TWO AUSTRALIAN TERTIARY NEOLAMPADIDS, AND THE CLASSIFICATION OF CASSIDULOID ECHINOIDS

by G. M. PHILIP

ABSTRACT. Two new neolampadids, *Pisolampas concinna* gen. et sp. nov. and *Notolampas flosculus* gen. et sp. nov., are described from the Tertiary of south-eastern Australia. The classification of cassiduloid echinoids is discussed, and it is suggested that the order Cassiduloida Claus should include three suborders, viz. Cassidulina s.s., Conoclypina Zittel, Neolampadina subord. nov.

ALTHOUGH the Tertiary echinoids of south-eastern Australia are being revised in a series of papers elsewhere (Philip, 1963a, b), it is desirable to present at an early stage aspects of this work of more general significance. In this note two new neolampadid genera are proposed, the phylogeny of the family discussed, and suggested alterations made to the current classification of the cassiduloid echinoids.

Up to the present no fossil neolampadids have been described. Living representatives (placed by Mortensen, 1948, in the family Neolampadidae of the order Cassiduloida), although rare, are cosmopolitan, widely distributed through tropical and subtropical seas. The absence of petals and the single or atrophied pores of the adapical ambulacra distinguish the group from other cassiduloids.

SYSTEMATIC DESCRIPTIONS

Genus PISOLAMPAS gen. nov.

Generic name. From the Greek πίσος, pea; λαμπάς, torch.

Type species. Pisolampas concinna sp. nov.

Diagnosis. Subhemispherical neolampadids with compact apical system possessing three genital pores. Oculars small, often separated from the central part of the apical disk. Adapical ambulacra with pores rudimentary or lacking. Periproct supermarginal, at the upper end of a shallow groove. Floscelle moderately well developed with well-defined bourrelets, and expanded phyllodes with an occluded plate in each posterior phyllode.

Remarks. Pisolampas is similar to Neolampas in the character of the compact apical system which has three genital pores. However, the separation of the oculars from the central part of the apical system is a feature not seen in Neolampas (although present in Tropholampas), and the position of the periproct, with its ventral groove, in particular distinguishes Pisolampas. The floscelle is better developed in Pisolampas, although similar occluded plates have been noted in the posterior phyllodes of some specimens of Neolampas rostellata (Agassiz, 1904, pl. 119, fig. 156).

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Pisolampas concinna sp. nov.

Plate 106, Plate 107, fig. 11; text-fig. 1

Echinobrissus concinnus Tate MS, museum label.

Material. Holotype A.U.G.D. T269A, the best preserved of thirteen specimens, mounted syntypes of R. Tate's MS species 'Echinobrissus concinnus', in the Tate Collection, Geology Dept., University of Adelaide. A.U.G.D. F15748–9 and four other uncatalogued A.U.G.D. specimens. National Museum of Victoria P.19252–3.

Locality and horizon. Aldinga, South Australia, St. Vincent Basin, Tortachilla Limestone, Upper Eocene.

Description. Test small, usually oval in outline, sometimes with greatest width posteriorly; adaptical surface usually subhemispherical, rarely with the posterior interambulacrum raised, so that the posterior part of the test is flattened; adoral surface flat, sunken around the peristome. Peristome anterior, elongate oval in shape. Periproct mounted high on the adaptical surface, narrow, with an introverted rim, and a prominent groove running downward to the ambitus. Test covered with small, irregularly disposed, sunken crenulate perforate primary tubercles between which are small closely spaced granules.

Apical system (text-fig. 1d, e) slightly anterior, compact, with genital pores 1, 2, 4 developed. Genital pores show marked dimorphism, being, in some specimens, much larger than in others. Oculars very small, and in some specimens well separated from the genital disk (text-fig. 1a, b). Usually three or four small, centrally located hydropores, but as many as twelve may be present.

Ambulacra narrow adapically with small plates and rudimentary or atrophied pores, seen only rarely on some plates (text-fig. 1b, e). Floscelle (text-fig. 1c) with moderately prominent, closely granulated bourrelets and expanded phyllodes with single pores and sunken peripodia, arranged in two irregular series, but with inner occluded plates in each posterior phyllode; two buccal pores in each phyllode.

Remarks. The enlarged genital pores of some specimens are seen in many living echinoids and are a characteristic of neolampadids (e.g. Agassiz, 1883, pl. 22, figs. 1, 13). They are due to sexual dimorphism, the specimens with large pores being females (Agassiz, op. cit.). It is reasonable to give a similar interpretation in these fossil forms.

Whether or not the adaptical ambulacral pores were absent cannot be decided positively; very small pores (text-fig. 1b) in some specimens suggests that their seeming absence in others could perhaps be a secondary effect due to fossilization.

Genus NOTOLAMPAS gen. nov.

Generic name. From the Greek νότος, south-wind; λαμπάς, torch.

Type species. Notolampas flosculus sp. nov.

Diagnosis. Somewhat posteriorly elongated neolampadids, with compact apical system possessing three genital pores, and pierced oculars; adapical ambulacral plates with single pores continuing to oculars. Periproct submarginal, overhung by posterior interambulacrum. Floscelle well developed, with prominent bourrelets and wide phyllodes with pores arranged in four irregular series in each.

Remarks. This combination of characters provides no basis for comparison with previously described genera. In particular, the floscelle is much better developed than in other neolampadids.

Notolampas flosculus sp. nov.

Plate 107, figs. 1-10; text-fig. 2

Pygorhynchus Vassali Wright; Tate, 1891, Trans. Proc. roy. Soc. S.A. 14 (12), p. 275.
(Non) Pygorhynchus Vassali Wright; Duncan, 1877, Quart. J. geol. Soc. Lond. 33, pp. 51, 67;
Duncan, 1887, ibid. 43, p. 420.

- = Catopygus elegans Laube, 1869, Sitz. k. Akad. Wissen. Wien, 59, pp. 190-1, figs. 8-8c.
- Studeria elegans (Laube).
- (Nec) Pygorhynchus vassali Wright; H. L. Clark, 1946, Pub. Carnegie Instn. 566, p. 358.
- = Studeria elegans (Laube).
- (Nec) Pygorhynchus vassali Wright; Ludbrook, 1961, Bull. Geol. Surv. S.A. 36, p. 44.
- = Progonolampas Novae-hollandiae Bittner, 1892, Sitz. k. Akad. Wissen. Wien, pp. 357-9, pl. 3, fig. 1.
- = Echinolampas novaehollandiae (Bittner).
- (Nec) Pygorhynchus Vassali Wright, 1864, Quart. J. geol. Soc. Lond. 20, p. 479, pl. 22, fig.

Material. Holotype A.U.G.D. F15747 (ex Mines Dept. S.A. Coll.). A.U.G.D. T277A-F, six mounted specimens in the Tate Collection.

Locality and horizon. Mannum, South Australia, Murray Basin, Mannum Formation, Lower Miocene.

Description. Test small, suboval in outline and somewhat pointed posteriorly, greatest width posteriorly, adaptical surface gently arched to the greatest height posterior to the apical system. Adoral surface tumid, markedly sunken around the peristome. Peristome anterior, elongate oval in shape. Periproct submarginal, overhung adaptically by the posterior interambulacrum, subquadrate in shape, with an introverted rim. Test covered with small, irregularly disposed, sunken primary tubercles and small granules.

Apical system (text-fig. 2a) central, compact with genital pores 1, 2, 4 present. Oculars abutting against genital disk, and subtending narrow ambulacra with single pores (text-fig. 2a). Up to six hydropores present.

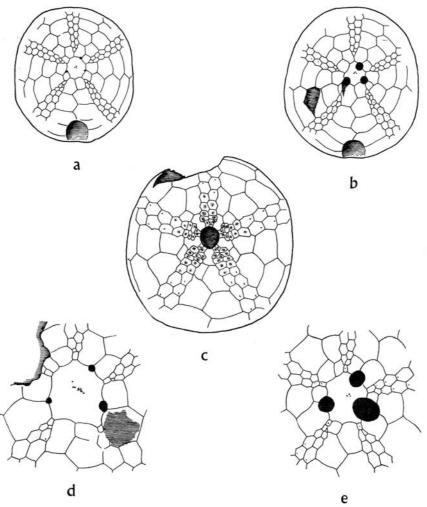
Floscelle (text-fig. 2b) well developed, with prominent granulated bourrelets, and expanded phyllodes, possessing single pores arranged in four very irregular series. Adoral pores with sunken peripodia. Two buccal pores in each phyllode.

Remarks. Small specimens of the Australian Miocene species Studeria elegans (Laube) are similar in shape to Notolampas flosculus, but differ obviously in the presence of petals. On such a specimen (British Museum Nat. Hist. E2375) is based Duncan's (1877,

EXPLANATION OF PLATE 106

Figures $\times 2$ unless otherwise stated.

Figs. 1–10. *Pisolampas concinna* gen. et sp. nov. 1, Adoral view. 2, Posterior view. 3, Anterior view. 4, Adapical view. 5, Left anterior view of holotype A.U.G.D. T269A (♂). 6, Left lateral view. 7, Adapical view of P.19252 (♀). 8, Enlargement of floscelle, P.19253, ×12. 9, Apical system of A.U.G.D. F15748 (♂), showing numerous hydropores, ×12. 10, Adapical surface of A.U.G.D. T269B (♂), showing apical system, sutures, and occasional ambulacral pores, ×12. All specimens from the Upper Eocene Tortachilla Limestone, Aldinga, South Australia.



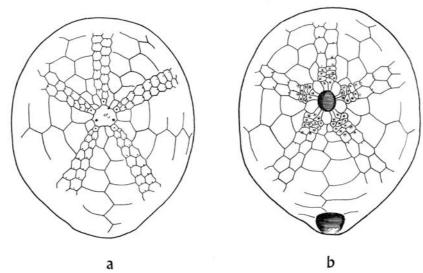
TEXT-FIG. 1. *Pisolampas concinna* gen. et sp. nov. *a*, Adapical plating of A.U.G.D. T269c (3), \times 5. *b*, Adapical plating of P.19252 (\mathcal{C}), \times 5. *c*, Adoral plating of P.19253, \times 5. *d*, Enlargement of apical system of P.19253 (\mathcal{C}), \times 10. *e*, Enlargement of apical system of A.U.G.D. F15749 (\mathcal{C}), \times 10.

p. 51) record of *Pygorhynchus vassali* Wright from 'East of the Glenelg River', Victoria. This record, in turn, gave rise to Tate's (1891) identification of the present species. *P. vassali*, currently placed in *Pliolampas* Pomel, has typical echinolampadid morphology, with prominent ambulacral petals.

The nature of the tubercles cannot be seen in the available material. As in *Pisolampas concinna*, some specimens show enlarged genital pores, which is interpreted as sexual dimorphism.

DISCUSSION

Mortensen (1948) included the Neolampadidae in the suborder Cassidulina of the order Cassiduloida. Kier (1962), on the other hand, did not mention the neolampadids in his revision of the order. The two Tertiary genera described above, with their well-developed floscelles, clearly establish the cassiduloid ancestry and affinities of the family.



TEXT-FIG. 2. Notolampas flosculus gen. et sp. nov. a, Adapical plating of holotype, A.U.G.D. F15747 b, Adoral plating of same. Both \times 5.

The neolampadids are, however, strikingly dissimilar from other cassiduloids in their non-petalloid adapical abulacra, the plates of which possess only single pores. Indeed, not only are petals absent, but also the ambulacral pores (and tube feet) may be atrophied, and the ambulacral columns and oculars even separated from the genitals (in *Tropholampas* and *Pisolampas*). The ambulacra thus are the most degenerate of all irregular echinoids. Because of this, a suborder is here proposed for the reception of the family.

Stefanini (1913) has suggested that the neolampadid ambulacra were neotenously derived from the cassiduloid ambulacra, and this view must be fully endorsed. Because the earliest neolampadids possess a floscelle, it seems that the absence of this in some living genera must be regarded as further neotenous simplification of the ambulacra. Mortensen (1948, p. 331) has suggested that, if *Aphanophora* possessed phyllodes, it

would 'be the most advanced of the Neolampadidae in this respect'. Rather than this, it would now seem that floscelle-bearing neolampadids should be thought of as the least modified and least degenerate.

The detailed derivation of the neolampadids is speculative. Because *Nannolampas* has disparate genital plates, it must be suggested that the family arose from forms such as the Nucleolitidae with a similar apical system. It must be noted that the Upper Eocene *Pisolampas* possesses advanced neolampadid characters suggesting that even older representatives of the family await discovery.

A complete summary of the classification of the Cassiduloida demands the brief introduction of broader issues, which are discussed in more detail elsewhere (Philip, 1963c).

Mortensen (1948) recognized two suborders of the Cassiduloida, viz. Cassidulina and Conoclypina. Durham and Melville (1957) removed the Conoclypina to the Holectypoida, and divided the remaining cassiduloids into two orders, viz. Cassiduloida emend. and Nucleolitoida. Grouped together were forms with unequal pores in the petals and disparate apical systems, as opposed to forms with equal pores in the petals and compact apical systems. Kier (1962, p. 23) rightly rejected this twofold subdivision of the Cassidulina, observing that 'As a matter of fact there are more genera with monobasal apical system and unequal pores than with equal pores'. As noted previously, Kier's usage of the Cassiduloida excluded the neolampadids.

Durham and Melville's (1957) removal of the Conoclypina to the Holectypoida stems from a particular emphasis on the value of the lantern and girdle in echinoid classification. They divide the irregular echinoids into two superorders, viz. Gnathostomata (roughly corresponding to the holectypoids and clypeasteroids) and Atelostomata (cassiduloids and spatangoids).

This return to nineteenth-century classification ignores the findings of the last sixty years.

It seems that, with the development of the irregular condition and the constriction of the peristome, the lantern became superfluous, and so must be considered as a truly regressive character, lost in different lines of descent. The adult holectypoid *Echinoneus* lacks a lantern and girdle, although these are present in early growth stages. A similar condition obtains in living cassiduloids such as *Apatopygus* and *Echinolampas*. Even among spatangoids MacBride (1918, p. 264) has described what he considered to be the rudiments of dental apparatus in the early larval stages of *Echinocardium cordatum*. Although this has been questioned (Mortensen, 1948, p. 6), the living meridosternous spatangoid *Pilematechinus* possesses 'well developed auricles around the peristome, indicating the probable existence in young stages of dental apparatus' (Mortensen, 1950, p. 116). These facts indicate that no clear-cut division into gnathostomatous and atelostomatous irregular echinoids is possible. It also follows that some so-called atelostomatous irregular echinoids, particularly the cassiduloids, are strictly gnathostomatous.

This clarified, the question of the systematic position of the Conoclypina can be discussed. The Tertiary Conoclypidae are virtually identical externally with some of the more advanced cassiduloids. Indeed, Kier (1957) gives as the distinctions between *Conoclypus* and *Echinolampas* the more slit-like outer pores in the petals, and the more longitudinally elongate peristome of the fomer. However, *Conoclypus* possesses a lantern

in adult stages, and hence Durham and Melville remove it to the largely gnathostomatous order Holectypoida.

The features unknown in holectypoids which indicate the manifestly cassiduloid morphology of the test of *Conoclypus* are:

- 1. The presence of petalloid ambulacra.
- 2. The presence of 'pseudo-phyllodes' and bourrelets around the peristome.
- 3. The disordered interambulacral ornament.
- The absence of gill-slits, which are present in all holectypoids which have a lantern in adults.
- 5. The compact apical system.

These characters indicate close similarity with advanced cassiduloids. This is also seen in other features such as the presence of single pores in the ambulacra outside the petals. Indeed, these, coupled with the compact apical system, are a combination of features found only in Cainozoic cassiduloids (with a few minor exceptions).

As various cassiduloid groups must strictly be considered gnathostomatous, this evidence suggests that it is far more probable that the Conoclypina were a neotenous derivative of advanced cassiduloid stock (such as the Echinolampadidae, which are known to possess a girdle and lantern in young stages) than primary descendants of the holectypoids. This interpretation is supported by the fact that no satisfactory holectypoid ancestor of the Conoclypina can be distinguished. The alternative view is to regard the Conoclypina as a sudden 'saltation' of the holectypoids to give a form of advanced cassiduloid morphology and the most remarkable example of homeomorphism in the class Echinoidea.

As an outcome of these considerations the following classification of the echinoid order Cassiduloida is advocated.

SUMMARY OF CLASSIFICATION

Order CASSIDULOIDA Claus, 1880 emend.

Diagnosis. Atelostomatous irregular echinoids (except Conoclypina) lacking gill-slits; ambulacra adapically petalloid (except Neolampadina) with petals usually all similar; floscelle usually well developed; apical system disparate or compact; plastron undifferentiated; fascioles absent.

EXPLANATION OF PLATE 107

Figures ×2 unless otherwise stated.

Figs. 1–10. *Notolampas flosculus* gen. et sp. nov. 1, Adapical view. 2, Adoral view. 3, Anterior view. 4, Left lateral view. 5, Posterior view of holotype, A.U.G.D. F15747 (3). 6, Enlargement of floscelle of holotype, ×10. 7, Left lateral view. 8, Adapical view of A.U.G.D. T277A (\$\varphi). 9, Adapical view of A.U.G.D. T277B. 10, Enlargement of floscelle of A.U.G.D. T277c, ×10. All specimens from the Lower Miocene Mannum Formation, Mannum, South Australia.

Fig. 11. Pisolampas concinna gen. et sp. nov. Enlargement of perforate crenulate primary tubercles at the ambitus of A.U.G.D. T269B, ×20. From the Upper Eocene Tortachilla Limestone, South Australia.

1. Suborder CASSIDULINA Claus emend.

Diagnosis. Cassiduloids lacking a lantern in adult stages; ambulacra adapically petalloid.

Families. Apatopygidae Kier, 1962; Archiacidae Cotteau & Triger, 1869; Cassidulidae L. Agassiz & Desor, 1847; Clypeidae Lambert, 1898; Clypeolampadidae Kier, 1962; Echinolampadidae Gray, 1851; Faujasidae Lambert, 1905; Galeropygidae Lambert, 1911; Nucleolitidae L. Agassiz & Desor, 1847; Pliolampadidae Kier, 1962.

Remarks. For present purposes, the families recognized by Kier (1962) in his restricted usage of the order Cassiduloida are listed as the complement of the Cassidulina. It is to be noted, however, that some of these are poorly differentiated (e.g. Nucleolitidae, Clypeidae; Echinolampadidae, Clypeolampadidae, Pliolampadidae) and probably should be considered at most as subfamilies.

2. Suborder CONOCLYPINA Zittel, 1879

Diagnosis. Cassiduloids possessing a lantern in adult stages; ambulacra adapically petalloid.

Families. Conoclypidae Zittel, 1879; ? Oligopygidae Duncan, 1891.

Remarks. As a lantern-bearing cassiduloid, Bonaireaster Pijpers finds its place with the Conoclypidae. Whether or not the other genera (Oligopygus, Haimea, Microlampas, Protolampas, and Ovulechinus), placed with Bonaireaster in the family Oligopygidae by Durham and Melville (1957), rightly belong together is uncertain. Durham and Melville's interpretation is followed to the extent that the family Oligopygidae is questionably referred to the Conoclypina.

3. Suborder NEOLAMPADINA subord. nov.

Type genus. Neolampas A. Agassiz, 1869.

Diagnosis. Cassiduloids lacking a lantern in adult stages; petals lacking, and adapical ambulacral plates with single pores.

Family. Neolampadidae Lambert, 1918.

Genera. Anochanus Grube, 1868; Aphanapora de Meijere, 1902; Nannolampas Mortensen, 1948; Neolampas A. Agassiz, 1869; Notolampas gen. nov.; Pisolampas gen. nov.; Tropholampas H. L. Clark, 1923.

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REFERENCES

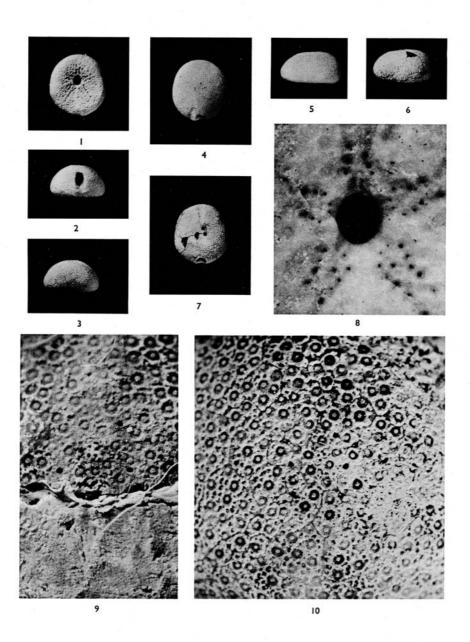
AGASSIZ, A. 1883. Report on the results of dredging . . . by the U.S. Coast Survey Steamer 'Blake'. Report on the Echini. *Mem. Mus. comp. Zool.* 10 (1), 1–94, 32 pl. —— 1904. The Panamic deep sea Echini. Ibid. 31, 1–243, 110 pl.

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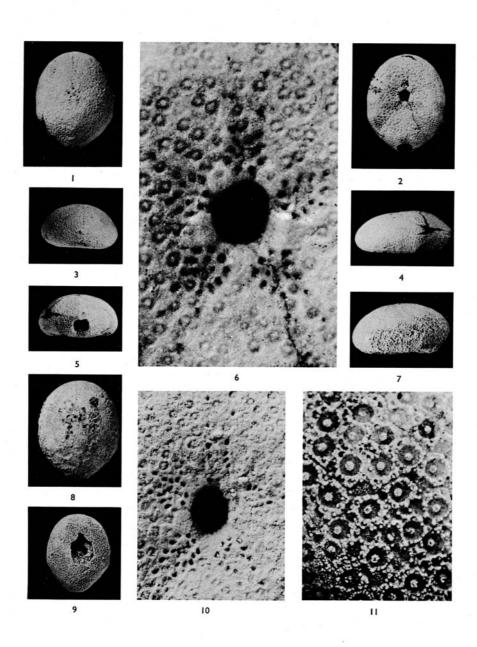
- BITTNER, A. 1892. Über Echiniden des Tertiärs von Australien. Sitz. k. Akad. Wissen. Wien (Math. Nat. Cl.), 101 (1), 331-71, pl. 1-4.
- CLARK, H. L. 1946. The echinoderm fauna of Australia. Its composition and its origin. Pub. Carnegie Instn. 566, 1-567.
- DUNCAN, P. M. 1877. On the Echinodermata of the Australian Cainozoic (Tertiary) deposits. Quart. J. geol. Soc. Lond. 33 (1), 42-71, pl. 3-4.
- 1887. A revision of the Echinoidea from the Australian Tertiaries. Ibid. 43 (3), 411-30.
- DURHAM, J. W. and MELVILLE, R. V. 1957. A classification of echinoids. J. Paleont. 31, 242-72.
- KIER, P. M. 1957. Tertiary Echinoidea from British Somaliland. Ibid. 31, 839-902, pl. 103-7.
- 1962. Revision of the cassiduloid echinoids. Smithsonian Misc. Coll. 144 (3), 1-262, 44 pl. LAUBE, G. C. 1869. Über einige fossile Echiniden von den Murray Cliffs in Süd-Australien. Sitz. k.
- Akad. Wissen. Wien (Math. Nat. Cl.), 59 (1), 183-98, 1 pl. LUDBROOK, N. H. 1961. Stratigraphy of the Murray Basin in South Australia. Bull. Geol. Surv. S.A. 37, 1-96, 8 pl.
- MACBRIDE, E. W. 1918. The development of Echinocardium cordatum. II, The development of the internal organs. Quart. J. Microsc. Sci. 63, 259-82.
- MORTENSEN, T. 1948. A Monograph of the Echinoidea, 4 (1), 1-363, 14 pl. Copenhagen.
- 1950. Idem. 5 (1), 1-432, 25 pl.
- PHILIP, G. M. 1963a. The Tertiary echinoids of south-eastern Australia. I, Introduction and Cidaridae (1). *Proc. roy. Soc. Vict.* **76**, 181–226, pl. 21–26. — 1963b. Idem., Cidaridae (2). Ibid. **77** (in press).
- 1963c. The classification of echinoids. J. Paleont. 37 (in press).
- STEFANINI, G. 1913. Probabile origine neotenica degli ambulacri apetali di Neolampas. *Padova Atti Acc. ven. trent.* 3 (6), 33–41.
- TATE, R. 1891. A bibliography and revised list of the described echinoids of the Australian Eocene with descriptions of some new species. Trans. Proc. roy. Soc. S.A. 14 (2), 270-82.
- WRIGHT, T. 1864. On the fossil Echinoidea of Malta. Quart. J. geol. Soc. Lond. 20, 370-1, p. 22.

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