BUBBLE-HEADED TRILOBITES, AND A NEW OLENID EXAMPLE

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ABSTRACT. Several trilobites developed an inflated cephalic lobe with a distinctive bubble-like profile. This happened polyphyletically in at least seven families ranging from the Cambrian to the Silurian. We describe a new species of Ordovician (Tremadoc) olenid trilobite, *Parabolinella bolbifrons*, having this morphology. A review of other trilobites with apparently similar cephala shows that the bubble-headed appearance was derived in several different ways and probably acquired different functions. In deiphonine cheirurids, staurocephalids and *Paraphillipsinella* all, or only the frontal part of the glabella, is involved in the inflation. These species have rigidly attached conterminant hypostomes, and glabellar inflation may have matched a comparable inflation of the stomach. In the new species, as in several Cambrian examples with natant hypostomes, inflation is confined to a median area of the preglabellar field. This is unlikely to have involved any modification of the alimentary system.

TRILOBITES displayed many modifications to their dorsal shields through their 300 million year history. The cephalon was particularly prone to drastic evolutionary change, such as loss of the eyes, general effacement, or becoming covered in coarse tuberculation. When we were reviewing evolutionary trends in trilobites (Fortey and Owens 1990) we recognized certain morphologies that had arisen repeatedly during trilobite history. Usually, these were morphological packages involving the entire exoskeleton. We termed these recurring designs morphotypes. The assumption was made that such morphotypes represented a specific mode of life, which trilobites adopted repeatedly. The olenid morphotype, for example, included such features as a low cephalic and axial convexity, multiplication of thoracic segments, which became narrow (sag.), but with wide pleurae, and a notably thin exoskeleton. The olenid morphotype arose on several occasions from different phylogenetic origins; we regarded it as an adaptation for life in oxygen-poor (dysaerobic) habitats. Another morphological modification that impressed us concerned the cephalon. We found a number of trilobites in which some part of the axial region was inflated dramatically into a perfectly spherical balloon, or bubble-like structure. These are the bubble-headed forms that we discuss in this paper, and we discuss whether or not these remarkable trilobites comprise another morphotype.

During the same period we were also investigating the faunas of the British Tremadoc (Fortey and Owens 1991*b*, 1992). In the course of this work we revised the olenid trilobite *Beltella* (Fortey and Owens 1991*a*) from material in the Bristol City Museum collected by M. L. K. Curtis and T. R. Fry from temporary exposures of the Breadstone Shales in the Tortworth Inlier, Gloucestershire. Unlike many Tremadoc fossils in the British Isles this material has suffered little tectonic distortion. In the same collection there is another, remarkable olenid assigned to the genus *Parabolinella*, which provides a beautiful example of bubble-head morphology; this new species is described below.

PHYLOGENETIC ORIGINS OF BUBBLE-HEADED TRILOBITES

It is clear that the bubble-headed morphology may have been derived from more than one phylogenetic source. It is a morphology which has been described from several families ranging from the Cambrian to the Silurian. In a few groups (Staurocephalidae, Nepeidae) the bubble-head

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construction has been accorded familial significance. In other cases, one or more genera within a family develop this feature, while its close relatives are more 'normal' trilobites. Many more trilobites exhibit a certain convexity in the antero-median region, without, however, displaying the independent convexity associated with bubble head morphology. In any case, there is no suggestion that all bubble-heads should be classified together. A selection of these trilobites is illustrated in Text-figure 1.

The following families include examples: Olenidae: – *Parabolinella bolbifrons*, described below; Phillipsinellidae – *Paraphillipsinella globosa* (Lu *in* Lu and Chang, 1974) is a typical example from the upper Ordovician of China and Thailand; Cheiruridae – *Deiphon barrandei* Whittard, 1934 (Silurian); *Sphaerocoryphe kingi* Ingham, 1974 (upper Ordovician); *Onycopyge liversidgei* Woodward, 1880 (Upper Silurian); Staurocephalidae – *Staurocephalus susanae* Thomas, 1981 (Silurian); Nepeidae – *Nepea* Whitehouse, 1939 (Middle Cambrian) and allied genera; Concoryphidae – a typical example is *Ctenocephalus barrandei* Hawle and Corda, 1847 (Middle Cambrian; see Šnajdr 1990, pl. 100). There are several additional genera whose familial affinities are under debate. The genus *Amzasskiella* Poletaeva, 1960 is a late Cambrian trilobite widespread through central and eastern Asia. *Toxotis* Wallerius, 1895 (middle Cambrian, Sweden) is probably not related to *Nepea.* Jell (1985) described another example, *Natmus*, from the lower Ordovician (Tremadoc) of Tasmania. Tumid glabellas which approach 'bubble-head' morphology in their convexity are known from such families as the Trinucleidae (e.g. *Tretaspis ceriodes* (Angelin, 1854) – see Owen 1980), Eodiscidae (e.g. *Acimetopus bilobatus* Rasetti, 1966) and Aulacopleuridae (e.g. *Cyphaspis hydrocephala* Roemer, 1843; see Přibyl and Vaněk 1981).

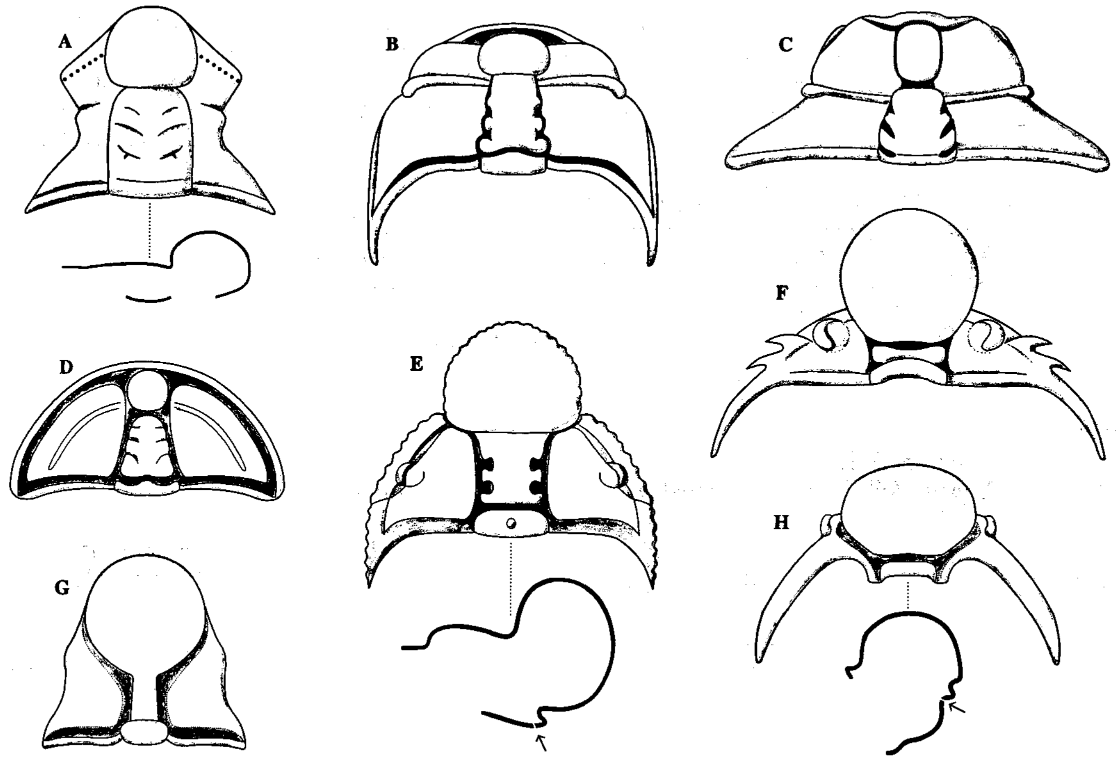
In the classification system employed in the *Treatise* (Moore 1959) or modified by Fortey (1990), Cheiruridae and Staurocephalidae are placed in the order Phacopida; Phillipsinellidae was assigned by Bruton (1976) and Fortey (1990) to the suborder Scutelluina, and possibly the order Corynexochida. Olenidae, Nepeidae and Conocoryphidae could be classified among the Ptychopariida. Hence the morphology arose independently in three different orders, and more if the examples with tumid glabellas are included. Furthermore, there is evidence that even within a given order the modification occurred independently in each example. *Staurocephalus* probably does not share a common ancestor with *Deiphon* and *Sphaerocoryphe* (Lane 1971). The olenid described below is evidently closer to other species in the same genus, *Parabolinella*, than it is to *Nepea* or *Ctenocephalus. Paraphillipsinella* is related to *Phillipsinella*, a small trilobite with a tumid glabella but hardly a spherical one. We consider it likely therefore, that bubble-headedness arose independently in all these examples. This carries with it the implication that for all its distinctiveness this drastic cephalic modification enjoys a relatively trivial phylogenetic burden. It could be relatively easily acquired. In this case the next question to address is whether the feature is homologous or even analogous in the different examples cited. In other words, it can be questioned whether bubble-heads truly characterize a morphotype, a design likely to have shared a common life habit.

ARE BUBBLE-HEADED TRILOBITES A DISTINCT MORPHOTYPE?

We consider it improbable that bubble-head development is homologous, or even analogous, in the various cases in which we have observed it. This is because the inflation in various examples is manifested in different parts of the cephalic axial anatomy.

Deiphon *type* (Text-fig. 1F, H). Much of glabella inflated in front of the occipital ring

In *Deiphon* (see Lane 1971; Holloway 1980, p. 39) and *Onycopyge* (see Holloway and Campbell 1974) inflation affects much of the glabella in front of the occipital segment. A relict L1 remains as a pair of inconspicuous nodes within the preoccipital depression. In *Sphaerocoryphe* this portion of the glabella is more conspicuous.



TEXT-FIG. 1. Examples of bubble-head morphology. A, Olenidae. *Parabolinella bolbifrons* sp. nov., with lateral view showing inferred position of hypostoma (based on specimens illustrated in Plate 1). B, Nepeidae. *Ferenepea hispida* Öpik, 1967, Middle Cambrian, north-west Queensland (after Öpik, 1967, pl. 39, fig. 8). C, Triplacephalidae. *Amzasskiella* [= *Triplacephalus*] *sanduensis* (Lu and Qian *in* Wang and Jin, 1977), Ordovician, Tremadoc Series, Guizhou Province, China (after Lu and Qian 1977, pl. 48, fig. 4). D, Conocoryphidae. *Ctenocephalus howelli* Resser, 1937, Middle Cambrian, south-east Newfoundland (after Hutchinson, 1962, pl. 12, fig. 18). E, Staurocephalidae. *Staurocephalus susanae* Thomas, 1981, Silurian, Wenlock Series, central England, dorsal and lateral views; arrow indicates hypostomal suture (after Thomas 1981, text-fig. 8, p. 66 and pl. 17, figs 2, 5, 9). F, Cheiruridae, Deiphoninae. *Sphaerocoryphe kingi* Ingham, 1974, Ordovician, Ashgill Series, Northern England (after Ingham 1974, text-fig. 22, p. 72). G, Phillipsinellidae. *Paraphillipsinella globosa* Lu *in* Lu and Chang, 1974, Ordovician, Caradoc Series, Gansu Province, China (after Zhou and Dean 1986, pl. 62, fig. 13). H, Cheiruridae, Deiphoninae. *Deiphon barrandei* Whittard, 1934, Silurian, Wenlock Series, central England, dorsal and lateral views; arrow indicates hypostomal suture (after Lane 1971, pl. 12, figs 1, 4, 6, 9).

Staurocephalus *type* (Text-fig. 1 E, G). Frontal lobe of glabella inflated

In *Paraphillipsinella* and *Staurocephalus* inflation affects only the anterior lobe of the glabella, while the posterior part of the glabella retains normal convexity.

Nepea *type* (Text-fig. 1 A–D). Preglabellar field inflated

In *Nepea*, as in *Parabolinella bolbifrons* described below, it is clear that the inflated area is derived entirely from that part of the exoskeleton lying anterior to the glabella. It is the preglabellar field in its median region which is transformed. A similar origin applies for the inflated areas in *Ctenocephalus*, *Amzasskiella*, *Toxotis* and *Natmus*.

These three cases are all different; they are certainly not homologous. It is extremely doubtful whether they are an expression of adoption of a similar life habit.

Ventrally, the structure of *Parabolinella bolbifrons* differs remarkably from that of cheirurid and *Paraphillipsinella* examples. We show below that the bulb is underlain by the preglabellar field in *P. bolbifrons*. Since the doublure is demonstrably narrow, and the natant hypostome is likely to have resided beneath the frontal lobe of the glabella, it is clear that the posterior part of the inflated area was underlain only by the ventral membrane (see Text-fig. 2), and it is likely that this also applied to the examples known from the Cambrian. However, in the younger examples, where all or part of the glabella is inflated, the ventral side of the bulb is continued posteriorly by the hypostome, together with the border and rostral plate (Text-fig. 1E, H; Lane 1971, pl. 13, fig. 12). Since the oesophagus and stomach were located under the cephalic axis it seems reasonable to infer that in these bubble-heads the stomach had become inflated likewise. This may reflect a change in diet, for example. This cannot have been the case in *Parabolinella bolbifrons* in which the inflation is unconnected with the glabella, and indeed specifically excluded it.

Ruedemann (1934) and Whittard (1934) regarded *Deiphon* and *Onycopyge* as planktic, arguing that the swollen glabella may have contained a low-density substance to aid flotation. Convincing arguments against this theory were advanced by Holloway and Campbell (1974). It is likely that all bubble heads were part of the benthos. Olenids such as *Parabolinella* appear to have been adapted to life in environments with low oxygen (dominated by this family; Henningsmoen 1957), whereas the other bubble-heads appear to have been inhabitants of diverse, open-shelf faunas.

Hence, despite a superficial similarity, bubble-headed trilobites are not comparable with regard to their structure, nor likely to have shared a common adaptation. There appear to be two major ways in which the morphology can be derived: by inflation of the preglabellar area, or by inflation of all or part of the glabella itself. These two morphologies are associated with natant trilobites, on the one hand, and conterminant ones on the other. There is no single bubble-head morphotype. This example shows that it is necessary to understand fully the genesis of a striking structure before assuming that all trilobites displaying it were the product of a similar adaptation.

SYSTEMATIC PALAEONTOLOGY

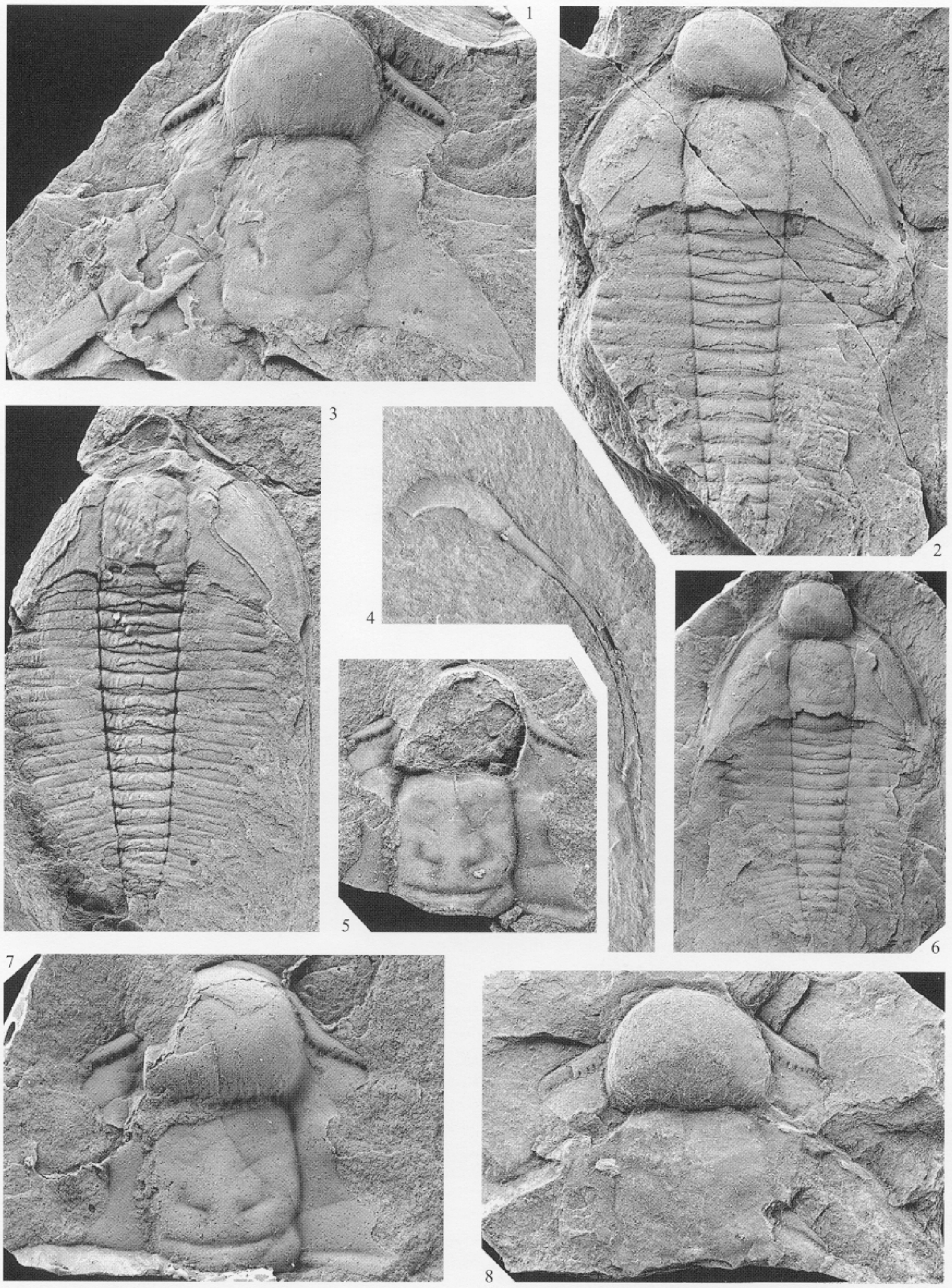
Family OLENIDAE Burmeister, 1843

Genus PARABOLINELLA Brøgger, 1882

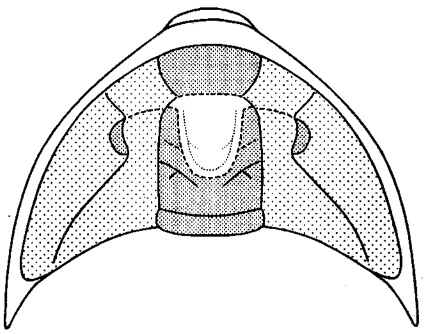
Type species. Parabolinella limitis, Brøgger, Tremadoc, Norway.

EXPLANATION OF PLATE 1

Figs 1–8. *Parabolinella bolbifrons* sp. nov.; Ordovician, Tremadoc Series, Breadstone Shales; Tortworth Inlier, Gloucestershire. 1, BRSMG Cc2133; cranidium showing pits in border furrow; ×1·5. 2, 6, BRSMG Cb4807; incomplete dorsal exoskeleton; 2, ×1·5; 6, latex cast from the counterpart; ×1. 3, BRSUG 26361; large, incomplete exoskeleton; ×1; 4, BRSMG Cc2132; doublure of free checks, preserved from the ventral side; ×1·5. 5, 7, BRSMG Cc2139; cranidium, preserving some relief; 5, ×2; 7 latex from counterpart; ×3. 8, BRSMG Cc2134; poor cranidium with well-preserved bulb; ×1.5. Figs 2, 6, holotype; all others paratypes. All internal moulds unless stated otherwise. BRSMG: Bristol City Museum; BRSUG: University of Bristol, Department of Geology.



FORTEY and OWENS, *Parabolinella*



TEXT-FIG. 2. *Parabolinella bolbifrons* sp. nov.; reconstruction of ventral side of cephalon, showing inferred position of hypostoma.

Parabolinella bolbifrons sp. nov.

Plate 1, figures 1–8; Text-figures 1A, 2

1996 *Parabolinella* sp. nov. Owens, p. 69, pl. 1, figs C–D.

Derivation of name. Latin, referring to its characteristic median anterior inflation.

Holotype. Incomplete dorsal exoskeleton, Bristol City Museum, BRSMG Cb4807.

Paratypes Incomplete dorsal and cephalic shields BRSUG 26361 (Bristol University), BRSMG Cc2127, Cc2128, Cc2133, Cc2134, Cc2139 Cc2141 and a doublure of yoked cheeks BRSMG Cc2132.

Occurrence. All material is from exposures of the Breadstone Shales (Tremadoc) in a temporary trench 192 m W 32° S of Crawless Old Barn, south-south-west of Breadstone, in the Tortworth Inlier, Gloucestershire [ST 7026 9997]. Curtis (1968) described the stratigraphy of this area and has made extensive new collections from temporary exposures in the soft shales. Fortey and Owens (1991*a*) redescribed the olenid trilobite *Beltella depressa* from the same exposures; this species occurs elsewhere in the Lower Tremadoc (Cressagian Stage in the terminology of Fortey *et al.* 1995; see also Owens 1996), which is thus the age of *P. bolbifrons*.

Diagnosis. *Parabolinella* with preglabellar field inflated into a balloon-like structure. Eye small, positioned anteriorly, and facial sutures moderately divergent both in front of and behind eyes.

Description. Like most *Parabolinella* species this trilobite is of medium size. None of our material is complete, but incomplete dorsal shields are more than 70 mm long and whole animals certainly exceeded 80 mm in length. All specimens are somewhat flattened, and it is not possible to say much about the original convexity, other than that it is likely to have been low, as in the rare examples of the genus preserved in relief (see Henningsmoen 1957). The degree of flattening is likely to have affected certain features, for example, the angular divergence of the facial sutures. However, the preglabellar bulb is invariably preserved in some relief. None of the specimens extends posteriorly to the pygidium.

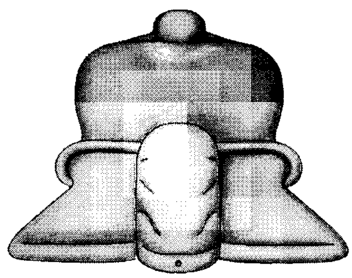
Cephalic shield about two-thirds as long (sag.) as wide. Glabella rectangular, length hardly exceeding width, front notably truncate, occupying less than one-third of transverse cephalic width. The large cranidium on Plate 1, figure 1 shows a bulge in width at the level of 1S. Occipital ring 20 per cent. of glabellar length, defined by deep occipital furrow which is effaced only at its extremities. Occipital tubercle present, but inconspicuous. Of glabella furrows, 1S especially is marooned in glabella, the result of lateral effacement not uncommon in *Parabolinella* species; outer end forked. 2S appears to be longer, more complete on most specimens, curved inwards and backwards and extending to just over one-third of glabellar width. On other *Parabolinella* species 3S and 4S are very short and isolated within the glabella, and 3S at least can be seen on the specimen on Plate 1, figure 5. Palpebral lobes are short (exsag.), having about the same length as the occipital ring, are approximately in line with the outer end of S2 in a forward position, and are removed from glabella by about one-third of the width of its adjacent part. Posterior border furrow on fixed cheek shallow. Facial suture diverges in front of, and behind eye at a similar angle, but the length of the anterior section is one-quarter to one-third the length of the posterior section. Divergence varies between 30° to 55° to sagittal line, but this angle may well have been affected by flattening. Anterior border furrow is comparatively deep, and was probably originally deeper than lateral and posterior border furrows. The best preserved specimens show seven to ten pits in the cranidial anterior border furrow to either side of the median inflation. This 'bulb' is a strongly inflated, subspherical structure which impinges on and grows over the border. Its transverse width is equal to, or slightly exceeds that of the glabella behind. Its posterior edge is usually marked with a few faint rugae, parallel to sagittal line. The dorsal surface lacks any sculpture.

Free cheeks are yoked. Narrow lateral border is prolonged into long and very gently curved, needle-like, genal spines which seem to extend alongside the whole length of the body. A ventrally preserved pair of cheeks (Pl. 1, fig. 4) shows that the doublure widened slightly, but distinctly across the median part having the bulb dorsally. On the largest specimen (Pl. 1, fig. 3) doublure preserved on the right is seen to extend about half-way across the preglabellar field. Assuming it was bounded at its outer edge by the median section of the facial suture, this proves that the doublure underlay only part of the bulb. Although the hypostome is not preserved it is likely to have sat beneath the frontal lobe of the glabella (Text-fig. 2) as it is in the similar olenid *Hypermecaspis* (see Fortey 1990, pl. 1, fig. 1) and in other natant trilobites. In all other olenids known to us the doublure is extremely narrow and retains the same width across the mid-line. Thus the widening in *P. bolbifrons* is probably connected with a partial ventral extension of the bulb, but falls well short of the anterior hypostomal margin.

No specimen is entire. There were 17 or 18 thoracic segments in total and presumably a comparatively small pygidium. The thorax is twice as long as the cephalic shield. Axis tapers very gently along the whole length of the thorax; half rings extend to almost half sagittal length of a ring. Pleurae are wider (tr.) than axis, and the pleural furrow extends almost along the length of each pleura as preserved, almost to spinose tips.

Remarks. The bulb distinguishes the new species from all others of *Parabolinella*. However, there is some evidence of preglabellar inflation in some of the Argentine specimens attributed to *Parabolinella argentinensis* by Harrington and Leanza (1957, fig. 37.5). Fortey and Owens (*in* Owens *et al.* 1982, pl. 1, fig. g) figured a specimen attributed to *Parabolinella argentinensis* from the Tremadoc of South Wales which also seems to show a similar glabella inflation; although this specimen is seriously flattened it shows proportions comparable to those of *P. bolbifrons*. However, the bulb does not grow across the anterior border as it does in *P. bolbifrons*, and it is unlikely they are conspecific.

TEXT-FIG. 3. *Bulbolenus bellus* Xiang and Zhang, 1983; reconstruction of cranidium for comparison with that of *Parabolinella bolbifrons* sp. nov. (based on Xiang and Zhang, 1983, pl. 33, figs 1, 3, 5); ×8 approximately.



We note that there are similar bulbs developed on several Cambrian genera, for example, *Amzasskiella* Poletaeva, 1960 (= *Triplacephalus* Lu and Qian *in* Wang and Jin, 1977) and *Nepea* Whitehouse, 1939. However, the glabella structure, genal spines, and features of the thorax all indicate that *P. bolbifrons* is an olenid. We do not consider the possession of a bubble-head alone as an adequate basis for the erection of a new genus, for in almost all its other morphological features *P. bolbifrons* is very similar to *Parabolinella triarthra* (Callaway) (see Lake 1913, p. 68, pl. 7, figs 4–12; Fortey and Owens *in* Owens *et al.* 1982, pl. 1, fig. k). We regard the inflated lobe as no more than an autapomorphy of *P. bolbifrons*. A small exoskeleton in the Bristol collections associated with *P. bolbifrons* (BRSMG Cc2140) is 15 mm long and hardly shows any sign of median inflation of the preglabellar field. It is possible that the inflation only developed late in ontogeny (although the specimen is very likely to have been an holapsis); alternatively, this is a specimen of *P. triarthra*.

Another olenid (or olenid-like) genus, *Bulbolenus* Xiang and Zhang, 1983 from the Cambrian of Xinjiang, China, has a swelling on the median part of the anterior border and anterior border furrow, but this does not involve the preglabellar field, as in *P. bolbifrons* (cf. Pl. 1, figs 1–8 with Xiang and Zhang 1983, pl. 33, figs 1–6 and pl. 34, figs 1–11, and Text-fig 1A and Text-fig. 3); therefore another, quite different type of anterior median swelling developed independently within the olenids.

Finally, it may be considered possible that the bubble is a teratology, caused by infection by a parasite. For example, among the living fauna deformities in infected fish and arthropods are caused by parasitic copepods. We think that this is unlikely for two reasons.

1. The consistent size and position of the inflation. All our examples seem to be developed to the same degree, overhang the border to a comparable extent and show similar inflation. It is improbable that an infestation would always express itself in exactly the same fashion.

2. The form appears to be stratigraphically limited to a distinct population. If a parasite was the cause, one might with reason expect to find occasional pathological individuals in a range of different *Parabolinella* species, which is not the case.

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REFERENCES

ANGELIN, N. P. 1854. *Palaeontologica Scandinavica 1: Crustacea formationis transitionis.* Fasc. II. Lund, i–ix, 21–92, pls 25–41.

BRØGGER, W. C. 1882. *Die silurischen Etagen 2 und 3 im Kristianiagebeit. &c.* Universitats – programme (Kristiania), 376 pp., 12 pls.

BRUTON, D. L. 1976. The trilobite genus *Phillipsinella* from the Ordovician of Scandinavia and Great Britain. *Palaeontology*, **19**, 699–714.

BURMEISTER, H. 1843. *Die Organisation der Trilobiten.* Georg Reimer, Berlin. 148 pp., 4 pls.

CURTIS, M. L. K. 1968. The Tremadoc rocks of the Tortworth inlier, Gloucestershire. *Proceedings of the Geologists' Association*, **79**, 349–362.

FORTEY, R. A. 1990. Ontogeny, hypostome attachment and trilobite classification. *Palaeontology*, **33**, 529–576.

—— HARPER, D. A. T., INGHAM, J. K., OWEN, A. W. and RUSHTON, A. W. A. 1995. A revision of Ordovician series and stages from the historical type area. *Geological Magazine*, **132**, 15–30.

—— and OWENS, R. M. 1990. Trilobites. 121–142. *In* McNAMARA, K. J. (ed.). *Evolutionary trends.* Belhaven Press, London, xviii + 318 pp.

—— 1991*a*. The early Ordovician trilobite *Beltella. Proceedings of the Bristol Naturalists' Society*, **49**, 69–79 [for 1989].

—— 1991*b*. A trilobite fauna from the highest Shineton Shales in Shropshire, and the correlation of the latest Tremadoc. *Geological Magazine*, **128**, 437–464.

—— 1992. The Habberley Formation, youngest Tremadoc of the Welsh Borderland. *Geological Magazine*, **129**, 553–566.

HARRINGTON, H. J. and LEANZA, A. F. 1957. *Ordovician trilobites of Argentina.* University of Kansas Press, Lawrence, Kansas, Department of Geology Special Publication 1, 276 pp.

HAWLE, I. and CORDA, A. J. C. 1847. Prodrom einer Monographie der böhmischen Trilobiten. *Abhandlungen der Königlichen Böhmischen Gesellschaft der Wissenschaften*, **5**, 1–176, pls 1–7.

HENNINGSMOEN, G. 1957. The trilobite family Olenidae. *Skrifter av det Norske Videnskaps-Akademie i Oslo, 1, Mat.-nat. Klasse for 1957*, **1**, 1–303, pls 1–31.

HOLLOWAY, D. J. 1980. Middle Silurian trilobites from Arkansas and Oklahoma, U.S.A. Part 1. *Palaeontographica, Abteilung A*, **170**, 1–85, pls 1–20.

—— and CAMPBELL, K. S. W. 1974. The Silurian trilobite *Oncyopyge* Woodward. *Palaeontology*, **17**, 409–422.

HUTCHINSON, R. D. 1962. Cambrian stratigraphy and trilobite faunas of southeastern Newfoundland. *Bulletin of the Geological Survey of Canada*, **88**, i–ix + 1–160, pls 1–25.

INGHAM, J. K. 1974. The Upper Ordovician trilobites from the Cautley and Dent districts of Westmorland and Yorkshire. Part 2. *Monograph of the Palaeontographical Society*, **128** (538), 59–87, pls 10–18.

JELL, P. A. 1985. Tremadoc trilobites of the Digger Island Formation, Waratah Bay, Victoria. *Memoirs of the Museum of Victoria*, **46**, 53–88, pls 19–33.

LAKE, P. 1913. A monograph of the British Cambrian trilobites, part 4. *Monograph of the Palaeontographical Society*, **66** (324), 65–88, pls 7–10.

LANE, P. D. 1971. British Cheiruridae. *Monograph of the Palaeontographical Society*, **125** (530), 1–95, pls 1–16.

LU YAN-HAO and CHANG WENG-TANG. 1974. [Ordovician trilobites.] 124–136, pls 49–56. *In* [*Handbook of stratigraphy and palaeontology in southwest China.*] Science Press, Beijing, iii + 454 pp., 202 pls. [In Chinese].

MOORE, R. C. (ed.). 1959. *Treatise on invertebrate palaeontology. Part O. Arthropoda 1.* Geological Society of America and University of Kansas Press, Lawrence, Kansas, 560 pp.

ÖPIK, A. A. 1967. The Mindyallan fauna of north-western Queensland. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics, Commonwealth of Australia*, **74**, 1–404.

OWEN, A. W. 1980. The trilobite *Tretaspis* from the upper Ordovician of the Oslo region, Norway. *Palaeontology*, **23**, 715–747.

OWENS, R. M. 1996. Trilobites of the Bristol district. *Proceedings of the Bristol Naturalists' Society*, **54**, 67–84 [for 1994].

—— FORTEY, R. A., COPE, J. C. W., RUSHTON, A. W. A. and BASSETT, M. G. 1982. Tremadoc faunas from the Carmarthen District, South Wales. *Geological Magazine*, **119**, 1–38, pls 1–7.

POLETAEVA, O. K. 1960. [New genera and species of Cambrian trilobites of western Siberia.] *Trudy Sibirskogo Nauchno-Issledovatel'skogo Instituta Geologii, Geofiziki i Mineral'nogo Syr'ya*, **8**, 50–76, pls 1–3. [In Russian].

PŘIBYL, A. and VANĚK, J. 1981. Studie zur Morphologie und Phylogenie der Familie Otarionidae R. & E. Richter, 1926 (Trilobita). *Palaeontographica, Abteilung A*, **173**, 160–208, pls 1–9.

RASETTI, F. 1966. New Lower Cambrian trilobite faunule from the Taconic sequence of New York. *Smithsonian Miscellaneous Collections*, **148**, 9, 1–52, pls 1–12.

RESSER, C. E. 1937. New species of Cambrian trilobites of the family Conocoryphidae. *Journal of Paleontology*, **11**, 39–42, pl. 7.

ROEMER, F. A. 1843. *Die Versteinerungen des Harzgebirges.* Hahn, Hannover, 40 pp., 12 pls.

RUEDEMANN, R. 1934. Paleozoic plankton of North America. *Memoirs of the Geological Society of America*, **2**, 1–141, pls 1–26.

ŠNAJDR, M. 1990. *Bohemian trilobites.* Geological Survey, Prague, 265 pp.

THOMAS, A. T. 1981. British Wenlock trilobites. Part 2. *Monograph of the Palaeontological Society*, **134** (559), 57–99, pls 15–25.

WALLERIUS, I. D. 1895. *Undersökningar öfver zonen med* Agnostus laevigatus *i Vestergötland jämte en inledande öfversikt af Vestergötlands samtliga* Paradoxides-*lager.* Uppsala University Dissertations, Lund, Sweden, 72 pp.

WANG XIAO-FENG and JIN YU-QIN (eds). 1977. [*Palaeontological atlas of central and southern China (1. Lower Palaeozoic).*] Geological Press, Beijing, 411 pp., 116 pls. [In Chinese].

WHITEHOUSE, F. W. 1939. The Cambrian faunas of north-eastern Australia. *Memoirs of the Queensland Museum*, **11**, 179–282, pls 19–25.

WHITTARD, W. F. 1934. A revision of the trilobite genera *Deiphon* and *Onycopyge*. *Annals and Magazine of Natural History, Series 10*, **14**, 505–533, pls 15–16.

WOODWARD, H. 1880. Description of a new species of trilobite, *Onycopyge liversidgei*, from the Silurian of New South Wales. *Geological Magazine*, **7**, 97–99.

XIANG LI-WEN and ZHANG TAI-RONG. 1985. Trilobita. 64–136. *In* [Stratigraphy and trilobite faunas of the Cambrian in the western part of northern Tianshan, Xinjiang]. *Geological Memoir of the People's Republic of China, Ministry of Geology and Mineral Resources. Series 2*, **4**, i–ix + 1–243 [In Chinese, English Summary].

ZHOU ZHI-YI and DEAN, W. T. 1986. Ordovician trilobites from Chedao, Gansu Province, North-west China. *Palaeontology*, **29**, 743–786.

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