

# *Acanthopleurella* Groom 1902: origin and life-habits of a miniature trilobite

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## Synopsis

The Tremadoc genus *Acanthopleurella* includes the smallest of mature trilobites. The type species, *A. grindrodi*, is revised and a new species *A. stipulae* described. They both have four thoracic segments and were derived neotenously from a shumardiid ancestor by suppression of the release of two (?) segments. They were specialized, secondarily blind, burrowing deposit feeders. The extremely small size of *A. stipulae* enabled it to co-exist with *Conophrys salopiensis*, inhabiting the same substrate.

## Introduction

In 1902 Professor Theodore Groom described the tiny trilobite *Acanthopleurella grindrodi* from the Tremadoc rocks of the Malvern Hills, but his material consisted only of internal moulds in an unsatisfactory state of preservation. Despite observations by Stubblefield (1926) and Lake (1946), and a figure by Bulman & Rushton (1973), the genus has remained little known. We have now, however, studied several good complete specimens, and not only confirm that *Acanthopleurella* is a valid genus with at least two species, but consider that it includes the smallest known adult trilobites. Its morphology is quite complex and it is possible to draw some functional conclusions concerning its mode of life and to investigate the possible causes of miniaturism in trilobites, a topic briefly considered by Robison & Campbell (1974).

In the form of its cranidium and glabella, the structure of the thoracic pleurae and the pygidium, *Acanthopleurella* is clearly related to *Shumardia* Billings, and in the discussion below we make many comparisons with the Shineton Shales species *Conophrys salopiensis* Callaway, a species formerly often referred to as *Shumardia pusilla* (Sars); this is not the place to discuss the validity of *Conophrys salopiensis*, but in using Callaway's name we intend to refer primarily to the well-known Shineton Shales form.

## Miniaturized trilobites

**Size.** Although tiny, *Acanthopleurella* is not based on the young stages of larger trilobites. The only similar-looking forms are shumardiids, but Stubblefield (1926) showed that the form named *A. stipulae* here could not be regarded as normal growth-stages of *C. salopiensis*. Furthermore, the known size range of holaspids of *A. stipulae* (with four free thoracic segments) is considerable, from 1.07 mm to 1.50 mm. This indicates a greater size range than in any of the meraspid degrees of *C. salopiensis* described by Stubblefield (1926).

With a sagittal length of 1.07 mm to 1.50 mm *A. stipulae* appears to be the smallest trilobite known. Agnostids generally enter the holaspid condition at a length of 3 mm or more; the eodiscid *Opsidiscus* is 2 mm or more in length (cf. Westergård 1946). A small complete *Schualenseeia* is 2.75 mm long (Westergård 1922 : pl. 1, fig. 19). The holotype of *Hospes clonograpti* Stubblefield (*in* Stubblefield & Bulman 1927 : 129) is 2.51 mm long; smaller specimens seem not

to be holaspides. *Thoracocare minutum* Robison & Campbell (1974 : 278) reaches the holaspid state at a length of 1.7 mm and is in the meraspid condition at 1.15 mm (1974 : fig. 1B). Shumardiids are generally considerably larger, but Stubblefield recorded a *C. salopiensis* 'meraspis of degree 6' – a holaspis in more general if less precise terms – only 1.81 mm long; and *Shumardia nericiensis* Wiman (1905) is only about 2 mm long.

**Origin.** *Shumardia* and *Conophrys* are in any case small and most species have six thoracic segments (but some species have five or seven). *Acanthopleurella* has only four, and part of the miniaturization of the genus is produced by reduction of the number of segments. But it is not as simple as that. *Acanthopleurella* holaspides with four segments are larger than degree 4 meraspides of *Conophrys salopiensis* (Fig. 12). Stubblefield has shown that in *Conophrys* the fourth, macropleural, segment, after being released from the transitory pygidium, migrates forwards in successive moults as the posterior two segments are added. In *Acanthopleurella* the process stops after the release of the fourth segment, which is presumed to be homologous with the macropleural fourth segment in *Conophrys*. The third thoracic segment on *Acanthopleurella* is also spinose, and on the meraspis three pairs of spines are present (Fig. 19). Hence during its ontogeny segments bearing the first two spines migrate forwards to be released as the two segments with spinose pleurae, while the posterior, third pair is aborted.

It is reasonable to assume that the *Conophrys* condition, generally with six segments, is primitive, and the *Acanthopleurella* condition, with four, is derived. The six-segment condition is also persistent, since the much younger species *Shumardia granulosa* Billings (redescribed in Whittington 1965) also has six segments. There may have been a five-segment stage between a *Conophrys*-like ancestor and *Acanthopleurella* (*C. ?curta* Stubblefield has five segments), but since there are

**Figs 1–4** *Acanthopleurella grindrodi* Groom. All  $\times 20$ . Fig. 1, IGS TW454A. Latex cast of dorsal exoskeleton. Figd Bulman & Rushton (1973 : pl. 6, fig. 6). Combe Abbey no. 1 Borehole, near Coventry, at 76 m depth. Fig. 2, IGS Zg184. Latex cast of dorsal exoskeleton. Bronsil Shales, south of Chase End Hill, near Malvern. Fig. 3, Holotype, University Museum, Oxford, A7. 'Dictyonema-shales' of the Malvern Hills. Imperfectly preserved internal mould, partly enrolled. Mould of the macropleural spine on the left appears as dark hole. Figd Groom (1902 : fig. 3) and Lake (1907 : pl. 4, fig. 3). Fig. 4, Paratype, University Museum, Oxford, A8. Internal mould of thorax and pygidium, loc. as for Fig. 3. Figd Groom (1902 : fig. 4).

**Figs 5–10, 13–15, 19** *Acanthopleurella stipulae* sp. nov. All  $\times 20$  except Fig. 19. Shinton Shales, Sheinton Brook, loc. 'RR2' of Stubblefield & Bulman (1927 : pl. 5). Fig. 5, Latex cast of holotype, complete exoskeleton, with associated cranium. IGS Zs6184. Note genal spines. Fig. 6, IGS Zs6186, cranium showing anterolateral lobes. Fig. 7, IGS GSM 58712, smallest holaspis, figd Lake (1907 : pl. 4, fig. 4). Fig. 8, BM(NH) In26816a, holaspis with damaged axis and pyritized spines. Figd Stubblefield (1926 : pl. 15, fig. 16). Fig. 9, IGS Zs6187, pygidium, poorly preserved internal mould but with pyritized border showing granules. Fig. 10, IGS Zs6182, pygidium showing large tubercles on pleural fields and well-developed anterior segment. Fig. 13, IGS Zs6185, meraspis of degree 3, showing pygidial doublure and pyritized spines on third thoracic segment and anterior of transitory pygidium. Fig. 14, IGS GSM 48713, largest holaspis, figd Lake (1907 : pl. 4, fig. 2). Fig. 15, Latex cast of BM(NH) In 26816b, showing large articulating half-ring on third thoracic segment. Fig. 19, Scanning electron micrograph of latex cast from meraspis of degree 0 on same rock chip as holotype. Note marginal spines and suture between cephalon and protopygidium.  $\times 90$ .

**Figs 11–12, 16–17** *Conophrys salopiensis* Callaway. Shinton Shales, Sheinton Brook, loc. 'RR2' of Stubblefield & Bulman (1927 : pl. 5). Fig. 11, BM(NH) In26819,  $\times 9$ , internal mould of complete exoskeleton in oblique side view to show facial suture. Figd Stubblefield (1926 : pl. 16, fig. 20). Fig. 12, BM(NH) In26815,  $\times 20$ , internal mould of meraspis degree 4 showing macropleural spine on fourth segment. Figd Stubblefield (1926 : pl. 15, fig. 15). Figs 16, 17, IGS Zs6188 (Stubblefield & Bulman coll.), latex cast of exceptionally well preserved complete exoskeleton, dorsal and oblique lateral views,  $\times 9$ , showing facial suture and free cheeks, possibly conjoined.

**Fig. 18** *Conophrys* sp. IGS RU5885. Entire exoskeleton showing seven thoracic segments,  $\times 15$ . Lower Tremadoc Series, tributary of Nant-y-Gist-faen, near Arennig Fawr, North Wales.



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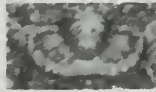
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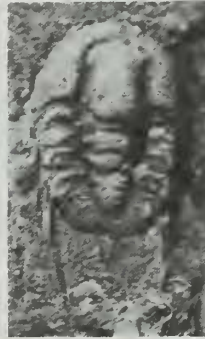
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examples (e.g. *Ceraurinella*, see Whittington & Evitt 1954) where several thoracic segments are released simultaneously into the thorax from the transitory pygidium, it seems perfectly possible to us that elimination of the release of two segments may have occurred as a single evolutionary step. Since *Acanthopleurella* had to be sexually mature, even at this small size, what essentially happened was a movement backwards (ontogenetically speaking) of sexual maturity – the process usually known as paedomorphosis.

A possibility that has to be reviewed is that *Acanthopleurella* was a sexual dimorph of *Conophrys*. This is improbable. In the first place the two forms are not invariably found together. For example, in the Amnodd Shales (near Arennig Fawr, Gwynedd) *Conophrys salopiensis* is common, but no example of *Acanthopleurella* has been discovered. Conversely at Malvern we have not noted a *Conophrys* from the same beds as *Acanthopleurella grindrodi*. If of opposite sex they would evidently have encountered one another very rarely! One might also expect, generally, *Shumardia*-like species would in that event tend to come in 'pairs', one male and one female morph occurring together. In our experience this is not so. In the early Ordovician of Spitsbergen, for example, where three species of shumardiid occur, they are found in sequence rather than together. Similarly the *Shumardia* Limestone in Quebec seems to contain only a single species, and that in great abundance.

### Life habits

The present example of miniaturization is not unique. Robison & Campbell (1974) have described a Cambrian corynexochoid trilobite *Thoracocare* with only two thoracic segments in the holaspide stage. It is likely that a similar process of miniaturization was involved in the genesis of the Agnostacea. Jell (1975) has discussed polymorphism in *Pagetta*, in which two- or three-segmented forms are recognized within a single species.

Robison (1972) and Jell (1975) concur that trilobites of the Agnostida (*sensu* Salter 1864) were pelagic or planktonic in habit. The same habits were deduced for *Thoracocare* (Robison & Campbell 1974). It should be noted, however, that some authors have proposed different life habits for the agnostids: for example, Bergström (1973) has suggested that they may have been parasitic on some (unspecified) free-swimming organism whereas Pek (1977) has presented evidence that some forms may have been epipelagic upon some floating seaweed, and Jago (1973) has suggested that they show some community behaviour related to former sea-bottom conditions, and hence may have included some benthic forms.

*Thoracocare* has large eyes and a very large pygidium, and is not really comparable to *Acanthopleurella* in its morphology. Agnostids were blind, like *Acanthopleurella*, but beyond this and their small size morphological comparisons cannot be extended in detail. Powerfully spinose agnostids are unusual, and we can only find one species in which the pleurae are spinose in the manner of *Acanthopleurella* (*Lejopyge laevigata armata* Westergård, 1946 : pl. 13, figs 32–36).

At the small adult size of *Acanthopleurella* genal and thoracic spines would have been effective in increasing frictional drag during descent through the water column. Many protaspides, which were supposedly planktonic, are well equipped with spines which would have inhibited sinking, as are Recent crustacean larvae. However, in this case we do *not* believe that the spines functioned as frictional brakes. In the first place they lie more or less horizontally alongside the thorax, so that in dorsal view they are not disposed in a way which would have been particularly effective in inhibiting sinking. If this had been their principal purpose one would have expected them to have been splayed out in the manner of odontopleurids, such as *Miraspis*, to present as large a surface area as possible. Second, the mid-thoracic spine would have had no influence on frictional drag. Third, *Acanthopleurella* seems to have had a very restricted distribution, being confined to Tremadoc shales of the Welsh borderlands and the English Midlands, not even extending over the whole region from which *Conophrys salopiensis* has been recovered. Fortey (1974 : fig. 4) has shown that pelagic trilobites tend to have an exceptionally elongate exoskeleton, whereas *Acanthopleurella*, the transverse width of which at mid-thorax is about three-quarters the length (sag.), is not unusual in this regard. The balance of the evidence suggests that *Acanthopleurella* was benthic,

and the fact that the meraspis degree 0 already had assumed the morphology characteristic of the adult further suggests that this habit was acquired from an early stage in ontogeny.

Some specimens (Figs 8, 15) show well-developed articulating half-rings, extending to almost the entire length of the preceding thoracic axial ring on the segments anterior to the macropleural segments. This implies considerable longitudinal flexibility. Given this fact, the lack of pleural spines on the first two thoracic segments can be explained: had spines been present on the first two segments any downward flexure of the cephalon (resulting in an upward swing of the genal spines) would have been prevented. Fig. 5 shows well how closely the genal spines approach the third thoracic segment.

Assuming benthic habits, we can extend the analysis of functional aspects of *Acanthopleurella* to enrollment. It is extremely unlikely that enrollment would have occurred by movement of the thorax relative to the cephalon, as this would have involved dragging the relatively enormous thoracic spines through the sediment. On the other hand, enrollment could have been achieved relatively easily by tucking the cephalon down and backwards beneath the pygidium; the short anterior thoracic pleurae permit unimpeded downward flexure of the cephalon. Most of the flexure seems to have been accommodated at the forward margin of the first, second and third segments, where, as we have noted, remarkably broad (sag.) articulating half-rings are developed. The resulting enrolled position might well have utilized the long backward-directed spines on the third and fourth thoracic segment as a means of support on the sediment surface during enrollment.

Both *Conophrys* and *Acanthopleurella* lack eyes, and, as in all trilobites, the blindness was secondary, as shown by the librigenal remnants figured in Figs 20a, b. We can eliminate great oceanic depth (Clarkson 1967) as a possible cause for this blindness because almost all the trilobites found in association with these shumardiids had normal eyes (except the agnostids), and were not different in eye development from other 'shelf' assemblages of the Tremadoc.

Blindness is explained by inferring that *Acanthopleurella* burrowed superficially in the surface layer of the argillaceous sediments with which it is associated, a life mode which rendered eyes superfluous. Reasonable support for this hypothesis is derived from a consideration of extant infaunal, minute crustacea. Even at 1–2 mm long *Acanthopleurella* is too large to be considered as a possible interstitial (meiofaunal) inhabitant, like the Mystacocarida, although visual surfaces are generally reduced in those forms. The best, and rather close, analogy is perhaps with cephalocarids (Sanders 1963). *Hutchinsoniella macraantha* has an adult length of 3 mm (excluding caudal spines) with a broadly hemispherical cephalon. It is blind, but secondarily so. It is benthic from early in its ontogeny, which, like that of shumardiids (but not of all trilobites), is a simple, progressive addition of segments without any profound morphological change. The principal morphological difference is the vermiform and flexible posterior segments of *Hutchinsoniella*. As we have inferred for *Acanthopleurella*, *Hutchinsoniella* lives in soft, muddy sediments. *Hutchinsoniella* extracts edible particles from detritus by using its limbs as a kind of filtration device. Whether or not *Acanthopleurella* used its limbs in the same way, it seems reasonable to suppose that it also extracted organic particles from the sediment. It is also worth noting that shumardiids occur in association with ostracods, with valve dimensions similar to the transverse cephalic dimensions of *Acanthopleurella* and *Conophrys* (Stubblefield & Bulman 1927; Bulman & Rushton 1973 : pl. 6). Benthic ostracods are also frequently deposit feeders, and it is not unreasonable to suppose that these arthropods were also concerned with exploiting the same source.

The occipital ring of *Acanthopleurella stipulae* is long (sag.) and produced backwards. This feature acquires significance if we assume that *Acanthopleurella* adopted an active feeding position with the cephalon tilted through an angle of perhaps 20° (Fig. 21c), in a manner similar to that shown by Clarkson (1969) for the Silurian odontopleurid *Leonaspis deflexa*. In this attitude the prolonged occipital ring serves to cover the 'gap' which would otherwise be created between thorax and cephalon. The genal spines then tilt upwards past the first two thoracic segments. Note that in *Leonaspis deflexa* the anterior thoracic pleural spines are (for an odontopleurid) also relatively abbreviated.

As a final comment on the function of the macropleural spines Ingham (1968 : fig. 3) has suggested that in *Cybelooides girvanensis*, a species equipped with long macropleurae, the spines

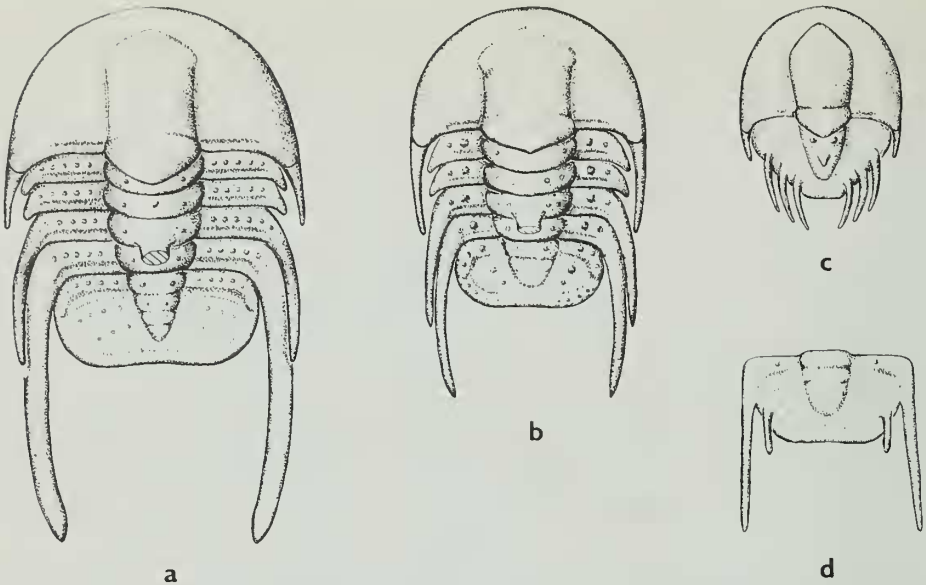


Fig. 20 (a) Reconstruction of *Acanthopleurella grindrodi* Groom,  $\times 30$ . (b–d) *A. stipulae* sp. nov.; (b) reconstruction,  $\times 30$ ; (c) meraspid of degree 0,  $\times 60$ , reconstructed from Fig. 19; (d) pygidium of meraspid degree 3,  $\times 60$ , based on an internal mould on the same rock-chip as the holotype.

functioned as an aid in burial, and that the long macropleural spine had a stabilizing function 'preventing excessive lateral rolling during arching of the thorax' while burial was in progress. *Acanthopleurella* may have spent a large part of its life buried at least within the semi-fluid surface layer of sediment. The vertical spine from the middle of the third thoracic segment, which we have not so far discussed, seems ideally placed to have acted as a sensor to make sure that burial did not proceed too far. At the minute size of *Acanthopleurella* we do not consider that the spines would have had a particular defensive function.

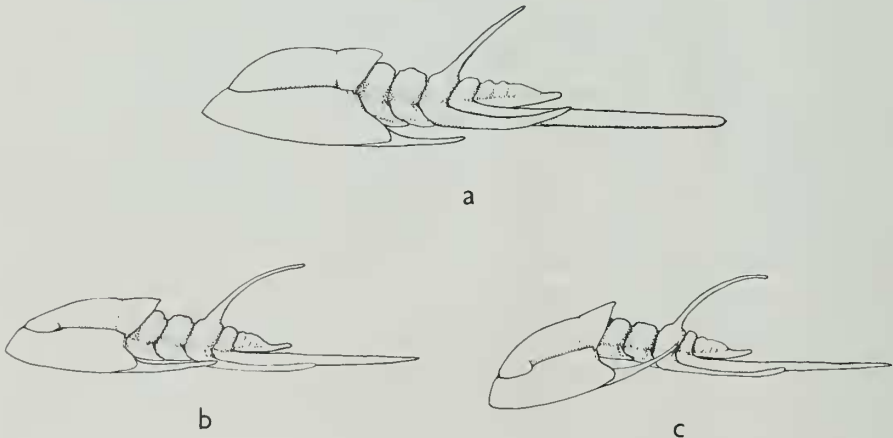


Fig. 21 (a) Lateral view of *Acanthopleurella grindrodi*,  $\times 30$ ; (b), (c) lateral view of *A. stipulae*,  $\times 30$ , in relaxed attitude (b) and in 'active' feeding or grubbing attitude (c). Length of dorsal axial spines and anterior course of facial sutures conjectural.

**Summary of life habits.** *Acanthopleurella* was derived from a *Conophrys*-like ancestor by suppression of release of two segments during ontogeny. It was a blind, benthic animal, but did not inhabit a particularly deep water environment. It was probably a burrowing deposit feeder, using its long macropleural spines as a support at or just below the sediment surface, during enrollment, and as an aid to burial.

### Resource partitioning and the relation of *Conophrys* to *Acanthopleurella*

Robison (1975) was the first to examine the effect of competitive exclusion in controlling the numbers of species and adult size of sympatric agnostids. Where related sympatric species utilize the same resource they can coexist without mutually exclusive competition if they exploit the resource in different ways, for example by taking different particle sizes if they are deposit feeders. May (1973) has given the mathematical basis for this kind of resource partitioning. Applications of this theory to marine benthos living on soft bottoms are relatively limited, but it has been applied to the small (c. 3 mm) benthic gastropod *Hydrobia* by Fenchel (1975). This is an appropriate example in the present case because *Hydrobia* is a small deposit feeder, and may exploit a resource and particle size not so very different from that utilized by shumardiids. Differences in particle-size utilization are reflected more or less directly in differences in adult size of the exploiting animal. Robison (1975) showed that the ratio between lengths of 'neighbouring' agnostids commonly approached the theoretically predicted value of 1.3 (and up to about 1.5). We do not have anything like the number of specimens of *Acanthopleurella* that Robison used for his agnostid example, but we can compare the length (sag.) of largest *A. stipulae* with average holaspid length of *Conophrys salopiensis* obtained from Stubblefield (1926). The length ratio of the latter to the former is about 2.2, which indicates that the size-difference between the two forms was more than adequate to allow them to exploit the same resource without direct competition. This ratio is far larger than the theoretical minimum. There is another small blind trilobite in the British Tremadoc, *Hospes clonograpti* Stubblefield (in Stubblefield & Bulman, 1927) which almost exactly serves to bridge the size gap: the length ratio of *Hospes* to *Acanthopleurella* is about 1.7, and that of *Conophrys* to *Hospes* is about 1.3. It is possible that *Hospes*, too, exploited the same environment. However, it has not so far been found in the beds that have yielded *Acanthopleurella* and *Conophrys*.

The shumardiid example is particularly interesting because we know the mechanism by which the morphological difference necessary to avoid competition was achieved, in this case the shortening of the thorax. There are other families of trilobites in which the number of thoracic segments is highly variable, for example the Olenidae, and similar adaptive reasons may prove to be behind otherwise inexplicable differences in thoracic development.

### Systematic descriptions

Family SHUMARDIIDAE Lake, 1907

Genus *ACANTHOPLEURELLA* Groom, 1902

TYPE SPECIES. *Acanthopleurella grindrodi* Groom, 1902, by monotypy.

DIAGNOSIS. Minute, blind, opisthoparian shumardiid trilobites. Glabella without lateral furrows, but faint anterolateral lobes may be developed. Occipital ring long sagittally but not spined. Genal spines present on free cheeks. Thorax of four segments, the third bearing an axial spine, the third and fourth having long pleural spines. Pygidium transverse, with border, pleural fields flat; anterior segment well defined, segmentation obscure posteriorly.

REMARKS. *Acanthopleurella* differs from *Conophrys* most obviously in the shorter thorax and the presence of macropleural spines on the third as well as the fourth segment. *Conophrys salopiensis* Callaway (= *Shumardia pusilla* auctt.), from the Shineton Shales, has six thoracic segments of which the fourth only has macropleural spines. Other *Conophrys* may have seven segments (e.g. *C. sp.* of Bulman & Rushton (1973 : pl. 6, fig. 5) and another undescribed species (Fig. 18) from

the lowest Tremadoc of North Wales) but in these only the fourth segment is macropleural. *C. ? curta* Stubblefield has five thoracic segments and again only the fourth is macropleural. No *Conophrys* are known to have thoracic axial spines.

The cephalon of *Acanthopleurella* is less distinctive: the anterolateral lobes are weaker than in *C. salopiensis* but are not weaker than those of *C. ? curta* or the *C.* sp. of Bulman & Rushton, or the cranidia referred to *Shumardia alata* Robison & Pantoja-Alor (1968 : 797). Whittington (1965 : 329) showed that *S. granulosa* has free cheeks and suggested that the Shineton Shales '*S. pusilla*' might also have them, although the evidence he cited, Lake's pl. 4, fig. 1, is based on a figure of a young *Asaphellus* (Lake 1942 : 324). Nevertheless, we find that Whittington's suggestion is supported by Shineton Shales specimens (Figs 11, 16, 17). Unlike *Acanthopleurella*, *C. salopiensis* does not show genal spines, although a possible *Conophrys* species, '*Shumardia oelandica* Moberg (1900 : pl. 14, fig. 4a), is illustrated with apparently fixiginal spines, and '*S. nericiensis* Wiman seems to have librigenal spines (Wiman 1905 : pl. 2, fig. 14).

The pygidia of *Conophrys* and *Shumardia* species vary greatly in shape and in the characters of the border and doublure. *Acanthopleurella* pygidia are short and wide with flat pleural fields and tend to be slightly emarginate behind the axis. In this they differ strongly from *S. granulosa* but resemble some *Conophrys*.

### *Acanthopleurella grindrodi* Groom, 1902

Figs 1-4, 20a, 21a

1902 *Acanthopleurella grindrodi* Groom : 70, figs 1-4.

1907 *Shumardia pusilla* (Sars); Raw in Lake : 42 (*pars*); pl. 4, fig. 3 only [figures holotype and places it in synonymy of *S. pusilla*].

1946 *Acanthopleurella grindrodi* Groom; Lake : 341 [revives *Acanthopleurella*].

1973 *Acanthopleurella* sp.; Rushton in Bulman & Rushton : 25; pl. 6, fig. 6.

TYPE SPECIMENS. Holotype OUM A7 (Fig. 3), the original of Groom's (1902) fig. 3. Paratype OUM A8 (Fig. 4), the original of Groom's fig. 4. Both are from the '*Dictyonema*-shales of the Malvern Hills', from beds correlated by Stubblefield & Bulman (1927) with parts of the *Dictyonema flabelliforme* Zone or the Transition Beds of the Shineton Shales.

OTHER MATERIAL. IGS Zg183, Zg184, J. C. Harper coll. From Bronsil Shales (Tremadoc) south of Chase End Hill, Malvern Hills. IGS TW454A from Tremadoc shales in the Combe Abbey no. 1 Borehole, 6 km east of Coventry; the age of these beds is a matter of some doubt (Bulman & Rushton 1973 : 7-8, 11).

DIAGNOSIS. *Acanthopleurella* without distinct anterolateral glabellar lobes; occipital ring about one-third the width of cranidium; posterior macropleura relatively massive, nearly as long as sagittal length of trilobite. Pygidial axis with four segments, pointed behind; pleural fields of thorax and pygidium with rows of many but inconspicuous granules.

MEASUREMENTS. IGS Zg184: sagittal length = 1.70 mm, length of cephalon (maximized) = 0.92 mm, width of cranidium (estimated) = 1.42 mm, length of fourth segment = 1.5 mm, length of pygidium = 0.55 mm, width of pygidium = 1.01 mm. TW454A: sagittal length = 2.03 mm. The holotype has a pygidium 0.48 mm long and 0.92 mm wide; the paratype pygidium is 0.60 mm long and 1.25 mm wide.

REMARKS. The type specimens are rather poorly preserved and do not show several features taken here to be characteristic of *A. grindrodi* (cf. Rushton in Bulman & Rushton 1973 : 26). We interpret the species by reference to IGS Zg184 (Fig. 2) and do not see any significant primary differences between that specimen and Groom's types. The holotype does not show the macropleura on the third segment, probably because the shale has split at a level lower than that at which the spine was preserved, but the mould of the spine on the fourth segment is clear (Fig. 3). We see no evidence for the four pairs of macropleurae shown in Groom's (1902) fig. 1. Groom's interpretation of the cephalon is based on its posterior half only, the anterior part of the cephalon being folded under and not clearly visible.



*A. grindrodi* was described by Rushton (*in* Bulman & Rushton 1973) on the basis of one specimen which resembles Zg184 in almost all particulars (Fig. 1). Rushton's description should be amended because he described the cranidium as a cephalon. IGS Zg183 shows small free cheeks with a genal spine about half as long as the cranidium. The punctate surface doubtfully observed by Rushton cannot be confirmed by other specimens. In Zg184 the thoracic axis is a little wider than the occipital ring. Pairs of small granules are placed exsagittally on the pleural and pygidial axial rings, and rows of small granules are present on the anterior bands of all the thoracic and pygidial pleurae as well.

This species is contrasted with the new form *A. stipulae* below.

*Acanthopleurella stipulae* sp. nov.

Figs 5–10, 13–15, 19, 20b–d, 21b, c

1907 *Shumardia pusilla* (Sars); Raw in Lake : 42 (*pars*); pl. 4, figs 2, 4.

1926 *Shumardia pusilla* variety ?; Stubblefield : 257–258; pl. 15, fig. 16 [distinguished from *S. pusilla*].

1946 *Acanthopleurella*; Lake : 341 (*pars*) [revives *Acanthopleurella*].

HOLOTYPE. IGS Zs6183–4, counterparts (Fig. 5), Stubblefield & Bulman coll. Shineton Shales, *Shumardia pusilla* Zone, Sheinton Brook, south of Sheinton, Salop. Locality 'RR2' of Stubblefield & Bulman (1927 : map, pl. 5).

PARATYPES. BM(NH) In.26816, complete specimen; IGS Zs6181–2, 6185–7, 4 complete specimens (2 immature), 4 cranidia, 3 pygidia (1 immature), all Stubblefield & Bulman coll. IGS GSM 48712, 48713, Rhodes coll. All are from the same locality as the holotype.

DIAGNOSIS. *Acanthopleurella* with distinct anterolateral lobes; occipital ring wider than fixed cheeks; posterior macropleura about half sagittal length of trilobite; pygidial axis short and blunt; pleural regions of thorax and pygidium with few but conspicuous granules.

NAME. 'Of stubble', with reference to Sir James Stubblefield.

DESCRIPTION. Cranidium convex, length two-thirds of width. Cephalic axis four-fifths or more of cranial length and two-fifths of its width. Glabella bluntly pointed in front, defined by distinct axial furrow; weak but distinct anterolateral lobes mark its widest part, behind which the sides of the glabella are slightly concave; no glabellar furrows. Occipital furrow weakly marked, nearly transverse. Occipital ring about as wide as widest part of glabella and nearly half as long, produced backwards in a broad curve, with a faint median node on its posterior edge. Fixed cheeks curved down frontally and laterally, without eyes or eye-ridges. Posteriorly the fixed cheek is two-thirds of the width of the occipital ring, abaxially curves somewhat backwards and downwards to the rounded posterolateral corner where the facial suture cuts off the genal spine. No border except posteriorly, where a short pleurooccipital furrow defines a narrow depressed border near the glabella, but dies out before reaching the facial suture. Facial suture appears to be nearly marginal for most of its course but cuts off the genal spines at the posterolateral corners. Genal spine depressed below the level of the first two thoracic pleurae but the tip curves up to clear the third pleura. Exoskeleton smooth.

Adult thorax of four segments. Axis of first two segments nearly twice as wide as pleura. Axis of third ring narrower and bears a large backwardly- and upwardly-directed spine of unknown length. The first and fourth axial rings bear pairs of small exsagittally-placed granules; the second and third axial rings have two pairs of such granules. First and second pleurae short, third and fourth pleurae have long spines, the macropleura on the fourth segment being over half the length of the rest of the trilobite. Stubblefield (1926 : 358) interpreted the specimen here refigured (Fig. 8) as having a spine on the second as well as the third and fourth pleurae. Our interpretation is that the genal spines have been displaced slightly backwards, perhaps during moulting, so that the spine has a somewhat anomalous position alongside the second and first segments. We believe that we can recognize the sutural margin on the spine that identifies its genal origin. The 'trace of a genal spine' also noted by Stubblefield cannot now be observed on the specimen. The

pleurae each have two granules on the anterior pleural band, the granule nearer to the axial furrow being the larger and comparatively conspicuous.

Pygidium with length about half the width, outline posteriorly faintly emarginate. The axis occupies just over one-third of the greatest width, is shorter than wide and truncate behind; composed of one well-defined ring, one or possibly two fainter ones behind and a terminal piece; the anterior ring carries a pair of small exsagittally-placed granules. Pleural fields flat, composed of one well-defined segment with a trace of one or two more behind. Conspicuous granules on the pleural fields continue the exsagittal arc of conspicuous granules seen on the thoracic pleurae. Posterior border weakly defined, furnished with small granules (Fig. 9). Width of doublure about one-fifth of pygidial length.

MEASUREMENTS. Holotype: sagittal length of trilobite = 1.32 mm, length of cranidium (maximized) = 0.70 mm, width of cranidium (estimated) = 1.1 mm, length of fourth segment = 0.78 mm, length of pygidium = 0.32 mm, width of pygidium = 0.65 mm. Length of BM(NH) In.26816 is 1.40 mm if allowance is made for the crushed front of the cephalon. IGS GSM 48713 and 48712 are 1.50 mm and 1.07 mm long respectively.

REMARKS. *A. stipulae* differs from *A. grindrodi* in its relatively wider axis. The glabella has more definite anterolateral lobes than in *A. grindrodi* and the occipital ring has a faint median node. In *A. stipulae* the pleural regions have fewer but larger granules than in *A. grindrodi* and the axes of the second and third segments have an extra pair of exsagittal granules. The macropleura on the fourth segment is not as massive as that of *A. grindrodi* but appears to have a sharper tip. The pygidial axis has a shorter, blunter axis with one or two fewer rings. The available material suggests that *A. stipulae* is a smaller species than *A. grindrodi*.

Stubblefield (1926 : 357–358) discussed the differences between the form named here as *A. stipulae* and meraspid specimens of *Conophrys salopiensis* ('*Shumardia pusilla*') with four thoracic segments (Fig. 12). The principal differences include the larger anterolateral glabellar lobes of *C. salopiensis*, its single macropleural segment and the stronger segmentation of the pygidium. We would emphasize also the large occipital ring and the axial spine on the thorax of *A. stipulae*. Meraspid of degree 4 reach 1.06 mm in length (Stubblefield 1926 : 356), and thus almost overlap the lower size-range of *A. stipulae* holaspid.

The presence of weak anterolateral lobes in *A. stipulae* recalls the condition of immature specimens of the associated shumardiid *C. salopiensis* (cf. Stubblefield 1926 : pl. 14, fig. 6; pl. 15, fig. 15). The only shumardiid known to be associated with *A. grindrodi* is the *Conophrys* sp. figured by Bulman & Rushton (1973 : pl. 6, fig. 5) which, like *A. grindrodi*, shows scarcely a trace of anterolateral lobes even though the specimen is apparently full-grown.

DEVELOPMENT. A meraspid of degree 0 is associated with the holotype of *A. stipulae*. It is 0.45 mm long and has a comparatively narrow axis. It has three pairs of spines which spring from the edge of the dorsal side of the transitory pygidium (Figs 19, 20c).

Also associated with these specimens is a transitory pygidium of a meraspid degree 3 (Fig. 20d). It is an internal mould with a sagittal length of about 0.22 mm, the 'true' pygidium being about 0.15 mm long. The long macropleural spine is that of the fourth thoracic segment, not yet released; behind this is a smaller macropleural segment (reconstructed here from the base of the spine on the internal mould and a trace of the external mould of the free spinose tip). It represents the third pair of spines seen in the meraspid of degree 0, partly reduced such that in the holaspid stage the pleural region of the pygidium is no longer spinose. The specimen shown in Fig. 13 is a complete meraspid, degree 3. The transitory pygidium has a sagittal length of 0.30 mm, the 'true' pygidium being about 0.22 mm long, and shows the bases of the reduced third pair of spines. It also shows the broad pygidial doublure. The smallest holaspid (Fig. 7) has a pygidium 0.25 mm long.

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