THE TAXONOMY, SHELL STRUCTURE, AND PALAEOECOLOGY OF THE TRIMERELLID BRACHIOPOD *GASCONSIA* NORTHROP

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ABSTRACT. The large trimerellid brachiopod *Gasconsia* Northrop is reassessed on the basis of the type species and abundant, well-preserved material from the upper part of the Bønsnes Formation (Rawtheyan: Ashgill Series) in the Ringerike district of the Oslo Region. Hitherto the genus was known only from indifferently preserved moulds from the upper Silurian of Quebec. The Norwegian specimens are assigned to a new species, *G. worsleyi*, and include valve interiors which permit a detailed analysis of the articulation and musculature. The shell has been replaced by sparry calcite which also characterizes the shells of the associated gastropods and cephalopods. This confirms the assumption that trimerellid brachiopods originally possessed an aragonitic shell. The unusual fauna containing *Gasconsia* in Norway is of low diversity and comprises articulate brachiopods, bryozoans, trilobites, ostracods, gastropods, corals, and calcareous algae. It is suggested that *Gasconsia* may have adopted a quasi-infaunal mode of life.

INTRODUCTION

TRIMERELLID brachiopods are rare in most Ordovician and Silurian faunas. Despite the detailed monographic study of the group by Davidson and King (1874) the internal features, for example the musculature and articulation, are poorly understood and not known in the majority of genera (Rowell 1965). To date the best preserved specimens of the Trimerellacea are incomplete silicified valves of *Dinobolus* from the middle Silurian of British Columbia described by Norford (1960) and *Eodinobolus* from the Caradoc of Fort Chute, Ontario, described by Norford and Steele (1969). Both studies revealed in detail internal features of the shells whilst the latter account speculated upon a viable mechanism for the relative movements of the valves.

The genus *Gasconia* was erected by Northrop (1939, p. 161) on the basis of several indifferently preserved moulds from the upper Silurian Gascons and Bouleaux formations of the Gaspé peninsula, Quebec. Although no valve interiors were described by Northrop, he provisionally referred the genus to the Trimerellidae, whilst noting the similarity of the Canadian material to *Dinobolus transversus* (Salter) from the Wenlock of England. Rowell (1965, p. H863) was uncertain as to both the status and affinities of *Gasconsia*. However, during the course of this study a slab containing topotype specimens has been located in the collections of the Peabody Museum with a number of valve interiors displaying features comparable with those of the better preserved Norwegian species. The generic validity of *Gasconsia* therefore is confirmed by both the Canadian and Norwegian samples whilst Northrop's assignment of the material to the Trimerellidae is correct.

Abundant and well-preserved shell and mould material of a new species of *Gasconsia* from the upper Ordovician rocks of the Oslo Region provides detailed information on the trimerellid musculature and articulation and permits a new interpretation of their functional morphology. The existing fabric of sparry calcite and the indications of an original structure of lamellae confirms the assumption that the trimerellid shell was initially aragonitic (Jaanusson 1966). The Norwegian species, *G. worsleyi* is described whilst the type species *G. schucherti* is redescribed from type and topotype specimens.

G. worsleyi is known from a few beds of limestone within a thick sequence of limestones and marls towards the top of the upper Ordovician Bønsnes Formation, near Stamnestangen (= Stavnestangen)

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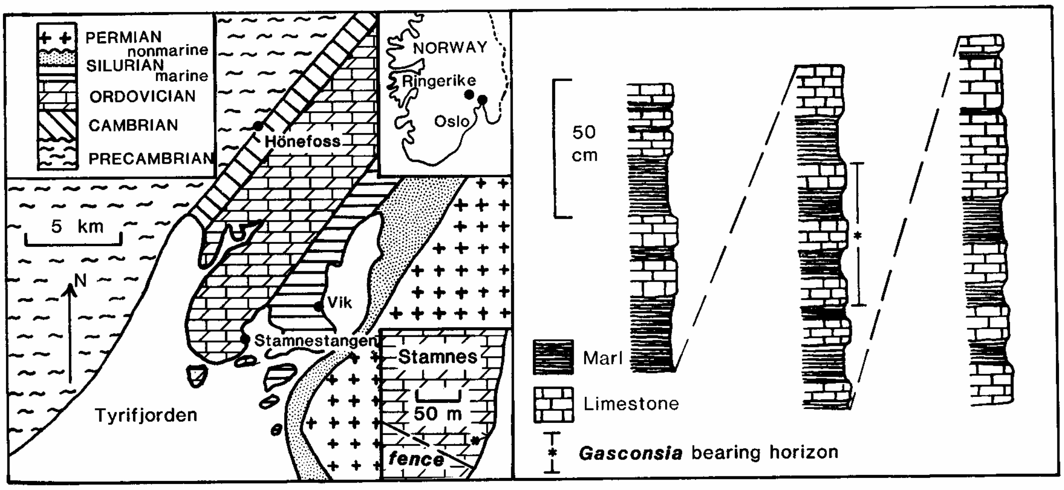
in the Ringerike district of the Oslo Region (text-fig. 1). Ringerike is the sixth of Størmer's districts of the region (1953, fig. 1) and is situated some 40 km north-west of the capital city. The gently folded Lower Palaeozoic succession youngs to the south-east and is best exposed around the margins of the Tyrifjord. Although the Ordovician succession is virtually complete only the upper Caradoc and Ashgill formations have been described in detail; Hanken and Owen (1982) summarized previous research. The Bønsnes Formation occurs near the top of the Ordovician succession and is correlated with the Rawtheyan Stage of the Ashgill Series (Owen 1979). The formation is well exposed around the Bønsnes peninsula, particularly at and near Stamnestangen. Here Professor Kiær collected in excess of fifty individuals of the trimerellid. Further collecting by the authors has confirmed Kiær's locality information (text-fig. 1).



TEXT-FIG. 1. Simplified geological map of the Ringerike district showing *Gasconsia* locality at Stamnestangen; measured profile at NM 6816.5961 indicates extent of the *Gasconsia* bearing horizon.

TECHNIQUES

In contrast to the poorly preserved moulds of *G. schucherti*, the valves of the Norwegian *Gasconsia* are preserved in a matrix of microspar with small amounts of clay and silt grade terrigenous material. Quantitative analysis of the calcium carbonate, following the procedure of Dreimanis (1962), has indicated a content of about 90% in the *Gasconsia* bearing horizon. Information regarding the shell interiors was derived by selective dissolution of the shell material. However, due to the small difference in carbonate content between the fossils and the matrix, over-etching of the limy moulds poses a serious problem. The best results were obtained if the moulds were exposed to 5% hydrochloric acid for a maximum of about two minutes. After etching the specimen was dried, and the newly exposed part of the mould impregnated with a solution of pioloform in alcohol. When the alcohol has evaporated the pioloform precipitates, thus causing surface particles to adhere. This thin skin is fairly impermeable and prevents further etching. The dissolution/impregnation process was repeated until all the shell material was dissolved and the pioloform impregnated mould was then cast in silicone rubber.

The fauna from the marly horizons, between the *Gasconsia* bearing strata, was recovered from a number of different levels. The marl weathers fairly easily under natural conditions, and samples with a mean weight of about one kilogram were collected from especially well-weathered beds. To achieve further breakdown of the matrix the marl was treated with petrol following the procedure of Allman and Lawrence (1972). After treatment the material was screened according to grain size and the samples were picked for fossils larger than 0·5 mm.

Petrographic observations were made from thin sections without cover glass. For the study of the microstructures of the shells a Nuclide Luminoscope mounted on a Leitz petrographic microscope was used making it possible to study the thin sections both by standard light-microscopy and by cathodoluminescence. For the latter a beam current of 0·7–0·9 mA at 13–14 kV and 50 torr vacuum was used.

The measurement, statistical, and photographic techniques used in this study are those described in Harper (1984) except where stated otherwise.

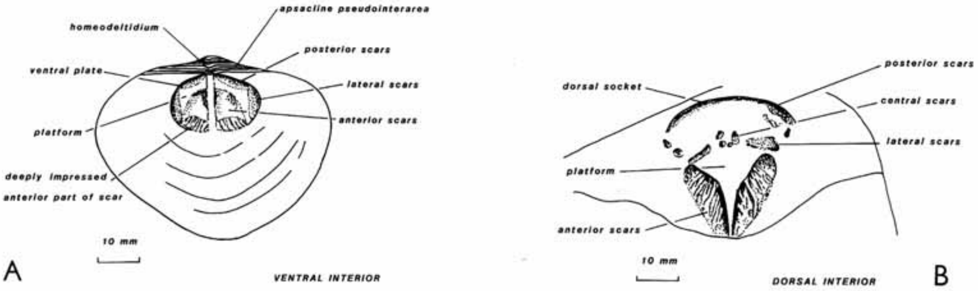
Repositories of specimens: PMO—Paleontologisk museum, Oslo; YPM—Peabody Museum, Yale University, New Haven.

SYSTEMATIC PALAEONTOLOGY

Superfamily TRIMERELLACEA Davidson and King, 1872
Family TRIMERELLIDAE Davidson and King, 1872
Genus GASCONSIA Northrop, 1939

Type species. By original designation, *G. schucherti* Northrop, 1939, p. 161; from the Gascons and Bouleaux formations (upper Silurian), Gaspé, Quebec, Canada.

Diagnosis. Large convexiplane to convexiconcave trimerellid of transversely suboval outline; dorsal and ventral platforms low, not vaulted and median ridges feeble or absent. Articulation achieved by curved ventral plate and corresponding dorsal socket. Ornament of locally thickened concentric growth lines and fine ribs usually restricted to inner shell layers.



TEXT-FIG. 2. *G. worsleyi* sp. nov. A, ventral interior, based on PMO 13091. B, dorsal interior, based on PMO 104.000

Remarks. Although the external diagnostic features of the genus are apparent in both *G. schucherti* and *G. worsleyi*, detailed data regarding the valve interiors were compiled from examination of the latter. Both known species of *Gasconsia* are large with well-defined ornaments of thickened concentric growth lines locally appearing as rugae. A small pooled sample of unbroken specimens of both species was investigated for size-independent morphological differences using Principal Components Analysis. *G. schucherti* consistently has a more transverse outline than that of *G. worsleyi*. Details of this analysis are housed with the figured material. *Gasconsia* is most similar to *Eodinobolus* in that both possess solid, not raised or vaulted platforms in both valves. *Eodinobolus*, however, possesses a different mode of articulation whereby a dorsal tooth fits into a ventral socket; furthermore the valves are relatively smaller and are subequally biconvex.

The large genera which characterize the Silurian trimerellid faunas, *Trimerella*, *Dinobolus*, *Monomerella*, and *Rhynobolus*, are subequally biconvex and possess raised or vaulted platforms in both valves. With the exception of *Dinobolus*, which possesses a dorsal plate and ventral socket, the articulating mechanisms of these genera are not well documented. None of the five trimerellid genera—*Sinotrimerella*, *Palaeotrimerella*, *Machaerocolella*, *Fengzuella*, and *Paradinobolus*—recently described from supposed early Caradoc rocks in western Zhejiang, China (Li and Han 1980) is comparable with *Gasconsia*.

Gasconsia schucherti Northrop, 1939

Text-fig. 4B–G

1939 *Gasconsia schucherti* Northrop, p. 161, pl. 12, figs. 6–8; pl. 13, fig. 7.

Material. Ten brachial and three pedicle valves; most are broken.

Lectotype. Selected herein, a pedicle valve YPM 13313A.

Diagnosis. A transverse *Gasconsia* species with about twelve ribs per 10 mm at the 30 mm growth stage and about 5–6 thickened concentric growth lines at a similar place.

Description.

Exterior. Very large convexiplane to convexiconcave valves of transverse outline with maximum width at or near mid-valve length; cardinal extremities obtuse and rounded. Anterior commissure rectimarginate. Pedicle valve about three-fifths as long as wide, roughly flat or weakly concave in both profiles but with local undulations; pseudointerarea short and apsacline with faint closely spaced growth lines. Brachial valve about three-fifths as long as wide and about one-fifth as deep as long. Anterior profile strongly but evenly convex with maximum convexity medianly; flanks feebly concave. Pseudointerarea reduced or obsolete. Lateral profile with greatest convexity over posterior third of valve surface; profile flattens slightly anteriorly. Ornament of thickened growth lines locally developed as rugae; about 5–6 per 10 mm are present medianly at 30 mm growth stage. Radial ornament of fine costae and costellae with uniformly rounded profiles apparently restricted to inner shell surfaces with about twelve per 10 mm medianly at 30 mm growth stage.

Valve interiors. Platforms and muscle scars poorly defined. Ventral interior with low, curved ventral plate and solid platform situated anteriorly; muscle scars not well defined. Dorsal interior with well-defined dorsal socket and bipartite, solid platform. Pair of oval anterior scars situated lateral to triangular anterior part of platform.

Remarks. Information regarding the valve interiors of *G. schucherti* is rather meagre but is sufficient to associate the Canadian species with the better preserved Norwegian material. *G. schucherti* possesses a dorsal socket and ventral plate together with solid platforms in both valves. The convexiplane valves are large and ornamented by rugae and ribs on their inner surfaces. These features characterise the genus and together they separate *Gasconsia* from all other trimerellid genera.

Gasconsia worsleyi sp. nov.

Text-figs. 3A–H; 4A, 2A, B

Derivation of name. For Dr. David Worsley.

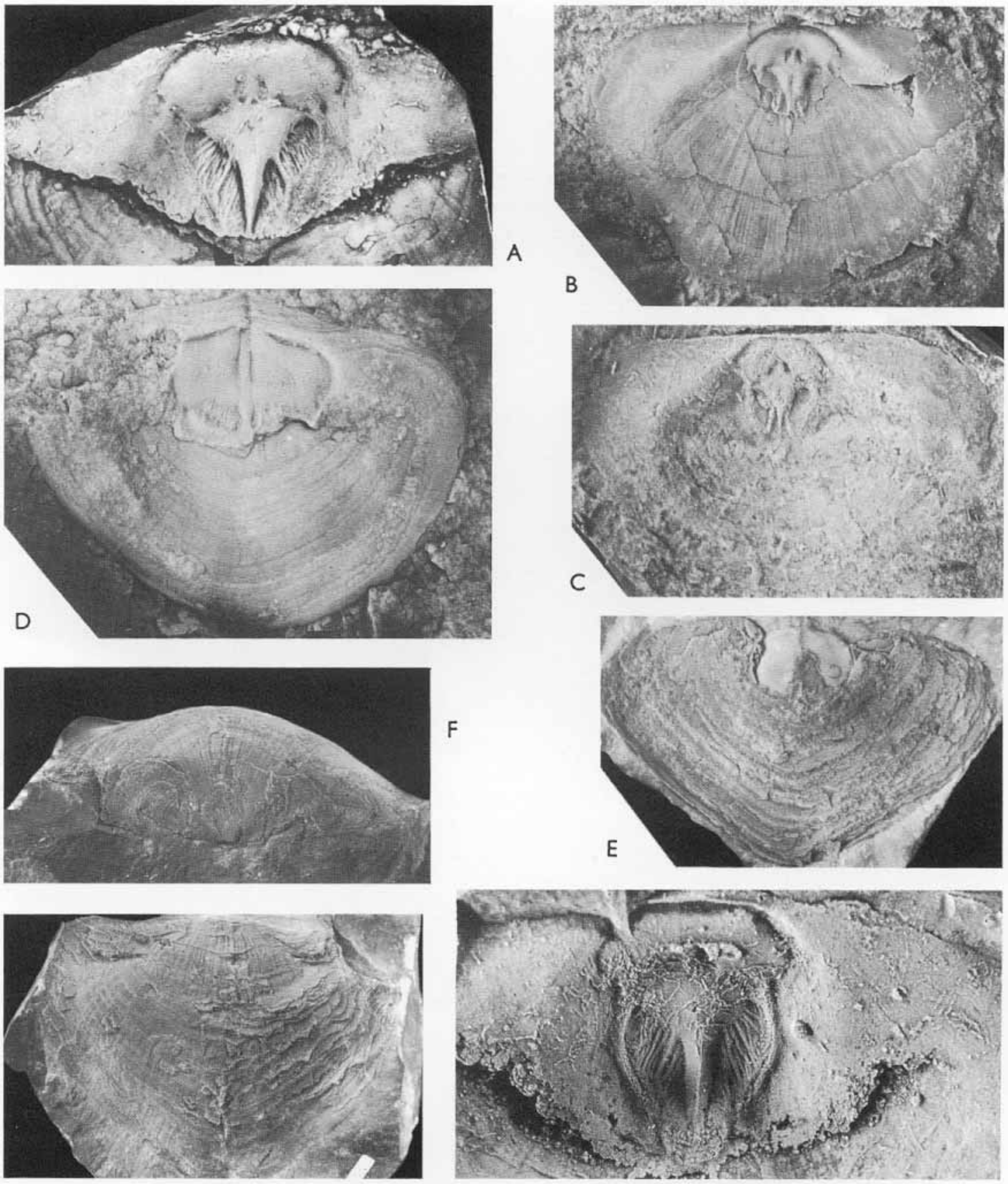
Material. Fifteen conjoined pairs, 12 pedicle valves, and 23 brachial valves; much of the material is represented by either broken or fragmentary valves.

Holotype. A pedicle valve, PMO 13091.

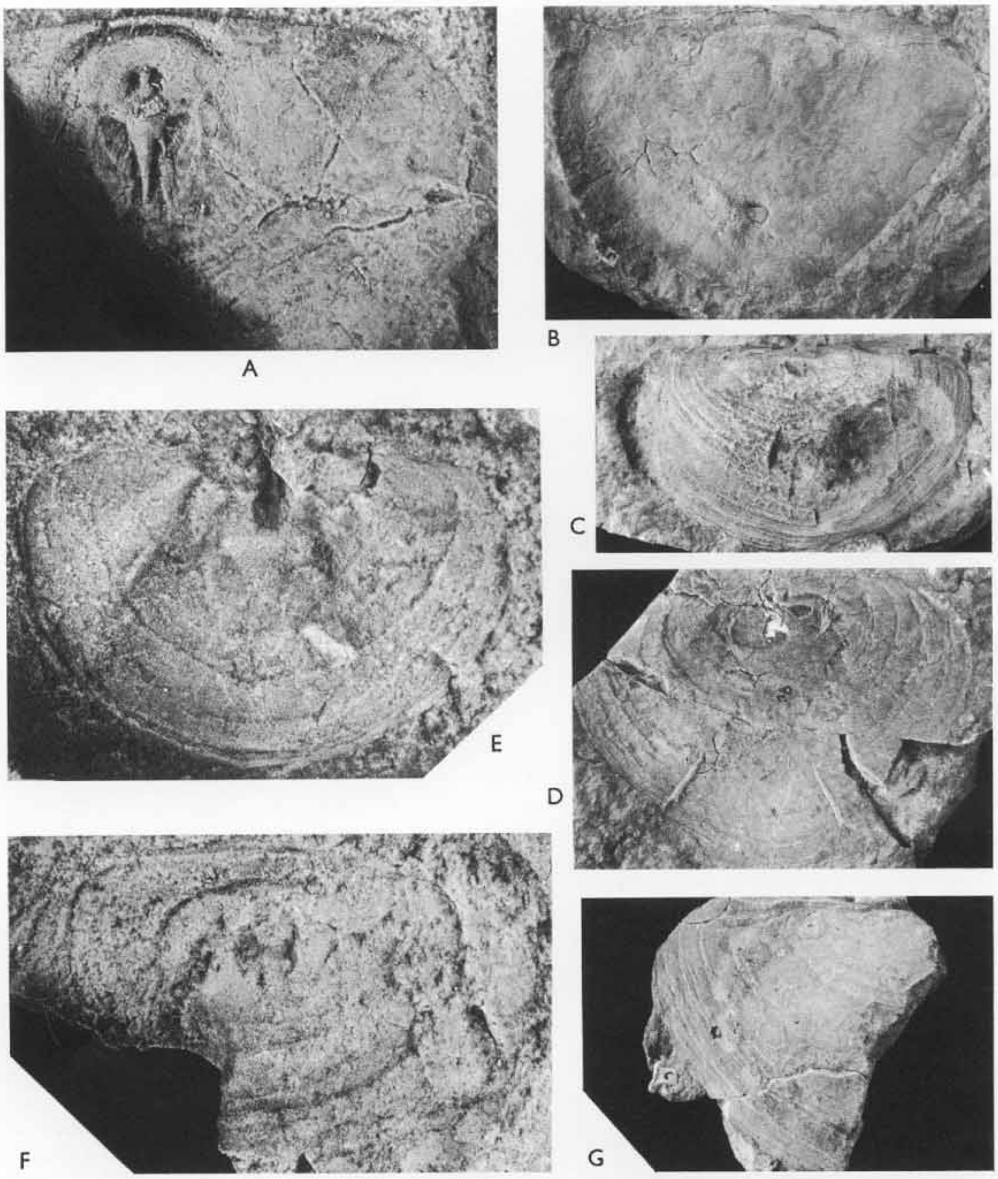
Diagnosis. An elongate *Gasconsia* with about 9–10 ribs per 10 mm at the 30 mm growth stage and about 3–4 thickened concentric growth lines per 10 mm at a similar place.

Description.

Exterior. Very large, thick, convexiplane to convexiconcave valves of elongate, rounded triangular outline with maximum width at or near mid-valve length; cardinal extremities obtuse and curved. Pedicle valve roughly flat or weakly concave in both anterior and lateral profiles, about three-quarters as long as wide. Well-defined but relatively short apsacline pseudointerarea about one-eighth as long as wide and about one-tenth sagittal valve length. Interarea modified by differentially thickened, transverse growth lines and narrow depressed homeodeltidium; latter occupies about one-fortieth width of interarea. Brachial valve about four-fifths as long as wide and about one-quarter as



TEXT-FIG. 3. A–H, *Gasconsia worsleyi* sp. nov., upper part of the Bønsnes Formation (Rawtheyan), Stamnestangen. A, silicone rubber replica of internal mould of brachial valve, PMO 104.000, × 1. B, dorsal interior, PMO 13831, × 2. C, silicone rubber replica of internal mould of brachial valve, PMO 103.999, × 1. D, holotype, ventral interior, PMO 13091, × 1. E, partly exfoliated ventral exterior, PMO S2275, × 0·5. F, G, posterior and dorsal views of dorsal exterior, PMO 17558, × 0·4. H, silicone rubber replica of internal mould of brachial valve, PMO 104.002, × 1·33.



TEXT-FIG. 4. A, *Gasconsia worsleyi* sp. nov., upper part of the Bønsnes Formation (Rawtheyan), Stamnestangen, silicone rubber replica of internal mould of brachial valve, PMO 104.001, ×2. B–G, *Gasconsia schucherti* Northrop, Gascons and Bouleaux formations (upper Silurian), Gaspé peninsula. B, lectotype, internal mould of pedicle valve, YPM 13313A, figured Northrop 1939, pl. 12, fig. 8; ×0·5. C, internal mould of brachial valve, YPM 13312, figured Northrop 1939, pl. 13, fig. 7; ×1·33. D, external mould of brachial valve, YPM 13313B, figured Northrop 1939, pl. 12, fig. 7; ×0·66. E, dorsal interior, YPM 13897; ×1·5. F, dorsal interior, YPM 13898; ×1·33. G, internal mould of brachial valve, YPM 13311; ×0·66, figured Northrop 1949, pl. 12, fig. 6. Figs. B, E, F are of specimens from the Bouleaux Formation (west side of Pointe Bouleaux Anse-A-la-Barbe, Gascons), the other figured specimens are from the Gascons Formation (locality 23 of Northrop 1939).

All specimens were whitened with ammonium chloride sublimate prior to photography; figs. E and F were photographed with a high-contrast film to enhance detail.

deep as long. Anterior profile strongly curved with maximum convexity medianly; flanks weakly concave, particularly near valve margins. Lateral profile strongly convex over posterior third of valve surface, anteriorly more evenly curved. Pseudointerarea short, virtually obsolete. Ornament of differentially thickened growth lines locally developed as rugae and over the anterior shell surface appearing as comae; 3–4 per 10 mm are present medianly at 30 mm growth stage. Rounded fine costae and costellae apparently restricted to inner shell surfaces number 9–10 per 10 mm medianly at 30 mm growth stage.

Ventral interior. Transverse semielliptical solid platform (text-fig. 2A) about two-thirds as long as wide and extending anteriorly to about two-fifths valve length. Platform delimited posteriorly by low, curved ventral plate rising vertically from floor of valve, lateral parts of which diverge widely anteriorly to near one-sixth valve length where they converge to describe evenly rounded curve. Large pair of anterior scars about three-fifths as long as wide, situated centrally on platform and divided medianly by low broad ridge, itself flanked by two deep grooves; anterior parts of muscle tracks deeply impressed. Lateral scars elongate and confined laterally by ventral plate; posterior scars transverse, partly attached to ventral plate.

Dorsal interior. Well-defined solid platform (text-fig. 2B) consisting of two parts. Curved dorsal socket marks posterior margin of rounded transverse and slightly convex rectangle bearing pair of small but deeply impressed central muscle scars and larger transverse posterior muscle scars. Anterior part of platform elongately triangular and marked laterally by deeply impressed anterior muscle scars, with numerous anterolaterally directed ridges. Lateral scars, relatively small, inserted on anterolateral edges of posterior part of platform.

Remarks. As previously noted the valves of *G. schucherti* are more transverse than those of *G. worsleyi* and moreover both the radial and concentric ornaments of the type species appear finer than those of the Norwegian form. However the lack of detailed information regarding the interiors of the type species prevents a comparison of the internal features of both species.

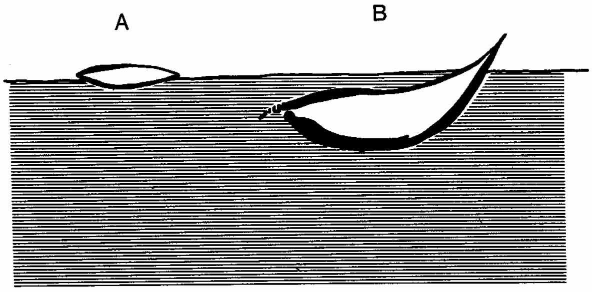
FUNCTIONAL MORPHOLOGY

Articulation of the valves of *Gasconsia* was achieved by the snug fit of the curved ventral plate into the dorsal socket. The muscles represented by the anterior and lateral scars when contracted would tightly close the two valves. The posterior muscles may also have contracted to supplement those adductors. Norford and Steele (1969, p. 164) suggested that to open the valves of the related trimerellid *Eodinobolus* Rowell muscles in the posterior part of the shells acted as diductors on contraction and therefore opened the valves about an axis delimited by the lateral edges of the interarea. This mechanism, however, is not feasible for *Gasconsia* as there is no area for muscle attachment behind the plate and socket whilst the function of muscles as diductors anterior to these structures is not possible. However, following the models of Gutmann *et al.* (1978) some of the muscles may have extended longitudinally from the posterior floor of one or both of the valves to attach directly to the coelom. Their contraction would have withdrawn the brachiopod animal posteriorly thus slightly forcing apart the shells. The central muscle scars of the lower brachial valve of *Gasconsia* do not appear to have counterparts in the pedicle valve. These scars may mark the site of attachment of such muscles; their contraction would have pulled the body posteriorly. Since lateral expansion of the body would have been inhibited by the lateral muscles, a dorsoventral distension of the animal's coelom would have raised the markedly lighter pedicle valve.

ONTOGENY AND AUTECOLOGY

Study of growth lines in different sized specimens of *Gasconsia* has permitted the reconstruction of the different growth stages of the shell during ontogeny. There is a distinct change in the type of growth between specimens less than 30–35 mm in length and larger ones. Specimens less than 30–35 mm in length have a gently convex brachial valve. In larger specimens, however, there is a sudden change from gently to strongly concavoconvex, reflected in a sharp change in convexity of the brachial valve. These changes in relative growth rates of the different parts of the shells are also combined with the development of great differential thickening of the brachial valve and the posterior part of the pedicle valve. This would have stabilized the shell against overturning, and the heavy posterior part of the shell may have partly sunk into the soft sediment.

The development observed in *Gasconsia* probably reflects different modes of life of young and adult individuals. Specimens less than 30–35 mm in length probably rested freely on the soft bottom with a more or less horizontal orientation of the commissural plane. The greater convexity of the brachial valve in larger specimens could be interpreted as an adaptation to a static, quasi-infaunal position (text-fig. 5). If sediment settled on to the concave pedicle valve, the shell may have been concealed except for the crescentic valve edges projecting above the surface of the sediment. This reconstruction of a quasi-infaunal position is very much like the presumed mode of life of many strophomenids, for example the productacean *Waagenoconcha* Chao (Grant 1966) from the Permian (see also Rudwick 1970, pp. 91–94).

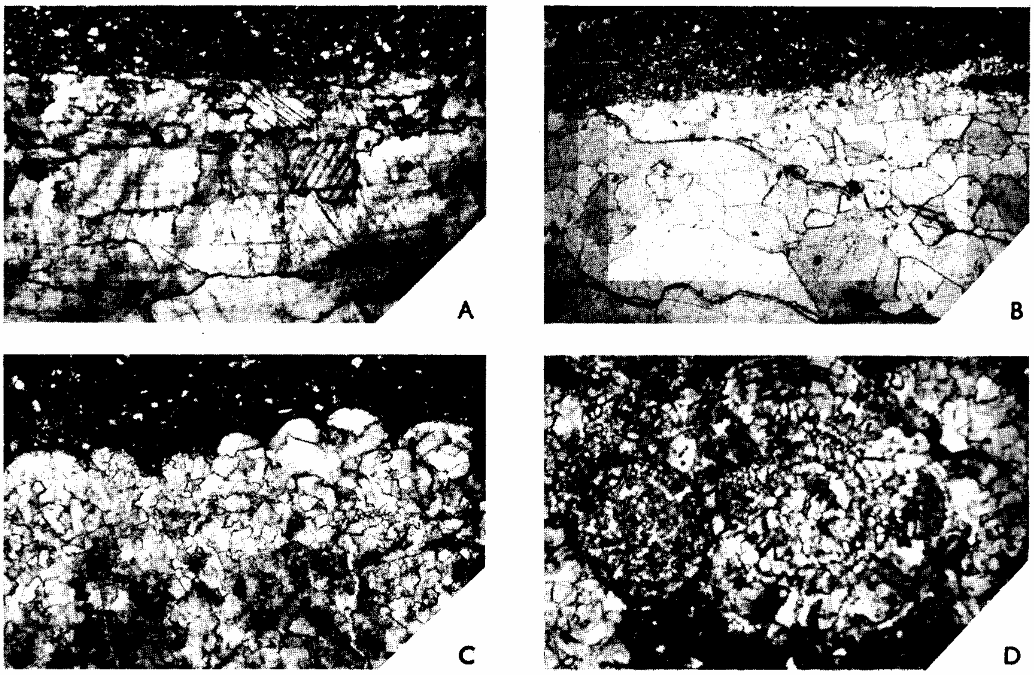


TEXT-FIG. 5. Reconstruction of life positions of young (A) and adult (B) specimens of *G. worsleyi* sp. nov. Young individuals probably lay on the sea floor while adults may have adopted a 'quasi-infaunal' mode of life. Both are sections through the median plane, the larger 75 mm in length, the smaller 30 mm.

Recent collecting at Stamnestangen has revealed a large conjoined pair of valves in a supposed life position. The orientation of the shells is consistent with the expected stable attitude of *Gasconsia* discussed above permitting the efficient opening and closing of the valves. The heavy umbonal region of the brachial valve was clearly anchored in the sediment whilst the markedly lighter pedicle valve could open freely.

SHELL STRUCTURE

Whilst the shells of the articulate brachiopods from the *Gasconsia* beds appear to display an original structure of fibres and lamellae of calcite (see e.g. Williams 1968*a*) the shell texture of the associated *Gasconsia* is strikingly different. (No shell material is available of the type species, *G. schucherti.*) The shells of *Gasconsia* are multilayered consisting of two intermixed phases (text-fig. 6A, B). The most prominent layers consist of a mosaic of sparry calcite; these are separated by thin indistinct zones, preserved as a diffuse linear arrangement of inclusions. These inclusions either cut the calcite mosaic, continuing without deviation across the intercrystalline boundaries, or separate the spar crystals in succeeding layers of sparry calcite. A similar microstructure has also been observed in gastropods and cephalopods from the same beds. Such a crystal fabric is evidence of an original aragonite shell diagenetically replaced by calcite with the retention of relict of 'ghost' texture (Bøggild 1930; Bathurst 1964). This supports the view of Jaanusson (1966) that trimerellid inarticulate brachiopods possessed the ability to secrete aragonite. Webby and Percival (1983, fig. 9B, E) have recently illustrated a similar secondary calcite fabric in shells of *Eodinobolus* from the Ordovician of New South Wales.



TEXT-FIG. 6. Photomicrographs of shell fabric of *G. worsleyi* sp. nov. A, part of shell, polarized light, × 25; the laminar relict shell structure is clearly visible whilst the grain boundaries of the secondary sparry calcite are less obvious. The shell-sediment interface is located near the top of the section. B, adjacent part of shell under cathodoluminescence, × 25; grain boundaries of secondary calcite are distinct whilst compactional fractures post-dating the calcite cement are pronounced. C, posterior part of shell showing development of warts, polarized light, × 25. D, detail of warts, polarized light, × 100; concentric primary structure clearly visible.

The inclusions, which represent traces of an original layered structure, indicate that the shells consisted of a number of sheet-like laminae orientated slightly oblique to the inner and outer shell surfaces (text-fig. 4A, B). Due to this oblique orientation the different laminae become exposed at the shell surface different distances from the umbo. The termination of these laminae at the outer surface are seen as growth lines. The most prominent and well-defined growth lines are composed of a series of thinner laminae whilst the more obscure lines consist only of a single lamina. In most cases the anterior termination of each lamina is separated from the shell surface and deflected outwards giving a characteristic serrated pattern in transverse section. This 'ghosted' original structure of *Gasconsia* is consistent with the well-established models of shell generation for the articulate brachiopods (e.g. Williams 1956, 1968*b*). The inversion to calcite prohibits speculation concerning the precise configuration and identity of individual lamellae. However since traces of an original fabric are locally preserved a form of replacement must have occurred rather than complete dissolution and recrystallization.

The shell interiors, particularly the posterior parts, are characterized by small rounded wart-like structures (text-fig. 6C, D). These are solitary or occur in irregular groups, and have sometimes grown along irregular lines making a complicated network (text-fig. 6C). There is a relationship between age and the number of warts in a shell with a general tendency for large shells to have a higher density than smaller ones. However the distribution pattern varies highly from individual to individual. In large specimens warts from the juvenile part of the shell are commonly completely engulfed by younger growth laminae, indicating that they ceased growing after some time. The warts vary in size, but most are about 0.5 mm in diameter. They are roughly hemispherical with growth laminae corresponding to the outer surface. The exact number of laminae in a wart is often difficult to discern due to replacement by sparry calcite, but in some well-preserved specimens more than twenty laminae could be counted. The distance between each lamina is about 0.08 mm. Although the warts may be explained as a response to some irritation which encouraged the brachiopod to secrete extra layers of aragonite there is no direct evidence for this view. Thin sections have not revealed any sign of associated foreign objects or borings. This may be preservational but more probably the irritant was organic and has since decomposed.

The shells have been extensively broken during compaction, but the resulting fractures are only visible in cathodoluminescence (text-fig. 6B). Since the now separated fragments of shell if reunited form a continuous crystal lattice, replacement of the original shell fabric occurred before breaking.

FAUNA AND DEPOSITIONAL ENVIRONMENT

Reconstruction of the depositional environment based on only one geological section is hazardous. In this case where lateral facies relationships are yet to be established in detail only a generalized picture of the depositional environment can be given.

In the Stamnestangen section the outcrop of the *Gasconsia* bearing beds is limited to a sequence about 20 m thick in the upper part of the Bønsnes Formation. *Gasconsia* is found as disarticulated or, less commonly, articulated shells in a microsparitic matrix. The associated fauna is characterized by a low species diversity (Table 1), in contrast to the rich shelly assemblages at the top of the Bønsnes Formation. The fauna is well-preserved, and except for tiny algal fragments, there is no sign of significant predepositional mechanical breakage or abrasion of skeletal material. The fauna and the fine-grained sediment indicate deposition in a rather constant low-energy environment influenced only by occasional stronger currents washing together skeletal fragments in thin horizons.

TABLE 1. List of associated species from the *Gasconsia* beds, Bønsnes Formation, Stamnestangen, Ringerike.

Articulate brachiopods	Sparse, minute dalmanellids, *Triplesia* sp., *Eospirigerina* sp. (all individuals minute).
Gastropods	*Maclurites* sp., *Murchisonia* (*Hormotoma*) sp., *Loxonema* (?) sp., *Lophospira* (?) sp., pleurotomariacean indet., holopeid spp.
Tabulate corals	*Palaeofavosites schmidti*, *P.* cf. *balticus*, *Catenipora tapaensis*, *Proheliolites dubius*, *Sarcinula organum*.
Rugose corals	*Streptelasma eccentricum*, *S. primum*, *S.* cf. *primum*, *Grewinkia anquinea*, *Bodophyllum eithum*.
Calcareous algae	*Vermiporella* sp., *Dasyporella* sp.
Trilobites	Illaenid indet.
Trace fossils	*Planolites* sp., *Chondrites* sp.
Ostracods	Not determined.
Crinoid ossicles	Not determined.
Bryozoan	*Hallopora* cf. *multipora*.

As shown by Kiær (1920) calcareous algae are very common in this part of the sequence, especially fragments of *Vermiporella*; in some horizons these fragments constitute more than 90% of the skeletal debris. The presence of algae throughout the profile suggests that deposition took place within the photic zone. The present-day distribution of living calcareous codiaceans provides a good basis for interpreting the environmental regimes of similar fossil forms. Most modern forms colonize sand and mud substrates where the rhizoids of the plant penetrate the soft bottom to develop holdfasts (Wray 1977). Because of the delicate construction of these plants they generally live below intense wave agitation and are most common and diverse at depths of a few metres, especially in tropical shelf and lagoonal environments. It is generally inferred that most fossil species also had similar distribution.

The Bønsnes Formation is also well known for the great abundance of gastropods; in the older literature the term 'Gastropod Limestone' was often used for these beds. Parts of this fauna have been described by Koken (1925). Little is known about the palaeoecology of these Lower Palaeozoic gastropods, but according to Dr. J. Peel (pers. comm. 1982) the assemblage is suggestive of an algal browsing, or at least quiet water filtration existence.

The tabulate corals are mostly found in growth position scattered throughout the sequence. Their stratigraphical ranges are not well known from the Oslo Region excepting the family Heliolitidae which was described by Kiær (1899, 1903). However, all these corals are also known from Estonia where they indicate an Ashgill age (Vormi and Pirgu stages; Dr. E. Klaamann, pers. comm. 1982). The solitary rugose coral fauna is fairly restricted comprising species which are all well known from the upper Ordovician of the Oslo Region (Neuman 1969). The corals have a ceratoid to trochoid shape except *Streptelasma primum* which is cylindrical. Specimens of *S. primum* commonly show sharp geniculations indicating a sudden change in growth direction. This is probably in response to being tipped over during stormy episodes, accompanied by rapid growth to re-orientate the calyx permitting continued feeding. A similar growth habit is also known for the Carboniferous coral *Caninia* sp. (Hubbard 1966).

The matrix is heavily bioturbated indicating aerobic bottom conditions throughout the sequence. The trace fossil fauna comprises at least three different species, but due to poor preservation only *Chondrites* sp. and *Planolites* sp. have been identified.

The evidence of the associated biota and lithofacies indicates that *Gasconsia* dwelt on or partly within a carbonate mud substrate in a shallow, warm, marine environment; the habitat was restricted and perhaps even lagoonal.

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