A NEW SILURIAN ECHINOID GENUS FROM SCOTLAND

by PORTER M. KIER

ABSTRACT. A new genus and species of echinoid, *Aptilechinus caledonensis*, is described from the Silurian (Llandovery) of Scotland. This species, the sixth known from the Silurian, is a flexible echinoid belonging to the family Lepidocentridae. It is unusual in having its largest spines attached to the ambulacra.

A NEW Silurian echinoid is described from the Pentland Hills of Scotland. This discovery is of great importance because of the rarity of echinoids of this age, and the sweeping evolutionary changes which were occurring in echinoids during this time. Only five Silurian echinoids are known: *Echinocystites pomum* Thomson, *Myriastiches gigas* Sollas, and *Palaeodiscus ferox* Salter from Great Britain, *Gotlandechinus balticus* Regnéll from Sweden, and *Koninckocidaris silurica* Jackson from the United States. The addition of the sixth adds considerably to our understanding of the evolution of these primitive species.

Although the specimens are preserved as moulds and are flattened, many minute details of their tests are visible. The most unusual morphological feature, one that would have given it a most 'peculiar' appearance in life, as reconstructed on text-fig. 4, is the presence of the largest spines on the ambulacra, and their absence on most of the interambulacral plates. One of these spines occurs beside each porepair; with presumably a function of protecting the tubefeet from predators. A few of the more adoral of these spines could have been used for locomotion, but probably the echinoid 'walked' mainly on the numerous peristomial spines.

Structurally, *Aptilechinus* possesses many of the characters which would be expected in a Silurian echinoid according to the evolutionary trends described by Kier (1965) for these flexible echinoids. The ambulacra are not expanded adorally, and the porepairs are near the perradial suture as typical in Silurian flexible echinoids. The radial water vessel is covered, as in many early Paleozoic echinoids, but it lacks the groove on the exterior along the perradial suture found in most of the other Silurian echinoids. The regularity of the shape of its plates coincides with that found in some other Silurian echinoids such as *Koninckocidaris* and *Myriastiches*, and its small, high test with few plates is typically primitive.

There appears to be in this genus only a single genital plate lacking genital pores. Although the apical area is not well preserved in any of the specimens, enough of the area is visible on several specimens to convince me that only one genital plate was present. Thus the absence of the other four genital plates and the lack of genital pores in the single madreporitic-genital plate is to be expected in echinoids from the Ordovician and Silurian. The Ordovician genera *Aulechinus*, *Ectinechinus*, and *Eothuria* have only one genital plate with no genital pore as does the Silurian *Echinocystites*. The apical system is not known in the Silurian *Myriastiches*, and the apical system is not clear in *Palaeodiscus*. According to Jackson (1912, p. 286, pl. 20, fig. 5)

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there is more than one genital plate in the Silurian *Koninckocidaris silurica* Jackson, but this figure shows no genital pores. However, this species is based on only a fragment showing the interior, and until this specimen has been found and re-examined, the presence and character of these genital plates is not certain. The earliest echinoid which definitely has more than one genital plate is the Devonian *Lepidechinoides whitnalli* in which Cooper (1931, p. 138) found a genital plate at the head of each interambulacrum, and each genital plate had numerous genital pores. This is also the earliest known Paleozoic echinoid that has genital pores. Therefore, it is apparent that the development of genital pores and more than one genital plate in the Paleozoic echinoids occurred at some time in the Silurian or Devonian.

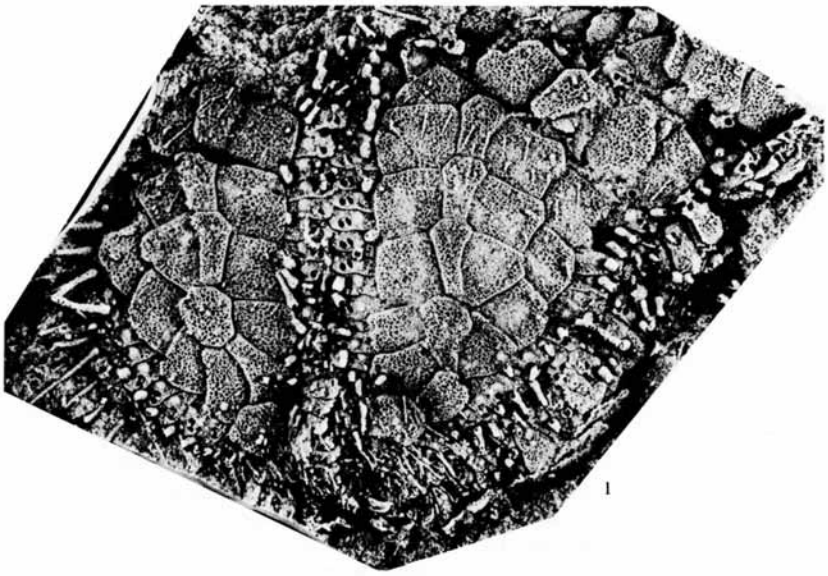
Stratigraphical and geographical occurrence of echinoids. These specimens were collected by Mr. David Hardie from Silurian rocks of the Pentland Hills, Midlothian, Scotland and purchased by the Royal Scottish Museum in Edinburgh in 1897. They are labelled 'Starfish Bed', Gutterborn Burn, Pentland Hills. Dr. Robin Cocks of the British Museum (Natural History) has examined the material and believes that the locality data are correct, and states that these beds belong to the *crenulata* Zone, which is latest Llandovery (Cocks, Holland, Rickards, and Strachan, 1971, fig. 9). The beds and their fauna have been described by Lamont (1947, pp. 193–208, 289–303), who later (1952, p. 27) proposed that they be referred to a new division of the Silurian System called 'Pentlandian'. He also considered them to be Gala-Tarannon (equivalent to latest Llandovery) in age.

Order ECHINOCYSTITOIDA Jackson
Family LEPIDOCENTRIDAE Lovén
APTILECHINUS gen. nov.

The test is flexible, composed of regularly shaped plates with the interambulacral plates imbricating adapically and laterally, and the ambulacral plates imbricating adorally and under the interambulacra. The apical system has one genital plate lacking genital pores and there are five ocular plates. The ambulacra are composed of two columns of plates in each area, and do not broaden adorally. The porepairs are situated near the perradial suture in well-developed peripodia. On the interior, each ambulacral plate has an elevated process forming an arched covering for the radial water vessel. The interambulacra are composed of four columns of regularly shaped plates. One large spine is attached to each ambulacral plate and to a few of the most adorally situated interambulacral plates. Small spines occur on the ambulacral and interambulacral plates, and pedicellariae were probably present. The surface of the plates are deeply pitted. The peristome is covered with many low, strongly imbricate

EXPLANATION OF PLATE 80

Figs. 1–3. *Aptilechinus caledonensis* sp. nov. 1, Adoral view of latex pull of RSM 1897.32.537A showing portion of two interambulacra and three ambulacra. Note small spines on some of the interambulacral plates, and larger spines on ambulacral plates, ×5. A drawing of the plate arrangement of this specimen is on text-fig. 3. 2, Side view of latex pull of RSM 1897.32.537B (holotype) showing presence of four columns of plates in each interambulacrum with the median column overlapping laterally the others, and the long ambulacral spines, ×5. A drawing of the plate arrangement of this specimen is on text-fig. 2. 3, Interambulacral plates of latex pull in fig. 2 showing the pitted surface of the plates, and the single protuberance or peg on each plate which probably served for attachment of a spine or pedicellaria, ×15.



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KIER, Silurian echinoid

ambulacral plates and a few interambulacral plates. Jaws, braces, and longitudinally ridged grooved teeth have been found.

Type species. Aptilechinus caledonensis sp. nov.

Comparison with other genera. This genus clearly belongs in the order Echinocystitoida because of its strongly imbricate plates with the ambulacral plates bevelling under the interambulacra and adorally over each other, and the interambulacral plates imbricating adapically. It is referred to the family Lepidocentridae because it has only two columns in each ambulacrum. *Aptilechinus* is easily distinguished from the Silurian genera of this family, *Palaeodiscus*, *Myriastiches*, and *Koninckocidaris*. *Myriastiches* has many more plates, lacks larger spines on the ambulacra, and has a much less developed covering over its radial water vessel. *Palaeodiscus* is easily distinguished by the external groove in its ambulacra, lack of covering over the radial water vessel, and wider ambulacra with lower plates, lacking larger spines. Too little is known of the Silurian species of *Koninckocidaris* to compare it with *Aptilechinus*. The holotype and only known specimen of *K. silurica* Jackson is a fragment showing only part of the interior of the test, and it is not possible from Jackson's figures to discern the character of the interior of the ambulacral plate. Unfortunately, this holotype is not at the University of Rochester, as reported by Jackson, and is presumably lost.

Aptilechinus differs from the Ordovician genera *Aulechinus*, *Ectinechinus*, and *Eothuria* in having more regularly arranged interambulacral plates, its porepairs more distant from the median suture, its pores completely divided from each other, and well-developed spines. It differs from the Devonian *Lepidechinoides* in having its radial water vessel covered, its porepairs much nearer the perradial suture, larger ambulacral spines, and smaller interambulacral spines. The Devonian *Albertechinus* and *Lepidocentrus* have primary tubercles on the interambulacra, and *Porechinus* is easily distinguished by its ambulacral plates which have the inner pore of each pair open.

Aptilechinus caledonensis sp. nov.

Material. The specimens are preserved as impressions in a silty shale whose grains are small enough to preserve minute details of the test. All the specimens are flattened, with the plates somewhat shifted but not disassociated. There are impressions of twenty-one specimens, six of which have been collected with their counterparts. Both the interior and exterior of portions of the echinoids are visible, but none of the calcite of the tests is preserved.

Presumably, the echinoids were covered and killed by the sediment in which they now occur. Although

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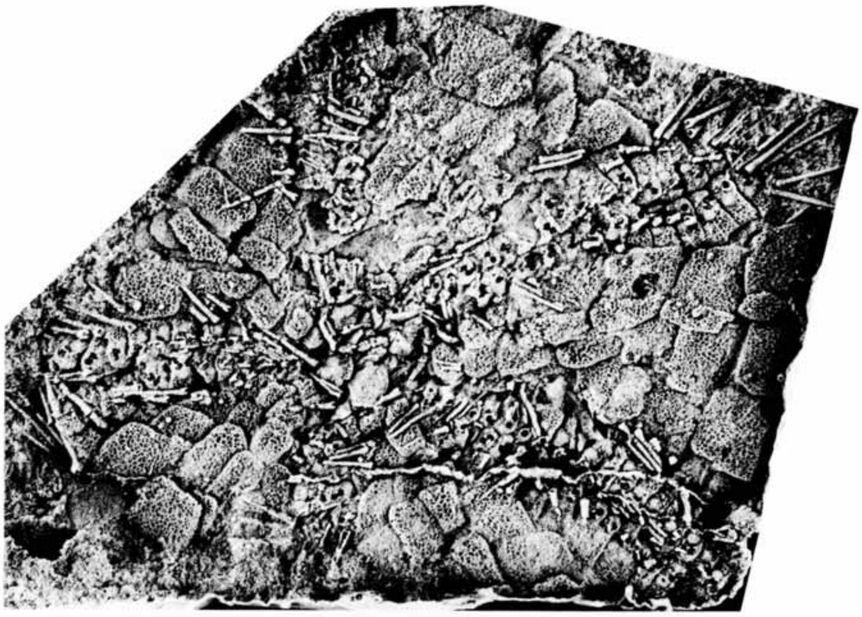
EXPLANATION OF PLATE 81

Figs. 1-3. *Aptilechinus caledonensis* sp. nov. 1, Adapical view of latex pull of RSM 1897.32.538B showing the small apical system. Several of the ocular plates are visible; the single large plate is probably the madreporite, ×5. 2, A brace on specimen in fig. 1, ×10. 3, View of portion of ambulacrum of specimen in fig. 1 showing position of porepairs near perradial suture, and greater height adradially of each plate when not overlapped by adjacent plates. Note long striated spines with deep concavity at their bases. These spines were evidently attached to the single nodes occurring on each ambulacral plate visible slightly adradial and adapical to the outside pore of each porepair, ×10. 4, Side view of latex pull of RSM 1897.32.551 showing two interambulacra and three ambulacra, ×5.



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KIER, Silurian echinoid

the spines have shifted slightly, they are still very near to where they were attached to the individual echinoid. Most of the ambulacral spines extend vertically from the ambulacra, showing that the echinoids were not disturbed after death by predators or currents.

Size. It is difficult to estimate the original size of the specimens because many are only partially preserved, and all are flattened. A rough estimate was possible on twelve of the twenty-one specimens, with the smallest estimated to have been 14 mm high, the largest 30 mm and the average 20 mm. These estimates are probably accurate to within 20%.

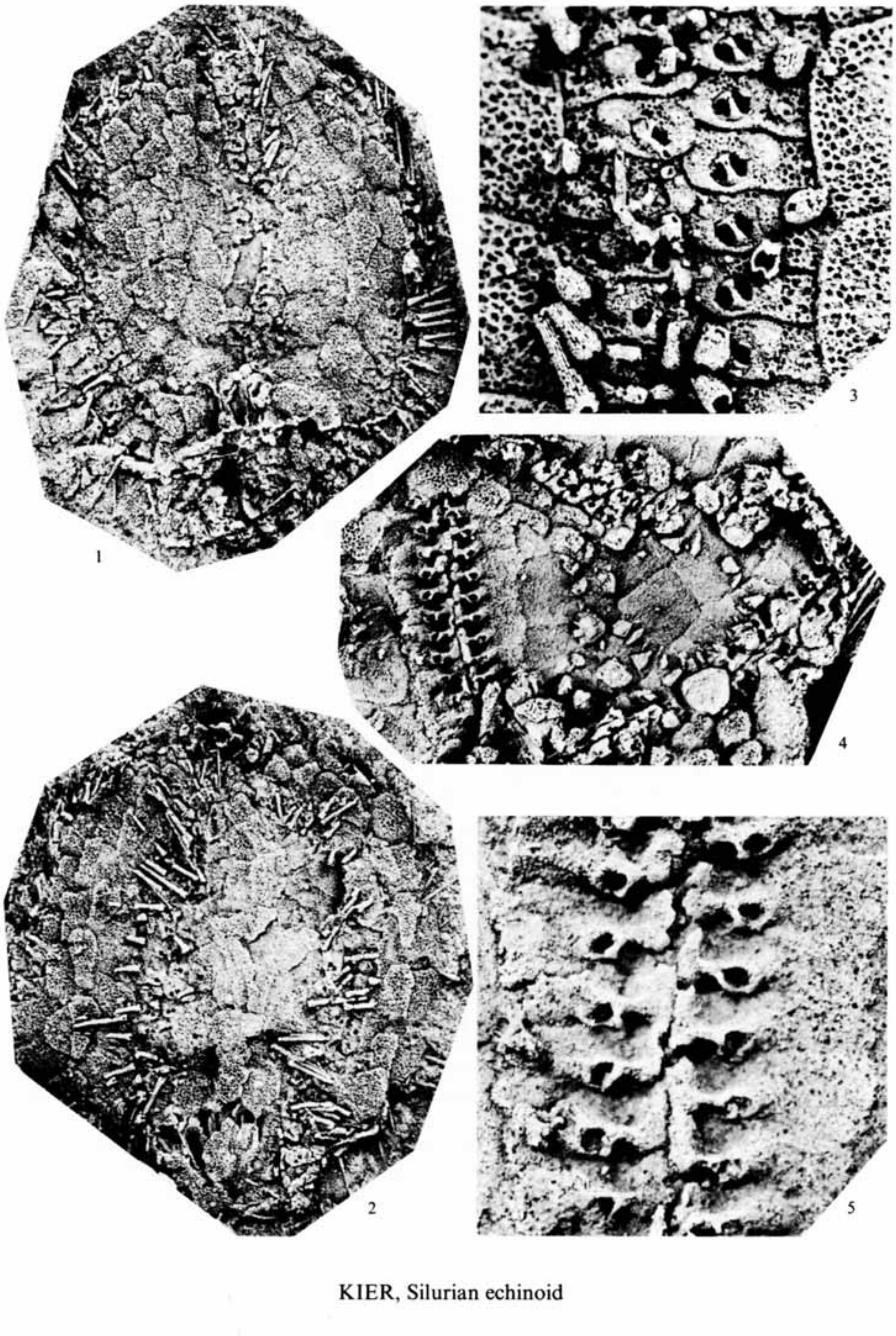
Shape. Three specimens are flattened sideways with little oblique distortion, therefore preserving what appears to be the original profile (Pl. 80, fig. 2; Pl. 82, figs. 1, 2). The test is higher than wide with a width approximately 80% of the height. A reconstruction of the original shape of the test is given on text-fig. 4.

Apical system. In none of the specimens is the apical system well preserved, but on three specimens portions of it are present. The system was very small, with a diameter equal to approximately 25% of the diameter of the test. There were five ocular plates but probably only one genital plate. Four ocular plates are preserved on specimen RSM 1897.32.5388 (Pl. 81, fig. 1). These plates are wider than high, approximately 1·1 mm wide, and have a smoothly curved dorsal margin, and a straight ventral margin. The dorsal part of the plate is thin with coarse-lattice structure, whereas the ventral part is thickened, prominently elevated, and lacks this coarse-lattice structure. A single indentation on the ventral portion of each plate may be the ocular pore. There is a single larger plate, 1·5 mm wide, on this specimen which is probably a genital plate and may be the madreporite. The indentations on the surface of this plate are smaller than the coarse-lattice structure on the interambulacral plates and are probably madreporic pores. No genital pores are visible. No similar plates are preserved on this specimen and probably this species, like the Silurian *Echinocystites pomum* Thomson, had only a single genital plate. Many small narrow angular plates occur in the centre of the apical system, and presumably they are the periproctal plates.

Ambulacra. The greatest width of each ambulacrum in specimens in which the plates are in position is 37–45% of the width of the interambulacrum. Each ambulacrum is approximately the same width above and below the midzone until near the apical system (Pl. 83, fig. 2) and peristome where they narrow gradually. Each has two columns of low plates (Pl. 82, fig. 3; text-fig. 2) which strongly imbricate adorally over each other, but are overlapped by the interambulacra. The height of each plate is approximately 40% of the width when the plates in proper position; the transverse

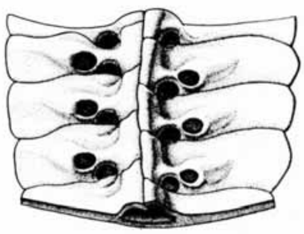
EXPLANATION OF PLATE 82

Figs. 1–5. *Aptilechinus caledonensis* sp. nov. 1, 2, Side views of latex pulls of RSM 1897.32.540B and 1897.32.540A in which most of exterior of the specimen is preserved, ×5. 3, Portion of ambulacrum of latex pull of RSM 1897.32.537A showing the well-developed peripodia, position of porepairs near perradial suture, imbrication of plates, and node for attachment of large spine, ×15. 4, View of interior of portion of test of latex pull of RSM 1897.32.552 showing the lack of pits on the inner surfaces of the plates and the interior structure of the ambulacrum, ×5. A more enlarged view of this ambulacrum is on fig. 5. 5, Interior of ambulacrum of specimen in fig. 4 showing arched covering over radial water vessel, ×15. A reconstruction of this structure is on text-fig. 1.



KIER, Silurian echinoid

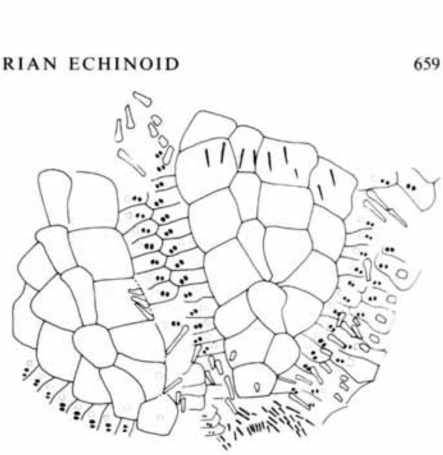
sutures are parallel. However, on specimens in which some of the ambulacral plates are isolated by post-mortem distortion and not overlapped by the adjacent interambulacra (Pl. 81, fig. 3), it can be seen that the ambulacral plates expand greatly in height adradially. When in proper position approximately 40% of the surface area of each ambulacral plate is covered by the overlapping interambulacral plate and adapical ambulacral plate. Due to the nature of the preservation, it is not possible to count the number of ambulacral plates in a full column on most of the specimens, but on two specimens a fairly accurate estimate can be made. One specimen, approximately 20 mm high has at least fifty plates in an ambulacrum (excluding the peristomial ambulacral plates), and another with a height estimated at 24 mm has sixty plates in an ambulacrum, plus another sixteen to twenty extending on to the peristome. The peristomial ambulacral plates are lower (Pl. 83, fig. 3) than the other ambulacral plates, more imbricate, and have peripodia approximately one-half as large. Approximately three ambulacral plates occur opposite each adjacent interambulacral plate. The porepairs are situated near the perradial suture (Pl. 82, fig. 3) approximately one-third the distance from the perradial to the adradial suture. The pores of a pair are oblique with the outer pore more adapical. This outer pore is narrower than its partner on some of the plates, but the same width on others, but this narrowing may be due to post-mortem distortion. The porepairs occur in well-developed peripodia (Pl. 82, fig. 3) with a high ridge separating the pores, and with a rim surrounding the porepair. This rim is absent on the adradial side of each outer pore but is well developed curving around the inner pore.



TEXT-FIG. 1. *Aptilechinus caledonensis* sp. nov. A reconstruction of the interior of part of an ambulacrum showing the arched covering which extends along the perradial suture, and served as a passageway for the radial water vessel.

Interior. The interior of each ambulacral plate has a prominent elevated process forming an arched covering extending along the perradial suture, and no doubt serving as a passageway for the radial water vessel (Pl. 82, fig. 5; text-fig. 1). A ridge extends transversely on each plate from this passageway and forms a high rim along the adapical edge of each porepair. This ridge extends approximately one-half the width of each plate. A deep depression occurs between this ridge and the adjacent porepair with a small gap extending from the inner pore and leading into the covered passageway presumably for the entrance of the side branch joining the tubefoot to the radial water vessel.

Interambulacra. Four columns of thin plates are present in each interambulacrum. They strongly imbricate adapically and laterally and are more or less regularly shaped. The median column (text-figs. 2, 3) is composed of narrower plates than in the other columns with a width equal to approximately only one-half the height. These plates are hexagonal with their greatest width adapical, and they imbricate laterally over the columns on their right and left. This median column varies in position on the same specimen and between different specimens. On some specimens (Pl. 81, fig. 1) all the median columns (as viewed from above) have two columns on the left of the



TEXT-FIG. 2. *Aptilechinus caledonensis* sp. nov. Plate arrangement of a latex pull of the holotype, RSM 1897.32.537B, showing four columns in each interambulacrum, two in each ambulacrum. The dotted circles on the ambulacral plates and a few of the adoral interambulacral plates mark the location of nodes where probably were attached the larger spines, $\times 5$. A photograph of this specimen is on Pl. 80, figs. 2, 3.

TEXT-FIG. 3. *Aptilechinus caledonensis* sp. nov. Plate arrangement of a latex pull of RSM 1897.32.537A showing adoral plate arrangement. Note the fragmental remains of the large spines which were attached to the ambulacral plates and a few of the adoral interambulacral plates. The dotted circles mark the location of nodes where these spines were probably attached, $\times 5$. A photograph of this specimen is on Pl. 80, fig. 1.

median column and one on the right, whereas in other specimens (Pl. 80, fig. 1) one interambulacrum has two columns on the right but another interambulacrum has one on the right.

The plates of the columns which border the ambulacra are less angular in outline and the edge of the plate which overlaps the ambulacra and adapical interambulacral plate is curved. Adorally, the first interambulacral plate is a single plate of the median column (Pl. 80, fig. 1; text-fig. 3), followed by two in the second row, three in the third, and four in the fourth. Approximately thirty-five plates are present in each interambulacrum with approximately ten plates in each column bordering the ambulacra. It is not clear how many interambulacral plates occur on the peristome.

Spines and tuberculation. One of the most unusual features of this echinoid is the presence of large spines on the ambulacra and their absence on the interambulacra, except on a few adoral plates. Two sizes of spines occur on the ambulacra. The largest are up to 3·4 mm long, gently tapering to a sharp point which is not preserved on most of the specimens. They are expanded near their bases where a deep concavity (Pl. 81, fig. 3) is present presumably for the insertion of muscle or ligament. These spines are longitudinally striated with approximately fifteen striations on each spine. One of the spines is attached to each ambulacral plate as indicated by the fact that the number of spines found on any specimen approximates but never exceeds the number of ambulacral plates. These spines were evidently attached to a single node that occurs on each plate slightly adradial and adapical to the outside pore of the porepair (Pl. 81, fig. 3; Pl. 82, fig. 3; text-figs. 2, 3). These nodes lack the coarse meshwork found on most of the surfaces of the ambulacral plates, and are simple protuberances lacking mamelons. The smaller spines are approximately one-third the size of the larger, are also striated and expanded at their bases, but the presence or absence of the basal concavity cannot be determined. The number of these smaller spines is not clear as most of them were removed during post-mortem sorting. However, they appear to have been attached to a single smaller node that occurs near the median suture adapical to the inner pore of each porepair (Pl. 82, fig. 3).

No large spines were attached to the interambulacra except adorally where a single large node similar to those found on the ambulacra is present on the first three plates of some specimens (Pl. 80, fig. 1; text-fig. 3) indicating that a large spine was attached there. Small spines approximately 0·9 mm long appear to have been attached to most of the interambulacral plates. They are slender, tapering to a sharp point, striated, and have expanded bases. I have not been able to find any nodes or tubercles for the attachment for these spines.

Many of the interambulacral plates bear a single protuberance with sharp sides and a flat upper surface. These pegs occur on the outer adapical corner (Pl. 80, fig. 3; text-fig. 2) of each plate except on the narrow median column where they occur on the middle of the adapical surface. They are approximately 0·2 mm in diameter. Similar but smaller pegs occur on the ambulacral plates (Pl. 82, fig. 3) with two to three on each plate, one between the porepairs and the adradial suture and two between the porepair and the median suture. Perhaps pedicellariae were attached to these pegs: several structures are present which appear to have been pedicellariae but they are too poorly preserved to be certain.

The peristomial region was covered with many small spines (text-fig. 3) which were attached to the narrow ambulacral plates which formed a very flexible surface extending between the end of the interambulacra and the mouth opening. These spines were attached to five or more nodes on each ambulacral plate.

Lantern. The lantern is not well preserved on any specimen, but enough of parts of it are visible on several specimens to show that the pyramids, braces, and teeth were well-developed. Although not enough of a pyramid is preserved on any specimen to be able to determine the depth of the foramen magnum, the height of the pyramid is estimated to have been approximately 2·7 mm. The pyramid appears to be small relative to a tooth which is at least 3 mm long and 0·7 mm wide. The tooth is grooved, and is typical of those found in Paleozoic echinoids. It has four to five longitudinal ridges (Pl. 83, fig. 3). The brace is likewise similar to those found in other Paleozoic echinoids, and is approximately 2·5 mm long, 0·9 mm wide, and expanded at its ends (Pl. 81, fig. 2).

EXPLANATION OF PLATE 83

Figs. 1–3. *Aptilechinus caledonensis* sp. nov. 1, Side view of latex pull of RSM 1897.32.543 showing most of length of two ambulacra with their long spines and part of the interior surface of the other side of the test showing the lack of pits on the interior surface of the plates, ×5. 2, Adapical region of latex pull of RSM 1897.32.541B, ×5. 3, Oral region of latex pull of RSM 1897.32.538A showing portions of pyramids, part of a striated tooth, and several peristomial ambulacral plates, ×10.

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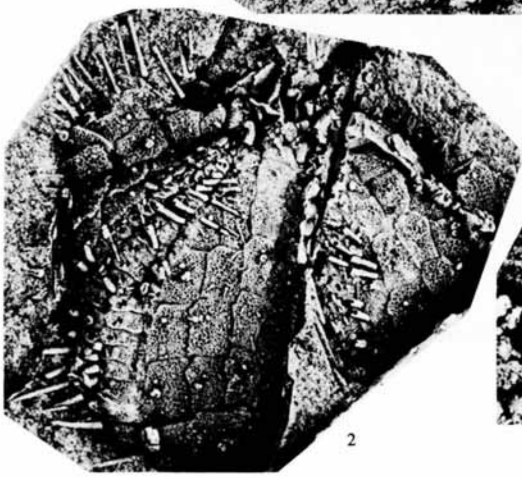

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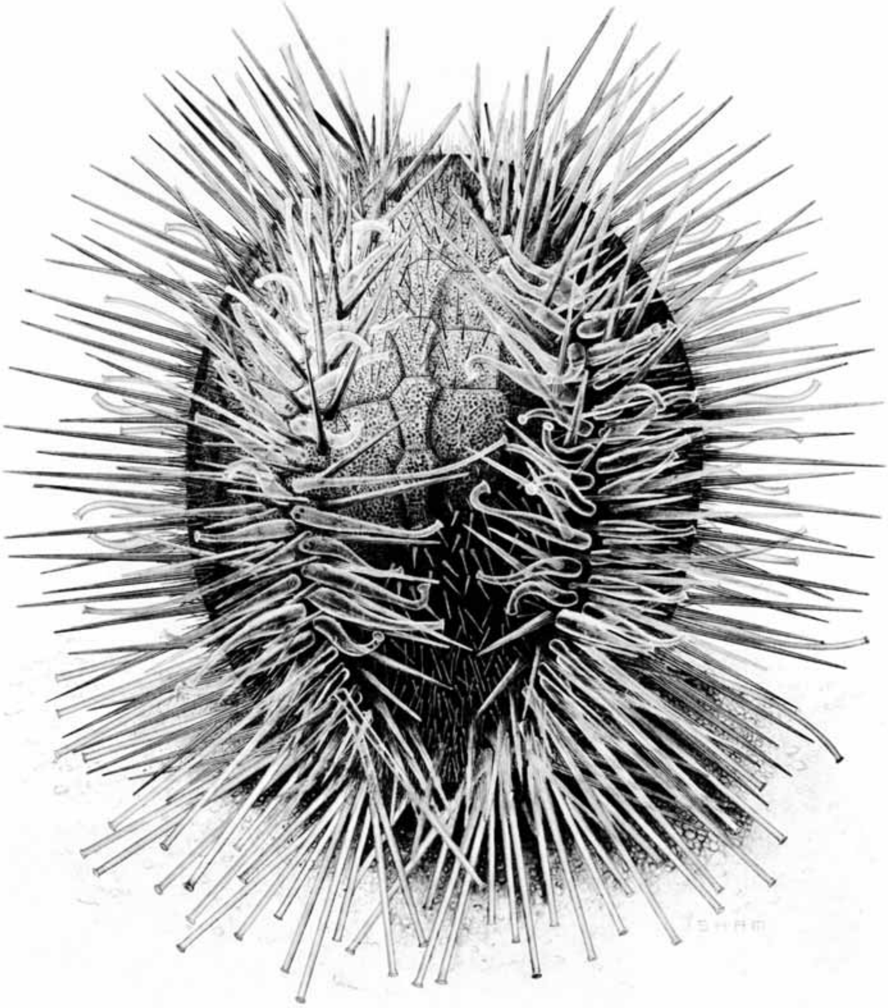

EXPLANATION OF TEXT-FIG. 4. A reconstruction of *Aptilechinus caledonensis* sp. nov. as it may have appeared in life.

Surface ornamentation. All of the exterior surface of the interambulacral plates and most of the exterior of the ambulacral plates is deeply pitted (Pl. 80, fig. 3). The largest of these pits are 0·8 mm in diameter, and they are irregularly arranged. At first appearance they appear to be the meshwork structure of the plates themselves but on some specimens parts of the interior of the plates are visible, and it can be seen that the true meshwork is much finer and is regularly structured in a latticework typical of echinoderms (Pl. 83, fig. 1). This pitted surface is absent on the ambulacral plates on the peripodia and on the nodes. Evidently, these pits served no exterior function for they are present on that part of a plate that is covered in life by adjacent plates (Pl. 81, fig. 3).

Type-specimens. Royal Scottish Museum, Edinburgh, Scotland. Holotype RSM 1897.32.537B, figured paratypes RSM 1897.32.537A, 1897.32.538A, B, 1897.32.540A, B, 1897.32.541B, 1897.32.543, 1897.32.551, 1897.32.552.

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