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TWO NEW BRACHIOPOD GENERA FROM DEVONIAN ROCKS IN VICTORIA

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Summary

Notoconchidium and *Notoleptaena*, new brachiopod genera, are described from Lower Devonian strata in Victoria. New species are *Notoconchidium thomasi*, *Notoleptaena linguifera*, and *Notoleptaena otophera*. As known at present, the former genus belongs to a sandy facies, while the latter has species in both sandy and muddy facies. The adaptation of these forms to their respective environments is discussed.

Introduction

While describing fossils of Upper Silurian and Lower Devonian age collected by Dr. D. E. Thomas from the Heathcote district of Victoria (Thomas 1937), the writer encountered unusual brachiopods which are now presented as new genera, viz., *Notoconchidium* and *Notoleptaena*. Search in other collections showed that the latter genus also occurs elsewhere in the State. The basement rocks of the Heathcote district consist of Cambrian, Ordovician, Silurian, and Devonian sediments. The Silurian and Devonian beds, on the whole, are of inshore or Rhenish facies, sandstones predominating. The sequence is of interest in that (1) it spans the Silurian - Devonian boundary, and (2) the Devonian rocks contain a fauna of inshore or Rhenish facies, contrasting with the contemporary offshore or Bohemian facies described from Lilydale and Killara (Gill 1939-1949).

Notoconchidium and *Notoleptaena* both appear in typical sandy facies horizons. The former is limited to the Heathcote area, as far as is known at present, but the latter has been found also in the Lilydale and Killara districts of Victoria. Different species of *Notoleptaena* occur in the two facies, and it is instructive to note the special features which suited these contemporaneous forms to their respective ecological settings.

Family PENTAMERIDAE McCoy
NOTOCONCHIDIUM gen. nov.

Genotype *Notoconchidium thomasi*, gen. et sp. nov.

Diagnosis. Multicostellate, rectimarginate, pentamerid brachiopods, in which both valves are of more or less equal convexity;

there is an angular deflection of the lateral margins of the dorsal valve, and often also of those of the ventral valve. The septal plates of the dorsal valve diverge slightly, then converge, and laterally to them thick callists develop with age. In the ventral valve a small spondylium is present and a median septum one quarter to one half of the valve in length. In adult shells, small tooth-like processes develop on the spondylial plates.

Taxonomy. The new genus is a typical pentamerid, allied to *Conchidium* in its external appearance, in having a spondylium and median septum in the ventral valve, and in the triple set of plates in the dorsal valve. On the other hand, the converging septal plates and lateral callists of the dorsal valve are conspicuous and taxonomically important variations from the genus *Conchidium* as at present understood. The dorsal steinkerns with their projecting septal areas are a conspicuous feature in the field, where these fossils occur in great numbers.

Etymology. The name of the genus is derived from the Greek word *notos* = south (to denote its description from Australia), and the name of the closely allied genus *Conchidium*.

Notoconchidium thomasi, gen. et sp. nov.
Pl. I, Figs. 1-15.

Conchidium knightii Chapman 1913, pp. 105-106, Pl. XI, fig. 11.

Type Material. 1. *Holotype,* consisting of the steinkern of a dorsal valve preserved in light greyish quartzitic sandstone stained in places with ferruginous infiltrations (M.D.V.* 46315), from locality F52, Parish of Redcastle (see maps published by Mines Department), i.e., in the Mt. Ida Beds.

2. *Paratype,* consisting of the steinkern of a ventral valve in a mottled (light grey and maroon) quartzitic sandstone (M.D.V. 39094) from loc. 6D, Parish of Dargile, also in the Mt. Ida Beds.

3. *Hypotypes,* consisting of two dorsal valves which show progressive thickening of the internal structures: (a) external mould (M.D.V. 46289A) and steinkern (46289B) preserved in brownish quartzitic sandstone; and (b) steinkern preserved in light greyish quartzitic sandstone (M.D.V. 46293). Two ventral valve steinkerns (M.D.V. 46252, 46284) are also included to illustrate growth stages. All hypotypes are from loc. F52, Parish of Redcastle, i.e., in the Mt. Ida Beds.

*Numbers in parentheses are registered numbers in the palaeontological collections of the following institutions: M.D.V. = Mines Department, Victoria; N.M.V. = National Museum of Victoria.

Descriptions. 1. *Holotype.* Dorsal valve sub-triangular, strongly convex, the median longitudinal profile rising about 7 m.m. above the plane joining the anterior and posterior margins. Length in plan, i.e., not following the profile, 2·1 cm.; maximum width, 1·7 cm. Hingeline narrow. Beak obtuse. Anterior commissure rectimarginate. Shell very thick in posterior region. Lateral margins of the shell deflected at right angles, and the resultant flange is costate. Umbo comparatively smooth, but rest of shell multicostate, there being 9 costae per cm. at the anterior margin.

Septal plates diverge slightly at first, then converge; they reach 1·6 cm. down the length of the shell, i.e., three-quarters of the length. The septal plates are thickest in the middle. The spaces between the septa and the lateral walls of the valve are filled with callists some 3 mm. thick. At the posterior end of the shell there is a bulbous swelling on each side of the central septa; at the posterior end of each swelling there is a ridge which is interpreted as a brachial support.

There is a low median septum between the septal plates, but it is not very well preserved in the holotype. Specimens in which this structure is well preserved show that it gradually gets deeper and wider posteriorly.

2. *Paratype.* Ventral valve strongly convex, the median longitudinal profile rising 7 mm. above the plane joining the anterior and posterior margins. The valve is evenly arched transversely, the lateral margins not being deflected at right angles as in the holotype dorsal valve. Length in plan 2·5 cm., and maximum width about 1·7 cm. Outline sub-triangular, but the lateral margins are not distinct in this specimen. Spondylium small, narrow, being 1 mm. wide at greatest breadth and 5 mm. long (outside measurements).

A narrow median septum extending anteriorly from the spondylium reaches 12·5 mm. along the profile of the valve, or 10 mm. in flat measurement. Specimens M.D.V. 46284 and 39222 show that the septum becomes higher in the middle; in the latter it is 4 mm. high. The costae commence fine and thin on the umbo, and gradually increase in size anteriorly, no intercalations or bifurcations being observed. This means that the young shell has quite a different appearance from that of the adult shell as far as ornamentation is concerned.

3. *Hypotypes.* Full description of the two dorsal valves is not necessary, they being included to illustrate growth stages. In specimen M.D.V. 46289B the septal plates are comparatively

thin and there are no callists. In the steinkern, the central part between the septa is on the same level as the impression of the shell floor. In M.D.V. 46293, however, the septa are thicker, and the callists have just begun to form. This stage is intermediate between that of the foregoing hypotype and that seen in the holotype. The three specimens are all about the same size, but there is a great difference in the character of the septa, and the degree of formation of callists. Specimen M.D.V. 46289A shows the nature of the external ornament.

On the specimen numbered M.D.V. 46252 there are the steinkerns of three ventral valves which provide three stages in the thickening of the internal plates, but the one chosen for illustration is marked with a black circle. The spondylial plates are thickened, and the median septum, instead of being a fine plate as in the paratype, is posteriorly 1·5 mm. thick at its base, and 1·5 cm. long. Specimen M.D.V. 46284 is the steinkern of a gerontic ventral valve showing an extreme of thickening of the spondylial and septal plates, and also markings on the ovarian areas consisting of elongate pustules. Two small teeth-like projections are present on the spondylial plates near where they unite with the median septum. They are apparently only developed to a recognizable degree in the older shells.

Comment. Chapman (1913) described a damaged steinkern of a dorsal valve (N.M.V. 12407) of this species as a ventral valve of *Conchidium knightii,* interpreting the septal plates as parts of a spondylium.

Notoconchidium thomasi is an index fossil in the Mt. Ida Beds, and was so used by Thomas (1937) to define the "*Pentamerus* (*Conchidium*) Beds."

The new species is a typical *Conchidium* in so far that it has a strongly multicostate exterior, strongly biconvex valves, and a thick shell in the posterior region, but it contrasts with the genotype of that genus (*vide* Schuchert and Cooper 1932) in that—

1. The septal plates of the dorsal valve are not simply divergent as in *Conchidium*; they diverge then converge. It was this characteristic which caused Chapman to interpret them as part of a spondylium.
2. The postero-lateral callists of the dorsal valve are so strongly developed as to give a characteristic appearance to the steinkerns.
3. The spondylium is very short.
4. The valves are more or less equally convex.

5. The angular deflection of the lateral margins of the dorsal valve is a notable feature, being present even in comparatively young specimens. The younger ventral valves are arched fairly evenly in cross-section, but a degree of deflection is developed in older specimens.

Palaeoecology. The heavy shells and costate surface are features characteristic of inshore (Rhenish) facies brachiopods. The extra weight and the friction of the costae with the sediments helped to hold them in place on the sea floor in an area where water currents were rife. The thick quartzitic sandstones in which the fossils are found are formed from sediments likewise characteristic of that facies. The shells contrast with those of *Conchidium polymitum* recently described from an offshore (Bohemian) facies of Lower Devonian rocks in another part of Victoria (Gill 1949e). The nature and extent of the Tasman Geosyncline, in which these strata were laid down, have recently been discussed (Brown 1942, Gill 1949d).

Notoconchidium thomasi was a very successful brachiopod, judging by its prolific occurrence in the specimens of rock sent for examination.

Family RAFINESQUINIDAE Caster

NOTOLEPTAENA gen. nov.

Diagnosis. Convexi-concave rafinesquid brachiopods with valves geniculated anteriorly and laterally, the dorsal valve being the more strongly geniculated. Ventral valve with tongue on anterior margin, and dorsal valve with accommodating recess. Ornamentation radially multistriate with concentric wrinkles on both the posterior and the geniculated parts of the valves. Ventral valve with high, smooth palintrope, while that of the dorsal valve is linear. Ventral and dorsal muscle fields of leptaenid type, with associated marginal ridges. Large bilobed cardinal process.

The new genus is readily recognized by the presence of the tongue (*die Zunge* of the German literature).

Taxonomy. Although *Notoleptaena* has the cardinalia, musculature, "ornamentation" and other features like those in *Leptaena,* it is convexi-concave and not concavo-convex like *Leptaena.* If Schuchert's (1913) classification of the Strophomenacea, which made the form of the valves rather fundamental, be followed closely, then the convexi-concavity of the new genus is a matter of some taxonomic importance. But there is some doubt as to whether this feature is taxonomically quite so fundamental. For instance, Caster (1939, p. 26) writes: "It appears after a rather

careful study of the better part of the entire group as developed in the Western Hemisphere that, in this stock at least, the character of resupination is not so important as former classifications would imply. Schuchert and LeVene, 1929, for example, dissociated the strophonellids from the strophеodontids mainly on resupination, it would seem, and referred the former to the Orthotetinae, with which they seem to show, omitting reversed convexity, no major classifactory correlation. It seems to express relationship much better to place both groups in a common family and recognize the resupination as principally a subfamily, or even less significant characteristic in this stock. In the strophеodontids *Douvillina* and *Douvillinella,* the latter being resupinate, the character is apparently not of more than generic value."

Secondly, the tongue is a feature of taxonomic interest. This character appeared in a number of different evolutionary lines of Palaeozoic brachiopoda, and this frequent appearance and continuance must surely be evidence of its biological worth. It is further discussed in the section on palaeoecology. *Notoleptaena* is founded as a new genus largely, although not completely, on the presence of this tongue.

Etymology. The name of the new genus is compounded from the Greek word *notos* = south, and the well-known generic name *Leptaena.* The latter element is included because *Notoleptaena* shares so many features with *Leptaena,* and the former word is to indicate its connection with Australia. It is considered better than the prefix *austral,* since this term has been used for a palaeogeographical province, which does not include Australia.

The trivial name of the genotype is intended to draw attention to the biocharacter which is taxonomically important and probably was biologically important—the tongue (Latin *lingua* = tongue, *fero* = I carry).

Notoleptaena linguifera, gen. et sp. nov.

Pl. I, Figs. 16-23.

Material. 1. *Holotype,* consisting of the steinkern of a ventral valve in whitish or light-greyish sandstone with tinges of ferruginous stain (M.D.V. 39470) from locality 3, Parish of Dargile, in the Mt. Ida Beds (*Pleurodictyum* Beds). Pl. I, figs. 16-17.

2. *Paratype,* consisting of the steinkern of a dorsal valve (M.D.V. 39477) in the same matrix and from the same locality. Pl. I, figs. 20-21.

3. *Hypotypes* as follows: (a) External mould and steinkern (M.D.V. 39480A and 39480B respectively) of a ventral valve to

show the nature of the "ornamentation." Only the former is figured (Pl. I, fig. 18). Same locality and matrix. (b) Steinkerns of two dorsal valves (M.D.V. 39469B) from the same locality and in the same matrix to show cardinalia and muscle field (Pl. I, figs. 19, 22-23).

Descriptions. 1. *Holotype.* Ventral valve large, sub-quadrate in outline, measuring 3·4 cm. wide and 2·5 cm. long. Hingeline straight; palintrope smooth (as far as can be judged from the impression in the sandstone matrix) and a little over 1 mm. high in the middle as preserved, but this is not the full height, part having broken away. Another specimen of about the same size and on the same slab indicates that the palintrope would be about 2 mm. high when complete, narrowing towards the cardinal extremities. The plane of the palintrope makes an angle of about 45° (judged by eye only) with the plane of the valve. Projections of the hingeline and lateral margins of the valve would make right angles, but the actual cardinal extremities are well rounded.

The anterior margin possesses a tongue which is at right angles to the postero-central part of the valve. The lateral margins are deflected ventrally, i.e., the opposite direction from that of the tongue.

On the interior of the valve the lateral margins are differentiated by a border half a centimetre wide which is delimited on the inner edge by a strong ridge or diaphragm such as has often been described for the ubiquitous "*Leptaena rhomboidalis.*" From the cardinal angles, the lateral margins begin to rise slowly in a ventral direction, then at about 1·3 cm. from the hingeline they rise suddenly so that in about half a centimetre the differentiated border stands at right angles to the general plane of the valve. At the front, the border is deflected dorsally to follow round the margin of the tongue.

The muscle field is of the typical leptaenid type, being deeply excavated, flabellate, and surrounded by a high and sharp ridge. Posteriorly this ridge merges with the teeth bases, but becomes less defined before doing so. The field is 1·3 cm. long and the same wide, including the ridges. The outline is broadly V-shaped posteriorly and rounded anteriorly. The umbo is well defined but not pronounced. On each side of it are the teeth, which are strong, divergent, and with bases of triangular outline.

A median septum divides the muscle field. About a third of its length from the umbo, the septum suddenly thickens, then thins out comparatively slowly towards the anterior margin of the field. This specialization in the septum was no doubt connected with

the attachment of the adductor muscles. Where the septum crosses the ridge bounding the muscle field, there is a localized thickening. The septum continues less strongly towards the anterior end of the valve, fading out where the valve is geniculated. This continuation of the median septum beyond the muscle field does not appear in all specimens, and is probably a gerontic feature.

Faint traces of the radial striae and concentric rugae of the exterior surface show on the steinkern.

2. *Paratype.* Dorsal valve 3·6 cm. wide and 2 cm. long; the geniculated part of the valve is about 1.4 cm. deep. The nature of the recess for the tongue in the anterior margin is shown by Pl. I, fig. 20; it is about 1·5 cm. wide. There is a differentiated lateral border marked by a ridge on diaphragm as in the ventral valve, but it is not quite complete in this specimen (M.D.V. 39477).

The musculature is of the leptaenid type. The muscle field is surrounded by a callosity consisting of a low broad ridge and not of a sharp ridge as in the ventral valve. The adductor muscle seats are excavated, though not as deeply as the diductors of the ventral valve. Anterior to these are two smaller scars. The median septum widens posteriorly to merge with the cardinalia. While in the field of the large adductors, the septum is relatively broad, but anterior to that it is narrow; it extends anteriorly as far as the point of geniculation.

Traces of the radiating striae and concentric rugae of the exterior surface appear in the steinkern both on the posterior part of the valve and on the geniculated part.

3. *Hypotype* (a). An external mould (M.D.V. 39480A), which has a counterpart steinkern (M.D.V. 39480B), is presented as a hypotype to demonstrate the nature of the prosopon. This is not well preserved owing to the coarse arenaceous type of matrix. However, there are radially disposed striae occurring 30-40 per cm., of rounded cross-section, and with interspaces of approximately the same width as the striae. Concentric rugae of low elevation occur both on the near-planate part of the valve and on the geniculated part.

The mould also reveals a slight flexure of the shell, consisting of a median fold with a faint sinus on each side. There is evidence of a corresponding flexure in the dorsal valve.

Yet another feature shown by this holotype is multitudinous minute pillars of secondary mineral, indicating the pseudopunctate character of the shell.

4. *Hypotype* (b). This is presented to show the nature of the cardinalia (M.D.V. 39469B). The median septum merges

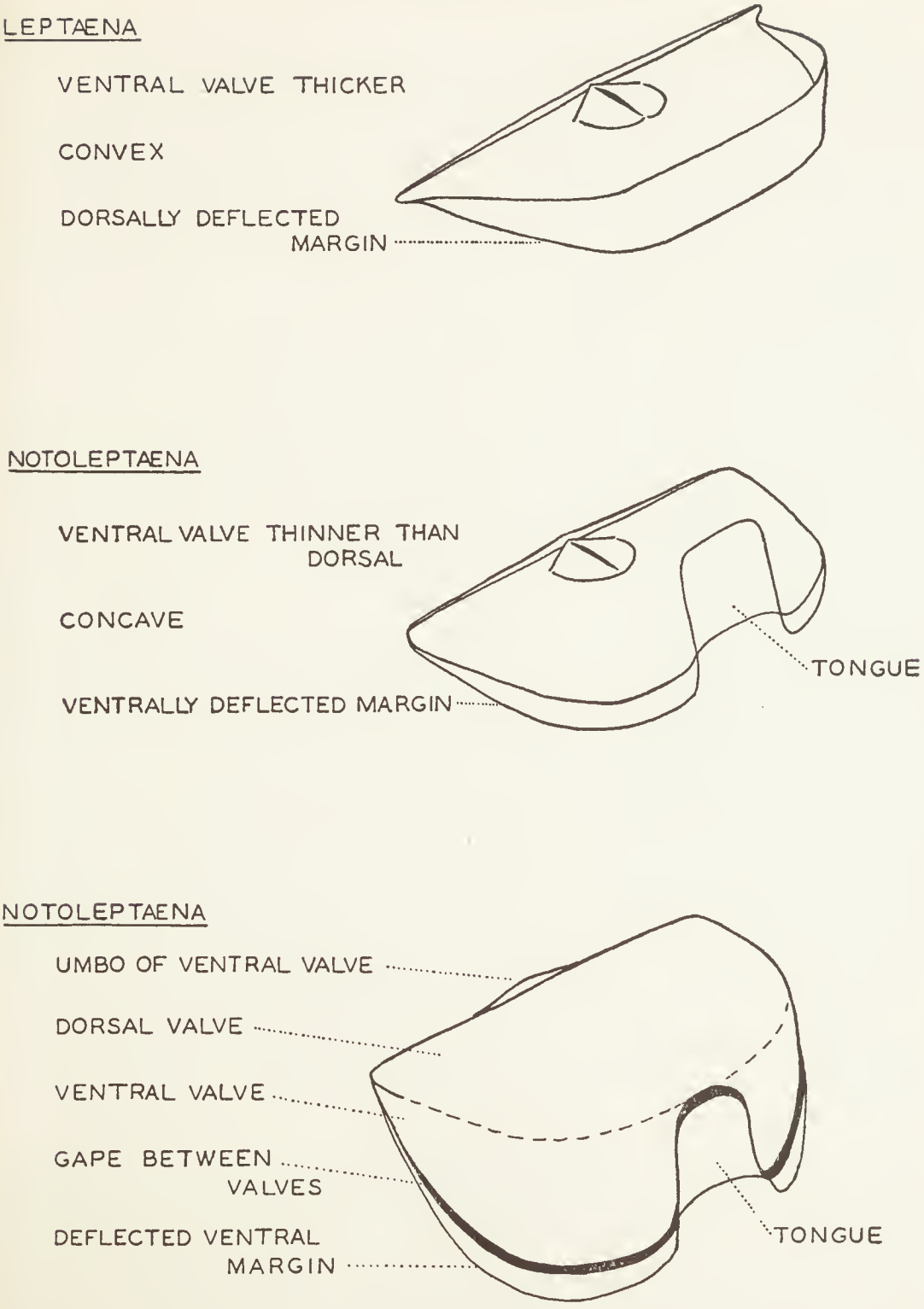

FIG. 1.

Diagrams showing nature and relationships of valves. (a) Ventral valve of *Leptaena*. (b) Ventral valve of *Notoleptaena*. (c) Ventral and dorsal valves together in *Notoleptaena*.

posteriorly into a large crural platform. Antero-lateral extensions thereof form an angle of about 90°, and outline the posterior edges of the sub-flabellate adductor scars. The large cardinal process is also merged with the crural platform, and it possesses two big prongs which jut ventrally more or less at right angles to the plane of the platform, and are very close together. The cardinal process extends a little beyond the hingeline. The palintrope is linear. Dental sockets occur on each side of the crural platform, and are of such size and shape as to accommodate the triangular teeth of the ventral valve.

The steinkern provides evidence of a low median sinus or flexure; this is to be seen also in specimen M.D.V. 39474.

On the same piece of rock as the hypotype just described is another dorsal valve in the form of a steinkern. It is a gerontic specimen with a recess for a large tongue, and with a high degree of secondary calcification of the diaphragm. The differentiated border is strongly developed. The external mould of this valve can be seen on specimen M.D.V. 39469A.

Palaeoecology. 1. *Relationship of Valves to each other.* In *Notoleptaena* the dorsal valve is the deep one, and the ventral the shallow one, a character in which it contrasts with *Leptaena.* The dorsal valve in *Leptaena* is like a lid to the ventral box, but the opposite is the case in *Notoleptaena* (contrast *b* and *c* in fig. I).

Moreover, the ventral valve is geniculated dorsally in *Leptaena*, but ventrally in *Notoleptaena* (leaving the tongue out of consideration, since this is a special structure). Thus instead of deflecting to meet the opposing valve, the edges of the ventral valve in the new genus turn towards the sea-floor. The edges therefore tend to lift the anterior part of the valve above the level of the sea-floor. It is said "tend," because the degree to which this elevation is effected will depend on the degree to which the edges sink into the sea-floor. In *Leptaena* the heavier valve is underneath, but in *Notoleptaena* the heavier valve is on top. This is assuming that the shells of both genera rested on their ventral valves.

2. *Relationship of Shell to Sea-floor. Leptaena rhomboidalis* was presumably so named because of its rhomboidal outline. Being without a functional pedicle (Arber 1939, 1940), the shell lived on the mud or sand of the sea-floor. The rugae would help hold the shell in position, as also would the rhomboidal outline of the shell. Lamont (1934, p. 167) observes: "If we take *L. rhomboidalis,* we find that the concentric folds on the ventral valve are most pronounced at points immediately behind the line of

geniculation. In this position no doubt they would help to maintain the stability of the shell on a muddy or sandy sea-floor. When the centre of gravity of the organism was changed and weight added posteriorly by the raising of the upper valve, these corrugations would be a means of preventing the ventral valve from sliding forward and sinking along the hinge-line. Such sinking, if it took place, might have allowed the ingress of foreign particles at the posterior angles. In some of the less transverse forms of *L. rhomboidalis* the rugae are particularly strong on the lateral parts of the shell. The writer correlates this with the fact that the more equi-dimensional shells would have a greater tendency to upset in a sideways fashion. From this argument it will be seen that, while rugae on the lower valve serve primarily to maintain stability, the final explanation lies in the principle of the exclusion of foreign material.''

Notoleptaena linguifera shared with *Leptaena* the advantages of rhomboid outline and rugose shell, only the latter feature was more extensive in *Notoleptaena,* the rugae appearing on the geniculated parts of the valves as well as on the non-geniculated areas.

When the valves of a strophomenoid shell were parted to admit water for respiration and nourishment, they were in contact at the hingeline whence the valves were parted in progressively greater measure to the anterior margin, where the maximum gape occurred. It was important to protect the animal from foreign bodies, and the greatest danger from these was along the anterior margin where the gape was greatest. If the margin could be lifted from contact with the sea-floor, there was less danger because clearer water was drawn in. This was attained in various ways which may be grouped in two categories:

(a) *Means of attachment,* e.g., pedicle, cementation, spines (Gill 1949d);
(b) *Means of elevation from sea-floor,* e.g., thickening of a valve (*Richthofenia*), shape of the valves.

In the last group come *Leptaena* and *Notoleptaena.* The former achieved elevation of the anterior margin by geniculation of the ventral valve. The latter genus achieved the same end, to a less extent probably, by the ventrally directed flanges of the ventral valve.

It is assumed in the foregoing discussion that these brachiopods had their ventral valves on the sea-floor, but this is not necessarily so. Lamont (1934, p. 180) claims that ''the Strophomenacea in general had the convex valve downwards; this is true of *Sower-*

byella, Leptelloidea, Leptaena, Rafinesquina, Stropheodonta, Christiania, Chonetes, etc., but *Strophomena* and *Schuchertella* rested upon the convex dorsal valve." However, even if *Notoleptaena* lived resting on its dorsal valve, the anterior margin would still be elevated above the sea-floor because of the strongly geniculate nature of the dorsal valve. But it should be remembered that the presence of the tongue in the anterior margin of *Notoleptaena* had the effect of lifting most of it above the sea-floor. This, combined with the effect of the downward turned ventral margins, leaves no need to postulate that *Notoleptaena* lived the other way from that of *Leptaena.*

3. *The Tongue.* A characteristic difference between *Leptaena* and *Notoleptaena,* and apparently a biologically significant one, is the presence of a tongue in the latter. Specimens of *Leptaena* have been described which have not a straight or evenly rounded anterior margin. For instance, Davidson (1865, Pl. XV) figures specimens of *L. rhomboidalis* with one (fig. 45) or more (fig. 46) shallow sinuses in the anterior margin. Other specimens, like the one figured in Zittel (1913, p. 384), show a slight fold.

It should be noted that a tongue is a different structure from the median fold and sinus, although the two are commonly associated. For example, some species of *Chonetes* (Gill 1945b) have median folds, but no tongue. Conversely, the tongue may be present but no fold and sinus structure, as Dr. Herta Schmidt (1937) has pointed out in her study of the morphogeny of the Rhynchonellidae. Dr. Schmidt also comments that the tongue structure is not yet fully understood. She says that the ecological significance of the tongue structure is clear in that in many cases the edge aperture is thereby increased in length. In a shell so equipped, a smaller gape will admit the same amount of water in unit time as a wider gape in a rectimarginate shell. The smaller gape will exclude foreign bodies which the wider gape would admit.

But as Schmidt indicates, this advantage does not accrue to the forms which have a tongue with sides at right angles to the general valve margin—in which class *Notoleptaena* falls. In such cases, the tongue slides up and down the sinus like a sleeve valve, so that when the shell valves part there is no aperture along the sides of tongue. The aperture then consists of three separated sections—the two lateral parts, and that at the tip of the tongue. The total length of these three secions is approximately the same as that of a shell without a tongue, i.e., rectimarginate. Schmidt therefore correctly infers that if there is an ecological significance in the tongue structure, it probably lies in its tripartite division

of the shell aperture. She suggests that incurrent streams flowed through the side openings and an excurrent stream through the middle opening, or *vice versa*. By such regulation, the streams are made stronger, and so the supply of food and oxygen enriched. The function of the tongue structure is thus somewhat analagous with that of the siphons in lamellibranchs. Where fold and sinus are present, they would support the function of the tongue structure as a stream regulator.

It appears to the writer that there is some ecological significance in the great length of the tongue as seen in *Notoleptaena*. Once a tongue is formed in such a way as to establish stream regulation, why should it be elongated until, as in *Notoleptaena* (Pl. I, fig. 26) it is over a centimetre long, i.e., more than half the length of the flat part of the valve? One would expect to find some ecological significance in the elongated tongues, since they appear and are maintained in different evolutionary lines. I suggest that there was a biological advantage in that the longer the tongue, the greater was the separation of the incurrent and excurrent streams, and so the less the danger of re-entry of ejected waters. If and when such re-entry occurred, it would mean—

(a) Reduction in amount of oxygen available per unit quantity of water, because oxygen had already been withdrawn from it. The effect would be analagous to our breathing "bad air" —our own or someone else's breath.
(b) Reduction in amount of food available per unit quantity of water, because food had already been gathered from that water.
(c) Increase in amount of any toxic excretory substances per unit quantity of water.

All these things would be biologically disadvantageous, and their avoidance a relative biological advantage.

4. *Gerontic Features.* There is but a limited amount of material from which to study the new genus, but what is present shows that with age—

(a) The shell becomes thicker through the deepening of the dorsal valve, and the accentuation of the ventrally directed flanges on the ventral valve.
(b) There is much secondary calcification, chiefly in the ridges bordering the muscle fields and the diaphragm. There is increased differentiation on the inside of the lateral and anterior border of the valves described above.

Occurrence. *Notoleptaena linguifera* has been noted in specimens from localities 3 (holotype) and 2D (M.D.V. 39190), Parish

of Dargile; also localities 32A (M.D.V. 47251) and 54 (M.D.V. 47197), Parish of Redcastle. Those from the latter parish are much smaller specimens and with better material may prove to be taxonomically distinct.

Age. Lower Devonian.

Notoleptaena otophera sp. nov.

Pl. I, Figs. 24-27.

Type Material. 1. *Holotype* consisting of the steinkern (N.M.V. 14687) and external mould (N.M.V. 14688) of a ventral valve in buff siltstone from Syme's Homestead, Killara, Victoria (for locality map see Gill 1945).

2. *Hypotype* consisting of the steinkern of another ventral valve (N.M.V. 14689) from the same locality.

Occurrence. Although a great deal of material from Syme's Homestead has been examined, only the figured specimens and some fragments of *Notoleptaena otophera* have been found. It is therefore not common. A smaller specimen referable to the same species has been collected from Syme's Tunnel, Killara (N.M.V. 14690). From Ruddock's Quarry in the Lilydale area (for locality map see Gill 1941) a specimen referable to the genus, but not specifically determinable at present, was collected by Mr. F. A. Cudmore (N.M.V. 14691). A ventral valve of *Notoleptaena* (counterparts N.M.V. 14708-9) was collected by the author from the limestone outcrop on Cemetery Hill Road, west of Whittlesea. It is notable in that radial costellae are absent.

Etymology. The trivial name of this species is derived from the Greek *ous, otos* = an ear, and *phero* = I carry, a reference to the auriculate nature of the cardinal extremities.

Descriptions. 1. *Holotype* ventral valve sub-semicircular in outline except for the auriculate cardinal extremities. Greatest width 4·5 cm. (calculated from the complete side), greatest length of planate part of valve 1·5 cm., and length along midline 1·4 cm. Hingeline long and straight, palintrope smooth and 1 mm. high as preserved on the external mould, but it was higher than this in the middle, probably about 2 mm. Palintrope narrows towards cardinal extremities. It is approximately at right angles to the planate part of the valve in the holotype, but sloping outwards slightly in the hypotype. Very fine growth lines are present on the palintrope parallel to the hingeline. The cardinal extremities are auriculate, and extend over half a centimetre beyond the semicircular part of the shell; their terminations are rounded.

The anterior margin possesses a tongue which is at right angles to the planate part of the valve. If the shell is viewed in plan, the line where the valve geniculates to form the tongue is incurved. A specimen of *"Leptaena rhomboidalis"* in the National Museum from Cooper's Creek, five miles S.W. of Walhalla (N.M.V. 671-2 counterparts) has a similar sinus in the geniculated part of the ventral valve, but without the formation of a tongue. The tongue in the holotype of the new species is 1·4 cm. wide and 1 cm. long. The sides are parallel, and the anterior margin only slightly curved.

The lateral margins of the valve are deflected nearly at right angles in the opposite direction to the tongue, i.e., ventrally, for a distance of about 3 mm. The "ornamentation" on the exterior of the valve consists of fine, somewhat irregular, concentric rugae, and of slightly sinuous radiating striae of a frequency of 25-30 per cm. Fine growth lines can also be seen. They suggest that the auriculations on the cardinal extremities were not present in youth, but developed with adult growth. There is a slight sinus down the middle of the valve.

The muscle field is of leptaenid type, deeply excavated, and with a strong bounding ridge. Anterior to the field is a very fine and faint median septum, but this cannot be seen in the hypotype. Fine radiating ridges occur on the diductor scars. Teeth strong, diverging, sub-triangular in cross-section, and vertically finely serrated on the outer edges, which are below the palintrope, but more or less in the same plane. The serrated area is 1·5 mm. long, and has about 18 serrations. The significance of this feature is discussed below.

Interior of valve finely papillate—closely in the area surrounding the muscle field and less so outside that.

2. *Hypotype* shows the full height of the palintrope. The ridges described for the holotype diductor field are almost absent in this specimen. The papillation of the interior of the valve is shown well, and some of the pallial sinuses can be recognized.

No dorsal valve of this species has yet been found.

Palaeoecology. In addition to the features already discussed relative to the genotype, there are specializations in *N. otophera* whereby it was adapted to the ecological conditions in which it lived. The general character of those conditions has been described elsewhere (Gill 1949a). The generally lighter build of *N. otophera,* compared with that of *N. linguifera,* matches its quieter environment. The auriculate cardinal extremities, on Lamont's (1934, p. 166) interpretation, are also an adaptation to a muddy sea-floor,

being "in response to the necessity of warding off silt from the lateral edges of the opening shell."

Relationships. In general structure, *N. otophera* is very close to that of *N. linguifera,* and so is included in the same genus. It possesses the tongue and the ventrally deflected margins which are so characteristic of the new genus. *N. otophera* differs in the generally lighter construction, presence of auriculate cardinal extremities, and teeth of slightly different shape and possessing a row of serrations. I regard the two species as isochronons occupying differing facial environments, *N. linguifera* belonging to the sandy facies and *N. otophera* to the muddy facies.

A taxonomic problem is posed by the presence of crenulations in the latter species. Of such I can find no evidence in *N. linguifera.* The matrix imposes limitations on the preservation of such fine structures, but they are seen on the margins of other strophomenids, and there was ample material for examination. *Amphistrophia* has small crenulated plates, but the shells are small, have a costellate-striate ornamentation without concentric rugae, and the ventral muscle field has no strong delimiting ridge as in *Leptaena* and *Notoleptaena. Cymostrophia* possesses rugae and a partly crenulated hinge, but the teeth files are longer and imposed on the palintrope (not limited to small plates below the hingelines as in *N. otophera*) ; also, the ornamentation is intercalated, and the rugae are interrupted to give a "seersucker" effect.

From Bohemia, Barrande described *Leptaena bouei* (Haidinger 1848, Barrande 1879) which, although different from *Notoleptaena* morphologically, shows ecological accommodations. Firstly, there are strong lateral flexures of the shell which are so pronounced that they would function like the reflexed ventral margins of *Notoleptaena* for holding the shell in place on the sea-floor. Secondly, the middle of the anterior margin is flexed strongly in a dorsal direction, i.e., in the opposite direction from the flexures just described, so that a tongue-like emargination is effected. The flexure would raise the anterior aperture above the sea-floor, and also increase the apertural length so that an opening smaller than otherwise necessary would suffice for respiration and feeding, but without admitting foreign bodies which could enter by the larger aperture. *Leptaena bouei* is found not only in Bohemia but also in the Lower Devonian of Western Europe (e.g., Haüsel and Richter 1936, Mailleux 1941).

Barrande (1879) also described *Strophomena emarginata,* a brachiopod possessing a tongue in its anterior margin. Kozlowski (1929, a work I have not been able to see) referred the species to *Leptaena,* though not without doubt. Kozlowski is quoted

in extenso in Northrop (1939), who refers Barrande's species to *Amphistrophia*. Northrop's comments were *à propos* his *Amphistrophia peroccidens*, which also has a tongue structure. Barrande stressed that *S. emarginata* developed its emargination only as a feature of the full-grown shell. He stated (p. 53): "L'échancrure du bord frontal est le principal charactère distinctif de cette espèce. Mais il faut remarquer qu'il n'est bien prononcé que dans les adultes. Il ne se manifeste pas dans les jeunes, ni dans les individus d'un âge moyen."

Kozlowski compared his *Leptaena emarginata* with *L. caudata* (Schnur 1854), which Reed (1908) referred to *Strophonella* and Mailleux (1941) to *Stropheodonta*.

Study of the above forms may reveal relationships with the new genus *Notoleptaena*.

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Description of Plate I

Fig. 1. *Notoconchidium thomasi,* gen. et sp. nov. Steinkern of ventral valve viewed from above. Paratype, M.D.V. 39094.
Fig. 2. Same specimen. Umbonal view to show spondylium.
Fig. 3. *N. thomasi.* Steinkern of ventral valve viewed from above. Hypotype M.D.V. 46252. Figures 1-7 illustrate the progressive thickening during growth of the spondylial walls and median septum. Figures 3-4 illustrate the intermediate stage.
Fig. 4. Same specimen. Latex impression.
Fig. 5. *N. thomasi.* Ventral view at gerontic stage showing maximum thickening of spondylial walls and median septum. Hypotype M.D.V. 46284 photographed from above.
Fig. 6. Same specimen. Umbonal view.
Fig. 7. Same specimen. Latex impression.
Fig. 8. *N. thomasi.* Steinkern of dorsal valve, viewed from above. Hypotype M.D.V. 46289B. Figures 8-15 illustrate the progressive thickening of septa during growth, and the accumulation of callus deposits laterally to them.
Fig. 9. Same specimen. Latex impression.


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Fig. 10. *N. thomasi.* Steinkern of dorsal valve viewed from above. Hypotype M.D.V. 46293.
Fig. 11. Same specimen. Latex impression.
Fig. 12. Same specimen. Umbonal view of steinkern.
Fig. 13. *N. thomasi.* Steinkern of dorsal valve viewed from above. Holotype M.D.V. 46315.
Fig. 14. Same specimen. Latex impression.
Fig. 15. Same specimen. View of steinkern from side.
Fig. 16. *Notoleptaena linguifera,* gen. et sp. nov. Steinkern of ventral valve viewed from above. Holotype M.D.V. 39470.
Fig. 17. Same specimen, viewed at an angle to show the deflected valve margin and the median sinus.
Fig. 18. *N. linguifera.* Hypotype 39480A. External moulds of two ventral valves to show fine costellation and rugae.
Fig. 19. *N. linguifera.* Steinkern of dorsal valve viewed from above. Hypotype M.D.V. 39469B.
Fig. 20. *N. linguifera.* Steinkern of dorsal valve, anterior view. Paratype M.D.V. 39477.
Fig. 21. Same specimen viewed from above.
Fig. 22. Enlargement of cardinalia of Fig. 19.
Fig. 23. *N. linguifera.* Side view of steinkern of dorsal valve on specimen 39469B. Note thickened margin, median sinus, median septum, and muscle field.
Fig. 24. *N. otophera,* sp. nov. Steinkern of ventral valve viewed from above. Holotype counterpart, N.M.V. 14687.
Fig. 25. *N. otophera.* External mould of ventral valve, and counterpart of Fig. 24. Holotype, N.M.V. 14688.
Fig. 26. *N. otophera.* Anterior view of holotype steinkern, N.M.V. 14687. Compare Fig. 24. Note anterior tongue.
Fig. 27. *N. otophera.* Steinkern of another ventral valve viewed from above. Hypotype, N.M.V. 14689.

Note. All figures are natural size except Fig. 22, which is enlarged one half.