THE SILURIAN BRACHIOPOD STEGERHYNCHUS

by BRIAN JONES

ABSTRACT. The brachiopod Stegerhynchus Foerste, 1909 occurs in Silurian strata in Canada, the U.S.A., the U.S.S.R., Gotland, and the United Kingdom. Review of the literature shows that Rhynchonella whiti praecursor Hall, 1863 is the true type species of Stegerhynchus. Although Stegerhynchus and Ferganella Nikiforova, 1937 are morphologically very similar, they can be separated because Stegerhynchus has an open notothyrial cavity that houses an elongate cardinal process based on the notothyrial platform, whereas Ferganella has a septal process extending anteriorly from the posteriorly conjunct hinge plates. The septal process joins the cardinal process distally. Stegerhynchus seems to be most common in Wenlock and Ludlow strata and less common in Ludlowery and Pridolian strata. Ferganella appears to be of Pridolian/Lower Devonian age. Species such as S. borealis and S. didonata are relatively long-ranging while other species such as S. anguicentis have a relatively short range. S. borealis is relatively common in the Upper Silurian Read Bay Formation of the Canadian Arctic islands, whereas S. anguicentis is relatively rare, being found only at the base of member C of the Read Bay Formation on the east coast of Cornwallis Island.

During a detailed study of the Ludlovian and Pridolian brachiopods from the Read Bay Formation of Arctic Canada it became apparent that there was considerable confusion surrounding the definition of Stegerhynchus and Ferganella. The literature covering these genera contains many conflicting statements. Amsden (1974, p. 67) commented that '... the distinction between Stegerhynchus and Ferganella is not at all clear ...'. This study outlines some of the main problems surrounding the genus Stegerhynchus. It is based on a review of all the North American species assigned to Stegerhynchus or Ferganella with a detailed analysis of the literature. Reference is also made to the European material for comparative purposes. In addition the rhynchonellids from the Read Bay Formation of Arctic Canada are described. I am particularly indebted to Dr. M. G. Bassett of the National Museum of Wales who provided me with information pertaining to European specimens of Stegerhynchus. Dr. Bassett also allowed me to see type material of Ferganella turkestana, F. borealis, S. decemplicatus anguicentis, and F. didonata which he had spent so much time and effort to collect and borrow. Dr. Bassett is currently studying the Stegerhynchus and Ferganella from Europe and is further investigating the taxonomic relationships in this group of brachiopods.

In this paper the following abbreviations are used for the numbering of type material: GSC = Geological Survey of Canada repository, Ottawa; UCLA = University of California, Los Angeles; OU = University of Oklahoma; UI-RX = University of Illinois, Rowe collection; NMW = National Museum of Wales; Br = Naturhistoriska Riksmuseet, Stockholm, and ETA = Eesti Teadusti Akademia; UA = University of Alberta.

TAXONOMIC HISTORY OF STEGERHYNCHUS

Foerste (1909, p. 98) introduced the name Stegerhynchus 'to distinguish the species typified by Rhynchotreta whiti praecursor, from the more typical species of Rhynchotreata ...'. Since Foerste (1909) did not designate a type species Schuchert and LeVene (1929) selected Rhynchonella whiti as the genolectotype of Stegerhynchus. Kozlowski (1929, p. 146) listed Stegerhynchus as a synonym of Stenochisma Conrad (1839), reasoning that the external and internal structures of Stegerhynchus as described by Foerste (1909) were exactly the same as those described for Stenochisma by Conrad (1839) (Kozlowski 1929, p. 148). However, Ager (1965, p. H629) included Stenochisma Conrad (1839) (not Stenochisma Hall, 1847; Stenochisma Hall and Clarke, 1894 or Stenochisma Grabau and Slicher, 1907) in the family Stenocostatidae Dehler (1883), since the type species, Terebratula schlotheimii,

Von Buch (1835), is a rhynchonelliform rhynchonellid with a well-developed stolidium. Stegerhynchus cannot be considered a synonym of Stenechisoma Conrad (1839).

Shimer and Shrock (1944, p. 360), ignored the work of Schuchert and LeVene (1929) and listed R. whitii praecursor as the type species of Stegerhynchus. Foerste 1909, Cooper (1955, p. 54) and Cocks (1978, p. 147) concluded that R. whitii Hall was the type species of Stegerhynchus since Schuchert and LeVene (1929, p. 42) had designated it as such. The Treatise lists R. whitii praecursor (= S. praecursor) as the type species of Stegerhynchus. The choice between the two species is critical because it has been shown by Cooper (1955, p. 54) and Amosden (in Amosden and Boucot, 1958, pp. 154-155) that R. whitii praecursor has a cardinal process while R. whitii does not. According to the Treatise, rhynchonellids in the subfamily Rhynchotretinae have a cardinal process while those in the subfamily Trigonirhynchidae do not. If R. whitii praecursor is the type species, Stegerhynchus would be assigned to the subfamily Rhynchotretinae. If R. whitii is the type species, Stegerhynchus would be placed in the subfamily Trigonirhynchidae. The problem of the type species of Stegerhynchus centres around the genoeletotype chosen by Schuchert and LeVene (1929). Foerste’s (1909) paper suggests that their choice was incorrect for the following reasons:

(a) Foerste (1909, p. 98) stated: ‘To distinguish the species typified by Rhyhochotretra whitii praecursor, from the more typical species of Rhyhochotretra, possessing an acuminate beak, long broad flattened sides, and a median depression along the posterior parts of the brachial valve, the term Stegerhynchus may be employed.’ It must be assumed that Rhyhochotretra was mistakenly used for Rhynchonella since it is clear from previous references to whitii praecursor (Foerste 1909, p. 96) that it belonged to Rhynchonella, not Rhyhochotretra.

(b) R. whitii praecursor was fully described by Foerste (1909, pp. 96-97) while R. whitii was only quoted in a list of species considered congeneric with R. neglecta and R. indusenosis.

(c) R. whitii praecursor and R. neglecta efflonensis were both figured by Foerste (1909, pl. III, figs. 47a, b, c and 48a, b, c respectively) while R. Whitii was not figured.

(d) R. whitii praecursor is the first described form linked with the name Stegerhynchus.

Cooper (1955, p. 54) considered that Schuchert and LeVene (1929) had chosen R. whitii as the type species since it was the first name in the list of species considered congeneric with the new varieties named by Foerste. From Foerste’s (1909, p. 98) concluding statement it is apparent that he considered R. whitii praecursor typical of Stegerhynchus. Also, R. whitii praecursor was the first name linked with Stegerhynchus and was better described and illustrated than R. whitii and thus should be given preference.

In view of the above considerations and the opinion given by Amosden (1968, p. 62) it is clear that R. whitii praecursor should be taken as the type species of Stegerhynchus.

COMPARISON WITH CLOSELY RELATED GENERA

Nikiforova (1937, pp. 77-78) erected the genus Fergusella, based on specimens from the northern slope of the Altai Range (Fergara). F. turkestanica, the type species, has a moderate to large, subrounded to subtriangular shell of variable convexity with a distinct fold and sinus. In the pedicle valve it has massive teeth supported by dental plates. In the brachial valve the massive, thick septum supports the notothyrial cavity in which the elongate cardinal process is housed. Joining the posteriorly conjunct hinge plates is a septal process which extends anteriorly before joining the cardinal process in a distal position (text-fig. 1). The crura extend from the inner edges of the hinge

### Text-fig. 1

Serial sections showing internal structures of Fergusella turkestanica. Diagrams based on illustrations in Nikiforova (1937, pl. 7, figs. 13 and 16). Exact positions relative from posterior not known, but a is closer than b.
plates. Nikiforova (1937, p. 37) transferred *R. borealis* Schlotheim to *Ferganella* because of the great similarity of the internal structures to those found in *F. turkestanica*.

Nikiforova (1937, p. 37) did not compare *Ferganella* directly with *Stegerhynchus*. Rather she compared *Stenochnisma* (considered the senior synonym of *Stegerhynchus* by Koéloowski 1929) with *Ferganella*, noting that *Stenochnisma* lacked a median septum which is well developed on *Ferganella*. Although *Ferganella* differs from *Stenochnisma* according to the criteria listed by Nikiforova (1937, p. 78) it does not follow that the same differences serve to separate *Stegerhynchus* from *Ferganella* as *Stegerhynchus* is not a synonym of *Stenochnisma*. Externally, two specimens of *F. turkestanica* from a locality on the River Djalkin in Fergana (NMW 76.9G.56 and NMW 76.9G.57) shown to me by Dr. M. G. Bassett are very similar to many of the species herein assigned to *Stegerhynchus*. However, comparison of the internal structures of *Ferganella* and *Stegerhynchus* shows that *Stegerhynchus* has an open notothyrial cavity, posteriorly disjunct hinge plates, and no septal process, whereas *Ferganella* has posteriorly conjunct hinge plates and a septal process which joins the cardinal process anteriorly. These internal structures of *Ferganella* are evident from the original description of *F. turkestanica* (Nikiforova 1937), from the illustrations of the internal structures of *F. turkestanica* (text-fig. 1) and from an original section of *F. turkestanica* shown to me by Dr. M. G. Bassett. These differences separate the two genera.

Rhomnitskaya (1959, p. 27) defined *Stegerhynchella* using *S. decemplicatus angusticostis* (Chernyshev) as the type species. However, Schmidt and McLaren (1965, p. 13556) and Lenz (1970, p. 488) suggested that *Stegerhynchella* is probably a synonym of *Stegerhynchus*. Inspection of twenty-two specimens of *S. decemplicatus angusticostis* (Chernyshev) from the toptotype locality in the Elegest Formation on the River Elegest, central Tuva, U.S.S.R., confirms this. Amsden recently named the new genus *Stegerhynchops* for non-lamellose rynchotrematids that lacked dental plates. The absence of dental plates clearly separate it from *Ferganella* and *Stegerhynchus*.

**DISCUSSION**

Until now *Stegerhynchus* and *Ferganella* have been maintained as separate genera even though the criteria for separating the two have not been clearly delineated. Since Cooper (1955, p. 54) considered *R. whitii* the type species of *Stegerhynchus*, he assigned *R. (Stegerhynchus) whitii procerus* Forste, 1909 and *R. (Stegerhynchus) neglecta eliphonensis* Forste, 1909 to *Ferganella* because they both possessed a cardinal process. Havlick (1961, pp. 89-91) and Kuklov (1963, 1967) followed Cooper's example, taking *R. whitii* as the type species of *Stegerhynchus*, and therefore considered that *Stegerhynchus* did not have a cardinal process. Johnson and Reso (1964, p. 80) assigned rynchotremids from the Sevy Dolomite of Nevada to *Ferganella*, on the basis that their external form was closer to *Ferganella* than to *Stegerhynchus*. Lenz (1970, p. 488) assigned rynchotremids from Prongs Creek to *Ferganella* rather than *Stegerhynchus* because of their external characteristics and because of the "... presence of the median septum, which though variable in height and development, is normally well developed". Although there is the implication that *Ferganella* and *Stegerhynchus* can be separated by virtue of the size and form of the median septum, the differences were not specified. Study of the various species of *Stegerhynchus* and *Ferganella* revealed no readily discernible differences at the generic level (Table 1).

The concept that the nature of the median septum could be used for separating the two genera was expanded by Johnson, Boucot, and Murphy (1976, p. 64) who considered that *Rynchotremata* and *Ferganella* both have a true median septum in their branchial valve while *Stegerhynchus* does not. This statement was made without supportive evidence or illustrations, but Johnson (1977, written comm.) considers that *Stegerhynchus* has a myophragm rather than a median septum. Although Johnson et al. (1976) considered the dichotomy between the genera to be quite rigid, study of the pertinent descriptions, illustrations, and, where possible, type material has shown that the length, height, and form of the median elevation is highly variable (Table 1). In *Stegerhynchus* the length of the median elevation ranges from 43 to 65% of valve length compared to 36 to 63% of valve length in *Ferganella* (Table 1). There is no difference in the length of the median elevations of species assigned to
### Table 1. Summary of main morphological attributes of the type specimens of *Steigerhynchus angaciensis*, *S. claritense*, *S. concina*, *S. antiqua*, *P. cf. F. lincolensis*, *P. chattertoni*, *F. didomata*, *F. lorendti*, and *F. turrustanica*. Abbreviations used are: c = complete; bv = Brachial valve; pv = Pedicle valve; pas = Posterior articulated shell.

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*Steigerhynchus* or *Pergamia*. Similarly, the height and development of the structure is also highly variable. For example, in *S. angaciensis* described by Lenz (1970) GSC types 25010 and 25013 both have well-preserved median septa. These two specimens show a marked contrast. GSC 25010 (text-fig. 2e) has a relatively short but high median elevation whereas GSC 25013 (text-fig. 2f) has a relatively long but low median elevation. This variability is emphasized further because the relatively high median elevation of GSC 25010 is skewed off to the right-hand flank of the shell (text-fig. 2e).
TEXT-FIG. 2. Internal structures of *Steigerhynchus*. a, brachial valve interior of *S. concinna* showing open notothyrial cavity housing elongate cardinal process. Medium septum supports notothyrial cavity. Specimen U1-RX-307; b, brachial valve interior of *S. concinna* showing same structures as in fig. 2a. Note medium septum is more prominent. Specimen U1-RX-310; c, pedicle valve interior of *S. concinna* showing dental plates and teeth. Specimen U1-RX-306; d, posterior portion of articulated specimen of *F. chattertoni* showing elongate cardinal process in open notothyrial cavity. Note crus extending from inner edges of hinge plates, well-developed medium septum and well-developed teeth in sockets. Specimen GSC 48076; e, brachial valve interior of *S. anguicrista* from Prong Creek showing 'right-skewed' medium septum and associated asymmetry of right flank of shell. Note open notothyrial cavity. Specimen GSC 25010; f, brachial valve interior of *F. chattertoni* showing open notothyrial cavity, elongate cardinal process, relatively broad medium septum, and curved hinge plates. Specimen GSC 48069; g, brachial valve interior of *F. cf. E. lincolnensis* from Prong Creek showing open notothyrial cavity, elongate cardinal process, sockets, triangular hinge plates, and relatively broad medium septum. Specimen GSC 25006; h, brachial valve interior of *S. anguicrista* from Prong Creek. Note difference in size, form, and location of medium septum compared to specimen in fig. 2c. Specimen GSC 25013.

*E. lincolnensis* described by Lenz (1970) has a median elevation that extends 57 to 63% of shell length. In specimens GSC 25001 and 25005 the median elevation is relatively low and merges imperceptibly with the central inter-rib space of the fold. By contrast, *F. chattertoni*, as defined by Lenz (1977), has a median elevation 36 to 40% valve length. Specimen GSC 48069 (text-fig. 2f) has a relatively high elevation whereas specimens GSC 48072 and 48073 have relatively low median elevations. In specimens GSC 48069 (text-fig. 2f) and GSC 48072 the anterior termination of the median elevation is relatively well defined, whereas in specimen GSC 48073 the termination is imperceptible and difficult to define. Similar variation can also be seen in *S. concinna* and Arndt (1974, p. 66) describes the presence of a median septum in *S. concinna*. Again, there is the implication that the size and form of the median elevation is highly variable and therefore difficult to use as a criterion for separating genera. If such a high degree of variation is evident from a limited number of specimens from widely scattered areas, then it is difficult to argue that a larger sample size would clarify the dichotomy suggested by Johnson et al. (1976). One important point to consider is demonstrated by study of specimen GSC 48076 (*Steigerhynchus?*) and an unnumbered specimen associated with specimen
GSC 48076. The brachial valve of the unnumbered specimen is more convex than the brachial valve of specimen GSC 48076 and has a correspondingly higher median elevation; implying that the height of the median septum is controlled by the distance between the floor of the brachial valve and the base of the notothyrial cavity. Therefore, the more convex valves will have the highest median elevation. This factor is probably partly responsible for the high septum in specimen GSC 25010 as opposed to the relatively low septum in specimen GSC 25013.

Summary. Review of the literature has shown that there is considerable confusion surrounding the genus Stegerhynchus. Moreover, the distinction between Stegerhynchus and Ferganella has been particularly difficult to delineate. There have been four main approaches to the latter problem; each with its associated problems, namely:

(a) The presence or absence of a cardinal process: this resulted from confusion over the type species of Stegerhynchus. However, since it is now clear that S. praecursor is the true type species of Stegerhynchus, this criterion cannot be used.

(b) Shell shape: although it has been stated that the external forms of the two genera differ, the differences have not been described in detail. Study of numerous specimens of Stegerhynchus suggests that there is a great range of shell shapes within the genus and that separation from another genus such as Ferganella on this basis of this criterion would probably prove very unsatisfactory.

(c) Form of median elevation in brachial valve: it has been stated that Ferganella has a true median septum whereas Stegerhynchus only has a myophragm. Study of all the available material suggests that the form of the median elevation is variable even amongst shells from the same locality. In this respect there does not appear to be a distinct dichotomy between the two genera.

(d) Internal structures: Stegerhynchus has an open notothyrial cavity whereas Ferganella has posteriorly conjunct hinge plates which partly cover the cavity and a septal process which joins the cardinal process in a distal position. This seems to be the only reliable way of separating Stegerhynchus from Ferganella.

Bassett (1978, written comm.) has also pointed out that Nkophoros's original specimen of F. turkestanae came from strata of Devonian age. Thus, it would appear that Ferganella is younger than Stegerhynchus which occurs mainly in Silurian strata. In view of the foregoing discussion the species herein considered part of Stegerhynchus are assigned on the basis of the last of the internal structures listed above.

SYSTEMATIC PALAEONTOLOGY

Order RHYNCHONELLIDA Kühn, 1949
Superfamily RHYNCHONELLACEA Gray, 1848
Family RHYNCHOTREMATAE Schuchert, 1913
Subfamily RHYNCHOTREMATINAE Schuchert, 1913

GENUS STEGERHYNCHUS Foerste, 1909

1909 Rhynchonella (Stegerhynchus) (pars) Foerste, pp. 96-97, pl. III, fig. 47a, n, and c.
1937 Stegerhynchus Foerste, 1909; Cherryshev, p. 29, pl. 1, figs. 15-16; text-figs. 1-2.
1937 Camarotoechia Hall and Clarke, 1894; St. Joseph, pp. 33-48, figs. 1-5.
1953 Stegerhynchus Foerste, 1909; Borisyak, pp. 46-47, pl. VI, figs. 6-11.
1955 Ferganella Nikiforova, 1937; Cooper, p. 55.
1959 Stegerhynchus Rzhonshtekov, 1959; Kheitina, p. 102, pl. 5-8, fig. 5a-c.
1960 Ferganella Nikiforova, 1937; Kheitina, p. 102, pl. 5-8, fig. 5a-c.
1960 Stegerhynchus Foerste, 1909; Zinchenko and Kultov, p. 103, pl. 5-8, fig. 7.
1929 Sianochisma Conrad, 1839; Kozlowski (pars), pp. 146-150.
1964 Ferganella Nikiforova, 1937; Johnson and Reso, p. 80, pl. 19, figs. 5-12.
1967 Ferganella Nikiforova, 1937; Kultov, pl. 75-76, text-fig. 31; pl. XII, figs. 7-11.
1968 Steigerhynchus Foerste, 1909; Amsden, pp. 61–63; text-fig. 47; pl. 17, fig. 1a–k.
1974 Fergamella Nikiforova, 1937; Basset and Cocks, p. 26, pl. 8, fig. 2a–b.
1974 Steigerhynchus Foerste, 1909; Amsden, pp. 66–68, text-figs. 41–42; pl. 14, figs. 3–4; pl. 15, figs. 1–4.
1975 Fergamella Nikiforova, 1937; Shchelkin, p. 729, pl. 5, figs. 1–5.
1975 Fergamella Nikiforova, 1937; Smith, p. 29, text-fig. 19; pl. 7, figs. 20–25.
1976 Steigerhynchus Foerste, 1909; Johnson et al., pp. 64–65, pl. 47, figs. 1–12.
1977 Fergamella Nikiforova, 1937; Lenz, p. 1542, pl. 8, figs. 1–16.
1977 Fergamella Nikiforova, 1937; Lenz, pp. 87–88, pl. 17, figs. 1–6 and 11.
1977 Steigerhynchus Foerste, 1909; Lenz, p. 85, pl. 17, figs. 7–10, 12–29.
1978 Steigerhynchus Foerste, 1909; Amsden, pl. 11, figs. 1–9.

nov. 1935 Steigerhynchus Foerste, 1909; Cooper, pp. 54–55.

nov. 1961 Steigerhynchus Foerste, 1909; Haukic, p. 80.


nov. 1964 Steigerhynchus Foerste, 1909; Drot, p. 103, pl. 19, figs. 6–8.

nov. 1970 Steigerhynchus Foerste, 1909; Gratsianova, p. 68, pl. 6, fig. 6.

Type species. S. praecursor Foerste, 1909 (= Rhynchonella (Steigerhynchus) whitii praecursor of Foerste, 1909).

Diagnosis. Shell outline subtriangular to transversely elliptical. Biconvex, plicate shell with erect to sub-erect pedicle umbo, round foramen, and triangular-shaped delthyrium which may be partly covered with small deltidial plates. Pedicle valve with teeth supported by dental plates which terminate anteriorly at level of teeth. Brachial valve with median septum of variable length, height, and width, posteriorly thickens and forms base of notothyrial cavity in which elongate blade-like cardinal process is housed.

Morphological summary. Shell, commonly but not always, with width equal to or greater than length. Biconvex, plicate shell, commonly with brachial valve more convex than pedicle valve. Sockets of variable form and size containing from 1 to 7 ribs. Each flank of pedicle valve occupied by 2 to 4 prominent ribs and 1 to 2 minor ribs. Pedicle umbo erect to suberect, foramen round and triangular delthyrium open or partly enclosed by small deltidial plates. Brachial valve contains median septum of variable length, height, and width (Table 1). Generally broadens posteriorly to form base of notothyrial cavity in which the elongate, blade-like cardinal process is housed. U-shaped sockets, which widen anterolaterally are bounded by elongate socket plates on inner edges. Triangular-shaped hinge plates curved ventrolaterally with crural bases at inner margins. Crus curve anterodorsally. In the pedicle valve the teeth are supported by dental plates which extend anteriorly to level of teeth before terminating sharply. Umbonal cavities are D-shaped.

Species assigned to Steigerhynchus. Since all of the species listed below have been described in detail elsewhere, only the pertinent remarks regarding each species is given. Representatives of the type material examined in detail are shown in Plate 18, and text-figs. 2 and 3. In the following descriptions the species are listed alphabetically.

Steigerhynchus anguicrnis Chernyshev, 1937
Plate 18, figs. 46–48; text-figs. 2a, b
1937 Steigerhynchus anguicrnis anguicrnis Chernyshev, p. 29; pl. 1, figs. 15–18; text-figs. 1, 2.
1955 Steigerhynchus anguicrnis Boriesyak, p. 46, pl. VI, figs. 9–11.
1955 Steigerhynchus anguicrnis var. tryplicata Boriesyak, p. 47, pl. VI, figs. 6–8.
1960 Steigerhynchus anguicrnis (Chernyshev); Zhonenskaya et al., pl. 43, fig. 7u–d; text-figs. 246–247.
1960 Steigerhynchus anguicrnis (Chernyshev); Khabina, p. 102, pl. S-28, fig. 5u–c.
Remarks. *S. decemplicatus angacienensis* Chernyshev, 1937 from the Late Silurian strata of western Mongolia and Tuva was used as the type species of the genus *Stiegerhynchella* by Rzhonsnitskaya (1959). However, I follow Schmidt and McLaren (1965, p. H356) and Lenz (1970, p. 488) in considering that *Stiegerhynchella* is probably a synonym of *Stiegerhynchus*. Lenz (1970) assigned rhyconellids from Prongs Creek to *S. angacienensis* (pl. 18, figs. 46–48) even though these specimens have fewer ribs on their flanks than was considered diagnostic for *S. decemplicatus angacienensis*. This was done because inspection of Chernyshev’s illustrations (1937, pl. I, fig. 15a–d) showed specimens that are very similar to the Prongs Creek specimens. Comparison of the material used by Lenz (1970) with *S. decemplicatus angacienensis* from the River Elsegate locality confirms this assessment. Like *S. praeursor*, *S. angacienensis* has a uniplicate sulcus. *S. angacienensis* differs from *S. praeursor* in having a higher brachial valve and a more elongate shell. These differences, however, may be ontogenetic or intraspecific in character.

Kul'kov (1967, p. 76) listed *S. angacienensis* Borisjak, 1955 and *S. angacienensis* var. *tripleata* Borisjak, 1955 as synonyms of *F. borealis* (Schlotheim). These species would be best considered synonyms of *S. angacienensis* rather than *S. borealis*. *S. diadonta* can be separated from *borealis* by virtue of its distinctive uniplicate sulcus (Bassett and Cocks, 1974, p. 26). It is extremely close to *S. angacienensis* Chernyshev, 1937; differing by being slightly more transverse and by having distinctive ruge.

*I. ingrata* (Savage, 1913)

Plate 18, figs. 34–39

1913 *Camaratoolithus antiqua* Savage, p. 128, pl. 7, figs. 1 and 2.

1964 *Fergusella incolomantis* Johnson, 1964; Johnson and Reso, p. 80, pl. 19, figs. 5–12.


1974 *Stiegerhynchus antiquis* (Savage, 1913); Amsden, p. 68, pl. 15, fig. 4a k.

1976 *Stiegerhynchus cf. S. incolomantis* (Johnson, 1964); Johnson et al., pp. 64–65, pl. 47, figs. 1–12.

Remarks. Savage (1913) named *Camaratoolithus antiqua* for rhyconellids from the Leeman Formation and the Noik Limestone of Illinois. Amsden (1974, p. 68) placed specimens UX 872, 4784 with question in *Stiegerhynchus* because the internal structures are unknown. Johnson and Reso (1964, p. 80) assigned rhyconellids from the Sevy Dolomite of Nevada to the new species

**Explanation of Plate 18**

Figs. 1–15. *Stiegerhynchus concordia* (Savage, 1913); 1–3, lateral, anterior, and pedicle views of the paratype, UI-RX-319; 4–6, lateral, anterior, and pedicle views of the paratype, UI-RX-316; 7–9, lateral, anterior, and pedicle views of the paratype, UI-RX-311; 10–12, lateral, anterior, and pedicle views of paratype, UI-RX-308; 13–15, lateral, anterior, and pedicle views of lectotype, UI-RX-855.

Figs. 16–21. *Fergusella charlottensis* Lenz, 1970 (synonym of *C. concordia* herein); 16–18, lateral, anterior, and pedicle views of the holotype, GSC 48067; 19–21, lateral, anterior, and pedicle views of paratype, GSC 48066.


All specimens ×2.
JONES, brachiopod *Siegerhynchus*
Lincolnensis (Pl. 18, figs. 25-30). Although the internal structures of these specimens had been obliterated by silification Johnson tentatively assigned the species to Ferganelia. However, Johnson et al. (1976, p. 64) later transferred Lincolnensis to Steigerhynchus, claiming that the internal structures of specimens from the Roberts Mountains Formation of central Nevada were more indicative of Steigerhynchus than Ferganelia as defined by those authors.

Comparison of the holotype of Lincolnensis (UCLA 3050, Pl. 18, figs. 25-27) with the lectotype of Antiqua (UI-RX-872, Pl. 18, figs. 34-36) shows that they have similar shell outline, similar profile, and similar ribbing both in the sulcus and on the flanks of the shell. More important, both have a sulcus that is poorly defined and developed only in the anterior portion of the shell. The internal structures of both Lincolnensis and Antiqua remain unknown. In spite of their morphological similarity Antiqua has been reported only from upper Ordovician strata whereas Lincolnensis has been reported only from Ludovician strata (text-fig. 4).

Pending discovery of internal structures Lincolnensis is provisionally placed as a synonym of Antiqua. S. antiqua is separated from S. concinna because it has a poorly defined sulcus which is well defined in the latter. S. antiqua has an unequally convex shell and this serves to distinguish it from other species of Steigerhynchus which have a brachial valve that is more convex than the pedal valve.

Steigerhynchus borealis (Von Buch, 1834)

1822 Anomia Terebratula laciniosa Linnaeus; Schlotheim, pl. 20, fig. 6a–c, non Linnaeus, 1758.
1832 Terebratula borealis Schlotheim, p. 65 nomen nudum.
1834 Terebratula borealis Von Buch.
1869 Rhynchoconcha borealis Schlotheim; Davidson, p. 174, pl. 21, figs. 14, 15, 17, 19, 20, and 24-27.
1937 Camarotoechia borealis (Von Buch); St. Joseph, p. 33, figs. 1-5.
1937 Ferganelia cf. F. borealis (Schlotheim); Nikiforova, p. 42, pl. 6, fig. 17a-d.
1954 Camarotoechia(?) borealis (Schlotheim); Nikiforova, p. 98, pl. X, fig. 4.
1967 Ferganella borealis (Schlotheim): Kuklov, pp. 76-79, fig. 1; pl. XII, figs. 7-11. *non* Ferganella lincolnensis Johnson and Reso, 1964, p. 80, pl. 19, figs. 5-12.
1976 Ferganella borealis (Schlotheim), Sheehan, p. 729, pl. 5, figs. 1-5.
1976 Ferganella cf. *F. turkestana* Nikiforova, 1937; Smith, p. 29, text-fig. 19; pl. 7, figs. 20-25.
1977 Ferganella chattertoni Lenz, p. 1542, pl. 8, figs. 1-16.

Remarks. In the literature there is some confusion over the authorship of the species borealis. Kuklov (1967, p. 76) and Sheehan (1976, p. 729) both attributed borealis to Schlotheim (1832) whereas Bassett and Cocks (1974, p. 26) attributed it to Von Buch, 1834. Schlotheim (1832, p. 65) used the name *Terebratula borealis* without illustrating or describing the specimens he was assigning to the species. Thus, the name remained a nomen nudem until Von Buch (1834) provided an adequate description of borealis. The species should therefore be assigned to Von Buch, 1834 as suggested by Bassett and Cocks (1974, p. 26). Although St. Joseph (1937, pp. 33 and 45) considered that Von Buch (1834) had formerly chosen the type specimen of the species, Bassett and Cocks (1974, p. 26) have shown that this is not the case. Thus, the description by St. Joseph (1937, p. 33) of the specimen figured by Schlotheim (1822, pl. 20, fig. 6a-c) should be regarded as the first description of the lectotype of the species (Bassett and Cocks, 1974, p. 26). The available descriptions suggest that *S. borealis* has a high degree of intraspecific variation. The problem is one of defining the exact range of variation for the species. For example, St. Joseph (1937, p. 46) considered *diodonta* Dalman, 1828 as a variety of borealis whereas Bassett and Cocks (1974, p. 26) considered them two separate species. Similarly, Kuklov (1967, p. 76) considered *F. lincolnensis* Johnson, 1964 a synonym of borealis while Sheehan (1976, p. 729) maintained the two as separate species. Lenz (1977, p. 1452) compared *F. chattertoni* with *F. borealis*, which Sheehan (1976) described from Utah. He considered the two distinct because the Mackenzie Mountains material lacked a deep, ventral muscle field, had 'normal' sized costae on either side of the sulcus and possibly a sharper, more pointed beak. Comparison of the type material of chattertoni with Sheehan's illustrations of *F. borealis* shows that these differences are probably valid. However, comparison of chattertoni with borealis as described by Kuklov (1967) and St. Joseph (1937) strongly suggests that chattertoni falls within the range of morphological variation of borealis. For this reason chattertoni is included as a synonym of borealis.

**Stegerhynchus claritense** Amsden, 1968

Plate 18, figs. 40-45

1968 *Stegerhynchus claritense* Amsden, pp. 61-63, text-fig. 47, Table 32; pl. 17, fig. 1a-k.

Remarks. *S. claritense* was named by Amsden (1968, pp. 61-62) for specimens from the Fitzhugh Member of the Clarita Formation of Arkansas. It is separated from other species of *Stegerhynchus* by virtue of its very distinctive subrounded ribs as compared to the angular ribs of other species.

**Stegerhynchus concinna** (Savage, 1913)

Plate 18, figs. 1-15; text-fig. 2a, b, c

1913 *Camarorochia concinna* Savage, pp. 128-129, pl. 7, fig. 3 (non Billings, 1866).
1974 *Stegerhynchus concinna* (Savage), Amsden, pp. 66-68, text-figs. 41-42, Table 9; pl. 14, figs. 3, 4; pl. 15, figs. 1-3.

Remarks. Since the original specimens of concinna Savage (1913) from the Edgewood Formation in Pike County, Missouri, and near Thebes, Alexander County, Illinois, could not be found, Amsden (1974, p. 67) designated specimen UI-RX-855 as the lectotype of the species. *S. concinna* differs from *S. praecursor* because it has more ribs (1 to 3 compared to 1) in its sulcus. It has subequally convex valves, whereas *S. praecursor* has a brachial valve that is more convex than the pedicle valve.
S. concinna was separated by Lenz (1977, p. 1425) from F. chattertoni because of its more distinctly rounded outline, fewer fold and sulcus costae, and its long median septum. However, comparison of the type series of the two species (Pl. 1, figs. 1–15 and 16–21) shows that chattertoni has three ribs in the sulcus while concinna has one to three ribs in the sulcus (Table 1). Thus, separation on this basis is not always possible. Although F. concinna is generally rounder than chattertoni, some of the more extreme forms have a very similar outline to chattertoni. The median septum in chattertoni is 36 to 40% of valve length (based on three specimens) while in concinna the septum is 55 to 65% of valve length (based on two specimens). However, this apparent difference in the length of the median septum should be treated with caution since study of other species of Stegerhynchus has shown that there can be a wide range of variation in the length of this feature even amongst shells from the same locality.

Stegerhynchus praecursor Foerste, 1909

Text-fig. 3

1909 Stegerhynchus whith-praecursor Foerste, pp. 96–98, pl. III, figs. 47a, b, c.
1944 Stegerhynchus whith-praecursor Foerste, 1909; Shimer and Shrock, p. 309.
1954 Ferganella praecursor (Foerste); Cooper, p. 55.
1965 Stegerhynchus praecursor Foerste, 1909; Schmidt and McLaren, p. 112.
1978 Stegerhynchus cliftonensis Foerste, 1909; Amsden, p. 28, pl. 11, figs. 1–9.

Remarks. The specimens of S. cliftonensis and S. praecursor figured by Foerste (1909, pl. III, figs. 47 and 48) are not available for further study. According to the original descriptions of the species (Foerste, 1909, pp. 96–98) they were considered to differ only in that S. cliftonensis had three ribs in its sulcus while S. praecursor had one rib in its sulcus. Both species were based on material from the Clifton Bed at Clifton, Tennessee (Foerste, 1909, p. 97). In the USNM collection there is a topotypic set of thirty specimens (collected by Foerste) which are labelled as S. praecursor. However, as noted by Amsden (1978, p. 23), most of these shells have three ribs in the sulcus and are thus more like S. cliftonensis as originally described by Foerste (1909, p. 97). Although Amsden (1978, p. 23) assigned these shells to S. cliftonensis, he noted that they could well be variants of S. praecursor rather than a separate species. The latter possibility seems more feasible since some shells in the topotypic collection have two ribs in the sulcus and could therefore be assigned to neither S. cliftonensis nor S. praecursor if Foerste’s original definitions were followed. Rather, there is the implication that this particular attribute alone is not very useful for separating species. This point is emphasized by the fact that other species, such as S. borealis, have anywhere from one to seven ribs in the sulcus. In view of these points S. cliftonensis is herein included as a synonym of S. praecursor. The available specimens from the Clifton Bed of Tennessee clearly show that Stegerhynchus has a well-defined median septum which tends for 50 to 60% of the length of the dorsal valve. The notothyrial cavity houses a long, narrow cardinal process (text-fig. 3).

EXPLANATION OF PLATE 19

Figs. 18, 25–33, 40–42. Stegerhynchus borealis (von Buch, 1834); lateral, anterior, and pedicle views of a series of specimens from assemblage M113 collected at Cape Admiral M'Climock, Read Bay Formation, Somerset Island; UA3701 to UA3702 inclusive.

Figs. 19–24, 34–39, 43–45. Stegerhynchus angustus Chernyshev, 1937; lateral, anterior, and pedicle views of specimens from basal unit of Member C of the Read Bay Formation at Goodsrir Creek, Cornwall Island, UA3710 to UA3714 inclusive.
CONSTITUTION AND AGE OF STEGERHYNCHUS

Species wrongly assigned to Stegerhynchus

In addition to the above species assigned to Stegerhynchus there are a number of species that have been wrongly assigned to the genus. In almost every case this resulted from confusion over the true type species of Stegerhynchus. Thus, Havlicek (1961, pp. 80-91) assigned daphne Barrande, 1847, infelix Barrande, 1879, incohans Havlicek, 1961, nympha Barrande, 1847, and pseudolovetius Barrande, 1847 to Stegerhynchus while Kulikov (1963, pp. 45-50) assigned daphne Barrande, 1879, nympha Barrande, 1879, and possibly dichotoma Khalfin, 1948 to Stegerhynchus. In his discussion of the genus, Kulikov (1963, pp. 45-50) also assigned pseudolovetius Barrande to Stegerhynchus. These assignments by Havlicek (1961) and Kulikov (1963) were made because they believed that R. whitii Hall was the type species of the genus as argued by Cooper (1955, pp. 54-55). None of these species possess a cardinal process and therefore cannot belong to Stegerhynchus. The affinity of these species is uncertain and requires further study before a definite assignment can be made. In 1967 Kulikov assigned mucilus Sowerby, 1839 to Stegerhynchus. However, inspection of the pertinent figures shows that the specimens sectioned do not contain a cardinal process (Kulikov, 1967, p. 83) and cannot, therefore be assigned to Stegerhynchus. Shimer and Shrock (1944, p. 309) also listed the species whitii, Hall, neglectum, Hall, indigenus, Hall, and acinus, Hall as members of Stegerhynchus. However, no information about internal structures was supplied; therefore, it is impossible to verify the validity of this assessment.

Age ranges of Stegerhynchus

Apart from isolated occurrences in the uppermost Ordovician of Missouri, Stegerhynchus is restricted to Silurian strata (text-fig. 4). Species such as S. borealis and S. diodonta have relatively long ranges while other species such as S. diodonta are relatively restricted. Apparently, Stegerhynchus does not occur in Devonian strata. S. borealis occurs in the Red Bay Formation of Arctic Canada in strata of upper Ludlovian age and this extends the range of the species as known from the literature. In the basal part of Member C of the Red Bay Formation at Goodsite Creek (text-fig. 5) S. borealis and S. angustiensis occur together thereby confirming the overlapping age ranges of these species.

![Text-fig. 4. Geographic and stratigraphic distribution of species assigned to Stegerhynchus.](image-url)
TEXT-FIG. 5. Geographic and stratigraphic locations of *Stegherhynchus borealis* and *S. angiacensis* in the Road Bay Formation of Somerset, Prince of Wales, and Cornwallis Islands. *S. borealis* is relatively common, especially in the lower part of the formation whereas *S. angiacensis* is relatively rare, occurring only in the basal part of Member C on eastern Cornwallis Island.
RHYNCHONELLIDS FROM THE READ BAY FORMATION
OF ARCTIC CANADA

The Upper Silurian Read Bay Formation of Somerset, Prince of Wales and Cornwallis Islands of Arctic Canada, contains an abundant fauna of brachiopods. Rhyynchonellids occur at many levels in the Read Bay Formation of these islands. S. borealis was collected from six localities on Somerset Island, three localities on Prince of Wales Island, and from members A and C of the type section of the Read Bay Formation at Goodsite Creek on Cornwallis Island. S. anguicostata has only been recorded from four localities on the east coast of Cornwallis Island (text-fig. 5).

*Stegerhynchus borealis* (Von Buch, 1834)

Plate 19, figs. 1–18, 22–30, 37–39, Plate 20

_Horizon and age._ *S. borealis* occurs at many horizons in the Read Bay Formation but is commonest in the lower part of the formation (text-fig. 5). Thus, it would appear to have a Ludlovian to Pridolian range on Somerset, Prince of Wales, and Cornwallis Islands.

_Preservation._ Most *S. borealis* in the Read Bay Formation are preserved as complete calcareous shells. However, silicified specimens have been recovered from localities on Prince of Wales and Somerset Islands and the description of the internal structures is based on this material.

_Description._ External morphology. *S. borealis* has a biconvex, plicate shell that attains a maximum length of about 2 cm. In small specimens (< 1 cm long) the valves are subequally convex (Pl. 19, figs. 37–39) whereas in larger, more mature shells the brachial valve is more convex than the pedicle valve (Pl. 19, figs. 1–15). Pedicle umbo generally erect. Deltihystrum triangular and commonly bordered by small deltoidal plates. Shell outline subtriangular with shell width generally exceeding shell length (text-fig. 7a). Sulcus commences 4 to 5 mm from the pedicle beak and becomes wider and deeper anteriorly (Pl. 19, figs. 2, 5, and 8). Most commonly, the sulcus contains three angular ribs (Pl. 19, figs. 5, 14, 23, and 26) but there is a wide range of variation about this mode (Pl. 19, figs. 2, 8, 11, and 29). For example, 80% of the shells in assemblage M13 have 3 ribs in the sulcus while the remaining 20% have 1, 2, 4, 6, or 7 ribs (text-fig. 6c). The number of ribs in the sulcus does not appear to be a function of ontogeny since there is no relationship between shell size and the number of ribs in the sulcus (text-fig. 7c). Each shell flank has 4 to 8 ribs which fade posteriorly (Pl. 19, fig. 39). Apical angle ranges from 66 to 95 degrees (text-fig. 6f).

On the pedicle valve slightly elongate and relatively stout teeth (Pl. 20, fig. 8) are supported by dental lamellae that diverge slightly anterolaterally (Pl. 20, fig. 4). The dental plates, which terminate abruptly, are short, being confined to the umbral region of the shell (Pl. 20, fig. 4). Umbonal cavities D-shaped. On the brachial valve the sockets widen anterolaterally (Pl. 20, fig. 2) and are bounded by blade-like dental socket plates (Pl. 20, figs. 2 and 6). The triangular-shaped hinge plates are convex anterolaterally and have eroded bases on their inner edges. Crus extend anterolongitudinally (Pl. 20, fig. 3). The notothyrial cavity is relatively large and has as its base the notothyrial platform which supports an elongate, blade-like cardinal process (Pl. 20, figs. 1, 2, and 7). The notothyrial platform is supported by a median septum which becomes narrower and lower anteriorly, eventually disappearing at about midlength (Pl. 20, fig. 6).

_Remarks._ These Read Bay rhyynchonellids are assigned to *S. borealis* because they are close to *S. borealis* as described by Basset and Cocks (1974, p. 26), St. Joseph (1937), Kulikov (1967, pp. 76–79), and Sheehan (1976, p. 728). They are also close to specimens Br 103764 and Br 103765 of *S. borealis_. Smith (1976) assigned rhyynchonellids from the Upper Silurian Douro Formation (equivalent to the Read Bay Formation of Somerset Island and Member A of the Read Bay Formation on Cornwall) to *F. turkestanica*. However, these specimens have internal structures more typical of *Stegerhynchus*. They are very similar to the specimens described as *S. borealis* in this paper.
TEXT-FIG. 6. Comparison of (a) number of ribs in sulcus, (b) length, (c) width, (d) height, (e) apical angle, and (f) number of ribs on each shell flank of pedicle valve for assemblage M113 of Stegerhynchus borealis and S. anguicinctus from the east coast of Cornwallis Island. The parameters are defined in fig. g. Note that the major difference between the two species is in the number of ribs in the sulcus.

TEXT-FIG. 7. Bivariate graphs comparing Stegerhynchus anguicinctus (from east coast of Cornwallis Island) and S. borealis (assemblage M113) for (a) length versus width and (b) width versus height demonstrating that the two species are very similar in these respects. (c) pictogram showing the absence of any relationship between the number of ribs in the sulcus and shell size of S. borealis.
**Siegerhynchus anguicinctus** Chernyshev, 1937

Plate 19, figs. 16-21, 31-36, and 40-42

**Occurrence and age.** *S. anguicinctus* has only been found in restricted numbers at four localities on eastern Cornwallis Island. *S. anguicinctus* occurs in the basal unit of Member C of the Read Bay Formation at Goodsr Creek (text-fig. 5). At localities (2, 3, and 4) to the south and north of Goodsr Creek, *S. anguicinctus* has only been found in the scree. However, their position in the scree and the associated fauna clearly points to them originating in the same stratigraphic position as the specimens at Goodsr Creek. Their occurrence at the base of Member C strongly suggests a late Ludovician age for the brachiopods since conodonts from Members A and C suggest that Members A, B, and part of Member C are of Ludovician age while the upper part of Member C is of Pridolian age (Ueno, 1977, fig. 41.2).

**Preservation.** All of the specimens of *S. anguicinctus* from eastern Cornwallis Island are preserved as articulated calcareous shells. Most of the shells are complete.

**Description.** Biconvex, plicate shell that attains a maximum length of about 2 cm. Brachial valve more convex than pedicle valve even in small specimens and this becomes even more pronounced in larger, more mature specimens. Pedicle umbo pointed, erect to sub-erect. Pedicle foramen is clearly visible. Shell outline subtriangular. In small specimens (<1 cm) width is approximately equal to length; however, in larger, more mature specimens width generally exceeds length. Well-defined uniplicate sulcus begins 2 to 3 mm from beak and is laterally bounded by steep-sided sulcus walls (Pl. 19, figs. 17, 20, 32, and 35). The brachial valve has a correspondingly strong fold with two angular ribs. Shell flanks are occupied by 5 to 6 strong, angular ribs and 1 to 2 minor angular ribs.

**Internal structures resemble those of** *S. borealis*.

**Remarks.** The specimens of *S. anguicinctus* from Cornwallis Island are very similar to those described and illustrated by Chernyshev (1937, pl. 1).

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**Explanation of Plate 20**

Figs. 1-8. *Siegerhynchus borealis* (von Buch, 1834): 1. Posterior portion of articulated shell showing the teeth in sockets, triangular-shaped hinge plates, and relatively large notothyrial cavity housing elongate, blade-like cardinal process. ×22. 2. Interior of brachial valve showing curved hinge plates, notothyrial cavity, elongate cardinal process, median septum becoming lower and narrower anteriorly, and muscle scars on either side of the septum. Note teeth broken off into sockets. ×20. 3. Posterior portion of brachial valve showing crus extending from hinge plates. ×23. 4. View of posterior portion of pedicle valve from anterior showing dental plates and D-shaped umbonal cavities. This valve matches the brachial valve shown in fig. 2. ×19. 5. Posterior portion of articulated shell. ×29. 6. Interior of brachial valve showing full extent of median septum. Note that septum is well developed even in this small shell. ×10. 7. View of the notothyrial cavity from anterior margin showing shape of cavity, shape of cardinal process, and height of cardinal process above cavity floor. ×26. 8. Enlarged view of tooth from pedicle valve. ×47.
JONES, brachiopod *Steiferhynchos*
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