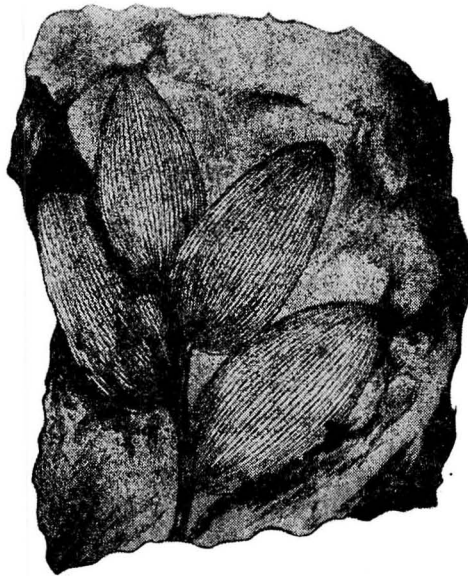


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The fossil on the cover: Original figure of *Podozamites Reinii* GEYLER, 1877, from the Tetori group. GEYLER's description marked the onset of modern palaeontology in Japan.

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691. ONTOGENETIC VARIATION OF *TRIGONIOIDES* (S.S.)  
*PAUCISULCATUS* (CRETACEOUS NON-MARINE BIVALVIA)\*

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**Abstract.** *Trigonioides* (s.s.) *paucisulcatus* shows positively the ontogenetic variation on its pseudocardinal teeth and V-shaped surface ornamentation. The number of the pseudocardinal teeth increases with growth, that is, from two on both valves (5, 3, PIII/4, 2, PII, PIV) in immature specimens, to four or five on both valves (5, 3, 1a, 1b, 1c, PIII/(6), 4, 2, 1'a, 1'b, PII, PIV) in adult specimens. The V-shaped ornamentation is gradually effaced with growth. From the comparison with *T.* (s.s.) *kodairai* from the lower stratigraphic horizon, it can be said that the phylogenetic trend is read at least on three characters; 1) The angle of the V-ribs on the surface decreases. 2) The surface ornamentation is effaced. 3) The number of the pseudocardinal teeth increases.

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### Introduction

*Trigonioides* (s.s.) *paucisulcatus* was proposed by SUZUKI (1940) as a subspecies of *T. kodairai* KOBAYASHI and SUZUKI (1936) based on the specimens from Baegandong, Yeongcheon-gun, Korea. At that time, the type-specimens were so strongly deformed and fragmental that its internal structures, especially of the hinge teeth, could not be completely described.

Subsequently, OTA (1959a) has reported its occurrence from Goshonoura (Cenomanian), Japan and raised it up to an independent species. But the Japanese specimen is also poorly preserved, so OTA himself left its hinge teeth undescribed.

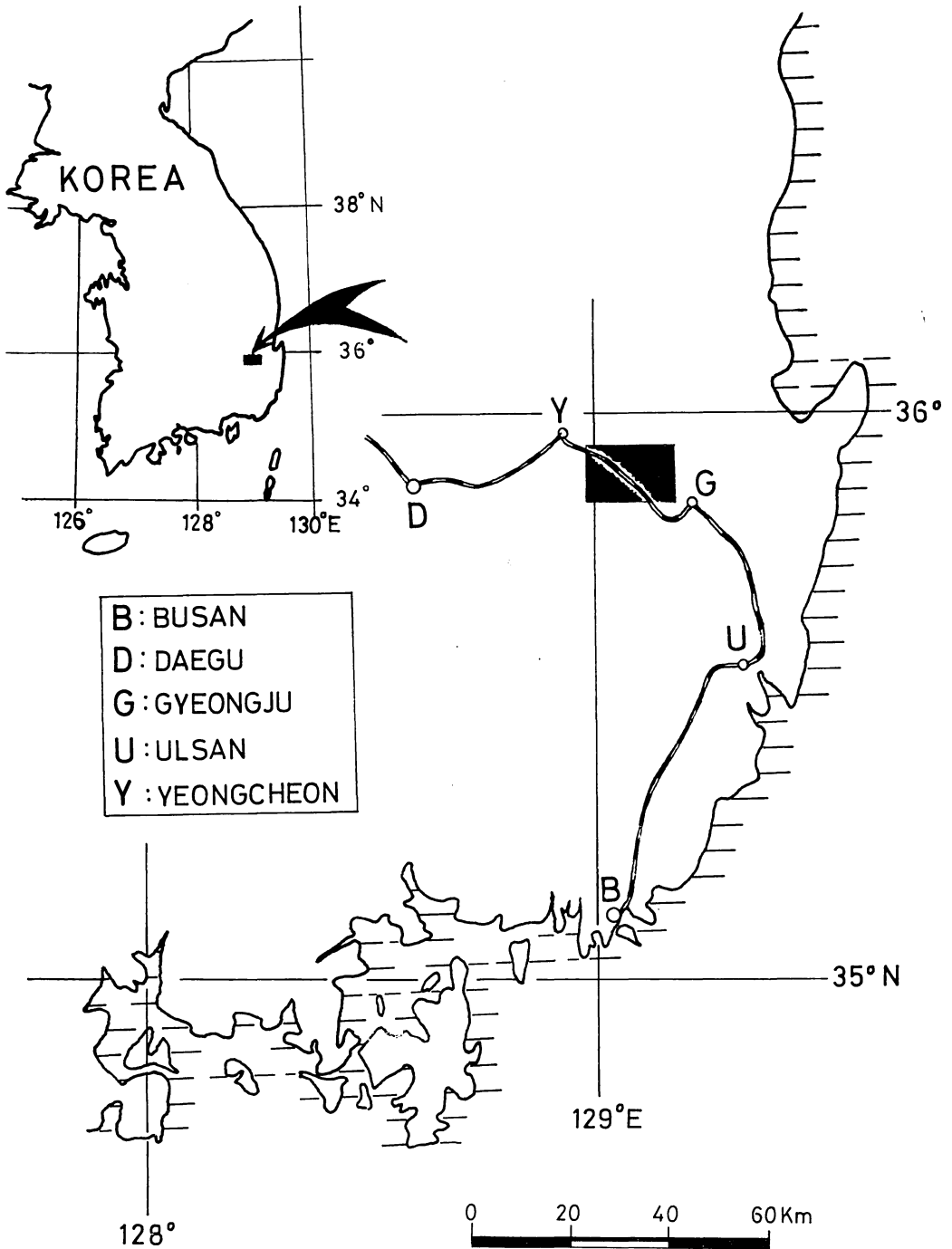
As previously mentioned (YANG, 1974), the genus *Trigonioides* is one of the most interesting and important non-marine

pelecypod genera in the upper Mesozoic of Asia. However, its evolutionary trend, phylogeny in one sense, has not been clearly understood yet. This deficiency has come firstly from that the relative stratigraphic positions of the fossil localities have not been confirmed, which is in turn because of their separate occurrences in dispersed basins, and secondly from that their genetic characters and their variations have not been grasped.

The two species, *T.* (s.s.) *kodairai* and *T.* (s.s.) *paucisulcatus*, are found from successively exposed Gyeongsang Group, Korea; the former is from the lower part and the latter from near the uppermost horizon. The comparison between the two, therefore, is quite important for understanding the evolutionary trend of the present genus. Recently I have found several new localities of *T.* (s.s.) *paucisulcatus* near its type-locality and made a fairly good collection. Present work is to report some of the results of the study

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\* Received September 30, 1977; read January 30, 1976, at Naruko.



Text-figure 1. Index map.

on the new acquisitions, putting special stress on the ontogenetic variation of the hinge structure and other characters.

*Acknowledgements*:—I would like to express my sincere gratitude to Emeritus Professor Tatsuro MATSUMOTO of Kyushu University for his continuous encouragement on my study and critical reading of the typescript of this paper, Professors Ki Hong CHANG and Yeong Gi KIM of Kyungpook National University for their introducing new fossil localities. My sincere thanks are also due to Mr. Gilsu LEE of the latter University for his assistance in field and laboratory works.

### Notes on Stratigraphy

Since TATEIWA (1929) first mapped the

Gyeongsang Group, the area around the fossil localities has been surveyed from time to time by several geologists (SON et. al., 1969, CHANG, 1970, PARK et. al., 1973). However, the stratigraphy of the area in the section of Waegwan-Daegu-Yeongcheon-Gyeongju has not been concretely established yet. This is because of lack of a pertinent key bed and little paleontological studies about the group. I have briefly investigated the geology around the fossil localities. It is illustrated in a simplified form in Text-figure 2. In order to show the relative stratigraphic horizons of the two species, a scheme of subdivision of Gyeongsang Group is presented in Table 1.

The Sinla Subgroup was correlated by SUZUKI (1940) to the Gyliaikian (Ceno-

Table 1. Subdivision of Gyeongsang Group.

GYEONGSANG GROUP	SILLA SUBGROUP	GEOCHEONRI FM.	JAYANGSAN FM.
			JAIN FM. .... <i>T. (s. s.) paucisulcatus</i>
		DAEGU FM.**	SONGNAEDONG FM.
			BANYAWEOL FM.
			HAMAN FM.
		SINLA CONGLOMERATE FM.	
	NAGDONG SUBGROUP	CHILGOG FM.	
		JINJU FM.*	
		HASANDONG FM. .... <i>T. (s. s.) kodairai</i>	
		NAGDONG FM.*	

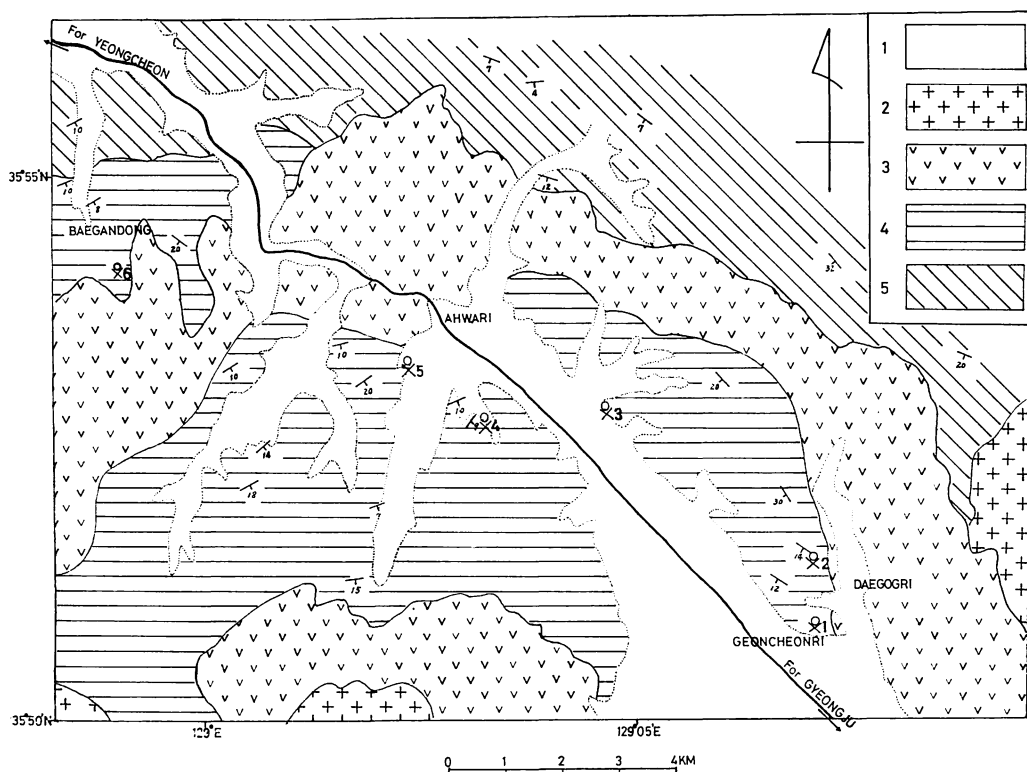
\*CHANG (1966) proposed Yeonhwadong and Dongmyeong formations for Nagdong (Naktong) and Jinju (Shinshu) formations, respectively, which were named by TATEIWA (1929), on account of remote distance from the type-section Waegwan-Daegu-Gyeongju. Recently CHANG (1975) withdrew his proposal by reason of priority.

\*\*Daegu formation (by TATEIWA, 1929) is subdivided into Haman, Banyaweol and Songnaedong formations in ascending order.

The porphyrite formations, that is, the so-called Hagbong (Kakubo), Chaeyagsan (Saiyakusan) and Jusasan (Shushazan), are excluded from the stratigraphy because of their intrusive relation to the adjacent formations. However, the extrusive features also are found here and there. And it has been in dispute that the porphyrite formations must be considered of stratigraphic units or not.

manian-Turonian) Mifune Group in Japan based on the common occurrence of *Thiara (Siragimelania) tateiwai*. The fossiliferous Lower Mifune is now referred to Middle to Upper Cenomanian (TAMURA and MATSUMURA, 1974; MATSUMOTO, 1977). And, as pointed out above, *T. (s. s.) paucisulcatus* also was reported by OTA

(1959a) from the Cenomanian Upper Goshonoura Group (see MATSUMOTO, 1977). Thus, in the present state, the Sinla Subgroup (strictly speaking, the fossil bed of Jain Formation, upper part of Sinla Subgroup) can be roughly correlated to Upper Cretaceous (Cenomanian-Turonian).



Text-figure 2. Geological map around the fossil localities.

1. Quaternary (Alluvium). 2. Bulgugsa granite. 3. porphyrite.
4. Jain Formation. 5. Songnaedong Formation.

### Material

Among the fossil localities, Loc. 6 is the type locality of *T. (s. s.) paucisulcatus* designated by SUZUKI (1940) and the others are new. I have visited several times the type-locality, but I have found no molluscan fossils except a gastropod,

*Thiara (Siragimelania) tateiwai*. The occurrence of fossils at the six localities is reviewed in Table 2.

As shown in Table 2, the fossils are commonly found in siltstone bed and the occurrence is not even but varies with localities. The present species occurs gregariously at Loc. 2 and 5, but has not

Table 2. Fossil occurrences and lithology at six fossil localities.

Loc.	Lithology	Fossils	Abundance
1	light grey siltstone	<i>T.</i> (s. s.) <i>paucisulcatus</i>	abundant
2	silicified light grey siltstone	<i>T.</i> (s. s.) <i>paucisulcatus</i> <i>Thiara</i> ( <i>Siragimelania</i> ) <i>tateiwai</i>	gregarious abundant
3	light grey siltstone	<i>T.</i> (s. s.) <i>paucisulcatus</i> <i>T.</i> (S.) <i>tateiwai</i>	rare frequent
4	grey siltstone dark grey siltstone	<i>T.</i> (S.) <i>tateiwai</i> <i>Estheria</i> sp.	rare frequent
5	light grey siltstone	<i>T.</i> (s. s.) <i>paucisulcatus</i> <i>T.</i> (S.) <i>tateiwai</i>	gregarious rare
6	light grey siltstone	<i>T.</i> (s. s.) <i>paucisulcatus</i> <i>T.</i> (S.) <i>tateiwai</i>	rare, not found gregarious

been found at Loc. 4 and 6. The siltstone beds yielding fossils seem to be of nearly the same stratigraphic horizon of lower Jain Formation.

More than 500 specimens of *T.* (s. s.) *paucisulcatus* have been collected from the above four localities (Loc. 1, 2, 3 and 5). The specimens are deposited at the Department of Earth Science, Kyungpook National University, Daegu, Korea.

#### Observation and Recognition of Ontogenetic Variation.

Since the fossiliferous beds are considered of nearly the same stratigraphic horizon, as mentioned above, and no specific difference can be confirmed among the samples from the different localities, it is evident that all of the trigonioidid samples fall within the same species.

The typical trigonioidid V-sculpture looks fairly variable at a glance. In general, the immature specimens (smaller than 2 cm in length) are ornamented all over the valve with the sculpture, while the adult specimens (larger than 4 cm) show complete effacement on the valve except weak and tough radial ribs on the

posterior side. However, it can be safely pointed out that these features are only ontogenetic, for the intermediate specimens (from 2 to 4 cm) shows the transitional state of the sculpture between the above two. On the angle of the V-sculpture, no marked variation has been observed.

Most of the specimens possess well preserved test except several of natural mould state and are secondarily deformed. The internal structures have been observed on the 55 specimens from which the tests were dissolved out by dilute hydrochloric acid. The muscle scars, i. e., adductor scars and pedal scars, and the ventral crenulation are observed constantly. The anterior adductor scar is more prominent, but smaller than the posterior one. The ventral crenulation changes its character with its position on the ventral margin. That is, on the posterior ventral margin it is fairly distinct while it becomes weaker towards the anterior and ultimately effaced on the anterior end. The crenulation is fine on the anterior side and rough and coarse on the posterior side, reflecting the coarseness of the radial ribs on the surface. However, no difference has

been observed on these internal structures between immature and adult ones.

On the other hand, fairly large variation of the hinge structure has been observed in accordance with the size of the specimens as shown in figures of Plate 46. On the smaller ones, the hinge structure is considerably simpler than the larger ones which possess a larger number of hinge teeth. When the specimens are arranged in order of size, these features show a gradual change which must be regarded as ontogenetic variation.

Ontogeny is generally understood as a life history of an organism and necessarily includes the development from the larval stage to the senility. And the recognition of the larval stage is most important in biological sense. However, in molluscan fossils, of which the initial stage, i.e., trochophore plus veliger, is not usually preserved, the ontogeny must be inevitably considered as partially after the deposition of the prodissoconch. Moreover, when the hinge structures of the Bivalvia are concerned, which cannot be observed even on the prodissoconch, the term 'ontogenetic' may be rather inappropriate in a strict sense. However, in such a case, the ontogeny is practically used in a broad sense as a continuous change with growth.

*On the Dental Formulae.*—The well-known BERNARD's scheme designed to give a concise expression on the bivalve hinge teeth and their disposition has been considered to be fairly suitable in regard to the taxonomy and phylogeny in some of the heterodonts based on the homologous dental structure. The adoption of the scheme to trigonioidids was made first by COX (1955). Subsequently, its usage had been current among the authors of trigonioidids. HAYAMI in HAYAMI and ICHIKAWA (1965) maintained that the BERNARD's scheme for the heterodonts should not be

used for the trigonioidids. However, after that it has been also used for trigonioidids without examination of the homology between the heterodonts and the non-heterodonts besides a little modification. As pointed out also by BOYD and NEWELL (1969), 'the scheme is difficult to apply widely even to heterodonts as well as non-heterodonts because homologies commonly cannot be readily recognized among dissimilar bivalves'. In BERNARD's formula, the cardinal teeth 1, 2 and 3 are meant to be ontogenetically originated from the anterior lateral teeth AI, AII and AIII, respectively. But in trigonioidids without any anterior lateral teeth, there is no yardstick on deciding which is 1 or 2, etc. Consequently, the formulae may be changeable due to which to decide arbitrarily. In order to reduce such a confusion, OTA (1975) proposed to nominate and fix the pseudocardinal tooth as 3 which is associated with the pedal scar in right valve and to arrange other symbols in order, that is, 5, 3, 1a and 1b from anterior extremity toward ventral on right valve and 6, 4, 2, 1'a and 1'b on left valve.

In some of the present specimens (see Pl. 46, figs. 14c, 15b), there appear obviously three pseudocardinals under the Ota's 3 in right valve. In such a case, it seems to be needed that another symbol 1c should be provided for presenting the new tooth ventrally found. The symbols 6, 5, 1'a and 1'b are considered quite strange as well as 1c in usual BERNARD's notation. The 'a' and 'b' are commonly provided for the teeth emerging from one cardinal divided anteriorly and posteriorly, respectively, while in trigonioidids they mean only order. In short, the current method of naming teeth in trigonioidids is quite peculiar in comparison to that in heterodonts.

BOYD and NEWELL (1969) proposed a



new method of recording hinge teeth with 1 and 0. And they presented several merits in their new system of being free from implication of uncertain homologies by avoiding specification of homologues for poorly understood group and of being able to be converted readily version of BERNARD's system whenever homologies are secure. However, there are some demerits also in their method. When all the hinge teeth and the sockets are recorded only with 1 and 0, it is difficult to point a certain one among the teeth, especially in trigonoidids of which hinge teeth are variable both with ontogeny and phylogeny. And as in their formulae the disposition is reversed anterior to right, posterior to left in contrast to BERNARD's scheme where anterior is to left, posterior to right, the abrupt adoption to trigonoidids may give rise to another confusion. It is rather convenient to use the conventional BERNARD's scheme with pointing out that the usage in trigonoidids has not relation to homologues of the heterodonts and is independent from phylogenetic relativity between.

In this paper, the both schemes are tentatively used for comparison.

To return to the main subject : the hinge structure of the present species can be expressed as Table 3. The left column is due to the modified conventional BERNARD's scheme in trigonoidids and the right column due to the new system of BOYD and NEWELL.

The length of the hinge teeth and the crenulation on the both of anterior and posterior sides are illustrated in Text-figure 3. As shown in the dental formulae and the Text-figure 3, it is evident that the posterior lateral teeth PII, PIII and PIV are constant, whereas the pseudocardinal teeth are considerably variable.

The hinge structure has been generally regarded as one of the most constant characters of the Bivalvia and used as a basis of high rank taxonomy. So at the beginning, I considered the hinge variety only apparent due to the state of preservation. However, through the careful examination of more than 50 specimens of wide range in size, I have ascertained that the variation must be regarded as ontogenetic. So far as I have observed, the specimens smaller than 20 mm in length all possess only two pseudocardinals on each valve. On the other hand the

Table 3. Variation of hinge structure of *Trigonioides* (s. s.) *paucisulcatus*.

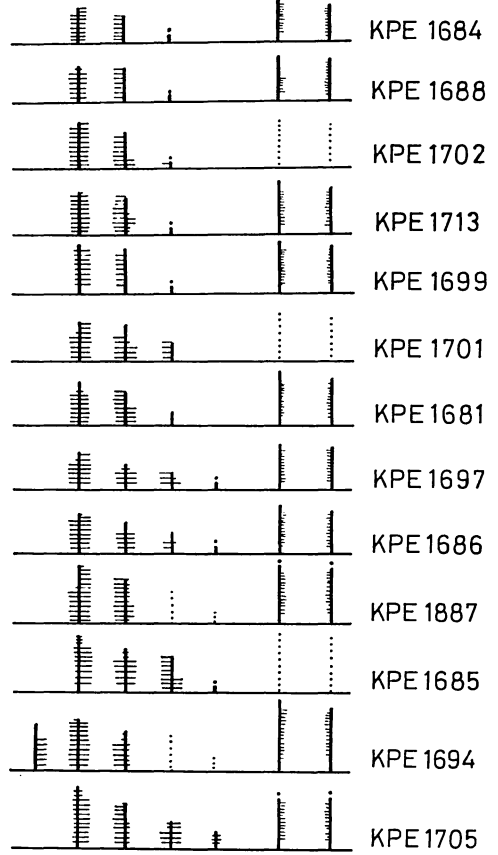
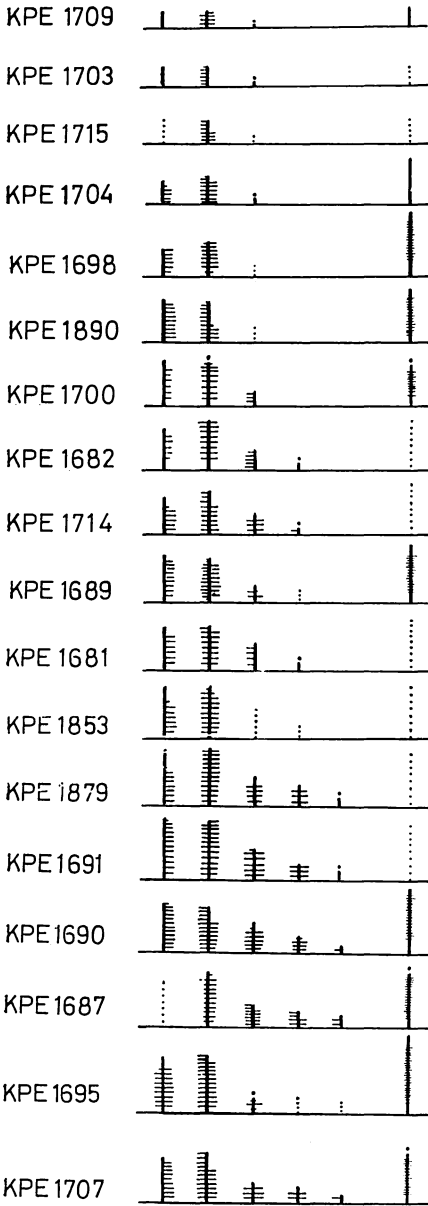
5 3	PIII	010—0101	RV
4 2	PII PIV	101—1010	LV
5 3 (1)	PIII	010—(1)0101	RV
4 2	PII PIV	101—0 1010	LV
5 3 1a	PIII	010—0 10101	RV
4 2 (1'a)	PII PIV	101—(1)01010	LV
5 3 1a (1b)	PIII	010—(1)010101	RV
4 2 1'a	PII PIV	101—0 101010	LV
5 3 1a 1b	PIII	010—0 1010101	RV
4 2 1'a (1'b)	PII PIV	101—(1)0101010	LV
5 3 1a 1b (1c)	PIII	010—(1)01010101	RV
4 2 1'a 1'b	PII PIV	101—0 10101010	LV
5 3 1a 1b 1c	PIII	010—101010101 0	RV
(6) 4 2 1'a 1'b	PII PIV	101—010101010(1)	LV

RIGHT VALVES

5 3 1a 1b 1c PIII  
a.p. a.p. a.p. a.p. a.p. a.p.

LEFT VALVES

6 4 2 1a 1'b PII PIV  
a.p. a.p. a.p. a.p. a.p. a.p. a.p.



15mm  
0

1: a.p.      2: KPE 0000

3:       4: 

5:       6: 

7:       8: 

specimens larger than 35 mm possess four or five cardinals, and the other ones of intermediate size three or four. The tooth indicated in parentheses is conventionally implied incipient presence as a point. As illustrated in Text-figure 3, this incipient hinge tooth becomes gradually prominent with growth.

Having a prejudice that the hinge teeth are constant, the previous authors paid little careful attention to the hinge variation. But according to my observation (YANG, 1974), the specific difference must be present at least between *T. (Kumamotoa) suzukii* and *T. (Kumamotoa) mifunensis*. Even though the hinge structure has not been investigated yet on a viewpoint of ontogenetic variation among other trigonioidids, this possibility cannot be completely eliminated. The hinge teeth are considered not to be always constant among the samples of *T. (Kumamotoa) matsumotoi*, *T. (Kumamotoa) mifunensis* and *Wakinoa wakinoensis*. According to the descriptions of the previous authors (TAMURA, 1970; OTA, 1975, the dental formulae are as follows;

TAMURA (1970)

*T. (K.) mifunensis*

$$\frac{5 \quad 3 \quad 1a \quad 1b \quad (PIII)}{(6) \quad 4 \quad 2 \quad 1'a \quad 1'b \quad PII \quad PIV}$$

*Wakinoa*

$$\frac{5 \quad 3 \quad (1) \quad PIII \quad PV}{(6) \quad 4 \quad 2 \quad (1') \quad PII \quad PIV}$$

OTA (1975a, b)

*Wakinoa wakinoensis*

$$\frac{5 \quad 3 \quad 1 \quad (PI) \quad PIII}{(6) \quad 4 \quad 2 \quad (1') \quad PII \quad (PIV)}$$

*T. (K.) suzukii*

$$\frac{5 \quad 3 \quad 1a \quad (1b) \quad PIII}{(6) \quad 4 \quad 2 \quad 1'a \quad PII \quad PIV}$$

*T. (K.) matsumotoi* & *T. (K.) mifunensis*

$$\frac{5 \quad 3 \quad 1a \quad 1b \quad PIII}{(6) \quad 4 \quad 2 \quad 1'a \quad (1'b) \quad PII \quad PIV}$$

*Hoffetrigonia kobayashi*

$$\frac{5 \quad 3 \quad 1a \quad 1b \quad PIII}{4 \quad 2 \quad 1'a \quad (1'b) \quad PII \quad PIV}$$

The teeth, 6, 1', 1b and 1'b expressed in parentheses may be brought to light as of ontogenetic variation, if the characters be examined on a larger number of large samples of a wider range in size.

### Systematic description

Superfamily Unionacea

Family Trigonioididae COX, 1952

Genus *Trigonioides* KOBAYASHI and SUZUKI, 1936

*Trigonioides* (s. s.) *paucisulcatus* SUZUKI, 1940 (emend)

Pl. 45, figs. 1-16; Pl. 46, figs. 1-26.

1940. *Trigonioides kodairai paucisulcatus* SUZUKI, *Japan. Jour. Geol. Geogr.*, 17, (3-4), p. 229, pl. 3, figs. 1-4, text-figs. 18-20.
1959. *Trigonioides paucisulcatus* SUZUKI, OTA, *Trans. Proc. Palaeont. Soc. Japan*, N. S., no. 34, p. 101, fig. 16.
1968. "*Trigonioides*" *paucisulcatus* SUZUKI, KOBAYASHI, *Geol. Palaeont. S. E. Asia*, 4, p. 128, pl. 23, fig. 4.

Text-figure 3. Crenulation and relative length of the hinge teeth.

1. a; anterior side, p; posterior side. 2. Specimen number preserved at Kyungpook National University. 3. Hinge tooth with crenulation on both sides illustrated by short horizontal lines and of length expressed by vertical heavy line. 4. Posterior lateral tooth with fine crenulation. 5. Hinge tooth with crenulation on both sides, but the crenulation on anterior side not observed. 6. Tooth not observed. 7. Hinge tooth of the length not measured exactly, may be longer than the length illustrated. 8. Incipient presence of subumbonal pseudocardinal tooth.

*Description.*—Shell medium in size, commonly about 30–45 mm in length, ratio of L/H about 1.3, subequilateral and equiv-alve; anterior margin well rounded, ventral one broadly arcuated, posterior margin rather straight or subtruncated, generally transversely subovate in outline; moderately inflated; umbo slightly prosogyrous, placed about two-fifths of the shell length from the anterior extremity; escutcheon and lunule narrow. The shells less than 20 mm in length, probably of immature stage, commonly covered with the characteristic V-sculptures, while those of later stages over 40 mm in length are ornamented only on the posterior area with rough carinae. On the intermediate ones the umbonal and the posterior parts both covered with the ornaments. The carinae on the postero-ventral part number commonly four or five. The angles of the V-ribs about 7°–10° and the radial ribs and grooves on the umbonal part fairly fine.

Hinge plate moderate in breadth, provided with the opisthocline pseudocardinal teeth and the posterior lateral teeth; the posterior lateral teeth one on right valve, two on left valve; the pseudocardinals two on each valve in immature ones; forming the dental formula as follows:

$$\frac{5 \quad 3 \quad \text{PIII}}{4 \quad 2 \quad \text{PII} \quad \text{PIV}}$$

but the number of the pseudocardinals increases successively with growth to five on right valve and four or five on left valve; forming the dental formula as follows:

$$\frac{5 \quad 3 \quad 1a \quad 1b \quad 1c \quad \text{PIII}}{(6) \quad 4 \quad 2 \quad 1'a \quad 1'b \quad \text{PII} \quad \text{PIV}}$$

The crenulation of the hinge teeth well developed; it is finer on the posterior lateral teeth than on the pseudocardinals. Adductor scars subequal in size and form, situated close to the outer ventral ends of the pseudocardinal teeth and the pos-

terior lateral ones; anterior one subcircular and more strongly impressed, accompanied with a distinct minute pedal scar; posterior one also subcircular but not so distinct. Ventral margin crenulated internally; the crenulation stout and strong on the posterior part, becoming weaker and finer towards the anterior and finally completely effaced at the anterior end. Umbonal cavity moderately deep.

*Comparison.*—The present species is similar to *T. (s. s.) kodairai* in surface ornamentation, but not identical in its confinement of the ornamentation to the posterior and the umbonal areas and in the angle of the V-ribs. In this respect, it is rather nearer to *T. (Kumamotoa) mifunensis*. The radial ribs on the umbo are finer and the angle of the V-ribs is smaller than in any other trigonioidid species.

The number of the hinge teeth of the present species is quite similar to *T. (Kumamotoa) matsumotoi* and *T. (K.) mifunensis* except possessing 1c. However, with respect to other features of the hinge structure, the present species is similar to *T. (s. s.) kodairai* rather than to *T. (Kumamotoa)* spp. The crenulation of the pseudocardinals in the present species are as fine as in *T. (s. s.) kodairai*, and not so prominently stout and strong as in *T. (Kumamotoa)*. The relative length of the pseudocardinals is also rather nearer to the former. And the hinge plate also is identical to that of *T. (s. s.) kodairai*. For this comparison, the hinge structure of *T. (Kumamotoa) mifunensis* is presented in Plate 46 (fig. 27).

*Phylogenetical remarks.*—From the comparison of *T. (s. s.) kodairai* with *T. (s. s.) paucisulcatus*, it can be safely said that at least three characters are phylogenetically varied. The first is that the surface ornamentation is gradually effaced with upward stratigraphic sequence. It is in-

Table 4. Measurements of *Trigonoides* (s. s.) *paucisulcatus*

Specimen	L	H	D	I	L/H	D/L	I/L
KPE 1651 (L)	64.5	50.9	28.8	16.1	1.27	0.45	0.25
KPE 1652 (L)	42.2	32.5	16.8	11.0	1.30	0.40	0.26
KPE 1653 (L)	42.6	32.6	15.7	9.8	1.31	0.37	0.23
KPE 1654 (L)	55.2	45.1	19.5	14.2	1.22	0.35	0.26
KPE 1656 (L)	25.6	19.2	8.8	—	1.33	0.34	—
KPE 1657 (R)	55.2	43.7	18.8	13.0	1.26	0.34	0.24
KPE 1658 (L)	44.6	32.7	17.5	—	1.36	0.39	—
KPE 1659 (L)	41.9	32.3	16.2	9.9	1.30	0.39	0.24
KPE 1660 (L)	30.9+	24.4	14.6	10.0	1.27	0.47	0.32
KPE 1662 (L)	42.2	30.4+	16.9	—	1.39	0.40	—
KPE 1664 (R)	26.7	20.9	9.3	—	1.28	0.35	—
KPE 1666 (R)	36.8	29.8	12.2	9.8	1.23	0.33	0.27
KPE 1668 (R)	37.8	31.5	13.9	9.8	1.20	0.37	0.26
KPE 1672 (L)	39.4	29.5	14.3	—	1.34	0.36	—
KPE 1673 (L)	37.8	26.9	15.1	—	1.41	0.40	—
KPE 1674 (L)	23.2	17.1	7.9	—	1.36	0.34	—
KPE 1675 (L)	39.5	28.8	17.5	—	1.37	0.44	—
KPE 1676 (L)	31.8	23.8	11.1	—	1.34	0.35	—
KPE 1678 (L)	20.8	15.2	8.7	—	1.37	0.42	—
KPE 1680 (L)	38.6	28.2	12.6	8.5	1.37	0.33	0.22
KPE 1684 (L)	29.9	21.8+	11.0	—	1.37	0.37	—
KPE 1694 (L)	42.0+	33.4	20.2	—	1.26	0.48	—

L: length, H: height, D: distance between umbo and anterior extremity, I: inflation, (L): left valve, (R): right valve. Mean of L/H: 1.31; standard deviation of L/H: 0.058, mean of D/L: 0.38; standard deviation of D/L: 0.044. (Based on 22 specimens, exclusive of the strongly deformed or broken specimens).

interesting to note that a similar feature was recognized also on the genus *Wakinoa*, that is, *W. wakinoensis*—*W. intermedia*—*W. obsoleta* (HASE, 1960). The second is the angle of the V-ribs on the median surface becomes also gradually smaller. It can be more prominently grasped when the *Koreanaia* is concerned. From this point, the *Wakinoa wakinoensis* is considered to be put phylogenetically between *Koreanaia* and *Trigonoides* (s. s.). The third is that the number of pseudocardinal hinge teeth is increased also with upward stratigraphic sequence.

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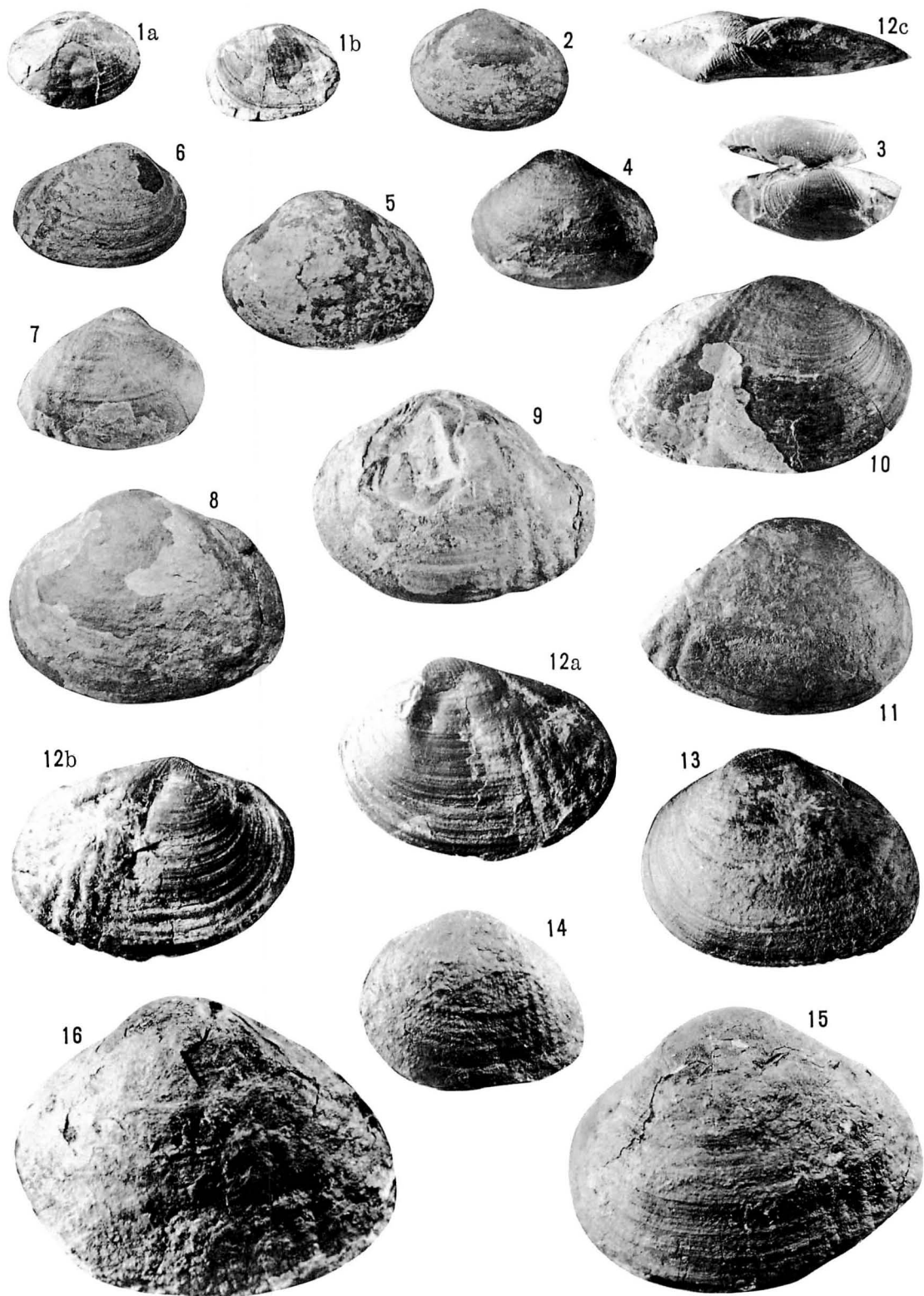
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#### Explanation of Plate 45

Figs. 1-16. *Trigonioides* (s. s.) *paucisulcatus* (SUZUKI, 1940)

1. Conjoined valves, immature specimen. (KPE 1665) 1a: right valve, 1b: left valve, showing radial ribs covering almost the whole shell.
2. Left valve (KPE 1656), immature specimen, showing radial ribs on the posterior part.
3. Conjoined valves (KPE 1669), opened ventrally, showing fine radial ribs.
4. Left valve (KPE 1660), showing fine radial ribs on umbo.
5. Left valve (KPE 1676), showing rough radial ribs on posterior half.
6. Right valve (KPE 1664), showing rough radial ribs on postero-ventral area.
7. Right valve (KPE 1661), showing radial ribs on posterior half.
8. Left valve (KPE 1659).
9. Left valve (KPE 1658), showing radial ribs on posterior half.
10. Right valve (KPE 1663), showing radial ribs on posterior half.
11. Right valve (KPE 1667), showing rough radial ribs on postero-ventral area.
12. Conjoined valves (KPE 1655), showing radial ribs on umbo and posterior half. 12a: left side view, 12b: right side view, 12c: dorsal view.
13. Left valve (KPE 1653), showing radial ribs on umbo.
14. Left valve (KPE 1652), showing radial ribs on posterior half.  $\times 0.9$ .
15. Left valve (KPE 1651), showing rough radial ribs on posterior half.  $\times 0.86$ .
16. Left valve (KPE 1654), showing rough radial ribs on posterior half.

All figures are of natural size unless otherwise stated. Loc.: at a point 1.5 Km northeast from Geoncheon-ri, Seo-myeon, Weolseong-gun, Gyeongsangbug-do, Korea. All of the above specimens are kept in the Department of Earth Science, Kyungpook National University, Daegu, Korea.



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Ahwa-ri 阿火里, Baegan-dong 百安洞, Banyaweol 半夜月, Chaeyagsan 採葉山, Chilgog 漆谷, Daegog-ri 大谷里, Daegu 大邱, Dongmyeong 東明, Geoncheon-ri 乾川里, Gyeongju 慶州, Gyeongsang 慶尚, Hagbong 鶴峰, Haman 咸安, Hasandong 霞山洞, Jain 慈仁, Jayangsan 紫陽山, Jinju 晋州, Jusasan 朱砂山, Nagdong 洛東, Seo-myeon 西面, Sinla 新羅, Songnae-dong 松内洞, Ulsan 蔚山, Waegwan 倭館, Weolseong-gun 月城郡, Yeongcheon 永川, Yeongcheon-gun 永川郡, Yeonhwa-dong 蓮花洞

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*Trigonioides* (s. s.) *paucisulcatus* の個体成長による変異について:—*T. paucisulcatus* の模式地付近から多くの標本を採集して、その内部構造、表面装飾などを調べた結果を報告する。*T. (s. s.) paucisulcatus* の pseudocardinal teeth には明らかに著しい変異が認められる。これは ontogenetic variation と解釈される。すなわち pseudocardinals は immature specimens では両殻ともに二つづつしかないので、成長によって次第に多くなって adult specimens では 5, 3, 1a, 1b, 1c, PIII/(6), 4, 2, 1'a, 1'b, PII, PIV になる。層序的に下位層準から産出する *T. (s. s.) kodairai* と比較した結果、系統進化の様式として三つの形質に変化がおこったことが明らかになった。

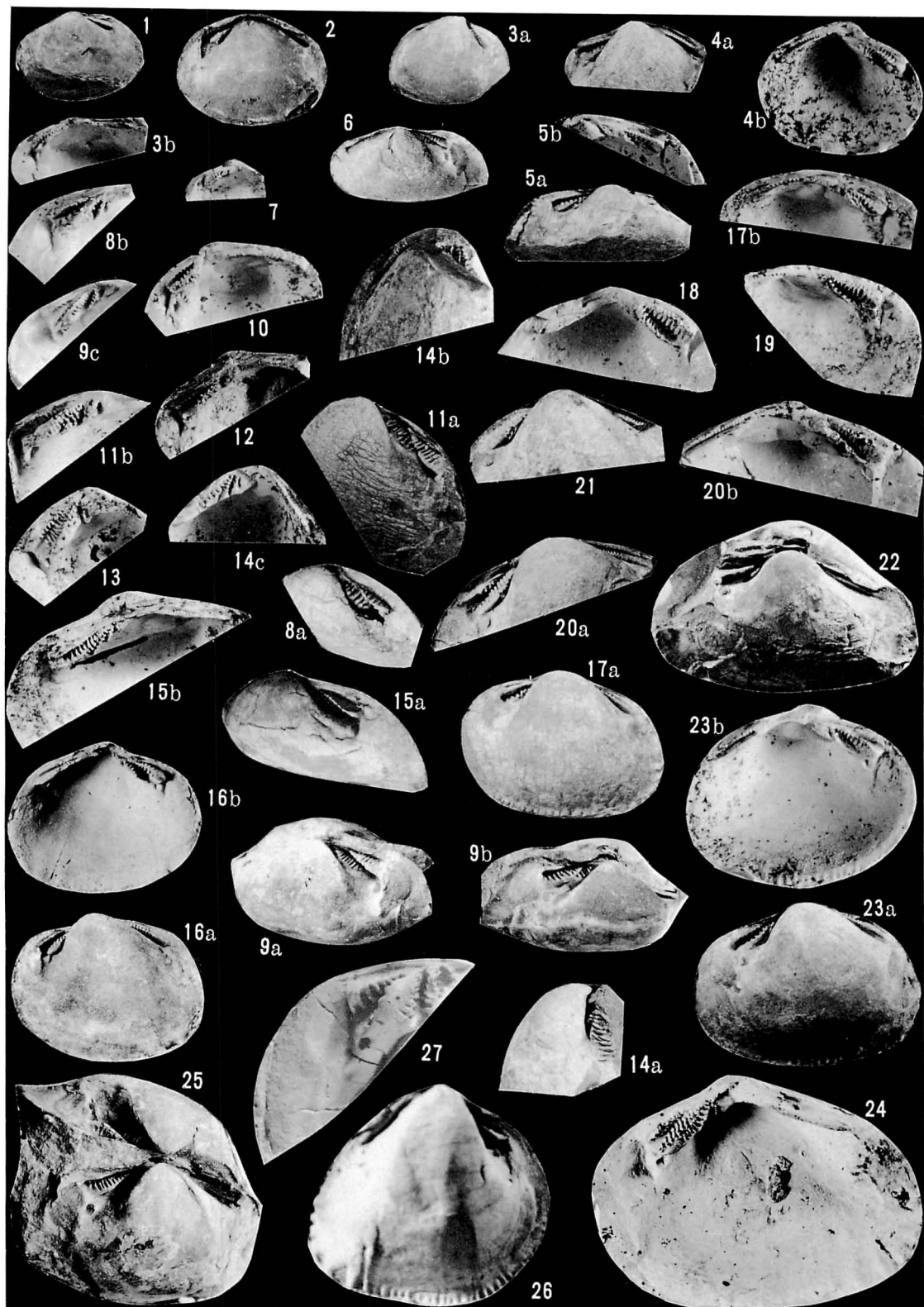
1. 表面のV字型装飾のV字の角度は小さくなる。
  2. 表面のV字型装飾はだんだん消失する。
  3. pseudocardinal teeth の数は多くなる。
-



## Explanation of Plate 46

Figs. 1-26. *Trigonioides* (s. s.) *paucisulcatus* (SUZUKI, 1940)

1. Right valve (KPE 1703), internal mould showing weak crenulation on pseudocardinal teeth.
2. Left valve (KPE 1683), internal mould showing muscle scars and weak crenulation on pseudocardinal teeth.
3. Right valve (KPE 1704), 3a: internal mould showing crenulation on pseudocardinal teeth, 3b: rubber cast of 3a, 5; crenulated on ventral side only, 3; crenulated on both sides, 1a; incipiently presented, PIII; not crenulated, but lamellar.
4. Left valve (KPE 1688), 4a: internal mould showing crenulation on both pseudocardinal and postero-lateral teeth, 4b: rubber cast of 4a, 4; crenulated on both sides, 2; crenulated on dorsal side only, PII, PIV; crenulated only one side, dorsal and ventral side, respectively.
5. Left valve (KPE 1701), 5a: internal mould showing crenulation on pseudocardinal teeth, 5b: rubber cast of 5a, 4; crenulated on both sides, 2; crenulated on both sides, situated vestigially between 4 and 1'a, 1'a; crenulated on dorsal side only. *Thiara* (*Siragimelania*) *tateiwai* associated with immediately below the umbo.
6. Right valve (KPE 1710), internal mould showing crenulated pseudocardinal teeth and muscle scars on anterior side.
7. Right valve, rubber cast of KPE 1709, showing pseudocardinal teeth, 5; not crenulated, 3; crenulated on both sides, 1a; presented incipiently.
8. Right valve (KPE 1714), 8a: internal mould showing crenulated pseudocardinal teeth, 8b: rubber cast of 8a, 5; crenulated on ventral side only, 3 and 1a; crenulated on both sides, 1b; crenulated on antero-dorsal side.
9. Conjoined valves (KPE 1682), internal mould ventrally opened, showing crenulated pseudocardinal teeth, 9a: right side view, 9b: left side view, 9c: rubber cast of 9a, 5; crenulated on ventral side only, 3; crenulated on both sides, 1a; crenulated on anterior side only.
10. Right valve, rubber cast of KPE 1698, showing crenulated hinge teeth, 5; crenulated on ventral side only, 3; crenulated on both sides, 1a, 1b; not preserved, PIII; crenulated on both sides.
11. Right valve (KPE 1879), 11a: internal mould, 11b: rubber cast of 11a, 5; crenulated on ventral side only, 3, 1a and 1b; crenulated on both sides, 1a closely associated with 3.
12. Right valve, rubber cast of KPE 1700, showing crenulated hinge teeth, 5; crenulated on ventral side only, 3; crenulated on both sides, 1a; crenulated on dorsal side, PIII; crenulated on both sides.
13. Right valve, rubber cast of KPE 1689, showing crenulated hinge teeth, 5; crenulated on ventral side only, 3 and 1a; crenulated on both sides, 1b; not observed, PIII; partly preserved, crenulated on both sides.
14. Right valve (KPE 1687), 14a: anterior side view, internal mould showing crenulated pseudocardinal teeth, 14b: right side view, the umbo cut out showing crenulated hinge teeth, the specimen strongly compressed antero-posteriorly, 14c: rubber cast of 14b, showing hinge teeth, 5; not preserved, 3, 1a and 1b; crenulated on both sides, 1c; crenulated on antero-dorsal side, PIII; crenulated on both sides.
15. Right valve (KPE 1690), 15a: internal mould, 15b: rubber cast of 15a, showing crenulated hinge teeth, 5; crenulated on ventral side only, 3, 1a and 1b; crenulated on both sides, 1c; crenulated on anterior side, PIII; crenulated on both sides.
16. Left valve (KPE 1684), 16a: internal mould showing crenulated hinge teeth, 16b: rubber cast of 16a, 4; crenulated on both sides, 2; crenulated on dorsal side, 1'a; incipient presence, PII, PIV; crenulated on upper and lower side, respectively.



17. Left valve (KPE 1697), 17a: internal mould showing crenulated hinge teeth and ventral crenulation, 17b: rubber cast of 17a, 4, 2 and 1'a; crenulated on both sides, 2 presented vestigially between 4 and 1'a, 1'b; incipient presence, PII, PIV; crenulated on upper and lower side, respectively.
  18. Left valve, rubber cast of KPE 1713, showing crenulated hinge teeth, 4 and 2; crenulated on both sides, 1'a; incipient presence, PII, PIV; weakly crenulated on upper and lower side, respectively.
  19. Left valve, rubber cast of KPE 1702, showing crenulated hinge teeth, 4 and 2; crenulated on both sides, 1'a; crenulated on anterior side, 1'b; not observed, PII and PIV; crenulated on upper and lower side, respectively.
  20. Left valve (KPE 1887), 20a: internal mould showing crenulated hinge teeth, 20b: rubber cast of 20a, 4 and 2; crenulated on both sides, 1'a; incipient presence, PII, and PIV; crenulated on upper and lower side, respectively.
  21. Left valve (KPE 1685), internal mould showing crenulated hinge teeth.
  22. Conjoined valves (KPE 1681), internal mould showing crenulated hinge teeth.
  23. Left valve (KPE 1686), 23a: internal mould showing crenulated hinge teeth and ventral crenulation, 23b: rubber cast of 23a, 4; crenulated on both sides, 2; crenulated on antero-dorsal side, 1'a; incipient presence, PII and PIV; crenulated on upper and lower side, respectively.
  24. Right valve, rubber cast of KPE 1695, showing crenulated hinge teeth and postero-ventral crenulation, 5, 3 and 1a; crenulated on both sides, 1b; not observed, PIII; crenulated on both sides.
  25. Conjoined valves (KPE 1706), opened ventrally about at right angle, internal mould, showing crenulated hinge teeth and the muscle scars.
  26. Right valve (KPE 1696), internal mould, compressed antero-posteriorly, showing ventral crenulation.
- Loc.: at a point 1.5 Km northeast from Geoncheon-ri, Seo-myeon, Weolseong-gun, Korea.
- Figure 27. *Trigonioides (Kumamotoa) mifunensis* TAMURA, 1970.
- Rubber cast of KPE 1023, showing strong and stout pseudocardinal hinge teeth.
- Loc.: See Tamura, 1970.
- All figures are of natural size.
- The specimens illustrated above are kept in the Department of Earth Science, Kyungpook National University, Daegu, Korea.

692. ONTOGENIES OF FOUR UPPER CAMBRIAN TRILOBITES FROM  
THE BONNETERRE DOLOMITE, MISSOURI\*

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**Abstract.** As one of the series of papers dealing with the ontogenic changes of various Trilobita the present study clarified the ontogenic development of four Upper Cambrian species from the Bonneterre Dolomite in Missouri, i.e., *Coosella prolifera*, *Holcacephalus tenurus*, *Welleraspis missouriensis* and *Meteoraspis globosa*. Among these four species, *Coosella prolifera* was investigated in great detail to distinguish the metaprotaspid, paraprotaspid, early meraspid and late meraspid stages. Moreover, two different morphologic groups were clearly shown in the *Coosella prolifera* and *Holcacephalus tenurus* samples respectively throughout the ontogenic changes. These bimodal phenomena were supposed to implicate a sexual dimorphism of the trilobites.

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**Introduction**

The present report describes the ontogenic development of *Coosella prolifera* LOCHMAN, *Welleraspis missouriensis* (LOCHMAN), *Holcacephalus tenurus* (WALCOTT) and *Meteoraspis globosa* (MILLER). The studied material was collected by Dr. Ch. LOCHMAN-BALK, New Mexico Institute of Mining and Technology, from the Bonneterre Dolomite, Upper Cambrian, Cedaria Zone, Saline Creek, 1.2 miles southeast of the School House at Avon, Ste Genevieve Co., Missouri, in 1940. Among the described species, *Coosella prolifera* is represented by four ontogenic stages: i.e., the metaprotaspid, paraprotaspid, early meraspid, and late meraspid stages, and those of the others are rather poorly known. They either lack the earlier stages or show discontinuity of the growth sequence. *Coosella prolifera* shows two different morphologic groups: the first is characterized by longer glabella, deep

frontal furrow, and narrower preglabellar field, and the pygidium has a narrower marginal border; the second group has a broader glabella, indistinct frontal furrow, broader preglabellar field, and the pygidium has a broader marginal border. The species *Holcacephalus tenurus* (WALCOTT) shows also two morphologic groups: the first has a narrow preglabellar field and a broader glabella; and the second is broader, and the glabella is slender. These bimodal phenomena are postulated as sexual dimorphism within each species population.

The morphogenesis of *Coosella prolifera* and *Meteoraspis globosa* are closely similar to those of *Syspacheilus dunoirensis* (MILLER), *Coosella convexa* TASCH, *Wilsonella pennsylvanica* HU, *Crepicephalus deadwoodensis* HU, and *Coosia albertensis* RESSER. The ontogenic development of *Welleraspis missouriensis* resembles *W. lochmanae* HU, and *Pemphigaspis bullata* HALL; and the instars of *Holcacephalus tenurus* are identical with those of material found from South Boulder Creek, Madison

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\* Received Nov. 18, 1977; read June 3, 1978 at Tsukuba.

Co., Montana by HU (1971). These ontogenetic similarities within each group certainly indicate close phylogenetic relationships.

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### Systematic Paleontology

Family Coosellidae PALMER, 1954

Genus *Coosella* LOCHMAN, 1934

*Coosella prolifica* LOCHMAN

Pl. 47, figs. 1-34

*Coosella prolifica* LOCHMAN, 1936, p. 39, pl. 9, figs. 4-11; Lochman & Duncan, 1944, p. 83, pl. 12, figs. 35, 36.

*Syspacheilus camurus* LOCHMAN, 1940, p. 42, pl. 3, figs. 21-25.

*Remarks.*—The present species is represented by two different morphologic groups: the first group has the cranidium with longer glabella (figs. 18, 22, 24), deep frontal furrow, and narrower preglabellar field, and the pygidium has a narrower marginal border (figs. 29, 31, 34); and the other one has a cranidium with broader glabella, indistinct frontal furrow, and broader preglabellar field (figs. 20, 21, 23), and the pygidium has broader marginal border (figs. 30, 32, 33). The author is of the opinion that these differences are minor and do not pertain to generic or specific level differences (as some think), since, both forms have a similar shaped

cranidium, glabella and pygidium, and similar depth of the dorsal furrow. They are probably instead represent sexual dimorphism within the same species population. The first group would be "female" and the second "male" forms. If this interpretation is tenable, then "*Coosella prolifica*" of LOCHMAN must be viewed as the female form, of LOCHMAN's (1940) "*Syspacheilus camurus*" which is based on male specimens of the same species.

*Coosella prolifica* LOCHMAN, ontogeny

*Metaprotaspid stage* (Pl. 47, figs. 1, 2).—The shield is rounded in outline, convex, and is about 0.30-0.40 mm in sagittal length; the axial and pleural lobes are not distinctly divided, except for a longitudinal furrow; a few glabellar lobes are rather faintly marked along the central axis; the frontal lobe is convex, and demarked with a pair of distinct pits laterally; the superciloid ridges are extended from the anterior lateral lobe, and curving posterolaterally for a short distance; the small occipital node is faintly elevated at the posterior shield margin; the pleural lobe is broader than the axis, and slopes downward around the margin. The skeletal surface is faintly covered by granules.

*Paraprotaspid stage* (Pl. 47, figs. 3-6).—The small shield is subrounded, convex, about 0.36-0.50 mm in length (sag.); the axial lobe is faintly delimited by dorsal furrow, slenderly cylindrical; no distinct glabellar segments are recognizable, except for a few faintly depressed impressions marked along the dorsal furrows, which suggest the presence of the axial segments; the frontal lobe is not distinctly elevated, and except for a pair of pits, is unmarked at the anterolateral margin; the paired superciloid ridges are short, and connected by a pair of elevated and well delimited palpebral lobes; the occipital

ring is transversely oval, highly convex, and well separated by a furrow; the fixigena is convex along the outer margin, and is wider than the axis; the posterior fixigenal border is about the same width as the occipital ring; the narrow lenticular protopygidium is divided by one to three segments, it slopes downward steeply; the skeletal surface is faintly granulated.

The morphogenesis of the skeleton during this stage saw the glabella developed from a cylindrical to slightly forwardly expanded; the frontal pit becomes shallower; the posterior fixigena increases in width; and the protopygidium increases in number of segments and from lenticular to semicircular in outline.

*Early meraspid stage* (Pl. 47, figs. 7-19).—The cranium is trapezoidal in outline, convex, about 0.60-1.0 mm in length (sag.); the slender cylindrical glabella is deeply defined by a dorsal furrow, and without distinct glabellar segments; the occipital ring is convex, bearing a minute median tubercle, and deeply separated by an occipital furrow; the narrow anterior border arches forwardly, and is well delimited by a frontal furrow; the fixigena is convex, broadly triangular, with the narrow medium-sized palpebral ridge located in front of the mid-line (tr.) of the glabella; the anterior facial suture is short and convex, and the posterior one is divergently convex; the posterior fixigenal border is convex, elevated from the broad and deep border furrow, and is about the same width as the occipital ring.

The morphogenesis of the instars during this stage saw the slightly forwardly expanded glabella become cylindrical, the anterior border increased in width; the palpebral lobe moved backward from the anterior border; the fixigena reduced the width from wide to narrower than the glabella. The surface of the skeleton is covered by faint granules and a few

coarse ones.

*Late meraspid stage* (Pl. 47, figs. 11-14).—The cranium is trapezoidal in outline, convex, about 1.0-1.8 mm in segittal length; the glabella is subquadrate, slightly tapering anteriorly and with a round anterior margin; the glabella furrows are not recognizable, except for the very faint occipital pair; the dorsal furrow is narrow and deep; the convex occipital ring is crescentic, bearing a medium sized occipital tubercle; the narrow preglabellar field is present, gently convex, and well defined by a broad anterior furrow; the anterior border is broad, convex, and arches forwardly; the convex fixigena is about one-third the width of glabella, has the medium-sized palpebral lobe situated on the mid-length of the glabella; the posterior fixigenal border is narrower than the occipital ring (tr.), and is deeply differentiated by a border furrow. The anterior facial suture line is short, slightly divergent-convex, the posterior one is divergent laterally and convex. The surface of the skeleton is covered by both faint and coarse granules; irregular ridges are elevated along the anterior border.

The skeletal morphogenesis during this stage sees the preglabellar field increases in width; the glabella becomes subquadrate and slightly deepens forwardly; the posterior fixigena grows narrower as the palpebral lobe moves backward from the mid-line of the shield (tr.).

The smallest pygidium is about 0.5 mm in length (sag.), it is convex and consists of 6-7 segments; the anterior thoracic segments are ankylosed with the terminal plate—the rudimentary pygidium—and show free pleural spines; the axial lobe is conical, tapering posteriorly, and reaches less than the full length of the shield. The surface is minutely granulated, and a few coarse nodes are present along the pleural bands.

The morphogenesis of the pygidium during these growth stages are: the rudimentary pygidium or the ankylosed posterior plate is changed from a rounded posterior margin to an inwardly directed bend; the surface granules on the pygidial surface are reduced.

*Remarks.*—The earlier ontogenic developmental stages of the present species are closely similar to those of *Syspacheilus dunoirensis* (MILLER) (HU, 1972), *Coosella convexa* TASCH, *Wilsonella pennsylvanica* HU (HU, 1968), *Crepicephalus deadwoodensis* HU (HU, 1972), *Coosia albertensis* RESSER (HU, 1975), and *Meteoraspis globosa* (MILLER) (LOCHMAN & HU, 1961, and present text). Thus, these genera possibly have close phylogenetic relationship.

*Figured specimens.*—UCGM. 43267, 43267a-43267z, 43267a'-g'.

Family Tricrepicephalidae PALMER, 1954

Genus *Meteoraspis* RESSER, 1935

*Meteoraspis globosa* (MILLER)

Pl. 48, figs. 23-36

*Blountia globosa* B.B. MILLER, 1936, p. 25-27, pl. 6, figs. 22-24.

*Meteoraspis globosa* (MILLER) in LOCHMAN & HU, 1961, p. 141, pl. 28, figs. 7-19.

*Prochuangia? berryi* LOCHMAN, 1940, p. 39, pl. 4, fig. 17 only (not 18-20).

*Remarks.*—The present species is represented by more than 30 small and large sized cranidia. The smallest cranidium, assigned as early meraspis, is about 0.65 mm in sagittal length, and the largest adult cranidium measures 6.0 mm long. They show a continuous growth sequence. The morphogenesis and the adult morphologic characteristics are identical with material found in the Wind River Mountains, Wyoming, reported by LOCHMAN & HU (1961), except that the librigena is

unknown in the present specimens.

Two incompletely preserved specimens, i. e., a cranidium and a pygidium are figured by LOCHMAN (1940) and referred to *Prochuangia? berryi* LOCHMAN. The cranidium has a subquadrate glabella, convex but faint glabellar furrows, and a narrow fixigena. It is possibly a member of the genus *Nisonella* or *Genevievella*; however, the specimen shows an incomplete postfixigena. The associated pygidium is semicircular in outline, with numerous marginal spines. These are certainly not the generic features of the genus *Prochuangia*, because *Prochuangia* has a pygidium with a pair of large caudal spines and a transverse subquadrate outline (KOBAYASHI, 1935). This pygidium belongs more likely to *Meteoraspis*, i. e., *M. globosa* (MILLER).

*Meteoraspis globosa* (MILLER), ontogeny

The ontogeny of the present species is incompletely known. The smallest instars are assigned to the early meraspis stage and are succeeded by late meraspis and holaspis stages, thus completing the post-paraprotaspis growth sequence. These are described as follows.

*Early meraspis stage* (Pl. 48, figs. 23, 24).—The cranidium is about 0.50-0.75 mm in sagittal length, convex, trapezoidal to truncatotriangular in outline, with narrow convex anterior border which arches slightly forward; the anterior border is well defined by a frontal furrow, and has a median niche toward the anterior glabellar margin; the glabella is cylindrical, convex, without distinct glabellar segments or furrows; the fixigena is convex, and is of about the same width as the glabella; the medium-sized palpebral lobe is a narrow, elevated ridge, well defined by a distinct palpebral furrow; the palpebral lobe is located in front of the mid-

transverse line of the cranium; the well elevated palpebral ridge arches anterolaterally from the anterolateral margin of the glabella and terminates in front of the palpebral lobe; the occipital ring is convex, lenticular, and bears a median tubercle; the posterior fixigenal border is elevated, and deeply separated by a border furrow, and is broader than the occipital ring; the dorsal surface of the cranium is deeply demarked by an axial furrow; a few coarse granules are sparsely scattered among the finer ones.

The earliest instar of the present stage is known by LOCHMAN & HU (1961, pl. 28, fig. 12) from the Wind River Mtns., Wyoming. It is about 0.5 mm in sagittal length, and shows a well defined dorsal furrow, and a cylindrical glabella, without a glabellar segmental furrow. This 1961 material possibly represents one step earlier than the material here illustrated (pl. 48, fig. 23).

*Late meraspis stage* (Pl. 48, figs. 25-33).—The cranium measures 0.70-1.0 mm in sagittal length; it is triangular in outline, convex, with an arched anterior border, and deep dorsal furrows; the anterior border is broad, convex, and distinctly separated by a frontal furrow; a narrow preglabellar field is present. It is narrow in the smaller instars but becomes broader and about the same width as frontal border in the larger ones; the glabella is cylindrical to slightly tapering forward from the deeply marked occipital furrow; no distinct glabellar segments are seen; the convex occipital ring is lenticular, arches posteriorly, and bears a minute median node. The fixigena is slightly narrower than the glabella, convex, and has the medium-sized palpebral lobe located on the mid-transverse line of the cranium; the posterior fixigena is about equal in width to the occipital ring, and deeply marked by a broader furrow; the

posterior fixigenal border is convex; the anterior facial suture line is convergently convex, and the posterior one is divergent laterally. The skeletal surface is marked by coarse and medium-sized granules.

The morphogenesis of the cranium during the present stage sees the preglabellar field change from narrow to broader, the glabella from cylindrical to conical, the fixigena from broad to narrower, and the palpebral lobe moves backward from near the anterior border to the mid-transverse line of the cranium. The present stage is correlated with what was reported as a "series of small holaspis crania" by LOCHMAN & HU (1961, pl. 28, figs. 13-17) from the Wind River Mtns., Wyoming.

When the cranium attained the holaspis stage (pl. 2, figs. 34-36) the glabella becomes oval, the fixigena narrower, two distinct pits are impressed in the frontal furrow, and the skeletal surface has fewer but coarse granules.

*Remarks.*—The ontogenic development of the present species is rather similar to that of *Coosella prolifica* LOCHMAN, except that in *Meteoraspis globosa* (MILLER) the skeletal surface is coarsely granular. They are possibly closely related.

*Figured specimens.*—UCGM. 43270, 43270a-43270m.

Family Lonchocephalidae HUPÉ, 1953

Genus *Welleraspis* KOBAYASHI, 1935

*Welleraspis missouriensis* (LOCHMAN)

Pl. 48, figs. 1-11

*Avonaspis missouriensis* LOCHMAN, 1940, p. 41, pl. 3, figs. 10-13.

*Diagnosis.*—Cranidium trapezoidal in outline, strongly convex; glabella subquadrate to oval, marked by pair of



traceable glabellar furrows; occipital ring bearing a stout median spine and a minute median tubercle; preglabellar field very narrow; anterior border narrow, convex, distinctly separated by frontal furrow; fixigena triangular, bearing small palpebral lobe. Librigena elongate with medium-sized genal spine. Pygidium roundly subtriangular in outline, convex, conical, axis divided by shallow furrows into four or more rings and a terminal portion; narrow marginal border horizontally convex. Skeletal surface covered by medium-sized granules.

*Description.*—The cranium is trapezoidal in outline, strongly convex; the glabella is broadly subquadrate to oval, highly convex, above the fixigena, and has two pairs of traceable glabellar furrows; the glabellar furrows are faintly impressed laterally to the dorsal furrows; the dorsal furrow is V-shaped, deeply surrounding the glabellar margin; the occipital ring is convex, triangular, narrow laterally and broadening to the central portion and then drawn out into a stout occipital spine; a transverse, elongate, minute tubercle is born on the center of the occipital ring; the preglabellar field is very narrow, convex, and slightly depressed in front of the glabella; the anterior border is narrowly crescentic, arching forward, and is distinctly delimited by the frontal furrow. The fixigena is narrowly triangular, convex along the free margin, and about one-fourth the width of the glabella between the palpebral lobe and the dorsal furrows; the medium to small-sized palpebral lobe is distinctly defined by a palpebral furrow, elevated, and located in front of the mid-line (tr.) of the glabella; the elevated palpebral ring is oblique toward the anterior lateral margin of the glabella; the anterior branch of the facial suture is convergently convex, and the posterior one is divergent pos-

terolaterally and convex; the posterior fixigenal border is narrower than the occipital ring (tr.) and deeply impressed by the border furrow.

The librigena is narrowly elongate and the ocular platform is about one and half the width of the lateral border, convex, and well defined by a broad lateral furrow; the ocular ring is medium-sized; the genal spine is medium-short, and has a broad base; no posterior border in known.

The pygidium is subtriangular in outline, convex; the axial lobe is conical, convex above the pleural lobe, tapers posteriorly, and is divided into five or more convex rings by furrows; the terminal portion extends to the posterior end of the pygidial margin; the pleural lobe is convex below the axis, about the same width as the axis, and divided into four deep furrows and faint interpleural grooves; the marginal border is slightly broader than the anterolateral margin—the facet region, and narrows posteriorly to the posterior terminal portion, and bears a few pairs of serrate nodes.

The skeletal surface is covered by medium-sized granules, and parallel ridges along the cephalic border, i. e., anterior border of the cranium and lateral border of the librigena.

*Remarks.*—The present species differs from the type species *Welleraspis jerseyensis* (WELLER, 1900), *W. swartzi* (TASCH, 1951) (RASETTI, 1954; HU, 1968), *W. lochmanae* HU, 1969, *W. lata* HOWELL, 1957 (HU, 1964), by the strongly convex, broader glabella, narrower preglabellar field, and round and less numerous pygidial segments.

*Welleraspis missouriensis* (LOCHMAN),  
ontogeny

The ontogenic development of the present species is comparable to that of *W.*

*swartzi* (TASCH) (HU, 1968; RASETTI, 1954), *W. lata* HOWELL (HU, 1964), and *W. lochmanae* HU, 1969 although the ontogeny of *W. missouriensis* is incompletely known. Two growth stages are recognizable in the ontogenic development, i. e., the early meraspid and the late meraspid stages.

*Early meraspid stage* (Pl. 48, figs. 7, 8).—The cranium is trapezoidal to rounded in outline, convex, about 0.45–0.65 mm in length (sag.); the glabella is expanded forward from the occipital furrow, convex above the fixigena, and marked by pairs of poorly separated glabellar segments; the triangular occipital ring is convex, and bears a medium-sized occipital spine; the anterolateral glabellar pits are well defined; a pair of short superciloid ridges extends from the anterolateral glabellar pits, and ends in front of the elevated

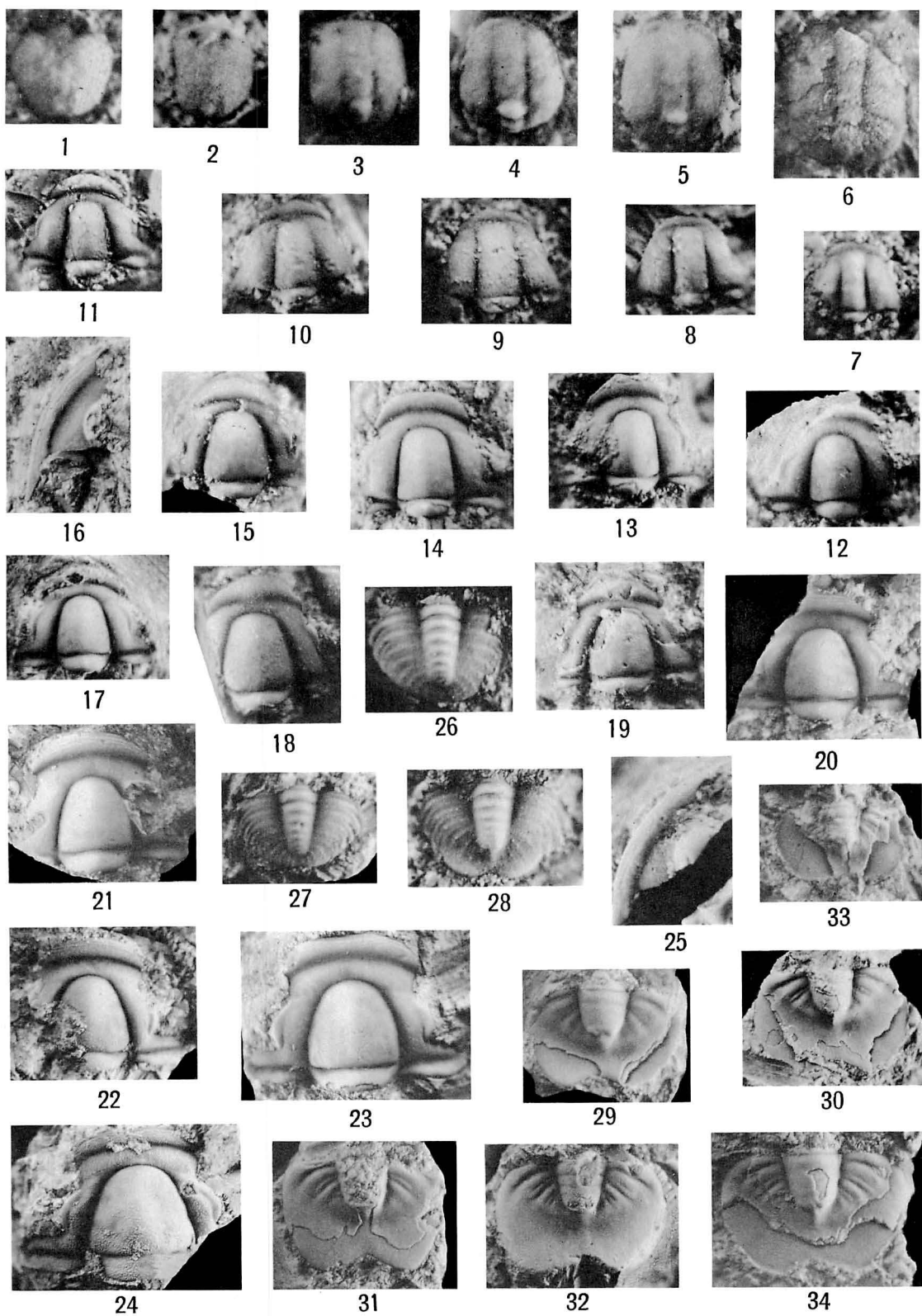
palpebral lobe. The triangular fixigena is convex, broad, and has the narrow and well defined palpebral ridge located at the first glabellar furrow (tr.); the rear border is elevated, distinctly demarked by a border furrow, and is about one and a half the width of the occipital ring (tr.). The skeletal surface is covered by medium-sized granules and scattered with sparse nodes.

*Late meraspid stage* (Pl. 48, fig. 6).—The cranium is trapezoidal in outline, highly convex, and is about 1.0–1.5 mm in length (sag.); the subquadrate glabella is convex, with both anterior and posterior margins rounded; the dorsal furrow is deep and v-shaped; three pairs of glabellar furrows are faintly impressed laterally to the dorsal furrows; the crescentic convex occipital ring is well defined by a deep

#### Explanation of Plate 47

##### Figures 1–34. *Coosela prolifica* LOCHMAN

- 1, 2, metaprotaspides, showing the indistinctly developed axial and pleural lobes. 1,  $\times 50$ , UCGM. 43267; 2,  $\times 43$ , UCGM. 43267a.  
 3–6, a few paraprotaspides, showing the well differentiated axial and pleural lobes and the presence of the protopygidium; 3,  $\times 39$ , UCGM. 43267b; 4,  $\times 42$ , UCGM. 43267c; 5,  $\times 42$ , UCGM. 43267d; 6,  $\times 30$ , UCGM. 43267e.  
 7–10, a few early meraspides, showing the presence of the anterior cranial border; 7,  $\times 17$ , UCGM. 43267f; 8,  $\times 19$ , UCGM. 43267g; 9,  $\times 21$ , UCGM. 43267h; 10,  $\times 17$ , UCGM. 43267i.  
 11–14, a few late meraspides, showing the presence of the preglabellar field and the subquadrate glabella; 11,  $\times 13$ , UCGM. 43267j; 12,  $\times 12$ , UCGM. 43267k; 13,  $\times 10$ , UCGM. 43267l; 14,  $\times 14$ , UCGM. 43267m.  
 16, 25, two nearly complete librigenae; 16,  $\times 9$ , UCGM. 43267w; 25,  $\times 10$ , UCGM. 43267x.  
 15, 19, 20, 21, 23, a few "male" cranidia, showing the short broad glabella and the wider preglabellar field; 15,  $\times 8.6$ , UCGM. 43267n; 19,  $\times 5.4$ , UCGM. 43267q; 20,  $\times 6$ , UCGM. 43267r; 21,  $\times 7$ , UCGM. 43267s; 21,  $\times 7$ , UCGM. 43267t; 23,  $\times 10$ , UCGM. 43267u.  
 17, 18, 22, 24, a few "female" cranidia, showing the narrow and longer glabella, narrower preglabellar field and the distinct frontal furrow; 17,  $\times 6$ , UCGM. 43267o; 18,  $\times 11$ , UCGM. 43267p; 22,  $\times 4.7$ , UCGM. 43267t; 24,  $\times 3.4$ , UCGM. 43267v.  
 26–28, three immature pygidia, notice the thoracic segments and the well ankylosed pygidial plate; 26,  $\times 17$ , UCGM. 43267y; 27,  $\times 10$ , UCGM. 43267z; 28,  $\times 11.5$ , UCGM. 43267a'.  
 30, 32, 33, three "male" pygidia, showing the round pygidial margin; 30,  $\times 2.3$ , UCGM. 43267c'; 32,  $\times 3.2$ , UCGM. 43267e'; 33,  $\times 5.6$ , UCGM. 43267f'.  
 29, 31, 34, three "female" pygidia, showing the narrower pygidial margin; 29,  $\times 5$ , UCGM. 43267b'; 31,  $\times 4$ , UCGM. 43267d'; 34,  $\times 5$ , UCGM. 43267g'.



occipital furrow; the occipital furrow is narrow across the sagittal line, and wider laterally to show a transverse W-shape; the broadly based, short occipital spine is extended posteriorly; the narrow, convex anterior border arches anteriorly; the triangular fixigena is convex and slopes downward along the lateral margin, and has the small-sized, well elevated palpebral lobe located in front of the glabella, between the anterior first and second glabellar furrows; the elevated palpebral ridge extends continuously from the palpebral lobe and ends at the anterior first glabellar furrow (tr.); the posterior fixigena is about the same width or slightly narrower than the occipital ring (tr.); the anterior facial suture line is convergently convex, and the posterior one is divergent and posterolaterally convex. The surface of the carapace is covered by medium-sized granules and bears scarce coarse ones.

The *meraspid pygidium* (Pl. 48, figs. 9, 10).—Two well preserved instar pygidia are assigned to the meraspid stage without any definitive differences separating them. They are about 0.45–0.55 mm in sagittal length, convex, and have 4–7 segments; the axis is conical, tapers posteriorly, and is divided by segmental furrows; the pleural lobe is either the same width as the axis or slightly broader; each of the pleural bands ends in a pair of short spines; the pleural spines are turned upward to reveal serrate nodes.

*Figured specimens.*—UCGM. 43268, 43268a–43268j.

Family Norwoodiidae WALCOTT, 1916

Genus *Holcacephalus* RESSER, 1938

*Holcacephalus tenurus* (WALCOTT)

Pl. 48, figs. 12–22

*Norwoodia tenurus* WALCOTT, 1916, p. 172, pl. 28, figs. 2–2g.

*Norwoodina tenurus* (WALCOTT) in LOCHMAN & DUNCAN, 1944, p. 137, pl. 13, figs. 15–17.

*Holcacephalus tenurus* (WALCOTT), LOCHMAN & HU, 1960, p. 823, pl. 98, figs. 1, 2, 4–7, 14–23, 28–32, 40–44, 52 only; Hu, 1971, p. 176, pl. 3, figs. 1–32, and text. fig. 4a–k.

*Holcacephalus* cf. *tenurus* (WALCOTT), PALMER, 1954, p. 742, pl. 84, fig. 3.

*Remarks.*—The present species is represented by a few adult skeletons and several earlier instars. The morphogenesis of these carapaces is closely comparable to that of a collection from the Pilgrim Formation, Upper Cambrian, Montana, reported by HU (1971). The adult cranidia are separated into two different morphologic groups: one has the cranidium with short, broad and cylindrical glabella, and narrow preglabellar field, while the other has an elongate, narrow, conical glabella, and broader preglabellar field. The general morphogenesis of the early instars shows the axial and the pleural lobes to be indistinct, but well separated laterally; the glabella expands forwardly, and becomes cylindrical to conical later; the preglabellar field changes from narrow to broad, the palpebral lobe moves from the anterior shield margin to the midline of the cranidium, and the posterior fixigena increases in width; the freely articulated pygidial segments are ankylosed.

*Figured specimens.*—UCGM. 43269, 43269a–43269i.

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Explanation of Plate 48

Figures 1-11. *Welleraspis missouriensis* (LOCHMAN)

- 1-4, few cranidia, showing the strongly convex glabella; 1,  $\times 8.6$ , UCGM. 43268; 2,  $\times 10$ , UCGM. 43268a; 3,  $\times 8.8$ , UCGM. 43268b; 4,  $\times 9$ , UCGM. 43268c.
- 5, a nearly complete librigena;  $\times 7$ , UCGM. 43268d.
- 6, a late meraspid cranidium; notice the quadrate glabella;  $\times 17$ , UCGM. 43268e.
- 7, 8, two meraspid cranidia; notice the forwardly expanded glabella; 7,  $\times 22$ , UCGM. 43268f; 8,  $\times 21$ , UCGM. 43268g.
- 9, 10, two meraspid pygidia; 9,  $\times 24$ , UCGM. 43268h; 10,  $\times 12$ , UCGM. 43268i.
- 11, a small nearly complete holaspid pygidium;  $\times 16$ , UCGM. 43268j.

Figures 12-22. *Holacephalus tenurus* (WALCOTT)

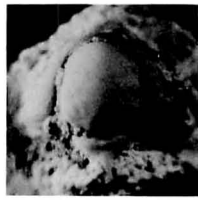
- 12, a complete anaprotaspis; notice the faint furrow along the central axis;  $\times 37$ , UCGM. 43269.
- 13, 14, two metaprotaspides, showing the well differentiated axial and pleural lobes; 13,  $\times 32$ , UCGM. 43269a; 14,  $\times 31$ , UCGM. 43269b.
- 15-17, three paraprotaspides, showing the presence of the protopygidium; 15,  $\times 33$ , UCGM. 43269c; 16,  $\times 33$ , UCGM. 43269d; 17,  $\times 32$ , UCGM. 43269e.
- 19, a broken cranidium, showing the quadrate glabella;  $\times 7$ , UCGM. 43269f.
- 18, 20, 21, three nearly complete cranidia, showing the narrower and elongate glabella; 18,  $\times 2.2$ , UCGM. 43269g; 20,  $\times 8$ , UCGM. 43269h; 21,  $\times 8.5$ , UCGM. 43269i.
- 22, a complete librigena;  $\times 12.5$ , UCGM. 43269j.

Figures 23-36. *Meteoraspis globosa* (MILLER)

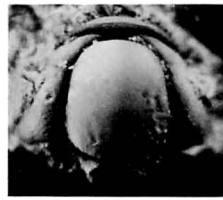
- 23, 24, two early meraspid cranidia; notice the presence of the anterior border; 23,  $\times 20$ , UCGM. 43270; 24,  $\times 20$ , UCGM. 43270a.
- 25-33, a growth series of late meraspid cranidia, showing the presence of the preglabellar field and the broaden of the glabella; 25,  $\times 17.5$ , UCGM. 43270b; 26,  $\times 17$ , UCGM. 43270c; 27,  $\times 16$ , UCGM. 43270d; 28,  $\times 15$ , UCGM. 43270e; 29,  $\times 14$ , UCGM. 43270f; 30,  $\times 15$ , UCGM. 43270g; 31,  $\times 15$ , UCGM. 43270h; 32,  $\times 12$ , UCGM. 43270i; 33,  $\times 10$ , UCGM. 43270j.
- 34-36, three holaspides, showing the oval, strongly convex glabella, and two pits in frontal furrow; 34,  $\times 5.8$ , UCGM. 43270k; 35,  $\times 2.1$ , UCGM. 43270l; 36,  $\times 4.4$ , UCGM. 43270m.



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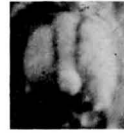
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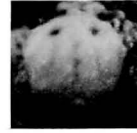
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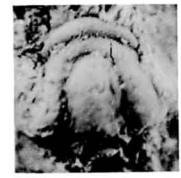
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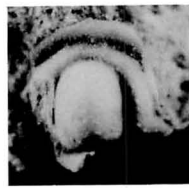
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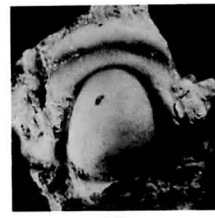
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本論文では *Coosella prolifera*, *Holcacephalus tenurus*, *Welleraspis missouriensis* および *Meteoraspis globosa* のカンブリア紀後期三葉虫4種の個体発生をとりあつかった。就中 *Coosella prolifera* の発生順序はほぼ完全に明らかにすることができたが、他の三種については十分な資料は得られなかった。しかし、*Coosella prolifera* ならびに *Holcacephalus tenurus* の2種に関しては、発生史中に二形態組を識別することが可能であり、それを同種異性型であると考えた。

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胡 忠 恒

693. ON THE GENERA *SIPHONOFUSUS* AND *EUTHRIA* OF  
THE INDO-WEST PACIFIC\*

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**Abstract.** The taxonomic and stratigraphic relation of three gastropod genera *Buccinulum*, *Euthria* and *Siphonofusus* is reexamined. The result shows that *Buccinulum* and *Siphonofusus* derived respectively in the Early and Middle Miocene from *Euthria* which appeared in the Eocene. *Siphonofusus*, an Indo-West Pacific element, reveals a morphoserries of enlarging shell and weakening sculpture in each of its three lineages.

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**I. Taxonomic status of *Siphonofusus* and related taxa**

A group of morphologically very characteristic species, both fossil and living, have been described under various generic names of *Buccinulum*, *Euthria* and *Siphonofusus* from the Indo-West Pacific region.

*Euthria* J. E. GRAY (in M. E. GRAY), 1850, with the type-species *Murex corneus* LINNAEUS (o. d.), *Buccinulum* DESHAYES, 1830, with the type-species *Buccinum lineatum* CHEMNITZ=*B. linea* MARTYN (s. d., IREDALE, 1921) and *Siphonofusus* KURODA and HABE, 1952, with the type-species *Siphonalia lubrica* DALL (o. d.) are so closely related with one another that their taxonomic distinction is debatable.

IREDALE (1918) recognized the generic separation of *Murex corneus* from *Buccinum lineatum* on the basis of critical difference in shell form and discordance in radular feature and placed them respectively in *Euthria* and *Evarne* H. and A. ADAMS, 1853. The latter genus was

later recognized by him (1921) as a synonym of *Buccinulum*. POWELL (1927) accepted IREDALE's idea and gave a comprehensive revision of *Buccinulum* of New Zealand. On the other hand, THIELE (1931) regarded *M. corneus* and *B. lineatum* as congeneric. When KURODA and HABE established (1952) and redescribed (1954) *Siphonofusus*, they did not make a comparison of that genus to any of the above noted taxa, but compared it with *Manaria* SMITH, 1906, from Arabian Sea.

As to the southeast Asian species in question, MARTIN (1895) and WANNER and HAHN (1935) described some species with a columellar plait under the generic name of *Siphonalia*. While MARTIN (1914) and OOSTINGH (1939) introduced *Euthria djocdjocartae* and *E. bantamensis*, respectively, ALTENA (1950) described *Buccinulum oostinghi*. BEETS (1942, 1944 and 1952) described several species under *Buccinulum* and made a revision (1942) of the related species from the Indonesian region. MACNEIL (1960) referred both BEETS' and ALTENA's species together with the species from Okinawa and Taiwan to *Afer* CONRAD, 1858 (type-species:

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\* Received Dec. 7, 1977; read Oct. 16, 1977 at Kumamoto.



*Fusus afer*: LAMARCK=*Murex afer* GME-LIN), and transferred, on that occasion, *Afer* into the Buccinidae from the Vasidae, although THIELE (1931), WENZ (1943) and many other authors treated that genus in the Vasidae. *Afer* is, however, featured by the low spire, laterally expanded body whorl and two columellar teeth and is clearly distinguished not only from those described by BEETS and AL-TENA, but also from those described by MACNEIL himself. SHUTO (1969) did not recognize any distinction between *Siphonofusus* and *Euthria* and treated them as synonymous. It is not easy to give a definite answer to the question whether these taxa really represent respectively one genus or not.

The type species of the above taxa show some important common morphological features.

Common characteristics of *Siphonofusus*, *Euthria* and *Buccinulum*: Shell is solid, moderate in size and fusiform with high spire and remarkably long snout. Axial sculpture shows retrogressive development. Aperture is oval and acuminate both posteriorly to the well defined gutter and anteriorly to the long and narrow canal. Labrum is sharp at the margin and provided with threads inside. Inner

lip is arcuately concave, covered by callus and has a parietal ridge, which demarcates the gutter. Columella is somewhat twisted and provided with a more or less distinct fold at the entrance of the canal. Operculum is ovate with nucleus at the acuminate anterior end.

Distinction: *Buccinulum* is devoid of the axial sculpture of the teleoconch except on the very early whorls and provided with a somewhat shorter snout than the others as illustrated in the type species (Fig. 1). The type species of *Euthria* and *Siphonofusus* show closely similar morphology in their early stage of growth. In that stage, they have distinct axial plicae reaching to both the upper and lower sutures. The axials become weaker in the later stages. However, weakening of plicae with growth is much more exaggerated in *Euthria* so that the penultimate and body whorls, at least, of adult shell of *Euthria* are devoid of the axials. In addition to the difference in axials, spiral sculpture of *Euthria* is much weaker than *Siphonofusus*. Comparison of the rhachidian radular teeth of *Buccinulum* (*Buccinulum linea*: THIELE, 1931) and *Siphonofusus* (*Siphonofusus lubricus*: KURODA and HABA, 1954) clarifies remarkable difference (Fig. 2). The central tooth of *S. lubricus* has three small cusps gathering at the central part of its arcuately protruded frontal margin. The lateral tooth has three stout cusps. While *Buccinulum linea* has triangular central tooth with rather large three cusps. Its lateral teeth are stouter and shorter than those of *Siphonofusus*. Radular teeth, particularly the central tooth of *Euthria* (*E. queketti* SMITH, BARNARD, 1959) is decidedly closer to *Buccinulum* than to *Siphonofusus*.

Living species belonging to *Buccinulum*, *Euthria* and *Siphonofusus* are distributed respectively in New Zealand-Tasmanian

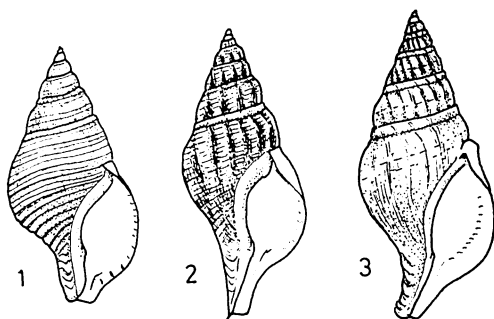


Fig. 1. Type-species of *Buccinulum*, *Siphonofusus* and *Euthria*. 1: *Buccinulum linea* (MARTYN), 2: *Siphonofusus lubrica* (DALL) and 3: *Euthria cornea* (LINNAEUS)

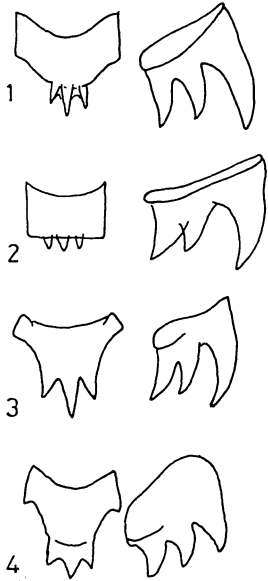


Fig. 2. Radulae of *Siphonofusus* and the related taxa. 1: *Siphonofusus lubrica* (DALL) [KURODA and HABE, 1954], 2: *Siphonalia fusoides* (REEVE) [KURODA and HABE, 1954], 3: *Euthria quaketti* SMITH [BARNARD, 1959] and 4: *Buccinulum linea* (MARTYN) [THIELE, 1931].

seas, Mediterranean-African seas and Indo-West Pacific. *Buccinulum* dates from the Earliest Miocene in its home area and some doubtful species (*Euthria bantamensis* OOSTINGH) has been known from the Pliocene of Java, Indonesia. The first appearance of *Euthria* in the Indo-West Pacific is the Middle Eocene of Java (*E. djocdjocartae* MARTIN). COSSMANN (1901) listed three Eocene species and three Oligocene ones of *Euthria* from the Mediterranean region. *Siphonofusus* was widely distributed in the Middle Miocene of the Indo-Malayan region, but is unknown in Early Miocene and earlier age. Its geographical range was expanded northward in Late Miocene and later age. *Fusus contorta* GRATELOUP, which COSSMANN referred to *Euthria*, from the

Mediterranean Burdigalian may be classified to *Siphonofusus*. Anyway the oldest known occurrence of *Siphonofusus* is in the Middle Miocene. Paleobiogeographical distribution of these taxa, particularly the known first occurrence of the taxa, suggests that *Euthria* is the group of the oldest origin among them.

*Euthria djocdjocartae* is very suggestive concerning the origin and phylogeny of *Buccinulum* which appeared in the Earliest Miocene of New Zealand. *E. djocdjocartae* has a peripheral angulation and distinct axial ribs on the first to fourth whorls and then becomes smooth so that the body whorl is roundly curved at side and provided with distinct growth lines and a few faint spiral lines on the lateral side, otherwise it is almost smooth (Fig. 3). The snout is rather short. That is to say, it shows an intermediate feature of *Euthria* and *Buccinulum*. It is strongly suggested that New Zealand-Tasmanian *Buccinulum* might have evolved from *E. djocdjocartae*.

*Siphonofusus* may be another derivative from *Euthria*. The former appeared in Middle Miocene both in the Indo-West Pacific and Mediterranean regions as mentioned above, but its post-Burdigalian history is not clear in the Mediterranean. It seems, at least, *Siphonofusus* did not succeed in growing up to a major group in the Mediterranean region. On the contrary it flourished in the Indo-West Pacific region. Geologic events in the Middle East must have been concerned

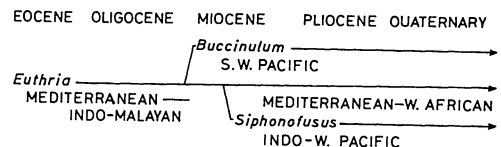


Fig. 3. Taxonomic relation and geographic distribution of the subgenera *Euthria*, *Buccinulum* and *Siphonofusus*.

in the above history of the taxon. Geological history of the Middle East involves events of closing Suez breach in Oligocene time and only a limited interchange of the Mediterranean and Indian marine faunas was probable mainly in Medial Miocene time through Iranian-Turkey channel. Larval type of *Siphonofusus* must be lecithotrophic as suggested by its paucispiral and globose protoconch and in consequence dispersion into the Mediterranean beyond the ephemeral Iranian-Turkey channel must be very difficult. *Siphonofusus*, therefore, is naturally regarded as a typical Indo-West Pacific element which evolved successfully after the Suez breach was closed. Not a small genetic difference worthy, at least, of subgeneric separation may be postulated between *Euthria* and *Siphonofusus*. In conclusion, the present author prefers to recognize subgeneric separation among *Euthria*, *Buccinulum* and *Siphonofusus*. SMITH (1906) established *Manaria* with the type-species *Manaria thurstoni* SMITH as a genus in the family Fascioliariidae. It has fusiform shell consisting of more than eight convex whorls sculptured by flat axial ribs and spiral lines. Its aperture is provided with six to seven denticles inside the labrum and an oblique fold on the columellar lip. Accordingly it is morphologically very close to *Siphonofusus*, but is distinguished from the latter in having decidedly shorter canal. KURODA and HABE (1954) reported a Japanese species which closely resembles *M. thurstoni* in typical features of the shell. According to them, this species, *Manaria* sp\*., has a rhachidian tooth, which is curved, laterally elongate rectangular and provided with three small

cusps gathering at the middle of the anterior margin. Its lateral tooth has long and stout cusps at both ends and a minute one between. The fact about the radular teeth reveals firstly that *Manaria* should be transferred firstly from Fascioliariidae to Buccinidae and secondly that *Manaria*, though closely allied to, is clearly distinguished from any of *Siphonofusus*, *Euthria* and *Buccinulum*.

## II. Evolutional lineages of *Siphonofusus*

Species in question of East and South Asia may be sorted into four groups.

They are *Siphonofusus orangensis* stock, *S. martini* stock, *S. chinensis* stock and *Euthria* group.

*Siphonofusus orangensis* stock: This stock includes *S. wanneri* (BEETS), *S. orangensis* (BEETS), *S. dinglensis* (SHUTO), *S. oostinghi* (ALTENA) and *S. longicanalis* (NOMURA and ZINBO). These species are together featured by the solid shell with the distinct spiral threads all over the shell surface and the prominent axial plicae running from suture to suture. Teleoconch whorls, at first, is concavoconvex in profile with distinct subsutural band and convex lateral side, between which is a narrow but distinctively concave band. Suture is somewhat clusping with distinct subsutural thread(s). Spiral sculpture is of adapical development in ontogeny (SHUTO, 1969 p. 47). The spirals generally consist of almost equally spaced and equally distinct five primary threads on the first whorl. The uppermost one (P1) is the distinct subsutural one, the second upper (P2) is on the concave band and the third to fifth threads (P3-P5) are on the convex lateral surface. P1 becomes broader and may be split into two threads on the later whorls. P2 abruptly becomes weak-

\* KURODA and HABE (1954, p. 230) cited this species as *Marania* sp., but this citation is simply an error for *Manaria* sp. as understood from their text.

er. Position of P3 is the peripheral angulation of the later whorls. The sixth primary thread (P6) and so on appear successively from the lower suture. Axial plicae are counted about eight (rarely seven or nine) for the first whorl and they are increased in number gradually to ten-eleven on the last whorl of the adult shell. They extend from suture to suture not only on the early whorls but also on the later ones. Growth lines are very gently opisthocyrt with its prosocline upper arm, slightly opisthocline lower arm and the apex of the very shallow sinus on the peripheral angulation. Species of this stock show a tendency of weakening of plicae in later growth stage. This tendency is more clearly exhibited

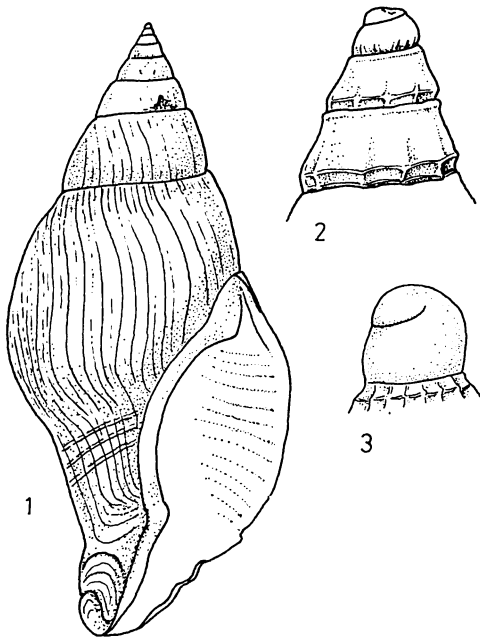


Fig. 4. 1: *Euthria djocdjocartae* MARTIN from Kali Poeroe, Central Java; Reg. No. St. 9173, Geol. Reichsmus. Leiden; 2: protoconch of the preceding specimen; 3: protoconch of *Euthria cornea* (LINNAEUS) [COSSMANN, 1901].

in the species of later geologic age. Size of adult shell is larger in the species of later age. The following species have been known hitherto.

- Siphonofusus wanneri* (BEETS, 1942), Middle Miocene, Rembang, Java, Indonesia.  
*S. orangensis* (BEETS, 1942), lower Upper Miocene, Kutei, Kalimantan.  
*S. dinglensis* (SHUTO, 1969), Upper Miocene, Panay, Philippines.  
*S. oostinghi* (ALTENA, 1950), Lower Pliocene, Java, Indonesia.  
*S. longicanalis* (NOMURA et ZINBO, 1934), Middle Pleistocene, Kikai-Jima, Japan.

*Siphonofusus martini* stock: *S. kelleitiformis* (VREDENBURG), *S. martini* (WAN-  
 NER and HAHN), *S. indicus* (DEY), *S. macneili*  
 sp. nov., *S. japonicus* sp. nov. and *S.*  
*lubricus* (DALL) constitute this stock. Species of the *S. martini* stock have characteristic shell with the whorls more or less distinctly angulated peripherally and with the axial sculpture being strong on the peripheral angulation and denuded above and below it. Profile of the first whorl of the teleoconch is rhomboid with sharp median angulation and the surfaces above and below the angulation are flat. Development of the spiral sculpture is adapical. Basic pattern of the spiral sculpture is represented by a strong subsutural thread (P1), P3 on the peripheral angulation and P4 between the angulation and the lower suture. A weaker primary spiral (P2) may be ready to appear from the lower suture in some species. Axial plicae are seven or eight on the first whorl and increased in number ontogenetically to nine or ten of the adult body whorl. The axials become weaker, particularly near the sutures, on the latter whorls, while the spiral threads persist their distinctness throughout growth stages. Weakening of the axial plicae is more exaggerated on the species of

youner geologic age. Growth lines are similar to those of the foregoing stock, but the opisthocyrt sinus is slightly deeper and the lower arm is more protruded opisthoclinally than in *S. orangensis* stock. *S. martini* stock is distinguished, furthermore, from *S. orangensis* stock in being provided with sharper peripheral angulation and weaker axials particularly near the suture. The following species belong to this stock.

*Siphonofusus martini* (WANNER et HAHN, 1935), Middle Miocene, Rembang, Java, Indonesia.

*S. kelleiiformis* (VREDENBURG, 1924), Middle Miocene, Myaukmigon and Thanga, Lower Burma.

*S. indicus* (DEY, 1962), Middle Miocene, Quilon, South India.

*S. macneili* sp. nov., Upper Miocene, Okinawa, Japan.

*S. japonicus* sp. nov., Pliocene, Kyushu, Japan.

*S. lubricus* (DALL, 1918), Recent, Southwest Japan.

*Siphonofusus chinensis* stock: Species of *Siphonofusus chinensis* stock exhibit sharply angulate profile of the spire-whorls. Above this angulation is a gently sloped ramp, on which the axial sculpture is extremely weak. Body whorl is distinctly biangulated with a peripheral and a basal angulation. Axial plicae are about six or seven on the first whorl and they are increased in number to eighteen on the adult body whorl. The spiral sculpture is close set and weak above the angulation, distinct and subequal on the lateral surface and unequal with weak secondaries intercalated on the basal surface. The snout is long and markedly recurved. The species belonging to this stock show some resemblance to *Afer* with defined shoulder slope and sharp peripheral angulation, but have definitely higher spire and relatively shorter snout than the latter. Three species are referred to this stock.

*Siphonofusus* sp. Middle Miocene, Sedan, Java, Indonesia.

*S. dentifera* (MARTIN, 1895), Upper Miocene, Tji-Odeng, Java, Indonesia.

*S. chinensis* (MACNEIL, 1960), Pliocene, Okinawa and Recent, Southwest Japan

*Euthria teschi* stock: Three species are known to belong to this stock. They are *E. djocdjocartae* MARTIN, *E. teschi* (BEETS) and *E. overmanae* (BEETS).

On *E. djocdjocartae* the spiral sculpture consists of the subsutural thread (P1), a thread on the peripheral angulation (P2) and a third one (P3) on the lateral surface. Profile of the whorl is sharply angulate at the lower one fifth of the whorl height. The surface between the distinct subsutural band and the peripheral angulation is steeply sloped and very slightly concavo-convex with an obsolete depression below the suture. The surface below the angulation is remarkably receded. Axial plicae are nine, eight and ten respectively on the first, second and third whorl. They are strong on and below the peripheral angulation but abruptly weakened above and do not reach to the upper suture. The peripheral angulation and axials persist on the early four whorls, but on the fifth whorl they disappear abruptly. Spirals on the later whorls are small in number, irregular in spacing and extremely weak.

*E. teschi* and *E. overmanae* are closely similar in the general morphology. Their spires are high, acute and rather straight-sided consisting of very slightly convex whorls. Whorls are provided with fine spiral threads. Growth-lines show shallow sinus. The most obvious difference between them is suggested by the axial sculpture. Morphology and developmental pattern of the axials on the early whorls of *E. teschi* are similar to those of *E. djocdjocartae*, but the axials disappear earlier in the former. *E. overmanae* has

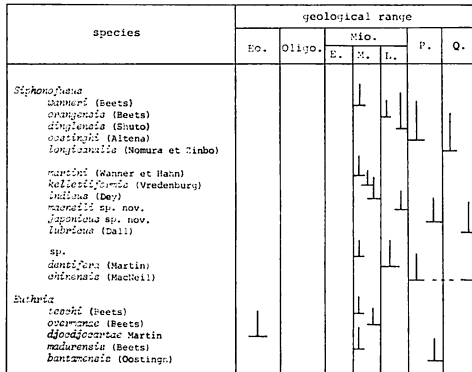


Fig. 5. Geological range of species of *Euthria* group and three lineages of *Siphonofusus* from Indo-West Pacific region. Horizontal and vertical lines in the columns respectively indicate the geological range and relative shell-size of each species.

only weak axials on the earliest whorl. In other words, the lineage of *E. djocdjocartae*, *E. teschi* and *E. overmanae* exhibits an evolutionary trend of earlier disappearance of axials in later species.

Diagnosis of *E. madurensis* is not clear because of poor preservation of the specimens, and its phylogenetic relation to any other species is not presumable. *E. bantamensis* is provided with coarse spiral threads on all the whorls and with rather distinct axials on early whorls so that it may be regarded as an intermediate form between *Buccinulum* and *Siphonofusus*.

### III. Biological aspect of *Euthria* and *Siphonofusus*

According to NORDSIECK (1968), *Euthria cornea* (LINNAEUS), the type-species of *Euthria*, dwells under stones of the rocky littoral zone or on the vegetated rocky bottom of nine to twenty-seven meters depth, while BARNARD (1959) noted that the living and dead shells of South African *Euthria* had been collected from the depth range of twenty-fifty fathoms. The latter

author did not refer to the substrate.

*Siphonofusus dinglensis*, Late Miocene species of the Philippines, is a minor element of the *Philindophos dijki* (MARTIN)-*Dendropoma javana* (MARTIN) association of muddy sand bottom of deeper shelf (SHUTO, 1969). *S. japonicus* from the Upper Pliocene of South Japan associates with *Anadara (Scapharca) castellata* (YOKOYAMA)-*Glycymeris rotunda* (DUNKER)-*Amussiopecten praesignis* (YOKOYAMA) association in the muddy sandstone, which was presumably deposited on the shallow shelf (SHUTO, 1962). MACNEIL (1960) mentioned that the Shinzato tuff member and Yonabaru clay member, from which *Siphonofusus chinensis* and *S. macneili* had been obtained, of the Shimajiri Group of Okinawa might have deposited respectively in bathyal depth of 200-400 fathoms and 150-300 fathoms. *S. chinensis* was dredged alive at the depth of fifty-nine fathoms in the Korean strait.

Concerning bathymetric range of the taxa in question, an idea may be acceptable that *Siphonofusus* is a dweller of sand or sandy silt bottom of the middle shelf and deeper zone in contrast to *Euthria*, at least a part of *Euthria*, which dwells on the rocky bottom of shallower depth under higher energy environment, although the data are not comprehensive. This is concordant with the fact that all the fossil species of Southeast Asian *Euthria*, *E. djocdjocartae*, *E. teschi*, *E. madurensis*, *E. overmanae* and *E. bantamensis*, lost their protoconchs and even the earliest part of the teleoconchs and are provided with a septum at the top of the preserved earliest whorl, although protoconchs of *Siphonofusus* species are generally preserved in more or less observable condition. These facts apparently suggest that *Euthria* and *Siphonofusus* differs from each other in their ecological adaptation.

Protoconch of *Siphonofusus* is paucispiral, consisting of about two (one and a half to two and one-third) smooth volutions. The nucleus is small, depressed and somewhat oblique, and the second volution is globose. The boundary between the protoconch and the teleoconch is indicated in most cases by abrupt appearance of the spiral and axial sculpture or a curved, oblique and smooth boundary riblet. *Euthria* has a quite similar protoconch to *Siphonofusus* judging from the figures (COSSMANN, 1901 and BARNARD, 1959). According to LO BIANCO (1899), the egg mass of *Euthria cornea* consists about forty semitransparent egg-capsules of eight-nine millimeters long and four millimeters wide, which contain respectively twenty-four ova on an average. This feature is comparable to the eggs of *Babylonia* and comparison leads to the supposition that ova of *E. cornea* must be large with a diameter of about 0.5 mm or more, although he did not state the size of ova. In other words, *Euthria cornea* must be a species of lecithotrophic larval type and is potentially a species of quick evolution and limited geographical distribution. Situation must be similar for other species of *Euthria* and also *Siphonofusus* and *Buccinulum*. This supposition is endorsed by the fact that many closely allied species have been differentiated in a single biogeographic province.

#### IV. Species reference list

- Siphonofusus wanneri* (BEETS)  
*Siphonalia martini* WANNER et HAHN [pars], 1935, *Zeitschr. Deut. Geol. Gesel.*, 87, (4), p. 222, 234, pl. 18, fs. 14 and 15 [excl. fs. 16-20].  
*Buccinulum wanneri* BEETS, 1942, *Leid. Geol. Meded.*, 13, (1), p. 228, pl. 24, f. 4.
- Siphonofusus orangensis* (BEETS)  
*Buccinulum orangense* BEETS, 1942, *Leid. Geol. Meded.*, 13, (1), p. 225-226, pl. 24, fs. 10-13.
- Siphonofusus dinglensis* (SHUTO)  
*Buccinulum (Euthria) dinglense* SHUTO, 1969, *Mem. Fac. Sci., Kyushu Univ.*, Ser. D. Geol. 19, (1), p. 122-124, pl. 9, fs. 19, 22-24.
- Siphonofusus oostinghi* (ALTENA)  
*Buccinulum oostinghi* ALTENA, 1950, *Leid. Geol. Meded.*, 15, p. 231, f. 19.
- Siphonofusus longicanalis* (NOMURA et ZINBO)  
*Siphonalia longicanalis* NOMURA et ZINBO, 1934, *Sci. Rep. Tohoku Imp. Univ.*, 2nd Ser. Geol. 16, (2), p. 159, pl. 5, f. 26.
- Siphonofusus martini* (WANNER et HAHN)  
*Siphonalia martini* WANNER et HAHN [pars], 1935, *Zeitschr. Deut. Geol. Gesel.* 87, (4), p. 222, 234, pl. 18, fs. 16-20 [excl. fs. 14-15].  
*Buccinulum martini* BEETS, 1942, *Leid. Geol. Meded.*, 13, (1), p. 222-225, pl. 24, fs. 1-3 (and 5-6?).
- Siphonofusus kelleiiformis* (VREDENBURG)  
*Siphonalia (Kelletia) kelleiiformis* VREDENBURG, 1924, *Rec. Geol. Surv. India*, 55, (1), p. 66-67, pl. 2, f. 11.
- Siphonofusus indicus* (DEY)  
*Siphonalia (Kelletia) indica* DEY, 1962, *Palaeont. Indica*, N. S., 36, p. 76, pl. 4, fs. 6-8.
- Siphonofusus macneili* sp. nov.  
*Afer* aff. *A. oostinghi* MACNEIL, 1960, *Prof. Pap. U. S. Geol. Surv.*, (339), p. 76, pl. 3, fs. 24, 25, 27, 28 and 33.
- Siphonofusus japonicus* sp. nov.  
*Siphonalia spadicea fuscolineata*: SHUTO, 1962, *Mem. Fac. Sci., Kyushu Univ.*, Ser. D. Geol. 12, (1), p. 36, pl. 7, fs. 5 and 9.
- Siphonofusus lubricus* (DALL)  
*Siphonalia lubrica* DALL, 1918, *Proc. U. S. Nat. Mus.* 54, (2134), p. 230.
- Siphonofusus lubricus*: KURODA et HABA, 1954, *Venus*, 18, (2), p. 95-97, fs. 16 and 20.
- Siphonofusus* sp.  
 2 specimens, Reg. No. Ge M. 556 with name "*Buccinulum sedanense* BEETS" MS, Museum Geol. Inst., Univ. Amsterdam
- Siphonofusus dentifera* (MARTIN)  
*Siphonalia dentifera* MARTIN, 1895, *Samml. Geol. Reichsmus. Leiden*, N. F., 1, (1), p. 96, pl. 15, fs. 215-217.
- Siphonofusus chinensis* (MACNEIL)  
*Afer chinensis* MACNEIL, 1960, *Prof. Pap. U. S. Geol. Surv.*, (339), p. 76, pl. 8, f. 19 and ? pl. 15, fs. 23-24.

*Euthria djocdjocartae* MARTIN

*Euthria jogjacartensis* MARTIN, 1914, *Samml. Geol. Reichsmus. Leiden*, N. F., 2, (4), p. 142, pl. 3, fs. 85, 85a, b and c.

*Pusio djocdjocartae* MARTIN, 1883-87, *Samml. Geol. Reichsmus. Leiden*, 3, p. 104, pl. 6, f. 105.

*Euthria teschi* (BEETS)

*Buccinulum teschi* BEETS, 1944, *Geol. Mijnb. N.S.* 6, p. 14-16, fs. 1-6.

*Euthria madurensis* (BEETS)

*Buccinulum madurensis* BEETS, 1944, *Geol. Mijnb.*, N. S. 6, p. 16, fs. 7 and 8.

*Euthria overmanae* (BEETS)

*Buccinulum overmanae* BEETS, 1942, *Leid. Geol. Meded.*, 13, (1), p. 226-227, pl. 24, fs. 7-9.

*Euthria bantamensis* OOSTINGH

*Euthria bantamensis* OOSTINGH, 1939, *Ingen. Ned. -Indië*, (8), p. 116, pl. 14, fs. 242a and b.

## V. Description of species

*Siphonofusus macneili* sp. nov.

*Afer* aff. *A. oostinghi*: MACNEIL, 1960, Prof. Pap. U.S. Geol. Surv., (329), p. 76, pl. 3, fs. 24, 25, 27, 28 and 33.

*Type-specimens*: holotype, USNM 562702 (pl. 3, f. 33) from loc. 17449, Kakazu, about 900 m south of Madama-bridge, Naha, Okinawa; paratypes, USNM 562700 (pl. 3, fs. 24 and 25) and USNM 562701 (pl. 3, fs. 27 and 28) from loc. 17451, north of Iwa, Kochinda, Okinawa, Japan. The holotype is an adult specimen and the paratypes are juvenile.

*Description*: Shell broadly fusiform and moderately small, attaining about 35 mm in height in the adult stage. Protoconch large and paucispiral, consisting of depressed first volution and broadly convex second one. Teleoconch whorls about seven, being bluntly angulated at the periphery, which is slightly anterior to the middle of the whorl. Axials prominent, from suture to suture and slightly oblique to the axis of coiling in the young

stage, but weakened above the peripheral angulation and becoming more vertical in the adolescent and later stages. Spiral threads close and moderately weak. Aperture rhomboidal in shape with distinct posterior notch and long, narrow and straight canal. Labrum teeth, parietal ridge and columellar plait distinct.

*Comparison*: The present species shows diagnostic characteristics of *Siphonofusus*. MACNEIL compared the above noted specimens with *Siphonofusus oostinghi* (ALTENA), but the former is readily distinguished from the latter in its one-half smaller size, abruptly narrowed entrance of the canal, sharper peripheral nodules and weaker spiral threads. Furthermore, axials of *S. macneili* are weakened in definitely earlier stage than *S. oostinghi*.

*S. macneili* is similar to *S. japonicus* sp. nov. from the Pliocene of south Kyushu, Japan. The former is, however, distinguishable from the latter in having a more contracted base, shorter aperture and 7-8 degrees wider apical angle than the latter.

*Horizon*: Upper Miocene Yonobaru Clay Member of the Shimajiri Group.

*Siphonofusus japonicus* sp. nov.

*Siphonalia spadicea fuscolineata*: SHUTO, 1962, Mem. Fac. Sci., Kyushu Univ., Ser. D, Geol., 12, (1), p. 36, pl. 7, fs. 5 and 9.

*Type-specimen*: holotype, GK-L 4891 (pl. 7, fs. 5 and 9) from loc. MI 6351, Hagenoshita, Takanabe-cho, Koyu-gun, Miyazaki Prefecture, Japan. Depository, Department of Geology, Kyushu University.

*Description*: Shell moderately small and broadly fusiform. Protoconch not observed. Teleoconch whorls more than seven, moderately angulate at the median periphery and slightly concave below the suture. Axials prominent from suture to suture in the young and weakened in the later



stage except on the periphery. Spirals close and moderately weak. Aperture elongately rhomboidal in shape, with oblique anterior canal and distinct and small posterior notch. Blunt columellar plait and sharp parietal ridge defining the entrance of anterior canal and posterior notch, respectively. Growth-lines sinuous and converging opisthocyrtly with upper suture by an angle of 45-50 degrees.

*Comparison:* Although the present species is close to the preceding one, it is clearly separated from the latter as mentioned above. Comparing with *S. kelleiiformis* (VREDENBURG), *S. japonicus* has a less contracted base, weaker axials, more sharply narrowed entrance of the canal and more deeply sinuous growth-lines. *S. indicus* (DEY) has distinctly stronger axials and more oblique canal than the present species. *S. lubricus* (DALL) has a longer canal, weaker parietal ridge, and more defined infrasutural depression than *S. japonicus*.

*Horizon:* Lower part of the Takanabe Member of the Miyazaki Group. Pliocene.

*Siphonofusus* sp.

*Specimen:* Ge M. 556, Museum Geol. Inst., Univ. Amsterdam.

*Locality:* Environs of Sedan, Java, Indonesia.

*Description:* Shell thick, fusiform and moderately small (32.4 mm in height). Whorls angulated at the periphery and concave below suture. Peripheral angulation blunt on early whorls and sharper on later whorls. Sutures clusping. Axial plicae 7-8 for a whorl, wider than interspaces, reaching to the lower suture and weakened above the angulation. Spirals weak, dense and equidimensional above the peripheral angulation and distinct and alternate below it. Body whorl large, about three-fourths of the total height of

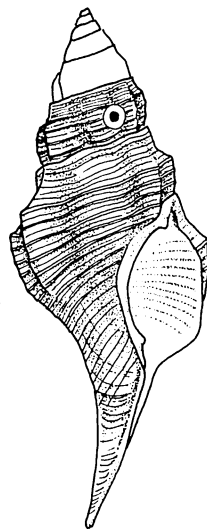


Fig. 6. *Siphonofusus* sp.

Museum Geol. Inst., Univ. Amsterdam, Reg. No. Ge M556 (labeled a2 *Buccinulum sedanensis*).

the shell, sharply angulate peripherally, contracted at the base to the very long, obliquely bent and tapered snout. Lateral surface below the peripheral angulation provided with 10 sets of distinct and slightly weaker threads. Aperture rhomboidal in shape with sharp posterior notch bordered by a parietal ridge at the entrance and with long and narrow canal anteriorly. Labrum sharp with thread-like teeth inside. Inner lip arcuate, covered with distinct but narrow callus. Columellar plait sharp at the lower part of the inner lip.

*Comparison:* The present species is characterized by its long, oblique and tapering canal, sharp peripheral angulation, pronounced infrasutural depression and prominent plicae. In this sense, it resembles *S. chinensis* (MACNEIL), but the former is readily distinguished from the latter in having much stouter plicae and more depressed shoulder slope. The present species differs from *S. dentifera*

(MARTIN), which has a distinct basal angulation.

*Horizon*: Rembangian (Lower Middle Miocene).

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*Buccinulum*, *Euthria* および *Siphonofusus* の分類上の関係を再検討し、それらが同一属の亜属を代表すること、始新世から知られる *Euthria* から *Buccinulum* が中新世初期に、*Siphonofusus* が中新世中期に派生したことを明らかにした。インド太平洋区の特徴的な要素である *Siphonofusus* は3つの種系列に分かれ、各系列では殻の大形化と縦彫刻の弱化という形態系列が認められる。

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首藤次男

- 第 1 条 本会は日本古生物学会という。
- 第 2 条 本会は古生物学およびこれに関係ある諸学科の進歩および普及を計るのを目的とする。
- 第 3 条 本会は第 2 条の目的を達するため次の事業を行なう。  
1. 会誌そのほかの出版物の発行。2. 学術講演会の開催。3. 普及のための採集会・講演会そのほかの開催。4. 研究の援助・奨励および研究業績ならびに会務に対する功勞の表彰その他第 2 条の目的達成に資すること。
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