Sapphicorhynchus, a new early Givetian rhynchonellid (brachiopod) genus from western New York State, USA, and Sapphicorhynchidae, n. fam.

by Paul SARTENAER

Introduction

The revision of the taxonomical status and the stratigraphical range of key rhynchonellid taxa of the New York Devonian, that started by the author with the late Givetian Tullypothyridina venustula (HALL, 1867) in 2003 and the late Eifelian Cherryvalleyrostrum limitare (VANUXEM, 1842) in 2004, is carried on with the re-examination of the early Givetian Rhynchonella sappho HALL, 1860.

The extensive stratigraphical range - Upper Helderberg to Lower Carboniferous - of the species, which has successively been assigned to the genera Rhynchonella FISCHER DE WALDHEIM, 1809, Stenoscisma CONRAD, 1839 (exceptionally), Camarotoechia HALL & CLARKE, 1893 (for about a century), and Cupularostrum SARTENAER, 1961, excludes the possibility to deal with the various forms to which its name has been given. It would lie outside the scope of the present study, which rests on the examination of the type species, field work, collections examined in various museums and scientific institutions, and scrutiny and pondering on the abundant literature on the subject.

Systematic palaeontology

Sapphicorhynchidae n. fam.

Type genus: Sapphicorhynchus n. gen.

Diagnosis

Shell of medium to medium-large size with strongly dorsibiconvex profile and subcircular to subpentagonal outline; top of shell posterior to front; short ventral interarea, well marked lunulae; angle of the cardinal commissure wide. Sulcus wide, moderately deep, fold
low, start at a short distance from beaks; costae well marked, simple, regular, in moderate number, start at the beaks, and strongly indent the commissure; parietal costae sometimes present. Delicate internal structures. Undivided hinge plate, crura raduliform. Dental plates separated from the wall by wide umbonal cavities; septum long; septalium wide and deep, amphora-shaped; connectivum covering anterior part of septalium.

Remarks
The diagnostic combination of characters allows separation of the family from all known families, and in particular from the family Trigonirhynchiidae SCHMIDT, 1965 here discussed.

Various reasons explain the remarkable prosperity of the family Trigonirhynchiidae. The main one, which has already been pointed out by SARTENAER (2001, p. 208), is the inclusion in the short diagnosis of the family of many alternative characters (see Fig. 2); the above-mentioned diagnosis does not contain any such characters. Consequently: 1) the family becomes an "accommodating drawer" and the few non-alternative remaining characters are shared with other families; 2) some other characters are omitted; 3) undue emphasis is placed on one or two or few characters; 4) genera are easily transferred from one family to another. These four points are exemplified.

Nine genera were added by McLAREN in SCHMIDT & MCLAREN (1965, pp. H559-562), three of them questionably (Lepidocycloides nikiforova in nikiforova & andreeva, 1961, Nekhoroshevia BUBLICHENKO, 1956, and Rostricellula ULRICH & COOPER, 1942) to the four genera (Cupulavrostrum SARTENAER, 1961, Nymphorrhynchia RZHONSNITSKAYA, 1956, Psychomalaetoechia SARTENAER, 1961, and Trigonirhynchia Cooper, 1942) originally assigned to the family Trigonirhynchiidae by SCHMIDT (1965, pp. 2, 3). Thirty years later the family numbered some 50 genera. In 2007 the number rose to about 80, making it the "richest" rhynchonellid family, the second "richest" being the Leiorhynchidae STAINBROOK, 1945. Out of them 54 (53 in 1996, 54 in 2002), 21 for the first time, were listed by SAVAGE (1996, table 3, p. 256; 2002, pp. 1052-1077) and distributed among five subfamilies: Hemitoechiinae SAVAGE, 1996 (17 genera), Ripidiorhynchinae SAVAGE, 1996 (four genera), Rostricellularinae ROZMAN, 1969 (four genera in 1996, five in 2002), Trigonirhynchinae SCHMIDT, 1965 (24 genera), and Virginiiatinae AMSDEN, 1974 (four genera).

It is not appropriate to single out a few characters or to decree that some are major and others minor. Characteristics of a family or a genus must be considered as a whole. Why should features such as the following be overlooked, omitted or rejected: location of top of shell; apical angle; depth, width and point of origin of sulcus and fold; regularity, strength, point of origin, number of costae; presence or absence of parietal costae; shape, depth, strength of the septalium; and the serration (undulation, indentation) of the commissure. In the case of Trigonirhynchia fallaciososa (BAYLE, 1878), the type species of Trigonirhynchia, its evident "globular, subcuboidal" shape mentioned by OEHLERT (1884, p. 420) in the first description of the species is not included in the diagnosis of the genus, and neither is the great deepness of the septalium illustrated by SCHMIDT (1965, fig. 1, p. 4) and reproduced by SCHMIDT in SCHMIDT & MCLAREN (1965, fig. 428, ff-q, p. H559) and SAVAGE (2002, fig. 710,1e-n, p. 1053). Furthermore, the internal structure of T. fallaciososa cannot be considered as fully known; in order to better understand the transverse serial sections given by SCHMIDT (1965), the author made sections in another topotype that show a stout septalium and connectivum, and dental plates separated from the wall by narrow umbonal cavities.

When few characters (sometimes one or two) are considered, the classification may move in various directions depending upon the weight put on them. Thus, AMSDEN (1974, p. 68) divided the family Trigonirhynchiidae into two subfamilies: Trigonirhynchiinae (forms with a fold and sulcus), and Virginiiatinae AMSDEN, 1974 (forms lacking a fold and sulcus). ROZMAN (1969, pp. 86, 94-96) erected the family Rostricellularinae embracing three genera (Evenkornirhynchia ROZMAN, 1969, Lepidocyclus, and Rostricellula ULRICH & COOPER, 1942) to which SAVAGE (1996, table 3, p. 256; 2002, p. 1065) added the genera Azamella LAURIE, 1991 in 1996 and Plectothyrella TEMPLE, 1965 in 2002. JIN et al. (1993, p. 54) adopted the subfamilies Trigonirhynchiinae and Rostricellularinae as the two divisions of the family Trigonirhynchiidae, and assigned eight genera to the former and 16 genera to the latter, but considered as distinctive the "septalial cavity covered completely or anteriorly by medially coalescent plates" (Trigonirhynchiinae), and the "septalial cavity commonly restricted, but not completely covered by medially projected crural ridges" (Rostricellularinae). BARANOV (1989, p. 42) had already proposed to follow a similar line, but with a different approach;
assuming that the structure of the cadinalia of the family Trigonirhynchiidae “did not undergo important changes in the course of evolution since the Ordovician”, he stated that divided and undivided hinge plates “interpreted by scientists as a taxonomical character of generic and family level” appeared independently in different phylogenetic branches, and that probably the “separation of Ancillotoechia-like [i.e. covered septalium] genera took place a few times in the course of iterative evolution”. Meanwhile, HAVLÍČEK & ŠTORCH (1990, p. 125) considered that the subfamily Rostricellulinae “was very close to the Oligorhynchiidae [COOPER, 1956] “judging from the inner and outer morphology”, and it is to this family that GARCÍA-ALCALDE (1998, p. 769) assigned five genera included by SAVAGE (1996) in the subfamily Trigonirhynchiinae [Ancillotoechia HAVLÍČEK, 1959, Aratoechia HAVLÍČEK, 1982, Myrmirhynx HAVLÍČEK, 1982, Sufetirhynchia HAVLÍČEK, 1982, and Iberirhynchia DROT & WESTBROEK, 1966; Ancillotoechia, Myrmirhynx and Sufetirhynchia were already assigned to the subfamily by JIN et al. (1993, p. 54)] plus a new genus Tectogonotoechia GARCÍA-ALCALDE, 1998 not mentioned by SAVAGE (1996, 2002).

Moving genera in and out of the family Trigonirhynchiidae is a common practice that is bound to last in the next future, e.g. Werneckeea. LENZ 1971 put by BRICE in BRICE et al. (2000, fig. 1, p. 68) in the family Trigonirhynchiidae is now included in the subfamily Leiorhynchinae STAINBROOK, 1945. Such shifts emphasize the deficiency and precariousness of the present classification. They can lead to the shrinking of a family to a few genera, when not only to its type genus. This has been the case of the family Camarotoechiidae SCHUCHERT & LE VENE, 1929, in which SCHMIDT & MCLAREN (1965, pp. 579-584) included twenty genera distributed among two subfamilies: Camarotoechiinae SCHUCHERT & LE VENE, 1929 (16 genera) and Septalariniiae HAVLÍČEK, 1960 (four genera).

To conclude, many discrepancies and/or contradictions result from the misleading diagnosis of the family Trigonirhynchiidae. Only one example is given here. What has the tiny lower-middle Eifelian genus Tetratomia SCHMIDT, 1941 in common with the medium-large to large Pragian [not Emsian as stated by SAVAGE (1996, table 3, p. 256; 2002, p. 1070)] genus Losvia BREIVEL & BREIVEL, 1976, the former assigned by SAVAGE (2002, p. 1070) to the subfamily Trigonirhynchiinae, the latter to the subfamily Hemitoechininae SAVAGE, 1996? (Tetratomia has a narrow and well marked sulcus and fold, an undivided hinge plate, no septalium, etc. Losvia has a weak sulcus and fold, a very low (almost none) tongue, an uncovered septalium, etc.)

**Sapphicorhynchus** n. gen.

**Derivatio nominis** Σαπφικός, η, ón (Greek, adjective) = sapphic. The name draws attention to the name given to the species, now type species, by HALL (1860).

**Type species**: Rhynchonella sappho HALL, 1860.

It is not to be excluded that some forms from the lower and middle Ludlowville Formation (Middle Givetian) of western and central New York State (Centerfield Limestone, Ledyard Shale, Wanakah Shale, and Otisco Shale Members) that have been assigned to the species could belong to the genus, if not to the species. Such forms have neither been figured nor described, and their examination would require more material than the one at hand.

**Diagnostic features**

Shell of medium to medium-large size, outline subcircular to subpentagonal, greatest thickness posterior to front. Ventral interarea short, angle of the cardinal commissure wide. Sulcus and fold start at a short distance from the beaks, sulcus moderately deep, fold low, forming a moderately high transverse-trapezoidal tongue, top of tongue lower than the maximum shell thickness. Costae in moderate number, start at the beaks. Parietal costae sometimes present. Internal structures delicate. Dental plates separated from the wall by wide umbral cavities. Hinge plate undivided, connectivum covering anterior part of septalium, septum long, septalium wide and deep, amphora-shaped, elongated raduliform crura.

**Description**

Shell medium- to medium-large-size, profile strongly dorsibiconvex (dorsal valve considerably thicker than ventral valve, the flanks of which are flattening near the front in medium-large specimens); ventral valve thickest at 1/4 to 1/3 shell length, dorsal valve thickest anterior to mid-length. Shell outline subcircular to subpentagonal (length about 3/4 to 4/5 width); half barrel-shaped in frontal view. Postero-lateral and lateral commissures sharp, strongly indented by the costae. Anterior commissure fused into the wall formed by the extremities of the costae. Wide angle of the cardinal commissure. Top of shell posterior...
to front. Elongated concave lunulae present in both valves with zero to two costae (two in the lectotype) on each of them; they are defined by faint beak ridges near the beaks. Ventral beak acute, slightly to strongly incurved; umbo low. Ventral interarea short; deltidial plates narrow. Sulcus and fold well marked, start imperceptibly at a short distance from the beaks. Sulcus wide, moderately deep and well delineated towards margin; bottom flat to slightly convex, extended dorsally as a moderately high tongue with subtrapezoidal outline, recurving slightly posteriorly in its uppermost part. Fold remains low throughout; top gently convex. In transverse profile, dorsal valve high, outer flanks deflected ventrally to be almost vertical near commissure. Median and lateral costae, in moderate number, start from the beaks [Remark: number of costae is not related to the ontogeny as implied by the founder of the species (HALL, 1860, p. 87; 1867, p. 340)]. Costae well marked, moderately high, wide, rounded, simple, and regular. Costae (with the exception of the posterolateral ones) interlock in high zigzags at the commissure. Parietal costae, when present, reach and indent the commissure.

Internal structures delicate. Dental plates subparallel posteriorly, becoming convergent anteriorly; umbonal cavities wide; teeth short, with wrinkled dorsal face. Inner socket ridges low. Septum long; septalium deep and wide (deeper than wide), amphora-shaped; hinge plate undivided, outer hinge plates flat to slightly convex passing without sign of crural bases into long crura; crura raduliform, Phrygian cap-shaped in section in their distal part where they are slightly curved ventrally; connectivum covering anterior part of septalium, and extending beyond.

Growth
With increasing size specimens become wider (transverse), and their angle of the cardinal commissure opens. Ventral lateral costae are often fan-wise in medium-large specimens; the term “flabelliform” used by HALL (1860, p. 87; 1867, p. 340) applies to such specimens, which HALL (1867, explanation of pl. 54, figs 38-42) and HALL & CLARKE (1893, explanation of pl. LVII, figs 10-14) considered as “large and characteristic” or “large and typical” (see Pl. 1, Figs 1-5).

Comparisons
The Lower Givetian (Upper Pompey Member of the Skaneateles Formation) genus Cupularostrum SARTENAER, 1961 has few characters in common with Sapphicorhynchus n. gen. It is only mentioned here because S. sappho has been included in it by GRIESEMER (1965, pp. 268-270), and since then, by North American and non-American authors (see Synonymy) [Remark: Three species were already assigned to the genus in 1964: the late Silurian Cupularostrum litchfieldense (SUCHCERHT, 1903) and the Lower Devonian C.? semiplicata (CONRAD, 1841) by BERDAN (1964, p. 16), and a new species, C. cantabricum, collected by WESTBROEK (1964, pp. 243, 244-246) near the Frasnian/Famennian boundary]. JOHNSON & PERRY (1976, pp. 622-624), who discussed the genus at length, ignored GRIESEMER’s paper in which, with the exception of the type species, C. recticostatum, SARTENAER, 1961, none of the twelve species and variety attributed to Cupularostrum belong to that genus [Camarotoechia ambiguia, FAGERSTROM 1961, C. edareensis, STAINBROOK, 1942, C. congregata var. parkheadensis CLARKE & SWARTZ, 1913, Rhynchonella depressa KINDLE, 1901, Atypa eximia, HALL, 1843, Camarotoechia formosensis FAGERSTROM, 1961, C. gregeri BRANSON, 1923, Rhynchonella orbicularis HALL, 1860, R. (Stenocisma) cf. prolifica HALL, 1867, Rhynchonella sappho, Camarotoechia scitulus CLELAND, 1911, and Rhynchonella tethys BILLINGS, 1860]. In general terms, Cupularostrum, to which some 50 species and subspecies + some 40 forms in open nomenclature have been assigned at one time or another, almost all of them incorrectly, is poorly understood and its alleged cosmopolitan status advocated by JOHNSON & BOUCOT (1973, p. 95), NORRIS (1979, p. A246), BRICE (in RACHEBOEUF et al., 2001, p. 147) , and SAVAGE (2002, p. 1056) is disputable. So is also its notable - Upper Silurian to Lower Viséan - and variable stratigraphical range, e.g. Upper Emsian to Middle Frasnian (SAVAGE, 1996, table 3, p. 256; 2002, p. 1056), latest Eifelian to earliest Frasnian (BRICE in BRICE et al., 2000, fig. 1, p. 68). SAVAGE et al. (1979), although they incorrectly accepted the presence of “Cupularostrum” in the Lochkovian, Pragian, and Emsian (table, p. 175), were right when they wrote (p. 195) that “Cupularostrum” is a poorly known Lower Devonian genus and the occurrences listed [table, p. 175] may include more than one genus”. MERGL et al. (2001, p. 178) were also certainly entitled to call Cupularostrum a “basket” genus.

Cupularostrum can easily be separated from Sapphicorhynchus n. gen. by its subglobular aspect and its thick and robust internal features (dental plates, septum, hinge plate, connectivum). Other
distinctive characters are a smaller size (the largest adult specimen of *C. recticostatum* reaches the size of the smallest adult specimen of *Sapphicorhynchus sappho*); a shell outline always subcircular or oval; a relatively higher ventral valve; the maximum thickness of the shell located more posteriorly; different l/w ratios (0.81 to 1 against 0.71 to 0.88 for *S. sappho*); narrower sulcus and fold; the uppermost part of tongue not slightly recurved posteriorly, but tending sometimes to become vertical; a different general costal formula \( \frac{4}{5} \) to \( \frac{1}{1}; \frac{8}{10} \) against \( \frac{5}{7} \) to \( \frac{1}{1}; \frac{6}{8} \) to \( \frac{1}{1} \) for *S. sappho*; generally narrower costae; parietal costae rarely present; a smaller angle of the cardinal commissure \( (97° \text{ to } 115° \text{ against } 115° \text{ to } 128° \text{ for } S. sappho) \); and lower inner socket ridges.

Before comparing *Sapphicorhynchus* n. gen. with *Oligoptycherhynchus* SARTENAER, 1970, the following remarks have to be made. When establishing the genus *Oligoptycherhynchus*, with type species *O. hexatomus* (SCHNUR, 1851) from the middle Eifelian (Ahrdorf Schichten) of the Gerolsteiner Mulde, SARTENAER (1970, pp. 20-21) also included: *Terebratula daleidensis* ROEMER, 1844 from the upper Emsian (Wiltz Schichten) of the Daleiden “Muldengruppe”, *T. elliptica* SCHNUR, 1853 from the middle Eifelian (Gondelsheimer Schichten) of the Gerolsteiner Mulde, *Rhynochonella imitatrix* FUCHS in SPIESTERSBACH & FUCHS, 1909 from the upper Emsian (Remscheider Schichten) of the Bergisches Land, and *Camarotoechia hexatoma* Wettoldorfensis SCHMIDT, 1941 from the uppermost Emsian (Heisdorf Schichten) of the Prümmer Mulde. Field work carried out since then in the Eifel area and in the Bergisches Land, and the study of collections housed in various museums and scientific institutions have convinced the author that the species and subspecies had a considerably shorter stratigraphical range (see above), and that they had to be rejected from the genus. Consequently, the wide range (middle Siegenian to Eifelian) advocated by the author in 1970 for *Oligoptycherhynchus* has become unacceptable, and the genus, now defined by its type species only, has to be emended. The emended diagnosis is as follows (changes in the initial diagnosis are in italics):

**Medium size.** Outline subcordiform. Uniplicate. Inequivalve. **Top of the 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. Short and robust teeth.

Another point that has commonly been overlooked is that the specimen of *Oligoptycherhynchus hexatomus* designated by SCHMIDT (1941, p. 9) as the representative of the species is not a specimen chosen in the original SCHNUR’s (1851, 1853) collection. It also comes neither from the **locus typicus,** nor from the **stratum typicum,** which are the “Kalk zu Pelm und Gees”, i.e. the Gees Horizon of the middle Eifelian Ahrdorf Schichten of the Gerolsteiner Mulde in the Eifel area. Assuming that the two specimens figured by SCHNUR (1853, pl. 23, figs 2a-g) were lost, SCHMIDT (1941, p. 9) took the unfortunate decision to consider a specimen coming from N. of Üxheim (“n. Ü. von Üxheim”) as the representative of the species and considered by her as approaching “am besten der Abbildung bei SCHNUR” the specimen (figs 2a-e) figured by SCHNUR. But Üxheim is located in a different syncline, the Hillesheimer Mulde, than Pelm and Gees. Moreover, SCHMIDT’s (1941, p. 9) statement that the “Horizont des Üxheimer Fundortes ist ja auch bei Gees vertreten” is contradicted by WEDEKIND (1924, pp. 86-90) and STRUVE in HOTZ et al. (1955, p. 59), who observed that the alleged Geeser Horizont N. of Üxheim is the Kirberg Member of the Lower Nohner Schichten (lower Eifelian).

The middle Eifelian genus *Oligoptycherhynchus* and *Sapphicorhynchus* n. gen. have many characters in common, e.g. a strongly biconvex profile; sharp postero-lateral and lateral commissures, strongly indented by the costae; an anterior commissure fused into the wall formed by the extremities of the costae; a short ventral interarea; well marked sulcus and fold, starting imperceptibly at some distance from the beaks; a wide, moderately deep sulcus, with flat to slightly convex bottom; a tongue slightly recurved posteriorly in its uppermost part; the top of fold gently convex; a
moderate number of well marked, moderately high, wide, rounded, simple, regular costae, starting at the beaks; dental plates converging anteriorly; wide umbonal cavities; a long septum; a deep amphora-shaped septum; a connectivum covering the anterior part of the septum and extending beyond (undivided hinge plate); short robust teeth; and long raduliform crura.

Many characters make Sapphicorhynchus n. gen. distinct from Oligopterhynchus: a smaller thickness; a greater width (this is only valid for middle-large specimens of Sapphicorhynchus sappho); the maximum thickness located posterior to front; better marked lunulae; a moderately high tongue with transverse-subtrapezoidal outline; a moderately high fold; ventral lateral costae arranged fan-wise (this is the maximum thickness located posterior to front; plates passing without sign of crural bases to Phrygian structures; horizontal or slightly convex outer hinge (undivided hinge plate); short robust teeth; and long umbonal cavities; a long septum; a deep amphora­

of Sapphicorhynchus hexatomus.

Sapphicorhynchus sappho (HALL, 1860)
Plate 1, Figs 1-33; Text-figure 1

1860 — Rhynchonella sappho (n.s.) — HALL, p. 87.
1867 — Rhynchonella (Stenocisma) sappho — HALL, pp. 340-341, pl. 54, figs 34-43.
non 1867 — Rhynchonella (Stenocisma) sappho — HALL, pl. 54, fig. 33.
non 1867 — Rhynchonella (Stenocisma) sappho var. — HALL, p. 354, pl. 55, figs 47-52.
non 1884 — Rhynchonella Sappho — WILLIAMS, p. 23.
non 1887 — Rhynchonella Sappho — WILLIAMS, table, p. 27.
non 1887 — Rhynchonella Sappho var. — WILLIAMS, p. 62.
non 1887 — Rhynchonella sappho var. — WILLIAMS, pp. 74, 77.
non 1887 — Rhynchonella Sappho var. — WILLIAMS, p. 88.
non 1887 — varieties of R. Sappho — WILLIAMS, p. 88.
non 1888 — Rhynchonella sappho, Hall — HERRICK, pp. 24, 25, 26, 40, table, p. 98, pl. VII, fig. 25.
non 1888 — Rhynchonella sappho (varieties of...) — HERRICK, pp. 39, 40.
non 1888 — Rhynchonella sappho (conditions of...) — HERRICK, p. 40.
non 1888 — Rhynchonella sageriana (= var. of R. sappho ?) — HERRICK, pl. II, fig. 15.
non 1888 — Rhynchonella sappho (Cf. cooperi) — HERRICK, pl. V, fig. 1.
non 1899 — Rhynchonella sappho — LESLEY, p. 900.
1890 — Stenoschisma sappho. (Rhynchonella sappho) Hall — LESLEY, p. 1060, figs 34-43, p. 1060 (= pl. 54, figs 34-43 in HALL, 1867).
non 1890 — Stenoschisma sappho. (Rhynchonella sappho) Hall — LESLEY, p. 1060.
1893 — Rhynchonella Sappho, Hall — HALL & CLARKE, pl. LVII, figs 10-14 (= pl. 54, figs 38-42 in HALL, 1867).
non 1893 — Rhynchonella Sappho — HERRICK in HALL & CLARKE, p. 192.
non 1896 — Rhynchonella sappho — WILLIAMS in KINDLE, p. 47.
non 1897 — Rhynchonella (Camarotoechia) sappho, HALL — PROSSER, p. 98.
non 1898 — Camarotoechia Sappho, Hall — WHITEAVES, pp. 386, 387.
non 1898 — Camarotoechia sappho (Hall) — WHITEAVES, p. 416.
non 1899 — Camarotoechia sappho (Hall) (?) — GIRTY, table, p. 485, pp. 541-542.
non 1899 — Camarotoechia sappho (?) — GIRTY, pp. 490, 492.
e.p. 1899 — Camarotoechia sappho — GIRTY, p. 492.
1899 — Camarotoechia sappho Hall — GRABAU, fig. 140, p. 230 (= pl. 54, figs 38-42 in HALL, 1867).
non 1899 — Camarotoechia sappho, Hall — GRABAU, p. 230.
non 1899 — Camarotoechia sappho Hall — KINDLE, pp. 13, 15, 16, 19, 28, 31. 58.
1901 — Camarotoechia sappho Hall — CLARKE, pp. 132, 134.
1901 — Camarotoechia sappho Hall — WOOD, pp. 150, 151, 162, 175, 179.
1901 — Camarotoechia sappho Hall — WOOD, p. 162.
non 1901 — Camarotoechia sappho Hall — KINDLE, pp. 568, 584, pl. VII, figs 4, 4a.
non 1902 — Camarotoechia Sappho (Hall) — SHIMER & GRABAU, table, p. 182.
non 1903 — Camarotoechia sappho? — BUTTS, p. 993.
non 1903 — Camarotoechia sappho Hall — BUTTS, pp. 994-995.
non 1903 — Camarotoechia sappho Hall — CLELAND, p. 42, appendix, p. 97.
non 1904 — Camarotoechia sappho Hall — RAYMOND, pp. 82, 151, 162.
non 1905 — Camarotoechia sappho Hall — CLARKE, p. 64.
non 1905 — Rhynchonella (Camarotoechia) cf. Sappho Hall — THOMAS, table, p. 286.
non 1905 — Camarotoechia sappho — KINDLE in WILLIAMS & KINDLE, pp. 21, 25, 32, 35, 120, table, p. 122.
non 1905 — Camarotoechia sappho — WILLIAMS in WILLIAMS & KINDLE, chart between p. 54 and p. 55.
non 1908 — Rhynchonella Sappho Hall — KNOX, p. 552.
non 1908 — Camarotoechia aff. sappho — GIRTY in KINDLE, p. 92.
non 1908 — Camarotoechia sappho — GIRTY in KINDLE, pp. 92, 98.
non 1909 — Camarotoechia sappho Hall — STAUFFER, table, p. 163.
1909 — Camarotoechia sappho Hall — GRABAU & SHIMER, figs 354 c.d, p. 287 = pl. 54, figs 39, 40 in HALL, 1867.
1911 — Camarotoechia sappho — CLELAND, p. 25.
non 1912 — Camarotoechia sappho Hall var. — PROSSER, p. 90.
Family Trigonirhynchiidae SCHMIDT, 1965

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<td>- meist einfach</td>
<td>- simple</td>
<td></td>
</tr>
<tr>
<td>- kantig oder gerundet-kantig</td>
<td>- angular or subangular</td>
<td></td>
</tr>
<tr>
<td>- im Schnabel beginnend</td>
<td>- extending from beak</td>
<td></td>
</tr>
<tr>
<td>- rarely bifurcate</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stirn und Schnabel können abgestutzt sein</td>
<td></td>
<td></td>
</tr>
<tr>
<td>In der Stielklappe meist gut ausgebildete Zahnstüten</td>
<td></td>
<td></td>
</tr>
<tr>
<td>In der Armklappe:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>- Septum</td>
<td>well-formed septalium that may be open or wholly or partly covered by plate uniting outer hinge plates</td>
<td></td>
</tr>
<tr>
<td>- gut entwickeltes Septalium, das bei einigen Gattungen offen, bei anderen ± bedeckt ist.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Schlossvorsatz fehlt</td>
<td></td>
<td>cardinal process absent</td>
</tr>
</tbody>
</table>

![Fig. 1](Original diagnosis of the family Trigonirhynchiidae SCHMIDT, 1965 parallel with those of the treatises (1965, 1996 + 2002). Italics indicate alternative characters.)

American Museum of Natural History, New York (AMNH34623–34629 (formerly 4382), and 5214); five specimens are figured (pl. 54, fig. 34–43 in HALL, 1867); four (figs 34–42) come from “limestone of the Marcellus shale” (HALL, 1860, p. 87) or from “calcareous layers in the Marcellus shale” (HALL, 1867, p. 341) “near Le Roy, Genesee County, New York” (HALL, 1860, p. 87; 1867, p. 341), the fifth one comes probably from near Le Roy, but WHITFIELD & HOVEY (1900, pp. 210–211) claim that it comes from Madison County. The ninth specimen (pl. 54, fig. 33) from the “Upper Helderberg limestones”, “assigned with some doubt to the species”, could not be located neither in the AMNH nor in any major American museum or scientific institution visited by the author. Six specimens (AMNH34630–34635) referring to a variety from Ohio, are not part of the type series, because they were first mentioned by HALL in 1867 (pl. 55, figs 47–52); two of them have been photographed (Pl.1, Fig. 34).

Lectotype, AMNH34626 (formerly 4382). Pl.1, Figs 1–5 = pl. 54, figs 38–42 in HALL, 1867. Limestone in the Marcellus shale, near Le Roy, Genesee County, New York. This specimen has been designated as the lectotype, because it was considered as a “characteristic specimen of the species” by HALL (1867) or a “typical example” by HALL & CLARKE (1893); figures of the lectotype have been reproduced many times in the literature (see Synonymy). Paralectotype A = pl. 54, fig. 33 in HALL, 1867. Upper Helderberg limestones”, “referred with some doubt to the species”. Paralectotypes B, AMNH34623 (formerly 4382), Pl.1, Figs 26–30 = pl. 54, figs 34, 35 in HALL, 1867, C, AMNH34624 (formerly 4382), Pl.1, Figs 21–25 = pl. 54, fig. 36 in HALL, 1867, D, AMNH34625 (formerly 4382), Pl.1, Figs 16–20 = pl. 54, fig. 37 in HALL, 1867, F, AMNH34627, G, AMNH34628, Pl.1, Figs 31–33, H, AMNH34629, Pl.1, Figs 6–10. Same locality and rock unit as the lectotype.
Paralectotype E, AMNH5214, Pl.1, Figs 11–15 = pl. 54, fig. 43 in HALL, 1867. Madison County, New York, according to WHITFIELD & HOVEY (1899, pp. 210–211).


Other material
Outside the type series, with the exception of Paralectotype A that anyhow does not belong to the species, eight specimens collected by the author in 1953 from the Stafford limestone, Batavia, Genesee County, New York, have been studied. Many specimens housed in various museums and scientific institutions have also been examined.

Description
Remark
The external characters of this “beautiful and symmetrical” species, as HALL (1860, p. 87; 1867, p. 341) qualified it, were adequately described by HALL (1860, p. 87), but it is only some years later that HALL (1867, pp. 340–341, pl. 54, figs 33–43) figured the species and completed its original description. Subsequent descriptions by various authors deal only partly or not at all with the species as redefined in the present paper.

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

Width of sulcus at front between 57 and 79 per cent (mostly between 61 and 74 per cent) of shell width. Top of tongue located lower than the highest part of the shell, i.e. between 16 and 25 per cent of shell thickness. Length of ventral interarea mostly between 24 and 35 per cent of shell width.

Measurements of the lectotype, seven paralectotypes, and two topotypes are given on Table 1; the lectotype and six paralectotypes have been photographed. Thickness of dorsal valve between 69 and 79 per cent (mostly 72 to 77 per cent) of shell thickness. Maximum thickness of dorsal valve, and thus of shell, between 12 and 43 per cent (mostly 24 to 30 per cent) of shell length anterior to the ventral beak. Maximum shell width between 45 and 65 per cent of shell length anterior to the ventral beak. Angle of the cardinal commissure between 115° and 128° (mostly between 120° and 128°).

The general costal formula in median, parietal, and lateral categories derived from at least 75 per cent of the specimens is: \[ \frac{5}{4} \text{ to } 6 \quad \frac{1}{0} \text{ to } 1 \quad \frac{1}{0} \text{ to } 1 \text{ to } 6 \text{ to } 8 \quad \frac{7}{1} \text{ to } 9 \text{ ratios of costae of the lectotype, six paralectotypes, and two topotypes are given in the explanation of Plate 1. Parietal costae present in about half the specimens. Width of median costae at front varies between 2 and 2.5 mm.}

Transverse serial sections of one specimen (topotype C IRSNBA12217) are shown on Text-figure 2; they are the first sections ever made from a specimen of the species.

Discussion of synonymy
Although rather complete, the synonymy list is by no means exhaustive. “e.p. “ in front of some references means that they include also, but not only, the species. The negative part of the synonymy is explained in the section Stratigraphical Range and Geographical Distribution.

Comparisons
Rhynchonella orbicularis HALL, 1860 from the “Chemung Group” of SW New York, and also present in NW Pennsylvania and NE Ohio, is one of the species assigned to the genus Cupularostrum by GRIESEMEN (1965, p. 270) (see above). DUTRO (1981, fig. 7, p. 79) mentions also C. orbicularis, although COOPER & DUTRO (1982, p. 71) prefer to put the species in the genus Ripidiorhynchus SARTENAER, 1966, an assignment already rejected by SARTENAER (1985, p. 323; 2001, p. 208). Rhynchonella orbicularis, which is “diagnostic of the Conewango Group” according to CHADWICK (1935, p. 328), is only mentioned here because CASTER (1930, pp. 152, 157, 158, 159 as Camarotoechia sappho) places the species described by HALL (1867) as Rhynchonella (Stenocisma) orbicularis and by HALL & CLARKE (1893) as Camarotoechia orbicularis into the synonymy of Sapphicorhynchus sappho. Although its appropriate generic assignment is not yet solved, Rhynchonella orbicularis, which is abundantly figured in the literature, differs from Sapphicorhynchus sappho, even in CASTER’S conception, by so many characters that there is no need to be more explicit.

Another species discussed in a PhD by HOLLAND (1959), and of which the generic status is also outstanding, is Rhynchonella Allegania WILLIAMS, 1887 known from SW New York and NW Pennsylvania as “highly characteristic” of Oswayo shales by BUTTS (1903, p. 99) and GOLDRING (1931, p. 428), “characteristic” of Oswayo beds by GOLDRING (1931, p. 426), a “Oswayo index fossil” by CASTER (1934, p. 95) and TESMER (1975, pp. 28, 66, 74, 79) or a “diagnostic species” of the Conewango...
1.3  1.35  1.5  1.55  1.7  1.8

1.9  2  2.05  2.1  2.2

2.3  2.35  2.4  2.45  2.6

2.8  2.95  3.05  3.25  3.4  3.65  3.8  3.95  4.1  4.2  4.3  4.35

Fig. 2 — *Sapphicorhynchus sappho* (HALL, 1860). Topotype C, IRScNBa12217. Transverse serial sections, figures are in mm from ventral umbo. Measurements: length = 17.1 mm; width = 20.7 mm; thickness = 13.2 mm. Costal formula: $\frac{6}{2}, 0; \frac{7}{8}$.

Group by CHADWICK (1935, p. 329). The species also lent its name to a zone (RICKARD, 1975, pl. 3), an Assemblage Zone (DUTRO, 1981, fig. 2, p. 70, p. 81) or a fauna (CARTER & KAMMER, 1990, p. 94). Generally attributed to *Camarotoechia*, the species has been questionably assigned to *Sinotectirostrum* SARTENAER, 1970 by DUTRO (1981, fig. 2, p. 70, p. 81), and SARTENAER (1970, p. 13) indicated that the possibility of its inclusion in the genus *Centrorhynchus* SARTENAER, 1970 should be considered. In any case, *Rhynchonella Allegania* is so strikingly different from *Sapphicorhynchus sappho* that any comparison is futile. The species is only alluded to here because CASTER (1930, p. 155) wrote that it “is in general appearance very similar to *Camarotoechia sappho*”. This statement does not correspond to the reality, while the following observation by WILLIAMS (1887, p. 88) is acceptable: “it [*Rhynchonella Allegania*] approaches more nearly *R. orbicularis*”.

**Sapphicorhynchus**, a new early Givetian rhynchonellid genus

Stratigraphical range and geographical distribution

*Sapphicorhynchus sappho* comes only from the Stafford Limestone of western New York, and its time equivalent, the Mottville Sandstone and Limestone of central New York, both being the lowermost members of the Lower Givetian Skaneateles Formation. This approximately corresponds to Dutro's (1981, fig. 1, p. 69) *Cupularorhynchus sappho* Occurrence Zone. All other references [Remark: It has been mentioned above (see Type species) that forms from the Centerfield Limestone, Ledyard Shale, Wanakah Shale, and Otisco Shale could belong to the genus, if not to the species] are indicative of other taxa and stratigraphical levels from the type area and outside New York State. The following concise review (New York references are in ascending stratigraphical order), which includes assignments with a query and varieties, runs parallel to the negative synonymy list.

**Western and Central New York**

*Upper Helderberg limestones*: Hall (1867 “referred with doubt to the species”), and by various authors referring to Hall, e.g. Lesley (1898), Knod (1908), Feruglio (1930), and Linsley (1994).

*Centefeller Limestone Member* (= lowermost member of the Middle Givetian Ludlowville Formation): Smith (1935, p. 104).


*Encrinal Limestone* (= base of the Moscow Formation): Grabau (1899), Shimer & Grabau (1902), Cleland (1903), Raymond (1904, Encrinal limestone and above), and Stauffer (1915, p. 171).


*Tully Limestone*: Williams (1887), Smith (1935, p. 110), Cooper & Williams (1935), and Linsley (1994, p. 100).

*Chemung Beds*: Williams (1884; 1887; in Kindle, 1896), Lesley (1890, p. 1060), and von Engel (1932).

*Sherburne Member* (in middle part of the Genesee Formation): Smith (1935, p. 111.)

<table>
<thead>
<tr>
<th>in mm</th>
<th>Paratype E A2514</th>
<th>Lectotype 34626</th>
<th>Paratype H 34629</th>
<th>Paratype F 34627</th>
<th>Paratype D 34625</th>
<th>Paratype C 34624</th>
<th>Paratype B 34623</th>
<th>Paratype G 34628</th>
<th>Topotype A</th>
<th>Topotype B</th>
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<tr>
<td>l</td>
<td>21.3</td>
<td>20.2</td>
<td>18.4</td>
<td>16.3</td>
<td>16.1</td>
<td>15.7</td>
<td>14.4</td>
<td>14.1</td>
<td>16.9</td>
<td>15.6</td>
</tr>
<tr>
<td>w</td>
<td>27.4</td>
<td>27.6</td>
<td>25.6</td>
<td>23.9</td>
<td>22.6</td>
<td>19.8</td>
<td>17.1</td>
<td>18.4</td>
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<td>19.4</td>
</tr>
<tr>
<td>lv unwound</td>
<td>34.5</td>
<td>32.5</td>
<td>30.5</td>
<td>23.9</td>
<td>26</td>
<td>25.2</td>
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<td>26</td>
</tr>
<tr>
<td>t</td>
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<td>17.8</td>
<td>17</td>
<td>12.6</td>
<td>15.1</td>
<td>15.4</td>
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<td>3.1</td>
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<tr>
<td>tdv</td>
<td>16.5</td>
<td>12.3</td>
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<td>7.9</td>
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<tr>
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<td>0.73</td>
<td>0.72</td>
<td>0.88</td>
<td>0.71</td>
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<td>0.84</td>
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<tr>
<td>t/vw</td>
<td>0.78</td>
<td>0.64</td>
<td>0.66</td>
<td>0.68</td>
<td>0.67</td>
<td>0.75</td>
<td>0.63</td>
<td>0.71</td>
<td>0.71</td>
<td>0.80</td>
</tr>
<tr>
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<td>0.92</td>
<td>0.77</td>
<td>0.94</td>
<td>0.95</td>
<td>0.75</td>
<td>0.93</td>
<td>0.82</td>
<td>0.99</td>
</tr>
<tr>
<td>angle of the cardinal commissure</td>
<td>128°</td>
<td>125°</td>
<td>126°</td>
<td>122°</td>
<td>124°</td>
<td>?</td>
<td>120°</td>
<td>120°</td>
<td>111°</td>
<td>115°</td>
</tr>
</tbody>
</table>

Table 1 — Measurements of the lectotype, seven paralectotypes, and two topotypes; the lectotype and paralectotypes B–E, G, H have been photographed. Abbreviations: l = length; w = width; t = thickness; vv = ventral valve; dv = dorsal valve.
Ithaca Member (in upper part of the Genesee Formation): CLARKE (1905).
Canadaway Group: CHADWICK (1935), and MANSPEIZER (1964).
Chadakoin Formation: CASTER (1930).
Conewango Group: CASTER (1930), and CHADWICK (1935).
Cattaraugus Formation: TESMER (1964).
Bradfordian, Oswayo Formation, Waverly Group, Olean Conglomerate, Knapp Conglomerate Salamanca Conglomerate: LESLEY (1890, above and below the Salamanca conglomerate, “Chemung” beds), BUTTS (1903, Oswayo shales, Knapp beds, Salamanca conglomerate, interval between the Wolf creek conglomerate and the top of the chocolate shales), and CHADWICK (1935, Oswayo–Knapp of BUTTS).
Carboniferous: Girty (1899, p. 492: “As is well known, Camarotoechia sappho and Spirifer subattenuatus occur in both Devonian and Carboniferous deposits”).

North America outside of New York
Ontario: In the upper Givetian Hungry Hollow and Widder Formations from the Thedford–Arkona region, SW Ontario, by WHITEAVES (1898), SHIMER & GRABAU (1902), RAYMOND (1904), STAUFFER (1915), and STUMM & WRIGHT (1958).
Pennsylvania: LESLEY (1889–1890, from the Upper Devonian of north–central Pennsylvania and from the Givetian Hamilton Group of central and north–central Pennsylvania (eight specimens of the collection identified by HALL)); KINDLE in WILLIAMS & KINDLE (1905, from the Upper Devonian Chemung Group of north–central Pennsylvania); CASTER (1930, from the Cassadaga (Chadakoin) and Bradford (Conewango, Olean, Oswayo) Stages; CASTER (1934, from the Strunian Bedford fauna of northwestern Pennsylvania); BUTTS in CHADWICK (1935, from the Conewango and Oswayo of northwestern Pennsylvania; and WILLARD (1939, from the Catskill Group of northeastern Pennsylvania.
Indiana: KINDLE (1899, pp. 13, 15, 16, 19) from the Lower Mississippian Riverside Sandstone of southern Indiana; 1901, from the uppermost Emsian–lower Eifelian Jeffersonville Limestone and the lower Givetian Sellersburg Beds of southern Indiana.
Iowa: LAUDON (1931) from the lower Famennian Sheffield Formation of north–central Iowa.
Kentucky: KINDLE (1899, from the Lower Mississippian Riverside Sandstone of central Kentucky; in WILLIAMS & KINDLE, 1905, from the Riverside Limestone and the Osagean Knobstone Formation of west–central Kentucky).
Maryland; PROSSER in PROSSER & KINDLE (1913) and in PROSSER et al. (1913) from the Givetian Hamilton Member of the Romney Formation of western Maryland.
Missouri: BRANSON & WILLIAMS (1922) from (probably) the Middle Devonian Grand Tower Limestone of southeastern Missouri.
Montana: Girty in KINDLE (1908) from the upper Carboniferous of southwestern Montana.
Virginia: KINDLE in WILLIAMS & KINDLE (1905) and WILLIAMS in WILLIAMS & KINDLE (1905) from the Kimberling Shale (Chemung fauna).
West Virginia: KINDLE in WILLIAMS & KINDLE (1905) and WILLIAMS in WILLIAMS & KINDLE (1905) from the Jennings blackish sandy shale (Chemung fauna) of southern West Virginia.
Wyoming: Girty (1899; in KINDLE, 1908) from the Mississippian Madison Limestone of the Yellowstone National Park.

Outside of North America
Brazil: THOMAS (1905) from the Devonian Maecurú Group of the States of Amazónas and Pará; KNOD (1908, referring to CLARKE, 1900); FERUGLIO (1930).
England (Devon): REED (1943) from the Pilton Beds (Devonian/Carboniferous boundary beds) of North Devon.
Iran: STEPANOV in ALAVI–NAJNI (1972) from the early Givetian part of the Bahram Formation.
Kazakhstan: NALIVKIN (1937, 1947) and SIMORIN (1956) from the Frasnian and Givetian.
Mongolia: BOBROV & MODZALEVSKAYA (1964) from the Middle Devonian.
Russia: Arctic region: NALIVKIN (1933) from the...
Upper Devonian at the mouth of the Lena River; For East: KRESTOVNIKOV in NAGIBINA & KRESTOVNIKOV (1959) and NALIKVIN et al. (1973) from the Givetian of the Amur River; Transcaussia: MAMEDOV & RZHONSNITSKAYA (1985) from the late Givetian of Nakhichevan.


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The author is grateful to the late Dr. N.D. Newell and to Dr. N. Eldredge, American Museum of Natural History, New York, for access to collections under their responsibility, long period loan, and permission to photograph types. In course of time the author had various fruitful conversations with the late Dr. G.A. Cooper, who allowed him to go through the collections of the National Museum of Natural History, Washington. Dr. G.J. Kloc, University of Rochester, kindly made some specimens of Sapphicorhynchus sappho available to the author. The author also wishes to express his appreciation to Prof. Dr. Michael R.W. Ammer, Ludwig Maximilians–Universität München for critically reading the manuscript, and for helpful comments.

References


grad.

288 pp. *Nedra*, Lenin­

gend.


SCHUCHERT, C., 1929. Classification of brachiopod genera, fossil and recent. *In: SCHUCHERT, C. & LE VENE, C.M, Brachiopoda (Genorum and Genotyporum Index
Sapphicorhynchus, a new early Givetian rhynchonellid genus


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Explanation of Plate 1
All figures are natural size

Figs 1-5 — Sapphicorhynchus sappho (HALL, 1860). Lectotype, AMNH34626 = pl. 54, figs 38-42 in HALL, 1867. Dorsal, ventral, anterior, posterior, and lateral views. Costal formula: $\frac{6}{5} \cdot \frac{1-0}{8} \cdot \frac{9}{9}$.

Figs 6-10 — Sapphicorhynchus sappho (HALL, 1860). Paralectotype H, AMNH34629. Dorsal, ventral, anterior, posterior, and lateral views. Costal formula: $\frac{6}{5}; \frac{7}{8}$.

Figs 11-15 — Sapphicorhynchus sappho (HALL, 1860). Paralectotype E, AMNH5214 = pl. 54, fig. 43 in HALL, 1867. Dorsal, ventral, anterior, posterior, and lateral views. Costal formula: $\frac{5}{4}; \frac{1-1}{8} \cdot \frac{7}{9}$.

Figs 16-20 — Sapphicorhynchus sappho (HALL, 1860). Paralectotype D, AMNH34625 = pl. 54, fig. 37 in HALL, 1867. Dorsal, ventral, anterior, posterior, and lateral views. Costal formula: $\frac{6}{5}; \frac{1-0}{8} \cdot \frac{7}{9}$.

Figs 21-25 — Sapphicorhynchus sappho (HALL, 1860). Paralectotype C, AMNH34624 = pl. 54, fig. 36 in HALL, 1867. Dorsal, ventral, anterior, posterior, and lateral views. Costal formula: $\frac{5}{4}; \frac{1-1}{8} \cdot \frac{6}{7}$.

Figs 26-30 — Sapphicorhynchus sappho (HALL, 1860). Paralectotype B, AMNH34623 = pl. 54, figs 34, 35 in HALL, 1867. Dorsal, ventral, anterior, posterior, and lateral views. Costal formula: $\frac{6}{5}; \frac{7}{8} \cdot \frac{8}{9}$.

Figs 31-33 — Sapphicorhynchus sappho (HALL, 1860). Paralectotype G, AMNH34628. Dorsal, ventral, anterior, posterior, and lateral views. Costal formula: $\frac{5}{4}; \frac{1-1}{8} \cdot \frac{7}{9}$.

Fig. 34 — Rhynchonella (Stenocisma) sappho var. AMNH34634 and 34631 = pl. 55, figs 51, 48 in HALL, 1867.