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Title	On the Trigoniinae
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Citation	Journal of science of the Hiroshima University. Series C, Geology and mineralogy , 4 (1) : 71 - 94
Issue Date	1961-05-15
DOI	
Self DOI	10.15027/53005
URL	https://ir.lib.hiroshima-u.ac.jp/00053005
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On the Trigoniinae

By

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With 1 Table and 1 Plate

ABSTRACT: In this paper, the writer discussed the classification and the complicated phyletic relationships of the Trigoniinae and described and listed a number of genera and species. *Pseudomyophorella* nov. is one of the most aberrant and interesting Trigoniids, and may be an off-shoot, belonging to a new subfamily, derived from *Trigonia* by the development of the diagonal and tuberculate costation on the flank.

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I. INTRODUCTION AND ACKNOWLEDGEMENTS

When the writer (1960) discussed the Trigoniids of the Mesozoic era, especially Cretaceous period, in Japan and her adjacent areas, he noted that the subfamily Trigoniinae KOBAYASHI, 1954 vary to a large extent in shell form and surface costation on the flank and area the latter of which is always sculptured with radial or concentric costae in the vicinity of the umbo. Moreover, he discussed that Frenguelliellinae nov. can be separable from KOBAYASHI's Trigoniinae on the basis of the ornamentation on the area.

In this paper, the writer dealt with the classification of the Trigoniinae and discussed their complicated phyletic relationships. As a result, this subfamily may be classified as shown on pages 79 and 92 and the distributions and possible phyletic relationships are tabulated on Tab. 1.

The Trigoniinae em. including 10 genera and a number of species and varieties, can be divided into 3 sections, i.e. *Trigonia*, *Pacitrigonia*, and *Indotrigonia* sections, by the costation on the flank and area. This subfamily appeared possibly in the Anician of Chile, and they continued to exist till the Cretaceous. In the Cretaceous, they vanished gradually from Europe and the Indo-African region. In the upper Senonian, *Pacitrigonia* which is a solitary genus of the subfamily and was limited to the Southern Pacific region. *Trigonia* forms a trunk of the subfamily, and prospered in Europe and the South American region from Dogger to Malm but suddenly declined in the Cretaceous. *Pseudomyophorella* nov. may be an off-shoot, belonging to a new subfamily, derived from the main trunk by the development of the diagonal and tuberculate sculpture on the flank. The genera of the *Pacitrigonia* section are considered to have been issued from *Trigonia* in the Pacific region through the Cretaceous by the change of the surface ornament on the flank and the shell form. From Malm to Neocomian, the remainders of the subfamily were derived probably from the trunk in the Indo-African region by the effacement of the radial costation on the area and the transfiguration of the shell form.

Here the writer tenders his cordial thanks to Professor Sotoji IMAMURA of Hiroshima University and Professor Teiichi KOBAYASHI of the University of Tokyo for their kind guidances and encouragements. The writer acknowledges also the kind helps given by Dr. M^{me} Suzanne FRENEIX of Laboratory of Palaeontology, Museum of Natural History at Paris, Dr. Minoru TAMURA of Kumamoto University, and Dr. Itaru HAYAMI of the University of Tokyo. The writer wishes to express his best thanks to Mr. Kimiyoshi SADA of Hiroshima University for his assistance in this study.

II. PALAEOONTOLOGICAL NOTES

Subfamily Trigoniinae KOBAYASHI, 1954 em.

Shell subtrigonal to subovate or sometimes pyriform, especially so when it is ros-

trate posteriorly, inequilateral, usually tripartite distinctly into a flank and an area and escutcheon; umbo rather prominent, mesial to antero-mesial and more or less opisthogyrous; area costellate radially and bipartite by a median carina or groove, but indistinct in some later representatives; escutcheon transversely costellate or smooth, but it is occasionally ill-defined; costae on flank plain and concentric to sub-concentric, but rarely undulate, tuberculate or broken into pustules; carinae and antecarinal groove distinct in many of them, but sometimes not well developed.

Some lengthened ridges recognized in the vicinity of the siphonal margin, presumably determined the positions of the siphon which is divided from the soft part of the other organ. Among them, inner one coinciding approximately with the middle of the area, separates the incumbent opening from the excurrent one.

In his study on the Trigoniidae, KOBAYASHI (1954) proposed the subfamily Trigoniinae nov. in the family. He noted that "Trigonians with the concentric costae on the disk and a distinct marginal carina; radial costellae present in the area in the most genera". Jointly with MORI, he (1954) has classified this subfamily into 3 sections including 13 genera and discussed their complicated phyletic relationships.

Their classification is summarized as follows:

Subfamily Trigoniinae KOBAYASHI, 1954

Laevitrigonia section

Genus *Psilotrigonia* COX, 1952 (*Trigonia beesleyana* LYCETT, 1874)

Genus *Laevitrigonia* LEBKÜCHNER, 1931 (*Trigonia gibbosa* SOWERBY, 1821)

Genus *Liotrigonia* COX, 1952 (*Trigonia lingonensis* DUMORTIER, 1869)

Trigonia section

Genus *Frenguelliella* LEANZA, 1942 (*Trigonia inexpectata* JAWORSKI, 1916)

Genus *Trigonia* BRUGUIÈRE, 1789 (*Venus sulcata* HERMANN, 1781)

Genus *Geratrigonia* KOBAYASHI, 1954 (*Trigonia hosourensis* YOKOYAMA, 1904)

Genus *Pleurotrigonia* VAN HOEPEN, 1929 (*Trigonia blanchenhorni* NEWTON, 1907)

Intotrigonia section

Genus *Pacitrigonia* MARWICK, 1932 (*Pacitrigonia sylvesteri* MARWICK, 1932)

Genus *Eselaevitrigonia* KOBAYASHI and MORI, 1954 (*Trigonia meridiana* WOODS, 1917)

Genus *Opisthotrigonia* COX, 1952 (*Trigonia retrosa* KITCHIN, 1903)

Genus *Indotrigonia* DIETRICH, 1933 (*Trigonia smeei* SOWERBY, 1840)

Genus *Nototrigonia* COX, 1952 (*Trigonia cinctula* ETHERIDGE, 1902)

Incerta sedis

Genus *Heterotrigonia* COX, 1952 (*Trigonia diversicostata* WHITEAVES, 1876)

In 1957, KOBAYASHI noted that the immature forms of *Nipponitrigonia* COX and *Rutitrigonia* VAN HOEPEN are essentially similar to *Frenguelliella* LEANZA in surface sculpture and shell form and they are probably the derivatives from *Frenguelliella* or his Trigoniinae. Succeedingly, he (1957) with TAMURA established *Latitrigonia* KOBAYASHI and *Ibotrigonia* KOBAYASHI based respectively on *Latitrigonia pyramidalis* KOBAYASHI and TAMURA nov. and *Ibotrigonia masatanii* KOBAYASHI and TAMURA nov. and they assigned to these genera the members of the Trigoniinae. But, their sectional positions are not pointed by them.

In describing a number of Trigoniids from the Lower Cretaceous of Manghysch-lack and Western Turkmen, SAHELIEV (1958) distinguished the subfamily Laevitrig-

oniinae nov. from KOBAYASHI's Trigoniinae and classified these subfamilies as follows:

Subfamily Trigoniinae KOBAYASHI, 1954

Genus *Trigonia* BRUGUIÈRE, 1789 (*Venus sulcata* HERMANN, 1781)

Subgenus *Trigonia* s.s.

Subgenus *Frenguelliella* LEANZA, 1942 (*Trigonia inexpectata* JAWORSKI, 1916)

Subgenus *Pleurotrigonia* van HOEPEN, 1929 (*Trigonia blanchenhorni* NEWTON, 1909)

Genus *Indotrigonia* DIETRICH, 1933 (*Trigonia smeei* SOWERBY, 1840)

Subgenus *Indotrigonia* s.s.

Subgenus *Opisthotrigonia* COX, 1952 (*Trigonia retrosa* KITCHIN, 1903)

Subgenus *Eselaevitrigonia* KOBAYASHI and MORI, 1954 (*Trigonia meridiana* WOODS, 1917)

Genus *Sphenotrigonia* RENNIE, 1936 (*Trigonia (Sphenotrigonia) frommurzei* RENNIE, 1936)

Genus *Nototrigonia* COX, 1952 (*Trigonia cinctula* ETHERIDGE, 1902)

Genus *Heterotrigonia* COX, 1952 (*Trigonia diversicostata* WHITEAVES, 1876)

Genus *Pacitrigonia* MARWICK, 1932 (*Pacitrigonia sylvesteri* MARWICK, 1932)

Genus *Eotrigonia* COSSMANN, 1912 (*Trigonia semiundulata* MCCOY, 1866)

Subfamily Laevitrigoniinae nov.

Genus *Laevitrigonia* DEECKE, 1925 (*Trigonia gibbosa* SOWERBY, 1821)

Genus *Geratrigonia* KOBAYASHI, 1954 (*Trigonia hosourensis* YOKOYAMA, 1904)

Genus *Liotrigonia* COX, 1952 (*Trigonia lingonensis* DUMORTIER, 1861)

Genus *Psilotrigonia* COX, 1952 (*Trigonia beesleyana* LYCETT, 1872)

Genus *Nipponitrigonia* COX, 1952 (*Trigonia kikuchiana* YOKOYAMA, 1891)

Genus *Quoieccchia* CRICKMAY, 1930 (*Quoieccchia aliciae* CRICKMAY, 1930)

Prior to KOBAYASHI and SAVELIEV, van HOEPEN (1929) proposed the Rutitrigoniinae and the Pleurotrigoniinae. However, KOBAYASHI (1954, 57) considered that these two subfamilies are to be included to his Trigoniinae. On the other hand, SAVELIEV (1958) pointed that the latter is a synonym of KOBAYASHI's Trigoniinae but the former is comprised to be the Megatrigoniinae van HOEPEN, 1929.

SAVELIEV's Trigoniinae is almost equivalent to KOBAYASHI's *Trigonia* section plus *Indotrigonia* section, while KOBAYASHI's *Laevitrigonia* section is nearly corresponded to SAVELIEV's Laevitrigoniinae which is chiefly composed of the members of the Laeves and the Grabrae. As already pointed out by COX (1952, p. 64), *Quoieccchia* may be better excluded from the Trigoniidae, because it is founded on the immature and imperfect specimens of the Trigoniidae and the similar forms have hitherto been undiscovered. In the shell form and the surface costation, Tertiary *Eotrigonia* has some resemblances to Mesozoic *Trigonia* in essential characters. Internally, the latter has the radial plications in the siphonal region and its ventral periphery is not well crenulated, while in the former the internal plications are absent and its siphonal margin is well crenulated. In this aspect, *Eotrigonia* is allied to Recent *Neotrigonia* having crenulate ventral margin and no internal plications, rather than Mesozoic *Trigonia*. Therefore, as suggested by KOBAYASHI, *Eotrigonia* may be included in his Neotrigoniinae. SAVELIEV considered that *Pleurotrigonia* might be issued from *Trigonia* and *Indotrigonia*, *Opisthotrigonia*, *Eselaevitrigonia*, and *Sphenotrigonia* were the derivatives from *Frenguelliella*. As already discussed by KOBAYASHI and MORI (1954) and others, they are, however, probably issued from *Trigonia* by the obsolescence of the carinae and the radial sculpture on the area, because their immature shells are in

many cases typical *Trigonia* as shown by some authors.

In KOBAYASHI's *Trigonia* section or his Trigoniinae s.s. which is approximately equivalent to Saveliev's genus *Trigonia* s.l., the radial costation on the area is recognized in *Trigonia* and *Pleurotrigonia*. These genera are respectively typified by *Venus sulcata* HERMANN from upper Lias of Alsace and *Trigonia blanckenhorni* NEWTON from Albian of Zululand. In *blanckenhorni*, the radial sculpture on the area is observed only in the vicinity of the umbo and the flank is ornamented with concentric to transverse costae as illustrated by RENNIE (1936, pl. 42, figs. 1-4). In *Frenguelliella*, on the other hand, the flank is provided with concentric to transverse costae and the area is transversely costellate or sometimes smoothened in latter representatives, i.e. *Trigonia indica* STOLICZKA (1871, pl. 15, figs. 14-15) and others. *Geratrigonia* typified by *Trigonia hosourensis* YOKOYAMA (1904, p. 11, pl. 1, figs. 3a-c) from Infrahettangian of Shizukawa district in Northeast Japan, is well represented by several forms from Hettangian to upper Lias of Japan. It has somewhat regular concentric costae on its flank, and the area is smooth but rarely weak concentric or transverse costae are found in the vicinity of the umbo. Therefore, this genus is possibly an off-shoot from *Frenguelliella*. Marginal carina is distinct in the early stage of *Pleurotrigonia*, but rounded off in its later growth stages. The other genera of the section have a fairly prominent marginal carina in all stages. *Trigonia* and *Frenguelliella* are two cosmopolitan and long-ranged genera, and they continued till the Cretaceous. In the surface sculpture and other morphologic characters, they bear some resemblances with each other. The area is, however, transversely costellate in the latter and radial ribs are well developed in the former. Recently, TAMURA (1959, pp. 213-214) established subgenus *Kumatrigonia* of genus *Frenguelliella* based on *Frenguelliella* (*Kumatrigonia*) *tanourensis* TAMURA (1959, pp. 214-215, pl. 2, figs. 1-6 and text-fig. 2) from Carnian at Tanoura in the south of Yatsushiro-city, Kumamoto Pref., Kyushu, Japan. This form is clearly provided with concentric or transverse costation on its area and its marginal carina is distinct in all stages. This is externally quite similar to konzentrischen skulptierte Myophorien represented by *Myophoria eleganse* DUNKER, *M. postera* QUENSTEDT, and others. *F. (K.) tanourensis* having internally crenulate cardinal teeth, is the oldest representative of *Frenguelliella*. *Frenguelliella* and *Kumatrigonia* have many aspects in common with each other. TAMURA noted that costae on the flank and area are less numerous in the former than the latter on which surface costation from the flank to the escutcheon are all connected to one another. He emphasized that in the former the escutcheon is smooth, but transversely costellate in the latter. As already pointed out by Cox (1952, pp. 54-55), *Frenguelliella* has the transversely costellate area and escutcheon on which sculpture is sometimes evanescent in adult stages. Costae on the flank are all connected to costellae on the area in some forms of the former, such as *Trigonia orientalis* STOLICZKA and others. Therefore, it is probable that *Kumatrigonia* is not separable from typical *Frenguelliella*. Judging from the occurrence of TAMURA's *F. (K.) tanourensis*, the writer is of opinion that *Frenguelliella* was derived already in the Upper Triassic from the konzentrischen skulptierte My-

ophorien.

In the members of *Indotrigonia* section which is nearly equivalent to the rest of Saveliev's Trigoniinae, it is recognized that surface costation and shell form are variable to a large extent. *Nototrigonia* is monotypic and typified by *Trigonia cinctula* Etheridge from Lower Cretaceous of Lake Eyre basin, South Australia. This genus has a distinct ante-carinal depression and a radially costellate area. *Pacitrigonia* typified by *Pacitrigonia sylvesteri* Marwick (1932, pp. 507-508, pl. 47, figs. 1-3) from upper Senonian of New Zealand, has irregular broken costae and a well developed ante-carinal groove on the flank. Its area is distinctly costellate radially, but sometimes the radial costation is later effaced. *Sylvesteri* is an aberrant form of this genus, because its characteristic sculpture on the surface and an ante-carinal depression are obsolete in later stages. "*Trigonia*" *papua* Glaessner (1958, pp. 207-209, pl. 26, figs. 1a-b) from Cenomanian of New Guinea may be the oldest of *Pacitrigonia*. The others of the genus are well known from Senonian of Southern Pacific region including New Zealand, Antarctica, Chile, and Patagonia etc. The other genera of the section, i.e. *Eselaevitrigonia*, *Indotrigonia*, and *Opisthotrigonia*, distribute in the Malm to Neocomian of the Indo-African region, excepting *Eselaevitrigonia meridiana* (Woods) occurred in the "Middle Cretaceous" of New Zealand. Costae on the surface of *Indotrigonia* typified by *Trigonia smeei* Sowerby from Argovian of India and Kimmeridgian to Neocomian of East Africa, are plain and concentric to subconcentric, but the immature forms of *smei* is typical *Trigonia* as shown by Kitchin (1903, pl. 4, figs. 9, 9a; pl. 4 figs. 1-3) and Lange (1914, pl. 20, figs. 8-13; pl. 21, figs. 1-7). *Eselaevitrigonia* typified by *Trigonia meridiana* Woods (1917, p. 6, pl. 1, figs. 2-7) from "Middle Cretaceous" of New Zealand, includes some forms from Tithonian of Cutch in India. This genus is characterized by an ante-carinal groove and numerous concentric costae the latter of which are sometimes effaced in some forms, i.e. *Trigonia cardiniiformis* Kitchin (1903, pl. 6, figs. 3-5) and others. Because its immature form is typical *Trigonia* as shown by Kitchin and Woods, this genus was probably derived from *Trigonia* by the obsolescence of carinae and radial costation on the area. As suggested by Kobayashi, *Opisthotrigonia* is monotypic and typified by *Trigonia retroa* Kitchin (1903, p. 57, pl. 6, fig. 10; pl. 7, figs. 1-2) from Tithonian of Cutch in India, and resembles a member of *Eselaevitrigonia*, *Eselaevitrigonia spissicostata* (Kitchin), in surface costation, if its peculiar form is overlooked. This genus might be derived from *Eselaevitrigonia* or *Trigonia* by the rostration of the shell form and the evanescent of the surface sculpture on the area, because its area is costellate by weak radial costae.

The third group, i.e. *Laevitrigonia* section typified by *Laevitrigonia*, is approximately equivalent to Saveliev's Laevitrigoniinae excepting *Quoiechhia*. In this group, the outline and the surface sculpture vary to a fairly small extent than those of the other section. The area is costellate transversely to obliquely or sometimes smooth, and the flank is ornamented with improminent concentric to subconcentric costae which are occasionally pustulate in later stages. *Laevitrigonia* ranges from Lias to Malm of

Western Europe, and its type species is *Trigonia gibbosa* SOWERBY (1821, p. 61, tabs. 235-236) from Portlandian of England. The sculpture on the flank is rather complicated than those of the other genera of the section, and the area is striated transversely or smooth. *Laevitrigonia damoniana* (de LORIO), *L. gibbosa* (SOWERBY), and *L. manseli* (LYCETT) have pustulate costae on the flank. Among them, the oblique arrangement of pustules is observed in *manseli* (LYCETT pp. 86-88, pl. 19, figs. 3-4). In this genus, an ante-carinal depression is commonly well developed. *Psilotrigonia* and *Liotrigonia* are both monotypic genera, and the types are respectively *Trigonia beesleyana* LYCETT (1874, pp. 91-92, pl. 17, figs. 2-4) from the Inferior Oolite of England and *Trigonia lingonensis* DUMORTIER (1861, p. 275, pl. 22, figs. 6-8) from middle Lias of France. The latter has subconcentric wrinkles on its flank, and the area is smooth. Oblique costellae as recognized in the youngster of *Rutitrigonia excentrica* (PARKINSON), are well developed in the whole area of *Psilotrigonia* which has slightly flexiate and oblique costae on the anterior part of the flank. As stated above, the young shells of the section have some resemblances to *Frenguelliella* in essential characters. Therefore, the genera in this section might be the derivatives from *Frenguelliella* by the change of the surface sculpture and the obsolescence of the carinae.

Nipponitrigonia and *Rutitrigonia* have the fairly simple sculpture on the surface and the marginal carina is weak in common forms and indicated only by an obtuse marginal angulation. The flank is sculptured with concentric to transverse costae which are sometimes obsolete later. Costellae on the area are transverse in the former and oblique in the latter, and they are in many cases evanescent in later stages. *Nipponitrigonia* is trigonally ovate to ovate in outline, and its type is *Trigonia kikuchiana* YOKOYAMA (1891, pp. 363-365, pl. 40, figs. 4-6) from Neocomian to Cenomanian of Japan excluding Hokkaido region. This genus is common in the Bajocian (?) to Cenomanian of Japan. Concentric costation presents at the umbonal region, but the rest of the flank is smooth or ornamented with concentric to transverse costae on the anterior part. As pointed out by KOBAYASHI (1957), its immature form is similar to *Frenguelliella* in essential characters, because its surface is concentrically costellate and distinctly tripartite by the carinae. *Rutitrigonia* is characterized by its pyriform outline and the obliquely costellate area, and the type species is *Rutitrigonia peregrina* van HOEPEN (1929, pp. 32-33, pl. 7, figs. 13-16) from "Middle Cretaceous" of Zululand in South Africa. Its distribution is Lower to "Middle" Cretaceous of cosmopolitan, but unknown in Australia. The immature shell of the genus is sculptured with several concentric costae and the surface is distinctly tripartite by a marginal and an escutcheon carina. Because of its appearance in the early stage, this genus might be a derivative from *Frenguelliella*.

Heterotrigonia is represented by a few species of upper Albian (?) to Santonian of the Northern Pacific, and its type is *Trigonia diversicostata* WHITEAVES (1876, p. 68, pl. 10, fig. 1) from the Haida formation (possibly upper Albian) of the Queen Charlotte series in British Columbia. Radial costae on the area seems to be a derivative from the Trigoniinae stock or *Trigonia*, but its youngest shell is distinctly tripartite

and the whole surface is concentrically costate. It is sometimes recognized that in the succeeding stage concentric costae on the flank change rapidly into L-shaped costae via V-shaped costae and the radial ornamentation on the area appeared suddenly. Accordingly, as suggested by KOBAYASHI (1954), it seems quite doubtful that this genus is a member of the Trigoniinae.

Sphenotrigonia typified by *Trigonia frommurzei* RENNIE (1936, pp. 369-375, pl. 45, figs. 1-3; pl. 46, figs. 1-4; pl. 47, figs. 1-4) from Neocomian of Zululand in South Africa is one of the most aberrant Trigoniids. This is similar to Astartid genus *Seebachia* in external characters. In *frommurzei*, RENNIE (1936) noted that in the vicinity of the umbo its flank is ornamented with pseudoconcentric costae and its area is bipartite by a median groove into two nearly equal anteal and postal parts on the latter of which two radial costellae are developed. In this respect, as pointed out by RENNIE, *Sphenotrigonia* may be a derivative from *Trigonia*.

Latitrigonia and *Ibotrigonia* are typified by *Latitrigonia pyramidalis* KOBAYASHI and TAMURA (1957, pp. 36-37, pl. 1, figs. 8a-b) from Bajocian of Soma district and *Ibotrigonia masatanii* KOBAYASHI and TAMURA (1957, pp. 38-39, pl. 1, figs. 5-6) from Callovian of the same district in Fukushima Pref., North Japan, respectively. They are small in size, and costae on the flank are parallel to the ventral periphery. Both genera have the smooth area except for the umbonal region where concentric or transverse costellae are sometimes well observed. In the early stage of growth, these genera are quite similar to *Frenguelliella*. So, they are probably two derivatives from *Frenguelliella*.

Recently, *Mesotrigonia* was reported by FRENEIX (1958, p. 165) from Senonian of New Caledonia, and its type species is *Mesotrigonia tarameahensis* FRENEIX (1958, p. 166, pl. 1, figs. 9-11) which has radial costellae on the area and oblique and geniculate costae on the flank. *Tarameahensis* is associated with *Pacitrigonia hanetiana neocaledonica* FRENEIX (1958, pp. 163-164, pl. 1, figs. 5-8). At a glance, the surface costation of *Mesotrigonia* is quite different from that of *P. h. neocaledonica*. *Mesotrigonia*-type costation is, however, sometimes observed in the young shells of *Pacitrigonia*. Therefore, it is probable that *Mesotrigonia* presents a youngster of *P. h. neocaledonica*.

Trigonia fortinensis LAMBERT (1944, p. 386, pl. 4, figs. 5-8) from Neocomian of Neuquen in Argentina bears radial costellae on its area, and its carinae are evanescent in a specimen on figs. 5-6 in pl. 4, but distinct in the other (pl. 4, figs. 7-8). It is distinctly rostrate and concentric costae are effaced in the posterior of the flank. Therefore, LAMBERT's specimen (pl. 4, figs. 5-6) is similar to *Rutitrigonia* rather than *Trigonia* in shell form and sculpture on the flank. This form is probably a derivative, belonging to a new genus, from *Trigonia* by the obsolescence of carinae and costae in the posterior part of the flank. The other form is probably a member of *Trigonia* as can be judged from the surface costation and shell form.

Myophorellinae gen. et sp. n.? by Saveliev (1960, pp. 91-93, pl. 7, figs. 3a-b) from Oxfordian (?) of Western Turkmen is one of the most aberrant and interesting Trigoniids. This form has some resemblances to *Myophorella* s.l. in surface costation,

but distinct from the members of the Myophorellinae by the characteristic radial sculpture on its area. Judging from the radial costation on the area, this form was issued probably from *Trigonia* by the development of the diagonal and tuberculate sculpture on the flank. On this occasion, the writer proposed *Pseudomyophorella* nov. typified by *Pseudomyophorella savelievi* gen. et sp. nov. which the writer gave the name for SAVELIEV's Myophorellinae gen. et sp. n.? This genus, belonging possibly to a new subfamily, is easily separable from the members of the Trigoniinae by its *Myophorella*-type sculpture on the flank. SAVELIEV's *Myophorella* (*Myophorella*) *signata* (AGASSIZ) (1960, pl. 11, fig. 2) from Dogger in Germany is quite similar to AGASSIZ's one in shell form and surface sculpture, but its area is ornamented with radial costae which are obsolete in later stages. Therefore, this is probably a member of *Pseudomyophorella* nov. as can be judged from the surface sculpture and shell form.

As already mentioned before, the sculpture on the flank and the shell form are variable to a large extent in this subfamily. It is an important fact that the obsolescence of carinae and the surface ornamentation and the complication of the sculpture on the flank are observed in various independent genera and species of the subfamily. The area is, however, ornamented with radial or transverse costellae which are sometimes evanescent in later stages. As pointed out by KOBAYASHI (1954), concentric costae on the flank and radial costellae on the area may be the most important and independent characters of the surface sculpture. Concho-ontogenetically, the costation on the area in the early stage may be important for classification of the subfamily. From this view-point, the writer is of opinion that the special attention must be noted in the sculpture of the area in early stage. As described above, *Frenguelliella* (*Kumatrigonia*) *tanourensis* TAMURA appeared in the Carnian of Kumamoto Pref., Kyushu, Japan. Therefore, the Trigoniinae having transverse costellae on the area appeared already in the Upper Triassic, should be segregated out of Trigoniinae KOBAYASHI 1954. Thus, Trigoniinae KOBAYASHI is separable into two groups called the Trigoniinae em. and the Frenguelliellinae NAKANO, 1960 on the basis of the sculpture on the area.

In summarizing above, the Trigoniinae KOBAYASHI, 1954 is tentatively classified as follows:

Subfamily Trigoniinae KOBAYASHI, 1954 em.

Genus *Trigonia* BRUGUIÈRE, 1789

Genus *Pacitrigonia* MARWICK, 1932

Genus *Nototrigonia* COX, 1952

Genus *Indotrigonia* DIETRICH, 1933

Genus *Eselaevitrigonia* KOBAYASHI and MORI, 1954

Genus *Opisthotrigonia* COX, 1952

Genus *Pleurotrigonia* van HOEFEN, 1929

Genus *Sphenotrigonia* RENNIE, 1936

? Genus *Pseudomyophorella* nov.

? Genus *Heterotrigonia* COX, 1952

Subfamily Frenguelliellinae NAKANO, 1960

Genus *Frenguelliella* LEANZA, 1942

Genus *Geratrighonia* KOBAYASHI, 1954
 Genus *Latitrigonia* KOBAYASHI, 1957
 Genus *Ibotrigonia* KOBAYASHI, 1957
 Genus *Laevitrigonia* LEDKÜCHNER, 1931
 Genus *Liotrigonia* COX, 1952
 Genus *Psilotrigonia* COX, 1952
 Genus *Nipponitrigonia* COX, 1952
 Genus *Rutitrigonia* VAN HOEPEN, 1929

With reference to the radial sculpture on the area and the costation of the flank 3 sections called the *Trighonia*, *Pacitrigonia*, and *Indotrigonia* sections can be distinguished in the subfamily Trighoniinae em.

1) *Trighonia* section includes *Trighonia* from lower Middle Triassic (possible middle or even lower Anician) to Senonian (?), and *Pseudomyophorella* nov. may tentatively be placed to this section. In Western Europe, this section is a single representative of the subfamily Trighoniinae em., ranges from late Middle Triassic or earliest Upper Triassic to Cenomanian. Its oldest may be *Trighonia zlambachiensis* HASS from Ladinian-Carnian of East Alps, but the youngest form in Western Europe is probably *Trighonia cardissa* AGASSIZ from Cenomanian of Switzerland. This genus culminated in the Middle to Upper Jurassic, and a number of species and varieties are known from various localities in Europe, but declined already in the Cretaceous. In the Senonian, its representative, *Trighonia anguste-costata* BEHRENDSEN, is reported only from Carylauhue of Argentina in South America, but its precise horizon seems uncertain. In South America, *Trighonia* (*Trig.*) *tabacoensis* BARTHEL (1958, pp. 353-356, pl. 19, figs. 1-8, text-fig. 1) is reported recently from probably middle or even lower Anician formation of Chile. It has a slightly prosogyrous umbo and the radially costellate area, and its flank is ornamented with numerous weak concentric costae. BARTHEL noted that this form was collected from the position of 400 to 500 m. below the beds containing the upper Anician Ammonites. In this region, the occurrences of *Trighonia* are very interesting, because it is collected from Middle to Upper Triassic, Dogger to Neocomian, and Senonian (?). It seems to have been undiscovered from Lias and "Middle Cretaceous". In North America, this genus appeared probably in the Upper Triassic of Yukon in Canada and its earliest form is *Trighonia textilis* LEES. Several forms of genus are known from Lias and Malm of this region. In Japan and Australia, it is reported from Lias to Dogger, but its occurrences are known from Dogger to Malm in India and Neocomian of Africa. As mentioned above, *Pseudomyophorella* nov. having *Myophorella*-type sculpture on the flank and radial costation on the area, occurs in the Callovian (?) of Western Turkmen and Dogger of Germany.

2) *Pacitrigonia* section including *Pacitrigonia* and *Nototrigonia*, has the characteristic radial costellae on the area and somewhat irregular costae and a broad ante-carinal depression on the flank. As discussed above, in this section the large variations are recognizable in the sculpture of the flank. This section distributes in the Southern Pacific region of the Cretaceous. *Pacitrigonia* has the irregular cord-like costation on the flank and radial costellae on the area, but these sculptures are sometimes evanescent

in later stage. The genus appeared probably in the Cenomanian of New Guinea, and flourished in the Senonian of South America, Antarctica, New Zealand etc. Sinuous costae are well developed in monotypic *Nototrigonia*, and its area is decorated by a few radial costae and numerous growth-lines. Judging from the surface sculpture, *Heterotrigonia* may be better included to this section rather than a member of the Vaugoniinae. This genus is characterized by the L-shaped costation on the flank and the radial sculpture on the area, but ante-carinal depression is obscure. It is represented by a few species from upper Albian (?) to Santonian of the Northern Pacific.

3) *Indotrigonia* section comprises *Indotrigonia*, *Eselaevitrigonia*, *Opisthotrigonia*, *Pleurotrigonia*, and *Sphenotrigonia*. In this section, the radial sculpture on the area is recognized only near the umbo, but in later stages the area is costellate with concentric costae or sometimes smoothed. Plain concentric costation is disposed somewhat regularly on the whole surface of *Indotrigonia* and *Eselaevitrigonia*, but it is restricted only to the flank in *Pleurotrigonia* and *Opisthotrigonia*. A remarkable radial groove beyond marginal angulation, i.e. ante-carinal depression, is well developed in *Eselaevitrigonia*, *Opisthotrigonia*, and *Pleurotrigonia*. The members of the section are distributed mainly in the Malm to Neocomian of the Indo-African region. *Eselaevitrigonia meridiana* (WOODS) occurs, however, in the "Middle Cretaceous" of New Zealand and *Trigonia gäwra* PHILIPPI assigned possibly to a member of *Sphenotrigonia* by Cox (1952, p. 63) is known from Upper Cretaceous of Chile.

In the Cretaceous, Trigoniinae KOBAYASHI em. declined gradually in Europe and the Indo-African region. In the upper Senonian, *Pacitrigonia* in this subfamily flourished in the Southern Pacific region. As mentioned before, this genus is a distinct off-shoot of *Trigonia* as can be judged from the surface costation and shell form, though a certain Senonian form of *Trigonia* has hitherto been missing from this region.

In the Tertiary, *Eotrigonia* appeared in the eastern part of Australia. As suggested by several authors, *Eotrigonia* is morphologically very close to Mesozoic *Trigonia*. Its shell is, however, thinner and smaller than that of *Trigonia*. Costae on its flank are concentric to transverse and the area is provided with numerous serrate radial costae. Marginal carina is obtuse but distinct. Radial weak threads presents on the posterior part of the flank and also on the very narrow and little escutcheon. Its shell form and surface costation are, therefore, very similar to those of *Trigonia* than *Pacitrigonia*. Judging from the surface costation, *Eotrigonia* was possibly derived from *Trigonia* by the development of the radial sculpture on the escutcheon and the dwarfing of the shell. Accordingly, it seems that *Trigonia* was probably outlived in the Southern Pacific region till the late Senonian.

Neotrigonia ranges from upper Miocene to Recent of Australia. The surface of the genus is ornamented with *Cardium*-like radial costation. This genus, however, grows through the *Eotrigonia* or *Trigonia* stage in its early ontogeny as shown by some authors, because of the presence of the radially serrate area and the concentrically costate flank. Internally, the ventral margin is all crenulate and the radial plications

along the positions of the carinae are absent. Therefore, this genus may be an offshoot issued from *Eotrigonia* by the development of the radial sculpture on the surface and the increasement of the internal crenulation on the ventral margin.

Genus *Trigonia* BRUGUIÈRE, 1789

Diagnosis:—Shell subtrigonal to subovate, often rostrate posteriorly; umbo prominent and angular; beak opisthogyrous and located anteriorly. Flank ornamented with numerous plain concentric to subconcentric costae; costae separated from the marginal carina in the left valve and sometimes also in the right valve by a smooth radial depression. Area wide and nearly flat or slightly concave, sculptured with strong radial costae and weak transverse striae the former of which are sometimes evanescent later; median carina or groove distinct but obscure in some forms. Escutcheon depressed and rather wide, provided with denticulate transverse costellae or smooth but sometimes radial threads developed in the vicinity of umbo. Marginal and escutcheon carinae distinct and strongly serrated.

Internally, radial plications along three carinae well developed and siphonal margin sometimes crenulated. Test very thick.

Type species:—*Venus sulcata* HERMANN, 1781. Up. Lias; Alsace.

Synonym:—*Lyridon* SOWERBY, 1823; *Lyriodon* BRONN, 1834; *Lyrodon* GOLDFUSS, 1837.

List of Species:—

- Trigonia acuta* KITCHIN, 1903. Oxfordian; Cutch, India.
- Trigonia alemanica* ROLLIER, 1912. Low. Bajocian; Germany.
- Lyridon alemanicum* var. *gingense* LEBKUCHNER, 1931. Low. Bajocian; Germany.
- Lyridon alemanicum* var. *helveticum* LEBKUCHNER, 1931. Dogger; Switzerland and Germany etc.
- Trigonia americana* MEEK, 1873. Malm; Montana and Utah etc.
- Trigonia (Trigonia) andrussovi* SAVELIEV, 1960. Callovian; West Turkmen.
- Trigonia anguste-costata* BEHRENDSEN, 1892. Senonian (?); Argentina.
- Trigonia (Lyridon) archinterlaevigata* WETZEL, 1937. Bathonian; Germany.
- Trigonia (Lyridon) ardenensis* ROLLIER, 1912. Up. Oxfordian; France.
- Trigonia bachelieri* d'ORBIGNY, 1850. Callovian; France.
- Trigonia baillycensis* de LORIO, 1893. Sequanian; France.
- Trigonia (Trigonia) bazarunasi* SAVELIEV, 1960. Callovian; Manghyschack and West Turkmen.
- Trigonia bella* LYCETT, 1877. Bathonian; Britain.
- Trigonia brevicostata* KITCHIN, 1903. Callovian; Cutch, India.
- Trigonia cardissa* AGASSIZ, 1840. Cenomanian of Switzerland and Lowest Oxfordian of West Turkmen.
- Trigonia carinata* AGASSIZ 1840. Hauterivian-Aptin; Germany, France, Britain, Argentina etc.
- Trigonia (Trig.) carinata caspica* SAVELIEV, 1958. Low. Valangian; Manghyschack
- Trigonia cassiope* d'ORBIGNY, 1850. Bathonian; France.
- Trigonia chariensis* KITCHIN, 1903. Bathonian-Callovian; Cutch, India.
- Trigonia charltonensis* DOUGLAS and ARKELL, 1928. Cornbrash; Britain.
- Trigonia conferticostata* CRAIG, 1905. Tithonian; Texas.
- Trigonia corderoi* LAMBERT, 1944. Callovian; Argentina.
- Trigonia costata* PARKINSON, 1815. Dogger; France, Britain, Germany etc.
- Trigonia costata* var. *elongata* GOLDFUSS. 1834. Bajocian; Germany.
- Trigonia costata* var. *lata* LYCETT, 1873. Great Oolite of Britain and Callovian of Chile.
- Trigonia costata* var. *pullus* MORRIS and LYCETT, 1853. Great Oolite; Britain.

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- Trigonia costata* var. *tenuicosta* WRIGHT, 1860. Inferior Oolite; Britain.
Trigonia costata var. *transversa* GOLDFUSS, 1834. Low. Dogger; Germany.
Trigonia costata var. *triangularis* GOLDFUSS, 1834. Up. Dogger; Germany.
Trigonia culleni LYCETT, 1877. Inferior Oolite; Britain.
Trigonia daphne de LORIO, 1893. Sequanian; France.
Trigonia densestriata BEHRENDSEN, 1892. Dogger; Argentina.
Trigonia denticulata AGASSIZ, 1840. Low. Dogger; France, Switzerland etc.
Lyridon denticulatum var. *curvatum* LEBKÜCHNER, 1931. Dogger; Germany.
Trigonia dhosaensis KITCHIN, 1903. Oxfordian; Cutch, India.
Trigonia distincta KITCHIN, 1903. Callovian; Cutch, India.
Trigonia (*Lyridon*) *ehningensis* ROLLIER, 1912. Up. Dogger; France and Germany etc.
Trigonia (*Trigonia*) *ehningensis kokbulakensis* SABELIEV, 1960. Callovian; Manghyschlack.
Trigonia elegantissima MEEK, 1893. Malm; Wyoming.
Trigonia elegantoides KÖRNER, 1937. Up. Trias; Peru.
Trigonia elongata SOWERBY, 1781. Bathonian of Britain and France etc. and Callovian of West Turkmen (?).
Trigonia elongata var. *angustata* LYCETT, 1877. Up. Bathonian-Low. Oxfordian; Britain.
Trigonia elongata var. *lata* LYCETT, 1877. Cornbrash; Britain.
Trigonia flumanni PHILIPPI, 1899. Horizon uncertain; Chile.
Trigonia fortinensis (pars) LAMBERT, 1944. Neocomian; Argentina.
Trigonia gaytani KLIPSTEIN, 1843. Up. Trias; East Alps.
Trigonia glasvillei MUNIER-CHALMAS, 1865. Low. Portlandian; France.
Trigonia harpa DESHAYES, 1842. Hauterivian-Gault; France.
Trigonia helena de LORIO, 1893. Sequanian; France.
Trigonia hemisphaerica LYCETT, 1853. Inferior Oolite; Britain.
Trigonia hemisphaerica var. *gregaria* LYCETT, 1877. Inferior Oolite; Britain.
Trigonia heva DOLLFUS, 1863. Gault; France.
Lyridon incrassatum LEBKÜCHNER, 1931. Dogger; Germany.
Trigonia infracostata LYCETT, 1881. Low. Lias; Spain.
Trigonia interlaevigata QUENSTEDT, 1858. Mid.-Up. Dogger; Germany.
Trigonia inostranzevi STREMOOUKHOV, 1896. Low. Portlandian; Moscow, U. S. S. R.
Trigonia kheraensis COX, 1952. Malm; Cutch, India.
Trigonia kiprinovi STREMOUKHOV, 1896. Low. Portlandian; Moscow, U. S. S. R.
Lyridon latezonatum LEBKÜCHNER, 1931. Up. Bajocian; Germany.
Trigonia langrunensis BIGOT, 1892. Up. Bathonian; France.
Trigonia (*Trigonia*) *latiarealis* SABELIEV, 1960. Lowest Oxfordian; West Turkmen.
Trigonia libanensis KRUMBECK, 1905. Dogger; Syria.
Trigonia lineolata AGASSIZ, 1840. Bajocian; Switzerland.
Trigonia littlei FIEBIGER, 1959. Sinemurian; British Columbia.
Trigonia lycetti WALFORD, 1885. Inferior Oolite; Britain.
Trigonia lycetti var. *corrugata* WALFORD, 1885. Inferior Oolite; Britain.
Trigonia meriani AGASSIZ, 1840. Low. Malm; Switzerland.
Trigonia miredensis LAMBERT, 1944. Kimmeridgian (?); Argentina.
Trigonia mollensis LAMBERT, 1944. Callovian; Argentina.
Trigonia monilifera AGASSIZ, 1840. Low. Malm; Switzerland and Britain etc.
Trigonia moorei LYCETT, 1870. Lias in Misol and Dogger in Australia.
Trigonia multicostata LYCETT, 1873. Inferior Oolite; Britain.
Trigonia munita CRAGIN, 1905. Tithonian; Texas.
Trigonia nitida KITCHIN, 1903. Oxfordian; Cutch, India.
Trigonia oehlerti BIGOT, 1893. Low. Callovian in France and Dogger in Argentina.
Trigonia papillata AGASSIZ, 1840. Oxfordian-Virgolian; Switzerland and Germany etc.
Trigonia parva KITCHIN, 1903. Tithonian; Cutch, India.
Trigonia (*Trigonia*) *pečincevae* SABELIEV, 1960. Callovian; West Turkmen.

- Trigonia popelaëvi* STREMOOKHOV, 1896. Callovian; Jaroslavl, U. S. S. R.
Trigonia postera QUENSTEDT, 1858. Lias; Germany.
Lyriodon praecassiope LEBKÜCHNER, 1931. Braun Jura γ ; Germany.
Lyriodon praecassiope var. *angusticostum* LEBKÜCHNER, 1931. Braun Jura; Germany.
Trigonia propinqua KITCHIN, 1903. Callovian; Cutch, India.
Trigonia prora KITCHIN, 1903. Bathonian; Cutch, India.
Lyriodon pseudosimile LEBKÜCHNER, 1931. Braun Jura β ; Germany.
Trigonia pullus SOWERBY, 1826. Dogger; Britain.
Trigonia reticulata AGASSIZ, 1840. Low. Malm; Switzerland.
Trigonia rolandi CROSS, 1875. Cornbrash; Britain.
Trigonia rudicosta CRAGIN, 1905. Tithonian; Texas.
Trigonia (Trigonia) rugosicostata Saveliev, 1960. Callovian; Manghyschlack.
Trigonia sculpta LYCETT, 1873. Inferior Oolite; Britain.
Trigonia sculpta var. *chellensis* LYCETT, 1877. Inferior Oolite; Britain.
Trigonia senex KOBAYASHI and MORI, 1954. Hettangian; North Japan.
Trigonia silicea QUENSTEDT, 1858. Malm; Germany.
Lyriodon simile var. *aberratum* LEBKÜCHNER, 1931. Braun Jura β ; Germany.
Trigonia similis AGASSIZ, 1840. Low. Dogger; Germany.
Trigonia spitiensis HOLDHAUS, 1913. Spiti shale (Malm); Himalaya, India.
Trigonia stelzneri GOTTSCHKE, 1878. Bajocian-Callovian; Argentina and Chile.
Trigonia stremmei LANGE, 1914. Neocomian; Tendaguru, East Africa.
Trigonia subcarinata ÉBRAY, 1858. Albion; France.
Trigonia (Trigonia) subpapillata Saveliev, 1960. Lowest Oxfordian; West Turkmen.
Trigonia subtriangularis WETZEL, 1911. Mid.-Up. Dogger; Germany.
Trigonia subtriangularis var. *alta* WETZEL, 1924. Mid. Dogger; Germany.
Trigonia subtriangularis var. *lata* WETZEL, 1924. Mid. Dogger; Germany.
Trigonia suevi STREMOOKHOV, 1896. Low. Portlandian; Moscow, U. S. S. R.
Trigonia (Lyriodon) sumiyagura KOBAYASHI and KASENO, 1947. Bajocian; North Japan.
Trigonia suprajurensis AGASSIZ, 1840. Sequanian-Virgolian; Switzerland.
Trigonia (Trig.) tabacoensis BARTHEL, 1958. Anician; Chile.
Trigonia tealei COX, 1937. Bathonian; Cutch, India.
Trigonia tenuicosta LYCETT, 1853. Inferior Oolite; Britain and Germany etc.
Trigonia tenuis KITCHIN, 1903. Tithonian; Cutch, India.
Trigonia (Lyriodon) tenuilaevigata WETZEL, 1937. Bathonian; Germany.
Trigonia textilis LEES, 1934. Up. Trias; Yukon, Canada.
Trigonia thetis PHILIPPI, 1899. Horizon uncertain; Chile.
Trigonia (Lyriodon) trigona WETZEL, 1950. Dogger; Germany.
Trigonia (Trigonia) tuarensis Saveliev, 1960. Callovian; West Turkmen.
Trigonia tumida KITCHIN, 1903. Callovian; Cutch, India.
Trigonia valfinensis de LORIO, 1888. Mid. Malm; France.
Trigonia zlabachiensis HAAS, 1909. Ladinian-Carnian; East Alps.

Remarks:—This genus is fairly constant in surface costation, while the outline varies to a large extent from subequilateral with a median umbo to highly inequilateral with a subterminal umbo. *Elongata* var. *angustata* has a tall outline, but pyriform in *culleni*. Common forms have the subtrigonal outline, but *thetis* is subcircular.

Costellae on escutcheon are transverse in many forms, but absent in Indian two species, i.e. *chariensis* and *parva*. Area is usually provided with strong radial costae and weak transverse striae, their intersections being thickened commonly into small tubercles or knods. *Parva* has, however, no concentric or transverse striae on its

area. Costae on the flank are fairly thick in most others and somewhat undulated near the anterior extremity, but fine in Upper Triassic *gaytani* and *zlambachiensis* from Alps.

Beak is opisthogyrous in common forms, but slightly prosogyrous in *tabacoensis*.

The earliest representative is *Trigonia* (*Trig.*) *tabacoensis* BARTHEL (1958, pp. 353–358, pl. 19, figs. 1–8, text-fig. 1) from possibly middle or even lower Anician of Chile. *Trigonia anguste-costata* BEHRENDSEN from Caryilauhue in Argentina is said to be of Senonian, but its precise horizon seems uncertain. Therefore, the youngest may be *Trigonia cardissa* AGASSIZ from Cenomanian of Switzerland.

Distribution:—Anician to Cenomanian of cosmopolitan, most flourished in Dogger to Malm of Europe and Southern America.

Genus *Pseudomyophorella* nov.

Diagnosis:—Shell subtrigonal to ovately quadrate, sometimes rostrate posteriorly; umbo rather broad, prominent and situated anteriorly; beak opisthogyrous. Marginal and escutcheon carinae distinct. Flank provided with diagonal and tuberculate, *Myophorella*-type costation; ante-carinal depression indistinct. Area fairly narrow, sculptured with radial costae and transverse threads which are sometimes obsolete in later stages; median furrow somewhat shallow and indistinct. Escutcheon depressed, of moderate width.

Type species:—*Pseudomyophorella savelievi*, gen. et sp. nov. Oxfordian (?); West Turkmen.

List of Species:—

Myophorella (*Myophorella*) *signata* (AGASSIZ) by SAVELIEV, 1960. Dogger; Germany.

Remarks:—This genus is one of the most interesting and aberrant Trigoniids, and its type is *Pseudomyophorella savelievi*, gen. et sp. nov. which the name is given for Saveliev's *Myophorellinae* gen. et sp. n.? (1960, pp. 91–93, pl. 7, figs. 3a–b).

This genus is distinct from *Trigonia* in having the characteristic *Myophorella*-type sculpture on its flank. *Myophorella* s.l. is distinguishable from this genus by the absence of the radial costation on the area.

Savelievi, sp. nov. has a small shell, and radial costae and a median furrow on the area are distinct. On the other hand, in Saveliev's *signata* (1960, pl. 11, fig. 2) a median furrow is indistinct and radial costae on the area are obsolete in later stages.

Clavotrigonia polonica LEBKÜCHNER (1931, p. 60, pl. 3, fig. 8; pl. 4, fig. 5) is represented by two interesting forms. Radial costae on the area are well observed in the later stage of the illustrated smaller one on fig. 8 in pl. 3, but its area is transversely costellate in the young stage. In the larger holotype specimen (pl. 4, fig. 5), the area is transversely costellate in the adult stage, but the costation in earlier stages is uncertain. Therefore, this species is easily separable from this genus by the character

of the area.

Distribution:—Dogger in Germany and Oxfordian (?) of Western Turkmen.

Genus *Pacitrigonia* MARWICK 1932

Diagnosis:—Shell trigonal-ovate to oblong, rarely rostrate posteriorly; umbo rather broad, prominent and located anteriorly; beak slightly prosogyrous. Marginal carina somewhat distinct in early stage, but sometimes rounded off later; median furrow or carina obscure. Escutcheon very narrow, depressed, with weak radial costellae which are often obsolete later; area rather narrow, slightly concave, provided with radial costae and transverse threads which are evanescent in later growth-stage. Flank with several plain concentric costae near umbo; rest of flank sculptured with oblique, more or less irregularly undulated costae which are obsolete or broken into pustules in the later. Ante-carinal depression distinct but obscure in some forms.

Test very thick.

Type species:—*Pacitrigonia sylvesteri* MARWICK 1932. Up. Senonian; New Zealand.

Synonym:—*Mesotrigonia* FRENEIX 1958

List of Species:—

Trigonia ecplecta WILCKENS, 1905. Up. Cret.; Patagonia.

Trigonia hanetiana d'ORBIGNY, 1847. Up. Senonian; New Zealand and Chile etc.

Pacitrigonia hanetiana neocaledonica FRENEIX, 1958. Up. Senonian; New Caledonia.

"*Trigonia*" *papuana* GLAESSNER, 1958. Cenomanian; New Guinea.

Trigonia regina WILCKENS, 1910. Up. Cret.; Seymour Island, Antarctica.

Remarks:—According to COX (1952, p. 62), *Trigonia patagonica* FERGULIO and *T. de-stefanini* FERGULIO are referable to be the genus.

Recently, FRENEIX (1958, p. 165) proposed *Mesotrigonia* based on *Mesotrigonia taramehaensis*, gen. et sp. nov. (1958, p. 166, pl. 1, figs. 9–11) from upper Senonian of New Caledonia. *Taramehaensis* is associated with *Pacitrigonia hanetiana neocaledonica*, and it has a small and subovate to ovately quadrate outline. On the costation, there are radial ornaments on the area and escutcheon but the geniculated sculptures are present on the flank. It is sometimes recognized that the similar sculpture is observable in the umbonal region of *Pacitrigonia hanetiana* and its allies. So, *Mesotrigonia* may indicate an immature stage of *Pacitrigonia*.

Like many other Trigoniids the genus presents somewhat remarkable change of characters in ontogeny.

The shell outline is subcircular in the young stage, but later it changes gradually into trigonal-ovate to oblong.

In the early stage of growth, the surface is ornamented with plain costae and costellae and tripartite distinctly by a marginal and an escutcheon carina into a flank, an area and escutcheon. Flank is sculptured with several concentric to transverse costae, and the area and escutcheon are ornamented with radial costae.

On the Trigoniinae

In the middle stage of growth, the flank is provided with plain, transverse to oblique costae which are geniculated in the anterior extremity. Costae on the area are usually well developed but sometimes absent. Costellae on the escutcheon are obscure.

In the adult stage, radial costae on the area are not well developed but transverse threads are sometimes well observable. Flank is smooth or provided with oblique, more or less irregularly, tuberculate and undulate costae.

As mentioned before, the shell in the early stage of the genus has some resemblances to that of *Trigonia* in surface costation and shell form. Therefore, this genus may be a derivative from *Trigonia*.

In this genus, the outline and surface sculpture vary to a fairly large extent. *Destefanini* has a remarkably rostrate outline, but subovate to trigonally ovate in *hanetiana* and its allies. On costae of the flank, irregular undulations are well observed in *hanetiana* and its subspecies *neocaledonica* but tubercles are well observable in *papuaana*. *Sylvesteri* has several plain costae near umbo, but soon smoothed, leaving rather distinct concentric bands which are restricted to the anterior half of the flank. Marginal carina and ante-carinal depression are distinct in many forms, but obscure in *sylvesteri*. Area is usually provided with radial costae, but smooth in *sylvesteri*.

Distribution:—Cenomanian to Senonian in New Guinea, New Caledonia, New Zealand, Antarctica, Patagonia, and Chile.

Genus *Nototrigonia* Cox, 1952

Diagnosis:—Shell pyriform, rostrate posteriorly, very inequilateral, moderately inflated. Umbo obtusely angular and somewhat improminent; beak almost orthogyrus and located anteriorly. Marginal and escutcheon carinae distinct near umbo, but rounded off later. Ante-carinal depression broad and distinct. Flank with oblique and sinuous costae which swell out and bent upwards at the margin of the depression. Area narrow, convex, with a small number of radial costae. Escutcheon broad, depressed and not impressed.

Growth-lines distinct and numerous in the posterior part of the shell; an internal ridge coincides approximately with the middle part of the area.

Type species:—*Trigonia cinctuta* ETHERIDGE, 1902. Low. Cret.; Lake Eyre basin, South Australia.

Remarks:—This genus is monotypic, being similar to *Heterotrigonia* in shell form and sculpture on the area, but distinct in costation on the flank.

Distribution:—Lower Cretaceous of South Australia.

Genus *Heterotrigonia* Cox, 1952

Diagnosis:—Shell small to medium in size, pyriform to trigonally ovate, inequilateral

eral, moderately inflated. Umbo narrow, rather prominent; beak opisthogyrous and antero-mesial. Marginal and escutcheon carinae visible only near umbo where surface is tripartite distinctly and ornamented with several plain concentric costae and costellae. Escutcheon fairly wide, depressed, provided with transverse, plain or tuberculate costellae. Area narrow, sculptured with several, radial, plain or tuberculate costae which are sometimes bifurcated or effaced later. Flank with two series of plain or tuberculate costae, except in the vicinity of umbo where a small number of costae exist; anterior series of costae first subconcentric, but become oblique and sometimes undulated or obsolete in the later; posterior series consists of radial or subvertical costae which are occasionally bifurcated; some radial or subvertical costae confluent with anterior subconcentric ones.

Growth-lines or concentric bands sometimes well developed on the whole surface; internally, a radial plication coincides approximately with the middle of the area.

Type species:—*Trigonia diversicostata* WHITEAVES, 1876. Haida formation (Up. Albian ?) of the Queen Charlotte series; British Columbia.

List of Species:—

Heterotrigonia granosa NAKANO, 1957. Santonian of Amakusa and Coniacian of Ikushumbetsu district in Central Hokkaido, Japan.

Trigonia subovalis JIMBO, 1894. "*Trigonia* Sandstone" (Cenomanian-Turonian) of Central Hokkaido in Japan and Peshina bay district in Kamtschatka; Urakawan formation (Coniacian-lower Campanian) of South Sachalin.

Remarks:—This genus is closely allied to *Apiotrigonia* and *Iotrigonia* in outline and surface costation, but easily distinguished by the presence of a small number of radial costae on the area.

In the early stage of growth, the whole surface is sculptured with several, plain concentric ribs and tripartite distinctly by a marginal and an escutcheon carina. It is sometimes recognized that in the umbonal region concentric costae rapidly become L-shaped costae via V-shaped costae and radial costae on the area appeared suddenly.

In the later stages, the characteristic L-shaped costae on the flank and radial costae of the area are well developed but sometimes evanescent.

As already discussed by the writer (1957a, 61), the shell outline is rather constant in this genus, but the ornamentation is somewhat variable. Costae in *granosa* are tuberculate, but plain in *diversicostata* and *subovalis*. *Diversicostata* has transverse and horizontal costae on the anterior part of the flank, and its area is provided with several distinct radial costae in all stages. In *subovalis*, transverse and horizontal costae are gradually becoming oblique, more or less undulated, and effaced in later stages when concentric bands are well developed on the whole surface. Its area is sculptured with several radial costae, but they are not well recognized in later stages. In shell outline, *granosa* is trigonal-ovate and small-sized, but pyriform in *subovalis* and *diversicostata*. *Diversicostata* has a medium-sized shell, while in *subovalis* the adult shell

measures 45–60 mm. long and 35–43 mm. high. Escutcheon is well developed in *subovalis* and *granosa*, but absent in *diversicostata*.

Distribution:—Upper Albian (?) to Santonian in the Northern Pacific.

Genus *Indotrigonia* DIETRICH, 1933

Diagnosis:—Shell triangularly ovate, strongly inequilateral, moderately inflated from umbo to venter and from anterior to posterior without marginal angulation. Umbo wide and rather prominent; beak opisthogyrous and located anteriorly. Marginal and escutcheon carinae effaced except near umbo where surface is distinctly tripartite. Flank with numerous, distinct, somewhat irregular, plain and concentric to subconcentric costae. Area convex, with rather distinct transverse costae but rapidly costellate near umbo. Median furrow sometimes well developed. Escutcheon narrow and depressed, sculptured with transverse costellae.

Internally, three radial plications along the carinae well recognized; test very thick.

Type species:—*Trigonia smeei* SOWERBY, 1840. Argovian of Northwest India and Kimmeridgian to Neocomian of East Africa.

List of Species:—

Trigonia beyschlagi MÜLLER, 1900. Barremian-Aptian; Tendaguru, East Africa.

Trigonia (Indotrigonia) katrolensis AGRAWAL, 1956. Kimmeridgian; Katrol, India.

? *Trigonia matapuana* KRENKEL, 1910. Neocomian; Tendaguru, East Africa.

Remarks:—This genus is constant in shell form and surface sculpture, though sometimes a median and an ante-carinal groove are well developed.

This genus is variable in ontogenetic development. The shell outline is subcircular to ovate in the young stage, but later it changes gradually into trigonal-ovate. In the immature stage, its shell is quite similar to that of *Trigonia* as shown by KITCHIN (1903) and LANGE (1914) etc. While, in the adult stage the whole surface is ornamented with concentric to subconcentric costae. Therefore, this genus must be an off-shoot from *Trigonia*.

COX (1952) and AGRAWAL (1956) considered that *Trigonia crassa* KITCHIN (1903, pl. 4, figs. 1–6; pl. 5, figs. 1–3) from the Upper Jurassic Oomia bed in Cutch of India is synonymized with *Trigonia beyschlagi* MÜLLER from Lower Cretaceous of Tendaguru, East Africa. In his study on *Rutitrigonia*, KOBAYASHI (1957, p. 58) transferred the latter to *Rutitrigonia*, because KRENKEL's *beyschlagi* (1900, pl. 20, figs. 6, figs. 8–9) has a rostrate shell and costae on the flank and area are oblique and gradually obsolete posteriorly.

Distribution:—Upper Jurassic to Aptian of Indo-African region.

Genus *Eselaevitrigonia* KOBAYASHI and MORI, 1954

Diagnosis:—Shell trigonally ovate to ovate, inequilateral, moderately inflated. Umbo broad and rather improminent; beak opisthogyrous and antero-mesial. Marginal and escutcheon carinae distinct near umbo, but obtuse or rounded off later. Flank with distinct, plain, concentric to subconcentric costae which are sometimes effaced in later growth-stages. Ante-carinal depression broad and more or less distinct. Area narrow and transversely costellate except for the umbonal region where several radial costae exist. Median furrow somewhat indistinct. Escutcheon narrow, depressed and smooth or rarely with transverse costellae.

Type species:—*Trigonia meridiana* Woods 1916. "Mid. Cret."; New Zealand.

List of species:—

*Trigonia cardinii*formis KITCHIN, 1903. Tithonian; Cutch, India.

Trigonia spissicostata KITCHIN, 1903. Tithonian; Cutch, India.

Trigonia trapeziformis KITCHIN, 1903. Tithonian; Cutch, India.

Remarks:—Ontogenetically, this genus is possibly a derivative from *Trigonia*, because its youngster is typical *Trigonia* as illustrated by KITCHIN (1903, pl. 5, fig. 4; pl. 6, figs. 1–9) and Woods (1917, pl. 1, figs. 2–7).

This genus is fairly constant in outline, but somewhat variable in surface costation. Regular concentric to subconcentric sculptures are well observed in *cardinii*formis and *meridiana*, but in *spissicostata* and *trapeziformis* the costation is somewhat irregular. In *spissicostata* ante-carinal depression is distinct, but obscure in *cardinii*formis and *meridiana*. Median furrow is well developed in *spissicostata*, but indistinct in the others.

Distribution:—Tithonian of India and "Middle Cretaceous" in New Zealand.

Genus *Opisthotrigonia* Cox, 1952

Diagnosis:—Shell pyriform or somewhat sickle-shaped, rather rostrate posteriorly, very inequilateral, moderately inflated. Umbo narrow and somewhat elevated; beak strongly opisthogyrous and pointed anteriorly. Marginal and escutcheon carinae distinct and strongly curved. Area narrow, sculptured with several radial threads and numerous weak transverse costae. Median furrow indistinct. Escutcheon narrow, depressed and smooth or provided with weak transverse striae. Flank with plain, somewhat irregular and subconcentric to transverse costae. Ante-carinal depression broad and distinct.

Type species:—*Trigonia retrosa* KITCHIN 1903. Tithonian; Cutch, India.

Remarks:—This genus is monotypic, resembling some forms of *Eselaevitrigonia*, i.e. *Eselaevitrigonia spissicostata* (KITCHIN) (KITCHIN, 1903. pl. 6, figs. 6–9), in surface costation and shell form, but very distinct in shape.

This genus is very variable in ontogenetic development. Its immature shell re-

sembles *Trigonia*, because its flank is provided with subconcentric costae and the area is radially costellate. So, this genus may be a derivative from *Trigonia*.

Distribution:—Tithonian of India.

Genus *Pleurotrigonia* van HOEPEN, 1929

Diagnosis:—Shell trigonal-ovate, somewhat elongated posteriorly, inequilateral, moderately convex. Umbo rather broad and prominent; beak opisthogyrous and located anteriorly. Marginal carina distinct and serrate in early stage, but rounded off later; escutcheon carina obscure. Ante-carinal depression broad and distinct. Flank with numerous, strong, plain concentric to subconcentric costae; anterior extremity of flank narrowly flattened in a plain almost at right angle to the commissure of the shell. Area somewhat broad and concave, sculptured with several radial threads which are obsolete in later stages. Escutcheon very narrow, depressed and smooth. Test very thick.

Type species:—*Trigonia blanckenhorni* NEWTON 1907. Albian; Zululand, South Africa.

Remarks:—This genus is monotypic. Its young shell is very similar to that of *Trigonia* in surface sculpture and shell form. Therefore, this is probably an off-shoot from *Trigonia*.

Distribution:—Albian of South Africa.

Genus *Sphenotrigonia* RENNIE, 1936

Diagnosis:—Shell large, cuneiform, elongately trigonal, very inequilateral, moderately inflated. Umbo obtuse and broad; beak prosogyrous and pointed at anterior extremity. Marginal and escutcheon carinae distinct and serrate in earliest stage, but evanescent in later. Area narrow and with some radial threads but soon become obsolete. Escutcheon indistinct. Flank with broad, plain and concentric undulations, except for the umbonal region where several subconcentric costae developed. Ante-carinal depression absent.

Type species:—*Trigonia (Sphenotrigonia) frommurzei* RENNIE 1936. Neocomian; Zululand, South Africa.

List of Species:—

? *Trigonia glabra* PHILIPPI, 1887. Up. Cret.; Chile.

Remarks:—This is the most aberrant Trigoniid, and is quite similar to Astartid genus *Seebachia* in shell form and surface sculpture.

According to RENNIE (1936, pp. 365–375), in the earliest stage the surface is distinctly tripartite by a marginal and an escutcheon carina into a flank, an area and escutcheon. Flank is sculptured with several, plain and subconcentric costae, and

the area is ornamented with some radial threads. Its youngest shell is similar to that of *Trigonia* in shell form and surface costation. Therefore, this genus is possibly a derivative from *Trigonia*.

In 1952, Cox (p. 63) pointed out that *Trigonia glabra* PHILIPPI from Upper Cretaceous of Chile may be a member of this genus.

Distribution:—Neocomian of Zululand in South Africa and (?) Upper Cretaceous of Chile.

III. CONCLUDING REMARKS

From the above discussion, the Trigoniinae KOBAYASHI 1954 em. can be classified as follows:

Subfamily Trigoniinae KOBAYASHI, 1954 em.

Trigonia section

Genus *Trigonia* BRUGUIÈRE, 1789

? Genus *Pseudomyophorella* nov.

Pacitrigonia section

Genus *Pacitrigonia* MARWICK, 1932

Genus *Nototrigonia* COX, 1952

? Genus *Heterotrigonia* COX, 1952

Indotrigonia section

Genus *Indotrigonia* DIETRICH, 1933

Genus *Eselaevitrigonia* KOBAYASHI and MORI, 1954

Genus *Opisthotrigonia* COX, 1952

Genus *Pleurotrigonia* van HOEPEN, 1929

Genus *Sphenotrigonia* RENNIE, 1936

The distributions and possible phyletic relationships of the Trigoniinae em. discussed above are tabulated on Tab. 1. *Trigonia* appeared in the Anician of Chile, forms a trunk of the subfamily. This genus mainly flourished in Europe and the South American region from Dogger to Malm, but suddenly declined in the Cretaceous. *Pseudomyophorella* nov. may be an off-shoot, belonging to a new subfamily, derived from the main trunk by the development of the diagonal and tuberculate sculpture on the flank. The genera of *Pacitrigonia* section are considered to have been issued from *Trigonia* in the Pacific region through the Cretaceous by the change of the surface ornamentation of the flank and the shell form. Among them, in the upper Senonian *Pacitrigonia* is a solitary genus of the subfamily and it was limited to the Southern Pacific region. From Malm to Neocomian, the remainders of the subfamily were derived possibly from the trunk in the Indo-African region by the effacement of the radial costation on the area and the transfigurations of the shell form.

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TABLE 1. Phylogeny and Geographical and Geological Distributions of the Trigoniinae Kobayashi, 1954 em.

[illegible]

EXPLANATION OF PLATE VIII

- FIG. 1. *Trigonia sumiyagura* KOBAYASHI and KASENO. Bajocian; Shizukawa district, Miyagi Pref., North Japan. $\times 1$.
- FIG. 2. *Frenguelliella inexpectata* (JAWORSKI). Middle Lias; Argentina. (After JAWORSKI). $\times 9/10$.
- FIG. 3. Same species, showing the costation on the area and escutcheon. (After JAWORSKI). $\times 9/10$.
- FIG. 4. *Indotrigonia smeei* (SOWERBY), Argovian of Northwest India and Kimmeridgian to Neocomian of East Africa. (After KITCHIN). $\times 5/9$.
- FIG. 5. Same species, showing the costation of the area and escutcheon in the young stage. (After KITCHIN). $\times 5/9$.
- FIG. 6. *Opisthotrigonia retrosa* (KITCHIN). Tithonian; Cutch, India. (After KITCHIN). $\times 2/3$.
- FIG. 7. Same species, showing the character of the area and escutcheon. (After KITCHIN). $\times 2/3$.
- FIG. 8. *Pleurotrigonia blanckenhorni* (NEWTON). Albian; Zululand, South Africa. (After RENNIE). $\times 2/3$.
- FIG. 9. *Eselaevitrigonia cardinii* (KITCHIN). Tithonian; Cutch, India. (After KITCHIN). $\times 2/3$.
- FIG. 10. Same species, showing the sculpture on the area and escutcheon.
- FIG. 11. *Heterotrigonia diversicostata* (WHITEAVES). Haida formation (possibly upper Albian) of Queen Charlotte series; British Columbia. (After PACKARD). $\times 2/3$.
- FIG. 12. *Pacitrigonia sylvesteri* MARWICK. Upper Senonian; New Zealand. (After MARWICK). $\times 1/2$.
- FIG. 13. *Sphenotrigonia frommurzei* RENNIE. Neocomian; Zululand, South Africa. (After RENNIE). $\times 2/3$.
- FIG. 14. Same species, showing the character of the area and escutcheon.
- FIG. 15. *Nototrigonia cinctuta* (ETHERIDGE). Lower Cretaceous; Lake Eyre basin, South Australia. (After Cox). $\times 2/3$.

