

EVOLUTION OF THE SILURIAN TRILOBITE  
*TAPINOCALYMENE* FROM THE WENLOCK  
OF THE WELSH BORDERLANDS

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**ABSTRACT.** Some calymenid trilobites from the Wenlock Series of the Welsh Borderland are described and assigned to a new genus *Tapinocalymene*, type species *T. nodulosa* (Shirley 1933). An evolutionary lineage from *T. volsoriforma* sp. nov. (early Wenlock) through *T. vulpecula* sp. nov. (late Wenlock) to *T. nodulosa* (late Wenlock) is proposed, involving an increase in the length and area of the preglabellar furrow. *Tapinocalymene* was probably benthic in habit, and occurs in somewhat offshore, generally deepish water, clastics. *Calymene diademata* Barrande, 1846 (Wenlock, Bohemia), *C. nasuta* Ulrich, 1879 (Llandovery, United States) and *C. blumenbachii* Brongniart, 1822 (Wenlock, England), respectively the type species of the calymenines *Diacalymene* Kegel, 1927, *Spathacalymene* Tillman, 1960, and *Calymene* Brongniart, 1822 are figured and compared with members of *Tapinocalymene*. *S. nasuta* and *T. nodulosa* both have a particularly long preglabellar area, but each differs in its form and derivation. Several Ordovician and Silurian calymenid genera, some only distantly related, evolved a long preglabellar area, the taxonomic value of which should be treated with caution.

SINCE the pioneer revisions made by Shirley (1933, 1936) on British Silurian calymenid trilobites, they have occasionally been discussed in studies on non-British faunas (Campbell 1967; Haas 1968; Schrank 1970; Whittington 1971*b*), but except for the work of Temple (1969, 1970, 1975) on Llandovery species, no direct attention has been paid to them. This paper is part of a wider project undertaken by the present author to investigate north-west European Silurian (and Ordovician) calymenids. The terminology, measurement, photographic and preparation techniques are those of Siveter (1977, 1979), except that surface sculptural terms are now used in the sense of Miller (1975, pp. 341, 343). Specimens used in this work are housed in the following museums: British Museum (Natural History), London (BM); Geological Museum, Institute of Geological Sciences, London (GSM); National Museum of Wales, Cardiff (NMW); Ludlow Museum, Salop (LM); Hunterian Museum, Glasgow (HM); Naturhistoriska Riksmuseet, Stockholm (RM); National Museum of Natural History, Smithsonian Institution, Washington (USNM).

SYSTEMATIC PALAEOLOGY

Family CALYMENIDAE Milne Edwards, 1840  
Subfamily CALYMENINAE Milne Edwards, 1840

*Discussion.* I have advocated (Siveter 1977, p. 353) that this subfamily should contain only those genera possessing the papillate-buttruss structure, but future work may provide exceptions to this general rule, with the possibility of buttressed forms giving rise to non-buttruss forms through the arrested development of this feature during ontogeny (Siveter 1979, p. 373).

Genus TAPINOCALYMENE gen. nov.

*Type species.* *Calymene nodulosa* Shirley, 1933; Wenlock Series, Coalbrookdale Formation, Burrington, Hereford, and Worcester.

*Derivation of name.* Greek, *tapeinos*, humble, alluding to the glabella which is fairly low and short relative to the fixed cheeks.

*Other species.* *T. volsoriforma* sp. nov., *T. vulpecula* sp. nov.

*Diagnosis.* A calymenine genus which combines the following characters: Preglabellar area relatively long, variably formed. Anterior glabellar margin normally lies behind anterior margin of fixed cheek, exceptionally both margins are in line (tr.); dorsal glabellar surface stands just above, or anteriorly is sometimes slightly below, fixed cheek. Glabellar lobe 2p is bridged across axial furrow to a genal buttress. Palpebral lobes are from twice to 2.5 times as wide (tr.) apart as glabellar width at 2p lobes. Hypostoma has ventral protuberance on middle of anterior lobe; maculae well developed. Pygidial axis almost flat (tr.); inner pleural region slopes gently abaxially; interpleural furrows are weak or obsolete. Numerous small to medium-sized granules uniformly and closely distributed on glabella; anterior adaxial part of fixed cheek, and often anterior border, coarsely granulate.

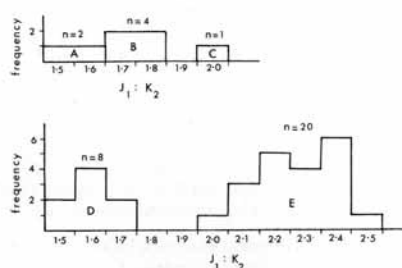
*Discussion.* Shirley (1936) advocated that calymenids showing a 'ridged' (or 'thickened') preglabellar area and a papillate 2p glabellar lobe joined to a genal buttress should be placed in his amended concept of *Diacalymene*; those species with this bridge across the axial furrow but without the 'ridged' preglabellar area should be placed in *Calymene*. The separation of *Diacalymene* on this basis has recently been questioned (Temple 1975; Ingham 1977; McNamara 1979) and certain British Ashgill and Llandovery species which Shirley placed in that genus are now held in abeyance in *Calymene (sensu lato)*. At present I prefer to consider the type species of *Diacalymene*, *C. diademata* Barrande, 1846 (late Wenlock age), and also several other related taxa such as *D. horbingeri* (Šnajdr, 1975) (Llandovery of Bohemia), as generically distinct from *C. blumenbachii* Brongniart, 1822 and related species. Nevertheless, assigning species to either *Diacalymene* or *Calymene* according to the nature of the preglabellar area was impracticable in the case of *Tapinocalymene nodulosa* (Shirley, 1933), *T. volsoriforma* sp. nov. and *T. vulpecula* sp. nov. These species all have the 2p lobe joined to a genal buttress, but whereas *T. volsoriforma* and *T. vulpecula* show a fairly distinct break in slope in the preglabellar area, where the anterior side of the preglabellar furrow meets the posterior edge of the less steeply sloping anterior border (Pl. 99, fig. 2; Pl. 100, fig. 2), similar to that in certain species variously referred to *Diacalymene* and *Calymene (s.l.)*, *T. nodulosa* (Pl. 97, fig. 11) has a preglabellar area similar to, though very much longer than, most *Calymene* species. All three species share characters which unite them as a genus distinct from other calymenines. The preglabellar area in *Tapinocalymene* is believed to have evolved quite rapidly and is useful for specific discrimination, though not for diagnosing the genus. None of the generic characters is completely exclusive, but in particular the low glabella which fails to protrude anteriorly beyond the fixed cheeks (Pl. 98, figs. 2, 3; Pl. 99, figs. 1, 2; Pl. 100, figs. 1, 2), the widely separated palpebral lobes (Pl. 98, fig. 6; Pl. 99, fig. 13; Pl. 100, fig. 4), and the style of cranial sculpture (Pl. 97, fig. 9; Pl. 99, fig. 14) all combine to distinguish *Tapinocalymene*. Other characteristic features include the axis, interpleural furrows, and inner pleural region of the pygidium. All *Tapinocalymene* species are closely associated in time and space.

Compared with *Tapinocalymene*, *Diacalymene* has a more raised, forwardly protruding glabella, narrowly separated palpebral lobes, and a more pointed inner, anterior corner to the fixed cheek (cf. Pl. 98, figs. 9–11; Pl. 101, figs. 5, 6, 10). Furthermore, *Diacalymene* lacks coarse granules on the inner part of the fixed cheek, though both genera have small, close-set glabellar granules. 'C.' *allportiana* Salter, 1865 (Much Wenlock Limestone Formation, Dudley) has the same type of cranial sculpture and pygidial axis as *Tapinocalymene* (Shirley 1933, pp. 58, 59, pl. 1, figs. 12–14); also the separation of its palpebral lobes falls just within the range of variation of the new genus (text-fig. 1). 'C.' *allportiana* is certainly more closely related to *Tapinocalymene* and *D. diademata* than to *C. blumenbachii*, but is excluded from *Tapinocalymene* as presently defined because of its more anteriorly, and (to a lesser extent) dorsally, projecting glabella. When *Diacalymene* is fully reassessed the generic position of 'C.' *allportiana* will become clearer. Most *Calymene* species differ from those of *Tapinocalymene* in the following features: a more dorsally and anteriorly projecting glabella having more variably sized, often larger, granules; less widely separated palpebral lobes; a steeper slope to the inner pleural region of the pygidium; a more convex (tr.) pygidial axis; better defined interpleural furrows, particularly distally. These differences are most obvious in the late Wenlock species *C. aspera* Shirley, 1936 and *C. blumenbachii* (cf. Pl. 97, figs. 1, 3, 10, 11; Pl. 100, figs. 9–12, 14, 16; text-fig. 1). Features characteristic of *Tapinocalymene* are occasionally exhibited, or closely

approached, by *Calymene* species. For example, *C. tuberculosa* Dalman, 1827, from the Wenlock of Gotland (and Wenlock Edge) has a gently convex pygidial axis, and *C. tenera* Barrande, 1852 from the Kopanina Formation (Ludlow) of Bohemia has very weak interpleural furrows. The Ludlow species *C. neointermedia* R. and E. Richter, 1954 has been allied with *T. nodulosa*, as both have similar scoop-like preglabellar areas (Schränk 1970, p. 122; Whittington 1971b, p. 463); the same character is present in *C. puellaris* Reed, 1920, also of Ludlow age. *C. neointermedia* and *C. puellaris* clearly belong within *Calymene*. The similarity in the preglabellar area of the three species is believed due to adaptive convergence.

Tomczykowa (1970) referred *Tapinocalymene nodulosa* to the monotypic genus *Spathacalymene* from the Osgood Formation (upper Llandovery; Berry and Boucot 1970), Indiana, an assignment made mainly because *S. nasuta* and *T. nodulosa* both have a long preglabellar area. However, it is not unusual for calymenid genera to independently develop a long preglabellar area and, in each genus, for it to be morphologically different. Compare, for example, that in *Thelecalymene mammillata* (Hall, 1861; Whittington 1971a, pl. 1, figs. 4, 5; pl. 2, fig. 1) from the upper Ordovician of the United States, *Prionocheilus foveolatus* (Törnquist, 1884; Warburg 1925, pl. 4, figs. 13, 16) from the middle Ordovician of Sweden, *Reedocalymene expansa* (Yi, 1957; Lu 1975, pl. 46, fig. 4) from the middle

TEXT-FIG. 1. Histogram of ratio of width between palpebral lobes to width of glabella at lobe 2p (= variates  $J_1$  and  $K_2$  of Siveter 1977, p. 338, fig. 1). A. *Spathacalymene nasuta*. B. *Diacalymene diademata*. C. '*Calymene*' *allportiana*. D. *Calymene blumenbachii*. E. *Tapinocalymene*: *T. volsoriforma*, n=6; *T. vulpecula*, n=4; *T. nodulosa*, n=10.



Ordovician of China, and *Calymenesun tingi* (Sun, 1931; Lu 1975, pl. 46, figs. 9-11) from the middle Ordovician of China. There is no resemblance in the preglabellar area of *Spathacalymene nasuta* and *Tapinocalymene nodulosa* apart from their uncommon length (see below and Pl. 98, figs. 6, 9, 12; Pl. 101, figs. 1, 4, 8). The former differs from the latter in its very convex (sag. and tr.), more dorsally and anteriorly projecting glabella, narrowly separated palpebral lobes (text-fig. 1), V-shaped rostral suture, subconical inner anterior corner to the fixed cheek, narrower thoracic and pygidial pleural region, and the lack of coarse granules on the inner, anterior part of the fixed cheek. I have no doubt that these species are not congeneric. The three calymenids with a spatulate preglabellar area from the Ludlow of Poland, which have been named *S. flexuosa*, *S. brevis*, and *S. linguata* by Tomczykowa (1970), should also be excluded from *Spathacalymene*. I agree with Whittington (1971b, p. 459) that these species represent a quite separate lineage (non-calymenine; but see Siveter 1979, p. 373). *Papillicalymene* Shirley, 1936 from the Ludlow of Gotland and Podolia, and Downton age glacial erratics of the north German plain, has a very advanced type of genal buttressing (Whittington 1971b, pls. 85, 86) which easily distinguishes it from *Tapinocalymene*.

*Occurrence.* *Tapinocalymene* has a stratigraphic range of early to late Wenlock; that is Sheinwoodian, probably *Cyrtograptus centrifugus* or *C. purchisoni* biozones, to Homerian, Gleadon Chronozone, *G. nassa* Biozone. It is limited to the main Wenlock outcrop of the Welsh Borderland from Rushbury, Ape Dale, through the core of the Ludlow anticline and the Wigmore Rolls area, to Dolgryn, Powys.

*Tapinocalymene nodulosa* (Shirley, 1933)

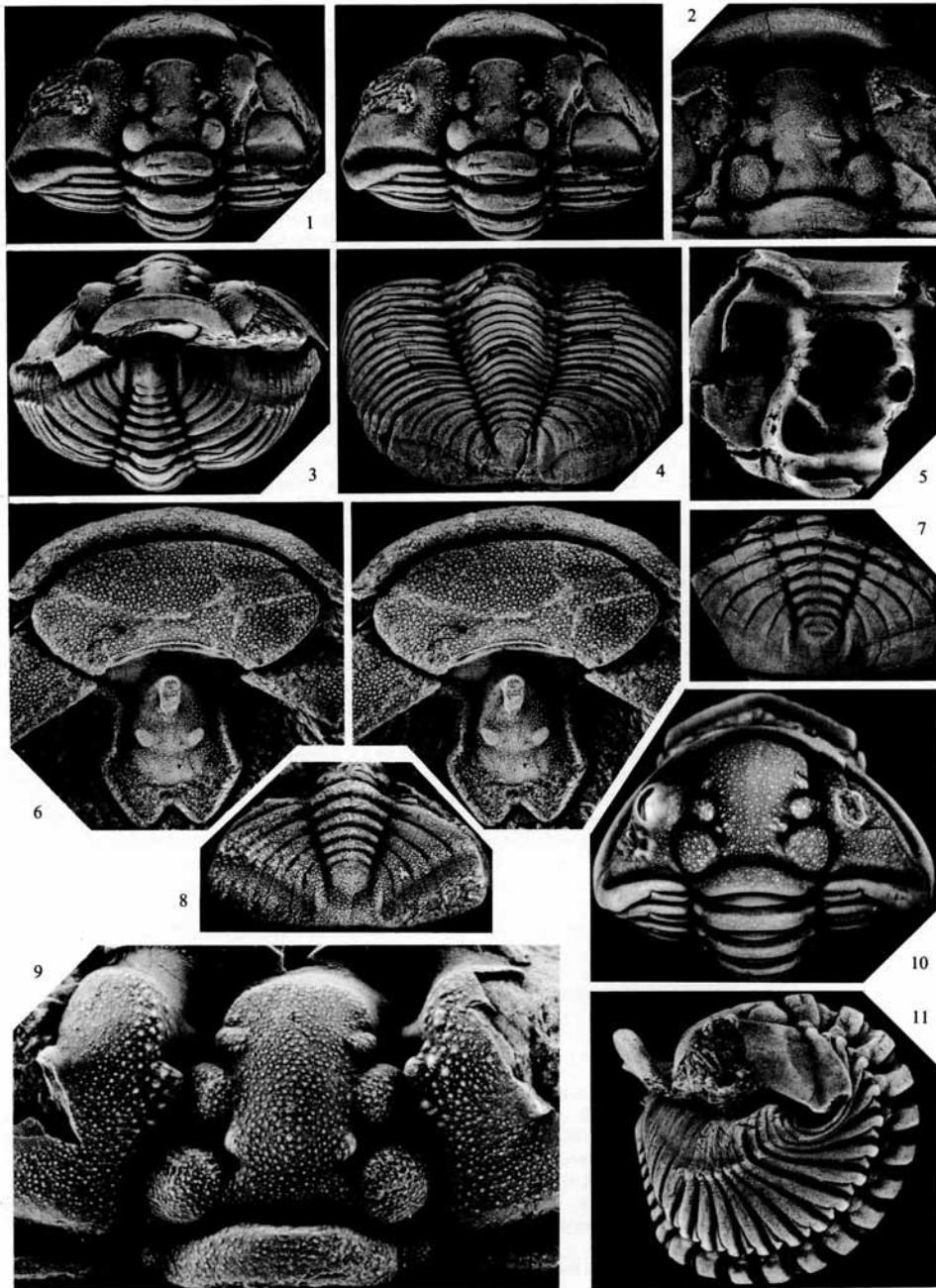
Plate 97, figs. 1-6, 8, 9, 11; Plate 98; text-fig. 2A-F

- non 1827 *Calymene blumenbachii* var *a*, *tuberculosa*; Dalman, p. 227.  
 v. 1839 *Calymene blumenbachii* Brongniart; Murchison (*pars*), p. 653, pl. 7, fig. 5 (GSM 6588), non figs. 6, 7.  
 v. 1848 *Calymene tuberculosa*, Salter; Salter, in Phillips and Salter, p. 342, pl. 12, figs. 1, 1a (GSM 19642), 2, 3, 5, ?fig. 4.  
 v. 1849 *Calymene tuberculosa* Salter; Salter, p. 1, pl. 8, figs. 1, 2 (GSM 19642), 1\*, 3-5, 7, ?fig. 6, non figs. 8\*, 8 (= *C. puellaris* Reed; GSM 19690).  
 non 1851 *Calymene tuberculosa* (Salter); McCoy, in Sedgwick and McCoy, p. 167.  
 v. 1859 *Calymene tuberculosa*, Salter; Murchison, pl. 18, fig. 11 (GSM 6588).  
 v. 1865 *Calymene tuberculosa*, Salter; Salter, p. 91, pl. 8, figs. 1, 2, 3 (GSM 19642), 4, 5 (GSM 19646), 6.  
 . 1873 *Calymene tuberculosa*, Salter; Salter (*pars*), p. 133, non p. 166.  
 v. 1884 *Calymene tuberculosa*; La Touche, p. 66, pl. 10, fig. 243 (GSM 6588).  
 . 1885 *Calymene tuberculosa* Salter non Dalman; Lindström, p. 66.  
 . 1888 *Calymene tuberculosa* Salter; Etheridge (*pars*), p. 46.  
 v. 1919 *Calymene blumenbachii* Brongniart; Reed, in Garwood and Goodyear, p. 20.  
 . 1925 *Calymene tuberculosa* Salter; Warburg, p. 158.  
 . 1927 *Calymene (Diacalymene) tuberculosa* Salter; Kegel, pp. 618, 620, text-fig. 2f.  
 v\* 1933 *Calymene nodulosa* nom. nov.; Shirley, p. 53, pl. 1, figs. 6-11.  
 . 1936 *Calymene nodulosa* Shirley; Shirley, pp. 388, 390, 393, 399, 400, text-figs. 1, 2 (*pars*).  
 . 1938 *Calymene nodulosa* Shirley 1933; Stubblefield, pp. 37, 38.  
 ? 1953 *Calymene nodulosa* Shirley; Williams, pp. 199, 200 (specimens not seen).  
 v? 1968 *Calymene nodulosa* Shirley; Greig, Wright, Hains, and Mitchell, p. 354 (specimens inadequate).  
 . 1970 *Calymene nodulosa* Shirley, 1933; Schrank, pp. 115, 122, 123.  
 . 1970 *Spathacalymene nodulosa* (Shirley); Tomczykowa, pp. 63, 70, 72, text-figs. 4k, 5f.  
 . 1971b *Calymene nodulosa* Shirley 1933; Whittington, p. 463.

*Holotype*. Nearly complete specimen lacking preglabellar area, with cuticle removed from abaxial part of cheeks and abaxial pleural region of thorax, GSM 19642; figured Salter 1848, pl. 12, figs. 1, 1a; 1849, pl. 8, figs. 1, 2; 1865, pl. 8, figs. 2, 3; Shirley 1933, pl. 1, figs. 6-10; pl. 98, figs. 1-3.

## EXPLANATION OF PLATE 97

- Figs. 1-6, 8, 9, 11. *Tapinocalymene nodulosa* (Shirley, 1933). All specimens are from the Wenlock Series, Homeric Stage, Coalbrookdale Formation, vicinity of Burrington, Hereford and Worcester; 2, 5, 8, 9 come from *C. lundgreni* Biozone strata, sunken lane south of Burrington (SO 442 718). 1, 3, 11, enrolled specimen lacking left, and most of the right, free cheeks, HM A212/1, dorsal stereo-pair, frontal view,  $\times 1\frac{1}{2}$ , left lateral view,  $\times 2$ . 2, slightly distorted cranidium, LM 4885, dorsal view,  $\times 2$ . 4, incomplete thorax and pygidium, NMW 75.35G.400, posterior view,  $\times 1.5$ . 5, incomplete cranidium and rostral plate, NMW 77.31G.10, ventral view,  $\times 2$ . 6, hypostoma and rostral plate, RM Ar38841, ventral stereo-pair,  $\times 3.5$ . 8, pygidium, NMW 77.31G.9, posterior view,  $\times 5$ . 9, cranidium, LM 4902, dorsal view,  $\times 4$ .  
 Fig. 7. *Tapinocalymene nodulosa?* (Shirley, 1933). Pygidium, NMW 77.31G.11, Wenlock Series, Homeric Stage, Coalbrookdale Formation, base of Farley Member, *G. nassa* Biozone, track section 252 m at 82° from St. Edith's Church, Eaton, Ape Dale, Salop (SO 5023 9002; Bassett *et al.* 1975, loc. 25, p. 16); posterior view,  $\times 1.5$ .  
 Fig. 10. *Calymene blumenbachii blumenbachii* Brongniart, 1822. Complete enrolled specimen, GSM 19668, Wenlock Series, Homeric Stage, Much Wenlock Limestone Formation, Dudley, West Midlands; dorsal view,  $\times 2$  figured Shirley 1933, pl. 1, figs. 4, 5.



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*Type locality.* Wenlock Series, Homeric Stage, Coalbrookdale Formation, Burrington, Hereford and Worcester. The Coalbrookdale Formation in the vicinity of Burrington includes strata of the *Cyrtograptus lundgreni*, *G. nassa*, and *Monograptus ludensis* biozones (Holland, Rickards, and Warren 1969). It is perhaps most likely that *lundgreni* Biozone strata yielded the holotype, and I have collected *T. nodulosa* from this horizon in the sunken lanes south of Burrington church.

*Additional material and occurrences.* At least 6 nearly complete individuals, 20 cranidia, 20 pygidia, 5 hypostomata. I have noted material in the British Museum (Natural History); Museum of the Institute of Geological Sciences, London; National Museum of Wales, Cardiff; Hunterian Museum, Glasgow; Ludlow Museum; Naturhistoriska Riksmuseet, Stockholm. The species occurs in the Coalbrookdale Formation of the following localities: Calcareous concretions within the small faulted patch of shales (= within the *C. rigidus* to *C. lundgreni* biozones; Bassett 1974, p. 759) above the Dolyhir Limestone, quarry 'D' of Garwood and Goodyear (1919, pl. 5, fig. 1, pl. 7), Dolyhir, Powys (SO 2412 5805); Birtley Lane, 6.5 km south-south-west of Leintwardine, Hereford and Worcester (SO 3687 6888); Homeric Stage, *C. lundgreni* Biozone, track section at St. Edith's Church, Eaton, Ape Dale, Salop (SO 5001 9002). A pygidium of *Tapinocalymene* (Pl. 97, fig. 7) from the base of the Farley Member, Coalbrookdale Formation, the track section at Eaton (SO 5023 9002), may also belong to *T. nodulosa*. Greig *et al.* (1968, p. 354) list the species from nearby Rushbury, Ape Dale (*C. lundgreni* Biozone; Bassett *et al.* 1975, p. 16, fig. 2); these specimens belong to *Tapinocalymene* but a specific assignment cannot be made with certainty. I cannot confirm Shirley's (1933, p. 56) record of Wenlock-age specimens from a quarry beside Nant Tresglen, behind Halfway Inn, 8 km east of Llandoverly (SN 828 328). Williams (1953, pp. 199, 200) cited *T. nodulosa* from his 'Lower' and 'Upper' Wenlock groups of the Llandeilo district. This material has not been seen but the *C. cf. nodulosa* figured (White, in Squirrell and White 1978, pl. 3, figs. 3, 4) from the Wenlock of the Cennen Valley near Llandeilo is not close to *T. nodulosa* and does not appear to be congeneric.

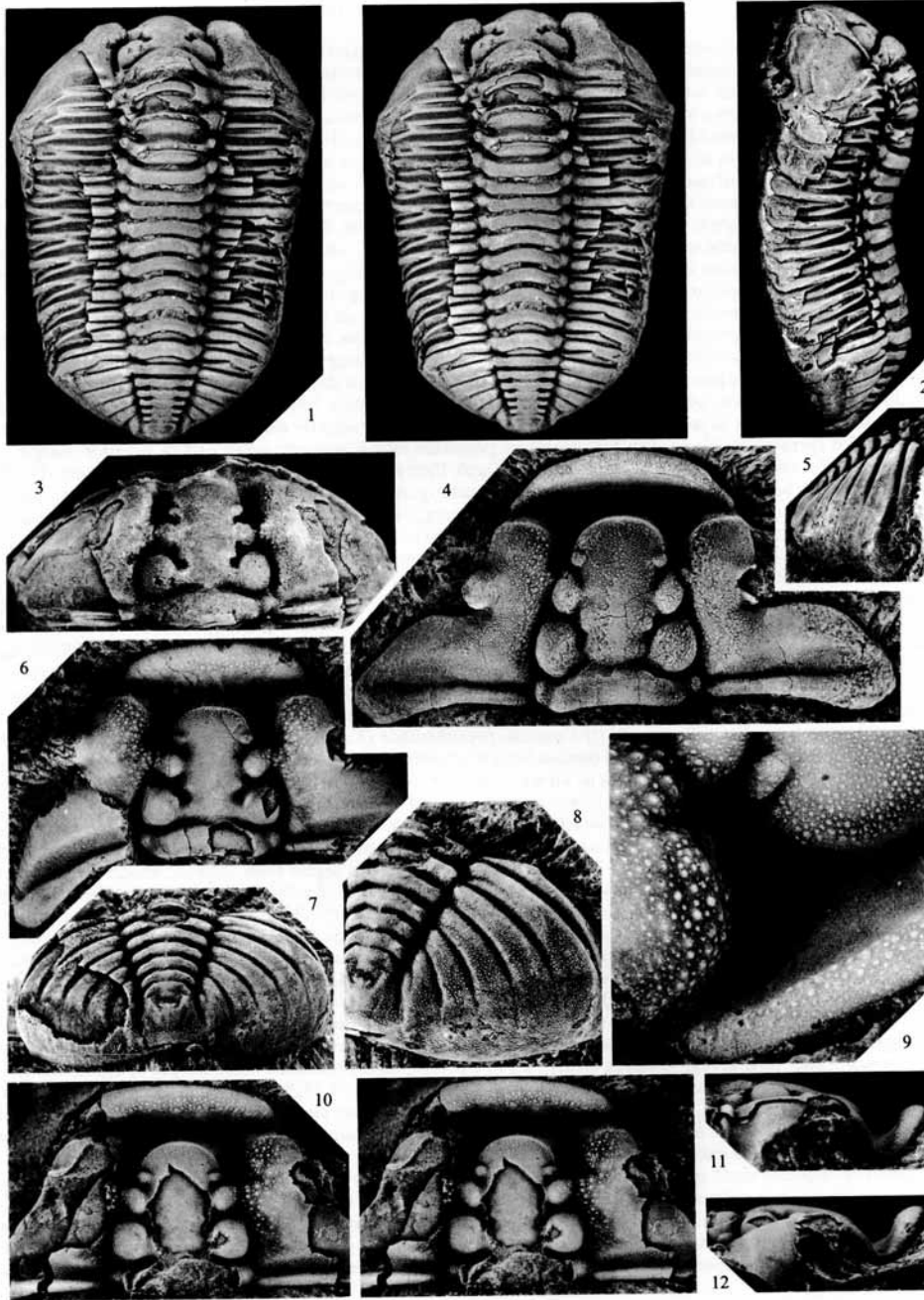
*Diagnosis.* Preglabellar area is from about two-fifths to almost one-half as long as glabella, directed forward, and curving progressively more steeply upward. Preglabellar furrow about three-fifths to three-quarters as long as preglabellar area; transition in slope between steep anterior side of this furrow and relatively short (sag. and exsag.), convex anterior border is gradual.

*Description.* Cranidium about twice as wide as long. Glabella slightly longer than wide with a subtrapezoidal to bell-shaped outline; in lateral profile dorsal surface is above fixed cheek at lobe 1p, is equal to or below fixed cheek at about furrow 2p (Pl. 97, fig. 11; Pl. 98, figs. 11, 12). Occipital ring about one-quarter as long (sag.) as wide, slightly wider than glabella at lobe 1p, is longest medially then shortens and swings forward laterally towards axial furrow where it is swollen. Occipital furrow longest and shallowest medially, shortens and deepens towards axial furrow, has a more steeply inclined posterior than anterior slope. Lobe 1p about one-third as wide as glabella. Abaxial part of 1p furrow deep, divides adaxially into two branches; posterior branch runs inward and obliquely backward, shallows before finally turning inward towards median line; weaker anterior branch directed forward and inward, not reaching as far adaxially as posterior branch. Shallow extension of posterior branch connects with occipital furrow to separate 1p lobe from frontomedian lobe. Small intermediate lobe within fork of furrow 1p (Pl. 97, fig. 9). Lobe 2p is papillate, joined to adaxially directed genal buttress. Furrow 2p directed inward and slightly backward, is continued as sharply flexed shallow depression which meets anterior branch of furrow 1p, thus semi-isolating lobe 2p. Lobe 3p much smaller than 2p, slightly elongate (tr.), sited on

#### EXPLANATION OF PLATE 98

Figs. 1-11. *Tapinocalymene nodulosa* (Shirley, 1933). 1-4 are from the Wenlock Series, Homeric Stage, Coalbrookdale Formation, vicinity of Burrington, Hereford and Worcester; 4 is from *C. lundgreni* Biozone strata, sunken lane south of Burrington (SO 442 718). 1-3, holotype, partial internal mould specimen lacking preglabellar area, GSM 19642, dorsal stereo-pair, left lateral view,  $\times 1.5$ , dorsal view (cephalon),  $\times 2$ ; figured Salter 1848, pl. 12, figs. 1, 1a; 1849, pl. 8, figs. 1, 2; 1865, pl. 8, figs. 2, 3; also Shirley 1933, pl. 1, figs. 6-10. 4, cranidium, NMW 77.31G. 8, dorsal view,  $\times 2$ . 5-12 are from calcareous concretions within faulted patch of Coalbrookdale Formation, Dolyhir, Powys (SO 2412 5808). 5, 7, 8, partial internal mould pygidium, NMW 53.288.G1, right lateral, posterior views,  $\times 1.5$ , oblique view,  $\times 2$ . 6, 12, cranidium, GSM Zs195, dorsal, right lateral views,  $\times 2$ . 9-11, partial internal mould cranidium, GSM Zs183, oblique view,  $\times 6$ , dorsal stereo-pair, right lateral view,  $\times 2$ .





SIVETER, *Tapinocalymene*

dorsolateral glabellar surface. Furrow 3p directed at about right angles to median line. Possible 4p furrow (not observed dorsally) expressed ventrally as a ridge joined to outer, posterior end of ridge which represents furrow 3p (Pl. 97, fig. 5). Frontal lobe bluntly rounded in outline, falls steeply to preglabellar furrow.

Axial furrow deep, steep-sided and narrowest around lobe 1p, is at least two to three times wider anterior to bridge of 2p lobe and genal buttress (Pl. 97, fig. 9). Anterior pit deep, situated very low down on adaxial side of axial furrow just anterior to furrow 3p; it is represented ventrally by a boss, the inner anterior slope of which is hollowed for reception of anterior wing process of hypostoma (Pl. 97, fig. 5). Some specimens show vestige of eye ridge running down abaxial side and across base of axial furrow opposite furrow 3p (Pl. 97, fig. 9; Pl. 98, fig. 9). In dorsal view anterior margin of preglabellar area is moderately (Pl. 98, fig. 10) to strongly (Pl. 97, fig. 2) convex forward, in lateral profile it is raised just above frontal glabellar lobe (Pl. 97, fig. 11), in frontal view it is sometimes slightly swollen upward opposite axial furrow. Long (sag. and exsag.) preglabellar furrow passes smoothly forward and progressively more upward on its anterior slope into short, convex (sag.) anterior border. Outer part of anterior border slopes downward and slightly backward to rostral suture (Pl. 97, figs. 6, 11).

Posterior border of cranium lengthens (exsag.) very slightly from axial furrow to fulcrum, abaxially from which it expands more quickly until shortening slightly and becoming less convex (exsag.) near facial suture. Posterior border furrow has a less steeply inclined anterior than posterior slope, both slopes become more gently inclined abaxially. Postocular part of fixed cheek slopes moderately downward to border furrow; convex preocular part projects beyond frontal glabellar lobe, is vertical or slightly overhangs abaxial continuation of preglabellar furrow (Pl. 97, fig. 11). Mid-length of palpebral lobe is opposite some part or anterior margin of lateral lobe 2p, initially it continues slope of fixed cheek then abaxially has a more horizontal attitude (Pl. 98, fig. 4). Posterior branch of facial suture runs outward and slightly backward then swings in broad curve to lateral border, finally turning more posteriorly to posterior margin (Pl. 98, fig. 6); anterior branches are abaxially convex, slightly convergent. Free cheek incompletely known, slopes steeply to open U-shaped lateral border furrow, doublure is sharply reflexed upward and outward from lateral border.

Border sector of rostral plate just greater than one-third to just less than one-half as long as wide, slightly more than three times as long (sag.) as outer part of anterior border (Pl. 97, fig. 6). Rostral suture moderately arched. Connective sutures gently convex outwards, converge posteriorly towards angular junction of border and doublure sectors. Inner arc of border sector about parallel to rostral suture, marked by a slight ridge (Pl. 97, fig. 6). Hypostoma 1.1 to 1.2 times as wide across anterior wings than long (sag.). Anterior margin broadly convex forward. Anterior border flexed ventrally; border furrow shallow. Anterior wing with deep pit. Lateral margin slightly convex abaxially between anterior wing and lateral shoulder; lateral border narrows (tr.) posteriorly; border furrow most distinct opposite (tr.) median protuberance of anterior lobe. Posterior border flattened, projecting into two broad spines. Faint median furrow connects two conspicuous, ovate maculae. Anterior lobe of median body about 2.25 to 2.5 times as long as posterior lobe; a spur-like protuberance is directed ventrally from centre of anterior lobe. Posterior lobe is crescent-shaped.

Thorax characteristically wide (tr.); anterior part of axis less wide than pleural region. Axis has thirteen rings, each of about constant length (sag. and exsag.) and flat to gently convex in lateral profile, flexed forward abaxially and swollen at axial furrow. Posterior band of each pleura higher than anterior, moderately convex (exsag.), forms posterior rim to articulating facet (Pl. 97, fig. 11; Pl. 98, fig. 2). Pleural furrow moderately deep and U-shaped at fulcrum, less well marked abaxially, dies out on articulating facet. Many specimens have slightly sinuous course to the distal, posterior margins of thoracic pleurae due to enrolment contact of free cheek; point of contact more dorsally positioned on posterior pleurae, becomes progressively lower on anterior pleurae, is continued posteriorly as a cincture on the pygidium (Pl. 97, figs. 4, 11).

Pygidial axis very gently convex (tr.), has six distinct and one indistinct axial rings and terminal axial piece. Each ring is almost flat (sag.); anterior rings slightly inflated at axial furrow. Ring furrows shallowest medially, become deeper towards axial furrow which becomes weaker posteriorly and scarcely present around terminal axial piece. Inner pleural region slopes gently (tr.) to cincture, thereafter much more steeply to lateral margin. Pleural region usually has five distinct pleural furrows to the cincture (Pl. 97, figs. 3, 8), one specimen (Pl. 98, figs. 5, 7, 8) has trace of a sixth. Interpleural furrows very faint. On outer pleural region pleural and interpleural furrows very weak (Pl. 97, fig. 8) or absent (Pl. 98, fig. 8), leaving smooth border. Postaxial sector falls almost vertically from terminal axial piece.

Small to medium-sized granules are evenly distributed on glabella; much larger ones on genal buttress, anterior adaxial part of fixed cheek, and sometimes anterior border (Pl. 97, fig. 9; Pl. 98, fig. 9). Abaxial inflations of occipital and axial rings have concentration of small granules. Small, closely spaced granules on border sector of rostral plate and lateral border of cheek (Pl. 97, fig. 6). Scattered fine granules on hypostoma, thorax, and pygidium. Maculae and deepest part of preglabellar, pleural, axial, and articulating furrows lack granules.



*Discussion.* Variation is present in the degree of upward curving of the preglabellar area and impression of cincture and interpleural furrows on the pygidium, though the latter are never strongly developed and may be almost completely absent. The largest cranidium (Pl. 98, fig. 4; ?gerontic specimen) is the only one to have the anterior glabellar margin transversely in line with the fixed cheek.

Cranidia from Dolyhir (Pl. 98, figs. 6, 9–12) have a more swollen anterior border, and thus a relatively shorter preglabellar furrow, than in typical Burrington specimens (cf. Pl. 97, fig. 2); in this character, therefore, they approach *T. vulpecula*. They are placed with *T. nodulosa* because they lack the more distinct break in slope between preglabellar furrow and anterior border that is diagnostic of the new species (cf. Pl. 98, figs. 6, 12; Pl. 100, figs. 1, 2), and because the anterior border of other specimens from Burrington is very similar to that in the Dolyhir material (cf. Pl. 97, figs. 1, 11; Pl. 98, figs. 10, 11).

*Tapinocalymene volsoriforma* sp. nov.

Plate 99, figs. 1–15; text-fig. 2t, j

1919 *Calymene blumenbachii* Brongniart; Reed, in Garwood and Goodyear, p. 19.

*Derivation of name.* Latin, *volsorium*, a curved archstone, referring to the cranial anterior border outline in dorsal view.

*Holotype.* Almost complete cranidium, GSM Zs63, Garwood Collection; Pl. 99, figs. 1–4.

*Type locality.* Wenlock Series, Sheinwoodian Stage, shale band included within the Dolyhir and Nash Scar Limestone Formation near its base, Dolyhir Quarries near Old Radnor, Powys (see Garwood and Goodyear 1919, p. 18, pl. 7). There are no specific horizon data given for *T. volsoriforma* specimens in the Institute of Geological Sciences Garwood Collection. Apart from the Pre-Cambrian, only the Dolyhir and Nash Scar Limestone Formation and a small faulted patch of Coalbrookdale Formation outcrop in this area. The lithology of the Coalbrookdale Formation here is different to the matrix surrounding the *T. volsoriforma* specimens and this patch yields instead *T. nodulosa*. The matrix is also unlike the mass of pure, crystalline Dolyhir Limestone, though Garwood and Goodyear's (1919, p. 18) description of a shale band included in the limestone near its base fits the IGS material. I have collected a *T. volsoriforma* cranidium from this shale band on the north side of the disused railway track, Dolyhir (SO 2410 5823). The exact location of the type locality amongst the Dolyhir Quarries is unknown. The Dolyhir and Nash Scar Limestone Formation is considered to span the *Cyrtograptus centrifugus*, *C. murchisoni* and part of the *Monograptus riccartonensis* biozones of the Sheinwoodian (Bassett 1974, p. 759).

*Additional material and occurrences.* At least three incomplete cranidia, GSM Zs62, GSM Z19983, LM 2850; one incomplete cephalon, GSM Zs65; one incomplete cephalon plus rostral plate GSM Zs58; one incomplete hypostoma GSM Z19696; seven incomplete pygidia GSM Zs22, GSM Zs24, GSM Zs57, GSM Zs59–61, GSM Zs64. Numerous other fragments of cranidia, pygidia, and thoracic segments are present in the Garwood Collection, Institute of Geological Sciences Museum.

Only recorded with certainty *in situ* from the type area, but it may also be present in the Coalbrookdale Formation of Salop (Pl. 99, fig. 16). One transported specimen (Pl. 99, fig. 5) was collected from a stream bed near English Bridge, Shrewsbury.

*Diagnosis.* Preglabellar area about one-third as long as glabella. Preglabellar furrow about one-sixth as long (sag.) as preglabellar area. Anterior border relatively long, it slopes fairly gently upward and forward from the more steeply inclined anterior side of preglabellar furrow. Axial furrow anterior to lobe 2p only slightly wider than around 1p lobe. Hypostoma with only moderately inflated subcircular protuberance on anterior lobe.

*Description.* Glabella essentially as in *T. nodulosa* but inflation within fork of 1p furrow generally weaker. Axial furrow deep and fairly narrow around lobe 1p, slightly wider beside lobe 3p and frontal lobe. Anterior pit is anterior to furrow 3p. Preglabellar furrow short and moderately deep medially, lengthens (exsag.) at anterolateral corner of frontal lobe, continues forward and outward between fixed cheek and anterior border into deep, narrow, lateral border furrow; steeply sloping anterior side of preglabellar furrow meets anterior border at change of slope. Anterior border about one-quarter (Pl. 99, fig. 5) to three-tenths (Pl. 99, fig. 1) as long as glabella, dorsal surface very gently convex (sag.), slopes forward and slightly upward. In lateral profile

anterior margin rises above anterior part of frontal lobe. Fixed cheek, palpebral lobe, and facial suture as in *T. nodulosa*. Free cheek has narrow eye socle (Pl. 99, figs. 7, 13), convex inner part of cheek falls steeply to U-shaped lateral border furrow; junction of border furrow with lateral border is more angular (tr.) than with inner part of cheek. Lateral border rolled under ventrally. Rostral plate (Pl. 99, fig. 11) imperfectly preserved but apparently similar to *T. nodulosa*. Hypostoma has moderate, subcircular inflation on anterior lobe (Pl. 99, fig. 8). Oval macula smooth; median furrow very faint. Posterior border expanded into two spines.

Thoracic segments (fragmentary) have axial rings inflated near axial furrow. Pygidium like that of *T. nodulosa*. Axis very weakly convex (tr.), has at least seven rings plus terminal piece. Axial rings longest (sag.) and ring furrows shallowest medially. Seventh ring furrow lacking abaxially; very faint trace medially of eighth furrow (Pl. 99, fig. 6). Inner pleural region descends gently abaxially, outer part falls more strongly. Five (possibly six) pleural furrows are best marked on inner pleural region; interpleural furrows much weaker.

Glabella, outer part of fixed cheek and free cheek have numerous small to medium-sized granules. Inner part of fixed cheek (especially anteriorly), genal buttress and anterior border are coarsely granulate (Pl. 99, fig. 14). Deepest parts of glabellar and preglabellar furrows lack granules; lateral and posterior border furrows have scattered small granules. Pygidium and hypostoma are finely granulate.

*Discussion.* Compared to the holotype (Pl. 99, fig. 1), a cranidium from outside the type area (Pl. 99, fig. 5) has a more rounded outline to the anterolateral corner of the frontal lobe, a shallower preglabellar furrow, a much weaker break in slope between preglabellar furrow and anterior border, and a relatively shorter anterior border (to the glabella). This variation is considered to be intraspecific as Dolyhir specimens vary in a like manner (for example, Pl. 99, fig. 13 in the first three of these characters).

Two other *Tapinocalymene* cranidia from Salop (Pl. 99, fig. 16; NMW 77.31G.13) may belong to *T. volsoriforma*, but are indifferently preserved. They are associated with *Monograptus flemingii* (identified by Dr. I. Strachan; pers. comm. Dr. C. N. Rodgers), indicating a post *M. riccartonensis* to *C. lundgreni* Biozone age. Apparently *T. volsoriforma*, or a species close to it, existed outside the type area at a later date.

*Tapinocalymene vulpecula* sp. nov.

Plate 100, figs. 1-8, 13, 15; text-fig. 2G, H

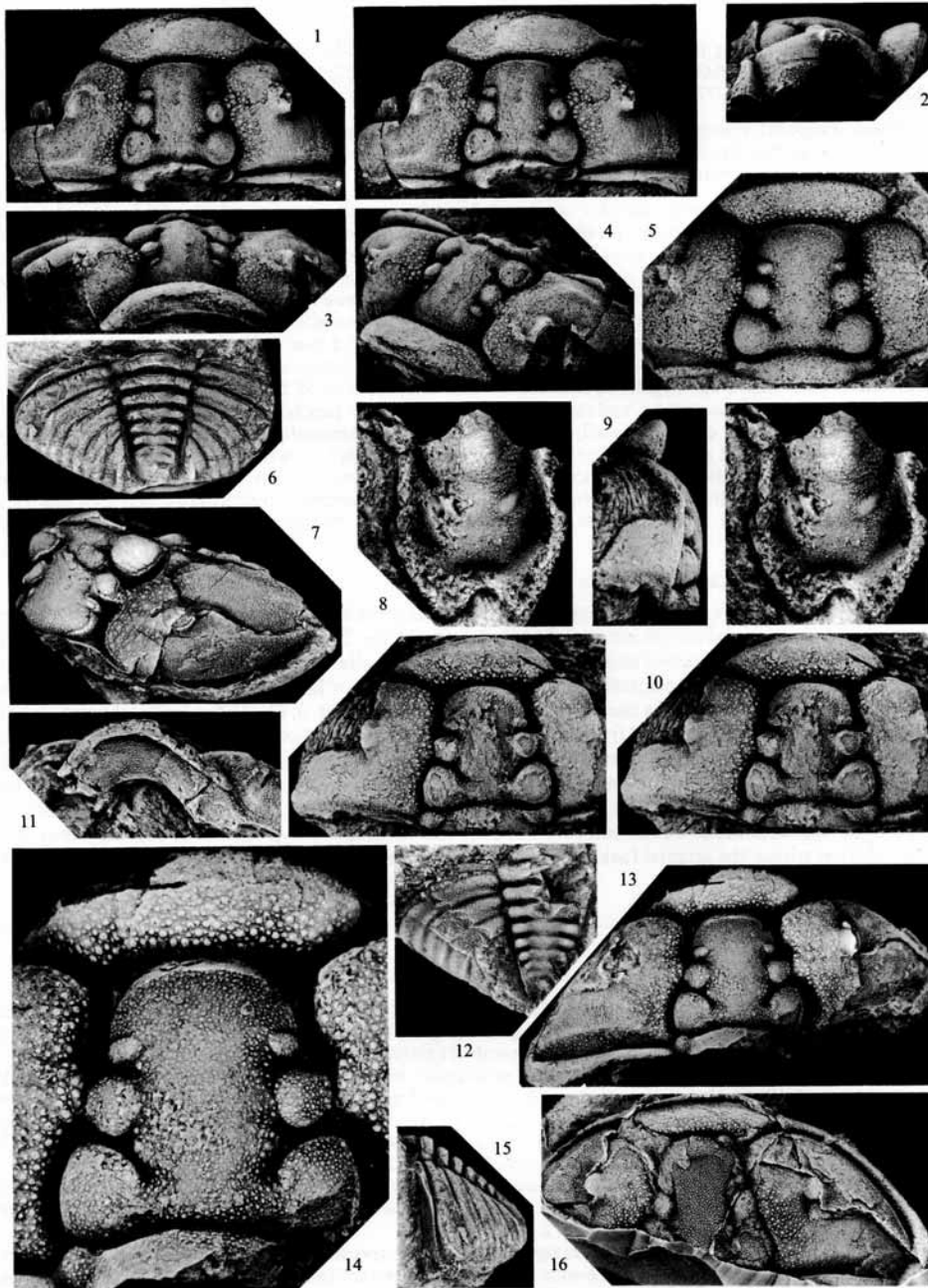
*Derivation of name.* Latin, diminutive of *vulpes*, fox, alluding to the appearance of the hypostoma.

*Holotype.* Incomplete cranidium, NMW 77.31G.1, collected D. J. Siveter 1971; Pl. 100, figs. 1, 2.

*Type locality.* Wenlock Series, small disused quarry on the west side of the road from Letton to Walford,  $\frac{1}{2}$  km north of Letton, Hereford and Worcester (SO 3790 7080). Graptolites (SM A80317-21, SM A80387-91) from this locality have been assigned to *M. flemingii*, and probably belong to the *lundgreni* Biozone (pers. comm. Dr. R. B. Rickards).

EXPLANATION OF PLATE 99

- Figs. 1-15. *Tapinocalymene volsoriforma* gen. et sp. nov. All specimens except fig. 5 are from the Wenlock Series, Sheinwoodian Stage, included shale band in Dolyhir and Nash Scar Limestone Formation, Dolyhir, Powys. 1-4, holotype cranidium, GSM Zs63, dorsal stereo-pair, frontal, left oblique views,  $\times 2$ , right lateral view,  $\times 2.25$ . 5, cranidium, silicone-rubber cast of external mould, LM 2850b, specimen from a water-transported pebble, found near English Bridge, Shrewsbury, Salop; dorsal view,  $\times 2$ . 6, 15, pygidium, GSM Zs61, dorsal, left lateral views,  $\times 2.25$ . 7, cranidium and left free cheek, GSM Zs65, left oblique view,  $\times 2$ . 8, hypostoma, GSM Z19696, ventral stereo-pair,  $\times 5$ . 9, 10, cranidium, GSM Z19983, left lateral view, dorsal stereo-pair,  $\times 2$ . 11, 13, 14, cephalon, GSM Zs58, ventral (rostral plate), dorsal views,  $\times 2$ , dorsal view,  $\times 4$ . 12, pygidium, GSM Zs64, dorsal view,  $\times 2.25$ .
- Fig. 16. *Tapinocalymene* cf. *T. volsoriforma* gen. et sp. nov. Cephalon, silicone-rubber cast of external mould, NMW 77.31G.12b, Wenlock Series, Coalbrookdale Formation, road cutting on A489 between Horderley and Plowden, south side of Long Mynd, Salop (SO 402 875); dorsal view,  $\times 2$ .



SIVETER, *Tapinocalymene*

*Additional material.* Only from type locality; three incomplete cranidia, NMW 77.31G.2-4; two pygidia, one with cuticle, NMW 77.31G.6, the other an internal mould, NMW 77.31G.7; one hypostoma, internal mould plus counterpart, NMW 77.31G.5a,b. Numerous other fragmentary cranidia, pygidia, and thoracic segments.

*Diagnosis.* Preglabellar area about two-fifths to one-third as long as glabella. Preglabellar furrow about as long (sag.) as anterior border and half as long as preglabellar area. Marked break in slope where anterior side of furrow meets posterior margin of border.

*Description.* Glabella similar to that of *T. nodulosa*. Axial furrow at least twice as wide at lobe 3p and frontal lobe than around lobe 1p. Anterior pit situated in axial furrow below lateral glabellar furrow 3p. Preglabellar furrow deep, U-shaped (sag.), about as long as anterior border medially, shortens (exsag.) abaxially where fixed cheek approaches anterior border; anterior side of furrow is about vertical and meets posterior part of anterior border in a sharp break of slope, border then continues less steeply forward and upward (Pl. 100, fig. 2). Anterior border is of about constant length abaxially from median line to opposite axial furrow, thereafter shortening (exsag.) towards facial suture. In lateral profile anterior margin is about level with or just above height of frontal lobe. Fixed cheek, palpebral lobe, facial suture, and hypostoma essentially like that of *T. nodulosa*. Free cheek and rostral plate unknown. Pygidium, showing no differences to that of *T. nodulosa*, has six complete, one incomplete, very gently convex (tr. and sag.) axial rings. Anterior six ring furrows shallowest at and just either side median line, deepen quickly abaxially; very faint seventh ring furrow does not reach axial furrow which is weakest around terminal axial piece. Pleural region slopes very gently to cincture, more steeply abaxially. Five pleural furrows run outward and backward to cincture, apparently absent from here to lateral margin though this part of pygidium is imperfectly preserved. Interpleural furrows extremely faint, best seen near axial furrow, not marked on internal mould (cf. Pl. 100, figs. 8, 13). Sculpture like that of *T. nodulosa* and *T. volsoriforma*.

#### *Distinctions between Tapinocalymene species*

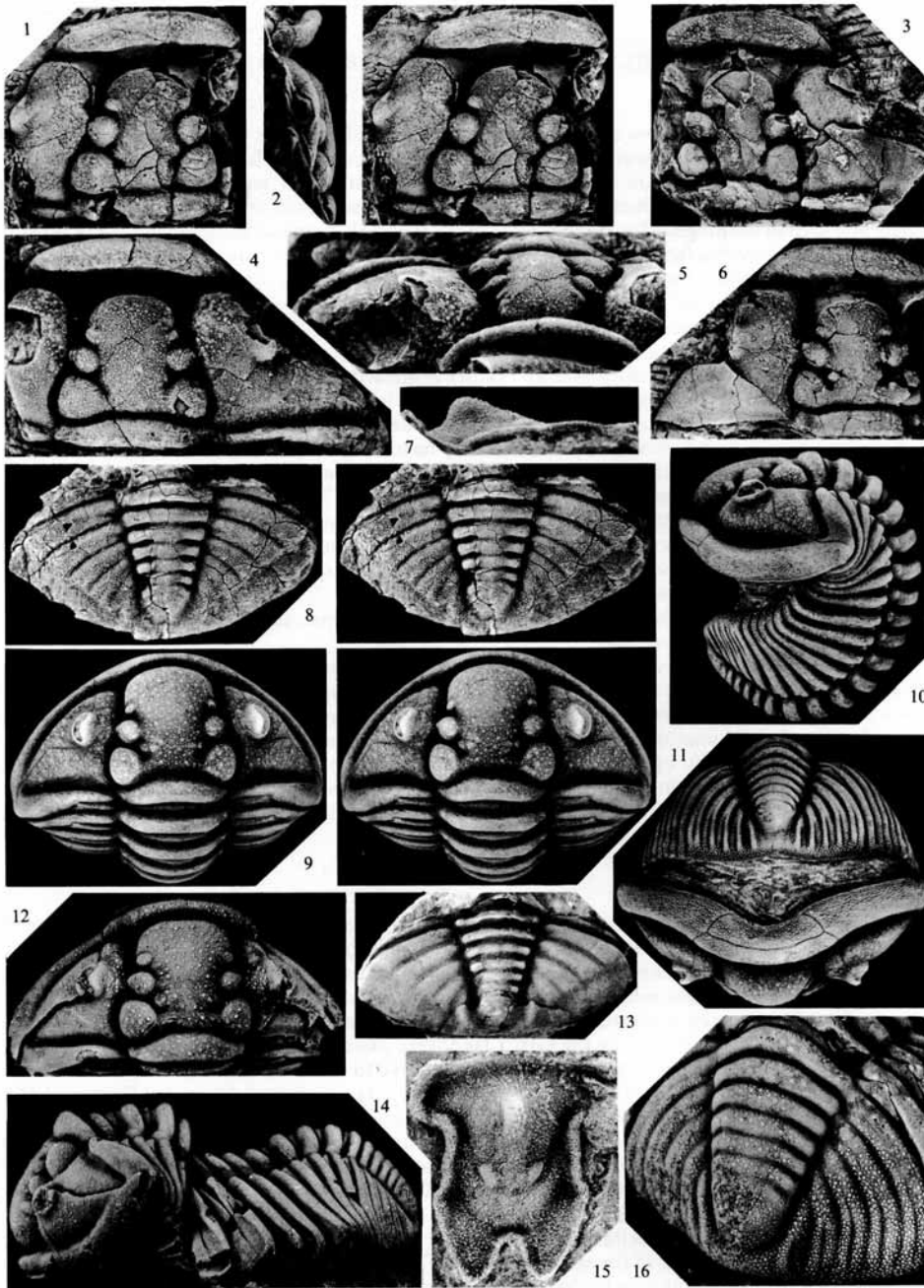
*T. volsoriforma* differs most obviously from *T. vulpecula* and *T. nodulosa* by its much shorter preglabellar furrow and longer anterior border (cf. Pl. 97, fig. 2; Pl. 99, fig. 1; Pl. 100, fig. 1). Further, *T. volsoriforma* has a narrower axial furrow anterior to glabellar lobe 2p (cf. Pl. 97, fig. 9; Pl. 99, figs. 13, 14; Pl. 100, fig. 1), and a ventral protuberance on the anterior lobe of the hypostoma which seems less well developed than that in the other two species (cf. Pl. 97, fig. 6; Pl. 99, fig. 8; Pl. 100, figs. 7, 15). *T. vulpecula* is best distinguished from *T. nodulosa* by its relatively shorter preglabellar furrow, longer anterior border, and sharper break in slope between these two features. In the change from *T. volsoriforma* to *T. nodulosa* through the Wenlock, in addition to a very marked change in the preglabellar area, the axial furrow anterior to lobe 2p becomes wider, the hypostomal protuberance seemingly becomes better developed (there is only one incomplete hypostoma of *volsoriforma*), and the inflation within the adaxial fork of furrow 1p becomes generally stronger (cf. Pl. 97, fig. 9; Pl. 99, fig. 14).

#### EXPLANATION OF PLATE 100

Figs. 1-8, 13, 15. *Tapinocalymene vulpecula* gen. et sp. nov. All specimens are from Wenlock Series, Coalbrookdale Formation, probably *Cyrtograptus lundgreni* Biozone, Homerian Stage, small old quarry on west side of road from Letton to Walford,  $\frac{1}{2}$  km north of Letton, Hereford and Worcester (SO 3790 7080). 1, 2, holotype cranidium, NMW 77.31G.1, dorsal stereo-pair, left lateral view,  $\times 2$ . 3, partial internal mould cranidium, NMW 77.31G.2, dorsal view,  $\times 2$ . 4, 5, cranidium, NMW 77.31G.4, dorsal, frontal views,  $\times 4$ . 6, cranidium, NMW 77.31G.3, dorsal view,  $\times 2$ . 7, 15, hypostoma, silicone-rubber cast of external mould, NMW 77.31G.5b, lateral, ventral views,  $\times 8$ . 8, pygidium, NMW 77.31G.6, dorsal stereo-pair,  $\times 2$ -25. 13, internal mould pygidium, NMW 77.31G.7, dorsal view,  $\times 2$ -25.

Figs. 9-11. *Calymene blumenbachii blumenbachii* Brongniart, 1822. Complete enrolled specimen, BM 44213, Wenlock Series, Homerian Stage, Much Wenlock Limestone Formation, Dudley, West Midlands; dorsal stereo-pair, left lateral, posterior views,  $\times 2$ .

Figs. 12, 14, 16. *Calymene blumenbachii* subsp. nov. Complete specimen, NMW 73.28G.3a, Wenlock Series, Sheinwoodian Stage, Woolhope Limestone Formation, temporary trench just north of church, Woolhope, Hereford and Worcester; dorsal, left lateral views,  $\times 2$ , posterior oblique view,  $\times 4$ .



SIVETER, Calymenid trilobites



ORIGIN OF THE GENERA *TAPINOCALYMENE* AND *SPATHACALYMENE**Tapinocalymene*

*T. volsoriforma* and *T. nodulosa* show the two morphological extremes in the preglabellar area of *Tapinocalymene*, that of *T. vulpecula* being intermediate in form. *T. volsoriforma* is from the lower Wenlock; *T. nodulosa* is from the upper Wenlock (*C. lundgreni* and ?*G. nassa* biozones), *T. vulpecula* being of probable *lundgreni* Biozone age. An evolutionary sequence involving an increase in the length and area of the preglabellar furrow through the Wenlock is postulated, from the sagittally short furrow in *T. volsoriforma* (text-fig. 2i, j), through the moderately long furrow of *T. vulpecula* (text-fig. 2g, h), to the scoop-like furrow and preglabellar area of *T. nodulosa* (text-fig. 2a, b). This trend is accompanied by a loss of the angular break in slope in the preglabellar area; the intraspecific variation attributed to *T. nodulosa* in the anterior border (Dolyhir specimens, text-fig. 2e, f) is taken as further evidence of the proposed phyletic series.

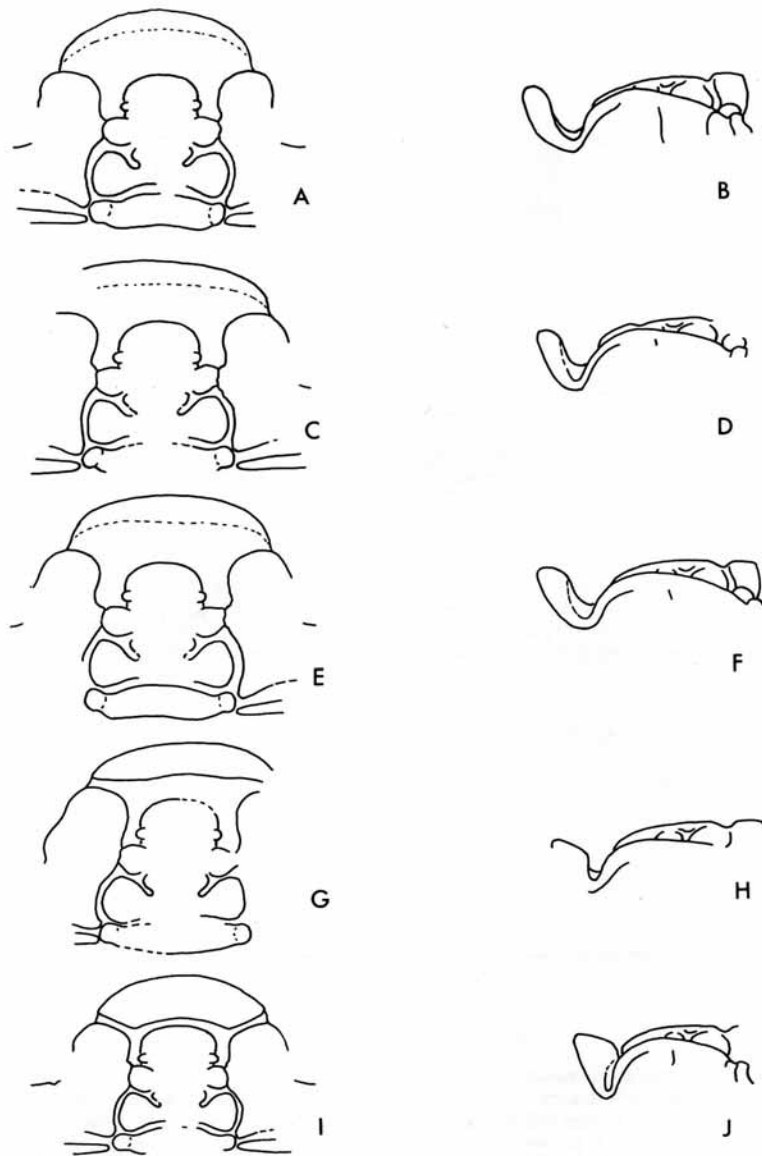
The exoskeleton of *T. nodulosa* is wide and rather depressed suggesting a benthic habit (cf. Fortey and Barnes 1977, p. 304 for broadly analagous conditions in certain olenids). Though the function of the distinctive preglabellar area is problematic, it may have been used in shallow burrowing, or to disturb superficial sediment in search of food. It may have been adapted to the carbonate mud facies of the Coalbrookdale Formation. *T. nodulosa* and *T. vulpecula* both occur in the same Wenlock calcareous shale facies, deposits interpreted (Bassett 1974, pp. 770-773, text-figs. 7, 8) as somewhat offshore, deepish-water clastics; in this context my own collections show that graptolites and small brachiopods invariably accompany these two species. The main mass of algal-rich Dolyhir and Nash Scar Limestone Formation was formed in shallow water deposited on a local offshore topographic high of faulted Pre-Cambrian rocks (Bassett 1974, p. 772, text-fig. 7; Hurst, Hancock, and McKerrow 1978, p. 204); the included shale band, which yields *T. volsoriforma*, suggests there may have been a temporary incursion of deeper water.

*Tapinocalymene* originated from *Diacalymene*, possibly from a stock broadly ancestral to *D. diademata*, rather than from *D. ? crassa* Shirley, 1936 and allied species. It is not related to *Calymene sensu stricto*. Specimens provisionally assigned to a new subspecies of *C. blumenbachii* are known from the Woolhope Limestone Formation of low Wenlock age (*C. centrifugus* and *C. murchisoni* biozones). These (Pl. 100, figs. 12, 14, 16) are approximately coeval with *T. volsoriforma*, yet are morphologically quite distinct (see differences between *Tapinocalymene* and *Calymene* in generic discussion). The *C. blumenbachii* species group, in contrast to *Tapinocalymene*, is characteristic of more onshore, generally shallower-water environments.

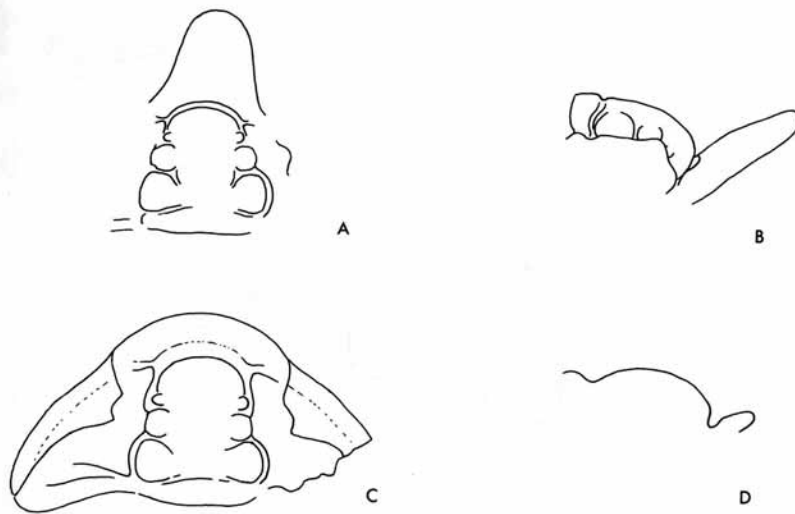
*Spathacalymene*

The preglabellar area of *Spathacalymene nasuta* has an inverted U-shaped, posteriorly divergent outline in dorsal view, with a long, dorsally flattened anterior border sloping moderately steeply posteriorly to meet a short, more steeply inclined preglabellar furrow. Apart from its length, this form is similar to the preglabellar area of certain calymenids assigned to *Diacalymene* by Shirley (1936); also similar is the pointed, forwardly and inwardly directed, anterior part of the fixed cheek. Both similarities apply to *D. ? crassa* from the early Llandovery (Rhuddanian) of Wales which, moreover, has a strongly convex (sag. and tr.), high glabella (relative to the fixed cheeks), as in *S. nasuta* (cf. Temple 1975, pl. 25, figs. 3, 4; Pl. 101, figs. 1, 4, 8 herein). The unrevised *C. vogdesi* Foerste (1887, p. 95, pl. 8, figs. 12, 13; 1893, p. 526, pl. 25, fig. 25; pl. 27, figs. 12, 13; 1919, pl. 19, fig. 5) from the lower Silurian of Ohio is a possible senior synonym of *crassa*, and it is also recorded (Foerste 1893, p. 527) from Indiana, where the upper Llandovery *S. nasuta* occurs. Foerste (1919, p. 393) regarded *vogdesi* as a 'typical Brassfield species'; his use of the term Brassfield included strata of middle to upper Llandovery age (Berry and Boucot 1970, p. 127).

The evolution of the preglabellar area of *S. nasuta* from that of '*C. vogdesi* or a similar species requires only the lengthening of the anterior border. This involves much less change in morphology from ancestor to descendant than in that proposed for *Tapinocalymene* (cf. text-figs. 2, 3).



TEXT-FIG. 2. Proposed evolutionary lineage in *Tapinocalymene* gen. nov. Dorsal and lateral outlines of cranidia, all  $\times 2$ . A, B. *T. nodulosa*, HM A212/1, pl. 97, figs. 1, 11. C, D. *T. nodulosa*, GSM Zs183, pl. 98, figs. 10, 11. E, F. *T. nodulosa* GSM Zs195, pl. 98, figs. 6, 12. G, H. *T. vulpecula*, holotype, NMW 77.31G.1, pl. 100, figs. 1, 2. I, J. *T. volsoriforma*, holotype, GSM Zs63, pl. 99, figs. 1, 2.

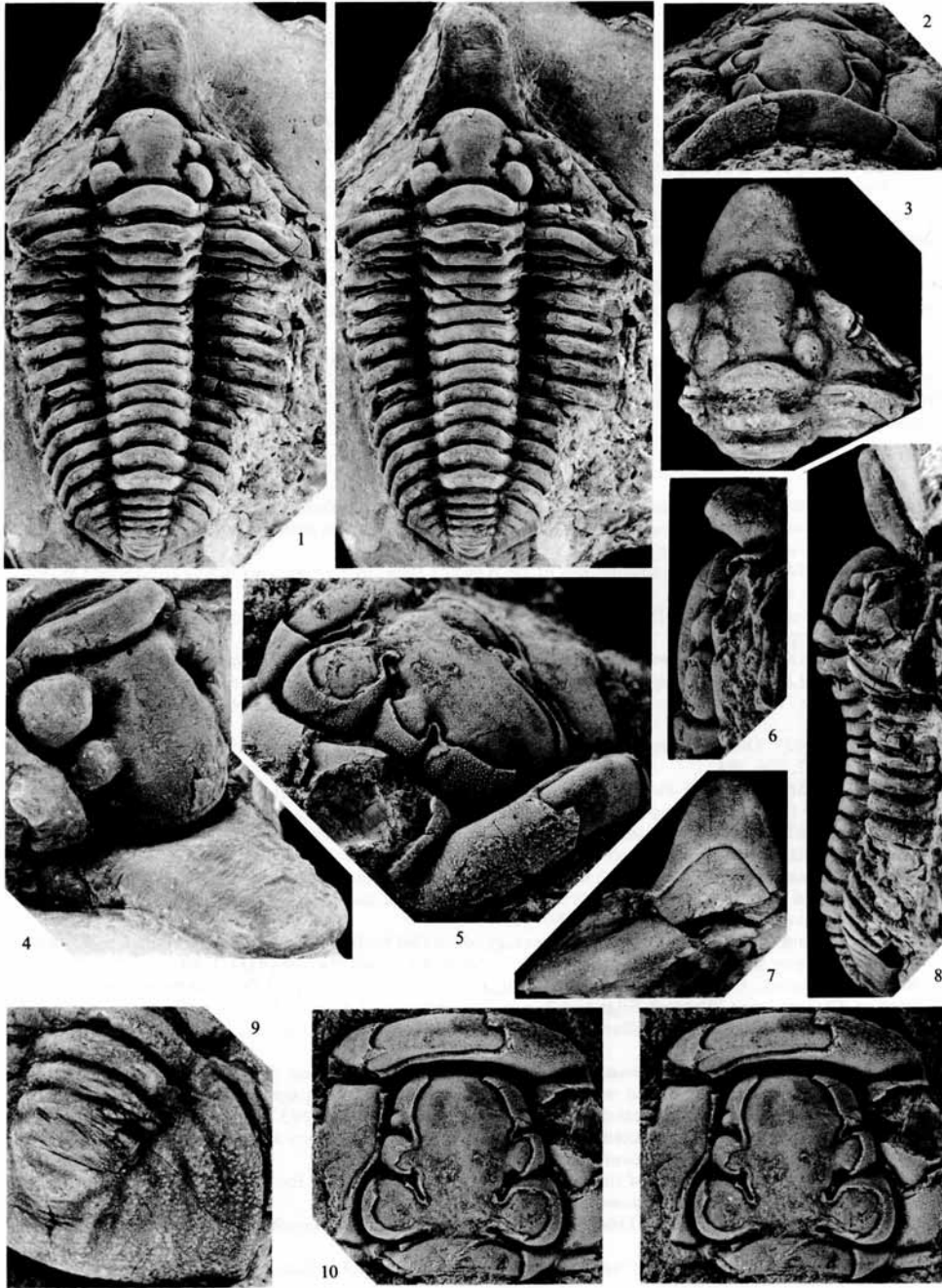


TEXT-FIG. 3. Possible origin of *Spathacalymene* Tillman, 1960. A, B. *Spathacalymene nasuta*, USNM 170363, dorsal and right lateral cranidial outlines,  $\times 1$ , pl. 101, figs. 1, 8. C, D. '*Calymene*' *vogdesi*, holotype, lower Silurian, Centreville, Ohio, U.S.A., dorsal and sagittal cranidial outlines; magnification unknown, but equal to Foerste's (1887, pl. 8, figs. 12, 13) original illustrations.

EXPLANATION OF PLATE 101

Figs. 1, 3, 4, 7-9. *Spathacalymene nasuta* (Ulrich, 1879). 1, 4, 8, 9, complete specimen, USNM 170363, Osgood Limestone (late Llandovery), quarry 1.3 km east of Napoleon, Ripley County, Indiana, U.S.A.; dorsal stereo-pair, right lateral view,  $\times 1$ , right oblique view,  $\times 2$ , posterior oblique view,  $\times 3.3$ ; figured Tillman 1960, pl. 116, figs. 1, 4, 5, 8, 9. 3, 7, paralectotype, cephalon, rostral plate and two thoracic segments, Osgood Formation (late Llandovery), Osgood, Indiana, U.S.A.; dorsal, ventral views,  $\times 1.5$ ; figured Tillman 1960, pl. 116, figs. 10-12.

Figs. 2, 5, 6, 10. *Diacalymene diademata* (Barrande, 1846). Cranidium, largely internal mould, NMW 71.8G.377, upper part of the Liteň Formation, *Cyrtograptus radians*-*Monograptus testis* biozones (late Wenlock), above path leading from Svatý Jan pod Skalou to Vraz, south-west of Prague, Czechoslovakia; frontal, right lateral views, dorsal stereo-pair,  $\times 2$ , right oblique view,  $\times 2.5$ .



SIVETER, Calymenid trilobites

## CONCLUSIONS

1. *C. nodulosa* Shirley, 1933, *T. volsoriforma* sp. nov. and *T. vulpecula* sp. nov. from the Wenlock Series of the Welsh Borderland belong to a new genus, *Tapinocalymene*.
2. *Tapinocalymene* shows plasticity in the form of its preglabellar area, which links the phyletic series *T. volsoriforma*, *T. vulpecula*, *T. nodulosa*.
3. *Tapinocalymene* was probably benthic and occurs throughout its stratigraphic range in somewhat offshore carbonate muds. The scoop-like preglabellar area of *T. nodulosa* developed in response to this mode of life and bottom conditions.
4. The possession of a long, conspicuous preglabellar area provides no basis for considering *T. nodulosa* and *S. nasuta* congeneric; details of its morphology and origin are distinctive in both taxa, and it is a feature that species of different calymenid lineages occasionally develop.

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