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TAIMANAWA, A NEW GENUS OF BRISSID ECHINOIDS FROM THE TERTIARY AND RECENT INDO-WEST-PACIFIC WITH A REVIEW OF THE RELATED GENERA *BRISSOPATAGUS* AND *GILLECHINUS*

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ABSTRACT. *Taimanawa* gen. nov. is erected to include two New Zealand fossil species, *T. pulchella* sp. nov. (taken as the type species) of early Miocene age and *T. greyi* (Hutton) of Oligocene age, as well as a poorly known extant species from the Kei Islands, Indonesia, *T. mortenseni* sp. nov., which had hitherto been tentatively referred to *Plagiobrissus* Pomel. In spite of possessing an internal fasciole, *Taimanawa* is referred to the Brissidae, with which it agrees in other morphological features. The closely related genera *Gillechinus* Fell and *Brissopatagus* Cotteau are re-evaluated using type material of the type species; they are maintained as distinct, but most of the species previously referred to *Brissopatagus* are here transferred to *Gillechinus*.

INTRODUCTION

In the course of a preliminary survey of the New Zealand Tertiary Spatangoida by one of us (H. B. F., 1947-55), the genus herein named *Taimanawa* was recognized as new. However, the two fossil species referable to the genus seemed to be congeneric with an unnamed and poorly known form from the Kei Islands, west of New Guinea, which had tentatively been referred to *Plagiobrissus* by Mortensen (1951). Therefore, it was deemed advisable to defer publication of the material until the fossils could be compared with the suspected living species. In the interim, the responsibility for describing the entire New Zealand collection of Tertiary spatangoids has been assumed by the second author. In consequence, this report has been prepared as a joint project.

Through the kindness of Dr. F. Jensenius Madsen (University Zoological Museum, Copenhagen) it has been possible to study fragments of two specimens from the Kei Islands and to confirm

that they represent a living species of *Taimanawa*. This species, together with *T. pulchella* (the type of the genus) and *T. greyi* (Hutton), which was described from New Zealand a century ago, are all treated here. Two additional species occur in the New Zealand Tertiary, but as they add little to the definition of the genus, they will be described in a monograph of New Zealand Tertiary Spatangoida now in preparation.

The closest relatives of *Taimanawa* are the genus *Gillechinus* Fell, 1964, based on *G. cudmorei* Fell, and a number of species which previously have been referred to *Brissopatagus* Cotteau, 1863. *Brissopatagus* is based on *B. caumonti* Cotteau, which is known from a single, poorly-preserved specimen. Recently Phillip (1966) has synonymized *Gillechinus* with *Brissopatagus*. In order to evaluate this contention and to determine the relationship of *Brissopatagus* and *Gillechinus* to *Taimanawa*, type material of *B. caumonti* and *G. cudmorei* have been compared. Paratypes of the former were supplied by Mr. T. A. Darragh (National Museum of Victoria), and the holotype of the latter was kindly lent to us by Professor J. Roger (Laboratory of Paleontology, University of Paris). As a result of this study, *Brissopatagus* and *Gillechinus* are here maintained as distinct, and most of the species previously referred to *Brissopatagus* have been regrouped in *Gillechinus*. *Taimanawa* is perhaps the direct descendant of *Gillechinus;* it is less closely related to *Brissopatagus*.

The authors wish to thank Dr. C. A. Fleming and Mr. I. W. Keyes (New Zealand Geological Survey), Mr. J. D. Campbell (Otago University), Mr. J. A. Grant-Mackie (Auckland University), Mr. D. R. Gregg (Canterbury Museum), and Dr. P. Kier (Smithsonian Institution) for the loan of specimens under their charge, and Mr. R. J. Foster (Hughesdale, Victoria, Australia) for a gift of specimens of *Gillechinus cudmorei*. The project was undertaken during tenure at Harvard University of a Frank Knox Memorial Fellowship and a Taranaki Post-Doctoral Fellowship by one of us (R. A. H.). The research was sponsored by a National Science Foundation grant, GB-3532.

Repositories. The repositories of type and other specimens are indicated by the following abbreviations: New Zealand Geological Survey (EC.); Geology Department, Otago University (OU.); Geology Department, Auckland University (E.); and Canterbury Museum (zfe.).

Localities. Localities of the New Zealand fossil specimens have been arranged in order of the sheet districts of the one mile to the

inch topographic map series (New Zealand Department of Lands and Survey, series N.Z.M.S. 1) on which they appear. The sheet districts are designated "N" and "S" for the North and South Islands and are arranged numerically from north to south on each island. Sheet Fossil Numbers of the New Zealand Fossil Record Form System (e.g. S164/496) are recorded for those localities to which they have been allocated.

Stratigraphy. The sequence of New Zealand Tertiary stage divisions relevant to the stratigraphic ranges of *T. pulchella* and *T. greyi,* listed in order from youngest to oldest, are as follows: Whaingaroan, Duntroonian (Oligocene); Waitakian, Otaian, Awamoan (Lower Miocene).

Order Spatangoida Claus, 1876

Family Brissidae Gray, 1855

Genus *TAIMANAWA* nov.

Type species. T. pulchella sp. nov. Other included species: *T. mortenseni* sp. nov.; *T. greyi* (Hutton).

Diagnosis. Large, flattened forms with peripetalous, subanal, and internal fascioles. Frontal ambulacrum deeply depressed, crossing the ambitus in a deep, narrow frontal notch. Paired petals long, narrow, shallowly depressed, and with subparallel pore series. Anterior pair widely splayed, posterior pair less so. Primary tubercles crenulate, restricted to the posterior plate series of the paired interambs within the peripetalous fasciole. Labrum very short, extending only halfway along the first plate of the adjacent ambulacra.

Etymology. The name *Taimanawa* is derived from the Maori words *tai* (= sea) and *manawa* (= heart); it is here treated as a Latin feminine first declension noun.

Description. Test large, flattened, cordiform in outline, and almost as wide as long. Aboral surface gently convex, oral surface flattened, ambitus sharp. Apical system at or near the axis of maximum height, usually slightly pre-central and ethmolytic, with four gonopores. Peristome crescentic, labiate, and anterior; periproct situated on the truncated posterior test surface. Well-developed peripetalous and subanal fascioles and a clear but less well-developed internal fasciole. Neither the peripetalous nor the internal fasciole continuous across the frontal ambulacrum. Both primary and secondary tubercles perforate and crenulate.

Aboral surface: Frontal ambulacrum apetaloid, deeply depressed, crossing the ambitus in a narrow, deep frontal notch; ornamented

with fine, dense miliary tubercles and perforated by minute, conjugate pore pairs. Paired petals long, narrow, and weakly depressed, with subparallel pore series. Anterior petals widely splayed, at an angle of approximately 120°; posterior petals less so, forming an angle of approximately 60°. Each pore pair weakly conjugate and separated from the next by a single row of miliary tubercles. Interambs with a broad, low ridge extending along or near the median suture of the plate series; ridges of the paired interambulacra subtend gently sloping, flattened surfaces posteriorly to the depression of each petal. Posterior plate series of the paired interambulacra bear prominent fields of primary tubercles located within the peripetalous fasciole. Tubercles surrounded by large, shallow scrobicules; those of each field generally arranged in a reticulate pattern with discernible rows both parallel and perpendicular to the axis of the adjacent petal. Median suture of the posterior interamb bordered on each side by a single or double row of well-spaced, coarse secondary tubercles. Each interambulacral plate of the two series bordering the frontal ambulacrum bears a small triangular field of coarse secondary tubercles. The remaining interambulacral areas of the aboral surface bear fine, dense secondary and miliary tubercles.

Oral surface: Plastron amphisternous, weakly keeled, and extending anteriorly almost to the peristome; it bears coarse, dense secondary tubercles arranged in lines radiating from the posterior of the keel. Subanal fasciole broad and reniform, enclosing a densely tuberculate area with an arcuate row of conjugate pore pairs on each side. Labrum very short, extending only halfway along the first plate of the adjacent ambulacra, twice as wide as long, and with a few secondary tubercles. Remaining interambulacral areas bear well-spaced secondary tubercles. Ambulacral areas not depressed, naked except for scattered miliary tubercles; those margining the plastron are conspicuous, being half as wide as the plastron itself. Secondary spines bear prominent longitudinal ribs and are akin to those of most other spatangoids.

Remarks. Judging from the fascioles alone, *Taimanawa* would be placed in the Loveniidae alongside *Breynia,* which is the only other spatangoid genus with peripetalous, subanal, and internal fascioles. However, its other characters show that it is unrelated to *Breynia* and that it cannot be referred to the Loveniidae in spite of possessing an internal fasciole. In general morphology it is very similar to the undisputed brissid genera *Gillechinus, Plagiobrissus, Brissopatagus, Macropneustes,* and *Eupatagus.* Its long, narrow petals with subparallel pore series, short labrum, crenulate primary

and secondary tubercles, and the absence of ampullae set it apart from the loveniids and necessitate its inclusion in the Brissidae.

Taimanawa, by virtue of its internal fasciole, is unique among the Brissidae. Its nearest relative is *Gillechinus,* which also has primary tubercles restricted to the posterior plate series of the paired interambulacra within the peripetalous fasciole and which has similar petals. Most members of *Gillechinus* possess flattened interambulacral surfaces subtended posteriorly from ridges of the paired interambs into confluence with the depressions of the paired petals, as in *Taimanawa.* However, *Taimanawa,* in addition to possessing an internal fasciole, is distinguished by its shorter labrum (Fig. 1), its much more deeply depressed frontal ambulacrum, and its much stronger frontal notch. It is interesting to note that the earliest species of *Taimanawa,* from the late Eocene of New Zealand (as yet undescribed), resembles contemporaneous *Gillechinus* in possessing a slightly depressed frontal ambulacrum and a relatively weak frontal notch. Such a relationship strongly suggests that *Taimanawa* was derived directly from *Gillechinus.* The genera *Eupatagus, Gymnopatagus, Macropneustes, Plagiobrissus,* and *Brissopatagus* all bear some resemblance to *Taimanawa.* Besides lacking an internal fasciole, they are distinguished by possessing primary tubercles on both plate series of at least the posterior paired interambs (with the exception of *E. ibericus* Lambert). *Eupatagus, Plagiobrissus,* and *Brissopatagus* possess a weak frontal groove and frontal notch, and even in *Macropneustes* and *Gymnopatagus,* where these structures are better developed, they are not as strong as in *Taimanawa. Eupatagus* and *Gymnopatagus* are further distinguished by possessing spatangiform petals with curved pore series, *Plagiobrissus* by possessing lateral branches of the subanal fasciole, and *Brissopatagus* by the concave depressions of its anterior paired interambulacra.

The presence of an internal fasciole in *Taimanawa* was initially a perplexing feature, since this structure has not previously been reported from any member of the Brissidae and, indeed, Mortensen's (1951) diagnosis of the family excludes forms with an internal fasciole. However, it will be recalled that a similar perplexity arose in reviewing New Zealand species of the spatangid genus *Paramaretia* (Fell, 1963), though in this case the fasciole proves to be a transitory feature that disappears in the adult. The relationship of fascioles to environmental features and the loss or acquisition of fascioles during the life-span of certain spatangoid echinoids have recently been studied by R. H. Chesher (private

communication), and the whole subject has now been considerably clarified by his recent publication (1968).

Most of the New Zealand Tertiary specimens of *Taimanawa* are from detrital limestones and from sandstones that were deposited in comparatively shallow water during the early and mid-Tertiary transgression of the New Zealand region. In contrast, the extant species is recorded by Mortensen (1951) from two deep-water stations (260 and 268 meters); the sediment type is known for only one of the stations and is recorded by Mortensen (1923) as mud and shells. The bottom temperature of the two stations is not known but is probably near 20° C and therefore some 8°-10° C higher than the mean annual temperature of surface water off the southeast coast of the South Island, New Zealand, where *Taimanawa* was abundant in Oligocene and earliest Miocene time. Such a relationship is consistent with the higher temperatures inferred for the mid-Tertiary marine environment of the New Zealand region on the basis of fossil echinoids (Fell, 1956), and by Beu (1966) and others on the basis of other fossil groups.

KEY TO SPECIES OF *TAIMANAWA*

1 (2) Crenulation of the primary tubercles strongly developed, contiguous with the mamelon, the platform therefore aborted 3

2 (1) Crenulation of the primary tubercles restricted to the periphery of the platform, widely separated from the mamelon ..... *mortenseni*

3 (4) 23-40 primary tubercles in each interambulacral field, 22-25 well developed pore pairs in the anterior petals ..... *greyi*

4 (3) 12-16 primary tubercles in each interambulacral field, 18-19 well developed pore pairs in the anterior petals ..... *pulchella*

TAIMANAWA PULCHELLA sp. nov.

Plate 2, fig. 2; Plate 3; Plate 4. Figures 1, 2a, 2c.

Holotype. OU. 8590, Karitane, Otago; S155/538.

Paratypes. S75: E. 310, Burnt Hill, Trelissick Basin, mid-Canterbury; S75/517. *S127:* EC. 405, Ngapara, south Canterbury; S127/561. *S155:* OU. 8540, Puketeraki, Dunedin district, Otago. E. 302, 304, Waikouaiti North Head, Matanaka Beach, Otago; S155/540. *S163:* EC. 426, Blackhead, Dunedin district, Otago; S163/495. OU. 4736, 8566a, b, 8567b-d, 8568a-d, Blackhead, Dunedin district, Otago. *S164:* EC. 437, Green Island district, Otago; S164/496. OU. 8585, New Zealand Cement Co. pit, Burnside, Otago. *Locality unknown:* EC. 671.

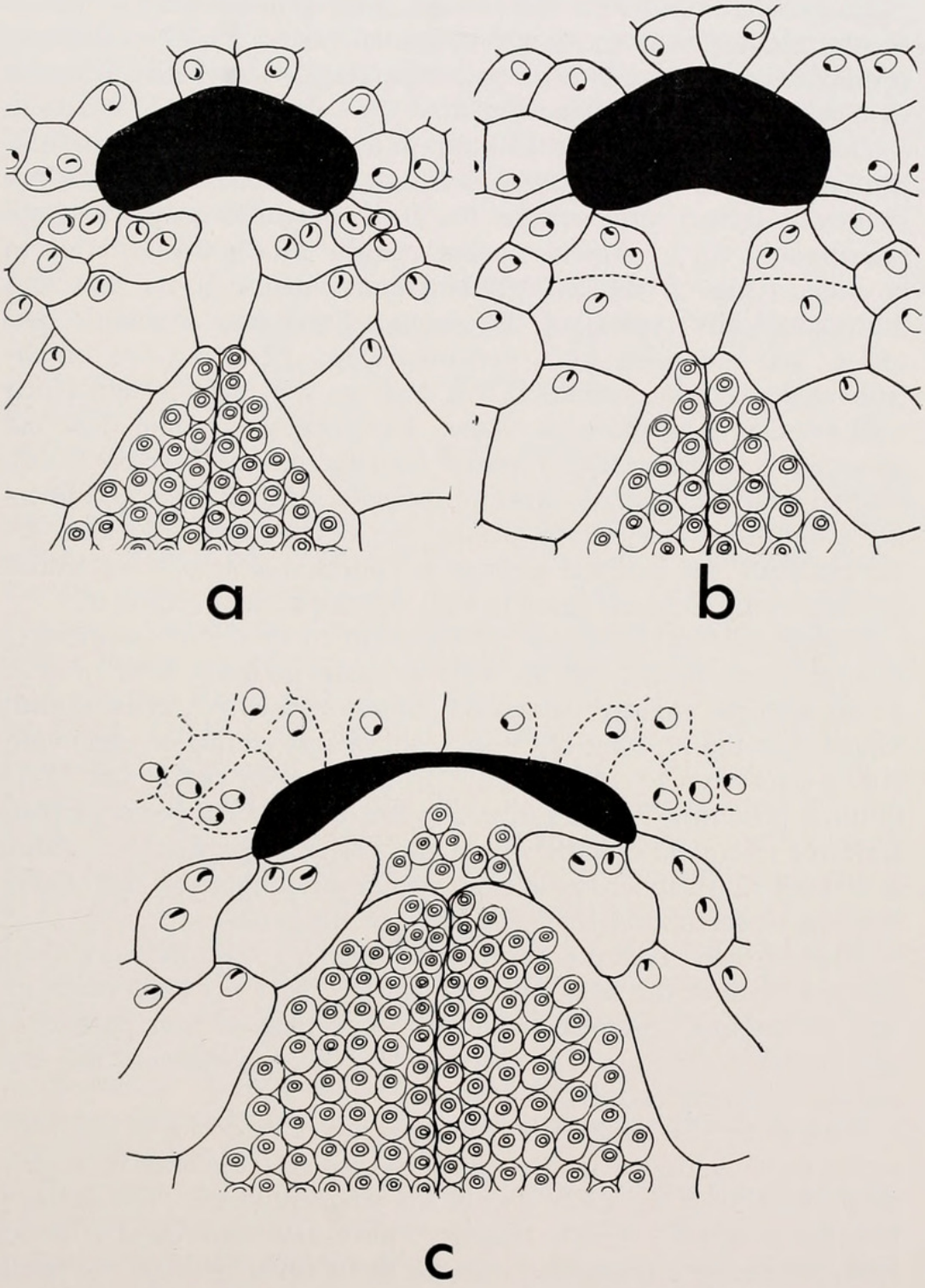

Figure 1. Comparison of the peristomial regions of *Gillechinus* and *Taimanawa*. a) *Gillechinus alabamensis* (Cooke), U.S. National Museum 562467; ×3.5. b) *Gillechinus cudmorei* Fell, Museum of Comparative Zoology 4147; ×3.5. c) *Taimanawa pulchella* sp. nov., holotype, OU. 8590; ×2.5.

Diagnosis. Adult tests compressed, with a moderately depressed frontal ambulacrum and a strong frontal notch; 18-19 well-developed pore pairs in the anterior paired petals, 12-16 primary tubercles in each lateral interambulacrum.

Description. Test up to 120 mm in length, cordiform in outline, almost as wide as long, with a sharp ambitus. Aboral surface shallowly arched, oral surface flattened; height/breadth ratio approximately 0.27. Apical system central to slightly anterior in position, lying on the axis of maximum height of the test and morphologically typical of the genus. Peristome crescentic, anterior, and margined by a prominent lip. Periproct lies on the truncated posterior surface of the test; no specimen is sufficiently well preserved to show its shape. Peripetalous fasciole thin, not indented between petals. Internal fasciole thin, of variable width, located near the median suture of the anterior interambs and forming a tight loop posteriorly around the apical system. Neither the peripetalous nor internal fasciole is continuous across the frontal ambulacrum. Subanal fasciole well developed and reniform.

Aboral surface: Frontal ambulacrum of moderate depression; frontal notch prominent, as wide as deep in adult tests. Paired petals straight, lightly depressed; anterior pair generally slightly longer than those posterior. Pore pairs weakly conjugate and ovate. Adult tests have 18-19 pore pairs in the anterior petals and 15-16 in those posterior. Primary tubercles restricted to the posterior plate series of lateral interambs within the peripetalous fasciole. Adult tests with 12-16 tubercles in each such interambulacral field. Other features of the aboral surface typical of the genus.

Oral surface: Labrum very short, reaching only halfway along the first plate of the adjacent ambulacra. There are eight pores inside the subanal fasciole, arranged in two lines of four parallel to the lateral portions of the fasciole. In other characters the oral surface is characteristic of the genus.

Remarks. The most distal row of primary tubercles in the interambulacral fields, as in the other species of *Taimanawa,* is generally flush with the distal end of the adjacent petal. The anterior interambs of OU. 8540, however, have two additional rows of tubercles nearer the ambitus than the distal tip of the adjacent petal, giving an unusually high number of tubercles (22) compared to that of more normal specimens (12-16). One specimen (EC. 671) has a conspicuous boring perforating the test at its anterior margin, evidently the result of an attack by a large, predatory gastropod.

Age. Lower Miocene; Waitakian — Otaian. OU. 8585 is known

to be of Waitakian age and EC. 405 has the age limits of Duntroonian — Waitakian. The remaining specimens, with the exception of E. 310, are from the Caversham Sandstone, which is largely of Otaian Age although Awamoan microfaunas are known from its uppermost horizons. The holotype is known to be of Otaian Age, and the other specimens from the Caversham Sandstone are most likely of Otaian Age also.

TAIMANAWA GREYI (Hutton)

Plate 1; Plate 2, fig. 1. Figure 2d.

Brissus greyi Hector, 1870: 192 (*nomen nudum*).
Eupatagus greyi; Hutton, 1873: 41.

Holotype. EC. 682, Cobden, north Westland; S44.

Additional material. N51: E. 296, near Waikawau Stream mouth, west Auckland; N51/677. *S37:* EC. 480, 481, Woodpecker Bay, north Westland; S37/528. *S44:* EC. 458, Cobden Limestone, Greymouth, north Westland; S44/465. EC. 543, Cobden Limestone Quarries, Greymouth, north Westland; S44/476. zfe. 286, 287, 290, Cobden Limestone, Greymouth, north Westland. *S102:* EC. 407, Kakahu River, south Canterbury; S102/1. OU. 8548b, Hanging Rock, Opihi River, south Canterbury. *S111:* E. 250, Lower Pareora Gorge, south Canterbury; S111/683. OU. 8606, Gordon Valley, south Canterbury. zfe. 284, Pareora Gorge, south Canterbury. *S127:* EC. 615, Pigeon Rock, Waitaki Valley, south Canterbury; S127/371. EC. 473, 474, Waihao River, south Canterbury; S127/376. EC. 472, Waitaki Valley, south Canterbury; S127/447. EC. 471, Awamoko Creek, Oamaru, south Canterbury; S127/450. E. 246, 248, Taylor's Road, Oamaru, south Canterbury; S127/639. OU. 8546, 8547, Waitaki Limestone, Duntroon, south Canterbury. OU. 8542, Ngapara, south Canterbury. OU. 8598, 8601, 8602, Earthquakes, Duntroon, south Canterbury. *S136:* OU. 8545, Weston, south Canterbury. *Locality unknown:* zfe. 278, Canterbury, unlocalised.

Diagnosis. Adult tests compressed, with a deeply depressed frontal ambulacrum, 22-25 well-developed pore pairs in the anterior petals, and 23-40 primary tubercles in each interambulacral field.

Description. Test up to 134 mm in length, cordiform in outline, almost as wide as long, with a sharp ambitus. Aboral surface shallowly arched, oral surface flattened; height/breadth ratio approximately 0.25. Apical system varies in position from slightly

anterior to slightly posterior of center; it lies on the axis of maximum test height, and its morphology is typical of the genus. Peristome crescentic, anterior, and margined by a prominent lip. Anal region not preserved on any available specimens. Peripetalous fasciole thin, not strongly indented between the petals. Internal fasciole extending for a short distance near the sutures of the two plate series of interambs 2 and 3 and forming a tight loop posteriorly around the apical system. Neither the internal nor the peripetalous fasciole closed across the frontal ambulacrum.

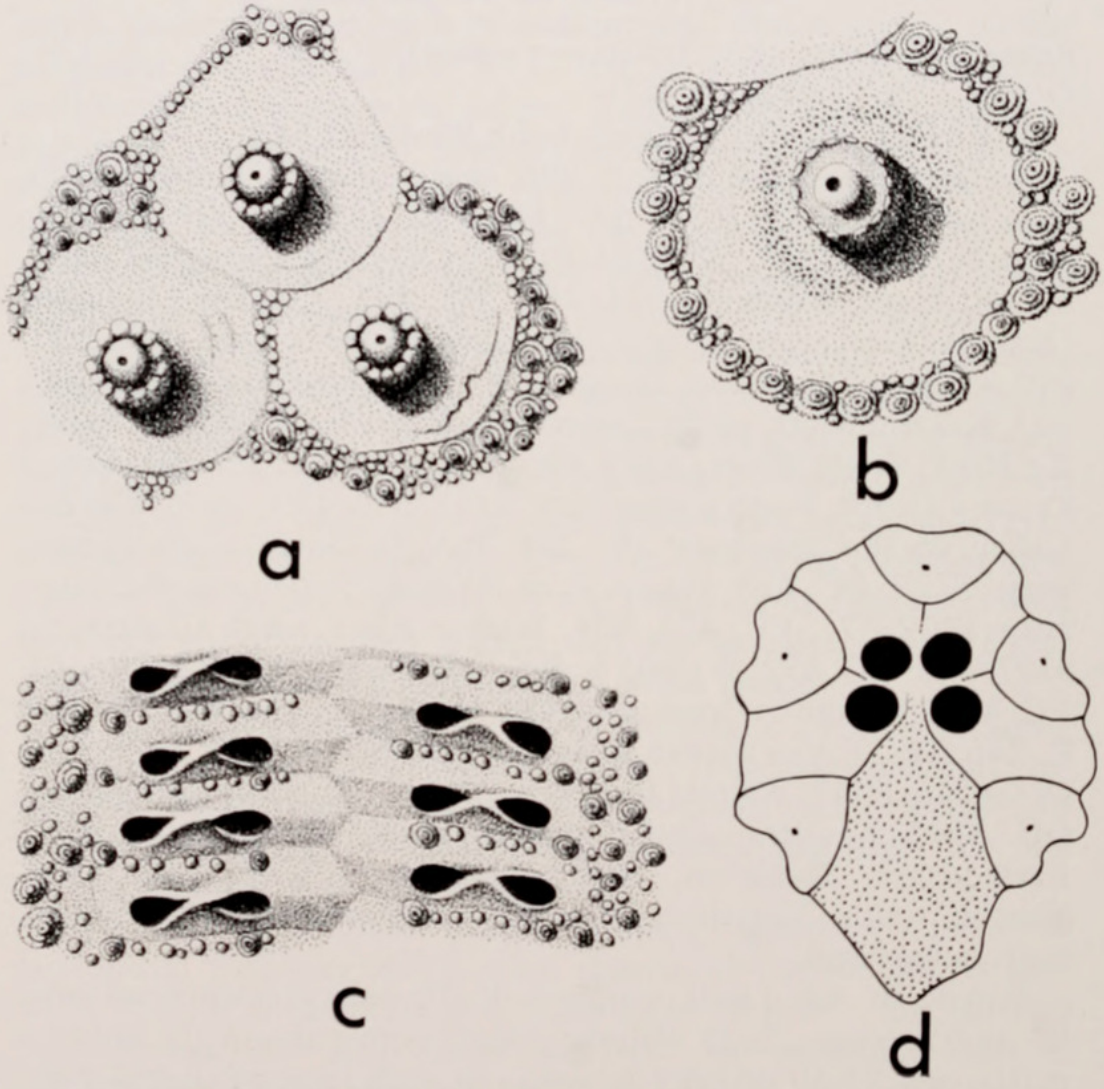

Figure 2. a) Primary tubercles of *Taimanawa pulchella* sp. nov., holotype, OU. 8590; ×7. b) Primary tubercles of *Taimanawa mortenseni,* holotype; ×7. c) Plates of ambulacrum V of *Taimanawa pulchella* sp. nov., holotype, OU. 8590; ×7. d) Apical system of *Taimanawa greyi* (Hutton), OU. 8598; ×7.

Aboral surface: Frontal ambulacrum deeply depressed, terminating in a conspicuous frontal notch that is as wide as deep on adult tests. Paired petals lightly depressed; anterior pair straight or gently curved towards the frontal ambulacrum and generally slightly longer than the posterior pair, which are straight or gently curved away from the posterior interamb. Pore pairs ovate and weakly conjugate; adult tests have 23-25 well-developed pore pairs in each anterior petal and 20-24 in each posterior petal. Fields of primary tubercles restricted to posterior plate series of the lateral interambs inside the peripetalous fasciole; 23-40 tubercles in each field on adult tests. Other features of the aboral surface as described for the genus.

Oral surface: As described for the genus. The anal region is poorly preserved on all the available specimens; the presence of a subanal fasciole cannot be confirmed, and the nature of the tuberculation within the anal fasciole is not known.

Remarks. The material, although abundant, offers but a single, indifferently preserved oral surface. The petals of different specimens are somewhat variable in length, breadth, and the degree to which they are depressed; the anterior petals of several specimens of about the same test width (114-119 mm) vary in length from 37 to 42 mm and vary in width from 5.0 to 6.5 mm. The number of primary tubercles in the interambulacral fields is also variable. Three specimens from the Cobden Limestone, Greymouth (zfe. 286, 287, 290), and a single specimen registered as from Ngapara, Oamaru (OU. 8542), differ from the remainder of the material in possessing more numerous primary tubercles (35-40 in each interambulacral field) and in bearing up to four rows of well-spaced, coarse secondary tubercles situated adjacent to and running parallel with the ambitus of the anterior interambs. The matrix of OU. 8542, a hard, fine-grained, muddy limestone, contrasts with the softer, coarse-grained, almost pure limestone that forms the matrix of other echinoids from Ngapara; it closely resembles the matrix of the Greymouth specimens. It may be that the locality of OU. 8542 has been incorrectly recorded.

Although the holotype has never been figured, it is known to be the specimen used by Hutton in the erection of the species. It is badly crushed and shows few of the characters of the species, but as it has at least 25 pore pairs in ambulacrum IV and approximately 36 primary tubercles in interambulacrum 4, it is undoubtedly conspecific with the other specimens herein referred to *T. greyi.*

Taimanawa greyi closely resembles *T. pulchella*, to which it was probably ancestral. It is distinguished by its petals, especially the anterior pair, having more numerous pore pairs (Fig. 3). Further differences include the deeper frontal goove and more numerous primary tubercles of *T. greyi*.

Age. Oligocene — lowermost Miocene; Whiangaroan — Waitakian. The exact age of the holotype is not known. From its locality and matrix, it can confidently be assigned to the Cobden Limestone, which ranges in age from Whiangaroan to Waitakian.

TAIMANAWA MORTENSENI sp. nov.

Plate 5, fig. 1. Figure 2b.

Plagiobrissus sp. ? Mortensen, 1951, p. 503, pl. 39, fig. 3.

Holotype. Fragments of a specimen from Station 32 of the Danish Expedition to the Kei Islands (1922), between Little Kei and Tajando Islands at a depth of 260 meters. Curated by the University Zoological Museum, Copenhagen.

Paratype. Fragments of a second specimen are represented in the collection from the same station.

Description. Known from fragments only, the largest of which comprises the anterior half of an aboral surface. Test large, and appears to be approximately as wide as long. Aboral surface inflated and ambitus more broadly rounded than in other members of the genus. Peripetalous fasciole well developed, not indented between the petals and not continuous across the frontal ambulacrum. Internal fasciole thin, of variable width, bordering the frontal ambulacrum for half the distance from the broken margin of the test, slightly anterior of the apical system, to the peripetalous fasciole. Subanal fasciole well developed and, as far as can be judged, reniform.

Aboral surface: Frontal ambulacrum deeply depressed, apetaloid, terminating in a pronounced frontal notch that is approximately as wide as deep. Amb plates bear a fine, dense, secondary and miliary tuberculation and are perforated by minute, conjugate pore pairs. Anterior petals slightly depressed, splayed at an angle of some 120°, and weakly flexuous, being concave away from the frontal ambulacrum proximally and concave towards the frontal ambulacrum distally. Each bears 25 ovate, weakly conjugate pore pairs; adjacent pairs are separated by a single row of secondary and miliary tubercles, and the interporiferous zone bears scattered miliary tubercles. Anterior plate series of the frontal interambulacra tumid, subtending a weakly concave surface posteriorly into confluence

with the depressions of the frontal petals. Primary tubercles restricted to the posterior plate series of the anterior interambs lying within the peripetalous fasciole, surrounded by prominent scrobicules, and very weakly crenulate. The partially preserved anterior plate series of interamb 4 devoid of primary tubercles, suggesting that tuberculation of the posterior lateral interambs is akin to those anterior. Frontal ambulacrum margined by a zone of coarse secondary tubercles. The remaining aboral interambulacral surfaces bear a dense miliary and secondary tuberculation.

Oral surface: Nature of the plastron and labrum unknown. Interambs bear well-spaced secondary tubercles; ambulacra naked except for scattered miliary tubercles. The area enclosed by the subanal fasciole bears dense secondary tubercles and is perforated on each side by seven conjugate pore pairs.

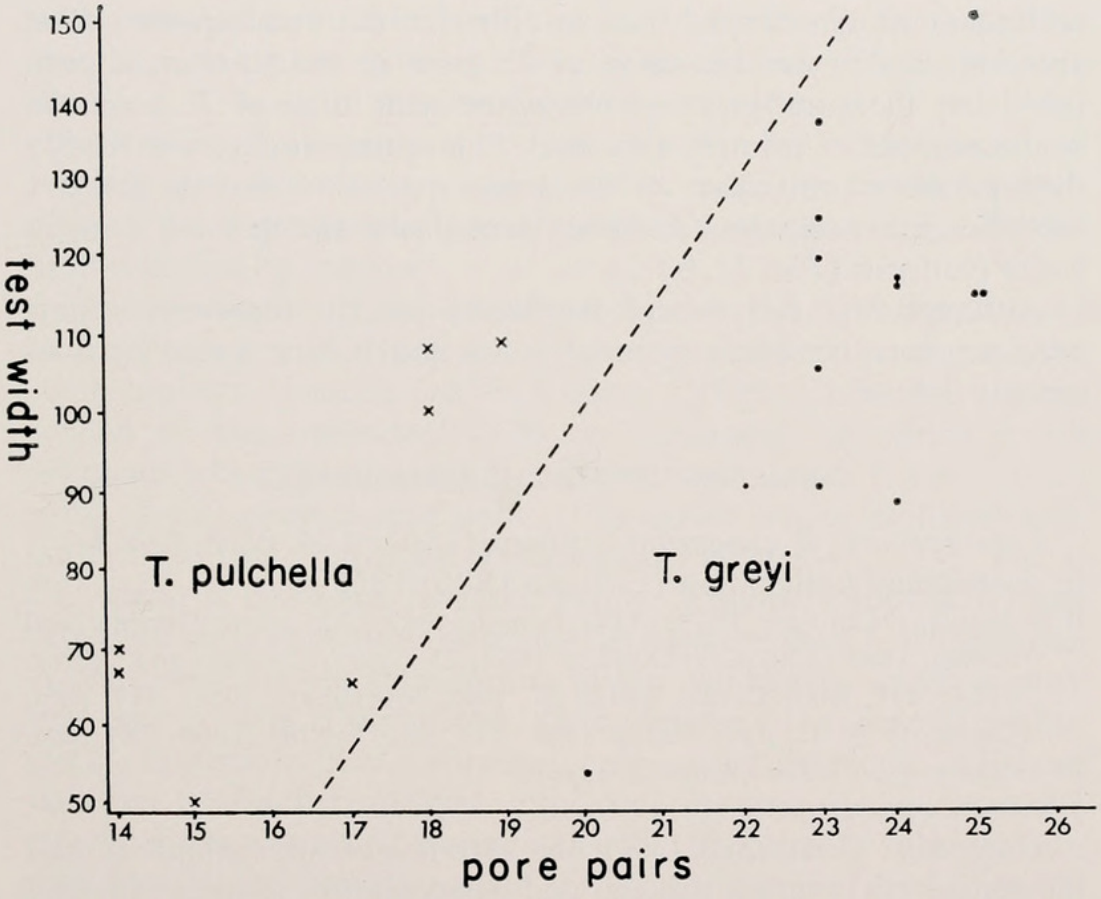

Figure 3. Plot of the number of fully developed pore pairs in each plate series of the anterior petals against test width for *Taimanawa pulchella* sp.. nov. and *T. greyi* (Hutton) showing the separation of the two species. Ordinate values have been estimated for many points and are accurate only to ± 5 mm.

Remarks. Mortensen (1951) also recorded fragments of this species from Station 44 of the Danish Expedition to the Kei Islands (1922), but the material is poor (Dr. F. Jensenius Madsen, private communication) and has not been examined in the preparation of this report. *T. mortenseni* is conformable in all its principal characters with the fossil *T. pulchella* and *T. greyi* but represents a discrete species. The possession of an internal fasciole and a strong frontal notch shows that *mortenseni* must be referred to *Taimanawa.* Indeed, the very close resemblance between the mid-Tertiary New Zealand species and the present form, which is living in the Kei Island area of the Indonesian region, is remarkable.

The holotype represented by the most complete set of fragments would have measured approximately 140 mm in width. The test height cannot be accurately estimated, but the aboral surface is more inflated than that of either *T. pulchella* or *T. greyi,* and the ambitus is more rounded than in either of the fossil species. The anterior petals resemble those of *T. greyi* in the number of pore pairs, but the anterior interambs agree with those of *T. pulchella* in the number of primary tubercles. The present species is readily distinguished from either of the fossil species in that its primary tubercles are much less distinctly crenulated and possess a much wider platform (Fig. 2a, b).

Although the Kei Island fragments clearly represent a new species, more complete material is needed before it can be adequately defined.

Genus *BRISSOPATAGUS* Cotteau, 1863

Type species. B. caumonti Cotteau (1863: 144, pl. 8, figs. 3-7); by subsequent designation (Cotteau 1886: 135).

Brissopatagus Cotteau, 1863: 144; Pomel, 1883: 32, *pars;* Duncan and Sladen, 1884: 226, *pars;* Duncan, 1889: 250, *pars;* Lambert and Thiery, 1924: 491, *pars;* Cooke, 1942: 57, *pars;* Mortensen, 1951: 453, *pars;* Cooke, 1959: 92, *pars;* Phillip, 1966: 114, *pars;* Fischer, 1966: 584, *pars.*

Brissospatangus Cotteau, 1886: 135, *pars.*

non Brissospatangus; Cotteau, 1890: 18.

Diagnosis. Test small, with the test height approximately half the test length, bearing subanal and peripetalous fascioles. Frontal ambulacrum narrow and lightly depressed, forming a narrow, shallow frontal notch. Petals lightly depressed with subparallel pore series; anterior pair widely splayed, posterior pair less so. Anterior interambs with conspicuous depressions confluent with depressions of the anterior petals. Primary tubercles present on the anterior plate series of the frontal interambs.

Remarks. Brissopatagus is a poorly defined genus. It was proposed for two incompletely known species: *B. caumonti* from the Eocene of France; and *B. javanicus* Cotteau (1863: 144), originally described as *Spatangus?* sp. by Herklots (1854: 13, pl. 3, figs. 2, 2a, 2b). The latter was reported from the Eocene of Java by Cotteau, but Gerth (1922: 520) revised the age to middle Miocene. Each of the species is apparently known from a single specimen; that representing *B. javanicus* is an internal mould and shows no tuberculation, whereas that representing *B. caumonti* is an eroded, somewhat deformed specimen. So far as their morphology can be observed, the two species show good agreement in test shape and in the nature of the ambulacra.

B. caumonti, the type species by subsequent designation, forms the basis of *Brissopatagus* and is redescribed and refigured below. The specimen shows traces of a peripetalous and a subanal fasciole which have not hitherto been recorded. Cotteau's figures of the specimen, as typical of fossil echinoid illustrations of that time, are idealized. The distribution of primary tubercles is of particular significance. Those shown in Cotteau's figures are fictitious; the original specimen shows traces of a few primaries on the anterior plate series of the anterior paired interambs, but the remainder have been removed by erosion.

Brissopatagus, in the sense of the type species, is closely related to *Eupatagus,* with which it has been grouped as a subgenus by some authors (Dames, 1878; Cooke, 1959). It is also closely related to *Macropneustes.* The only character by which it can adequately be differentiated from these two genera is the depressions of the anterior interambs. The genus is also affiliated with *Gillechinus* Fell (based on *G. cudmorei* Fell, 1964, p. 213, pls. 1, 2), which is discussed in detail below. Phillip (1966: 114) has proposed that *Gillechinus* be treated as a synonym of *Brissopatagus.* A comparison of the type species of the two genera shows at once that such a view is untenable. *G. cudmorei* lacks the interambulacral depressions of *B. caumonti,* an essential character of *Brissopatagus,* as Fischer (1966) indicates. Further, *G. cudmorei* is clearly distinct from *B. caumonti* in that its primary tubercles are restricted to the posterior plate series of the paired interambs. If *Brissopatagus* is to be taken as including forms lacking interambulacral depressions and possessing primary tubercles on the anterior plate series of the paired interambs, then it is transitional to *Eupatagus* through species like *E. lamberti* Fourtau and *E. cordiformis* Duncan and Sladen and is indistinguishable from *Macropneustes.*

Subsequent to its erection, a number of species have been referred to *Brissopatagus*. Several possess characters of both *Brissopatagus* and *Gillechinus*, so that their correct generic assignment is not immediately apparent. For the reasons given in the discussion of *Gillechinus*, those with primary tubercles restricted to the posterior plate series of the paired interambs are referred to that genus. The remaining species are *B. colligoni* Lambert (1933: 37, pl. 4, fig. 21) from the Eocene of Madagascar and *B. sundaicus* Böhm (1882: 365, pl. 2, figs. 2a, b) from Madura Island north of Java. *B. sundaicus* is no older than Miocene in age, as no Lower Tertiary rocks are known to crop out on Madura Island (van Bemmelen, 1949: 106). This species, like *B. javanicus*, possesses distinct interambulacral depressions, but both species are represented by internal moulds alone, so that the nature of their tuberculation is not known and they cannot be referred to either *Brissopatagus* or *Gillechinus* with certainty. *B. collignoni* was described from crushed material that shows primary tubercles on both plate series of the paired interambulacra, and thus it agrees with *Brissopatagus* rather than *Gillechinus*. However, its interambulacral depressions are very weakly developed, and it may prove to be best included in *Eupatagus* or *Macropneustes*. The existence of transitional species showing characters of more than one genus is, of course, an inevitable consequence of evolution, since intermediate stages must often persist after generic stocks have differentiated. While such species are valuable indications of the relationships and origins of generic stocks, it becomes a matter of practical convenience to tolerate these transitional inter-generic taxa, whilst maintaining the validity of the formal genera which they seem to link. Any other course would result in the fusion of large groups of species in ever larger generic categories, as more intermediate forms are discovered from intermediate horizons, and as clines are elucidated from wider geographic sampling. Under the Linnaean system of taxonomy, we are compelled to base our generic diagnoses upon the characters seen in the original genotypes. In the case of *Brissopatagus* and *Gillechinus*, these characters are given by the type material, and they confirm the opinions of Mortensen (1951), Fell (1964), and Fischer (1966).

In summary, *Brissopatagus* as here restricted has but a single undoubted representative, *B. caumonti* from the Eocene of Biarritz, France. It is doubtfully represented in the Eocene of Madagascar (*B.? collignoni*) and may occur in the Miocene of the Javanese area (*B.? javanicus, B.? sundaicus*).

BRISSOPATAGUS CAUMONTI Cotteau

Plate 5, figs. 2-4.

Brissopatagus caumonti Cotteau, 1863: 144, pl. 8, figs. 3-7.
Brissospatangus caumonti; Cotteau, 1886: 136, pl. 30, figs. 1-4.

Holotype. 409- 1A- Co 1-2- b 132 (École des Mines, Paris).

Description. Test of moderate size, low vaulted, elongate; apical system anteriorly excentric, apex near the posterior margin. Anterior ambitus broadly rounded and cut by a narrow, shallow, frontal notch. Posterior ambitus somewhat tapered and more narrowly rounded. Apical system cannot be clearly seen but appears to possess four gonopores. Traces of peripetalous and subanal fascioles are present, the former not indented between the petals and the latter complete and reniform. Peristome small, crescentic, anterior; periproct vertically elongate and situated on the truncated posterior test surface.

Aboral surface: Frontal ambulacrum depressed on the adambital half of its length; its pores not preserved. Paired petals distinctly depressed with ovate pores. Anterior pair short, widely splayed, and anteriorly concave; each has about 12 well-developed pore pairs. Posterior pair somewhat longer, set close together, and straight, with about 20 well-developed pore pairs. Interambulacra 2 and 3 with conspicuous depressions forming concavities in the test continuous with those of the anterior paired petals. Ornament almost entirely lacking due to erosion of the specimen; a few primary tubercles preserved on the anterior plate series of interambulacra 2 and 3. The few patches that have escaped severe erosion suggest that much of the adoral surface was originally ornamented with small, dense, secondary tubercles.

Oral surface: Not well preserved. Plastron with a well-developed median keel and ornamented with dense secondary tubercles. Labrum appears to be long and narrow. Other interambulacral areas also bear dense secondaries. Ambulacra adjacent to the plastron appear to be narrow and, like the anterior ambulacral areas, naked except perhaps for miliary tubercles.

Remarks. The specimen is badly eroded and somewhat deformed. The interambulacral depressions adjacent to the anterior petals, although undoubtedly natural structures, have been accentuated by deformation. As far as can be deduced from Cotteau's descriptions, the specimen to hand is the only known representative of *B. caumonti.* The illustrations given by Cotteau are strongly idealized, as may be suspected from the discrepancies between those given in the two reports. The nature of the apical system and

arrangement of the plates on the oral surface as depicted by Cotteau are fictitious. On the original specimen, the groove of the frontal ambulacrum does not reach as close to the apical system as depicted by Cotteau, nor are the posterior petals as divergent.

Genus *GILLECHINUS* Fell, 1964

Type species. G. cudmorei Fell (1964: 213, pls. 1, 2); by original designation.

Gillechinus Fell, 1964: 213; Phillip, 1966: 114; Fischer, 1966: 584.

Diagnosis. Test of moderate size, with the test height approximately half the test length, bearing peripetalous and subanal fascioles. Frontal ambulacrum weakly depressed, frontal notch broad and shallow. Petals lightly depressed, narrow, with subparallel pore series; anterior petals widely splayed, posterior pair less so. Interambulacra of the aboral surface ridged at or near the suture of the two plate series, with ridges of the paired interambs subtending flattened or concave surfaces posterior to the adjacent ambulacral depressions. Primary tubercles restricted to posterior plate series of the paired interambulacra within the peripetalous fasciole.

Remarks. As already pointed out, *Gillechinus* cannot be synonymised with *Brissopatagus,* as advocated by Phillip (1966), because the interambulacral depressions diagnostic of *Brissopatagus* are not shown by the type species of *Gillechinus.* A further distinction is provided by the restriction of primary tubercles to the posterior plate series of the paired interambs of *Gillechinus,* a feature not shown by *Brissopatagus.* There are, however, a number of species that have previously been referred to *Brissopatagus* and that possess both interambulacral depressions and tuberculation of the *Gillechinus* style. To classify these forms, it is necessary to decide which of the two characters is taxonomically significant. The species concerned are as follows:

G. alabamensis (Cooke) (1942: 58, pl. 4, figs. 7, 8) from southeast U.S.A. and possibly Cuba. = *B. georgianus* Cooke (1942: 58, pl. 7, figs. 8-11) and possibly *B. avilensis* Sánchez Roig (1951: 45, pl. 33, figs. 2, 3). Eocene and possibly Oligocene.

G. beyrichi (Dames) (1878: 82, pl. 11, figs. 2a, b) from north Italy. Eocene.

G. humei (Fourtau) (1908: 218, pl. 2, fig. 8) from north Africa. Eocene.

G. lummaui (Castex) (1930: 82, pl. 4, fig. 1) from France. Eocene.

G. sindensis (Duncan and Sladen) (1884: 226, pl. 38, figs. 19-21) from India. Eocene.

One further species, originally referred to *Macropneustes,* must be added:

G. mexicanus (Dickerson and Kew) (1917: 134, pl. 24, fig. 3, pl. 25, figs. 1a, b) from northeast Mexico. Upper Oligocene or Lower Miocene.

Gillechinus georgianus was synonymised with *G. alabamensis* by Cooke (1959: 92). *G. avilensis* is not well known, but the grounds for maintaining it as distinct, given by Sánchez Roig (1951) as its more depressed petals and less pronounced groove for the frontal ambulacrum, are slight and likely to be due to infraspecific variation. *G. lummaui* and *G. alabamensis* may prove to be synonymous; *G. lummaui* appears to be less inflated, and its anterior interambs have more primary tubercles than those posterior, while the reverse is true of *G. alabamensis.* The first distinction could be due to the slight crushing evident from Castex's (1930) figure, and the second could be due to infraspecific variation. *G. mexicanus* is closely related to *G. cudmorei,* differing mainly in its less inflated posterior oral surface. *B. sindensis* is more elongate than any of the other species, and *B. humei* is likewise readily distinguished by its more depressed frontal ambulacrum and deeper frontal notch. *G. beyrichi* is characterized by possessing more prominent interambulacral depressions than any of the other species.

The six species show considerable variation in the development of interambulacral depressions. In *G. beyrichi* they are well developed, apparently forming actual concavities on the test surface. The anterior depressions of *G. sindensis* are recorded by Duncan and Sladen (1886) as forming concavities on the test. However, in the remaining species the paired interambulacra appear to possess flattened surfaces subtended posteriorly from a tumid zone near the median suture of the two plate series. The flattened surfaces pass into confluence with the depressions of the paired petals and give the impression of interambulacral depressions. Homologous structures are well developed in *Taimanawa* and *Plagiobrissus,* and can be recognized on the type species of *Gillechinus, G. caumonti.* Such structures cannot be regarded as identical with the strong interambulacral concavities of *Brissopatagus.* It is significant that the interambulacral depressions of all six species are developed in all four of the paired interambs, whereas in *Brissopatagus* these structures are restricted to the anterior paired interambs. There is little doubt that the six species are closely related; it must be concluded that interambulacral depressions are a variable character in

this species group, and the point at which they can be regarded as present or absent is not easily defined.

The restriction of the primary tubercles to the posterior plate series of the paired interambs is a conspicuous feature of all six species and is highly unusual for members of the *Brissidae*. This feature not only shows the six species to be very closely affiliated with *G. cudmorei* but provides a convenient diagnostic character for *Gillechinus*, separating it from all other brissid genera with the exception of *Lajanaster* Sánchez Roig. *Lajanaster* differs in possessing an elongate, strongly flattened test, and its oral surface, like that of *Plagiobrissus*, has a narrow plastron and very narrow ambulacral areas. In consequence, the six species here discussed are referred to *Gillechinus*.

Brissopatagus vilanovae Cotteau (1890: 19, pl. 2, figs. 9-13) is somewhat transitional between *Gillechinus* and *Eupatagus*. It has primary tuberculation of the *Gillechinus* style, but its petals are spatangiform with curved pore series rather than with subparallel pore series as in *Gillechinus*. For this reason the species is probably best referred to *Eupatagus*, whereupon it becomes a homonym of *B. vilanovae* Cotteau (1890: 10, pl. 1, figs. 1-4) and has been renamed *E. ibericus* by Lambert.

Gillechinus enjoyed a wide distribution in tropical and subtropical seas during Eocene time. It may range as high as the Miocene, but the Oligocene age given for *G. avilensis* by Sánchez Roig (1951) and the Upper Oligocene — Lower Miocene age given for *G. mexicanus* by Dickerson and Kew (1917) are unsupported and must be treated with caution.

TABLE I

DIMENSIONS OF TAIMANAWA AND BRISSOPATAGUS

	tl	tw	th	aa	apl	apw	aps	ap	ppl	ppw	pps	pp	at	pt	nw	nd
*OU. 8568c	*c*70.0	*c*67.0	*c*19.0	*c*30.0	19.0	4.0	35.0	14	20.0	4.0	19.5	14	7	10	13.5	*c*6.7
*OU. 8590	*c*110.0	*c*108.0	*c*30.0	55.0	34.0	6.3	*c*60.0	18	29.0	6.0	31.0	16	12	15	17.0	14.0
*EC. 426		*c*109.0	*c*30.0	*c*64.0	34.0	6.2	59.5	19	31.0	6.0	34.0	17	14	16		
†EC. 474	*c*58.0	*c*54.0		*c*31.5	17.0	3.3	29.0	20	15.0	3.2	17.0	17	10	12	10.0	5.5
†EC. 615	*c*123.0	*c*114.0		*c*58.0	37.0	5.0	*c*58.0	25	35.0	4.8	c38.5	24	*c*20	*c*22		
†OU. 8547	*c*123.0	*c*116.0		64.0	35.0	5.0	*c*62.0	24	34.0	5.0	*c*36.0	20	24	27	14.5	13.0
†OU. 8598	133.5	*c*114.0	43.0	65.5	42.0	6.0	68.0	25	40.0	6.0	41.5	23	31	34	15.0	14.0
†OU. 8545		*c*115.0	*c*35.0	*c*71.0	39.0	6.4	65.0	24	38.0	6.4	38.5	23	24	28	15.0	16.0
†EC. 471	134.0	119.0		68.0	41.0	6.5	69.5	23	41.0	6.0	41.0	22	27	23	15.5	16.0
†OU. 8601		124.0		65.0	42.0	6.0	67.5	23	37.0	6.0	*c*38.5	22	24	27	17.5	13.0
†OU. 8606	151.0	136.0		77.0	43.0	7.0	73.0	23	40.0	6.5	44.0	20	24	35	17.0	15.5
B. caumonti	40.5	35.0	19.5	14.5	10.5	2.5	18.5	12	13.5	2.5	*c*8.0	20			7.5	0.6

* *T. pulchella;* † *T. greyi.* Test length (tl); test width (tw); test height (th); distance from apical system to anterior margin (aa); length of anterior petals (apl); width of anterior petals (apw); distance between distal tips of anterior petals (aps); number of fully developed pore pairs in each anterior petal (ap); length of posterior petals (ppl); width of posterior petals (ppw); distance between distal tips of posterior petals (pps); number of fully developed pore pairs in each posterior petal (pp); number of primary tubercles in each anterior interamb (at); number of primary tubercles in each posterior interamb (pt); width of frontal notch (nw); and depth of frontal notch (nd). All measurements in millimeters.

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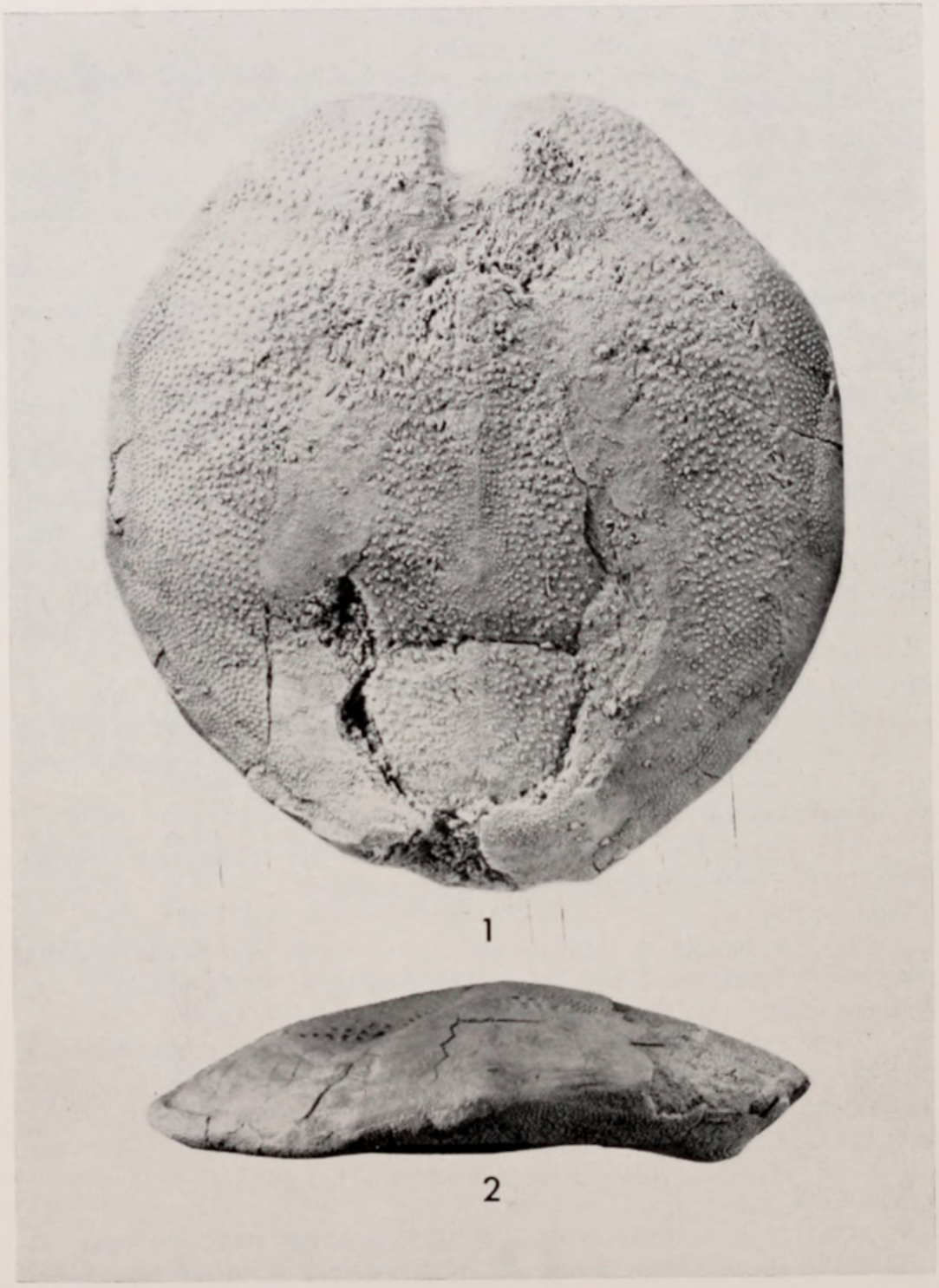

PLATE 1

FIGS. 1, 2. *Taimanawa greyi* (Hutton), dorsal view (Fig. 1), lateral view (Fig. 2). OU. 8598, test length 135.5 mm; (×⅔).

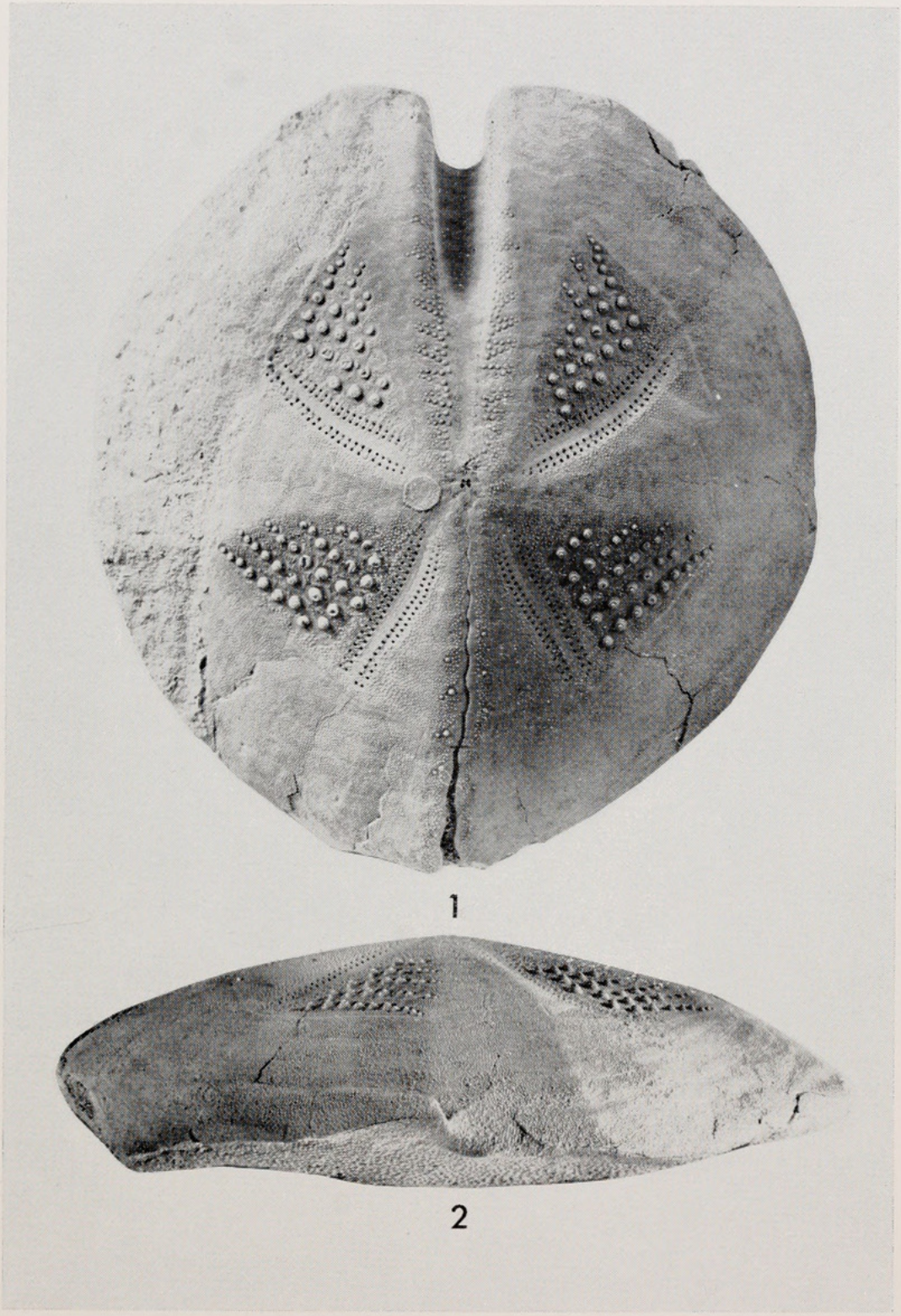

PLATE 2

FIG. 1. *Taimanawa greyi* (Hutton), ventral view. OU. 8598, test length 133.5 mm; (×⅔).

FIG. 2. *Taimanawa pulchella* sp. nov., lateral view. Holotype, OU. 8590, test length *c* 110.0 mm; (×⅔).

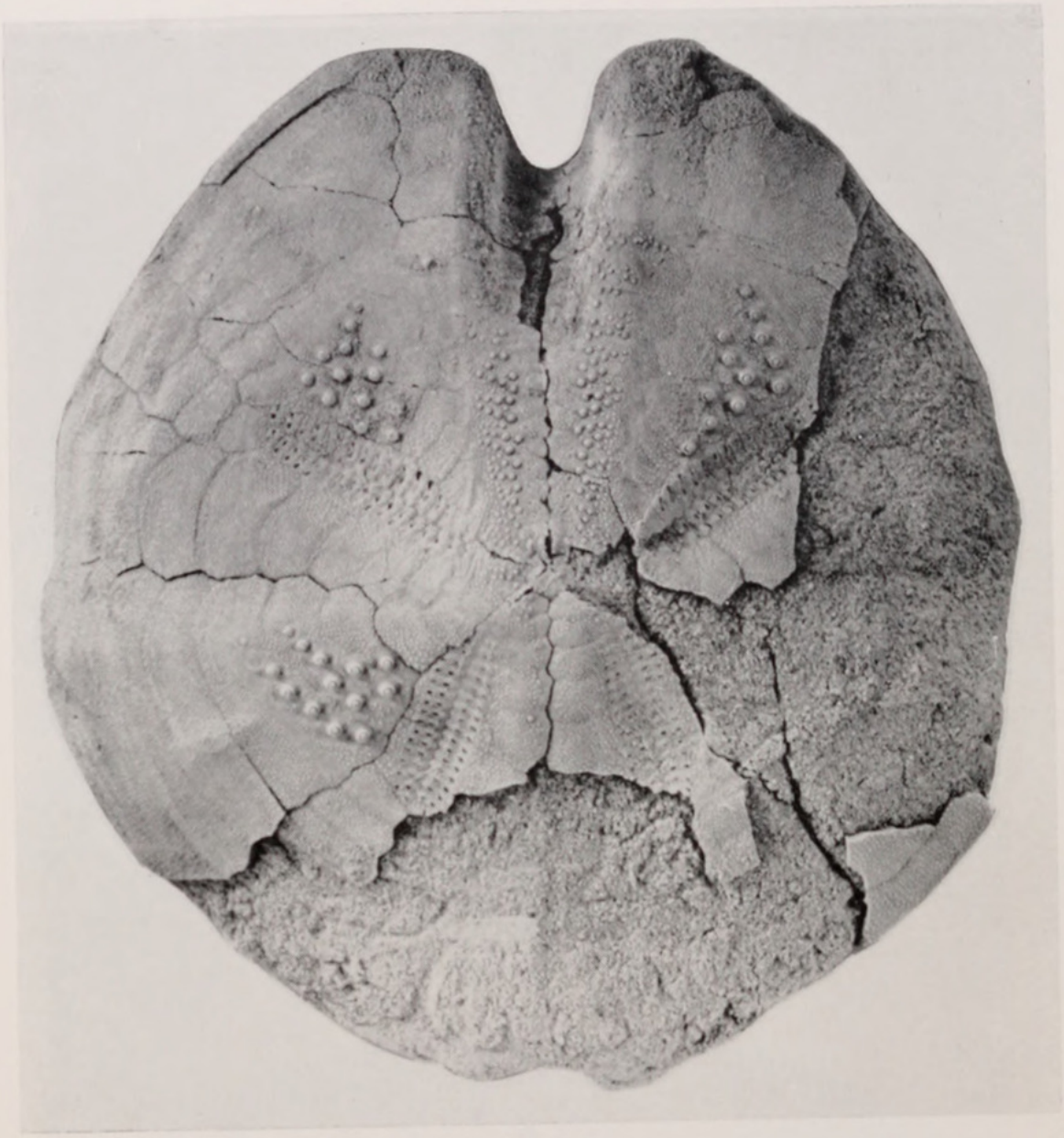

PLATE 3

Taimanawa pulchella sp. nov., dorsal view. Holotype, OU. 8590, test length *c* 110.0 mm; (×1).

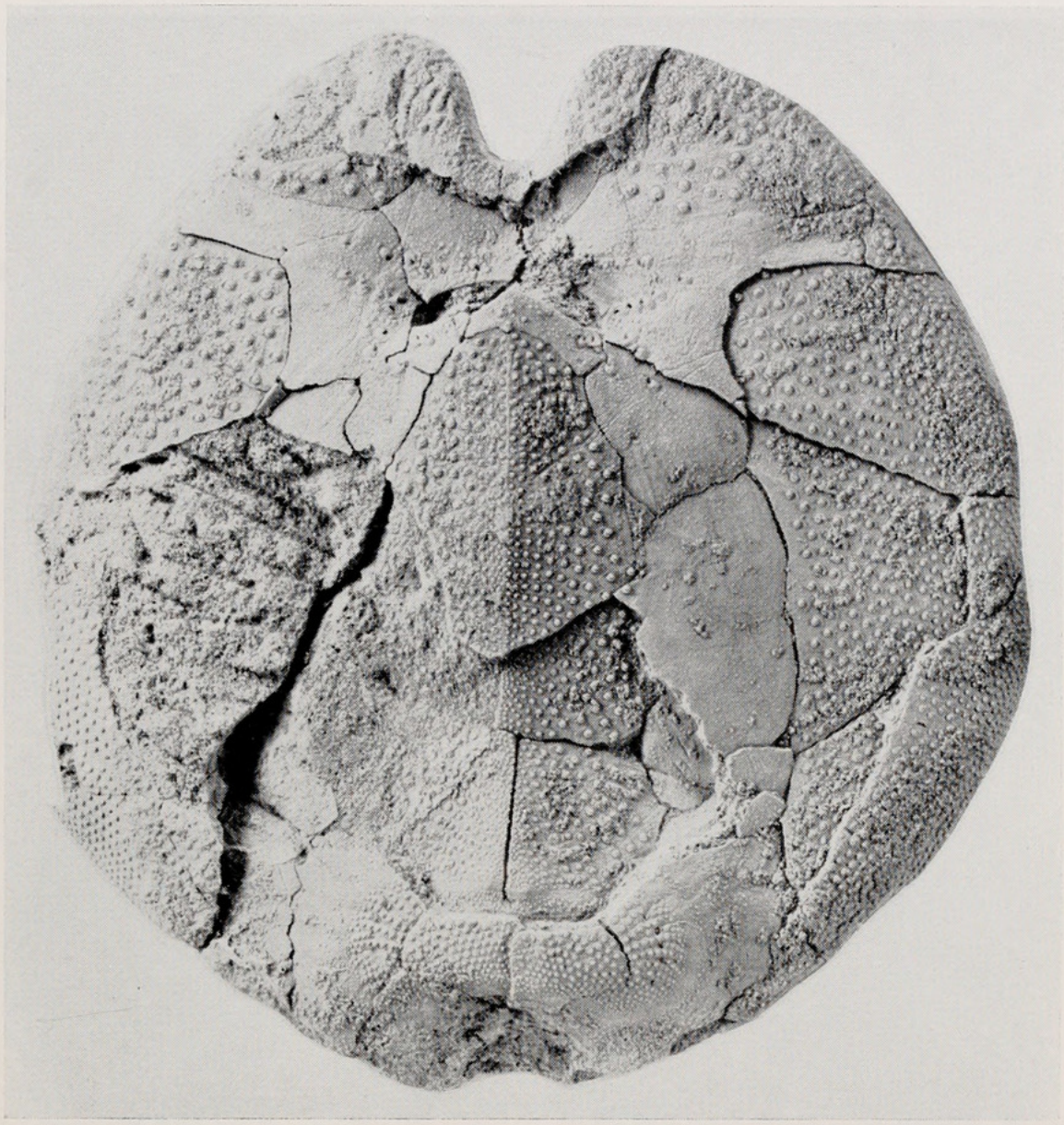

PLATE 4

Taimanawa pulchella sp. nov., ventral view. Holotype, OU. 8590, test length *c* 110.0 mm; (×1).

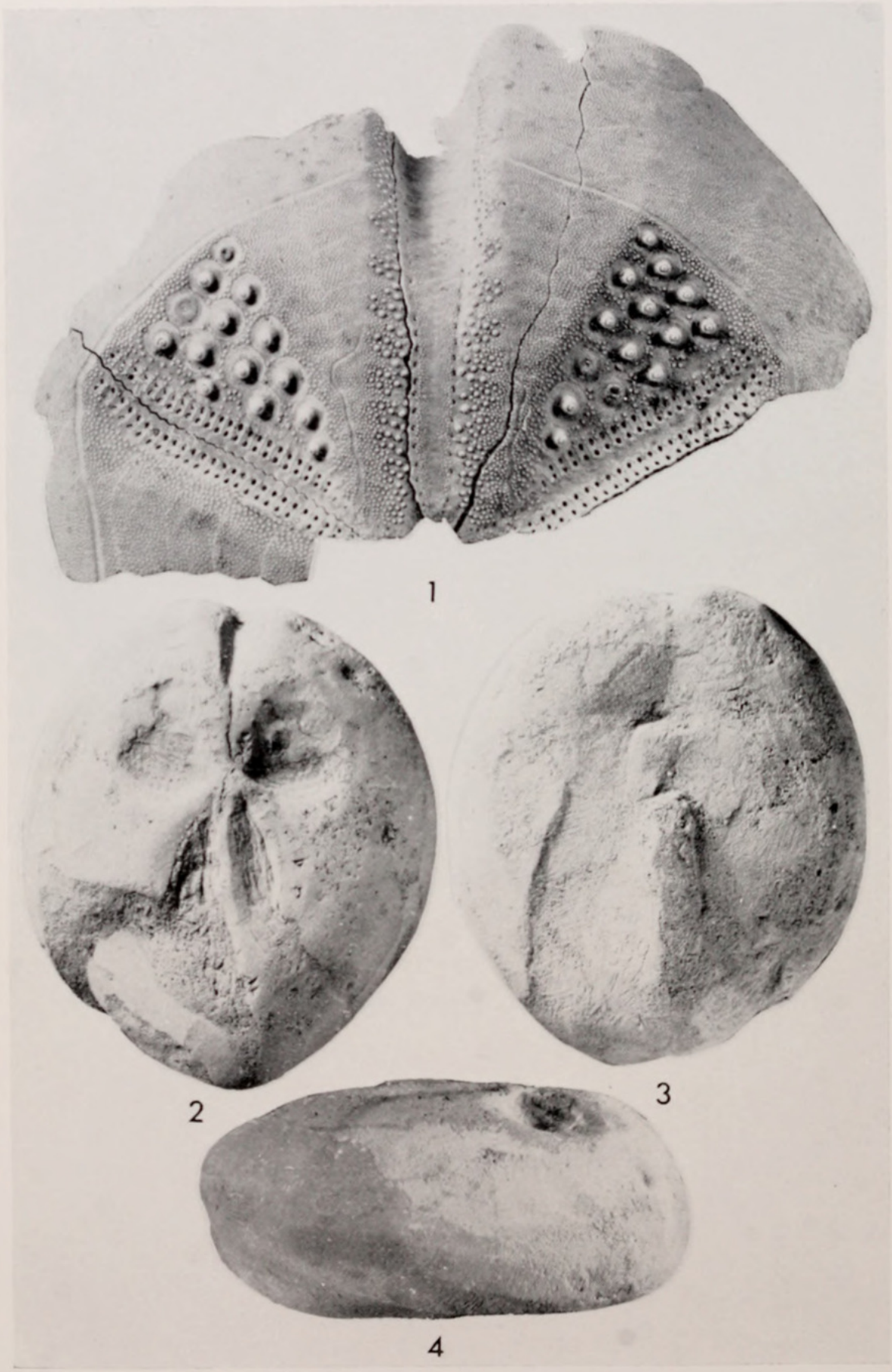
1
2
3
4

PLATE 5

FIG. 1. *Taimanawa mortenseni* sp. nov., dorsal view. Holotype, fragments of a specimen from Station 32 of the Danish Expedition to the Kei Islands (1922), University Zoological Museum Copenhagen, width of fragment 105 mm; (× *c* 1).

FIGS. 2-4. *Brissopatagus caumonti* Cotteau, dorsal view (Fig. 2), ventral view (Fig. 3), lateral view (Fig. 4). Holotype, 409- 1A- Co 1-2- b 132, École des Mines, Paris, test length 40.5 mm; (Xc1).