Rinetrigonia and Its Allies

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With 1 Table

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ABSTRACT: In this paper, the writer has re-examined and discussed the classification, the complicated phyletic relationships and the mode of life of the Pterotrigoniinae van HOEPEN, 1929 em. KOBAYASHI and NAKANO, 1957 and described and listed a number of species. *Metacanthotrigonia* nov. typified by *Pterotrigonia* (*Rinetrigonia*) *yeharai* NAKANO and NUMANO is a new subgenus of *Acanthotrigonia* van HOEPEN, 1929 and is characterized by having the discrepant ribbing on the anterior and the posterior part of the flank. It is known in the Aptian to the Turonian of Japan and Manghyschlack.

CONTENTS

I. INTRODUCTION

Rinetrigonia van HOEPEN, 1929 and its allies equivalent nearly to GILLET's Groupe de *Trigonia ventricosa* KRAUSS des Scabres, are well characterized by their own outline and surface sculpture. They are the members of the subfamily Pterotrigoniinae van HOEPEN, 1929 em. KOBAYASHI and NAKANO, 1957, and they are characteristic and inhabited in the Tithonian to the upper Senonian of the so-called Gondwanaland and her adjacent regions.

Since 1957, KOBAYASHI and NAKANO has proposed a tentative classification of the subfamily Pterotrigoniinae on the basis of the surface ornament on the convex area and the flank, a number of interesting papers for the subfamily were published by FRENEIX (1972), LEVY (1967), SAVELIEV (1958), SKWARKO (1963, 1966, 1968), TAMURA and his co-workers (1967, 1968), etc. As the result, the knowledge of the subfamily has been

increased rapidly over the last decade.

In this paper, the writer takes a new look at the subfamily Pterotrigoniinae and tries to discuss the phyletic relationships and the mode of life of the subfamily. As a result, the subfamily Pterotrigoniinae may be classified here as shown on page 105 and their distribution and possible phyletic relationships are tabulated on Table 1. It is interesting to see that *Rinetrigonia* and its allies can be separable into two groups called *Rinetrigonia* and *Metacanthotrigonia* nov. by the sculpture on the area where costae, if present, are transversal in the former but diagonal or oblique in the latter. *Metacanthotrigonia* nov. based on *Pterotrigonia* (*Rinetrigonia*) *yeharai* NAKANO and NUMANO is a new subgenus of *Acanthotrigonia* van HOEPEN, 1929 and the new subgenus is known in the Aptian to the Turonian of Japan and Manghyschlack. Because the youngsters in many species belonging to *Scabrotrigonia* and *Acanthotrigonia* s.l. bear many aspects of *Pterotrigonia* s.s., the former two may have been issued respectively from the last one. As already suggested by the writer (1970), it seems that the most shells of the Pterotrigoniinae stand on sandstone layers with the anterior extremity downward and the siphonal part upward and in this condition they may have been in clusters and their venter looking toward a calm water in neritic sea.

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II. PALAEONTOLOGICAL NOTES

Subfamily Pterotrigoniinae van HOEPEN, 1929

Describing a number of the interesting Cretaceous Trigoniids from Zululand in Africa, van HOEPEN (1929) distinguished the Pterotrigoniinae nov. in the family Trigoniidae and placed in the subfamily the following new genera:

Subfamily Pterotrigoniinae nov.
- Genus *Pterotrigonia* nov. (*Pterotrigonia cristata* nov.)
- Genus *Acanthotrigonia* nov. (*Trigonia sheptonei* GRIESBACH, 1871)
- Genus *Linotrigonia* nov. (*Linotrigonia linifera* nov.)
- Genus *Pisotrigonia* nov. (*Pisotrigonia salebrosa* nov.)
- Genus *Rinetrigonia* nov. (*Trigonia ventricosa* KRAUSS, 1847)
- Genus *Ptilotrigonia* nov. (*Ptilotrigonia lauta* nov.)

Before this work, DEECKE (1925) proposed *Scabrotrigonia* without its type species. Van HOEPEN's proposal was accepted by CRICKMAY (1932) who condidered, however, *Pisotrigonia* and *Rinetrigonia* to be the subgenera of genus *Pterotrigonia*. Succeedingly, DIETRICH (1933) established *Scabrotrigonia* and *Notoscabrotrigonia* based respectively on *Trigonia scabra* LAMARCK and *T. tocaimaana* LEA. In 1952, Cox accepted only *Linotrigonia* and *Pterotrigonia* as the valid genera in the family Trigoniidae, but remaining genera of van HOEPEN's and DIETRICH's ones were assigned by him to the synonyms of *Pterotrigonia*. Later, he (1969) treated *Scabrotrigonia* as a subgenus of genus *Pterotrigonia*.

In his comprehensive study on the Trigoniidae, SAVELIEV (1958) accepted Cox's proposal for *Linotrigonia* and *Pterotrigonia* but assigned *Scabrotrigonia* as a valid genus in

his subfamily Pterotrigoniinae.

His classification is as follows:

Subfamily Pterotrigoniinae van HOEPEN, 1929
  Genus *Pterotrigonia* van HOEPEN, 1929 (=*Acanthotrigonia* van HOEPEN, 1929=*Pisotrigonia* van HOEPEN, 1929=*Rinetrigonia* van HOEPEN, 1929=*Ptilotrigonia* van HOEPEN, 1929=*Notoscabrotrigonia* DIETRICH, 1933)
  Genus *Linotrigonia* van HOEPEN, 1929
    Subgenus *Linotrigonia* s.s.
    Subgenus *Oistotrigonia* COX, 1952 (*Trigonia spinosa* PARKINSON, 1811)
  Genus *Scabrotrigonia* DEECKE, 1925 em. DIETRICH, 1933 (*Trigonia scabra* LAMARCK, 1819)

Van HOEPEN's and SAVELIEV's Pterotrigoniinae are roughly corresponded to LYCETT's Aliformis and Spinosa groups of the Scabrae section, the latter group of which is considered to be a substitute of *Linotrigonia* s.l. having a sharp marginal craina on the concave area, but the former has no distinct carina on the convex area. Therefore, it seems to the writer that they are quite different to each other in many aspects. As already suggested by KOBAYASHI and NAKANO (1957), in this respect, it may be better to segregate *Linotrigonia* s.l. out of the Pterotrigoniinae because it belongs to KOBAYASHI's Myophorellinae rather than to the Pterotrigoniinae.

Earlier than SAVELIEV, KOBAYASHI and NAKANO (1957) revised the knowledges for the Pterotrigoniinae at that time and they noted that the costation on their convex area may be most important for classification of the subfamily which are variable to a large extent in shell form and sculpture on the flank. According to them, in the subfamily Pterotrigoniinae costellae on the area, if present there, are transversal in *Pterotrigonia*, but diagonal or oblique in *Acanthotrigonia* and chevron-shaped in *Scabrotrigonia*.

Their classification is summarized as follows:

Subfamily Pterotrigoniinae van HOEPEN, 1929
  Genus *Pterotrigonia* van HOEPEN, 1929
    Subgenus *Pterotrigonia* s.s. (=*Ptilotrigonia* van HOEPEN, 1929=*Notoscabrotrigonia* DIETRICH, 1933)
    Subgenus *Rinetrigonia* van HOEPEN, 1929 (=*Pisotrigonia* van HOEPEN, 1929)
  Genus *Scabrotrigonia* DIETRICH, 1933
  Genus *Acanthotrigonia* van HOEPEN, 1929

As mentioned before, the Pterotrigoniinae by KOBAYASHI and NAKANO including *Pterotrigonia* s.l., *Scabrotrigonia* and *Acanthotrigonia*, correspond roughly to the typical Scabrae or LYCETT's Aliformis group. According to them, *Pterotrigonia* s.s. and *Rinetrigonia* have some resemblance with each other in essential character and the former inhabited in the Neocomian to the Senonian of cosmopolitan, but diagonal ribbing on the flank is discrepant between the anterior and the posterior part in the latter which is limited to the Tithonian to "Middle Cretaceous" of the austral region such as India, East and South Africa, Chile (?) and Peru (?). In this respect, *Rinetrigonia* was reserved by them as a subgenus of *Pterotrigonia*.

KOBAYASHI and NAKANO's proposal for the subfamily Pterotrigoniinae is followed by SKWARKO (1963, 1966, 1968), TAMURA and his co-workers (1967, 1968), LEVY (1967) FRENEIX (1972) and others, and a number of species belonging to the Pterotrigoniinae, especially *Rinetrigonia* and its allies, were reported and added by them from various locali-

ties.

In 1958, KOBAYASHI and NAKANO reported the occurrence of a few fragmental specimens under the name of *Pterotrigonia* (*Rinetrigonia*?) sp. *a* and *b* from the Aptian Hinagu formation in Yatsushiro district, Kyushu, Japan, which reveal close affinity to *Rinetrigonia*. Succeedingly, the writer (1961) with NUMANO described *Pterotrigonia* (*Rinetrigonia*) *yeharai* sp. nov. and *P.* (*R.*) sp. nov. from the Turonian strata of the Goshonoura group and the Mifune group in Kyushu, respectively. At that time, they noted that *Pterotrigonia cubanica* (pars) (SINZOW) in SAVELIEV (1958, pl. 34, figs. 2–6 non figs. la-b) from the upper Aptian of Manghyschlack, *P. subpiriformis* SAVELIEV from the upper Albian of the same region, and *Trigonia subventricosa* STANTON from the lower Neocomian of Patagonia in Argentina are possibly the members of *Rinetrigonia* because of the discrepant costation between the anteal and the posteal portion of the flank but the other *Rinetrigonia*-type specimens (pl. 34, figs. la-b only) of *cubanica* by SAVELIEV seem to be the members of *Acanthotrigonia* as can be judged from the obliquely costellate area.

In 1963, SKWARKO described *Pterotrigonia* (*Rinetrigonia*) *capricornia* sp. nov. from the upper Neocomian to the Aptian of Northern Territory in Australia and he suggested that Neocomian *Pterotrigonia australiensis* COX may be a member of *Rinetrigonia*. Succeedingly, he (1968) described *Pterotrigonia* (*Rinetrigonia*) *verrucosa* sp. nov. and *P.* (*R.*) *capricornia* SKWARKO from the late Neocomian of Queensland in Australia and these forms look to be the most interesting and aberrant forms of *Pterotrigonia* (*Rinetrigonia*) because tubercles on the costae of the anterior part in the flank are developed into short spines.

In 1967, TAMURA and TASHIRO pointed out that *Pterotrigonia* (*Rinetrigonia*) sp. nov. by NAKANO and NUMANO (1961) has some resemblance to *Rinetrigonia* in shell form and surface sculpture but its area is diagonally or obliquely costellate. So, this form was considered by them to be a member of *Acanthotrigonia* and they gave a new specific name, *Acanthotrigonia higoensis* sp. nov. Succeedingly, TAMURA et al. (1968) transfered *Pterotrigonia* (*Rinetrigonia*) *yeharai* NAKANO and NUMANO to *Acanthotrigonia* because of oblique ribbing on its area. Consequently, they emphasized that there is no species of *Rinetrigonia* in Japan, if *Pterotrigonia* (*Rinetrigonia*?) sp. *a* and *b* by KOBAYASHI and NAKANO (1958) are excluded, and that Japanese and Manghyschlackan forms, i.e. *Pterotrigonia subpiriformis* SAVELIEV, *P. cubanica* (pars) (SINZOW) in SAVELIEV, *P.* (*Rinetrigonia*) *yeharai* NAKANO and NUMANO, and *Acanthotrigonia higoensis* TAMURA and TASHIRO, having the discrepant sculpture on the flank are far aprt from typical *Rinetrigonia*.

The opinion by TAMURA et al. to *Rinetrigonia* and its allies is very interesting and it may be a good key to the division of the Pterotrigoniinae.

As mentioned before, with reference to the areal ornament the subfamily Pterotrigoniinae are classified by KOBAYASHI and NAKANO (1957) into three genera such as *Pterotrigonia* s.l., *Scabrotrigonia* and *Acanthotrigonia*, and the first one is splitted into two subgenera called *Pterotrigonia* s.s. and *Rinetrigonia* based on the sculpture of the flank. In the same way, *Acanthotrigonia* having oblique ribbing on the convex area seems, also, to be separable into two groups named as *Acanthotrigonia* s.s. and *Metacanthotrigonia* nov. on the basis of the costation on the flank. *Metacanthotrigonia* nov. is typified by *Pterotrigonia* (*Rinetrigonia*) *yeharai* NAKANO and NUMANO from the Turonian member of the Goshonoura group in Kyushu, Japan and the similar forms are reported from the Aptian to the Turonian of Japan and Manghyschlack as mentioned before. *Metacanthotrigonia nov.* is well characterized by the discrepant costation between the anterior and the posterior part of the flank.

In this character, this new subgenus is distinguishable from typical *Acanthotrigonia*. On the sculpture of the flank this new subgenus is quite similar to *Rinetrigonia* but is distinct in having oblique costellae on the area.

As summarized above, the Pterotrigoniinae are tentatively classified as below.

Subfamily Pterotrigoniinae van HOEPEN, 1929
  Genus *Pterotrigonia* van HOEPEN, 1929
    Subgenus *Pterotrigonia* s.s. (=*Ptilotrigonia* van HOEPEN, 1929=*Notoscabrotrigonia* DIETRICH, 1933)
    Subgenus *Rinetrigonia* van HOEPEN, 1929 (=*Pisotrigonia* van HOEPEN, 1929)
  Genus *Scabrotrigonia* DIETRICH, 1933
  Genus *Acanthotrigonia* van HOEPEN, 1929
    Subgenus *Acanthotrigonia* s.s.
    Subgenus *Metacanthotrigonia* nov. (*Pterotrigonia* (*Rinetrigonia*) *yeharai* NAKANO and NUMANO, 1961)

As already pointed out by KOBAYASHI and NAKANO (1957), the subfamily Pterotrigoniinae are variable to a wide extent in shell form and surface costation and comprises a great number of species and varieties as listed by KOBAYASHI and NAKANO (1957), NAKANO (1958, 1973a), NAKANO and NUMANO (1961) and others. In this occasion, some additional notes are described hereunder.

On the phyletic relationships of the Pterotrigoniinae, SAVELIEV (1958) considered that this subfamily including *Pterotrigonia, Linotrigonia* s.l. and *Scabrotrigonia* were directly derived from *Apiotrigonia* Cox of his Megatrigoniinae.

On the other hand, KOBAYASHI and NAKANO (1957) emphasized that their Pterotrigoniinae containing *Pterotrigonia* s.l., *Scabrotrigonia* and *Acanthotrigonia* were issued from KOBAYASHI's Myophorellinae or most probably from *Haidaia* of *Myophorella* because Pterotrigonians bear many aspects of *Myophorella* in their juvenalium. Although the oldest of the subfamily may be *Trigonia ventricosa* KRAUSS from the Tithonian Umia (Oomia) bed of Cutch in India, which ranges from the Tithonian to the Neocomian, they assigned that later Pterotrigonians were derived from an unknown Pre-Tithonian ancestor because *ventricosa* is considered by them to be so far specialized in outline and sculpture.

In 1961, the writer with NUMANO accepted KOBAYASHI and NAKANO's proposal and they pointed out that the immature shells of many species in the subfamily are quite similar to those of *Haidaia* of *Myophorella* in the presence of distinct carinae, diagonal *Haidaia*-type crenulate costae on the flank, and transversely costellate area. Therefore, they emphasized the ancestor of the subfamily were issued possibly from *Haidaia* of *Myophorella*.

In 1967, TAMURA and TASHIRO pointed out that *Scabrotrigonia* was derived probably from *Acanthotrigonia* on the basis of the ornamental change of *Acanthotrigonia pustulosa* (NAGAO). On the other hand, the writer (1973a) did not agree with their opinion and he suggested that *Acanthotrigonia* and *Scabrotrigonia* may have been issued possibly from *Pterotrigonia* s.s. by the development of the oblique ribbing or the chevron-shaped sculpture on the area based on the costation near the umbo, respectively.

The shell of the Pterotrigoniinae is well characterized by its own outline and surface ornament as mentioned above and, in this aspect, it is easily distinguishable and separable from that of the other groups in the family Trigoniidae. On the outline the shell is very inequilateral, lunate to subtrigonal and very inflated anteriorly but attenuated and depressed posteriorly, and the anterior extremity of the bivalved shell is broadly flattened in a plane which is almost perpendicular to the commissure. Costae on the flank of the shell

are diagonal, tuberculate or plain and rarely spinose, and they are steep on the anterior or umbonal side but gently inclined on the other.

As already suggested by the writer (1970), these facts seem to be one of the most important key to analyse the problem of the mode of life because the shells of the Pterotrigoniinae at hand having these features, such as, *Pterotrigonia inezana* (PACKARD), *P.* (*Rinetrigonia*) *ventricosa* (KRAUSS), *Scabrotrigonia clavigera* (CRAGIN) and others, stand easily and fix steady on a plane with antero-dorsal part, i.e. anterior extremity, downward and the siphonal margin upward. On the fossil occurrence, the shells of the Pterotrigoniinae come, in many cases, out of sandstone layers in which they are sometimes crowded together as a fossil bank. In this part, we can rarely recognized the bivalved specimens are preserved in the condition mentioned above.

From the viewpoint of functional morphology and fossil occurrence, therefore, on the mode of life, the writer is of opinion that the shells of many species belonging to the Pterotrigoniinae stand on the sandstone strata with anterior extremity downward and the siphonal part upward and in this state they may have been in clusters and their ventral margin meeting against a calm water in neritic sea.

Genus *Pterotrigonia* van HOEPEN, 1929

Type species: — *Pterotrigonia cristata* van HOEPEN, 1929. "Mid. Cret."; Zululand, South Africa.

Remarks: — This is a typical member of the Pterotrigoniinae having transverse costae on the convex area where the ribbing is commonly obsolete later, and is variable to a wide extent in shell form and surface sculpture. As mentioned before, on the bsais of the sculpture on the flank this genus can be divided into two subgenera named as *Pterotrigonia* s.s. and *Rinetrigonia* van HOEPEN, 1929 the latter of which has the discrepant ribbing between the anterior and the posterior part.

Subgenus *Pterotrigonia* s.s.

Synonym: — *Ptilotrigonia* van HOEPEN, 1929 = *Notoscabrotrigonia* DIETRICH, 1933

Remarks: — This subgenus is cosmopolitan in the Cretaceous, and comprises a great number of species and varieties as listed by KOBAYASHI and NAKANO (1957, pp. 225–226) and NAKANO and NUMANO (1961, p. 90). The followings may be added to this subgenus.

Pterotrigonia aliformis schapsugensis (MORDVILKO) by EBERSIN, 1960. Low. Cret.; Caucasas.
Trigonia akuschaensis ANTHULA, 1899. Aptian; Caucasas.
Trigonia churchi ANDERSON, 1958. Campanian; California.
Trigonia hemphilli ANDERSON, 1958. Low. Campanian; California.
Pterotrigonia (s.s.) *hottingeri* FRENEIX, 1972. Up. Albian; Central Morocco.
Trigonia klamathonia ANDERSON, 1958. Turonian; California and Oregon.
Trigonia limbata LAMARCK by ABBASS, 1962. Cenomanian; Egypt.
Trigonia melhasei ANDERSON, 1958. Up. Turonian; California.
Pterotrigonia peroni FRENEIX, 1972. Up. Albian; Tunisia.
Trigonia scabra (pars) LAMARCK in STOLICZKA, 1871. Turonian; India.
Trigonia scabra LAMARCK in ABBASS, 1962. Vranconian; Sinai Peninsula.

This subgenus varies to a large extent in surface ornamentation and shell form. Its outline is subtrigonal in common forms, but lunate or crescentic and attenuate posteriorly

in *aliformis, brevicula, cristata, pocilliformis* and *yokoyamai* etc. The quadrate forms, i.e. *columbiana, sakakurai,* and *wendleri* etc., are collected from the "Middle Cretaceous" of Japan and North America.

Ante-carinal depression is distinct and it is broad and shallow in many species, but obscure in *bowersiana* and *melhasei* etc. Median furrow is distinct in common forms, but indistinct in some large ones, such as *plebeia* and *sakakurai.*

Costae on the flank are distinct, diagonal and tuberculate in many others, but they are plain in some Northern Pacific "Middle Cretaceous" species, i.e. *columbiana, sakakurai* and *yokoyamai* etc. and they are evanescent in the anteal part of *chivensis* (ARCHANGELSKI, 1916; pl. 4, fig. 6). Area is as a rule smooth except near the umbo, but transversally costellate in *caudata, etheridgei, hottingeri, scabricola* and others which occur in the Lower and "Middle" Cretaceous of Europe and North Africa. Escutcheon is sculptured with tuberculate or plain costellae in most species, but sometimes smooth in *brevicula.*

As already pointed out by KOBAYASHI and NAKANO (1958) and NAKANO (1973a), *Trigonia scabra* Lamarck in STOLICZKA (1871, pl. 15, figs. 24–26; pl. 16, figs. 35–40) seems to be a heterogeneous aggregate as can be judged from the sculpture on the area. The oblique ribbing is well recognized in some forms (pl. 15, figs. 25 and 25a; pl. 16, figs. 35, 35a–b and 36), but smooth in the others (pl. 15, figs. 24, 24a and 26; pl. 16, figs. 37, 40 and 40a). Therefore, the obliquely striated forms are possibly belonged to *Acanthotrigonia* and the smooth ones are probably *Pterotrigonia* s.s.

Trigonia elisae BRIART et CORNET was tentatively placed by KOBAYASHI and NAKANO (1957) in this subgenus, but it is better to be referred to *Acanthotrigonia* because of the obliquely costellate area. COSSMANN'S *T. elisae* (1912, pl. 2, figs. 1, 10–12; pl. 4, figs. 18) is, however, a typical *Quadratotrigonia* as can be judged from the surface sculpture and shell form.

As already suggested by the writer (1961) with NUMANO, *Pterotrigonia vectiana* (LYCETT) in SAVELIEV (1958, pl. 39, figs. 1–3) seems to be a member of *Linotrigonia* because of the distinct marginal carina and the obliquely costellate area.

ABBASS' *Trigonia limbata* LAMARCK and *T. scabra* LAMARCK (1962, pp. 88–92, pl. 15, figs. 1–9) derived respectively from the Cenomanian of Eastern Desert in Egypt and the Vranconian of Sinai Peninsula have some resemblance to the members of *Scabrotrigonia* in essential character, but the chevron-shaped sculpture on the convex area is not discernible in his ones. Therefore, they are possibly belonged to *Pterotrigonia* s.s. as already pointed out by the writer (1973a, p. 264).

Very recently, FRENEIX (1972, p. 190) referred *Trigonia coihuicoensis* WEAVER (1931, pp. 268–270, pl. 27, figs. 151; pl. 28, figs. 155–160) to this subgenus, but it seems to be a member of *Promyophorella* of *Myophorella* as can be judged from the slightly concave area where the marginal carina is sharp and prominent.

Distribution: — Cretaceous of cosmopolitan. Upper Cretaceous members inhabited mainly in North America.

Subgenus *Rinetrigonia* van HOEPEN, 1929

Type species: — *Trigonia ventricosa* KRAUSS, 1847. Neocomian of East Africa and Tithonian to Neocomian of India.

Synonym: — *Pisotrigonia* van HOEPEN, 1929

Remarks: — This is characterized by having the discrepant sculpture between the anteal

and the posteal part of the flank. The synoptic lists were shown by KOBAYASHI and NAKANO (1957, p. 230) and NAKANO and NUMANO (1961, p. 94). The additional forms are as follows:

Pterotrigonia australiensis COX, 1961. Neocomian; Western Australia.

Pterotrigonia (Rinetrigonia) capricornia SKWARKO, 1963. Up. Neocomian-Aptian; Northern Territory and Queensland in Australia.

Pterotrigonia (Rinetrigonia) verrucosa SKWARKO, 1968. Up. Neocomian; Queensland.

This subgenus is fairly constant in shell form, but somewhat variable in surface ornament. Costae on the anterior part of the flank are as a rule tuberculate but plain in *subpiriformis* and spiny in *capricornia* and *verrucosa*. Posterior costae are plain and slender in *kraussi* and *australiensis*, but tuberculate and fairly thick in *salebrosa*. Escutcheon is transversely costellate in most others, but it seems to be smooth in *australiensis* and *tuberculifera*. Median furrow is obscure in large forms, such as *kraussi* and *salebrosa* etc., but distinct in small ones, i.e. *subpiriformis, ventricosa* and others.

SKWARKO (1963) and TAMURA and TASHIRO (1967) emphasized that *capricornia* has the oblique ribbing on the area near the umbo. According to SKWARKO's illustration (pl. 2, figs. 2–8), *capricornia* seems to be represented by not so well preserved specimens and it is considered to be strongly compressed by secondary deformation. Succedingly, SKWARKO (1966, pl. 7, figs. 11 and 14; 1968, pl. 14, figs. 9 and 12) reported and described two and one fairly well preserved specimens under the name of *capricornia* from the late Neocomian of Northern Territory and Queensland, respectively. The areas of them are provided with distinct transverse costae in the vicinity of the umbo as can be judged from their gypsum casts at hand. Therefore, *capricornia* is possibly a member of *Rinetrigonia*.

Recently, LEVY (1967) referred *Trigonia feruglioi* PIATNIZKY, 1938, *T. windhauseniana* WILCKENS, 1921 and *T. bustamatiana* FERUGLIO, 1935 to *Rinetrigonia* of *Pterotrigonia* without their illustrations. They are collected from Patagonia of Argentina, and the first is the Albian in age but upper Senonian in the others.

Distribution: — Tithonian to Senonian of the so-called Gondwanaland and its adjacent areas such as India, Africa, Australia, South America and Caspian sea region. This appeared in the Tithonian of India, and migrated gradually into the other regions.

Genus *Scabrotrigonia* DIETRICH, 1933

Type species: — *Trigonia scabra* LAMARCK, 1819. Albian-Turonian; France, Britain, Madagascar etc.

Remarks: — The chevron-shaped ribbing on the convex area is the most important characteristic of the genus. As already suggested by KOBAYASHI and NAKANO (1957) and NAKANO (1958, 1973a), the genus is fairly variable in surface sculpture but somewhat constant in shell form and it comprises a number of species and varieties as listed by them.

Trigonia pseudocrenulata NOETLING from the Aptian of Lebanon and Sinai Peninsula is very close to a member of the Pterotrigoniinae in essential character. Its convex area is, however, provided with 3–4 radial ribs which become obsolete later as already pointed out by the writer (1973a, p. 264; 1973b, p. 66). Therefore, this is a member of *Arabitrigonia* NAKANO, 1973.

Trigonia ethra COQUAND from the Cenomanian of Asia Minor, Sicily and Algeria etc. was tentatively considered by KOBAYASHI and NAKANO (1957, p. 226) to be a member

of *Pterotrigonia* s.s., but it may be better to be placed in this genus because of the chevron-shaped ribbing which was illustrated by FRENEIX (1972, p. 116, text-fig. 15–C).

Distribution: — Aptian to Maestrichtian of cosmopolitan; very abundant in Campanian to Maestrichtian of North America.

Genus *Acanthotrigonia* van HOEPEN, 1929

Type species: — *Trigonia sheptonei* GRIESBACH, 1871. Up. Santonian-Maestrichtian; Natal, Mozambique, Madagascar etc.

Remarks: — This is characterized by the oblique ribbing on the convex area. The genus is somewhat constant in shell form but varies to a large extent in sculpture on the flank. In this respect, this genus seems to be separable into two groups called *Acanthotrigonia* s.s. and *Metacanthotrigonia* nov. the latter of which has the discrepant ribbing between the anteal and the posteal part of the flank.

Subgenus *Acanthotrigonia* s.s.

Remarks: — This subgenus has some resemblance to *Pterotrigonia* s.s. and *Scabrotrigonia* in essential character, but differs in having the diagonal or oblique costae on the area. This subgenus comprises a number of species as already listed by KOBAYASHI and NAKANO (1957, p. 232). The followings are possibly added to the subgenus.

Trigonia elisae BRIART et CORNET, 1863. Low. Cenomanian; Belgium.
Pterotrigonia gokderensis SAVELIEV, 1958. Aptian; Manghyschlack.
Acanthotrigonia mashikensis TAMURA and TASHIRO, 1967. Turonian; Mifune district, Kyushu, Japan.
Acanthotrigonia mifunensis TAMURA and TASHIRO, 1967. Turonian; Mifune district, Kyushu, Japan.
Trigonia scabra (pars) LAMARCK in STOLICZKA, 1871. Turonian; India.
Pterotrigonia subaliformis SAVELIEV, 1958. Up. Albian; Manghyschlack.
?*Trigonia umkwelanensis* ETHERIDGE, 1904. Low. Cret.; Natal, South Africa.

The shell form and the surface sculpture are variable to a wide extent in this subgenus. Shell size is fairly large in common forms, but small in *mashikensis, mifunensis* and others. The shell outline is crescentic in most others, but subtrigonal in *dilapsa* and *ogawai* and rostrate posteriorly in *longiloba*. Ante-carinal depression is broad and shallow in many forms, but obscure in *dilapsa, ogawai* and others. Median furrow is in many cases distinct, but indistinct in *dilapsa* and *ogawai* etc.

Costae on the flank are as a rule tuberculate, but spiny in *sheptonei* and plain in *dilapsa* and *longiloba*. The *Haidaia*-type crenulate costae are well developed and recognized in all stage of *moriana*. Horizontal short striae in the antero-dorsal part below the umbo are distinct and well developed in *gokderensis, mashikensis* and *subaliformis*, but they are lacking in the others. Tuberculate or plain costae on the area are as a rule gradually obsolete in the later, but they are well developed on the whole surface of *ludovicae* and *moriana*, the latter of which has the fairly distinct marginal angulation on the slightly concave area. They are broken into rows of pustules in *pustulosa*.

Pterotrigonia gokderensis SAVELIEV (1958, p. 33, figs. 4–6) and *P. subaliformis* SAVELIEV (1958, pl. 33, figs. 3a–d) are the interesting forms, and they are possibly the members of *Acanthotrigonia* because of the obliquely costellate area.

SOARES and da SILVA (1970, p. 41, pl. 5 figs. 6–8) reported the occurrence of *Acanthotrigonia sheptonei* (GRIESBACH) from the Maestrichtian of Moçambique, but its areal charac-

ter is uncertain.

Distribution: — Aptian to Maestrichtian, most flourished in Aptian to Turonian of the eastern hemisphere.

Subgenus *Metacanthotrigonia* nov.

Type species: — *Pterotrigonia* (*Rinetrigonia*) *yeharai* NAKANO and NUMANO, 1961. Turonian; Goshonoura-jima, Amakusa, Kyushu, Japan.

Diagnosis: — This subgenus having oblique costae on the convex area, is characterized by the discrepant sculpture between the anterior and the posterior part of the flank.

List of Species: —

Pterotrigonia cubanica (pars) (SINZOW) in SAVELIEV, 1958. Up. Aptian; Manghyschlack.
Acanthotrigonia higoensis TAMURA and TASHIRO, 1967. Turonian; Mifune district, Kyushu, Japan.
?*Pterotrigonia* (*Rinetrigonia*?) sp. *a* and *b* by KOBAYASHI and NAKANO, 1958. Aptian; Yatsushiro district, Kyushu, Japan.

Remarks: — This is distinguishable from typical *Acanthotrigonia* by the discrepant ribbing on the flank where the ante-carinal depression is well develpoed. This is quite similar to *Rinetrigonia* in sculpture on the flank, but differs in having oblique costae on the area.

The shell form and surface sculpture are fairly constant in this subgenus. Median furrow is somewhat obscure in *cubanica*, but it is distinct in *yeharai* and *higoensis* the latter of which has two radial grooves on its area.

Distribution: — Aptian to Turonian of Japan and Manghyschlack.

III. CONCLUDING REMARKS

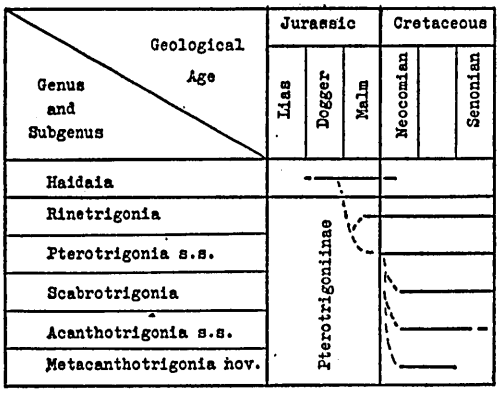
The followings are summarized as a conclusion from the above discussion.

The subfamily Pterotrigoniinae are tentatively classified as belows.

Genus *Pterotrigonia* van HOEPEN, 1929
  Subgenus *Pterotrigonia* s.s.
  Subgenus *Rinetrigonia* van HOEPEN, 1929
Genus *Scabrotrigonia* DIETRICH, 1933
Genus *Acanthotrigonia* van HOEPEN, 1929
  Subgenus *Acanthotrigonia* s.s.
  Subgenus *Metacanthotrigonia* nov. (*Pterotrigonia* (*Rinetrigonia*) *yeharai* NAKANO and NUMANO, 1961)

The geological distribution and the possible phyletic relationships of the Pterotrigoniinae are tabulated on Table 1. *Metacanthotrigonia* nov. based on *Pterotrigonia* (*Rinetrigonia*) *yeharai* NAKANO and NUMANO, is a subgenus of genus *Acanthotrigonia* van HOEPEN, 1929 and this is characterized by having discrepant costation between the anterior and the posterior part of the flank. It is known in the Aptian to the Turonian of Japan and Manghyschlack. *Scabrotrigonia* and *Acanthotrigonia* were considered to be the issues from *Pterotrigonia* s.s. as can be judged from the youngsters of them. On the mode of life, it seems that the shells of many species in the subfamily stand on the sandstone strata with anterior extremity downward and the siphonal part upward and in this state they may have been in clusters and their ventral margin meeting against a calm water in neritic sea.

Table 1. Phylogeny and Geological Distribution of the Pterotrigoniinae.



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