THE ONTOGENY OF *THERIOSYNOECUM FITTONI* (MANTELL)

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ABSTRACT. The carapaces of *Theriosynoecum fittoni* (Mantell) from the uppermost Weald Clay (Lower Cretaceous) of four English localities have been measured. Nine growth stages were recognized and the shape and ornament of each stage recorded. Though change in shape is considerable, the tubercles are generally constant in number and relative position throughout development. A lectotype for the species is designated, figured, and described.

SAMPLES of Weald Clay from the Cuckmere Brick Pit, near Berwick, Sussex, at a horizon 15 feet below the base of the Atherfield Clay have been examined independently by both writers, whose results have been combined in this account. In addition the second writer measured specimens of *T. fittoni* occurring in the upper part of the Weald Clay from three boreholes, i.e. at Warlingham, Surrey; St. Margaret's Bay and Oxney, Kent.

These studies have made it possible to trace the ontogenetic development of *T. fittoni* from an instar, probably the first hatched, through eight other stages, of which the last was the adult and the first to show any marked sexual dimorphism.

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Genus THERIOSYNOECUM Branson 1936

Morrisonia Branson 1935 (*non* Grote 1874), p. 521.
Theriosynoecum Branson 1936, p. 323 (new name for *Morrisonia* Branson 1935).

Type species (*monotypic*). *Morrisonia wyomingensis* Branson 1935, p. 521, pl. 57, figs. 17–21. Morrison formation, Wyoming.

The reason why *Theriosynoecum* has had only one species for so many years is that the generic characters as originally defined were identical with the characters of the type species *T. wyomingense* (Branson). The orientation of Branson's original illustration (1935, p. 57, fig. 17) should be transposed left to right. It is of a right valve and not a left valve as indicated by Branson (1935, p. 520). Correct orientation shows the species to be bisulcate in the anterior half. Topotypes (USNM 75502) are dimorphic in width of posterior. Both dimorphs have nodes and ridges. Branson described the hinge of the genus (1935, p. 521), and of the type species (1935, p. 522) as 'Hinge straight, short, a ridge on the right valve fitting into a groove in the left valve in the central part of the hinge'. The blade-like teeth were not mentioned.

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Single valves of *T. wyomingense* from the Morrison formation of the Black Hills of South Dakota and Wyoming (USGS localities 26897, 26910, 26916, 26921, 26922) have hinges with terminal dentition that are illustrated in text-fig. 1*g* and *j*. The muscle scars of this genus were not discussed by Branson, but the single valves mentioned above have a vertical row of four scars located below the median sulcus similar to those illustrated here on Plate 15, figs. 18, 20, 25.

Our present studies suggest that Mandelstam (1956, p. 138) was probably correct in considering the bisulcate Mesozoic species hitherto assigned to *Metacypris* and *Gomphocythere* as belonging to *Theriosynoecum* Branson. This matter has also been discussed by Grekoff (1958).

Theriosynoecum fittoni (Mantell)

Plate 15, figs. 1–35; text-figs. 1*a–f*, *h*, *i*; 3, 4

1836 *Cypris tuberculata* J. de C. Sowerby (part), *in* Fitton, p. 345, pl. 21, fig. 2*a* (*non* 2*b*, *c*; 2*c* is *Cypridea tuberculata*).
1844 *Cypris fittoni* Mantell, p. 545, pl. 119, fig. 2.
1878 *Cypridea? fittoni* (Mantell); Jones, p. 277.
1885 *Cythere fittoni* (Mantell); Jones, p. 333.
1888 *Metacypris fittoni* (Mantell); Jones, *in* Prestwich, p. 263, fig. 137*a*.
1940 *Gomphocythere berwickensis* Martin, p. 344, pl. 12, figs. 176–81, text-figs. 1, 2; p. 340, pl. 6, figs. 95–97; pl. 7, figs. 98–100.
1957 *Gomphocythere fittoni* (Mantell); Wicher, p. 270, pl. 2, figs. 4*a–c*, 5*a–c*.
1958 '*Metacypris*' *fittoni* (Mantell); Grekoff, p. 26, pl. 2, fig. 19.
1961 *Theriosynoecum berwickense* (Martin); Branson, p. 247.

Lectotype. GSM Mik(M) 1905001 (*ex* Geological Society of London Collection, No. 2479). A complete carapace, adult female.

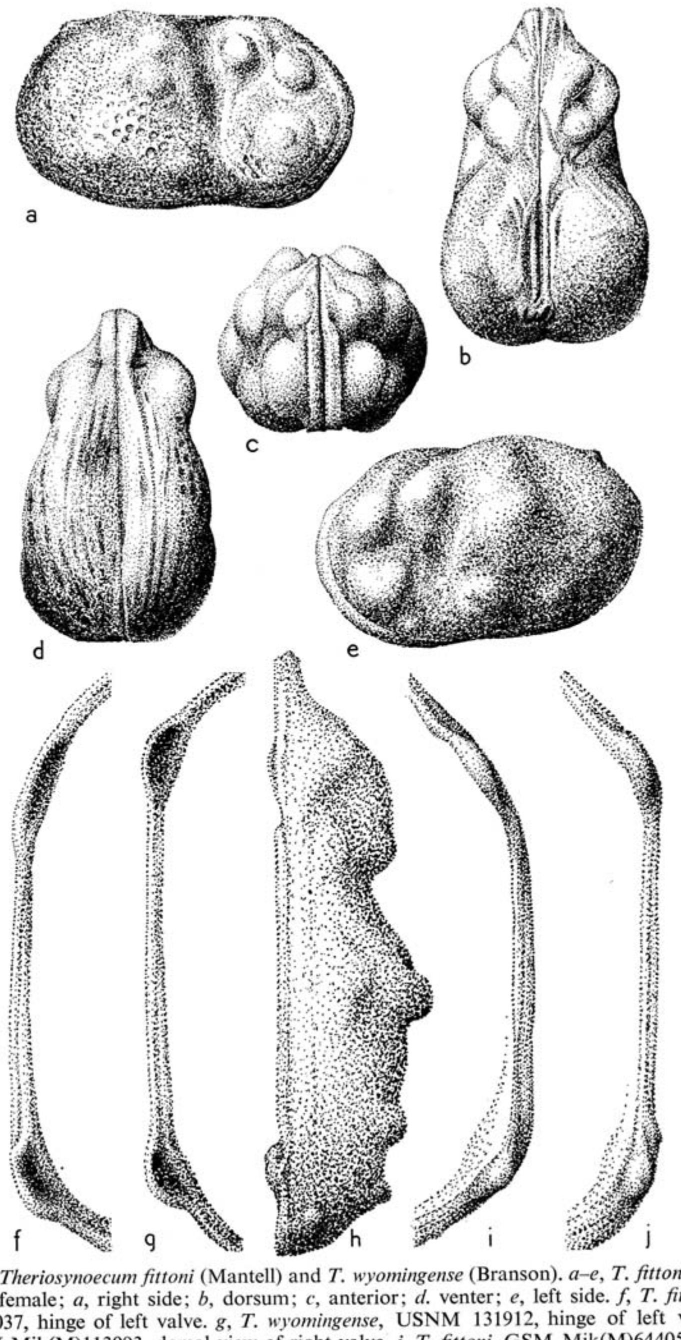
Dimensions. Length 0·950 mm., height 0·580 mm., width 0·575 mm.

Locality. Punfield Cove, Swanage Bay, Dorset.

Horizon. Uppermost Wealden, i.e. Wealden Shales, 34 ft. 6 in. thick.

Diagnosis. In lateral view an oblong carapace with anterior and posterior margins evenly rounded, but with marked antero- and postero-dorsal angles. Adductor muscle scar anterior to centre of valve and a little below the middle line, consisting of a vertical row of four longitudinally elongate scars. Two vertical, slightly sinuous sulci in anterior dorsal quadrant, one running from the muscle-scar to the dorsal margin and the other, shorter and shallower, anterior to this.

Description. The hinge in the lectotype is not visible, but in other specimens the articulation in the right valve consists of an anterior flange-like tooth and a posterior, more conspicuous, peg-like tooth. These are connected by the thickened shell margin, which is slightly excavated on the inner side. In the left valve are sockets to correspond, joined by a narrow, rounded bar. End margins with simple, widely spaced radial pore canals. The outer surface is rather coarsely punctate. The ornament consists of large blunt tubercles or rounded bosses. Sexual dimorphism well marked. In both sexes the carapace is wider behind the centre, but in the female the posterior is much more swollen than in the male. In the adult male there are usually four swellings or tubercles anterior to the



TEXT-FIG. 1. *Theriosynoecum fittoni* (Mantell) and *T. wyomingense* (Branson). *a–e*, *T. fittoni*, lectotype ×50, adult female; *a*, right side; *b*, dorsum; *c*, anterior; *d*. venter; *e*, left side. *f*, *T. fittoni*, GSM Mik(M)644037, hinge of left valve. *g*, *T. wyomingense*, USNM 131912, hinge of left valve. *h*, *T. fittoni*, GSM Mik(M)113093, dorsal view of right valve. *i*, *T. fittoni*, GSM Mik(M)644059, hinge of right valve. *j*, *T. wyomingense*, USNM 131913, hinge of right valve.

adductor muscle scar and six posterior to it, with sometimes additional minute auxiliary tubercles near the anterior and posterior margins. In the adult female the ornament is reduced, especially in the posterior half, where the tubercles are sometimes barely detectable. In juveniles, except for the earliest instars, all ten tubercles are present.

Discussion. This species was first described by J. de C. Sowerby, together with another quite different form, as *Cypris tuberculata*. In his fig. 2, three forms were illustrated. That in fig. 2*a* is recognizable as the one later named *Cypris fittoni* by Mantell; fig. 2*b* is not recognizable, whilst fig. 2*c* remains as *Cypridea tuberculata*.

Sowerby stated that the specimen illustrated as fig. 2*a* came from Swanage. The type material consists of a small fragment of rock covered with numerous examples of the species *Theriosynoecum fittoni*. It is impossible to identify the specimen actually figured by Sowerby, and a lectotype has therefore been selected from this material.

The allocation of the species *fittoni* to the Recent genus *Metacypris* by T. R. Jones (1888) has caused much discussion in recent years. Martin (1940), working with immature moults from the Weald Clay of Berwick, Sussex, renamed the species *berwickensis*, referring it to the Recent genus *Gomphocythere* Sars, 1924. Wicher (1957) relegated *berwickensis* to a subspecies of *fittoni* in *Gomphocythere*. In 1958 Grekoff made a critical study of the systematic problems involved and came to the conclusion that *fittoni* could not be satisfactorily assigned to either *Metacypris* or to *Gomphocythere* and proposed using these names only in parentheses or alternatively, following Russian workers (Lubimova 1956), in allocating *fittoni* and related species to the genus *Theriosynoecum*. The hingement in *Theriosynoecum* is not very different from that of *Metacypris* but clearly differs from that of *Gomphocythere*. In the type of *Metacypris cordata* Brady and Robertson (BMNH 1900.3.6.171) the two valves are firmly closed, and the hinge cannot be seen.

The species to be considered are the Wealden *fittoni* and the Purbeck *forbesi* allocated by Jones to *Metacypris*, and the two Purbeck species *striata* and *silvana* allocated by Martin to *Gomphocythere*. These four are similar in hinge structure and adductor muscle scars, and if Grekoff is correct in his interpretation of the hinge in *Gomphocythere*, none of them can be allocated to that genus. On the other hand Grekoff's illustrations of the hinge in *Metacypris cordata* (1958, pl. 2, fig. 18*a–d*) differ from those of the original authors, Brady and Robertson (reproduced by Grekoff 1958, pl. 1, figs. 3–6), who showed a hinge closer to that of *fittoni*. Thus, at present, the distinction between *Theriosynoecum* and *Metacypris* is not clear and the writers are uncertain as to the correct generic assignment of these apparently related species from the Purbeck beds, i.e. *M. forbesi* Jones 1885, *Gomphocythere striata* Martin 1940, and *G. silvana* Martin 1940.

GROWTH STAGES IN *THERIOSYNOECUM FITTONI*

The fact that living ostracods pass through a series of moult stages during their life history has been known for many years, and the dimensions of the successive instars of a number of species have been published.

Since Jones recognized juvenile forms in 1849 most authors writing on ostracods have from time to time referred to immature individuals. The fact that earlier instars may be very different in appearance from the adult, and the difficulty of recognizing as the same species carapaces which differ in size, shape, ornament, and hinge-structure, has always proved an embarrassment to the systematist.

Though it is obvious that an ostracod species is incompletely known until all its growth stages have been described, little attention has been paid to this until comparatively recently. In 1945 Le Roy studied the development of *Cythereis simensis* (Le Roy) and *C. holmani* Le Roy, and in the same year Cooper described the developmental stages of *Ectodemites plummeri* Cooper. Since then a number of such studies have been published, and are critically examined in the immediately following paper by Anderson (1964). Nevertheless there remain a number of questions which have not yet been unequivocally answered, namely, whether it is possible to recognize individual instars by size alone; the number of moults required to reach maturity; the number of instars present in any one species, and whether this number is constant for the species; whether or not there are post-maturation moults; and what is the law of growth in the Ostracoda.

Material. For this study of the growth stages in *Theriosynoecum fittoni* samples of ostracod-bearing shale were taken from strata of approximately the same age, i.e. a horizon high in the Weald Clay (Lower Cretaceous) from four widely separated localities, Berwick (Sussex), St. Margaret's Bay and the Oxney boreholes (Kent), and the Warlingham Borehole (Surrey). In each case the ostracod fauna consisted almost entirely of the one species and in no case was any other species of the genus present. It was therefore a reasonable presumption that all the juveniles found were those of *T. fittoni*. Four different localities were selected in order to discover if the growth-rate was constant for the species. In every case early instars were deliberately sought, so that the numbers recorded for each instar do not bear any relation to the natural distribution of individuals in the instars.

1. *The Warlingham assemblage*. Horizon: 1,076 feet, i.e. 29 feet below the base of the Atherfield Clay at 1,047 feet. The length and height of 382 carapaces and separated valves were measured. Since the two valves differ very little in size they were not recorded separately. In text-fig. 2 length is plotted against height. The approximate position of the mean in each instar is apparent whenever a reasonable number of individuals has been measured. It is equally clear that the amount of growth between moults increases with age. Nine growth stages appear to be represented. They range in size from a mean

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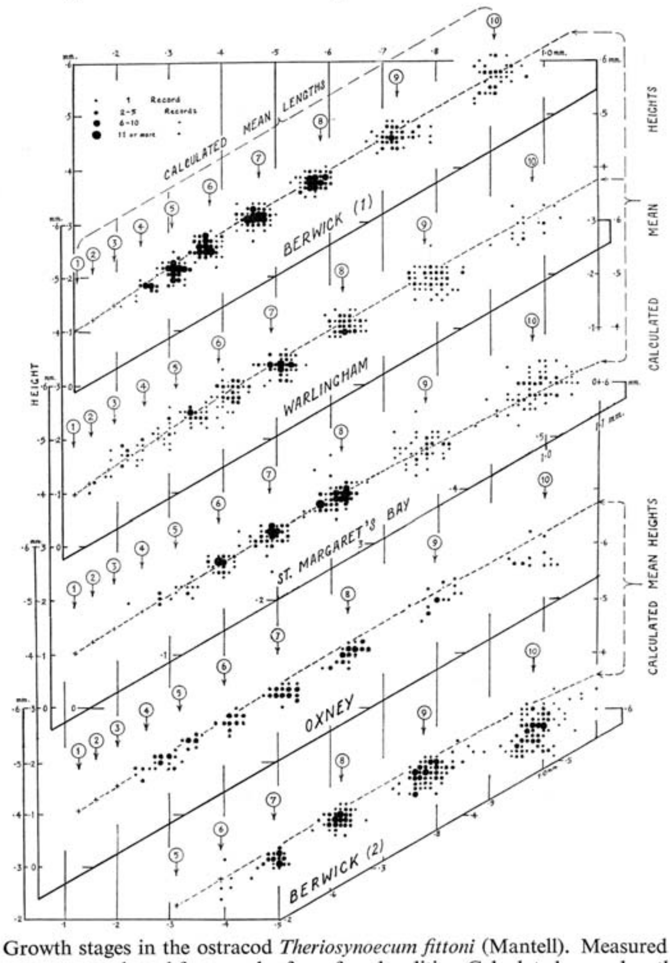
EXPLANATION OF PLATE 15

Theriosynoecum fittoni (Mantell). Magnification approximately ×30.

Figs. 1, 2. Inside and outside of left valve, USNM 131231. 3, 4, Dorsal and outside of left valve, USNM 131232. 5, 6, Dorsal and outside of right valve, USNM 131233. 7, 8, Dorsal and outside of right valve, USNM 131234. 9, 10, Dorsal and outside of right valve, USNM 131235. 11–13, Dorsal, outside and posterior of left valve, USNM 131236. 14, 15, Outside and dorsal of right valve, USNM 131237. 16, Left valve, paratype, Senck.-Mus. No. X/E 2053. 17–19, Dorsal, inside and outside of right valve, male, USNM 131238. 20, Inside of left valve, female, USNM 131239; the spot anterior to vertical row of muscle scars is matrix. 22–23, Dorsal, outside and posterior of left valve, female, USNM 131240. 24–27, Dorsal, interior, posterior and outside of right valve, female, USNM 131241. 28–31, Posterior, dorsal, inside and outside of left valve, male, USNM 131242. 32, Right view of carapace, male; paratype, Senck.-Mus. No. X/E 2504. 33–34, Dorsal and right views of carapace, female; paratype, Senck.-Mus. No. X/E 2055. 35, Left valve, male, node 5 missing, USNM 131243.

length of 0·158 mm. and height of 0·115 mm. to mature individuals of average length 0·961 mm. and height 0·585 mm.

2. *The Berwick assemblage*. Horizon: 15 feet below the base of the Atherfield Clay. From this fauna 918 complete carapaces and single valves were measured. In this case only eight growth stages were identified, the last being the mature adult, which averages 0·904 mm. in length and 0·568 mm. in height in Anderson's material and 0·986 mm.



TEXT-FIG. 2. Growth stages in the ostracod *Theriosynoecum fittoni* (Mantell). Measured lengths and heights of carapaces are plotted for samples from four localities. Calculated mean lengths (see immediately following paper by Anderson 1964) are indicated by an arrow for each growth stage and heights by means of a broken line. Growth-stage numbers are shown within a circle. Too few well-preserved specimens of early instars were found to compensate for the pressure effect on these very delicate shells. This diagram illustrates clearly the difficulty of determining mean dimensions in early instars.

long and 0·561 mm. high in Sohn's. Sohn's material, probably collected from a different level, gives results that differ slightly from those Anderson obtained from Berwick, but coincide almost exactly with those from Warlingham. Anderson's measurements are plotted on text-fig. 2 as 'Berwick (1)' and those by Sohn are shown as 'Berwick (2)'.

3. *The St. Margaret's Bay assemblage*. Horizon: 6 inches below the base of the Atherfield Clay. The 400 specimens measured from St. Margaret's Bay also show that here the growth rate is greater than in Berwick (1), leading to an average size for the mature carapace of 0·980 mm. in length and 0·590 mm. in height. Here only seven instars were recognized, the earliest of which is growth stage 4.

4. *The Oxney assemblage*. Horizon: 8 inches below the base of the Atherfield Clay. The 199 individuals from this locality again represent seven growth stages.

Morphological changes during development

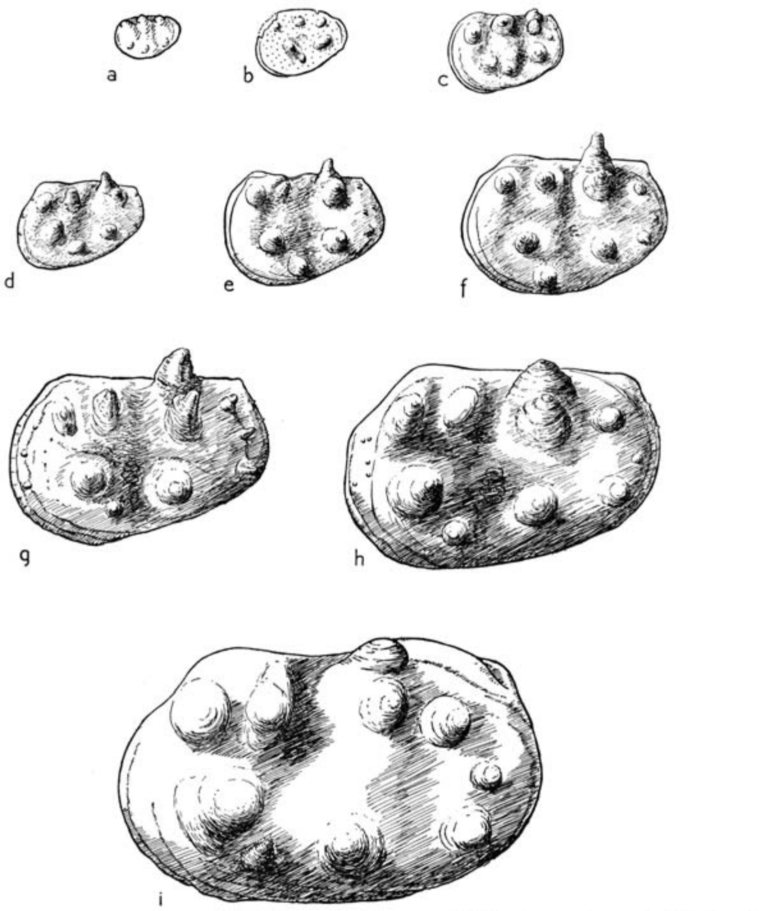
(i) The earliest instar seen; according to the system of notation used by Anderson (1964), this is recorded as *growth stage 2*. Only four examples of this stage have been seen, all from Warlingham. Three of them are thin-shelled and partly damaged, 0·160 mm. long and 0·120 mm. high, and one, apparently uncrushed, is 0·150 mm. long and 0·100 mm. high (text-fig. 3*a*). The mean of these measurements is 0·158 mm. and 0·115 mm. The dimensions, calculated by the method described in the immediately following paper by Anderson, could be expected to be 0·158 mm. and 0·126 mm. No examples of a comparable instar were recovered from any of the other localities.

The shell is extremely thin. It is oval in outline with its greatest height well anterior to the centre (text-fig. 3*a*). The dorsal margin is almost straight, anterior and posterior margins smoothly rounded and joining it without the characteristic angles seen in most of the later instars. Anteriorly and posteriorly the shell bears a narrow marginal flange. The radial pore canals are plainly visible and evenly distributed, but are relatively widely spaced. Tubercles are only faintly indicated as low rounded bosses. Six primary tubercles appear to be present, the lumbar pair (text-fig. 4, *Fa*, *Fb*) being represented by a single tubercle, whilst the posterior tubercles (text-fig. 4*g*, *h*, *i*) are missing. The length of shell anterior to the rudimentary sulcus is 1·80 times that behind. If an earlier instar ever existed it would probably have been 0·126 mm. long and 0·103 mm. high, and may have been without tubercles.

(ii) *Growth stage 3*. Sixteen examples of this stage were recovered, fifteen from Warlingham, averaging 0·207 mm. in length and 0·164 mm. in height; and one from Berwick, 0·215 mm. in length and 0·150 mm. in height. In outline the shell is similar to that of the previous instar but a little less ovate. Six tubercles are still present (text-fig. 3*b*). The ratio between anterior and posterior portions of the shell is now 1·75. The sulcae are not yet evident.

(iii) *Growth stage 4* (text-fig. 3*c*). Thirty-six examples were measured: 11 from Warlingham, with average length 0·248 mm. and height 0·182 mm.; 14 from St. Margaret's Bay, average length 0·276 mm., height 0·201 mm.; 5 from Berwick, average length 0·246 mm., height 0·182 mm.; and 6 from Oxney, average length 0·244 mm., height 0·188 mm. The anterior–posterior length ratio is 1·66.

With this instar there is marked change of shape. The carapace has now developed an evident postero-dorsal angle and is more oblong than ovate. The tubercles are now clearly seen and all six primaries are present, with the addition of several minute



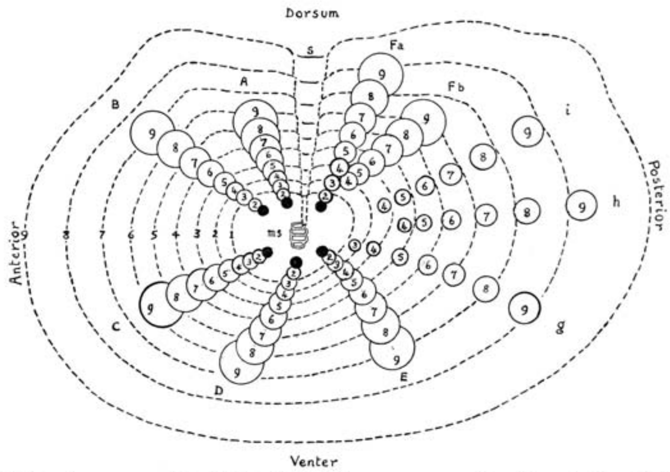
TEXT-FIG. 3. *Theriosynoecum fittoni* (Mantell). Growth stages, all left valves. *Camera lucida* drawings. *a*, Growth stage 2. Length 0·150 mm. Warlingham borehole. GSM Mik(M)637060. *b*, Growth stage 3. Length 0·215 mm. Berwick. GSM Mik(M)386067. *c*, Growth stage 4. Length 0·260 mm. Berwick. GSM Mik(M)388064. *d*, Growth stage 5. Length 0·315 mm. Berwick. GSM Mik(M)388042. *e*, Growth stage 6. Length 0·370 mm. Berwick. GSM Mik(M)338062. *f*, Growth stage 7. Length 0·450 mm. Berwick. GSM Mik(M)388040. *g*, Growth stage 8. Length 0·585 mm. Berwick. GSM Mik(M)387082. *h*, Growth stage 9. Length 0·720 mm. Berwick. GSM Mik(M)385100. *i*, Growth stage 10. Length 0·920 mm., male. Berwick. GSM Mik(M)385012.

posterior tubercles. The lumbar (*F*) is now divided into two divergent tubercles with a common base (*Fa*, *Fb*). The radial pore canals are distinct, relatively large, and more closely set than before, and the shell surface is now very finely punctate.

(iv) *Growth stage 5* (text-fig. 3*d*). Two hundred and thirty-four examples were measured: 40 from Warlingham, with average length 0·314 mm., height 0·235 mm.;

12 from St. Margaret's Bay, average length 0·310 mm., height 0·215 mm.; 131 from Berwick, average length 0·303 mm., height 0·213 mm.; and 51 from Oxney, average length 0·318 mm., height 0·225 mm. The anterior–posterior length ratio is 1·56. All six primary tubercles are present and are conical rather than dome-shaped. The lumbar tubercles are clearly seen to be a closely set pair confluent at the base and with vertical axes diverging at about 45°. Three or more secondary tubercles are again present posterior to the lumbar-furcal line, and there may be three or four minute tubercles on the anterior flange.

(v) *Growth stage 6* (Pl. 15, figs. 1, 2; text-fig. 3*e*). Two hundred and thirty-three examples were measured, 68 from Warlingham, average length 0·405 mm., height 0·273 mm.; 46 from St. Margaret's Bay, average length 0·397 mm., height 0·269 mm.; 98 from Berwick, average length 0·373 mm., height 0·259 mm. (Anderson), 0·400 mm. and 0·270 mm. (Sohn); and 21 from Oxney, average length 0·412 mm., height 0·275 mm. The anterior–posterior length ratio is 1·44. The tubercles are relatively larger and more spinose, the lumbar pair (text-fig. 4, *Fa*, *Fb*) being especially large and sharp.



TEXT-FIG. 4. *Theriosynoecum fittoni* (Mantell). Diagram representing the exterior of a left valve and showing the positions of the nodes at each growth stage. The six primary nodes are shown in solid black and their position in each subsequent growth stage by circles enclosing the growth stage number. Carapace outlines are shown by the broken lines.

(vi) *Growth stage 7* (Pl. 15, fig. 16; text-fig. 3*f*). Three hundred and eighty-four examples were measured, 92 from Warlingham, average length 0·509 mm., height 0·337 mm.; 83 from St. Margaret's Bay, average length 0·490 mm., height 0·323 mm.; 166 from Berwick, average length 0·465 mm., height 0·314 mm. (Anderson), 0·494 mm. and 0·318 mm. (Sohn); and 43 from Oxney, average length 0·513 mm., height 0·325 mm. The anterior–posterior length ratio is 1·32. The outline of the carapace is a little more oblong than in the previous instar as a result of the more rapid growth of the posterior half of the shell. The anterior sulcus is now less clearly defined than the median. All the

TABLE 1. Number of specimens measured in each growth-stage with their measured and calculated mean lengths and heights

Growth stage	Warlingham Borehole K_L 0·099, K_H 0·086					Berwick (1) K_L 0·096, K_H 0·083					Berwick (2) K_L 0·099, K_H 0·086				
	Measured means (mm.)			*Calculated means (mm.)*		*Measured means (mm.)*			*Calculated means (mm.)*		*Measured means (mm.)*			*Calculated means (mm.)*	
	Length	*Height*	*No.*	*Length*	*Height*	*Length*	*Height*	*No.*	*Length*	*Height*	*Length*	*Height*	*No.*	*Length*	*Height*
0	—	—	—	0·100	0·085	—	—	—	0·100	0·085	—	—	—	0·100	0·085
1	—	—	—	0·126	0·103	—	—	—	0·125	0·103	—	—	—	0·126	0·103
2	0·158	0·115	4	0·158	0·126	—	—	—	0·156	0·124	—	—	—	0·158	0·126
3	0·207	0·164	15	0·198	0·154	0·215	0·150	1	0·194	0·150	—	—	—	0·198	0·154
4	0·248	0·182	11	0·249	0·187	0·246	0·182	5	0·242	0·182	—	—	—	0·249	0·187
5	0·314	0·235	40	0·313	0·228	0·303	0·213	131	0·302	0·220	—	—	—	0·313	0·228
6	0·405	0·273	68	0·393	0·278	0·373	0·259	93	0·377	0·267	0·400	0·270	5	0·393	0·278
7	0·509	0·337	92	0·493	0·339	0·465	0·314	126	0·470	0·323	0·494	0·318	40	0·493	0·339
8	0·630	0·409	68	0·620	0·413	0·580	0·381	111	0·586	0·391	0·618	0·444	74	0·620	0·413
9	0·793	0·500	64	0·778	0·504	0·730	0·470	67	0·731	0·473	0·783	0·480	103	0·778	0·504
10	0·961	0·585	20	0·977	0·614	0·904	0·568	42	0·912	0·573	0·986	0·561	120	0·977	0·614

Growth stage	St. Margaret's Bay Borehole K_L 0·099, K_H 0·086					Oxney Borehole K_L 0·100, K_H 0·087				
	Measured means (mm.)			*Calculated means (mm.)*		*Measured means (mm.)*			*Measured means (mm.)*	
	Length	*Height*	*No.*	*Length*	*Height*	*Length*	*Height*	*No.*	*Length*	*Height*
0	—	—	—	0·100	0·085	—	—	—	0·100	0·085
1	—	—	—	0·126	0·103	—	—	—	0·126	0·104
2	—	—	—	0·158	0·126	—	—	—	0·159	0·127
3	—	—	—	0·198	0·154	—	—	—	0·200	0·155
4	0·276	0·201	14	0·249	0·187	0·244	0·188	6	0·251	0·189
5	0·310	0·215	12	0·313	0·228	0·318	0·225	51	0·316	0·231
6	0·397	0·269	46	0·393	0·278	0·412	0·275	21	0·398	0·282
7	0·490	0·323	83	0·493	0·339	0·513	0·325	43	0·501	0·344
8	0·610	0·385	114	0·620	0·413	0·638	0·400	46	0·631	0·421
9	0·777	0·472	49	0·778	0·504	0·800	0·500	17	0·794	0·514
10	0·980	0·590	82	0·977	0·614	0·982	0·575	15	1·000	0·628

tubercles are spinose with large, spreading, swollen bases. The lumbar pair (text-fig. 4, *Fa, Fb*) are relatively larger and more conspicuous than the others. Three of the posterior tubercles become clearly defined, and presumably represent the tubercles *g, h*, and *i* (text-fig. 4). These three are constant in position and number in later growth stages.

(vii) *Growth stage 8* (Pl. 15, figs. 7–10, 16; text-fig. 3*g*). Four hundred and thirteen examples were measured, 68 from Warlingham, average length 0·630 mm., height 0·409 mm.;114 from St. Margaret's Bay, average length 0·610 mm., height 0·385 mm.; 185 from Berwick, average length 0·580 mm., height 0·381 mm. (Anderson), 0·618 mm. and 0·444 mm. (Sohn); and 46 from Oxney, average length 0·638 mm., height 0·400 mm. The anterior–posterior length ratio is 1·16. The shape of the carapace is similar to that in the previous instar, but the posterior half is relatively larger so that the adductor muscle scar is now almost on the vertical axis. All primary tubercles are well-developed and spinose, the lumbar pair being especially prominent.

(viii) *Growth stage 9*. Three hundred specimens of this, the pre-maturation instar, were measured, 64 from Warlingham, average length 0·793 mm., height 0·500 mm.; 49 from St. Margaret's Bay, average length 0·777 mm., height 0·472 mm.; 170 from Berwick, average length 0·730 mm., height 0·470 mm. (Anderson), 0·783 mm. and 0·480 mm. (Sohn); and 17 from Oxney, average length 0·800 mm., height 0·500 mm. The anterior–posterior length ratio is 0·98, i.e. the posterior half of the shell is now longer than the anterior half but is still not quite so high. The outline of the carapace is a little more oblong and the tubercles are less spinose, now bluntly conical.

(ix) *Mature adult* (*growth stage 10*) (Pl. 15, figs. 17–35; text-fig. 3*i*). Two hundred and seventy-nine examples were measured, 20 from Warlingham, average length 0·961 mm., height 0·585 mm.; 82 from St. Margaret's Bay, average length 0·980 mm., height 0·590 mm.; 162 from Berwick, average length 0·904 mm., height 0·568 mm. (Anderson), 0·986 mm. and 0·561 mm. (Sohn); 15 from Oxney, average length 0·982 mm., height 0·575 mm. The anterior–posterior length ratio is 0·80. The maturation moult produces marked changes in the shell. The dorsal and ventral margins are now almost parallel so that the outline is rectangular, with evenly rounded, more or less semicircular anterior and posterior margins. The tubercles are now all rounded bosses or blunt cones and the lumbar pair (text-fig. 4, *Fa, Fb*) are clearly separated and no longer dominant. The anterior sulcus is barely perceptible and the adductor muscle-scar is well anterior to the middle line. Sexual dimorphism is pronounced; in the female the posterior half of the carapace is swollen (Pl. 15, figs. 21–23) and the tubercles are low and inconspicuous, sometimes absent; in the male the posterior half is much narrower and all the tubercles are well developed (Pl. 15, figs. 17–19, 28–31). In both sexes the posterior-dorsal margin is swollen and raised so as to hide the dorsal margin in side view.

RECOGNITION OF INSTARS

When length of carapace is plotted against height as in text-fig. 2, it is obvious that the later growth stages can be identified by size alone provided a sufficient number of individuals are measured and provided they are from the same horizon and locality. But since the growth-rate in *T. fittoni* is not absolutely constant it is evident that if the measurements of length and height were not plotted on a separate graph for each locality it would not always be possible to distinguish the instars. Though the growth rate is evidently not constant for *T. fittoni*, this may be a feature peculiar to brackish-water species, since the data published by Neale (1959) for the Recent marine species *Normanocythere leioderma* (Norman), the specimens of which came from various localities though mainly from Spitzbergen, show very little evidence of a variable growth rate. Similarly, Anderson's (1964) study of *Pterygocythere jonesi*, for which specimens were collected from various localities in the Irish Sea, show very little deviation from the mean of each instar so that the growth rate cannot have differed greatly from place to place.

Apart from size the changes in shape and ornament enable a rough assessment of the growth stage to be made. It was noted during measurement that some specimens were atypical in that one or more of the posterior three nodes (text-fig. 4*g*, *h*, *i*) were missing (Pl. 15, fig. 35), and all the material on hand then was examined for atypical specimens. Out of 2,000 specimens examined, only 16 atypical specimens were found. These are similar to the rest in all respects except that one of the posterior nodes is missing. Only one of these specimens has two of the posterior nodes missing. The shell is smooth in the area where the node should be, indicating that its absence is not due to preservation. These specimens range in greatest length from 0·51 mm. to 1·06 mm., suggesting that the abnormality persisted through the entire ontogeny of the individual. These exceptions are considered to represent genetic sports, and as such do not alter the conclusion that in this species the number of nodes, and their relation to each other on the surface of the valve, are constant. This interpretation of genetic control argues against the hypothesis proposed by Wicher (1957, p. 269) that nodosity in this plexus is caused by outside influences, namely environment. According to him, a change in the salinity caused the development of nodes.

CONCLUSIONS

This study demonstrates that in *Theriosynoecum fittoni* (Mantell) the number of nodes is normally ten in adult males as well as in most of the younger growth stages. It is usually possible to see the remains of these nodes in adult females even though they are resorbed. The position of the nodes relative to each other is constant on the surface of the valve.

This principle of constancy of nodes may be used to discriminate between bisulcate brackish-water Mesozoic species, and may prove to apply as well to marine species in other ostracod genera. For example, Wicher (1957) illustrated and discussed specimens from north-west Germany that he assigned to *Gomphocythere fittoni berwickensis*. The German specimens figured have only nine nodes, and are stated to have from eight to nine nodes (1957, p. 270). The arrangement on the surface of the valve (Wicher 1957, pl. 2, figs. 4*a–c*, 5*a–c*) differs from that of *T. fittoni*, so that these specimens may not be conspecific with the English species. Grekoff (1958, p. 26) considers the *G. pahasapensis* (Roth) of Martin 1940, as synonymous with *G. berwickensis* Martin 1940, and refers both to '*Metacypris*' *fittoni* (Mantell) 1844. Martin's illustrations (1940, pl. 6, figs. 95–97; pl. 7, figs. 98–100) are of specimens that are probably not conspecific with *T. fittoni* since the number and arrangement of the nodes differ from the species illustrated by Martin (1940, pl. 12, figs. 176–81; text-figs. 1, 2), and also in this paper.

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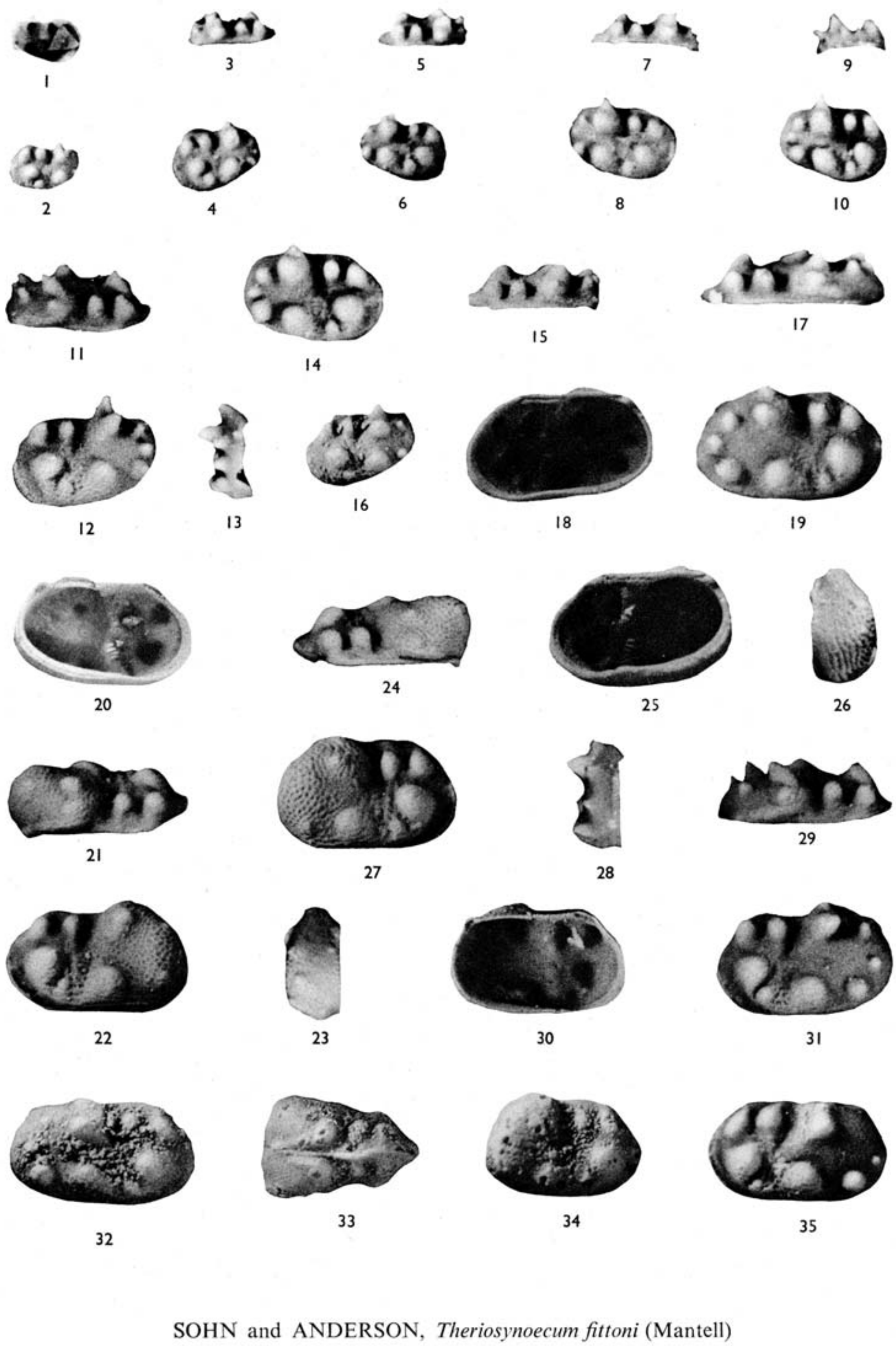
ADDENDUM. The monograph entitled 'A Complete Revision of the Genera *Bisulcocypris* and *Theriosynoecum* (Ostracoda)', by I. D. Pinto and Y. T. Sanguinetti (1963, *Esc. Geol. P. Alegre Publ. Esp.* **4**) appeared after this paper had been completed and contains several controversial issues which require discussion. At the moment the present authors find no reason to change their allocation of '*Metacypris*' *fittoni* from the genus *Theriosynoecum* to the genus *Bisulcocypris*.



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