

MALAYOMAORICA GEN. NOV. (FAMILY
AVICULOPECTINIDAE) FROM THE
INDO-PACIFIC UPPER JURASSIC;
WITH COMMENTS ON RELATED
FORMS

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ABSTRACT. Critical reinvestigation of the aviculopectinid form '*Aucella*' *malayomaorica* Krumbeck from the late Jurassic of the Indo-Pacific region indicates that it does not belong either to the genus *Buchia* (= *Aucella*) or to any other known aviculopectinid genus. A new genus *Malayomaorica* is erected to receive '*Aucella*' *malayomaorica*. This genus is characterized by: (1) presence of a submedian furrow-like excavation in the ligamental pit of the left valve; (2) presence of an irregularly shaped tooth-like bulge in front of the ligamental pit at the anterior margin of the left ligamental plate; (3) presence of a strong ligamental ridge rising above the true dorsal shell margin in the right ligamental plate; and (4) a wide to very wide byssus notch.

Malayomaorica gen. nov. is much more closely allied to *Meleagrinnella*, *Aucellina*, and *Arctotis* than to *Buchia*. This genus is, accordingly, placed in subfamily Oxytominae and not in Buchiinae (= Aucellinae). The genus *Aucellina* is also placed in the Oxytominae, as it appears to be an independent offshoot of *Meleagrinnella* unrelated to *Buchia*.

The boreal genus *Arctotis* is the closest known ally of *Malayomaorica*. The latter is accordingly interpreted as an offshoot of the *Arctotis* lineage, which immigrated, together with the true *Buchia* species, into the Indo-Pacific region during the early part of the Upper Jurassic.

THE purpose of this paper is to establish a new genus for a peculiar aviculopectinid pelecypod from the Upper Jurassic (Kimeridgian) of Indonesia and New Zealand, as well as to investigate the morphological distinctions and probable phylogenetic ties of this biochronologically important genus.

'*Aucella*' *malayomaorica* Krumbeck 1923 has been the source of a considerable taxonomical and biochronological confusion ever since its original description by Boehm (1911) under the name of *Aucella plicata* Zittel. This species has been assumed to be an 'archaic' member of the genus *Buchia* (better known as *Aucella*) closely allied to the so-called *Buchia radiata-impressae* species group from the Oxfordian stage of Europe (Krumbeck 1923, pp. 70-74). It was, consequently, widely assumed to be of the early Upper Oxfordian age in terms of the international standard stages by the European workers who studied Upper Jurassic rocks and faunas of Indonesia and New Zealand (e.g. Krumbeck 1923, 1934; Wandel 1936; Stolley 1929). At about the same time, however, Crickmay (1932, p. 5) has made an astute but undeservedly neglected observation that: '*Aucella* from the more southerly localities, e.g. India, and New Zealand, are very different, and hardly congeneric.' This conclusion appears to be quite correct, at least so far as '*Buchia*' *malayomaorica* (and possibly '*Buchia*' *misolica*) is concerned.

The Oxfordian dating of '*Aucella*' *malayomaorica* beds has been recently refuted by Fleming (1958, p. 379; 1960, p. 267, table 1), who was able to demonstrate their early to mid-Kimeridgian age. Fleming (1958, p. 380) has, furthermore, concluded that: 'two parallel lineages [of *Buchia*; writer's remark], one represented by *malayomaorica* and

misolica, the other by the *plicata-subpallasi* group, lived in the south-east Tethyan region during the Kimeridgian-Tithonian.'

Several Upper Jurassic *Buchia* forms of the Canadian Western Cordillera appear to be closely allied to and are possibly conspecific with *Buchia spitiensis* (Holdhaus), *B. leguminosa* (Stoliczka), and *B. blanfordiana* (Stoliczka) of the Indo-Pacific region (Jeletzky 1950, pp. 28-29; 196-). The present paper explains the reasons for the statement (Jeletzky 196-) that ' "*Buchia*" *malayomaorica* is rather different from and probably not congeneric with either the boreal *Buchia* (better known as *Aucella*) or the *Buchia plicata-subpallasi* species group of the Indo-Pacific region.'

The writing of this paper has been facilitated by valuable comments from Dr. C. A. Fleming, Senior Palaeontologist of the New Zealand Geological Survey, who also has kindly provided the writer with several well-preserved specimens of '*Aucella*' *malayomaorica* Krumbeck 1923 from the Kawhia section. It is published by permission of the Director, Geological Survey of Canada.

SYSTEMATIC DESCRIPTION

Family AVICULOPECTINIDAE Etheridge, Jr., 1906 emend. Newell 1938

Subfamily OXYTOMINAE Ichikawa 1958

Genus MALAYOMAORICA gen. nov.

Plate 21, figs. 1-2

Derivation of name. Malayo for the Malay Archipelago; maorica for Maori, the name of the New Zealand native people. Gender feminine.

Type species. *Aucella malayomaorica* Krumbeck (1923, pp. 65-76, pl. clxxiii, figs. 2-12, 17; pl. clxxvii, figs. 13a-b). Early to mid-Kimeridgian beds of Indonesia and New Zealand.

Diagnosis. Ligamental plate of the left valve separated into two parts by a submedian transverse furrow. This transverse furrow is a modification of the spoon-like excavation of the ligamental pit of some other members of the family. This furrow extends all across the ligamental plate from the very tip (underside) of the beak to its lower margin. The lower margin of the ligamental plate is indented at the lower end of the furrow.

The anterior part of the ligamental plate is markedly thickened; it carries an irregularly shaped bulge and an articulation furrow (= 'Gelenkgrube') near the anterior margin.

The byssus notch of the right valve is wide to very wide and broadly triangular in shape. The middle part of the ligamental plate of the right valve has an irregularly swollen, strong ligamental ridge, which rises above the true dorsal shell margin and is directed obliquely upward and forward. This ligamental ridge fits into the transverse furrow of the left ligamental plate.

Type specimen and synonymy. No previous selection of the type specimen of *Malayomaorica malayomaorica* (Krumbeck 1923) is known to the writer. The left valve represented in pl. clxxiii (2), fig. 4 of Krumbeck's (1923) work is, therefore, selected herewith as the lectotype of the type species of the genus *Malayomaorica*. It is from the so-called *Aucella* horizon of Portuguese Timor, and was collected between Bele and Tooï near Kampong Kamlachi, in calcareous marl with *Inoceramus*. According to Dr. Fleming, it is preserved in Geol. Pal. Inst., Bonn.

Fleming (1958, p. 378), Glaessner (1945), and Marwick (1953) have placed *Aucella boehmi* Marwick 1926 into the synonymy of '*A.*' *malayomaorica* Krumbeck 1923. Most other workers concerned (beginning with Krumbeck 1934) have, of course, been aware of the fact that '*Aucella*' *plicata* Boehm non Zittel from Kawhia Point is conspecific with '*Aucella*' *malayomaorica* Krumbeck; they have, however, overlooked the fact that this New Zealand form was formally named by Marwick.

There is little doubt that '*Aucella*' *boehmi* Marwick 1926 is both congeneric and conspecific with *Malayomaorica malayomaorica* (Krumbeck 1923). The characteristic furrow-

EXPLANATION OF PLATE 21

(Unless otherwise indicated, all specimens are reproduced natural size. To facilitate the comparison of their shapes, the valves of the pelecypods figured are, as a rule, oriented with their hinge margins uppermost.)

Figs. 1A-G. *Malayomaorica malayomaorica* (Krumbeck 1923). New Zealand, North Island, north-east coast of Heteri Promontory, Kawhia Harbour. Heterian stage (early to mid-Kimeridgian). A topotype of *Buchia boehmi* Marwick 1926. GSC Cat. No. 17006.

Left valve of a variant with a strongly reduced anterior ear. The semi-smooth appearance of most of the anterior part of the valve (fig. 1E) appears to be due to its abrasion. 1A: Dorsal view of the beak part. 1B: Oblique posterior view of the ligamental plate. Note the furrow-like excavation of the middle part of the ligamental pit. The ligamental plate occupies all of the underside of the beak. 1C: Posterior view. Note the predominance of the concentric, lamellar growth-lines on this part of the valve. 1D: Anterior view. Note the rounded, tooth-like bulge at the anterior rim of the ligamental plate and the pronounced embayment of the valve's margin underneath it. 1E: View from the left. Note the strongly reduced anterior ear and well-developed posterior ear. 1F: The beak part and the ligamental plate, $\times 3$. Oriented exactly as in fig. 1B. 1G: Inside view.

Figs. 2A-F. *Malayomaorica malayomaorica* (Krumbeck 1923). Same locality and age as for the specimen shown in figs. 1A-G. GSC Cat. No. 17007. Complete shell with its valves almost in normal position relative to each other. A variant with typically developed anterior and posterior ears of the left valve and typically developed and well-preserved sculpture of both valves. The flattened, folded appearance of the toothlike bulge at the anterior margin of the ligamental plate of the left valve (figs. 2A and 2F) appears to be an individual feature peculiar to this specimen.

2A: Right valve viewed from the right. The transversally grooved ligamental plate of the left valve and the underside of the left beak are clearly visible. Note that the ligamental plate occupies all of the underside of the left beak up to its very tip. The wide gap between the byssus ear and the anterior ear of the right valve is characteristic of *Malayomaorica*. 2B: Left valve viewed from the left. Note the predominance of radial ribbing over the concentric growth-lines and the nodose to spinose appearance of radial ribs at their intersections with the concentric growth-lines. This ornament contrasts strongly with that of *Buchia erringtoni* (Gabb) shown in figs. 8A, B, F, 2C: Anterior view of both valves. 2D: Posterior view of both valves. 2E: Dorsal view of the beak parts of both valves. 2F: Beak part of the right valve, $\times 3$ viewed from the right. Oriented as in fig. 2A. Note the sculpture of the surface of the byssus ear and the marked bend of the latter toward the left valve.

Fig. 3. *Buchia mosquensis* (Buch non Keyserling non Lahusen). Canada, N.W.T., Mackenzie District, Richardson Mountains, East slope of Aklavik Range, southern side of nameless creek falling into Husky Channel, about $\frac{3}{4}$ mile south of the top of Mount Gifford. Collected on the float of the basal part of lower shale-siltstone division. Middle to late Kimeridgian. GSC Cat. No. 17008. An early form of the species somewhat transitional to *Buchia* ex gr. *concentrica* (Sowerby)-*erringtoni* (Gabb). An internal cast of right valve viewed from the right. The central part of the valve, including its beak part, is strongly abraded.

Fig. 4. *Buchia mosquensis* (Buch non Keyserling non Lahusen). Same locality and age as for the specimen shown in fig. 3. GSC Cat. No. 17009. An early form of the species somewhat transitional to *Buchia* ex gr. *concentrica* (Sowerby)-*erringtoni* (Gabb). Inside view of the right valve with the well-preserved shell layer. The concentric ornament is just as well developed as on the surface of the shell.

like excavation of the ligamental pit is neither visible in Krumbeck's (1923) drawings nor clearly described in the text. This feature was, however, excellently figured and described by Wandel (1936, p. 457, pl. xvii, figs. 2-3), who has been able to study Krumbeck's (1923) original material of the species.

Age and correlation. Krumbeck (1923, expl. of pl. clxxii (2), fig. 2) has tentatively dated the *Malayomaorica malayomaorica* beds of Indonesia as of early Upper Oxfordian age. Fleming (1958, p. 379; 1960) has recognized more recently, however, that in New Zealand

while the radial ornament is subdued compared with its development on the shell's surface. Note the simply grooved, *Meleagrionella*-like appearance and orientation of the inside surface of the byssus ear, which differs from that of the younger *Buchia* species (e.g. *B. piochii* var. *russiensis* shown in figs. 5D, E).

Figs. 5A-E. *Buchia piochii* (Gabb) var. *russiensis* (Pavlov). Canada, N.W.T., Franklin District, Prince Patrick Island, Mould Bay, lat. 76° 16' 30" N., long. 119° 27' 9" W. Collected on the float of Mould Bay Formation (restricted). Late Portlandian (s. str.) GSC Cat. No. 17010. A well-preserved right valve.

5A: View from the right. Note the pronounced bend of the byssus ear toward the left valve. The byssus ear of *Buchia mosquensis* (Buch) shown in figs. 3-4 is, in contrast, oriented more or less in the plane of contact of the valves. 5B: Anterior view. Note that the anterior surface of the byssus ear is oriented almost perpendicular to the plane of contact of the valves. 5C: Posterior view. 5D: Inside view. $\times 3$. Note the pronouncedly spoonlike appearance of the inside surface of the byssus ear contrasting with the simply grooved appearance of the same in *Buchia mosquensis* (Buch) shown in fig. 4. 5E: Dorsal view of the beak part, $\times 3$, to show structural detail of the right ligamental plate and byssus ear. Note that the byssus ear is oriented almost perpendicularly to the plane of contact of the valves (plane of symmetry of the shell).

Figs. 6A-C. *Buchia keyserlingi* (Lahusen 1888) s. lato. East Greenland, Trail O. Locality 92 of Donovan (Medd. om Gronl. Bd. 111, No. 4, 1953, pp. 51-52). Middle or late Lower Valanginian. Property of Min. og Geol. Mus., Copenhagen.

A *Buchia crassicolis*-like variant of the species, possibly identical with *B. crassicolis* var. *gracilis* Sokolov, 1908 non Lahusen 1888. A well-preserved internal cast of the left valve with considerable patches of well-preserved shell layer. Note the pronouncedly lamellar appearance of concentric growth-lines and the absence of any radial ornament.

6A: Anterior view. 6B: Viewed from the left. 6C: Inside view of the beak and hinge areas, $\times 3$.

Figs. 7A-B. *Buchia piochii* (Gabb) var. *russiensis* (Pavlov). Same locality and age as for the specimen shown in figs. 5A-E. GSC Cat. No. 17011. A somewhat distorted and cracked left valve with excellently preserved shell layer.

7A: Inside view of the complete valve. 7B: Inside view of the beak part, $\times 3$, to show structural detail of the beak and ligamental plate. The ligamental plate is broken in the middle of the ligamental pit. The structure of the ligamental plate and the beak is closely similar to that of *Buchia keyserlingi* s. lato shown in figs. 6A-C.

Figs. 8A-F. *Buchia concentrica* (Sowerby) var. *erringtoni* (Gabb). Canada, Western Cordillera of British Columbia, Tyaughton Lake area, north side of a pass 1 $\frac{3}{4}$ miles north-west of Peak of Sheba. Lower part of Eldorado Group. Early Kimeridgian? GSC Cat. No. 17012.

A complete internal cast with valves in approximately normal position relative to each other. Small patches of the inner shell layer are preserved around the right beak and near the posterior margin of the right valve. The byssus ear is largely preserved as an internal cast. 8A: Left valve, viewed from the left. 8B: Right valve viewed from the right. The ligamental plate and beak of the left valve are clearly visible above the beak of right valve. 8C: Anterior view; 8D: Posterior view. 8E: Dorsal view of the beak part. 8F: Beak part of the right valve and the inside view of the left valve, $\times 3$. Note the far-reaching similarity of the structure of the byssus ear to that of *Buchia mosquensis* (Buch) shown in fig. 3 and its dissimilarity with that of *B. piochii* var. *russiensis* shown in figs. 5A-E. The left beak is clearly separated from the ligamental plate and protrudes above the latter as is the case in younger *Buchia* species.

this species occurs in early to mid-Kimeridgian rocks. The *M. malayomaorica* beds of Indonesia are, therefore, believed by the writer to be of early to mid-Kimeridgian age.

Morphological and taxonomic remarks. The morphology and infra-specific variability of *M. malayomaorica* have been described in detail by Krumbeck (1923), Marwick (1926), and Wandel (1936). The present discussion of its morphology can, therefore, be limited to description, illustration, and taxonomic analysis of those morphological features that are diagnostic or otherwise significant at the generic and family level.

The generally accepted reference of *M. malayomaorica* to the genus *Buchia* (= *Aucella*) is based exclusively on its morphological similarity to such European forms as '*Aucella impressae* Quenstedt and '*A. radiata* Trautschold. This is stressed in the following statement made by Krumbeck (1923, p. 73) in the original description of *M. malayomaorica*: 'Im ganzen kann es nach meiner Ansicht nicht zweifelhaft sein, dass *Aucella malayomaorica* den älteren Aucellen und zwar vor allem der *Impressae-Radiata*-Gruppe am nächsten steht und in dieser mit *A. impressae* die meisten und engsten Berührungspunkte aufweist. Von den übrigen mir bekannten Aucellen — vielleicht ausgenommen *A. plicata* Zitt, sp. — weicht sie . . . ab.' This conclusion has been accepted by all subsequent workers in its entirety. As we shall see, however, only Krumbeck's claim of the far-reaching similarity of *M. malayomaorica* to '*A. impressae* and '*A. radiata* is apt and valid. His assumption that these two European forms are true representatives of *Buchia* is, on the contrary, erroneous and based on their misinterpretation by Pompeckj (1901).

Malayomaorica malayomaorica typically possesses a fairly well-developed anterior ear in the left valve (Krumbeck 1923, p. 66; Wandel 1936, p. 457; this paper, Pl. 21, figs. 2A, B, F), although this ear can become strongly reduced and barely noticeable in some specimens (Wandel 1936, pl. xvii, figs. 9, 11; this paper, Pl. 21, figs. 1A, E, G).

The taxonomic significance of the presence or absence of the anterior ear in the left valve of *Buchia* has been discussed by Pompeckj (1901) in connexion with his reference of such aberrant forms as '*A. radiata* Trautschold and '*A. impressae* to this genus. The interpretation of these two Oxfordian forms as 'archaic' representatives of *Buchia* connecting this genus with *Pseudomonotis* (*Meleagrinnella* of recent usage) led Pompeckj (1901, pp. 327, 339, pl. xv, figs. 12, 16) to the revision of the generally accepted diagnosis of the former genus. Pompeckj concluded that the oldest representatives of *Buchia* possess a distinct, although short, anterior ear in the left valve, which becomes lost in the younger representatives of the genus. This conclusion has been strongly criticized by Sokolov (1908, 1912, and elsewhere).

Sokolov (1908, p. 3) insisted that the possession of an anterior ear in both valves and the peculiar shape of their beaks excludes '*Aucella radiata* and '*A. impressae* from the genus *Buchia*. Only the right valve figured by Pompeckj (1901, pl. xv, figs. 2, 5) under the name of *Aucella impressae* is a representative of *Buchia* according to Sokolov (1908, p. 3, footnote). A new name, *A. pompeckii*, was proposed for this form by Sokolov (1908), only to be passed later (Sokolov 1912, pp. 115–16) into the synonymy of *Buchia lata* (Trautschold).

To strengthen his argument Sokolov (1912, pp. 108–13; pl. 2, figs. 11a, b, 12a–13b) has redescribed and refigured the original specimens of '*Aucella radiata* Trautschold and was able to show that this species is in all respects a typical representative of the group of species formerly included in *Pseudomonotis* s. lato but now separated under the name

of *Meleagrinnella*. Sokolov (1912, pp. 115–16) points out in the same paper that the oldest-known true *Buchia* species, such as *B. lata* (Trautschold), occur already in middle to late Callovian rocks of Russia. They antedate, therefore, the Oxfordian '*A. impressae*' and '*A. radiata*', which have been assumed to be the oldest representatives of *Buchia* by Pompeckj (1901, pp. 327, 337). *B. lata* (Trautschold) is, moreover, already a typical representative of the genus in the complete absence of the anterior ear of the left valve and in the sculpture (see below). There is little doubt that Sokolov's (1908, 1912) criticisms of Pompeckj's (1901) treatment of '*A. radiata*' and '*A. impressae*' are fully valid.

Although published in German, in part at least (Sokolov 1908, pp. 26–27), Sokolov's conclusions have been completely ignored by those European workers who have made the most thorough study of *Malayomaorica malayomaorica* and unreservedly accepted Pompeckj's (1901) interpretation of *Buchia*. Krumbeck (1923, p. 71) actually stated that he did not use Sokolov's works, except for his plates.

As already seen, the presence of the anterior ear in the left valve suffices to exclude *M. malayomaorica* from the genus *Buchia*, as all its true representatives are characterized by the complete absence of the same. Its placement in this genus would probably never have been seriously contemplated except for the authority of Pompeckj's (1901) work and the unfortunate neglect of Sokolov's (1908, 1912) research.

Only Krumbeck (1923, p. 67) describes the ornamentation of *M. malayomaorica* in any detail. He stresses the strong variability of the ornamentation and the common occurrence of the specimens with more or less obsolete sculpture in all population samples available. Specimens characterized by the presence of the concentric ornament alone on parts or all of the shell are also common in his material.

Judging by the New Zealand specimens in the writer's possession (Pl. 21, figs. 1–2), the marked variation in strength and character of ornamentation from one specimen to another (or from one part of the shell's surface to another within a single specimen) is at least partly related to the degree of abrasion of the shells concerned prior to or after their burial. This abrasion (e.g. in specimen shown in Pl. 21, figs. 1A–G) was apparently facilitated by the restriction of ornamentation to the outer layers of the shell. The writer does not deny the strong variability of the ornamentation and the presence of specimens with obsolete sculpture. The sculpture of the specimen of *M. malayomaorica* shown in Plate 21, figs. 2A, B, F is, nevertheless, assumed to be typical of the species. The specimens of *M. malayomaorica* figured by Boehm (1911, pl. 2, figs. 2–4, non 1) and the specimen figured by Marwick (1926, pl. 71, fig. 10) are similarly strongly sculptured. The same is, finally, true of the herewith selected lectotype of the species (see above).

The ornament of the well-preserved specimens studied (Pl. 21, figs. 2A, B, F) consists of closely spaced, fine, sharp, and straight radial ribs intersecting more widely spaced concentric growth-lines (or growth-ridges). In our material the radial ribs are generally speaking stronger developed on the left valve, where they tend to be about as strongly developed as the concentric growth-lines (Pl. 21, fig. 2B). In the right valve the concentric growth-lines or growth-ridges are generally speaking more strongly developed than the radial ribs (Pl. 21, figs. 2A, F). The concentric growth-lines tend to be imbricated and lamellar in appearance in the best-preserved specimens; they also tend to become markedly frilled and to form small, ill-defined tubercles and spines whenever intersected by the radial ribs (Pl. 21, figs. 2A, B, F). The intersection of the radial and concentric elements of sculpture, which are about equally strongly developed, results in the markedly

reticulate appearance of some parts of the shell's surface. In the specimens available, I was not able to observe clearly the intercalation of the second-order radial ribs with the first-order radial ribs observed by Krumbeck (1923, p. 67).

The sculpture of *Malayomaorica malayomaorica* described above is quite unlike that of *Buchia*. As it can be seen in Plate 21, figs. 3, 6A, B, 8A, B, F, the ornament of *Buchia* is usually visible on the surface of internal casts as well as on the surface of the shell. Furthermore, as already noted by Sokolov (1912, p. 110), the concentric growth-lines (or growth-ridges) of *Buchia* are always much more pronounced than the radial ribs. The latter are either of a very low relief or almost unnoticeable, even in *Buchia ex gr. concentrica* (Sowerby) (= ? *B. bronni* Rouillier) (Pl. 21, figs. 8A, B, F), and are mostly completely absent in the majority of younger *Buchia* species (Pl. 21, figs. 6A, B). The imbricated appearance of the concentric growth-lines of *Malayomaorica malayomaorica* and the presence of small tubercles and spines on them is also quite foreign to *Buchia* and characteristic of *Meleagrinnella*. The same is true of the intercalation of the second-order radial ribs observed by Krumbeck (1923, p. 67). On the whole the ornamentation of *Malayomaorica malayomaorica* is distinctly more similar to that of *Meleagrinnella* than to that of *Buchia*. It differs, however, from that of *Meleagrinnella* in much greater strength of the concentric growth-lines (or growth-ridges). In *Meleagrinnella* the radial ribs are, indeed, always much stronger developed than the concentric growth-lines, which can be sometimes quite weak (as, for example, in *Meleagrinnella radiata* Trautschold, see Sokolov 1912, pl. 2, figs. 11a, 12a, c). The intercalation of the second-order radial ribs with those of the first order is, finally, much better developed in *Meleagrinnella* than in *Malayomaorica*.

The sculpture of *Arctotis* (Bodylevsky 1960, p. 44) differs from that of *Malayomaorica* in the same way as that of *Meleagrinnella*. It is, furthermore, coarser in the best-known representatives of the genus (Bodylevsky 1960, pl. 7, figs. 1a, b, 2a; Borissiak 1915, pl. 11, figs. 3, 6, 12).

The sculpture of *Aucellina aptiensis* (d'Orbigny) Pompeckj 1901 and other Barremian-Aptian representatives of the genus is essentially similar to that of *Meleagrinnella* and *Malayomaorica*. The radial ribs strongly predominate over the concentric growth-lines. The latter are, furthermore, often imbricated, tuberculate and/or spinose whenever they cross the radial ribs (Pompeckj 1901, pp. 353-4, pl. xvi, figs. 1a, 5a, and the writer's own observations on Canadian specimens). The sculpture of *Aucellina gryphaeoides* (Sowerby), on the contrary, is more like that of *Buchia* than that of older *Aucellina* species. This is, however, probably a secondary phenomenon, reflecting the convergent development of *Aucellina* and *Buchia*.

Pompeckj's (1901, pp. 328-32, 336, expl. of plates) nomenclature of morphological elements of the ligamental plate of Aviculopectinidae is used in the following discussion with some additions (e.g. excavations of the ligamental pit).

The edentulous ligamental plate of the left valve of *Malayomaorica malayomaorica* is wider than that of any other aviculopectinid genus (Pl. 21, figs. 1B, 1F). The ligamental pit of this plate is subdivided into two parts by a deep transverse groove, which is broadly V-like in cross-section (Pl. 21, figs. 1B, F). This groove begins underneath the very tip of the short, blunt, centrally located beak, and extends right across the ligamental plate. Both parts of the ligamental plate slope markedly toward this groove in its proximity. The lower margin of the ligamental plate is more or less clearly indented at the lower

end of the transverse groove discussed above (Pl. 21, figs. 1B, F, G). In the specimens available to the writer, as well as in those figured by other workers, the posterior part of the ligamental pit is one and a half to three times longer than its anterior part (Pl. 21, figs. 1F, 2E). It is covered by numerous, more or less sinuous, longitudinal striae (Pl. 21, figs. 1F, 2F). An oblique, more or less sharp rim slanted posteriorly separates the posterior part of the ligamental pit from the still longitudinally striated inner surface of the posterior ear (Pl. 21, figs. 1F, 2F). A curved, low, longitudinal ridge may occur in the middle of the posterior part of the ligamental pit (Pl. 21, figs. 1F, 1G).

The anterior part of the ligamental pit is covered by sinuous, longitudinal striae, similar to those of its posterior part. The shell is markedly strengthened underneath this part of the pit. A more or less pronounced bulge occurs in front of the anterior part of the ligamental pit (Pl. 21, figs. 1B, D, F, G, 2A, E, F). This bulge is often more or less regularly rounded (Pl. 21, figs. 1D, 1F), but it may also be quite irregularly shaped, flat-topped, and folded over (Pl. 21, figs. 2A, C, F). This bulge occupies the inner surface of the anterior ear of *M. malayomaorica*. The inner surface of the bulge described above is also covered by irregularly curved, fine or coarse striae. An irregularly curved groove or depression, corresponding to the articulation pit (= 'Gelenkgrube' of Pompeckj 1901, p. 336) of *Buchia* and other aviculopectinid genera, separates this bulge from the ligamental plate proper. This articulation groove or depression persists right across the ligamental plate, is finely or coarsely striated, and may ramify in some of the specimens studied. The presence of striations on the bulge and articulation groove of *Malayomaorica* described above suggests that these features have also been covered by the ligament.

The anterior margin of the left valve is usually more or less markedly concave just below the above-described bulge (Pl. 21, figs. 1A, B, D, 2C). In some of the specimens studied the anterior margin of this valve forms a broadly rounded, deep embayment at that place. This embayment sharply separates the anterior ear from the rest of the shell (Pl. 21, figs. 1A, B, D).

The above-described structure of the left ligamental plate of *Malayomaorica* differs sharply from that of *Buchia*. In *Buchia* the bottom of the ligamental pit is essentially flat and appears to lack any excavations or furrows similar to the transverse furrow of *M. malayomaorica* (Pl. 21, figs. 6C, 7A, B; Pompeckj 1901, pl. xv, figs. 17, 18, 21; pl. xvi, figs. 4, 6d). The left beak of *Buchia* is, at that, situated at the extreme anterior end of the ligamental plate, well forward of the ligamental pit and immediately above the articulation pit (= 'Gelenkgrube'). The articulation pit of *Buchia* differs, furthermore, from that of *Malayomaorica* (and from that of all other Jurassic and Cretaceous aviculopectinid genera) in its regularly hoof-like shape, greater depth, and well-outlined, near vertical rims (Pl. 21, figs. 6C, 7A, B; Pompeckj 1901, pl. xv, figs. 17-18). Finally, no structure homologous to the ligamental bulge of *Malayomaorica* discussed above is present in *Buchia*.

The structure of the left ligamental plate of *Aucellina* is only imperfectly understood. Judging by the description and figures of Pompeckj (1901), and some Canadian specimens available to the writer, *Aucellina* is more similar, in this and other respects, to *Meleagrinnella* and *Arctotis* than to *Buchia*. It can, accordingly, hardly be a member of the subfamily Buchiinae Cox (see below).

The structure of the left ligamental plates of *Meleagrinnella* and *Arctotis* is much more

similar to that of *Malayomaorica* than to that of *Buchia*. To begin with, all better-known representatives of *Meleagrinnella* possess an irregularly rounded, more or less transverse excavation of the middle part of the ligamental pit equivalent to the transverse furrow of *Malayomaorica*. The anterior rim of this excavation may, furthermore, become steep and furrow-like in appearance (Pompeckj 1901, pl. xv, fig. 15; Borissiak 1909, pl. ii, fig. 14a; Bodylevsky 1960, p. 44). The central excavation of *Meleagrinnella* and *Arctotis* differs, nevertheless, from the homologous transverse furrow of *Malayomaorica* in being broad, irregularly rounded in outline, and broadly concave in cross-section. *Malayomaorica* differs, furthermore, from *Meleagrinnella* (but apparently not from *Arctotis*) in lacking, completely, the tooth-like bulge separating the ligamental pit from the articulation pit. This tooth-like bulge appears to be present in all better-known species of *Meleagrinnella* (Pompeckj 1901, pl. xv, figs. 15–16; Borissiak 1909, pl. i, fig. 12e; pl. ii, figs. 14e, 15e). The ligamental plate of *Malayomaorica* has, instead, an irregular, tooth-like bulge at its anterior rim forward from the furrow-like articulation pit (= 'Gelenkgrube') (Pl. 21, figs. 1A, B, D; 2A, F). This bulge appears to be absent in *Meleagrinnella* and *Arctotis*.

The articulation pit of *Meleagrinnella*, *Arctotis*, and probably *Aucellina*, differs strongly from that of *Malayomaorica* (and *Buchia*, see above) in being more like a slight sinus than a regular pit or furrow. The articulation pit of *Meleagrinnella*, *Arctotis*, and probably *Aucellina*, is an only slightly depressed and ill-defined area of pronouncedly bent and lamellated concentric growth-lines situated on the underside of the anterior ear of the left valve well forward from its beak (Pompeckj 1901, pl. xv, figs. 15–16, 19; pl. xvi, figs. 3a, 6b, 10a; Borissiak 1909, pl. i, fig. 12e; pl. ii, figs. 14e, 15e; 1915, pl. 11, figs. 7–9; Bodylevsky 1960, pl. 7, fig. 1a).

The ligamental plate of the left valve of *M. malayomaorica* occupies all of the underside of its short and blunt beak (Pl. 21, figs. 1B, F, 2F). The left beak is, thus, not separated at all from the ligamental plate. In typical representatives of *Buchia* and *Aucellina*, in contrast, left beaks are more or less clearly separated from and protrude above the left ligamental plate (Pl. 21, figs. 6A, C, 7A–B; Pompeckj 1901, pl. xv, fig. 14; pl. xvi, figs. 6c, 10a). This separation of left beaks from the ligamental plates apparently exists also in the true 'archaic' *Buchia* species (Pl. 21, figs. 8B, C, F), although it is not so well expressed in these forms. The beak structure of Barremian–Aptian *Aucellina* species is unknown.

The structure of the left beak of *Meleagrinnella* is much more similar to that of *Malayomaorica* than to that of *Buchia* and *Aucellina*. As pointed out by Borissiak (1909, p. 10, pl. i, fig. 12e), the left beak of *M. echinata* var. *donetzensis* protrudes only slightly beyond the upper margin of the ligamental plate. Pompeckj's (1901, p. 325, pl. xv, figs. 15, 16) descriptions and drawings indicate that similar relationships prevail also in *Meleagrinnella echinata* and *M. impressae*.

The best-known representatives of *Arctotis* are indistinguishable from *Malayomaorica* in the structure of their left beaks. In *Arctotis lenaensis* (Lahusen), the type species of this genus, the ligamental plate occupies all of the underside of the short, blunt, and centrally located left beak (Borissiak 1915, pl. 11, figs. 7–9), just as in *Malayomaorica malayomaorica*. The same appears to be true also of *A. intermedia* (Bodylevsky 1960, pl. 7, fig. 1a).

The ligamental plate of the right valve of *Malayomaorica malayomaorica* possesses a strong ligamental ridge in its middle part. This ridge has been well described and figured

by Wandel (1936, p. 458, pl. xvii, figs. 1a-c, 4b-c, 11); it rises above the true dorsal shell margin and is directed obliquely forward.

The above-described ligamental ridge of *Malayomaorica* is completely absent in the right valve of *Buchia* to the best of the writer's knowledge (Pl. 21, figs. 3, 4, 5A, D, E, 8B, F; Pompeckj 1901, pl. xv, figs. 2, 5, 6, and 9). A similar ligamental ridge, is however, present at least in some (probably in all) representatives of *Aucellina*, *Meleagrinnella*, and *Arctotis* (Pompeckj 1901, pl. xv, fig. 7; pl. xvi, figs. 1a, b; Bodylevsky 1960, pl. 7, figs. 2a, b). The ligamental ridge of *Arctotis intermedia* Bodylevsky 1960 is, moreover, particularly similar to the ligamental ridge of *Malayomaorica malayomaorica* in its shape, position on the ligamental plate, &c.

Other characteristic features of the right valve of *Malayomaorica malayomaorica* are: the stoutness and exceptionally large size of the byssus ear (Pl. 21, figs. 2A, F), the large size, the great to very great width and the broadly triangular shape of byssus notch, the marked bend of the byssus ear toward the left valve, and strong ornamentation of the external surface of the byssus ear (Pl. 21, fig. 2F). In some specimens (Pl. 21, figs. 2A, F) the anterior end of the byssus ear is covered by a fold-like flap of the previously described tooth-like bulge of the left valve. If considered in relation to the total shell's dimensions, the byssus ear of *M. malayomaorica* is probably larger and stouter than that of any other Jurassic and Cretaceous aviculopectinid genus, with the possible exception of some small-sized representatives of *Arctotis* (e.g. *A. intermedia* Bodylevsky 1960).

The byssus ear and notch of *Malayomaorica malayomaorica* differ strongly from the homologous features of the true 'archaic' *Buchia* species of the northern hemisphere (*Buchia* of the *B. lata-concentrica-mosquensis* species group); they are at the same time relatively more similar to the byssus ear and notch of the younger *Buchia* species.

The mid-Callovia to Kimeridgian 'archaic' *Buchia* of the *B. lata-concentrica-mosquensis* species group are characterized by the relatively small byssus ear extending forward and upward more or less in the plane of contact of the valves (Pl. 21, figs. 3-4, 8B, F; Pompeckj 1901, pl. xv, fig. 2). The groove occurring on the inner surface of the byssus ear in these *Buchia* species is, unlike that of younger *Buchia* species, open at its anterior end (Pl. 21, figs. 4, 5D). The byssus ear of the presently discussed 'archaic' *Buchia* species is thus rather similar to that of *Meleagrinnella* (Pompeckj 1901, pl. xv, figs. 1, 7). This explains the previously discussed erroneous assignment of such *Meleagrinnella* species as *M. radiata* and *M. impressae* to *Buchia* (Pompeckj 1901).

In the latest Jurassic and early Lower Cretaceous *Buchia* species, beginning with *B. piochii* (Gabb, s. lato) (= *B. russiensis* Pavlow and *B. mniovníkensis* Pavlow) (Pl. 21, figs. 5A-E), the byssus ear gradually becomes relatively larger and stouter and bends more and more toward the left valve. In the Valanginian *Buchia* forms, such as *B. keyserlingi* s. lato (Pompeckj 1901, pl. xv, figs. 6, 8-10, 21) the external surface of the byssus ear is directed almost perpendicularly to the plane of contact of the valves (plane of symmetry of the shell). At the same time, the anterior margin of the byssus ear begins to extend, ridge-like, across the anterior end of the canal that runs on the inner side of the byssus ear. A distinctly spoon-like shape of byssus ear (when seen from inside; Pl. 21, figs. 5D, E) results; this biochronologically important feature also reaches its maximum development in the Valanginian *Buchia keyserlingi-crassicollis* species group. These morphologically progressive changes of the byssus ear in the course of evolution of

Buchia have already been clearly recognized by Pompeckj (1901, p. 326). They have however, been, completely neglected by later workers.

In spite of its greater similarity to the byssus ear of the younger *Buchia* species, the byssus ear of *Malayomaorica* differs from it in its large and widely gaping byssus notch. As noted by Pompeckj (1901, p. 326, pl. xv, figs. 6, 8-10, 20-21), the byssus notch of the younger *Buchia* species is all but closed. Only a short and extremely narrow fissure remains at the anterior end of the ear in these species. The byssus notch of all Jurassic *Buchia* species, including that of its true 'archaic' representatives (Pl. 21, figs. 3, 4, 8b, t), is also much narrower than that of *Malayomaorica*.

The byssus ear and byssus notch of *Meleagrinnella* differ from those of *Malayomaorica* in about the same way as do the byssus ear and notch of the true 'archaic' *Buchia* species (see above). The byssus ear and notch of *Meleagrinnella* are, furthermore, proportionally smaller than those of any known *Buchia* species (see Pompeckj 1901, pl. xv, figs. 1, 4, 7).

The byssus ear and notch of *Arctotis* are more similar to those of *Malayomaorica* than are those of any other Jurassic and Cretaceous aviculopectinid genus. As noted in the description, and clearly visible in the figures, of Bodylevsky (1960, p. 45, pl. 7, figs. 1a, 2a-b), *Arctotis intermedia* possesses a short, stout, and large byssus ear accompanied by a widely gaping byssus notch. The byssus ear of *A. lenaensis* (Borissiak 1915, pl. 11, fig. 10, text-fig. 1) is also similarly large and stout; it is, however, much longer than the byssus ear of *Malayomaorica* and *A. intermedia*. The byssus ears of the *Arctotis* species mentioned above differ from the byssus ear of *Malayomaorica* in the apparently complete absence of the inward bend described above.

Because of the morphological peculiarities of its hinge described above, the articulation of valves of *Malayomaorica* differs markedly from that of *Buchia*. In the latter genus, the byssus ear of the right valve enters the articulation pit of the left valve (Pompeckj 1901, pl. xv, figs. 20-21). In *Malayomaorica*, however (Wandel, 1936, p. 458): 'dient die Gelenkgrube nicht, wie Krumbeck annimmt, zur Aufnahme des Byssusohres, sondern zur Aufnahme des wulstig verdickten und schräg nach oben gerichteten Vorsprungs "v" der Bandplatte der rechten Klappe (Taf. XVII, Fig. 1b, c u. 11), der wie ein Zahn in sie eingreift (vgl. Taf. XVII, Fig. 4b). Das Byssusohr schmiegt sich dem präumbonalen Teil der Bandplatte der linken Klappe an (Taf. XVII, Fig. 4a).'

The above description of Wandel (1936) is quite apt, except that his 'Gelenkgrube' corresponds to the furrow-like excavation of the ligamental pit of the writer rather than to the true articulation pit (= 'Gelenkgrube') of Pompeckj (1901).

In *Meleagrinnella*, *Arctotis*, and *Aucellina*, the articulation of valves is essentially similar to that of *Malayomaorica*. For *Aucellina* and *Meleagrinnella* this is clearly indicated by drawings of Pompeckj (1901, pl. xv, fig. 19; pl. xvi, figs. 4, 6b). For *Arctotis* this is clearly indicated by Bodylevsky's (1960, pl. 7, fig. 1a) figures of *A. intermedia*. The writer was, furthermore, able to check on the reliability of the above data when studying the still undescribed Canadian representatives of *Aucellina* and *Arctotis*.

Malayomaorica malayomaorica (Krumbeck 1923) itself and *M. aff. malayomaorica* (Fleming 1958) are the only species that can be placed with assurance in the genus *Malayomaorica* at the present time.

The generic nature of '*Aucella sp.?*' aus der Gruppe der *A. malayomaorica*' (Wandel 1936, pp. 461-2, text-figs. 1a-c) from the Demu limestone and Lilinta marly limestone of Misol is uncertain, although the apparent absence of a ligamental ridge in the

drawings of its right valve does not favour its assignment to *Malayomaorica*. A detailed study of well-preserved ligamental plates of the left valves of this form is needed for its definite generic assignment.

The generic position of '*Aucella misolica*' of Krumbeck (1934, pp. 454-5, pl. xv, fig. 10a-b) is also uncertain, as the type material of this species consists of a unique, poorly preserved right valve. It probably is a representative of *Malayomaorica*, however, as *Buchia* aff. *misolica* (Krumbeck) from the Lower Tithonian of New Zealand has been recognized by Fleming (1958, p. 379; 1960, p. 267, table 1) as a younger representative of *Malayomaorica malayomaorica* lineage. It is to be hoped that *Buchia* aff. *misolica* will be described and figured in the near future.

All other *Buchia* species hitherto described from the Indo-Pacific region seem to be true representatives of the genus, in the present state of our knowledge at least (compare Jeletzky 196-).

CONCLUSIONS

'*Aucella malayomaorica* Krumbeck, 1923' neither belongs to the genus *Buchia* (= *Aucella*), as hitherto assumed, nor is closely allied to this genus. It differs from *Buchia* in all diagnostic morphological features and so cannot even be placed in the subfamily Buchiinae Cox, 1953 (= Aucellinae Fischer, 1887).

'*Aucella malayomaorica*' is much more closely allied to such aviculopectinid genera as *Meleagrinnella*, *Aucellina*, and *Arctotis*. It is particularly similar morphologically to the boreal genus *Arctotis*. From this genus it differs, however, in the furrow-like appearance of the excavation of its left ligamental pit, the occurrence of a tooth-like bulge in front of the articulation pit (= 'Gelenkgrube') of the left valve, and in the marked bend of the byssus ear toward the left valve. These morphological distinctions fully warrant the erection of a new genus *Malayomaorica* for '*Aucella malayomaorica*', particularly as it differs even more strongly from *Meleagrinnella* and *Aucellina*. *Malayomaorica* is sufficiently close to *Arctotis* and *Meleagrinnella* to be included in the subfamily Oxytominae Ichikawa, 1958. *Aucellina* is also a member of the Oxytominae in the writer's opinion. This genus differs strongly from *Buchia* in most of its diagnostic morphological features, while being rather similar to *Meleagrinnella* in these same features. It is inferred, therefore, that *Aucellina* is only homoeomorphically similar to *Buchia*, and that it is an independent offshoot of *Meleagrinnella*.

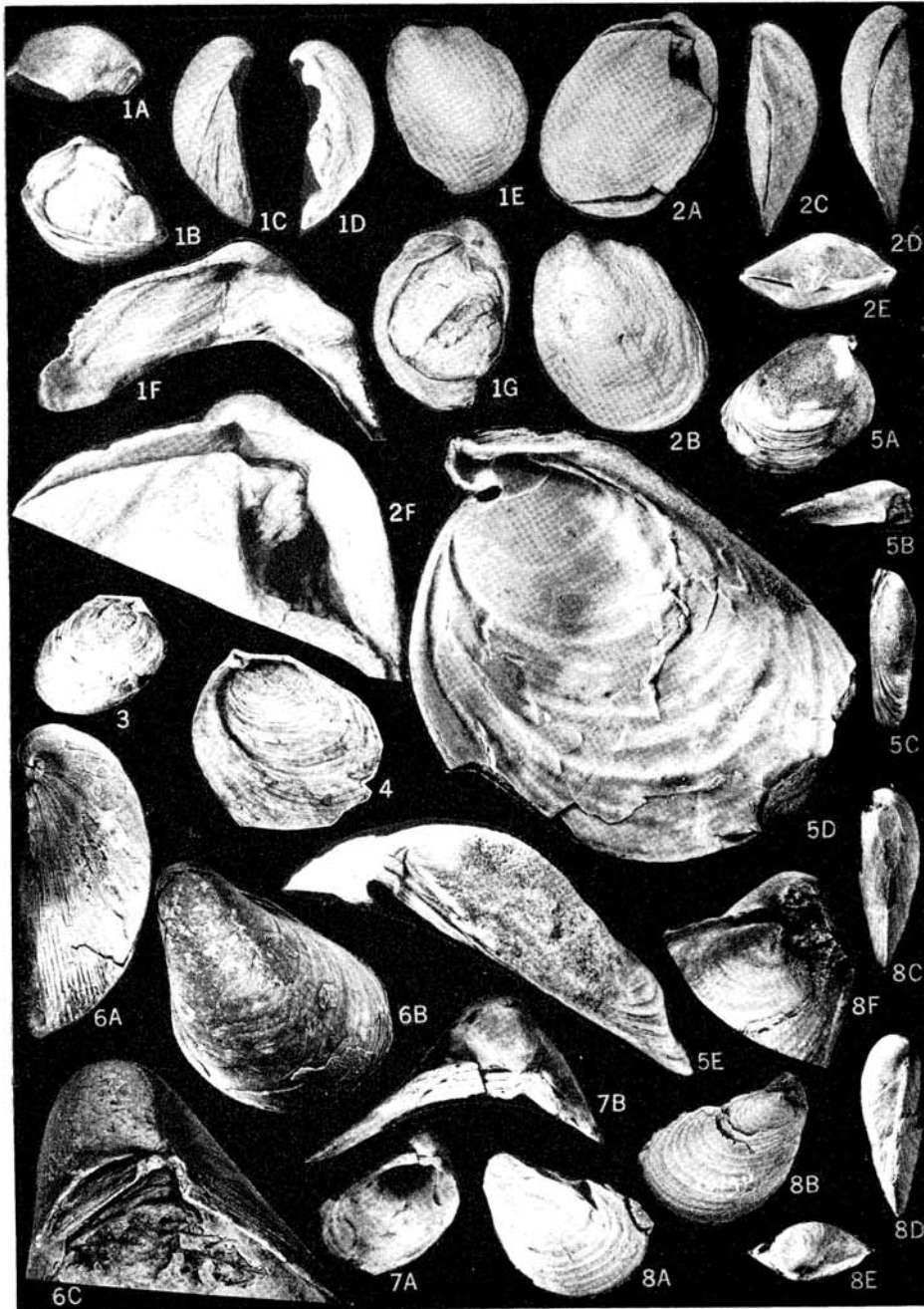
Malayomaorica is considered provisionally to be an offshoot of *Arctotis* lineage, which had penetrated the Indo-Pacific region during the early part of the Upper Jurassic together with true *Buchia* species belonging to the *Buchia lata-concentrica-mosquensis* species group. The morphological similarities of *Malayomaorica* to *Meleagrinnella* and *Aucellina* are not sufficiently far-reaching to assume its being directly related phylogenetically to either of these two genera.

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