstimmung”) with the “6-rippigen Sötenicher Form” that “eine Abtrennung nicht möglich ist, zumal da die Gesamtzahl der Rippen die gleiche ist”.

These are only two examples of the damaging consequences resulting from focusing essentially on one external character (number of median costae), and neglecting all others. The picture becomes blurred and judgement is affected. An extreme example, from which any stratigraphic consideration is excluded, is the following one: MAILLIEUX (1931, pp. 21-24) stated that BARROIS’s (1889, pp. 86-87, pl. V, figs 2a-e) *Rhynchonella nympha* from the Armorican Massif, having $\frac{5}{4}$ median costae could just be (“il est possible qu’elle doit être rapportée à”) *Rhynchonella Pareti*, a species with $\frac{4}{3}$ median costae that he includes in the synonymy of *Camarotoechia daleidensis*. Therefore

it is only on account of the $\frac{5}{4}$ median costae that MAILLIEUX questionably included BARROIS’s taxa, possibly identical according to him, in the synonymy of *Camarotoechia daleidensis*, implying that this restriction would be lifted if these taxa had $\frac{4}{3}$ median costae.

As for *daleidensis*, the two following remarks must be borne in mind. Firstly, although $\frac{4}{3}$ and $\frac{6}{5}$ represent the number of median costae of a large majority of specimens of *daleidensis* and *hexatoma*, respectively, other ratios exist and indicate some degree of variability. Secondly, there are more rhynchonellid species (and genera) with $\frac{4}{3}$ and $\frac{6}{5}$ median costae than just *daleidensis* and *hexatoma* known from the Emsian and Eifelian. Within the Wiltz Beds (Upper Emsian) alone, there is one species of which the majority of specimens possesses $\frac{4}{3}$ median costae (*daleidensis*), and another of which the majority of specimens possesses $\frac{6}{5}$ median costae (*Xahetomus hexadaleidensis* = one of the two varieties of *daleidensis* mentioned by SCHNUR, 1853, p. 172).

Stratigraphic range and geographic distribution of daleidensis according to the literature

Daleidensis has been commonly mentioned in beds ranging in age from the Siegenian to the early Eifelian; it has also been occasionally mentioned in the Lower Ludlow, Gedinnian, Upper Devonian, Frasnian, and Strunian.

Rhenish facies E and W of the middle Rhine valley

In Bergisches Land, Dill Syncline, Hunsrück, Kellerwald, Lahn Syncline, Mosel valley, Siegerland, Taunus, and Westerwald, *daleidensis* has been reported from the whole Lower Devonian (e.g. KAYSER, 1889, p. 43, table, p. 110, 1908, pp. 139, 143; MAURER, 1896, p. 657; VIËTOR, 1918, p. 438, table, p. 466) or from the middle and upper Lower Devonian (e.g. PAECKELMANN & SIEVERTS, 1932, p. 55). It means: Lower and Upper Siegenian, and Lower and Upper Emsian (Hunsrück), Lower and Upper Siegenian, and Lower Emsian (Siegerland), Middle Siegenian (Westerwald), Upper Siegenian and Lower Emsian (Kellerwald, Taunus), Upper Siegenian and Lower and Upper Emsian (Mosel valley), Lower and Upper Emsian (Dill Syncline), Lower and Upper Emsian, and Lower Eifelian (Bergisches Land, Lahn Syncline).

Eifel area

- In the Eifel area considered as a whole, *daleidensis* has been mentioned from the “Cultrijugatusstufe” by SCHULZ (1883, table, p. 167), from the lower Middle Devonian by FUCHS in SPRIESTERSBACH & FUCHS (1909, p. 80), and from the Upper Emsian Beds by SPRIESTERSBACH (1942, table, p. 90).
- In the “Eifelkalkmulden”, aside of the Daleiden “Muldengruppe” (type area, see below under the description of *daleidensis*), the species has been mentioned from the Lower Devonian of the Sötenich Syncline by QUIRING (1915, pp. 92, 107, table between p. 160 and p. 161), from the Upper Emsian Wetteldorf Beds of the Gerolstein Syncline by HEIBEL (1969, table 2, p. 548), from the Upper Emsian of the northern margin of the Prüm Syncline by WERNER (1969, table 2, pp. 170-171, table 3, pp. 180-182, 184, table 4, p. 189, p. 218), and from the Lower Emsian and Upper Emsian Wetteldorf Sandstone of the Prüm Syncline by GOSSELET in DUPONCHELLE (1880, pp. 326-327), ASSELBERGHS (1913, p. 156; 1928, pp. 9-10) and various authors (e.g. SCHMIDT, 1942, p. 390, tables 1, 2, p. 401; BULTYNCK 1970, pl. XXXVII), respectively. KAYSER (1871b, p. 520; 1889, p. 43, table, p. 110) accepted the presence of the species also in the Middle Devonian of the “Eifelkalkmulden”, because (see above) he considered the Eifelian *Terebratula hexatoma* as the “Fortläuferin” of *T. Daleidensis*.
- *Region SE and E of the “Eifelkalkmulden”*. The presence of *daleidensis* has been mentioned in the Middle Siegenian (MITTMEYER, 1982, pp. 30, 33, 35, 36, 39-41), in the Middle and Upper Siegenian, and Lower Emsian (SIMPSON, 1940, p. 11, 18-22, table 4, p. 60, table 8, p. 66-67), in the Upper Siegenian and the three substages (Ulmen, Singhofen, and Vallendar) of the Lower Emsian [e.g. MAILLIEUX, 1910, table, p. 207, p. 218; RÖDER, 1960, pp. 10, 11, 18, 20, 22-24, 29, 30, 32, 33, 35-38, 40, 41, 43, 44, 46, table 1, p. 50, pp. 53, 54, 57; FUCHS (1974, pp. 25, 32, 33, table 1, pp. 35-36, p. 40, table 2, pp. 44, 46, pp. 50, 56-59, 61, 62, 64, 68, 71, 74, 77, 78, 82, 83, 85, 86, 88, 95, 97-100; 1982a, pp. 233-237, fig. 10, p. 253, p. 254; 1982b, pp. 157, 159, 161, 164, 169, 172; NEGENDANK, 1983, pp. 21-24, 27, 29-30, 149; KÖLSCHBACH *et al.*, 1993, table 1, pp. 306-308], in the Lower Emsian (e.g. FRECH, 1889, p. 195; DREVERMANN, 1902, p. 103; DIENST, 1914, table, pp. 604-605; MAUZ, 1935, pp. 23, 78; SOLLE, 1956, pp. 8, 10, 11; RÖDER, 1957, pp. 134-135, 137, 138; NEGENDANK, 1974, fig. 9, pp. 22, 24, 89; DOHM, 1976, fig. 9, p. 19; KOWALSKI, 1976, pp. 236-237, 241-244; FÜRSICH & HURST, 1980, p. 307; FUCHS & PLUSQUELLEC, 1982, p. 26; FUCHS, 1989, p.111; MITTMEYER, 1997, pp. 22-23), in the Upper Emsian (“Stufe der *Spirifer cultrijugatus*”) (e.g. SCHULZ, 1883, table, p. 167), in the Lower and Upper Emsian (e.g. SOLLE, 1937, pp.7, 9, 11, table, p. 17, p. 22, table, p. 34, table, p. 43, table 1; 1976, table, p. 22, pp. 43-44, table, pp. 52-53, table, pp. 90-91, table, p. 109, p. 117, table, p. 125, table, p. 139).
- *Region W and SW of the “Eifelkalkmulden”*. *Daleidensis* has been reported from the middle Emsian of Üttfeld and Brandscheid areas, and the Upper Emsian of Irrhausen by ASSELBERGHS (1928, pp. 9, 15), the Nasinger Schichten (lowermost Lower Emsian) and the Stadtfelder Schichten (uppermost Lower Emsian) by NÖRING (1939, pp. 69-72), and the three subdivisions (from base to top: “Nasingen-“, “Niederraden-“, and “Neuerburg-Schichten”) of the lower Lower Emsian Ulmen Substage, of which *daleidensis* is characteristic (“bezeichnend”), and the two subdivisions (“Altscheuern-“ and “Merlbach-Schichten”) of the middle Lower Emsian Singhofen Substage of the Neuerburg area by FUCHS (1989, p. 111-117, 119-122).
- *Region N of the “Eifelkalkmulden”*. *Daleidensis* has been mentioned by SAUER (1968, pp. 500-501) in the Lower Emsian of the neighbourhood of Zülpich.

Regions close to the type area

Not too far away from the type area, *daleidensis* has been reported from the Upper Emsian and Lower Couvinian of the Vesdre Massif and from the Lower Siegenian to the Lower Emsian of the Aachen area. The species has been mentioned from the Middle Siegenian to the Upper Emsian of the Oesling Basin (Grand Duchy of Luxemburg), and from the Lower Siegenian to the Lower Couvinian of the Ardenne [Dinant Basin (Belgium and France), Ardenne Anticline, Neufchâteau Syncline, Laroche-Houffalize Syncline, Bastogne Anticline, and eastern border of the Stavelot Massif (Belgium), and northern border of the Givonne Massif (France)]; a single Frasnian occurrence on the southern border of the Dinant Basin is due to MOURLON (1881, p. 15). In Sauerland, the species is known from the Upper Emsian, and in the Harz Mountains from the Lower and Upper Emsian, and the Lower Eifelian.

Other regions of the world

According to the literature, the stratigraphic range and the geographic distribution of *daleidensis* is as follows: Algeria (Siegenian, Lower and Upper Emsian,

Strunian), Canada (New Scotland, Pragian), China (Inner Mongolia, Upper Emsian), England (Siegenian to Eifelian), France (Gedinnian, Siegenian, Emsian, Lower Couvinian), Iran (Siegenian to Upper Emsian), Kazakhstan (Emsian, Eifelian), Libya (Lower Devonian, Givetian-Lower Frasnian), Mauritania (Siegenian to Lower Couvinian), Morocco (Lower and Upper Siegenian, Lower and Upper Emsian, Lower Eifelian), Poland (Upper Ludlow, Upper Emsian), Rumania (Gedinnian, Siegenian), Spain (Gedinnian, Siegenian, Emsian), Turkestan (Upper Devonian), Turkey [Lower Devonian (Siegenian, Emsian)], Uzbekistan (Upper Devonian).

Conclusions

Before trying to get out of the fix we are in, it is useful to examine clearly the succession of steps that allowed the confusion to progressively install itself in a process that is common for many species of old standing:

- wrong understanding, and thus incorrect identifications (often based on one or two external characters) that resulted in incorporating of various forms in the Eifel species *Terebratula daleidensis* and *T. hexatoma*, and in proposing arbitrary groupings; the word “group” being used with various meanings;
- erroneous and not substantiated generic assignments;
- spreading of the two species from their *loci typici* (Daleiden “Muldengruppe”, and Gerolstein Syncline, respectively) to other parts of the Eifel area, to other regions of Germany (both species: Bergisches Land, Dill Syncline, Hörde, Harz, Lahn Syncline, Moselle valley, middle Rhine valley, Sauerland, Taunus; *daleidensis* alone: Aachen area, Hessisches Hinterland, Hunsrück, Kellerwald, Siegerland, Westerwald), to bordering and near-by regions (both species: Ardennes, Dinant Basin, France, Grand Duchy of Luxemburg; *daleidensis* alone: Vesdre Massif; *hexatoma* alone: Namur Basin), to other European countries (both species: England, Poland, Russia, Spain; *daleidensis* alone: Rumania; *hexatoma* alone: Kuznetsk Basin), and to the rest of the world (both species: Iran, Libya, Mauritania, Morocco, Uzbekistan; *daleidensis* alone: Algeria, China, Kazakhstan, Nova Scotia, Turkey; *hexatoma* alone: Canadian Arctic);
- considerable stratigraphic range: for *daleidensis*: Eifel area [Siegenian to Lower Eifelian (chiefly upper part of Lower Emsian, and Upper Emsian)],

other regions of Germany [Siegenian to Lower Eifelian (chiefly Lower and Upper Emsian)], and other parts of the world [Gedinnian to Middle Eifelian, and Frasnian (chiefly Siegenian to Emsian)] not to mention exceptional occurrences in beds of late Ludlow, Gedinnian, Frasnian, and Strunian ages; for *hexatoma*: Eifel area [Lower Emsian to Givetian (chiefly Upper Emsian to Middle Eifelian)], other regions of Germany (Upper Emsian to Lower Givetian), and other parts of the world (Pragian to Lower Givetian, Frasnian, and Lower Famennian);

- quasi general lack of any information on the precise location or range of species within lithostratigraphic units, rarely smaller than a formation, with, as a result, the impossibility to trace eventual transition forms and to follow evolutionary lineages;
- usual preservation as moulds of the fossils obtained from the Rhenish “Grauwacke” involving more disadvantages than advantages.

Systematic Palaeontology

Family **Sapphicorhynchidae** SARTENAER, 2007

Genus ***Oligoptycherhynchus***

SARTENAER, 1970, emend. 2007

SARTENAER (2007, p. 45) acknowledged that “the wide range (middle Siegenian to Eifelian) advocated by him in 1970 for *Oligoptycherhynchus* has become unacceptable”, with, accordingly, the elimination from the genus of all other species than the type species, the Middle Eifelian *O. hexatomus*. The revaluation of the Upper Emsian *daleidensis* in the present paper convinced the author that this species had to remain in the genus, and that its assignment to a new genus suggested by him (SARTENAER, 2009, p. 34) had to be refuted.

Type species: Terebratula hexatoma SCHNUR, 1851.

Diagnosis

The emended diagnosis of the genus, which is here assigned to the family Sapphicorhynchidae, is as follows: medium size; outline subcordiform; uniplicate; inequivalve; top of dorsal valve at front; commissure sharp; well marked sulcus and fold, starting at a short distance from the beaks; sulcus moderately deep with flat to slightly convex bottom, wide at front; high fold with slightly convex top; high subrectangular tongue with sharp borders, sometimes recurved posteriorly in its upper part; ventral beak slightly to strongly

incurved; narrow ventral interarea; costae in moderate number, regular, simple, moderately elevated to elevated, angular or angular with rounded top, starting at the beaks; parietal costae common; apical angle wide; moderately thick shell; moderately thick dental plates, diverging in the apical region, becoming parallel to convergent anteriorly, long and moderately thick septum; deep septalium, amphora-shaped in transverse serial sections, covered by a moderately robust connectivum; hinge plate composed of two horizontal to slightly concave parts; inner ridges of dental sockets high; teeth short and robust.

Oligoptycherhynchus daleidensis (ROEMER, 1844)

Pl. 1, Figs 1-35

Figured specimens are deposited in the collections of the Royal Belgian Institute of Natural Sciences, Brussels, with registration numbers prefixed IRScNBa.

Lectotype, locus typicus, stratum typicum

The only syntype figured by ROEMER (1844, pl. I, figs 7a-c) from the "Grauwacke" near Daleiden ("Daleiden Muldengruppe", Eifel area) is here selected as the lectotype of the species, and reproduced (Pl. 1, Figs 6-10). Four specimens identified in 1843 by ROEMER are deposited in the "Hauptsammlung" of the "Paläontologisches Museum, Museum für Naturkunde, Berlin",

Other material

The 665 (~) specimens examined come from the *stratum typicum* and the *locus typicus*: 500 (~) specimens in the collections of the "Preussische Königlich geologischen Landesanstalt" housed in the "Paläontologisches Museum, Museum für Naturkunde, Berlin" (nine of them = topotypes A-I, IRScNBa12703-12711); 31 specimens deposited in the Department of Palaeontology of the British Museum (Natural History), London, purchased or accepted as a gift in the beginning of the twentieth century; 141 specimens being part of the collections of the "Senckenberg Forschungsinstitut und Natur Museum", 35 of them collected by J. Schnur (the specimen XVII 180w figured by SCHMIDT, 1941, pl. 1, figs 1a-c, belongs to this collection), and 99 by K. Jaeger. All specimens are internal moulds.

Description

Remarks: On account of the following three conclusions reached in the present paper no description of *Oligoptycherhynchus daleidensis* after 1844 is reliable, although the descriptions may include

some pertinent features: 1) the difference between *Rhynchonella inaurita* and *Terebratula Daleidensis sensu* SCHNUR, 1853, a possibility already envisaged by GOSSELET (1887) (see above), resulting in the assignment of *Rhynchonella inaurita* to a new genus, *Inaequalibellirostrum*, described below; 2) the absence of the species in Germany outside the Eifel area; 3) the absence of the species in other countries of the world. Therefore, our understanding of the species relies on the original description by ROEMER (1844, p. 65, pl. I, figs 7a-c), which contains some of the most characteristic features of the species. ROEMER's figures are also the best ones existing so far, in spite of the slight discrepancy in the number of median costae mentioned in the text and seen on one of the three figures (fig. 7b); this problem has been discussed above. Photographs (Pl. 1) of six specimens and the plaster cast of the lectotype of *O. daleidensis* show that the species was originally well figured and well described.

None of the many specimens examined by the author showed a preserved shell, although according to ROEMER (1844, p. 65), the species was represented by "zahlreichen völlig unverdrückten Exemplare, zum Theil mit erhaltener Schale". This is the reason why there are no published transverse serial sections [*Remark*: SCHUMANN (1965, fig. 22, p. 95), made sections from a specimen of *Rhynchonella paretii* (now *Inaequalibellirostrum paretii*) mistaken for *Camarotoechia daleidensis*]. Nevertheless, most of the internal features of the species can be inferred from moulds; the author confirmed the presence of a connectivum in making sections in a specimen.

What follows refers only to specific characters in need of further elaboration. Width of sulcus at front between 54 and 73%, mostly between 57 and 67%, of shell width. Maximum shell width located between 52 and 72%, mostly between 62 and 67%, of shell length anterior to ventral beak. Apical angle between 112° and 126°, mostly 112° to 118°. Ratios $\frac{l}{w}$: 0.70 to 0.90, mostly 0.70 to 0.82; $\frac{t}{w}$: 0.80 to 0.97, mostly 0.85 to 0.97; $\frac{t}{l}$: 1 to 1.31, mostly 1 to 1.16. The general costal formula in median, parietal, and lateral categories derived from at least 75% of the specimens is: $\frac{4}{3}$; 0; $\frac{7-9}{8-10}$. The ratios of costae are given in Table 1. Width of median costae near front between 2.5 and 3 mm.

Measurements of ten specimens, of which seven have been photographed, are given on Table 2. Columns 3, 5-7 refer to specimens of usual size. The distorted specimen figured by SCHNUR (1853, pl. 22,

| Median costae | | | Lateral costae | | |
|------------------|---------------------|-----|------------------|---------------------|------|
| Number of costae | Number of specimens | % | Number of costae | Number of specimens | % |
| $\frac{2}{1}$ | 12 | 3.3 | $\frac{5}{6}$ | 1 | 0.3 |
| $\frac{3}{2}$ | 10 | 2.8 | $\frac{6}{7}$ | 7 | 2.2 |
| $\frac{4}{3}$ | 313 | 87 | $\frac{7}{8}$ | 64 | 20 |
| $\frac{5}{4}$ | 20 | 5.5 | $\frac{8}{9}$ | 107 | 33.8 |
| $\frac{6}{5}$ | 5 | 1.4 | $\frac{9}{10}$ | 103 | 32.5 |
| | 360 | 100 | $\frac{10}{11}$ | 28 | 8.9 |
| | | | $\frac{11}{12}$ | 6 | 2 |
| | | | $\frac{12}{13}$ | 1 | 0.3 |
| | | | | 317 | 100 |

Table 1 – Number of median and lateral costae of *Oligoptycherhynchus daleidensis* (ROEMER, 1844).

figs 1a-d) falls into a small category of particularly wide specimens such as toptype I, IRScNBa12711 (column 10). The enlarged (x1.5) specimen figured by SCHMIDT (1941, pl. 1, figs 1a-c) is similar to the one of figures 31-35 of Plate 1.

The percentage of specimens from the type area with $\frac{5}{4}$ median costae includes those that have been qualified as rare by SCHNUR (1853, p. 172), and by FUCHS in SPIRSTERSBACH & FUCHS (1909, p. 70), who considered them as mutations. STEININGER (1853, p. 58) mentioned one specimen with five, another with six costae on the fold, and even one with six costae in the sulcus. SCHMIDT (1941, p. 8) mentioned “vereinzelte Stücke in den Wiltzer Schichten haben 6 Rippen auf dem Sattel”; these specimens belong to the species *Xahetomus hexadaleidensis*.

Comparisons

The major difference between the abundant Upper Emsian *O. daleidensis* and the rare upper Lower and lower Middle Eifelian *O. hexatomus* is the number of median and parietal costae ($\frac{4}{3}$; 0 for *O. daleidensis*; $\frac{6}{5}$; $\frac{1-1}{1-1}$ for *O. hexatomus*); the number of lateral costae is similar ($\frac{7-9}{8-10}$) [Remark: the total number of costae, 16

to 18, indicated by SCHMIDT (1941, p. 8) for *hexatomus* is a *lapsus calami* for 26 to 28]. Parietal costae are very rare in *O. daleidensis*, but the external costae of fold are commonly slightly lower than the others, and the ventral internal lateral costae slightly higher than the others. In *O. hexatomus*, ventral flanks flatten or even reverse their curvature near the antero-lateral commissures, where they end as spurs, the sulcus is generally slightly deeper, the anterior commissure is lower than the front margin, and the frontal parts of sulcus and fold form together a convex surface with flattened costae. The largest specimens of *O. hexatomus* never reach the size of the largest specimens of *O. daleidensis*.

SCHMIDT (1941, pl. 5, figs 4a-i as *Camarotoechia hexatoma hexatoma*) published transverse serial sections from one specimen of *hexatoma* coming from the lower Nohn Beds (upper Lower Eifelian) of Üxheim (Hillesheim Syncline). More detailed sections (including the crura) from another specimen (IRScNBa12712) from the same locality are given in Fig. 1. As already mentioned, the “Geeser Horizont” of the Nohn Beds is older than the “Geeser Horizont” of Gees and Pelm (Gerolstein Syncline), which is the *stratum typicum* and the *locus typicus* of *Oligoptycherhynchus hexatomus*. But, because no toptype of the species has been spotted so far in existing collections, the

| in mm | Topotype G IRScNBa 12709 | Topotype A IRScNBa 12703 | Topotype B IRScNBa 12704 | Topotype D IRScNBa 12706 | Topotype C IRScNBa 12705 | Lectotype | Topotype H IRScNBa 12710 | Topotype E IRScNBa 12707 | Topotype F IRScNBa 12708 | Topotype I IRScNBa 12711 |
|--------------|-----------------------------------|-----------------------------------|-----------------------------------|-----------------------------------|-----------------------------------|-----------|-----------------------------------|-----------------------------------|-----------------------------------|-----------------------------------|
| l | 13 | 14.9 | 17.3 | 18 | 15.7 | 18.2 | 17.7 | 17.3 | 20.1 | 18.6 |
| lvv unrolled | 24 | 30 | 34 | 36.5 | 30 | 31 | 31 | 36.5 | 37 | 37.5 |
| w | 17.9 | 18.8 | 19.2 | 20.7 | 20.8 | 21.1 | 22.3 | 23.9 | 24.6 | 26.4 |
| t | 14.8 | 18.1 | 18.6 | 20.9 | 17.6 | 18.3 | 17.9 | 22.8 | 21.9 | 23 |
| tvv | 5.2 | 5.5 | 6 | 5.7 | 5.5 | 5 | 5.2 | 6.2 | 5.4 | 5 |
| tdv | 9.6 | 12.6 | 12.6 | 15.2 | 12.1 | 13.3 | 12.7 | 16.5 | 16.5 | 18 |
| l/w | 0.73 | 0.79 | 0.90 | 0.87 | 0.75 | 0.86 | 0.79 | 0.72 | 0.82 | 0.70 |
| t/w | 0.83 | 0.96 | 0.97 | 1 | 0.85 | 0.87 | 0.80 | 0.95 | 0.89 | 0.87 |
| t/l | 1.14 | 1.20 | 1.08 | 1.16 | 1.12 | 1 | 1.01 | 1.31 | 1.09 | 1.24 |
| Apical angle | 117° | 116° | 112° | 114° | 121° | 115° | 113° | 118° | 118° | 126° |

Table 2 – Measurements of ten specimens of *Oligoptycherhynchus daleidensis* (ROEMER, 1844). Abbreviations: l = length; w = width; t = thickness; vv = ventral valve; dv = dorsal valve.

author, like SCHMIDT, had to be contented with making sections from a rare specimen presented to the author by Dr. K.-W. Wendorf (collected by Berd Trost) that is externally similar to the specimen figured by SCHNUR (1853, pl. 23, figs 2a-e as *Terebratula hexatoma*). This specimen is here formally designated as the lectotype of the species. It could be argued that such a designation already took place. As a matter of fact, SCHMIDT (1941, p. 9) declared that among the subspecies of *Camarotoechia hexatoma* described by her, *C. hexatoma hexatoma* seemed to be the typical one, as best corresponded to SCHNUR's figures ("scheint mir die typische zu sein, denn sie entspricht am besten der Abbildung bei SCHNUR"). Such a statement cannot be considered as the designation of a lectotype, because it does not comply with Article 74.7 of the ICZN. Moreover, the German word "Abbildung" used in the singular covers the two syntypes figured by SCHNUR (figs 2a-e and figs 2f, g, plate 23). With the designation of a lectotype, the specimen of figures 2f, g becomes a paralectotype. This status is questionable in the present case, because SCHNUR, as explained by SARTENAER (2009, p. 35), figured this specimen under the name *Terebratula hexatoma*, but described it (SCHNUR, 1853, p. 172) as one of the two varieties of *T. Daleidensis*. Anyhow, paralectotype or not, this specimen has been chosen as the holotype of *Xahetomus hexadaleidensis*.

The Lower Givetian species *Sapphicorhynchus sappho* (HALL, 1860) and *Oligoptycherhynchus daleidensis* share several characters, e.g. a strongly dorsibiconvex profile; the dorsal valve thickest posterior to front; deeply serrated antero-lateral and lateral commissures; a short interarea; well marked sulcus and fold starting at a short distance from the

beaks; a wide, moderately deep sulcus, with flat to slightly convex bottom; a clearly delineated tongue slightly recurving posteriorly in its uppermost part; the top of fold gently convex; a moderate number of well marked, wide, simple costae starting from the beaks; similar internal characters (detached dental plates, long septum, deep and wide septalium, undivided hinge plate, connectivum).

Many characters make *Sapphicorhynchus sappho* distinct from *Oligoptycherhynchus daleidensis*: a smaller thickness indicated in the $\frac{t}{w}$ and $\frac{t}{l}$ ratios ($\frac{t}{w}$: 0.63 to 0.80, mostly 0.66 to 0.80, for *S. sappho* against 0.79 to 0.99, mostly 0.79 to 0.93, for *daleidensis*); $\frac{t}{l}$: 0.75 to 1, mostly 0.88 to 1, for *sappho* against 0.95 to 1.12, mostly 0.95 to 1, for *daleidensis*); a more constant outline; a greater width*; the maximum shell width located more posteriorly (45 to 65% of shell length anterior to ventral beak for *sappho* against 60 to 65% for *daleidensis*); the ventral flanks flattening near the front*; the anterior commissure fused into the wall formed by the extremities of costae; a lower tongue with transverse-subtrapezoidal outline; the top of tongue lower than maximum shell thickness; a different general costal formula ($\frac{5-6}{4-5}$; 0 to $\frac{1-0}{1-0}$ and $\frac{1-1}{1-1}$; $\frac{6-8}{7-9}$ for *sappho* against $\frac{4}{3}$; 0; $\frac{7-9}{8-10}$ for *daleidensis*); the common presence of parietal costae; a wider angle of the cardinal commissure; more delicate internal features (the preservation as moulds of the specimens of *daleidensis* does not allow a detailed examination of most features, and, in particular, of the crura). (* = only valid for middle-large specimens of *sappho*).

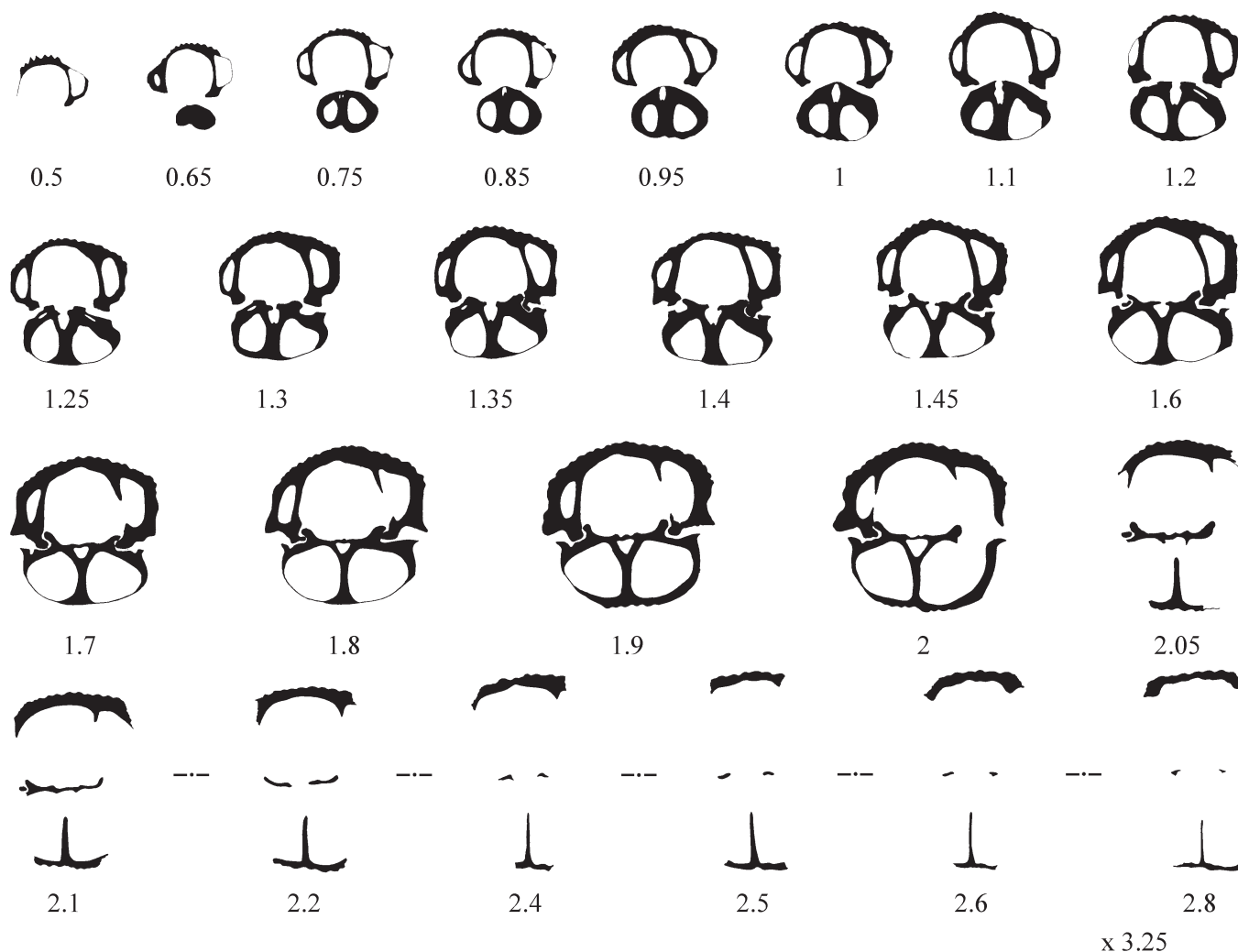


Fig. 1 – *Oligoptycherhynchus hexatomus* (SCHNUR, 1851). Camera lucida drawings of serial transverse sections; figures are distances in mm forward of the ventral umbo. IRScNBa12712. Üxheim (Hillesheim Syncline, lower Nohn Beds, upper Lower Eifelian). Measurements: length = 16.3 mm; width = 21.7 mm; thickness = 15.8 mm.

Trigonirhynchia COOPER, 1942 differs from *Oligoptycherhynchus* in most characters. The genus is only mentioned here, because SCHMIDT (1965, p. 6), although underlining obvious differences, considered that *Camarotoechia daleidensis* and *C. hexatoma* had some features (outline, profile, costae) in common with its type species *Trigonirhynchia fallaciosa* BAYLE, 1878 (Pragian, Armorican Massif).

Stratigraphic position and geographic location

In a remote past, *Oligoptycherhynchus daleidensis* has been mentioned in the type area (Daleiden “MuldenGruppe” and adjoining region of the Grand Duchy of Luxembourg = type area *stricto sensu*, and Prümer Syncline = type area *lato sensu*) from the “Spiriferensandstein”, the Daleiden-, Eifel-, Hierges-, Rhine (Rhenish)-, and Waxweiler-“Grauwacke”, and

from the Daleiden-Waxweiler beds. A more precise lithostratigraphic unit, covering the upper part of the “Grauwacke”, the “Oberk(c)oblenschichten” came progressively in use.

O. daleidensis is now restricted to the Upper Emsian Wiltz Beds (“Wiltz-Schichten”), of which it is a characteristic species (see e.g. STRUVE, 1964, p. 227; WERNER, 1980, p. 14; KOWALSKI, 1983, p. 101).

The presence of the species in Germany outside the type area has still to be substantiated. The undue importance given to a given number of median costae ($\frac{4}{3}$), considered the most important character, if not the only one, of *O. daleidensis*, has led to the assignment to that species of a long string of Siegenian and Emsian forms. No specimen has been spotted in the various collections examined by the author. Evidence

is lacking for the abundant isolated and embedded valves from the “Singhofen-Gruppe” (middle Lower Emsian) of the Taunus (near the “Loch-Mühle” NW Gemünden) assigned by KUTSCHER & MITTMEYER (1970, pp. 43-44, 45-46, 49, pl. 15, figs 11-14) to the “Normalform” of Daleiden, to which they remarkably (“in bemerkenswerter Weise”) correspond, for the only reason that they show an almost constant number ($\frac{4}{3}$) of median costae.

The presence and the stratigraphic range of *daleidensis* in other parts of the world (see above) must be disregarded.

Inaequalibellirostridae n. fam.

Type genus: Inaequalibellirostrum n. gen.

Diagnosis

Shell of medium to medium-large size, with right angle triangle profile, subtrigonal outline, and convexo-concave ventral valve; apical angle moderately wide; thickest at front margin; top of shell = top of tongue; well marked *lunulae*; short ventral interarea; pointed, projecting ventral beak; sulcus, fold, and costae start from beaks; sulcus wide and deep; fold high; tongue high; costae well marked, in moderate number, sharp, high, simple, regular, deeply indenting the commissure; no parietal costae; dental plates separated from the wall by wide umbonal cavities; long septum; wide, deep, cupula-shaped septalium, covered by a thin connectivum in its anterior part; undivided hinge plate; raduliform crura; high internal socket ridges; well marked denticula; and slightly impressed, longitudinally elliptical and narrow ventral muscle field.

Comparisons

The new family Inaequalibellirostridae differs from the family Sapphicorhynchidae in a subtrigonal outline; a right angle triangle profile; a convexo-concave ventral valve; better marked *lunulae*; a pointed, projecting ventral beak; a deeper sulcus; a higher fold with strongly convex top; sharper, higher costae; the absence of parietal costae; a larger, wider, and deeper septalium (connectivum occupies more than half the width of hinge plate); teeth entering the dental sockets vertically in serial transverse sections (not laterally as in the family Sapphicorhynchidae); dental plates divergent posteriorly, subparallel anteriorly, i.e. not convergent; higher internal socket ridges; and inverted L-shaped crura in their distal part. [*Remark*: constancy

of the last two differences needs confirmation; other internal characters shown in Fig. 3 are supported by the serial transverse sections and drawings to be found in the literature (DROT, 1964, fig. 75, p. 181 as “*Camarotoechia*” *pareti*; SCHUMANN, 1965, fig. 22, p. 95 as *C. daleidensis*, standing for *pareti*, and WESTBROEK, 1967, fig. 7, p. 8, fig. 32, p. 30 as *Trigonirhynchia pareti*].

Before comparing the families Inaequalibellirostridae and Trigonirhynchiidae SCHMIDT, 1965, some points need to be clarified.

Reasons for re-examining the contents of the family Trigonirhynchiidae, and its five subfamilies (Hemitoechiinae SAVAGE, 1996, Ripidiorhynchinae SAVAGE, 1996, Rostricellulinae ROZMAN, 1969, Trigonirhynchiinae SCHMIDT, 1965, and Virginiatiinae AMSDEN, 1974) have been examined at length by SARTENAER (2007, pp. 42-43, fig. 1, p. 48).

A first step in that direction has been the elevation by SARTENAER (2001, p. 208; 2003, p. 183) of the subfamily Ripidiorhynchinae to the family rank, with *Ripidiorhynchus* SARTENAER, 1966 as sole representative. The genera *Cyphoterorhynchus* SARTENAER, 1964, *Hemiplethorhynchus* von PEETZ, 1898, and *Pseudosinotectirostrum* YUDINA, 1991 are excluded from the family Ripidiorhynchidae. At the same time, SARTENAER chose not to include in the family various genera resulting from a revision of that genus, and to establish monogeneric families. Therefore, the following genera were provisionally included, with reservation, in the family Trigonirhynchiidae: *Hypselorhynchus* SARTENAER, 2001, *Kedridorhynchus* SARTENAER, 2001, *Orophomesorhynchus* SARTENAER, 2001, *Piridiorhynchus* SARTENAER, 2001, *Poleomesorhynchus* SARTENAER, 2001, *Paropamisorhynchus* SARTENAER, 2001, *Porthmorhynchus* SARTENAER, 2001, *Saxuli-rostrum* SARTENAER, 2001, and *Gesoriacorostrum*, SARTENAER, 2003.

SAVAGE (2007, pp. 2703-2707) added to the four genera included earlier by him (SAVAGE, 1996, table 3, p. 256; 2002, pp. 1074-1077) in the subfamily Ripidiorhynchinae the eight genera proposed by SARTENAER (2001) plus *Hunanotoechia* MA, 1993, while the genus *Gesoriacorostrum* was omitted. This is acceptable for some of these genera as long as they are not included in a subfamily (Ripidiorhynchinae) of the family Trigonirhynchidae, but in the family Ripidiorhynchidae as recommended by SARTENAER (2001, 2003).

On the other hand, SAVAGE suggested that *Hypselorhynchus* and *Kedridorhynchus* were

synonyms of *Porthmorhynchus* and *Saxulirostrum* respectively. Diagnoses of these genera by SARTENAER (2001, pp. 199-201, 203) indicate that differences between these genera are important.

The Middle-Upper Frasnian *Porthmorhynchus ferquensis* (GOSSELET, 1887) from Boulonnais can easily be separated from *Hypselorhynchus farsani* (BRICE in BRICE & FARSAN, 1977) (Middle-Upper Frasnian, western Afghanistan) by a large size; stronger and higher costae; a usually smaller number of median and lateral costae; parietal costae only occasionally present; clearly detached dental plates and septum; and wide umbonal cavities. The Upper Frasnian *Saxulirostrum saxatilis* (HALL, 1867) from NC Iowa can easily be separated from *Kedridorhynchus cedarensis* (STAINBROOK, 1942) (Upper Givetian, NE and CE Iowa) by a larger size; a deeper sulcus; higher fold, tongue, and costae; slender internal structure; and an undivided hinge plate.

These are only two of the 43 genera synonymized by SAVAGE (2002, 2007). With the exception of the few genera already considered synonyms by specialists, most of these synonymies are not accepted by the present author. Neither are most of the 52 *nomina dubia* of SAVAGE in the same publications [SARTENAER (2004, p. 8) commented on *Platy glossariorhynchus* considered a *nomen dubium* by SAVAGE]. On the other hand, some genera considered for a long time as synonyms have been treated as valid genera. Thus, *Bergalaria* SCHMIDT, 1975, considered a synonym of *Flabellulirostrum* SARTENAER, 1971 by DROT (1982, p. 74), BRICE in BRICE & MORZADÉC (1983, pp. 549, 563), and SARTENAER (1985, p. 312), has been included by SAVAGE (2002, pp. 1095, 1159) in the family Septalariidae HAVLÍČEK, 1960, while *Flabellulirostrum* has been included in the family Uncinulidae RZHONSNITSKAYA, 1956.

The establishment of the Family Sapphicorhynchidae SARTENAER, 2007 represented a second step in the dismantling of the family Trigonirhynchiidae. The genus *Xahetomus* SARTENAER, 2009 was added to the type genus of the family.

There is no doubt that the breaking up of the family Trigonorhynchiidae will be pursued, as the introduction by GARCÍA-ALCALDE (2009) of the family Iberirhynchiidae (+ subfamily Iberirhynchiinae), with type genus *Iberirhynchia* DROT & WESTBROEK, 1966, and the subfamily Myrmirhynxinae, with type genus *Myrmirhynx* HAVLÍČEK, 1982, indicates. With the exception of its inclusion in the family Oligorhynchiidae COOPER, 1956 by GARCÍA-ALCALDE (1998, p. 769), *Iberirhynchia* has been initially assigned to the family

Trigonorhynchiidae, and maintained in it thereafter. SARTENAER (2007, p. 43) criticized both this transfer and the contents of this family. Both type genera were included by SAVAGE (1996, table 3, p. 256; 2002, p. 1056) in the subfamily Trigonirhynchiinae; JIN *et al.* (1993, p. 54) had already assigned *Myrmirhynx* to the same subfamily. All this explains why, in the following comparison, the definition of the family Trigonirhynchiidae will essentially rest on the definition of its type genus, *Trigonirhynchia fallaciosa*.

The family Inaequalibellirostridae differs from the family Trigonirhynchiidae in an outline that is constantly subtrigonal (subtrigonal to subrounded in the family Trigonirhynchiidae); a right angle triangle profile (half an ellipse to half a circle in the globular to subcuboidal family Trigonirhynchiidae); a convexo-concave ventral valve; a deeply serrate commissure; a deeper sulcus; higher fold and tongue; a lower number of higher and sharper costae; the absence of parietal costae (but external median costae are lower, sometimes markedly, than the others) on the slopes of the high fold; the maximum thickness at front margin and corresponding to the top of tongue (in the family Trigonirhynchiidae the fold curves more or less abruptly and flattens towards the middle part of the anterior commissure that is located around one third, exceptionally one half, of front below the maximum shell thickness); dental plates separated from the wall by narrow umbonal cavities as already mentioned by SARTENAER (2007, p. 42) [*Remark:* as mentioned by SARTENAER (2007, p. 42) serial transverse sections made from two topotypes of *Trigonirhynchia fallaciosa* do not show the wide umbonal cavities figured by SCHMIDT (1965, fig. 1, p. 4), and duplicated by SCHMIDT in SCHMIDT & McLAREN (1965, figs 428, 1f-q, p. H559), and SAVAGE (2002, figs 710, 1e-n, p. 1053)]; a deep septalium; and a smaller (narrower and less elongate) ventral muscle field.

Inaequalibellirostrum n. gen.

Derivatio nominis

Inaequalis, *is*, *e* (Latin, adjective) = unequal; *libellus*, *i* (Latin, masculine) = level; *rostrum*, *i* (Latin, neuter) = beak. The name draws attention to the unequal level of the middle and external median costae of the species assigned to the genus.

Type species: *Hemithyris Pareti* de VERNEUIL, 1850a.

Species assigned to the genus

Besides the type species, *Rhynchonella inaurita* from

the “Spiriferensandstein” of the middle Rhine valley described by the SANDBERGER brothers (1856, pp. 336-338, 444, 459, 470-472, 474, 477, 541, pl. XXXIII, figs 5, 5a-c) is assigned to the genus. Three specimens of the species are figured (Fig. 2). Some Lower Emsian (“Untercoblenschichten”) forms identified as *daleidensis* in the regions E (Antweiler) and SE (Stadtfeld, Oberstadtfeld) of the “Eifelkalkmulden” probably belong to the genus. They are very close to *inaurita*, but somewhat smaller. On account of lack of material, the author is compelled to go no further in the matter.

It has been mentioned above that the confusion of *R. inaurita* with various species (*Terebratula livonica* as understood at that time, *T. Huotina*, and *T. Daleidensis*) was unacceptable as were the wide stratigraphic range and geographic distribution that such confusion implied.

The name *inaurita* chosen by the SANDBERGER brothers indicate that the absence of ears (read: *lunulae*) in the dorsal valve (“Die Rückenklappe ist gänzlich ohne Oehrchen”) is a major character of this description. They also considered the *lunulae* observed

on both valves of *Rhynchonella Pareti* as the main difference between the two species, but expressed as such, this is only partly true. As a matter of fact, ears are present in *R. inaurita*, although not as strongly marked as in *R. Pareti*. This is acknowledged by the SANDBERGER brothers, who stated that the dorsal valve is “gänzlich ohne Oehrchen oder nur sehr kurz geöhrt”.

GOSSELET (1887), the first author to accept that *R. inaurita* could be a valid species (see above) reached such a conclusion in examining SCHNUR’s (1853, pl. XXII, figs 1a-c) figures of *R. Daleidensis* that he considered different from the original ones of ROEMER (1844, pl. I, figs 7a-c). It is easy to find in the literature specimens identified as (*Terebratula*, *Rhynchonella*) *daleidensis* that belong to *R. inaurita*, e.g. QUENSTEDT (1871, pl. 42, fig. 59; “Grauwacke” Daun, Eifel area) duplicated by ROEMER (1876, pl. 23, fig. 7), GÜRICH (1909, pl. 45, figs 6a-d = pl. 33, figs 5, 5a-c in SANDBERGER, G. & F., 1856).

Figures of three specimens [topotypes (*largo sensu*) IRScNBa12714-12716) from the Vallendar Substage (upper Lower Emsian) at Speckgraben im

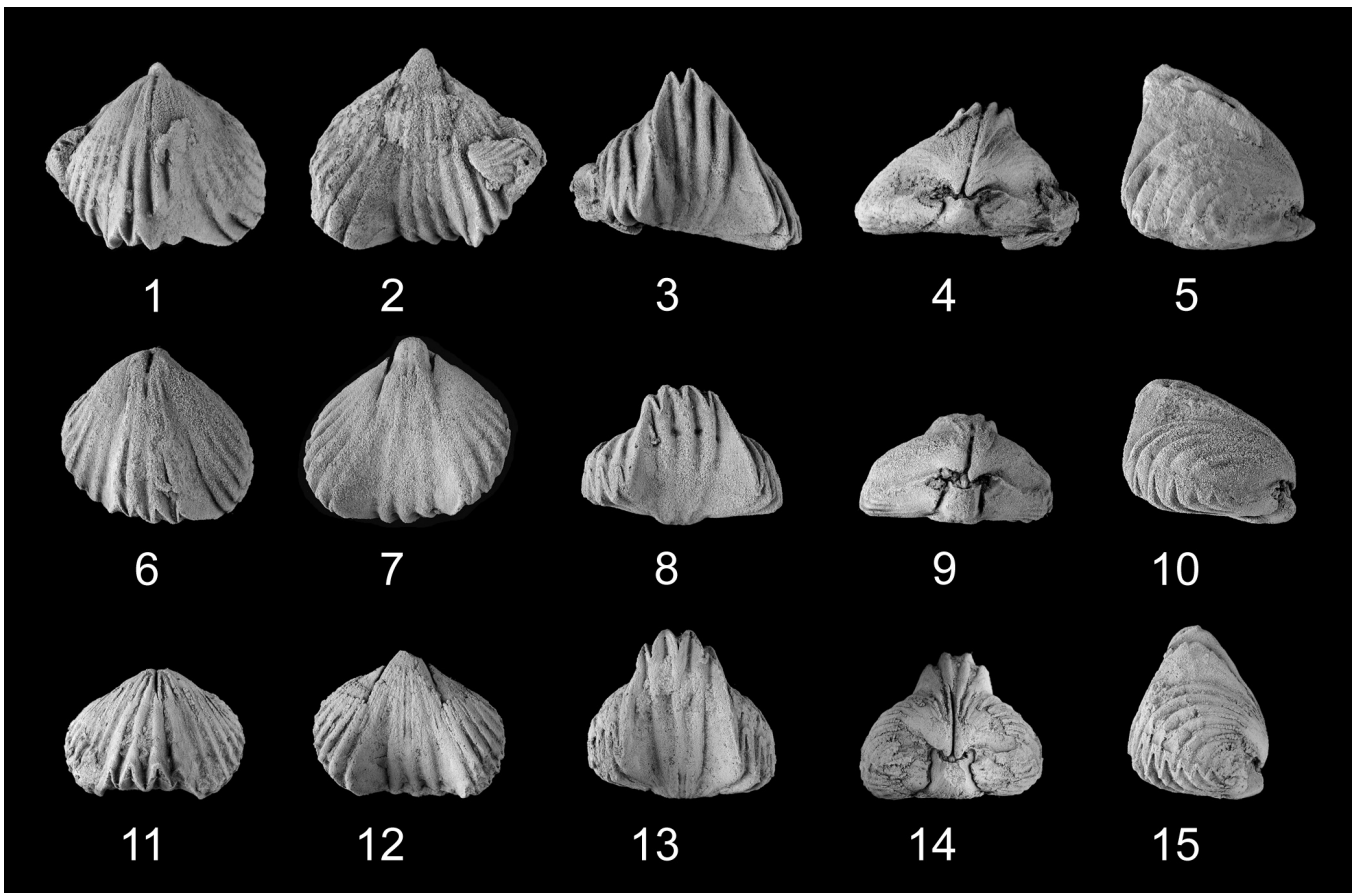


Fig. 2 – *Inaequalibellirostrum inauritum* (SANDBERGER, G. & F., 1856). Dorsal, ventral, anterior, posterior, and lateral views of three specimens. Topotypes (*largo sensu*) A-C, IRScNBa12714-12716. Speckgraben im Feisternachtal near Vallendar, topographic map 1: 25.000 Bendorf, middle Rhine valley, Vallendar Substage (upper Lower Emsian).

“Feisternachtal” near Vallendar (Middle Rhine valley)] are shown on Fig. 2; they are part of a collection of more than one hundred specimens made by Dr. K.-W. Wenndorf, and were generously presented to the author. *Inaurita* is restricted to the Vallendar Substage. Some isolated embedded valves suggest that it could also be present in the lower Upper Emsian Emsquarzit, Lahnstein Substage, and in “Hohenrheiner Schichten” of the middle Rhine valley, but there is no conclusive evidence for it.

Only two German geologists identified as *R. inaurita* specimens collected from two very different stratigraphic levels in the Middle Rhine valley. These are MAURER (1886, pp. 27, 37, 53), and FUCHS (1899, p. 68), who reported *R. inaurita* from the “*Cultrijugatus*-Stufe” (= Stufe VIII = uppermost Emsian) at Laubach and Michelbach), and the basal *Hercynia* Zone (middle Lower Emsian) at Bellsgraben in the Lorelei area, respectively. MAURER (1896, p. 658) even suggested that *R. inaurita* could eventually be considered as the dominant species (“vorherrschende Art” of what he defines as the lower subdivision [= Stufen I (“Taunusquarzit”), II (“Hunsrückschiefer”), and III (“untere Grauwacke”)] of the Lower Devonian on the east of the Rhine, and *R. daleidensis* as the dominant species of the upper subdivision [= Stufen IV (“Haliseritenschiefer”), V (“Coblenzquarzit”), VI (“Chondritenschiefer”), VII (“Hohenrheiner-Stufe”), and VIII “*Cultrijugatus*-Stufe”)]. The pertinence of these identifications cannot be assessed by the author.

The “very abundant” Devonian form from Devonshire identified as *Rhynchonella inaurita* by DAVIDSON (1870, pp. 72, 73-75, 78, 79, 80, pl. V, figs 1-3; 1881, pp. 336, 340, 341, 343, 351-353, pl. 38, fig. 21?, 35, 35a,b), and the Frasnian (sic!) form from NW Poland (borings) identified as *Camarotoechia* (*C.*) ex gr. *inaurita* by ŁOBANOWSKI (1968, pp. 768, 774, 775, 783, pl. II, figs 4-5) do not belong to that species.

Description

Shell medium- to medium-large-size, profile a right-angle triangle, strongly dorsibiconvex, and width always the largest dimension. Shell outline subtrigonal. Maximum shell width located anteriorly. Ventral *lunulae* much lower than the dorsal ones on account of the convexo-concave ventral valve; these postero-lateral concavities, also called ears, may extend as far as mid-length and are separated from the flanks proper by ridges that are well pronounced in the umbonal region. One, exceptionally two, faint costae present in the *lunulae*.

Anterior and antero-lateral commissures deeply serrate, postero-lateral commissures only slightly. Apical angle moderately wide. Sulcus and fold strongly marked, start from beaks. Ventral flanks narrow. Beak pointed, projecting, slightly to strongly incurved. Interarea very narrow. Deltidial plates short. Sulcus deep, widening rapidly, wide at front, with flat bottom, extended dorsally as a high and clearly delineated tongue with variable outline (trapeze, semicircular arch, and gothic arch). Tongue high, recurving slightly to strongly posteriorly in its uppermost part in the largest specimens. Crest of tongue variously (slightly to strongly) curved.

Dorsal valve very high, thickest at front margin, vertical or almost vertical in the umbonal area. Fold very high, rapidly gaining in height anteriorly, sometimes a sharp rise near front. Slope of flanks sharply interrupted postero-laterally by the *lunulae*, abrupt antero-laterally. Costae few, simple, regular, high, wide, angular (acute, sharp), starting from beaks. No parietal costae. Shell thin. Teeth stout, wide, short, cyrtomatodont, entering the dental sockets vertically in serial transverse sections. Denticula well developed. Dental plates slender, subparallel, separated from the wall by wide umbonal cavities. Delthyrial cavity wide. Hinge plate undivided. Outer hinge plates narrow. Septum extending until mid-length. Septalium wide, deep, with variable shape, median ridge sometimes present on bottom of septalium. Connectivum covering anterior part of septalium. Crura long, raduliform, aliform in section in their proximal part, walking-stick-shaped in their distal part, where they are curved. Dental sockets shallow, bottom wrinkled, inner socket ridges high. Muscle fields slightly impressed.

Comparisons

Inaequalibellirostrum can easily be separated from *Oligoptycherhynchus* by a right-angle triangle profile, a subtrigonal outline, well marked *lunulae*, a slightly wider apical angle, a slightly deeper sulcus, a tongue with variable outline, a higher fold with (sometimes) a sharp rise near front, acute and slightly higher costae, a different number of median costae, the absence of parietal costae; a deeper septalium; longer crura; and teeth entering the dental sockets vertically in serial transverse sections (laterally in *Oligoptycherhynchus*). Representatives of the genus *Inaequalibellirostrum* may also reach a larger size.

Inaequalibellirostrum differs from *Sappichorhynchus* SARTENAER, 2007 by many features, the major ones being a right-angle triangle profile, a subtrigonal outline, well marked *lunulae*, a smaller apical angle, a

deeper sulcus, a higher tongue with variable outline, a higher dorsal valve thickest at front, a higher fold with (sometimes) a sharp rise near front, acute costae, a different general costal formula [$\frac{4}{3}; \frac{5}{6}$ to $\frac{7}{8}$ for *I. paretii* against $\frac{5-6}{6-5}$; 0 to $\frac{0-1}{0-1}$, and $\frac{1-1}{1-1}; \frac{6-8}{7-9}$ for *S. sappho*].

Inaequalibellirostrum paretii (DE VERNEUIL, 1850a)

Fig. 3

The following generic assignments were given in succession to the species: *Terebratula* MÜLLER, 1776, *Rhynchonella* FISCHER de WALDHEIM, 1809, *Camarotoechia* HALL & CLARKE, 1893, "*Camarotoechia*", *Trigonirhynchia* COOPER, 1942, *Stegerhynchus* FOERSTE, 1909, and *Oligoptycherhynchus* SARTENAER, 1970.

In more recent time, not to mention the assignment to *Trigonirhynchia* COOPER, 1942 by WESTBROEK (1967, fig. 7, p. 8, pp. 9-10, 20-21, fig. 19, p. 21, fig. 21, p. 22, figs 26-28, p. 26, p. 27, fig. 27, p. 27, pp. 28-29, p. 30, fig. 32, p. 30, fig. 35, p. 32, pp. 34, 66, 69, 70, pl. III, figs 1, 7, 7a, pl. V, figs 1, 2, 2a, 3, pl. VI, figs 1a-c, pl. VIII, figs 1a,b, 2, 3) with a considerable stratigraphic range (Upper Siegenian - Lower Eifelian), and questionably to *Stegerhynchus* FOERSTE, 1909 by GARCÍA-ALCALDE *et al.* (1979, fig. 16, p. 27), the species has since 1984 continuously been mentioned as *Oligoptycherhynchus paretii*.

Lectotype

The only specimen figured by de VERNEUIL (1850a, pl. III, figs 11a,b) is here designated as the lectotype of the species. de VERNEUIL does not indicate from which of the two localities specifically mentioned in his description of the species (Sabero in the Province of Leon, and Ferroñes in the Province of Asturias) this specimen comes from.

The author is inclined to believe that Colle, referred to by de VERNEUIL, 1850a, p. 164 as "the richest locality of the Sabero district", is the locality from where the specimen has been collected. The species is particularly abundant there, and de VERNEUIL (1866, p. 11) wrote that he found it «pour la première fois dans les calcaires dévoniens inférieurs de Sabero».

Description and Remarks

Besides the original description of the external characters by de VERNEUIL (1850a, p. 177, pl. III, figs 1a,b) a

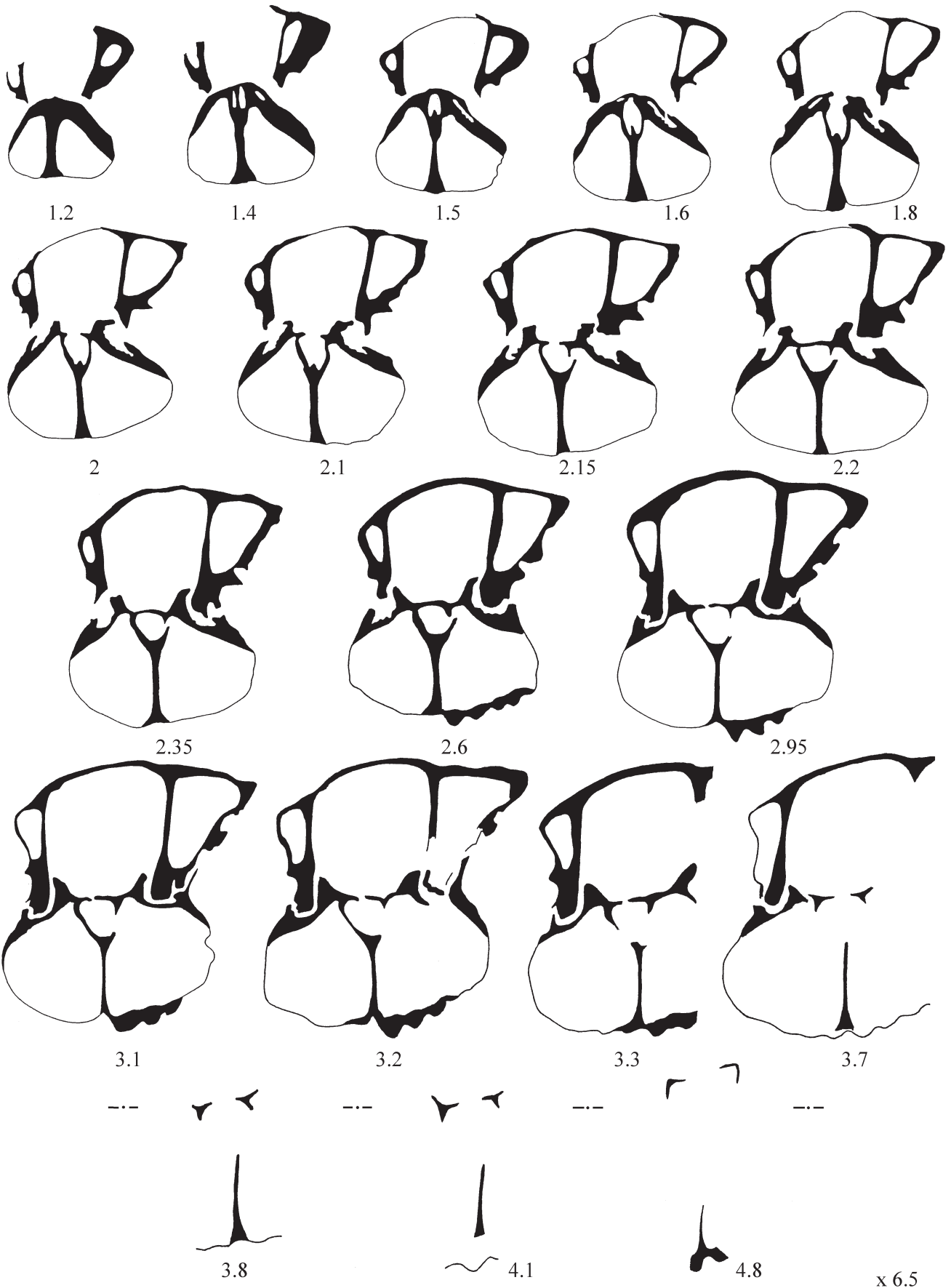
more detailed one has been given by OEHLERT (1884, pp. 415-416, pl. XIX, figs 2, 2a-i). The description by SCHUMANN (1965, p. 93, fig. 2, p. 95, p. 96, pl. 4, figs 10a-c as *Camarotoechia daleidensis*) includes internal characters.

BARROIS's (1889, pp. 84-85, pl. V, figs 3a-c) description of the alleged Armorican *Rhynchonella Paretii* is almost a word for word transcription of OEHLERT's description of the Spanish species. No comparison to *R. subpareti* OEHLERT, 1884 is attempted; *R. subpareti* is only listed (p. 328) in "la faune coblenzienne des calcaires de Bretagne".

The description that follows refers only to specific characters in need of further elaboration. Length and thickness similar, but thickness is usually slightly larger ($\frac{t}{l}$ between 0.81 and 1.23, mostly between 0.85 and 1.10; $\frac{1}{w}$ between 0.74 and 0.87; $\frac{t}{w}$ between 0.66 and 0.94). Width of sulcus at front between 63 and 85%, mostly between 70 and 80%, of shell width. Maximum shell width between 60 and 71% of shell length anterior to the ventral beak. Maximum thickness of dorsal valve, and thus of shell, between 81 and 70% (exceptionally less) of shell length anterior to ventral beak. $\frac{4}{3}$ median costae (very exceptionally $\frac{5}{4}$ or even $\frac{6}{5}$), $\frac{4}{5}$ to $\frac{7}{8}$ (exceptionally $\frac{8}{9}$) lateral costae; mere undulations of the postero-lateral commissures are not included in the counting. Median costae 3 to 4 mm wide near front. External costae of fold, distinctly lower than the others, and the ventral internal lateral costae, higher than the others, could rigorously be called parietal, but slopes of the fold are free of costae, as suggested by the name of the species (*paries, etis*, Latin = wall, flank). Apical angle between 103 and 115°, mostly around 105°. Transverse serial sections from one topotype (IRScNBa12713) are shown in Fig. 3. Sections made in five more specimens indicate that the septalium is either cupula-, amphora- or tumbler-shaped.

Excellent transverse serial sections have been made by DROT (1964, fig. 75, p. 181) from a specimen from the Province of Asturias (no precise locality given), and by SCHUMANN (1965, fig. 22, p. 95 as *Camarotoechia daleidensis*) from a specimen from the type area (Aguasalio syncline). Another transverse section and excellent reconstructions of the internal characters of the species have been figured by WESTBROEK (1967, fig. 7, p. 8, fig. 32, p. 30, fig. 35, p. 32).

Collections mentioned by ALVAREZ (1990, pp. 306-307) at two localities of the Province of Leon (Colle E of Boñar, and Villayandre S of Crémenes) were loaned



to the author by Prof Fernando Alvarez; they allowed assessing the variability, the ontogenetic development, and the number of costae of the species.

Comparisons

Various characters make *pareti* distinct from *daleidensis*: a right-angle triangle profile, a subtrigonal outline, well marked *lunulae*, a smaller apical angle, a lower ventral umbonal region, a projecting ventral beak, flat ventral flanks, a slightly deeper, better marked, and often wider sulcus, a tongue with variable outline, a relatively higher dorsal valve, always thickest at front, a higher fold with (sometimes) a sharp rise near front, a different general costal formula [$\frac{4}{3}$; $\frac{5}{6}$ to $\frac{7}{8}$ (exceptionally $\frac{8}{9}$) for *pareti* against $\frac{4}{3}$; 0; $\frac{7-9}{6-10}$ for *daleidensis*], external costae of fold distinctly lower than the others.

Inaequalibellirostrum inauritum can easily be separated from *I. pareti* by a larger size, a deeper sulcus, a higher fold, a higher tongue, and a slightly higher number ($\frac{7}{8}$ to $\frac{9}{10}$) of lateral costae. Although variable in both species, the tongue outline of *I. inauritum* is more often a gothic arch than in *I. pareti*. In extremely rare specimens, the external costae of fold of *I. inauritum* are not only lower than the others as in *I. pareti*, but they are significantly lower, and have to be called parietal.

Stratigraphic range and geographic distribution

DE VERNEUIL (1866, p. 11), who previously (1850a, 1850b) had only indicated a Devonian age for the species, was more precise when he declared that he found the species he established in the “calcaires dévoniens inférieurs de Sabero”.

In the type area (Province of Leon), *Inaequalibellirostrum pareti* is found in the part of the La Vid Group corresponding to the upper part of the Valporquero Formation and the Coladilla Formation, i.e. in the middle Emsian Faunal Intervals 11 to 13 introduced by GARCÍA-ALCALDE (1994). It means, in terms of the conodont zonation, the middle and upper parts of the undifferentiated *Polygnathus laticostatus/inversus* Zone + the lower half of the *P. serotinus* Zone [GARCÍA-ALCALDE in GARCÍA-ALCALDE *et al.*, 1979, fig. 16, p. 27; in TRUYOLS *et al.*, 1990, fig. 1, p. 14; 1994, fig. 2, p. 78; 1995, fig. 6, p. 21; 1996, fig. 2, p.

60; 2001, fig. 1, p. 548), and ALVAREZ & BRIME (1990, table 1, p. 15)].

Remark: Spanish geologists prefer to include Faunal Intervals 11 to 13 in the lower part of the Upper Emsian, because they subdivide the Emsian into two parts: a Lower Emsian (= most of Pedrosa Formation), and an Upper Emsian (= uppermost part of Pedrosa Formation + Valporquero Formation + Coladilla Formation + most of the Santa Lucia Formation).

Is *pareti* present outside the type area?

According to the literature, the species is present in three countries: France (Armorican Massif, Ardennes, Belfort Territory in the “Département de la Franche-Comté”, Pyrenees), Spain (Cantabrian Cordillera, Central Iberian Zone), and Turkey (Asia Minor), and ranges from the Gedinnian to the Lower Eifelian. This has little interest.

The species has been mentioned in the Asturian Devonian by various authors since de VERNEUIL (1850a, pp. 160, 177; 1850b, table, p. 780, p. 784; 1866, p. 11), and de VERNEUIL & BARANDE (1855, p. 1016).

BARROIS (1882, pp. 267-268, 473-475, table, p. 503, table, p. 518) collected the species from the “calcaire(s) de Nieva” (or “schistes et calcaires de Nieva” or “zône de Nieva”) at various localities of the Asturian coast, and attributed to them an early Coblencian age (i.e. late Siegenian and early Emsian). The Nieva Formation is considered nowadays of late Lochkovian- early Pragian age, thus indicating a considerably older age than the beds containing *pareti* in the type area.

From the beginning the species has been mentioned in Puerto del Ciervo and Chillón in the Sierra Morena (Central Iberian Zone) by de VERNEUIL in de VERNEUIL & BARRANDE (1855, p. 1016; 1866, p.11). Recent investigations by PARDO & GARCÍA-ALCALDE (1984a, p. 83; 1984b, p. 475; 1994, fig. 2, p. 155; 1996, fig. 3, p. 75, p. 79) and PARDO-ALONSO (in GARCÍA-ALCALDE *et al.*, 2000, fig. 4, p. 138) have indicated that *Oligoptycherhynchus* cf. *pareti*, *O. gr. pareti* and *O. aff. pareti* are part of a middle Emsian fauna in the Central Iberian Zone and in the northern part of the Ossa-Morena Zone.

The occurrence of *pareti* in the Ardennes rests on BARROIS's (1882, p. 512) statement that the species was common to the “Nieva limestone” and the “Montigny fauna”. BARROIS, however, had in mind *daleidensis* that he considered, as previously indicated, as closely

Fig. 3 – *Inaequalibellirostrum pareti* (DE VERNEUIL, 1850). Camera lucida drawings of serial transverse sections; figures are in mm forward of the ventral umbo. Topotype IRScNBa12713. Measurements: length = 17.9 mm; width = 19.2 mm; thickness = 17 mm. (opposite page)

related to *pareti*, *livonica*, and *inaurita*. The presence of *daleidensis* in the late Siegenian Montigny Greywacke had already been mentioned by French and Belgian geologists, especially by GOSSELET in many of his papers published between 1863 and 1880.

ROUSSEL (1904, p. 18), and ASSELBERGHS (1926, p. 72) mentioned the presence of the species in the Pyrenees and in the Belfort Territory (Parisot-Chevillard collection) respectively.

The presence of *pareti* in the regions just mentioned must be disregarded, but what about the Armorican Massif, where its presence has been widely accepted during the second half of the 19th century?

In his original description of *Hemithyris Pareti*, de VERNEUIL (1850a, pp. 159-162, 177, pl. III, figs 1a,b) made a distinction between this Devonian species “propre à l’Espagne” (Asturias and Leon) and a species “presque identique” from Viré-en-Champagne (“Département de la Sarthe”, Laval Syncline). The same year (1850b, table, pp. 780-781, pp. 784-785, 786 as *Terebratula Pareti*), however, he abandoned this distinction, and declared the species present not only in the Cantabrian Cordillera, but also in the Sierra Morena, at Viré-en-Champagne, Brûlon, and Joué (“Département de la Sarthe”, Laval Syncline), and Néhou (“Département de la Manche”, Cotentin peninsula, Lower Normandy); he even explicitly mentioned the “*Terebratula Pareti* de notre pays”.

Pareti from the Laval Syncline, to which BARROIS (1889, p. 85) gave the same qualification («type») as to the Spanish species. OEHLERT (1877, pp. 592, 601) named *Terebratula Pareti* specimens collected from the “Calcaire à *Spirigera undata* de la partie moyenne du dévonien inférieur” (probably middle Pragian) at la Baconnière, Saint-Germain, and Saint-Jean (“Département de la Mayenne”); in 1884 (p.414) he replaced this identification with *T. cypris*.

No *pareti* has been spotted in the various collections from Néhou, where its presence has been indicated by de VERNEUIL (1850b), by OEHLERT (1884, p. 416, and since then by various authors. Outside of the Laval Syncline and Néhou, *pareti* has been mentioned thereafter from the “Rade de Brest”, and Erbray.

Pareti was recorded from the “Rade de Brest” (Châteaulin Syncline, “Département du Finistère”) by de TROMELIN & LEBESCONTE [1876, p. 611 as *Rhynchonella Paretoi* (*R. Cypris*, d’Orb.); Lower Devonian], BARROIS [1886, p. 691; 1899, p. 239, «grauwacke du Faou» now considered as middle Pragian-early Emsian in age, and «grauwacke du Fret» (late Emsian in age). No available collection allows substantiating these claims. It is doubtful that these

references could indicate the small “*Rhynchonella*” cf. *subpareti* described by BRICE (1980, pp. 238-239, figs 58A, B, p. 237, fig. 59, p. 241, pl. 33, figs 6a, b; 1981, p. 197), and revived by MORZADÉC *et al.* (1988, fig. 7, p. 12-13; 1991, fig. 4, p. 907) from the Lower Pragian of the “Pointe de l’Armorique” located in the same syncline (see below); however, this age differs from those just mentioned. Although BRICE (1980, pp. 238-239, figs 58A,B, p. 237, pl. 33, figs 6a,b), who figured one specimen and made transverse serial sections from two others, considered her identification as questionable, it cannot be disregarded.

BARROIS (1887), after having mentioned the presence of *pareti* in the “Faune d’Erbray” (p. 160 as *Rhynchonella pareti*), he (1889, pp. 84-85, 87, table, p. 251, pp. 258, 261-262, 273, 328, pl. V, figs 3a-c), described *R. Pareti* from the Erbray Limestone at Erbray [Saint-Julien-de-Vouvantes Syncline, «Département de Loire-Inférieure” now “Département de la Loire-Atlantique”)]. The species had been already mentioned there by CAILLIAUD (1861, p. 333 as *Terebratula Pareti* or *hemithyris*) and de TROMELIN & LEBESCONTE (1876, pp. 606-607) [*Remark*: the word “unknown” used by BARROIS (1889, p. 261) to qualify CAILLIAUD’s *Terebratula Pareti* from the Erbray Limestone is misleading. Does it mean that he did not find the specimen(s) in CAILLIAUD’s collection that he had at his disposal? Otherwise, it is a contradiction, because he described *Rhynchonella Pareti* from the same limestone].

BARROIS’s description indicates, on one hand, that he had a sizeable collection at his disposal, and on the other, that more than one species was present in the material on hand, among others the “petites coquilles trigones” that he considered as juveniles.

The only figured specimen is easily separable from *pareti* by its proportions, in particular by its smaller thickness. It lacks the following characteristic features of *pareti*, i.e. the right-angle triangle profile, the well-marked *lumulae*, the very high fold, the usual number ($\frac{4}{3}$) of median costae (although $\frac{4}{3}$ is mentioned by BARROIS as the general ratio), the external costae of fold markedly lower than the others, and the high median costae. The present author is inclined to believe that this specimen belongs to a species of its own. This seems to be implied by BARROIS himself, who notes (1889, p. 85) that *Rhynchonella Pareti* from the Erbray Limestone, that he incorrectly dates as Gedinnian (late Pragian – early Emsian is the prevailing age nowadays), “se distingue un peu, de mes types de l’espèce, de la Sarthe [*subpareti*, according to the present author] et

de l'Espagne [*pareti*], par sa forme plus transverse, moins haute à l'état adulte". This opinion is supported by a small collection of the "Musée des Sciences" in Laval, comprising four specimens from the Lower Devonian of la Jaillerie near la Baconnière in the nearby "Département de la Mayenne", all of them of the same size as the specimen figured by BARROIS, and with $\frac{4}{3}$ median costae.

After 1889 mentions of *pareti* disappeared almost completely from the French literature related to the Armorican Massif, with the exception of indication of its presence in a given area (COUFFON, 1925, p. 45 as *Rhynchonella pareti*, "Département de Maine-et-Loire") and the confirmation of its occurrence in various localities (PÉNEAU, 1929, p. 263 as *R. pareti*, Erbray, Lower Devonian; COMTE, 1938, p. 59, Brittany, Coblencian). In short, *pareti* is not present in the Armorican Massif.

What about *subpareti*, which is a poorly known Middle Pragian species from the Armorican Massif? Its name alone imposes a comparison with *pareti*.

OEHLERT (1884) gave a new and more complete description of the Spanish *pareti* (pp. 415-416, pl. XIX, figs 2a-i as *Rhynchonella Pareti*), the presence of which he still accepts in Néhou (p. 416), and established (pp. 412, 414-417, pl. XIX, figs 3, 3a-e) *Rhynchonella subpareti* OEHLERT, 1884 that he had once considered «comme une simple variété de *R. Pareti*», and that he now sees as a «modification locale de la *R. Pareti* d'Espagne, mais dont les caractères sont suffisamment fixés pour qu'il soit nécessaire de lui donner un nom distinct» or a «forme représentative de la *R. Pareti* d'Espagne, mais qui, pour ses caractères constants, mérite d'être désignée par un nom distinct» or as offering «des modifications suffisamment constantes et distinctes du type d'Espagne, pour qu'il soit nécessaire de la mettre à part». This phraseology presupposes the extreme and not acceptable plasticity of a «type» similar to the one of *R. livonica* advocated by KAYSER (1871b) (see above): «ces espèces [*R. cypris*, *Pareti*, *subpareti*, *livonica*, *nympha*, *pseudolivonica*, etc.] ne sont sans doute qu'un même type, modifié dans le temps ou dans l'espace». A similar plasticity is advocated by BARROIS *et al.* in GOSSELET *et al.* (1922, p. 97) for a group including *R. nympha*, *R. daleidensis*, *R. livonica*, *R. sub-livonica*, *R. Pareti*, and *R. sub-pareti* (see above).

The two specimens of *Rhynchonella subpareti* figured by OEHLERT (1884, pl. XIX, figs 3, 3a-e; the specimen of figs 3, 3a,b is here formally designated as the lectotype of the species) went astray *fide* BRICE (1980, p. 238). According to DROT (1964, p. 177) and

DROT & L'HOTELLIER (1976, p. 268), OEHLERT's figures of *Rhynchonella subpareti* represent a juvenile form (figs 3c-e) with the aspect of *R. cypris* d'ORBIGNY, 1847, which could be "*Camarotochia paretiiformis*" DROT, 1964 from the Lower Gedinnian of the Dra Plains (Anti-Atlas, Morocco). Very few specimens of this taxon collected at that time are available, although OEHLERT (1884, p. 415) stated that the species he established was quite frequent in the Devonian outcrops of the "Département de la Sarthe". BRICE *in* MORZADEC *et al.* (1988, p. 52) also reminds that OEHLERT collected the species from the very fossiliferous Pragian (Saint-Cénére Formation) shales and limestones of the old quarry La Roussière SW of Saint-Germain-le-Fouilloux ("Département de la Sarthe").

The four localities mentioned by OEHLERT in 1884 (Saint-Cénére in the "Département de la Mayenne", and Viré, les Courtoisières, and Vieux-Michel in the adjoining "Département de la Sarthe", all localities in the Laval Syncline) were dropped by OEHLERT (1886, p. 23). Instead a fifth locality of the same syncline, Sablé ("Département de la Sarthe"), was added. BARROIS (1889, p. 328) did not discuss *Rhynchonella subpareti* that he only listed in the "faune coblencienne du calcaire de Bretagne".

As a matter of fact, *subpareti* never gained wide acceptance in the literature related to the Armorican Massif. Except for the mentions by REED (1922, p. 96) and BARROIS *et al.* in GOSSELET *et al.* (1922, p. 97) (see above), and by GIOVANNONI & ZANFRA' (1979, p. 214 as *Camarotoechia subpareti*), *subpareti* has been reported by COUFFON [1925, p. 78 as *Rhynchonella subpareti*, "Département de Maine-et-Loire", Lower Givetian (sic!)], PÉNEAU [1929, pp. 84, 231, 263 as *R. sub.Pareti*, Angers-Saint-Julien-de-Vouvantes Syncline, "Département de Maine-et-Loire", Calcaire de Vern (Middle Siegenian, now Upper Lochkovian-Lower Pragian)], and PILLET (1953, p. 17, Calcaires de Vern-d'Anjou).

Still, as previously indicated, *subpareti* popped up again in another part of the Armorican Massif when BRICE (1980, 1981) described "*Rhynchonella*" cf. *subpareti* from the Lower Pragian of the "Pointe de l'Armorique" (Châteaulin Syncline, "Rade de Brest", "Département du Finistère"). The stratigraphic range of this species was again given by MORZADEC *et al.* (1988, 1991). BRICE (1980, p. 239) stated that "*R.*" cf. *subpareti* seemed to belong to the same genus as "*R.*" *nympha* that had still to be defined. Consequently BRICE (1981, pp. 195, 197, p. 214, figs 1A, B, p. 196, fig. 7, p. 213, pl. 25, figs 1a-c, 2a-d, 3a,b, 4, 5) proposed the genus *Stenorhynchia* BRICE, 1981 with type species

Terebratula nympha BARRANDE, 1847 and included in it the varieties proposed by BARRANDE. At the same time, she assigned OEHLERT's *Rhynchonella subpareti* to it, and described as *nympha* an Upper Emsian small form from the la Lézais trench in the Ménez-Bélair Syncline ("Département d'Ille-et-Vilaine") assigned by SARTENAER (2009, p.34) to the genus *Xahetomus* SARTENAER, 2009. MORZADEC *et al.* (1981, fig. 4, p. 12, fig. 5, p. 14, pp. 16-17) and MORZADEC (1983, p. 276, fig. 6, p. 286) confirmed the presence of *nympha* in the Upper Emsian of the la Lézais trench, and mentioned it also from beds of the same age in the Reun ar C'hrank en Lanvéoc section ("Rade de Brest"), which LARDEUX & MORZADEC (1979, pp. 14, 17) had already reported *Stenorhynchia nympha* from.

This brings up questions regarding the presence of the Bohemian species in the Armorican Massif and the contents of the genus *Stenorhynchia*. The presence of *nympha* in the Armorican Massif, covering the form identified and figured as such by BARROIS (1889) and also various other forms, has been accepted by many authors, e.g. CAILLIAUD (1861, p. 332), de TROMELIN & LEBESCONTE (1876, pp. 606-607), KAYSER (1878, p. 143: *Pareti* "gehört wahrscheinlich zu *nympha*"), OEHLERT (1884, p. 416; his opinion has been mentioned above), FRECH (1887, p. 410), BARROIS [1889, pp. 86-87, table, p. 241, p. 328, pl. V, figs 2a-e; *nympha*, of which he had only six specimens, is figured for the first time and considered distinct from *Pareti* present in the same limestone (Erbray Limestone)], MAURER (1896, p. 659), VENYUKOV (1899, p. 157), SCUPIN (1906, pp. 236-238, table, p. 302), REED (1922, p. 96; refers to *nympha* "as figured by BARROIS"), PÉNEAU (1929, p. 230, table, p. 263), LE MAÎTRE (1934, pp. 210-211, table, p. 229, pp. 230, 235, 239; 1944, pp. 11, 12, table, p. 20, pp. 47, 48), COMTE (1959, p. 276), HAVLÍČEK (1961, p. 87), PILLET (1962, p. 49), DROT (1964, p. 105). MAILLIEUX (1931, pp. 21, 24) also indicated the presence of *nympha* in the Armorican Massif and envisaged the possibility that it belongs to *Pareti*, and, as a consequence, falls into synonymy of *daleidensis*),

L'HOTELLIER-VIDEAU, who devoted her PhD (1970) to the rhynchonellids from some outcrops in the southeastern part of the Armorican Massif, discussed neither *R. pareti* nor *R. subpareti*, but described eight distorted specimens from existing collections from the Erbray Limestone as *Stegerhynchus? nympha* and *S.? cf. nympha*. She figured three specimens representing two, probably three, taxa, none of them approaching *R. Pareti* or *R. nympha* figured by BARROIS (1889, pl. V, figs 2a-e, 3a-c).

The Upper Emsian *S. nympha* from la Lézais is also

not identical with the Pragian *S. nympha* from Bohemia (age *fide* HAVLÍČEK, 1961, pp. 85, 87) [Remark: the species described as *S. nympha* by BRICE (1981) is completely different from *Rhynchonella nympha* described by BARROIS (1889)].

Various characters make the Bohemian *nympha* distinct from the Armorican *nympha*: a ventral valve almost completely excavated by the sulcus, a wide and shallow sulcus with flat bottom, a larger number of lateral costae (8 to 13), the almost systematic presence of parietal costae, and the absence of a connectivum [HAVLÍČEK (1961, p. 86) writes: "Das Septalium wird von ventraler Seite durch zwei dünne Fortsätze eingeengt, die den oberen Septaliumränder aufsitzen und deren freien Enden gegeneinander orientiert sind. Diese Fortsätze berühren sich jedoch niemals"; (see also fig. 29, p. 86 of *Stegerhynchus nympha*)]. [Remark: GARCÍA-ALCALDE in TRUYOLS-MASSONI & GARCÍA-ALCALDE (1994, p. 232), taking into account a personal communication from BRICE, declares that transverse serial sections made by her from two Bohemian specimens presented by HAVLÍČEK have shown a delicate tectiform connectivum in the anterior part of the septalium].

Nympha from la Lézais does not belong either to the genus *Stenorhynchia*. "*Rhynchonella*" *cf. subpareti* from the "Pointe de l'Armorique" also cannot be assigned to the genus *Stenorhynchia*, and the assignment of *Terebratula Nympha pseudo-livonica* BARRANDE to *Stenorhynchia* is also disputable.

GARCÍA-ALCALDE in TRUYOLS-MASSONI & GARCÍA-ALCALDE (1994, pp. 232-233) included BRICE's Upper Emsian species from la Lézais in *Stenorhynchia briceae* GARCÍA-ALCALDE, 1994, a frequent species from the upper third of the La Ladrona Formation and the basal part of the Aguión Formation of the Cantabrian Cordillera, i.e. from the middle Emsian Faunal Intervals 9 to basal 12 of GARCÍA-ALCALDE (Remark: these Faunal Intervals are put in the Upper Emsian by Spanish geologists because they subdivide the Emsian into a Lower Emsian restricted to the lower half of the La Ladrona Formation, and an Upper Emsian corresponding to the upper half of that formation + the Aguión Formation + most of the Moniello Formation). This substitution, accepted by BRICE (2000, p. 15), does not make the generic assignment more acceptable.

Terebratula nympha, a characteristic species of the Koněprusy (Pragian) Limestone, has successively been assigned to the following genera (in parentheses are indicated the main periods): *Rhynchonella* FISCHER de WALDHEIM, 1809 (1856-1963), *Camarotoechia* HALL & CLARKE, 1893 (1934-1990), *Nymphorhynchia*

RZHONSNITSKAYA, 1956 (1956-1987), *Stegerhynchus* FOERSTE, 1909 (1961-1969), *Stenorhynchia* BRICE, 1981 (1979-2000); assignments to *Ancillotoechia* HAVLÍČEK, 1959 (1975), *Felinotoechia* HAVLÍČEK, 1961 (1982), and *Microsphaeridiorhynchus* SARTENAER, 1970 (1983) remain exceptions. *Nympha* is not present in most of the regions of the world where it has been mentioned; it is one of the various Lower Devonian Bohemian species that have been unduly “exported”.

The genus *Stenorhynchia* has followed the unfortunate usual pattern, shared with many genera, in being as from its establishment overloaded with species that are foreign to it. Today twenty-two species, subspecies, and forms in open nomenclature have been assigned to the genus. For example, neither the Upper Emsian *S. briceae* already mentioned nor the five small middle and late Silurian Bohemian species and subspecies of *Stenorhynchia* described by HAVLÍČEK in HAVLÍČEK & ŠTORCH (1990, pp. 28, 30, 38, 40, 42, 142-144, pl. XXXVII, figs 6a-c, pl. XLII, figs 1a-c, 2a-c, 4a-c, 5a,b, pl. XLIII, figs 4a-c, 5a,b, 6a-c, 7a-d, 8a-c, 9) belong to it.

A middle Silurian to early Zlichovian age advocated for *Stenorhynchia* by HAVLÍČEK (1992, table 1, p. 56, p. 80) due to the extended (in relation with the previous Pragian range) stratigraphic range he gives to *S. nympha*, and to his questionable assignment, in 1990 (in HAVLÍČEK & ŠTORCH), of new Silurian species to the genus [Remark: CHLUPÁČ *et al.*, 1972, pp. 122, 148, 171 as *Nymphorhynchia* aff. *nympha*, and CHLUPÁČ *et al.*, 1979, p. 146 as *N. cf. nympha*, already indicated that *Stenorhynchia nympha* could be present in the Lower Lochkovian and in the Upper Zlichovian respectively].

Other stratigraphic ranges are also found in the literature, e.g. Ludlow-Přídolí in the European Province (RONG *et al.*, 1995, appendix 2, p. 60) (it means that the *stratum typicum* of the type species is excluded), and those including the Emsian species incorrectly assigned to the genus: Pragian-Emsian (SAVAGE, 1996, table 3, p. 256), uppermost Lochkovian-Pragian-Emsian (BRICE in BRICE *et al.*, 2000, fig. 1, p. 68), and Upper Silurian (Ludlow) to Lower Devonian (Emsian) (SAVAGE, 2002, p. 1062).

Compilation of the literature suggests long range of the genus *Stenorhynchia* (Middle Silurian - Upper Frasnian) and wide geographic distribution, since it has been reported from Algeria (various regions), Armenia, Belgium, Bohemia, Canada (various regions), Carnic Alps, England (various regions), France (various regions), Germany (various regions), Kazakhstan, Lettonia, Libya (Fezzan), Mauritania (Zemmour),

Mongolia, Morocco (various regions), North America (various States), Podolia, Russia (many regions), Spain (various regions), Tadjikistan, Turkestan, Turkey (Bithynia), Uzbekistan. It is clear that the contents of the genus are unduly inflated and that, in particular, the world distribution of its type species is not acceptable.

According to the author, the genus *Stenorhynchia* is restricted to the Pragian, with the suspicion that further investigations will allow to restrict its stratigraphic range even more within that stage.

Subpareti was “imported” into the Iberian Cordillera by COMTE (1959, p. 282, Coblencian, as *Camarotoechia subpareti*), in the Ossa-Morena Zone by PARDO ALONSO & GARCÍA-ALCALDE (1996, p. 79 as *Oligoptycherhynchus* gr. *subpareti*, Upper Emsian), and, as from 1992, as *Stenorhynchia subpareti* in the Upper Pragian and Emsian Intervals 7 to 10 of the Cantabrian Cordillera by GARCÍA-ALCALDE (1992, fig. 4, p. 59; 1994, fig. 2, p. 78; in TRUYÓLS-MASSONI & GARCÍA-ALCALDE, 1994, fig. 2, p. 223, pp. 232, 233; 1996, fig. 2, p. 60), and by GARCÍA-ALCALDE & TRUYÓLS-MASSONI (1994, p. 86, fig. 2, p. 87).

In the absence of any description of the Spanish *subpareti*, it is not possible to accept the presence of the Armorican species in any region of Spain. GARCÍA-ALCALDE (1997, p. 243; 1998, p. 243) found *S. subpareti* in Lower Emsian beds from the Dra Plains (Anti-Atlas, Morocco); it is only mentioned here for the sake of completeness.

How does *subpareti* compare with the Spanish *pareti*? *Subpareti* did not benefit of a clear-cut definition when it was established. As already indicated, its original description is obscured by sybillic phraseology. OEHLERT (1884, pp. 414, 417) opposed diminished (“amoidries”), attenuated (“atténuées”), and exaggerated (“exagérées) specimens (or forms) of *subpareti* and *pareti* to “typical” specimens (or forms) or “normal types” of both species. Are we faced with the ontogenetic development of one species or with the transition from one species to another, an opinion evoked by OEHLERT himself (p. 414)? In any case the wording used for establishing *subpareti* is ambiguous.

In his original description of *subpareti*, which is more a comparison with *pareti* than the description of an independent species, OEHLERT (pp. 416-417) states that the new species is smaller, less cuneiform, has a more clearly marked outline, a more globular profile, weaker and less angular costae, and less pronounced *lumulae*. He also stresses that the relative depth of valves and the development of the lateral and median parts are different. The occasional secondary median costae (read: parietal costae) mentioned by OEHLERT

do not appear on the figures of the lectotype, formally designated in the present paper, and on three specimens from the Lower Devonian of Viré housed in the “Musée des Sciences” of Laval. It is regrettable that *subpareti*, which, according to OEHLERT (1884, p. 415), is rather frequently found in the Devonian outcrops of the “Département de la Sarthe”, is poorly represented, and more generally even not, in the available collections from the Armorican Massif.

Proper collecting by regional geologists is needed for improving our information on *subpareti* and the Armorican *pareti* that are still insufficiently known and not stratigraphically dated. It will then become possible to deal with their generic status. In particular it will allow finding out if the middle-sized *R. subpareti* from the Laval Syncline belongs to the same genus as the “*nympha*” of the same size and the larger “*pareti*” from the Saint-Julien-de-Vouvantes Syncline. The problem of the presence or absence of *subpareti* in Spain could then also be solved.

An important conclusion of the present study is that neither *Inaequalibellirostrum pareti* nor *Stenorhynchia nympha* is present in the Armorican Massif.

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Explanation of Plate 1

All figures are natural size

Oligoptycherhynchus daleidensis (ROEMER, 1844)

- Figs 1-5 – Topotype A, IRScNBa12703. Dorsal, ventral, anterior, posterior, and lateral views. Costal formula: $\frac{4}{3}$; 0; $\frac{9}{10}$ and $\frac{10}{11}$.
- Figs 6-10 – Lectotype. Dorsal, ventral, anterior, posterior, and lateral views. Costal formula: $\frac{4}{3}$; 0; $\frac{7}{8}$ and $\frac{8}{9}$. Dorsal, anterior, and lateral views of this specimen have been figured by ROEMER (1844, pl. 1, figs 7a-c as *Terebratula Daleidensis*).
- Figs 11-15 – Topotype B, IRScNBa12704. Dorsal, ventral, anterior, posterior, and lateral views. Costal formula: $\frac{4}{3}$; 0; $\frac{9}{10}$.
- Figs 16-20 – Topotype C, IRScNBa12705. Dorsal, ventral, anterior, posterior, and lateral views. Costal formula: $\frac{4}{3}$; 0; $\frac{7}{8}$.
- Figs 21-25 – Topotype D, IRScNBa12706. Dorsal, ventral, anterior, posterior, and lateral views. Costal formula: $\frac{4}{3}$; 0; $\frac{9}{10}$.
- Figs 26-30 – Topotype E, IRScNBa12707. Dorsal, ventral, anterior, posterior, and lateral views. Costal formula: $\frac{4}{3}$; 0; $\frac{8}{9}$ and $\frac{9}{10}$.
- Figs 31-35 – Topotype F, IRScNBa12708. Dorsal, ventral, anterior, posterior, and lateral views. Costal formula: $\frac{4}{3}$; 0; $\frac{9}{10}$.

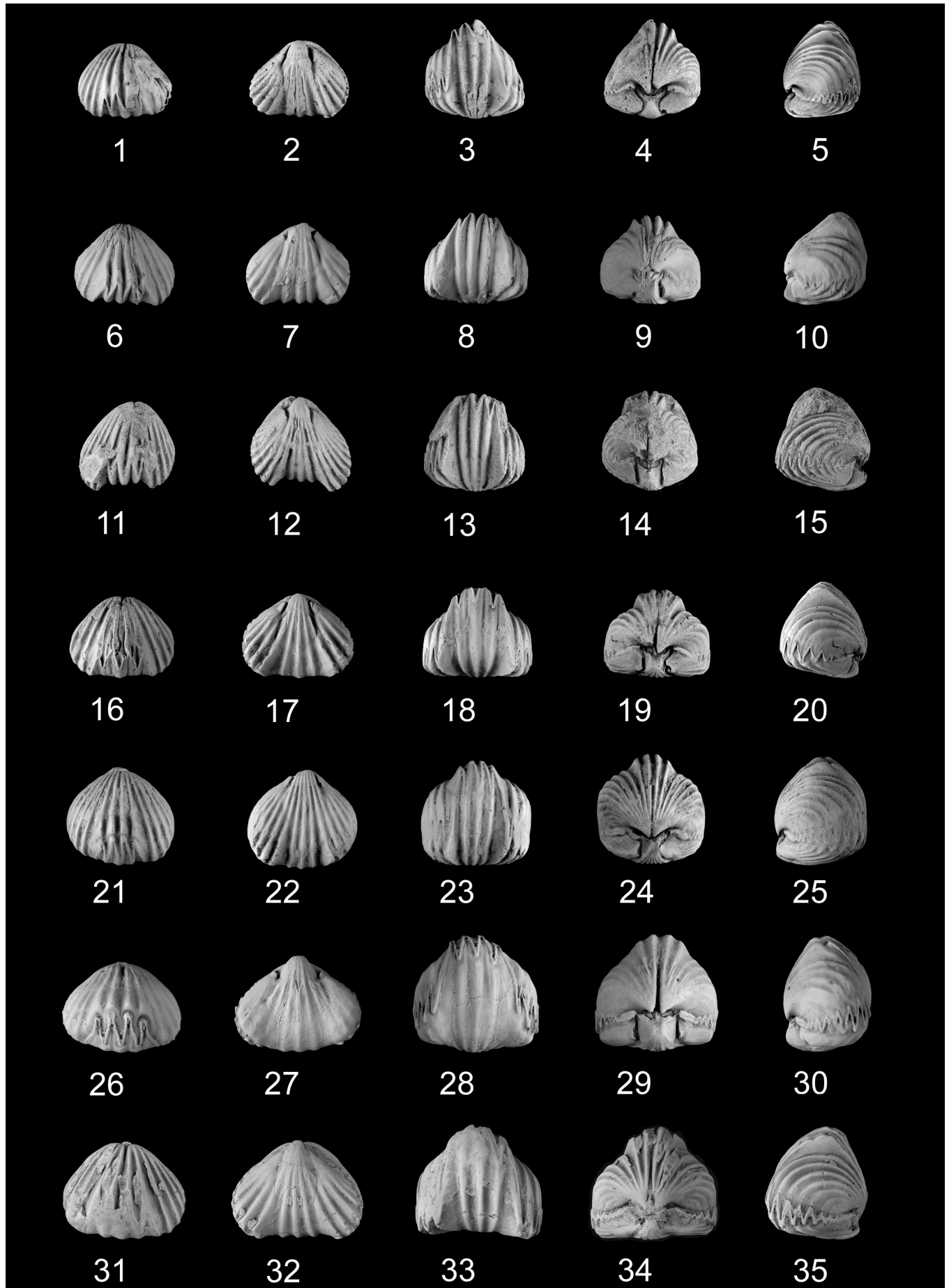


PLATE I