

THE TRILOBITE GENUS *PHILLIPSINELLA*  
FROM THE ORDOVICIAN OF SCANDINAVIA  
AND GREAT BRITAIN

by D. L. BRUTON

ABSTRACT. *Phillipsinella fornebuensis* sp. nov. and *P. preclara* sp. nov. are described from the Caradoc Lower Chasmops Shale (4b $\alpha$ ) and the Upper Chasmops Limestone (4b $\delta_{1-2}$ ) respectively of the Oslo Region, Norway, together with figured but unnamed specimens from equivalent horizons and older in Sweden. Material of *P. preclara* sp. nov. is also figured from the highest Pugsillian of northern England. The Norwegian material provides new information on muscle-scar patterns and exoskeletal surface sculpture. Well-defined glabellar lobes and furrows are described for the first time, there being three lobes in *P. preclara*, one lobe in *P. fornebuensis*. A new diagnosis is given for the genus which is retained in a separate family on account of the distinctive hypostoma. Relationship to the early scutelluids, especially *Raymondaspis* and *Stygina*, is considered likely. A classification based on the morphology of various known cranidia allows the recognition of two species groups, an Arenig-Ashgill group embracing forms from Balto-Scandinavia, eastern Ireland, Turkey, Kazakhstan, and Uzbekistan, and an Ashgill species group centred around *P. parabola sensu lato* known from Britain, Bohemia, Poland, and southern Sweden.

THIS work represents part of a larger project concerned with the vertical stratigraphical distribution and description of Middle Ordovician fossils from several sections in the Oslo Region, Norway. Detailed collecting has produced a wealth of material amongst which are specimens belonging to two new species of *Phillipsinella* described herein from the Caradoc Lower Chasmops Shale (4b $\alpha$ ) and the Upper Chasmops Limestone (4b $\delta_{1-2}$ ) respectively. Further specimens from equivalent horizons or older are described from Sweden, none of which has been previously figured, although occurrences have been listed by Jaanusson (1960, 1963) from the Uhaku Stage (zone of *Glyptograptus teretiusculus*) of Öland and the Siljan district.

The importance of the Norwegian and Swedish material is that it is all of pre-Ashgill age and thus helps to shed some light on the origin and distribution of the genus *Phillipsinella* otherwise best known through its type species, *P. parabola* (Barrande), which is abundantly represented in rocks of Ashgill age in Bohemia, Britain (for discussion see Whittington 1950, 1966, 1968; Ingham 1966, 1970; Price 1973), eastern Ireland (Dean 1974), Poland (Kielan 1960), Kazakhstan (Appolonov 1974), and Usbekistan (Abdullaev 1972). In discussions on trilobite migration, Kielan (1960, p. 38) suggests a Scandinavian origin for *Phillipsinella*. The material described herein and that recently described by Dean (1973, p. 309) from the Arenig of Turkey, shows that the early history of the genus appears to lie within the Asaphid Province.

Family PHILLIPSINELLIDAE Whittington, 1950  
Genus PHILLIPSINELLA Novák, 1885

*Type species.* By original designation, *Phacops parabola* Barrande, 1846, p. 6, from the Králuv Dvůr Formation (Ashgill), Bohemia.

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*Diagnosis.* Cephalon as long (sag.) as wide, moderately convex; glabella clavate, defined by deep furrows, narrowest between palpebral lobes, widest across frontal lobe. Three glabellar furrows on suitably preserved material, otherwise shallow to lacking. Dorsal furrows end in anterior pit alongside frontal lobe; second (posterior pit) in furrow nearly opposite front of palpebral lobe. Facial sutures opisthoparian, anterior branch diverging forward, curving to meet along anterior margin. Connective sutures diverge inwards and backwards, rostral plate long (sag.), lying beneath frontal glabellar lobe. Hypostoma elongate (sag.) covering posterior half of glabella and slightly beyond posterior margin; middle body oval in outline, anterior wings short. Free cheek with genal spines extending the length of thorax. Thorax with six segments, pleural furrows shallow. Pygidium semicircular to quadrate in outline with small postero-median notch. Rachis long, slightly tapered, moderately convex with post-rachial ridge best seen on internal moulds; three to six rachial rings; pleurae smooth or with at least three shallow furrows. Glabella with raised line pattern with or without associated pits. On pygidium, raised lines along postero-lateral border and doublure.

*Stratigraphical and geographical range.* Ordovician (Arenig to Ashgill); Scandinavia, Turkey, Kazakhstan, Uzbekistan, Czechoslovakia, Poland, Britain, and eastern Ireland.

*Discussion.* The new diagnosis is emended from that of the Treatise (Harrington *et al.* in Moore 1959, p. O408) so as to incorporate new material together with study of topotype material of the type species from the Králuv Dvůr Shale, Czechoslovakia, and from the Upper Drummuck Group, Girvan (Begg Collection, Hunterian Museum, University of Glasgow), the Ashgill of Wales and northern England (Sedgwick Museum, Cambridge), and from northern England figured by Ingham (1970).

The large collection of *Phillipsinella preclara* sp. nov. is excellently preserved and provides much new information on morphology, but difficulties arise in comparing it with material assigned to *P. parabola* and allies which are mainly described from siltstone and shale, or as external moulds from decalcified limestone.

#### REMARKS ON MORPHOLOGY

*Glabellar lobation.* *P. preclara* shows for the first time details of glabellar lobes and furrows which, following Jaanusson (1956, pp. 36-37), are numbered and lettered from the posterior forwards, using the notation *L* (glabellar lobe) and *S* (glabellar furrow); (see Pl. 106, fig. 2). The lobes and furrows occur on the narrow posterior half of the glabella adjacent to the wide dorsal furrow, the lobes being accentuated on account of the granulation covering them, and which is absent from the furrows. There are no traces of furrows in front of *S*<sub>3</sub>, on the large, forwardly expanded frontal glabellar lobe and which, on the ventral side, is underlain by the large rostral plate (Pl. 105, fig. 6; see also Whittington 1950, pl. 75, figs. 4, 6). The basal glabellar lobe (*L*<sub>1</sub>) is the most prominent and forms a lateral expansion of the hindmost part of the glabella immediately in front of the occipital furrow. This expansion together with *S*<sub>1</sub> is on specimens of *P. fornebuensis* (Pl. 107), on the cranidium of *Phillipsinella* sp. indet. B (Pl. 105, fig. 7), and on *P. parabola hibernica* (see Dean 1974, pl. 29, fig. 6). In these, however, unlike in *P. preclara*, additional lobes and furrows are faint or lacking. One specimen of *P. parabola*, illustrated by Kielan (1960, Pl. 5, fig. 1; lowermost), shows what may be a basal glabellar lobe, while other specimens do not, and lobes are lacking on material figured by Whittington (1966, pl. 25, figs. 1, 6) and Ingham (1970, pl. 5, figs. 13, 15, 16, 18). However, on the latter material, absence of lobes may be a result of preservation.

*Median occipital tubercle.* Unlike specimens of *P. parabola sensu lato*, *P. preclara* (Pl. 104, figs. 3, 5, 6; Pl. 105, fig. 8) and the cranidium of *Phillipsinella* sp. indet. B (Pl. 105, fig. 7) possess a median occipital tubercle. In *P. preclara* suitably preserved specimens show the tubercle to contain four tiny pits arranged to outline corners of a square. A similar arrangement of pits is also seen on the occipital ring of *P. fornebuensis* (Pl. 107, fig. 4), but in this species there is no occipital tubercle. Such a feature has been termed a median occipital organ by Whittington (1965, p. 297) in connection with scutelluids such as *Bronteopsis* and *Raymondaspis* and it is also known from several other trilobites, among them certain odontopleurids (Whittington 1956, p. 177; Burton 1967, p. 220).

*Muscle scars.* Cranidia of *P. preclara* and *P. fornebuensis* show small, slightly depressed smooth areas along the median line of the frontal glabellar lobe. These are here termed *frontal glabellar scar(s)*. In *P. preclara* (Pl. 104, fig. 5; Pl. 105, fig. 2) a single scar occurs on the frontmost part of the glabellar lobe, whereas in *P. fornebuensis* (Pl. 107, fig. 2) at least three separate oval scars occur along the median line. In both species these scars are accentuated by a disruption in the raised line pattern surrounding them and Plate 106, fig. 3 shows how, in *P. preclara*, the raised lines do not cross the scar.

On the pygidium of *P. preclara* (Pl. 106, fig. 1) there are smooth areas at the inner ends of each rachial ring furrow and adjacent to the dorsal furrow: these are interpreted as areas of muscle attachment. This is supported by a pygidium of *Phillipsinella* sp. indet. (Pl. 108, fig. 12), from the Lower Jonstorp Formation, Västergötland, Sweden, where similar muscle scars correspond to raised areas on the internal mould. This pygidium also has a drawn out post-rachial ridge of the rachis, which seems to be a generic characteristic and is seen even on a dorsal exoskeleton, as a light reflective area (cf. Pl. 105, fig. 4; Pl. 108, figs. 5, 6). A similar muscle-scar pattern was figured by Whittington (1965, pl. 57, fig. 13) on the pygidium of *Raymondaspis reticulatus*.

*Anterior and posterior pit.* The new species of *Phillipsinella* show two prominent pits in the dorsal furrow of cranidia, termed anterior and posterior pits by Kielan (1960, p. 73). These have been identified on Ashgill material by Whittington (1966, p. 79) and Ingham (1970, p. 36) and recently by Dean (1973, p. 311) on the holotype of *P. borealis* described by Kummerow (1927, pl. 1, fig. 7) from an ?Arenig erratic boulder in East Germany.

The anterior pit, which is known on certain scutelluids such as *Stygina* (see Skjeseth 1955) and *Raymondaspis* (see Whittington 1965, pl. 55, fig. 9; pl. 59, fig. 7), occurs alongside the frontal glabellar lobe and inside where the anterior branch of the facial suture crosses the border. It is especially prominent on *P. fornebuensis* (Pl. 107, fig. 1), less so on *P. preclara* (Pl. 104, fig. 1), but in both it is associated with a slight swelling on the frontal glabellar lobe when viewed from above. On the ventral surface of the dorsal exoskeleton the anterior pit corresponds to a slight boss which protrudes ventrally and is covered by the doublure of the free cheek. There is no corresponding feature on the external surface of the doublure (Pl. 105, fig. 6).

The posterior pit occurs in the dorsal furrow level with the anterior edge of the palpebral lobe where the glabella becomes constricted. Unlike the anterior pit, which is oval, the posterior pit is narrow and slit-like. On external moulds this is difficult to see, but from its position it might lie beneath the outer tip of the anterior wing of the hypostoma, and be some form of attachment point. The reconstruction given for the ventral side of the cephalon by Kielan (1960, p. 74, fig. 19) is quite misleading. Furthermore she states (p. 73) that 'p 1' (anterior pit) is situated at the level of the most anterior portion of the eye (whereas on her text-fig. 18 it is shown in front of the eye), and 'p 2' (posterior pit) is a little in front of 'p 1' (in fact it is behind 'p 1'). As far as can be judged, however, the position of the pits shown on her figure (loc. cit., fig. 18) corresponds to that observed for *P. preclara*, *P. fornebuensis*, and others.

*External exoskeletal surface.* *P. preclara* and *P. fornebuensis* have been collected from fresh, dark-grey limestone and have needed little preparation except for removal of matrix from furrows and adjacent to suture lines. The illustrated material shows details of exoskeletal sculpture of pits, granulation, and raised lines, or a combination of all three types, which are now described for *P. preclara*.

*Pits.* A dense irregular network of pitting without associated raised lines occurs on the anterior border of cranidia and is concentrated around the base of the frontal glabellar lobe (Pl. 105, fig. 2). Laterally, the concentration diminishes and adjacent to the anterior facial suture the border is smooth (Pl. 104, fig. 5). On the outer part of the palpebral lobe a larger, more regular pitting occurs in a series of subparallel lines,

while the remainder of the lobe is smooth. A similar irregular network of pits to that on the anterior border occurs between the raised lines on the frontal glabellar lobe and on the median and posterior portion of the glabella where raised lines are lacking. Pits also occur on the free cheek but are lacking on the pygidium.

*Granulation.* On two cranidia (Pl. 104, figs. 1-3; Pl. 106, fig. 2) a dense granulation covers the entire fixed cheek, posterior border, and occipital ring but is less obvious on the holotype (Pl. 104, figs. 4, 5) and a second specimen (Pl. 104, fig. 6) where the concentration is less. On all specimens there is granulation on the glabellar lobes (Pl. 106, fig. 2), the basal part of the glabella immediately in front of the occipital furrow, and in the spaces between the pits on the posterior part of the glabella, where rows of granules also occur on the tops of many of the raised lines (Pl. 104, fig. 6; Pl. 105, fig. 2); sometimes rows of granules merge to form raised lines (Pl. 106, fig. 2).

On the pygidium granulation occurs on the pleural areas, the posterior half of the articulating half-ring, the first rachial ring, and the median portion of the remaining rachis. The distribution of granules around the smooth muscle-scar areas serves to outline the latter.

*Raised lines.* These occur in more or less concentric rows on the frontal glabellar lobe and outline the latter. The outermost lines start low down on the frontal glabellar lobe where they are inclined upwards and slightly outwards (Pl. 104, fig. 4). From here towards the median line, successive lines become less inclined, lower in profile, and are progressively lengthened backwards, the penultimate line always extending backwards to reach the back of the glabella. Considerable variation in the arrangement of the raised line pattern is exemplified by the illustrated specimens, for example, the three innermost raised lines on the cranidium illustrated on Plate 104, fig. 3, all reach the back of the glabella. On the largest specimen (Pl. 104, fig. 6), the outermost raised lines all curve parallel to the anterior margin, whereas those inside become straighter and extend more or less transversely across the glabella. Not all lines are continuous, those antero-medially terminating at the edge of the smooth frontal glabellar scar (Pl. 106, fig. 3) and not crossing it, while spaces between adjacent lines are occasionally taken up by short discontinuous lines with or without associated granules (Pl. 106, figs. 3, 4). Stereoscan photographs of the surface of the holotype show the raised lines to be symmetrical in section with rounded tops; they do not appear to be of the same terrace-line type described for illaenids by Whittington (1965, p. 386) in which the pattern is the result of a steep scarp and shallow-angled dip-slope topography of the exoskeletal surface.

On the pygidium, raised lines with or without granules along their length, are restricted to the articulating facet and the outer, antero-lateral part of the pleurae. The lines run subparallel to the angle of the articulating facet, and, on reaching the margin, curve sharply backwards and downwards and continue along the ventral edge of the doublure.

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#### EXPLANATION OF PLATES

Except where stated, dorsal, lateral, and anterior views of cranidia have the specimen oriented so that the plane passing through the posterior margin of the occipital ring is vertical. All specimens painted with dilute 'Opaque' and coated with ammonium chloride.

#### EXPLANATION OF PLATE 104

*Phillipsinella preclara* sp. nov. from Upper Chasmops Limestone (4b<sub>2</sub>), 1.5-1.6 m below Tretaspis Shale, Frognøya, north-west shore, Ringerike, Norway (except fig. 6).

Figs. 1, 2. PMO 94287. Cranidium, dorsal and oblique left lateral view,  $\times 16$ . Coll. Bruton and Hamar.

Fig. 3. PMO 8980. Cranidium, dorsal view,  $\times 20$ . Loose block. Coll. J. Kiær.

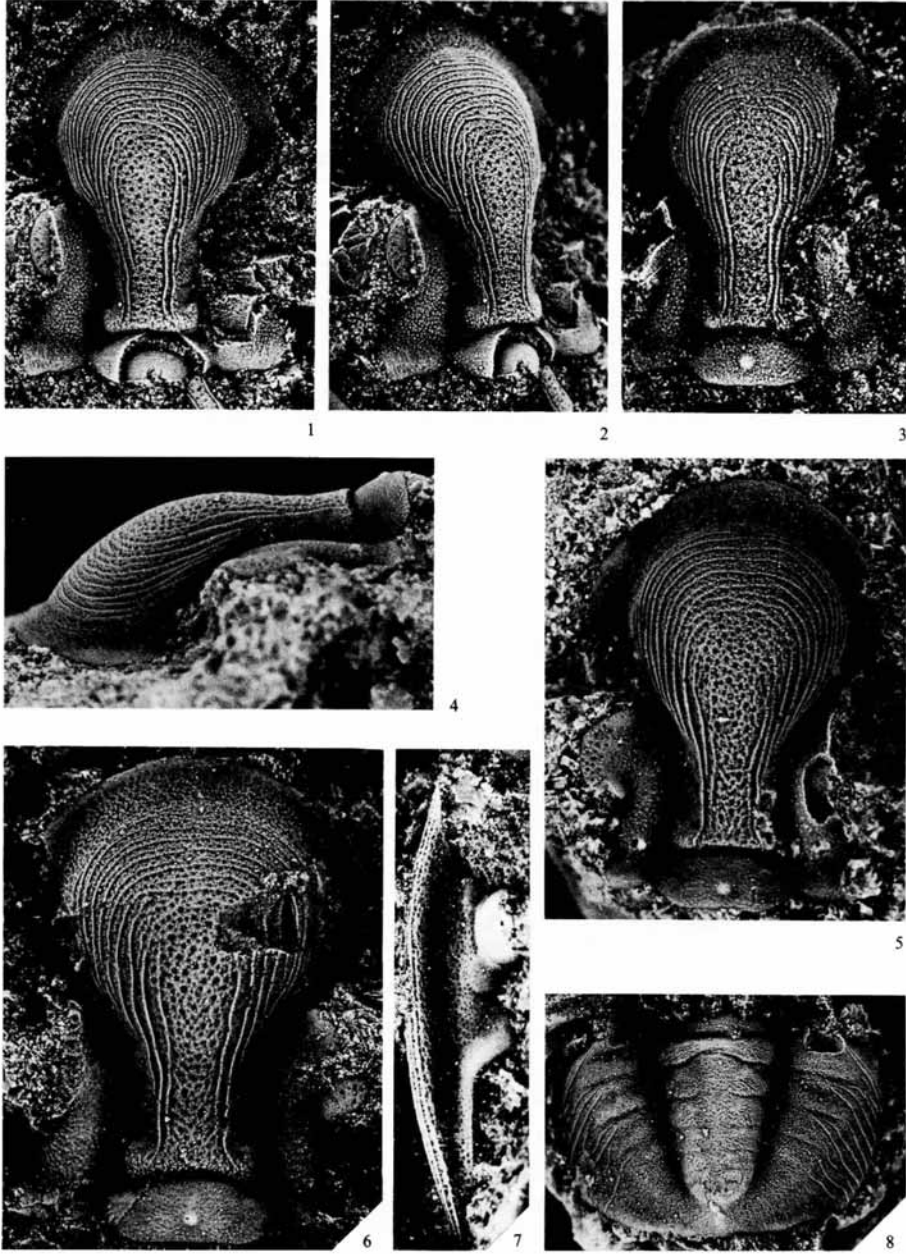
Figs. 4, 5. Holotype, PMO 94278. Cranidium, left lateral and dorsal view,  $\times 18$ .

Fig. 6. PMO 94288. Cranidium, dorsal view,  $\times 16$ . Upper Chasmops Limestone (4b<sub>1</sub>), approximately 2 m from top, Terneholmen, Asker, Oslofjord. Coll. J. Kiær.

Fig. 7. PMO 94286. Pygidium, dorsal view,  $\times 16$ .

Fig. 8. PMO 9107. Free cheek, latex cast of external mould, dorsal view,  $\times 15$ .

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BRUTON, *Phillipsinella*

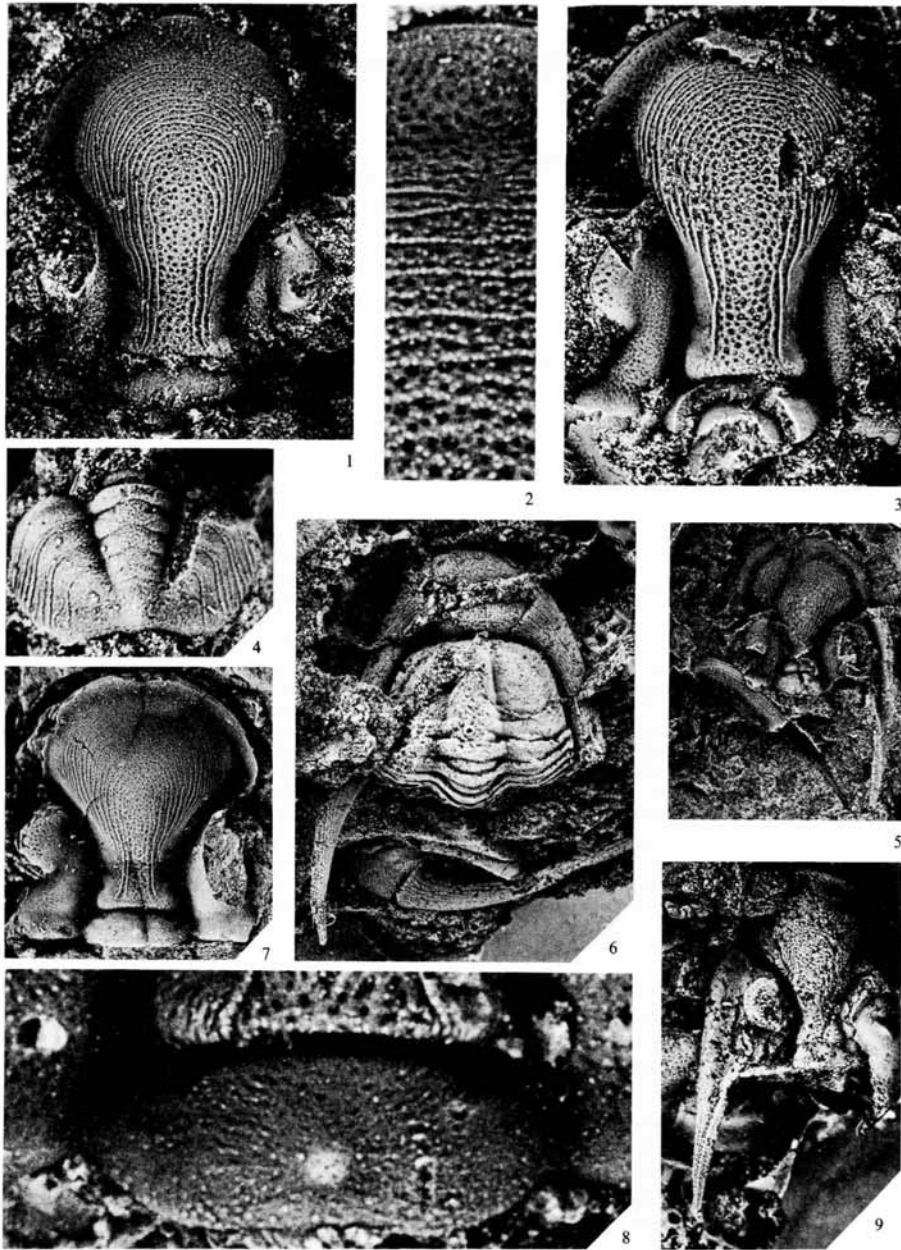
## AFFINITIES AND RELATIONSHIPS

*Phillipsinella* can be compared with early scutelluid genera (Whittington 1963, p. 83), particularly *Stygina* and *Raymondaspis*. Points of cephalic similarity are: three pairs of glabellar furrows, forwardly expanding glabella, course of anterior branch of facial suture, and presence of anterior pit. These dorsal features, together with the presence of a frontal glabellar scar, median occipital organ, post rachial ridge of the pygidium, and the arrangement of muscle scars, suggests that *Phillipsinella* is more closely related to *Raymondaspis* (cf. *R. reticulatus* Whittington, 1965, pl. 55, fig. 9; pl. 56, figs. 1-10; pl. 57) than to *Stygina*. Poulsen (1969, p. 409) has shown how cranidia and pygidia of *Stygina* can be separated from those of *Raymondaspis*. There is considerable difficulty in distinguishing external moulds of small pygidia of *S. minor* (see Skjeseth 1955, pl. 3, figs. 4, 6) from those of *P. preclara* occurring in the same beds. The similarity between *Phillipsinella* and *Stygina* was mentioned by Reed (1931, pp. 11-12), but was dismissed by Whittington (1950, p. 561), mainly on account of the distinctive hypostoma and rostral plate in *Phillipsinella*. More recent descriptions of the hypostoma of *Phillipsinella* by Kielan (1960) and Ingham (1970), and based on better material than was available at the time to Whittington, shows the presence of anterior wings and a more oval outline, but even this material shows that the hypostoma is unlike that known for the scutelluids including that of *R. reticulatus* (cf. Whittington 1965, pl. 55, figs. 2, 3, 5-8).

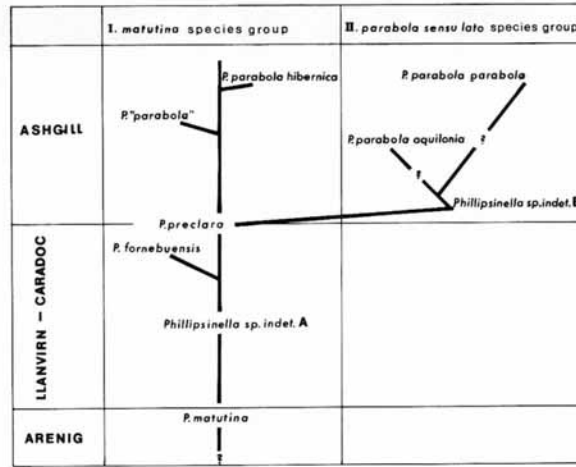
The distinctiveness of the hypostoma of *Phillipsinella* leads me to retain the genus in a separate family, the Phillipsinellidae, although the genus was probably derived from the same root stock which gave rise to the early scutelluids. Text-fig. 1 illustrates the relationship between species of *Phillipsinella* from the Arenig (Dean 1973) to Ashgill. Lack of clear-cut differences between the various pygidia which have been figured indicates that it is very difficult to separate them. Study of well-preserved *P. preclara* shows that smaller specimens have a more steeply sloping pleural margin than do larger specimens, and the indented posterior margin is more accentuated. Variation

## EXPLANATION OF PLATE 105

- Figs. 1-3, 4, 8. *Phillipsinella preclara* sp. nov. 1, PMO 8979. Cranidium, dorsal view,  $\times 16$ . Loose block, same locality and collection as Pl. 104, fig. 3. 2, segment of frontal glabellar lobe of holotype showing details of surface sculpture,  $\times 56$  approx. 3, PMO 94276. Cranidium, dorsal view,  $\times 16$ . Upper Chasmops Limestone (4b $\delta_2$ ), Frognöya, Ringerike, Norway. Coll. Henningsmoen and Nikolaisen. 4, PMO 94284. Pygidium, dorsal view,  $\times 22$ . Same locality and collection as Plate 104, fig. 1. 8, detail of occipital ring of holotype showing median occipital organ. The centre mark is a blemish on the specimen and not a pit,  $\times 56$ , approx.
- Fig. 5. *Phillipsinella* cf. *parabola* (Barrande 1846). RM Ar. 9880. Incomplete cephalon, dorsal view,  $\times 3.5$ . Upper Jonstorp Formation (= Red Tretaspis Mudstone), Kungslena, Västergötland, Sweden.
- Figs. 6, 9. *Phillipsinella preclara* sp. nov. 6, HM A7331/1. Rubber cast from external mould of enrolled specimen, ventral view showing rostral plate, connective sutures, and form of enrolment,  $\times 4$ . 9, HM A7331/2. Rubber cast from external mould of incomplete cephalon, dorsal view,  $\times 6$ . Highest Pusgillian Stage, Billy's Beck, Cross Fell Inlier, Cumbria, England.
- Fig. 7. *Phillipsinella* sp. indet. B. LO 1941t. Cranidium, dorsal view,  $\times 6$ . Tretaspis Shale, Röstånga, Kyrkabäck, Scania, Sweden. Specimen the original of Olin 1906, pl. 2, fig. 18.



BRUTON, *Phillipsinella*



TEXT-FIG. 1. Stratigraphical distribution of *Phillipsinella* and relationship between the *matutina* species group and the *parabola sensu lato* species group. I. *matutina* species group: *P. matutina* Dean, Upper Arenig (Volkhov Stage), Turkey. *Phillipsinella* sp. indet. A. Llandeilo (Uhaku Stage), Öland and Siljan district, Sweden. *P. fornebuensis* sp. nov., Caradoc. Lower Chasmops Shale (4b<sub>α</sub>), Oslo Region, Norway; Skagen Limestone, Siljan district, Sweden. *P. preclara* sp. nov. Caradoc-low Ashgill. Upper Chasmops Limestone (4b<sub>δ1-2</sub>), Oslo Region, Norway; high Pusgillian, Cumbria, England. *P. parabola hibernica* Dean. Ashgill, Chair of Kildare Limestone, eastern Ireland. *P. 'parabola'*. Ashgill, zone of *Staurocephalus clavifrons*, Kazakhstan (see Appolonov 1974) and Bukantau, Uzbekistan (see Abdullaev 1972). II. *parabola sensu lato* species group: *Phillipsinella* sp. indet. B. Tretaspis Shale, Scania, Sweden. *P. parabola aquilonia* Ingham. Ashgill. Cautleyan Stage, Cumbria, England, Upper Drummuck Group, Girvan, Scotland, Rhiwlas Limestone and Crugan Mudstones, North Wales. *P. p. parabola* (Barrande). Ashgill, Králuv Dvůr Shale, Bohemia; zone of *S. clavifrons*, Poland; Jonstorp Formation, Västergötland, Sweden.

in the number of rachial rings is also considerable, and in many cases their recognition depends on suitability of preservation of the dorsal exoskeleton, or if only internal moulds are available for study. Dean (1974, pp. 69-71) has used rachial ring count in order to distinguish the subspecies *P. parabola hibernica* Dean from the Kildare Limestone of eastern Ireland, and his specimens show four well-defined rachial rings on the dorsal surface and two to three more rings on the internal mould (see Dean 1974, pl. 29, figs. 8, 9, 12). However, rachial ring count is not a reliable taxonomic criteria because on all pygidia of *P. preclara* the first three rachial rings are clearly defined, but behind them the number of rings varies, there being three additional rings on the specimen illustrated on Plate 104, fig. 7, two rings on the specimen



illustrated on Plate 105, fig. 4, and one ring on the specimen illustrated on Plate 108, fig. 9. The additional two muscle scars on the terminal portion of the rachis of the latter specimen, may also be interpreted as the sites of rachial segmentation, thus giving a total of six segments on this rachis. Similar features are more clearly shown on the internal mould of the specimen of *Phillipsinella* sp. illustrated on Plate 108, fig. 12, where a total of six segments and a terminal portion with post-axial ridge can be distinguished.

Study of crania shows that two morphological groups can be recognized, the Arenig-Ashgill *matutina* species group and the Ashgill *parabola sensu lato* species group.

*The matutina species group.* This group includes *P. matutina* (see Dean 1973, p. 309, pl. 5, figs. 2-5, 9-11) from the Arenig of Turkey, *P. borealis* Kummerow, from an ?Arenig erratic boulder (for discussion see Dean 1973, p. 311), *Phillipsinella* sp. indet. A (Pl. 108, fig. 11) from the Uhakuan of Öland, Sweden, *P. preclara* sp. nov. from the Upper Chasmops Limestone (4b $\delta_{1-2}$ ) of the Oslo Region, Norway, and from the highest Pusgillian Stage, Cross Fell Inlier, Cumbria, England, *P. fornebuensis* sp. nov. from the Lower Chasmops Shale (4b $\alpha$ ) of the Oslo Region, *P. parabola hibernica* (see Dean 1974, p. 69, pl. 29, figs. 1, 4, 6-15; pl. 30, figs. 1-3) from the Chair of Kildare Limestone, eastern Ireland, specimens from the Ashgill of Kazakhstan assigned to *P. parabola* by Appolonov (1974, p. 44, pl. 9), and specimens from the Ashgill of Bukantau, Uzbekistan, assigned to *P. parabola* by Abdullaev (1972, p. 113, pl. 45, figs. 4-9). In all but *P. fornebuensis*, crania are characterized by having a relatively long glabella (sag.) which is pinched in opposite the anterior edge of the palpebral lobe, the frontal glabellar lobe is smoothly rounded, and the posterior part of the glabella is relatively long (sag.) and parallel sided. The line of the anterior border follows the rounded profile of the frontal glabellar lobe and is narrowest (sag.) in the oldest species. Details of glabellar lobes are not known for the oldest crania, though in *P. matutina*, Dean (1973, p. 309) notes that the hindmost portion of the glabella expands slightly in front of the occipital furrow. This is best seen in the lateral view (Dean 1973, pl. 5, fig. 3) and could represent a basal glabellar lobe of the type shown in *P. fornebuensis* (Pl. 107, figs. 1, 3-7) and further well developed together with additional lobes and furrows in *P. preclara* (Pl. 104, figs. 1-6; Pl. 106, fig. 2). The crania of *P. parabola hibernica* (Dean 1974, pl. 29, fig. 6) also shows a basal glabellar lobe and faint traces of additional lobes.

The coarse raised line pattern with accompanying pits known from *P. matutina* is shared by the cranium from the Uhakuan of Öland, Sweden (Pl. 108, fig. 11), and by *P. preclara* and *P. parabola hibernica* suggesting a direct relationship between them. Crania of *P. fornebuensis* from the Lower Chasmops Shale (4b $\alpha$ ) of the Oslo Region and the cranium of *P. cf. fornebuensis* from the Skagen Limestone, Sweden (Pl. 108, fig. 13), on the other hand, have a finer raised line pattern without pits. The latter cranium is too incomplete for detailed comparison but shows the broad (tr.) frontal glabellar lobe and straighter dorsal furrows characteristic for *P. fornebuensis*. The latter is considered to represent a short-lived stock confined to the Baltic and Scandinavia.

*P. preclara* from the Upper Chasmops Limestone in Norway is considered to be

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the same as specimens from the highest Pugsillian of northern England (Pl. 105, figs. 6, 9) indicating a migration into Britain of the *matutina* species group of Balto-Scandinavian origin. Whether a species like *P. preclara* gave rise to succeeding Ashgill members of the *parabola sensu lato* group in Wales, Scotland, and northern England is not known but it seems possible (text-fig. 1).

Material assigned to *P. parabola* by Appolonov (1974, p. 44, pl. 9) and by Abdullaev (1972, pl. 45, figs. 4-9), from the Ashgill of Kazakhstan and Bukantau, Uzbekistan respectively, clearly belongs to the *matutina* species group on account of glabella shape and narrow anterior border. The cranidia from both collections are most like those of *P. preclara* and *P. parabola hibernica*, but differ from these in having smaller palpebral lobes. The pointed outline of the anterior border of cranidia figured by Apollonov (1974, pl. 9, figs. 1, 2, 5, 6) is also seen in certain specimens of *P. preclara* (cf. Pl. 104, fig. 1; Pl. 105, fig. 1).

*The parabola sensu lato species group.* This group includes specimens figured from the Middle Ashgill of Poland by Kielan (1960, pl. 4, figs. 2-7; pl. 5, figs. 1-3), Scottish specimens figured by Whittington (1950, pl. 75, figs. 3-7), specimens from the Rhiwlas Limestone and Crugan Mudstones (Whittington 1966, pl. 25, figs. 1, 5, 6), material from the Cautleyan Stage (Zone 3) of northern England (see Ingham 1970, pl. 5, figs. 13, 15, 18), a cranidium of *P. cf. parabola* (Pl. 105, fig. 5) from the Upper Jonstorp Formation (= Red Tretaspis Mudstones), Västergötland, Sweden, and a cranidium, *Phillipsinella* sp. indet. B (Pl. 105, fig. 7) from the Tretaspis Shale of Scania. In all these specimens, even allowing for compression in some, the glabella differs from that of the *matutina* species group in being shorter (sag.), strongly pinched in at a point behind the anterior edge of the palpebral lobe, and the strongly diverging dorsal furrows produce a broader (tr.) frontal glabellar lobe. The highest part of the glabella is at a position where the glabella is pinched in, and slopes downwards and backwards from this point to the shorter (sag.), flatter posterior part of the glabella.

*P. parabola aquilonia* was described (Ingham 1970) as differing from *P. parabola* on account of the large flap-like palpebral lobes, and Ingham put all previously described Welsh and Scottish material in this subspecies. *P. preclara* (Pl. 104, fig. 5) also has large palpebral lobes as does the cranidium of *Phillipsinella* sp. indet. B (Pl. 105, fig. 7) from the Tretaspis Shale of Scania, Sweden, but the latter has a short

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EXPLANATION OF PLATE 106

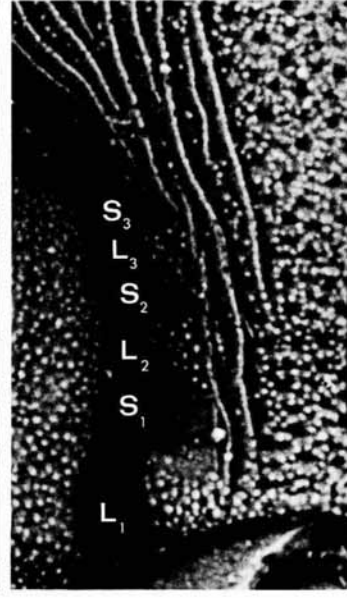
*Phillipsinella preclara* sp. nov.

Fig. 1. PMO 94286. Oblique view of right pleural area of pygidium illustrating rachial muscle scars and surface sculpture,  $\times 36$ . Specimen the same as Plate 104, fig. 7.

Fig. 2. PMO 94287. Enlargement of glabella showing glabellar lobes (L) and furrows (S),  $\times 40$ . Specimen the same as Plate 104, fig. 2.

Figs. 3, 4. Stereoscan enlargements of exoskeletal sculpture on frontal lobe of holotype. Area of enlargement shown on Plate 105, fig. 2. 3, pitted anterior border and frontal glabellar scar. Note how the raised lines do not cross this area,  $\times 264$ . 4, details of raised lines lateral and posterior to frontal glabellar scar. Note that raised lines are both continuous and discontinuous and appear symmetrically rounded in profile; also pitted areas between lines,  $\times 270$ . Angle of tilt, 10 degrees.

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BRUTON, *Phillipsinella*

pinched in glabella and thus resembles *P. parabola sensu lato*. However, unlike other members of the *parabola sensu lato* species group, *Phillipsinella* sp. indet. B has glabellar lobes and a median occipital tubercle known also from the Middle Ordovician *P. preclara* and *P. fornebuensis*, thus suggesting a link between the *matutina* and *parabola sensu lato* species groups.

Thus from the Arenig to Ashgill, representatives of *Phillipsinella* show variation on the same basic plan, but do not exhibit sufficient features to separate them as genera. Such variation includes size of eyes, shape of glabella (long, drawn out, short, pinched in), presence or absence of occipital tubercle, and minor differences in outline of anterior border. A combination of two or more of these characters in populations approximately the same age, but geographically separate, would indicate subspeciation. Ingham (1970) recognized this in *Phillipsinella* from the Ashgill of Britain, and it may well be true elsewhere. However, differences between specimens in pre-Ashgill rocks are more clear-cut, and the new material described below shows reliable specific differences between *P. preclara* and *P. parabola sensu lato* and between *P. fornebuensis* and the former two.

*Phillipsinella preclara* sp. nov.

Plate 104, figs. 1-8; Plate 105, figs. 1-3, 4, 6, 8-9; Plate 106, figs. 1-4; Plate 108, fig. 9

1953 *Phillipsinella parabola*: Störmer, p. 87.

1970 *Phillipsinella parabola aquilonia* Ingham (pars.), p. 38.

*Material*. Holotype: PMO 94278, a cranidium (Pl. 104, figs. 4, 5) from the Upper Chasmops Limestone (4b<sub>2</sub>), 1.5-1.6 m below the Tretaspis Shale, Frognøya, north-west shore, Ringerike, Norway.

Other specimens from the Upper Chasmops Limestone (4b<sub>1</sub>), at approximately 2 m below the top of the unit at Terneholmen, Asker, and at East Raudskjær, Asker.

As well as the holotypes and paratypes there are three cranidia and eleven pygidia.

*Derivation of name*. From the Latin *preclarus*—very beautiful.

*Description*. Cranidium with maximum width (tr.) across palpebral lobes. Glabella clavate, broadly expanded anteriorly, constricted level with anterior edge of palpebral lobe, from here backwards, parallel sided with width (tr.) in front of occipital furrow approximately half that of frontal lobe. Anterior of frontal glabellar lobe broadly rounded and separated by change in slope from flat to gently concave anterior border. Glabella with three lobes, the basal, L<sub>1</sub>, a well-marked swelling expanding outwards and forwards towards dorsal furrow. L<sub>2</sub> and L<sub>3</sub> obliquely directed, weakly raised swellings separated by short, shallow, smooth glabellar furrows, S<sub>1</sub>-S<sub>3</sub> (Pl. 106, fig. 2). Latter extend from deep dorsal furrow and are delimited at their inner ends by the raised lines on the postero-lateral side of the glabella. Dorsal furrow broad and deep opposite basal lobe, becoming shallower and directed slightly outwards and backwards to delimit occipital ring. Anteriorly, dorsal furrow becomes narrower and shallower around lateral expansion of frontal lobe and terminates in deep oval anterior pit (Pl. 104, fig. 1). A second smaller pit occurs in the dorsal furrow at a position level with the anterior edge of the palpebral lobe and where the glabella becomes constricted. Occipital ring moderately convex, longest sagittally, tapering laterally with inwardly curved posterior margin reaching ends of dorsal furrows. Occipital furrow narrow and deep medially, becoming broader and incised behind

basal glabellar lobe. Small occipital node situated approximately one-third distance from posterior margin of ring. Median occipital organ with four minute pits arranged to form corners of a square (Pl. 105, fig. 8). Palpebral lobe broad and flap-like, its anterior margin level with outer end of  $S_1$ . Lobe separated from adjacent fixed cheek by shallow palpebral furrow which becomes deepened at anterior and posterior margins. In dorsal view, lobe asymmetrical with rounded posterior margin, gently curved lateral margin, and long oblique anterior margin (Pl. 104, fig. 5). Behind palpebral lobe, posterior branch of facial suture directed outwards, then curving straight backwards from shallow transverse posterior border furrow, to cross margin. Latter longest (exs.) at suture, narrowing inwards to where dorsal furrow delimits occipital ring. Inner end of anterior branch of facial suture directed outwards at about 50 degrees until a point just inside an exsagittal line through outer edge of palpebral lobe; from here, curving inwards and following curve of antero-lateral border. On all but the largest specimen (Pl. 104, fig. 6), the anterior border is slightly wider (sag.) anteriorly than laterally, thus giving the cranium a pointed outline. On the larger specimen the curve of the anterior margin parallels that of the frontal glabellar lobe. Anterior border with thickened edge accentuated by two to three raised lines. Only one specimen of a free cheek has been found from the type locality (Pl. 104, fig. 8). The cheek is blade-like with a maximum width (tr.) across the base of the librigenal spine. Border furrow shallow anteriorly and lateral to eye lobe, deepening posteriorly and extending on to base of librigenal spine dividing latter into two parts, a raised outer edge accentuated by raised lines of the lateral border, and a narrow pitted inner edge. Lateral border flat, about half maximum width. Lateral border and furrow with fine pitted surface, bilobed base of eye socle and posterior border inside suture, smooth. A specimen (Pl. 105, fig. 6) shows details of rostral plate and connective sutures similar to *P. parabola* (Whittington 1950, pl. 75, figs. 3, 4, 6).

*Pygidium*. Largest pygidium (Pl. 104, fig. 7) trapezoidal with broad rachis tapering backwards and not reaching posterior margin. Dorsal furrow deepest anteriorly, shallowing backwards but outlining curved terminal portion of rachis. Latter with six ring furrows, the first crossing the rachis, curving forwards medially to form a notched posterior margin of the rachial ring. Succeeding furrows shallow and not crossing the rachis medially. Inner part of pleura flat to gently sloping outwards and crossed by three shallow pleural furrows. Latter do not reach lateral margin which slopes more steeply down and is slightly concave postero-laterally and weakly notched medially. A smaller specimen (Pl. 108, fig. 9) shows a more tapered rachis and signs on the dorsal exoskeleton of the post-rachial ridge which reaches the margin; latter indented medially. Four rachial furrows cross the rachis, and laterally there are four pleural furrows, the last one only faint. An even smaller pygidium (Pl. 105, fig. 4) shows all these features but with an additional fifth rachial ring, a more tapered rachis, very steeply sloping pleurae, and a marked posterior marginal notch.

For discussion and description of exoskeletal sculpture see p. 701.

*Discussion*. Material assigned by Ingham (1970, p. 38) from the high Pusgillian of Billy's Beck (Cross Fell Inlier, Cumbria), to his Cautley subspecies *P. parabola*

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*aquilonia*, is figured on Plate 105, figs. 6, 9, and assigned to *P. preclara*. Like the Norwegian specimens, this material has a relatively long glabella (sag.) which is pinched in opposite the anterior edge of the palpebral lobe, the frontal glabellar lobe is smoothly rounded, and the wide (sag.) anterior border likewise. Details of the glabellar lobes are not present on the Pusgillian material which consists of external moulds, but the raised line pattern and regular network of coarse pits on the glabella and anterior margin is very like that described from the better-preserved Norwegian material.

Specimens from the type horizon occur abundantly in a thick limestone bed 1.5–1.6 m below the Tretaspis Shale, together with a rich fauna including *Tretaspis kiaeri*, *Stygina minor*, *Telephina* (*Telephina*) *wegelini*, and undescribed species of *Stauraccephalus*, *Sphaerexochus*, *Diacalymene*, and *Lonchodomas*. Many of these genera are also known from Pusgillian and younger strata in Britain. The significance of this fauna in terms of interregional correlation is being assessed by A. Owen (University of Glasgow), and part of the Upper Chasmops Limestone at Ringerike may be younger than previously thought (see also discussion by Dean 1971, pp. 14, 47–48).

Small cranidia of *P. preclara* from 4b $\delta_1$  in Asker cannot be distinguished from those of similar size from 4b $\delta_2$  in Ringerike. However, the largest cranidium known for the species is from 4b $\delta_1$  on Terneholmen, Asker (Pl. 104, fig. 6), and it is this specimen which shows a slightly different raised line pattern and a more rounded anterior border than usual.

*Phillipsinella fornebuensis* sp. nov.

Plate 107, figs. 1–7; Plate 108, figs. 1–6

*Material.* Holotype: PMO 94297, a cranidium (Pl. 107, figs. 4, 7) from the Lower Chasmops Shale (4b $\alpha$ ), Fornebu foreshore profile, Oslo-Asker, Norway. Other specimens from the Lower Chasmops Shale at Langmannen, Snarøya, close to the type locality, from Nakholmen, Oslofjord, and Rodelokken (Bygdøy profile 38–39 m), Oslo.

As well as the holotype and figured paratypes four cranidia and eight pygidia.

*Description.* The broader (tr.) glabella outlined by straighter forwardly diverging dorsal furrows in dorsal view (Pl. 107, figs. 1, 4, 5), the steeply sloping glabellar profile in lateral view (Pl. 107, figs. 6, 7), and the weaker raised line pattern and limited pitting, separates cranidia of this species from those of *P. preclara*. Other

EXPLANATION OF PLATE 107

*Phillipsinella fornebuensis* sp. nov. All from limestone in upper part of Lower Chasmops Shale (4b $\alpha$ ), Fornebu foreshore profile, Oslo-Asker, Norway. The height above base (normal sea level) of measured section is given in metres.

Figs. 1, 2, 6. PMO 70246: 3.20 m. 1, cranidium, dorsal view showing well-developed anterior pit,  $\times 20$ . 2, anterior view showing three frontal glabellar scars and discontinuous and branching raised lines,  $\times 36$  approx. 6, right lateral view,  $\times 20$ .

Figs. 3, 5. PMO 94293: 3.20 m. 3, cranidium, oblique right lateral view,  $\times 16$ . 5, dorsal view,  $\times 16$ .

Figs. 4, 7. Holotype, PMO 94297: 3.20 m. 4, cranidium, dorsal view,  $\times 22$ . 7, right lateral view; specimen oriented with palpebral lobe horizontal,  $\times 22$ . Much of the glabella has an overgrowth of secondary calcite which fortuitously gives the appearance of a partly exfoliated exoskeleton.



1



2



3



4



5



6



7

BRUTON, *Phillipsinella*

differences include the smaller, more rounded palpebral lobe situated on a narrower (tr.) fixed cheek (Pl. 107, fig. 5), and the broad, deep dorsal furrows. The latter end anteriorly in a conspicuously deep oval anterior pit. Only the basal glabellar lobes are developed and are outlined by the narrow, deep  $S_1$  furrows which reach the occipital furrow. The median occipital organ, represented by four minute pits, occurs in the same position as in *P. preclara*, but an occipital tubercle is not developed (Pl. 107, figs. 1, 4). Pitting occurs only on the highest part of the glabella where it is restricted to a small oval area inside the innermost raised lines. The latter are much finer than in *P. preclara*, and on the frontal glabellar lobe are seen to anastomose (Pl. 107, fig. 2). On all specimens there are at least three smooth frontal glabellar scars (Pl. 107, fig. 2), and an interruption of the raised line pattern occurs adjacent to each scar. None of the raised lines extend as far as the back of the glabella which is covered by a dense, fine granulation. A similar granulation covers the occipital ring and anterior and posterior borders. One incomplete free cheek (Pl. 108, fig. 4) is known and this is wider (tr.) than that of *P. preclara* and lacks the pitted surface and smooth eye socle. Details of the thoracic segments are known from one partly flexed specimen showing four segments and articulated pygidium (Pl. 108, fig. 6). In shape each pleura resembles the first segment of the pygidium with short (trans.) inner portion crossed by a shallow transverse pleural furrow, and a longer outer portion which becomes bent strongly downwards and terminates bluntly. A diagonal raised line marks the shoulder of the articulating facet, and two to three shorter raised lines occur on the shoulder proper.

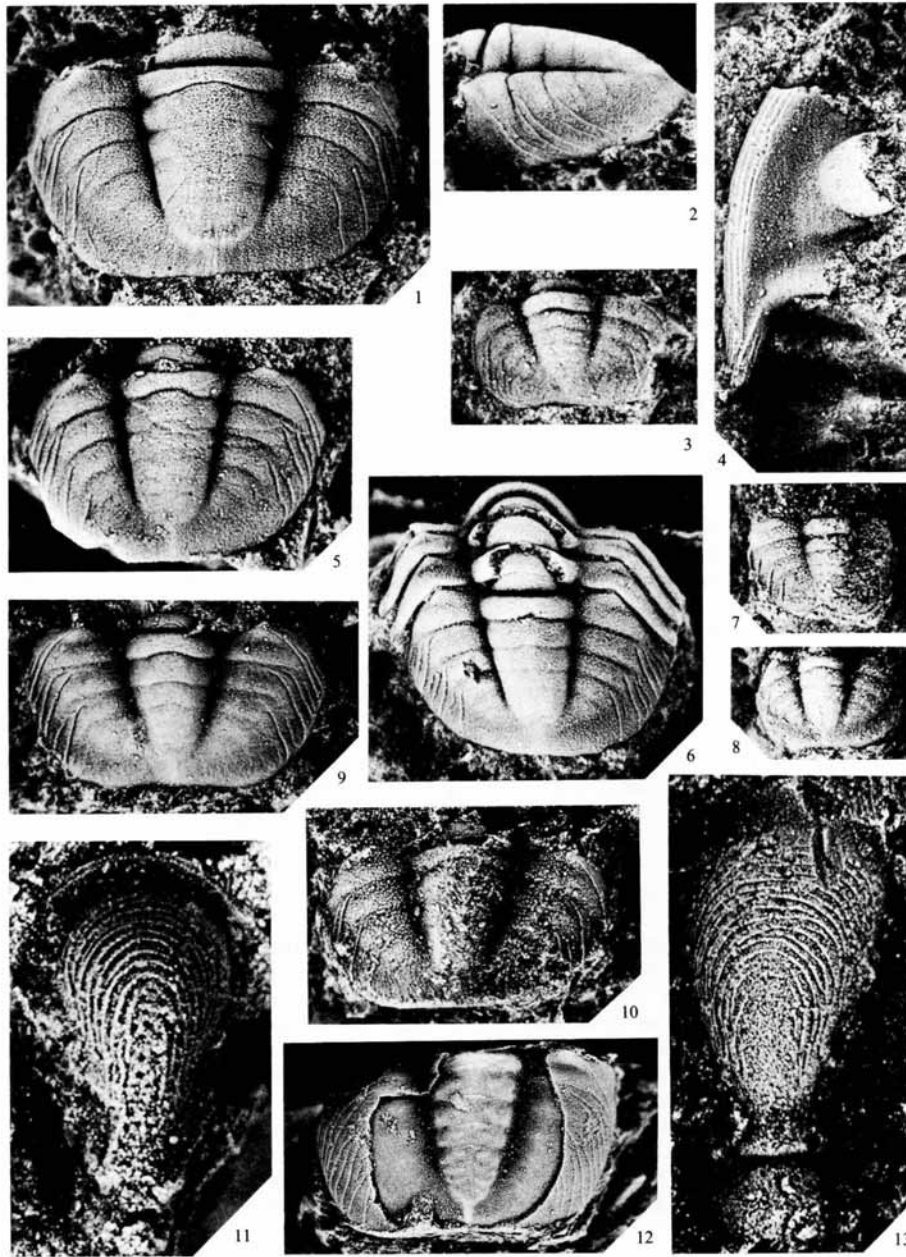
*Pygidium*. Like that described for *P. preclara*, but differing from that species in that the rachis has four rachial rings all of which cross the rachis, and there is a corresponding number of pleural furrows throughout ontogeny. Additional differences between mature *P. fornebuensis* and *P. preclara* (cf. Pl. 108, fig. 1; Pl. 104, fig. 7) are

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EXPLANATION OF PLATE 108

- Figs. 1-6. *Phillipsinella fornebuensis* sp. nov. All from the same locality as Plate 107. 1, 2. PMO 94295: 4-80 m. 1, pygidium, dorsal view,  $\times 10$ . 2, left lateral view,  $\times 10$ . 3, 4. PMO 94300: 4-0 m. 3, small pygidium, dorsal view,  $\times 30$ . 4, incomplete free cheek,  $\times 25$ . 5, PMO 70247: 3-20 m. Pygidium, dorsal view,  $\times 22$ . 6, PMO 94296: 4-80 m. Partly enrolled exoskeleton with four thoracic segments and articulated pygidium,  $\times 21$ .
- Fig. 9. *Phillipsinella preclara* sp. nov. PMO 94285. Pygidium, dorsal view,  $\times 24$ . Upper Chasmops Limestone (4b $\delta_2$ ), 1.5-1.6 m below Tretaspis Shale, Frognöya, north-west shore.
- Figs. 8, 13. *Phillipsinella* cf. *fornebuensis* sp. nov. 8, UMD 2000. Pygidium, internal mould, dorsal view,  $\times 10$ . Skagen Limestone, 9.3-9.4 m from top of Macrourus Limestone, Fjäckå section, Siljan district, Sweden. 13, UMD 2001. Incomplete cranidium, dorsal view,  $\times 18$ . Skagen Limestone, Fjäckå section, level 8.95-9.05 m.
- Figs. 7, 10, 11. *Phillipsinella* sp. indet. A. 7, UMD 2002. Pygidium, dorsal view,  $\times 22$ . Furudal Limestone, Profile D92, Fjäckå, Siljan district, Sweden. 10, UM Öl 1330. Pygidium, internal mould,  $\times 18$ . Persnäs Limestone, Böda Hamn bore core, level 7.8 m, Öland, Sweden. 11, UM Öl 1329. Cranidium, dorsal view,  $\times 30$ . Level 7-26 m, same locality and horizon as fig. 10.
- Fig. 12. *Phillipsinella* sp. RM Ar. 9881. Partly exfoliated pygidium showing muscle-scar pattern on rachis and post rachial ridge, dorsal view,  $\times 10$ . Lower Jonstorp Formation, Mösseberg, Västergötland, Sweden.
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BRUTON, *Phillipsinella*

the broader (tr.) and shorter rachis in the former and the lack of smooth muscle-scar areas. Otherwise details of exoskeletal granulation and raised line pattern are the same.

*Discussion.* The steeply sloping glabellar profile in lateral view, the straight, forwardly diverging dorsal furrows, and the fine raised line pattern are features shared by the incomplete cranidium (Pl. 108, fig. 13) from the Skagen Limestone of the Siljan District, Sweden (for stratigraphy see Jaanusson 1964, pp. 8, 10, 56–58), which is here referred to as *P. cf. fornebuensis*. A small pygidium (Pl. 108, fig. 8) from a similar horizon is also assigned here.

The type species is common in the Lower Chasmops Shale (4b $\alpha$ ), for which it appears to be a reliable index fossil for the topmost 5 m of this unit, occurring with a rich fauna including *Platylichas validus*, *Asaphus (Neosaphus) glabratus*, *Remopleurides* sp., *Chasmops cf. conicophthalmus*, and *Decoroproetus cf. gyratus*. All but the last-named species are listed by Jaanusson (1964, p. 56), together with *Phillipsinella* sp., as being distinctive for the Skagen Limestone in the type area of Västergötland, Sweden, indicating a correlation between this unit and the upper part of the Lower Chasmops Shale of the Oslo Region. Jaanusson (1964, p. 53) has already indicated that at least part of the Lower Chasmops Shale of the Oslo Region is also equivalent to the upper pelitic member of the underlying Dalby Formation in Västergötland on the basis of the ostracod fauna. The Dalby Formation ostracods listed by Jaanusson have not been identified in the topmost 5 m of the Lower Chasmops Shale in the Oslo Region, according to G. Qvale.

*Phillipsinella* sp. indet A

Plate 108, figs. 7, 10, 11

*Discussion.* The pygidium (Pl. 108, fig. 10) and the cranidium (Pl. 108, fig. 11) are those listed by Jaanusson (1960, p. 234; p. 236, fig. 5) from the Persnäs Limestone (Uhakuan Stage) of the Boda Hamn bore core, northern Öland, Sweden. The cranidium is incomplete, but the glabella shows the well-rounded frontal lobe and long (sag.) and narrow posterior part characteristic for the *matutina* species group. The frontal lobe slopes steeply downwards anteriorly and laterally as in *P. matutina* (see Dean 1973, pl. 5, figs. 2, 3, 9), but is longer (sag.) than in that species. The surface of the glabella is covered with a pattern of strong raised lines similar to that of *P. preclara*, and pits occur on the highest part of the glabella and on the posterior portion. The small pygidium (Pl. 108, fig. 10), an internal mould, resembles *P. preclara* (Pl. 108, fig. 9) in being more rectangular in outline than is usual for the genus, and has a straight posterior margin. The rachis has three well-defined ring furrows which laterally correspond to the same number of pleural furrows. A second pygidium (Pl. 108, fig. 7) from the Uhakuan Furudal Limestone at the main section of Fjäckå, Siljan district, Sweden, and most resembles *P. matutina* in its sub-semicircular outline. Jaanusson (1963, p. 27, fig. 10) lists a *Phillipsinella* sp. nov. from the same locality of Fjäckå at level 19.00 m in the profile. This specimen is an incomplete cranidium but shows a well rounded, narrow anterior border like that of *P. matutina* and of the specimen (Pl. 108, fig. 11) from the Uhakuan of Öland.

*Phillipsinella* sp. indet. B

Plate 105, fig. 7

*Discussion.* This cranidium was described by Olin (1906, p. 60, pl. 2, fig. 18) from the Tretaspis Shale of Scania, Sweden, but there is no evidence from his text or from the specimen label, where in the succession at Röstånga the specimen was collected, and he records *Phillipsia* [sic] *parabola* from various horizons (loc. cit., p. 78). Comparison between this cranidium and those of *P. parabola* from Poland (Kielan 1960, pl. 5, figs. 1, 3), shows how similar they are in glabella shape and raised line pattern, the difference between them being the larger palpebral lobe in the Swedish specimen. In glabella shape and size and position of eyes, the Olin specimen is indistinguishable from topotype material of *P. parabola* from Czechoslovakia and from the specimen (Pl. 105, fig. 5) referred to *P. cf. parabola* from the Upper Jonstorp Formation of Västergötland, Sweden. However, unlike these and other Ashgill members of the *parabola sensu lato* species group from Britain and Poland, the Olin specimen has glabellar lobes and furrows clearly developed, the basal lobe especially so, and the occipital ring bears a median tubercle.

Dr. J. K. Ingham has kindly shown me an incomplete internal mould of a cephalon, the only known *Phillipsinella* from the red mudstone unit of the Upper Whitehouse Beds on the foreshore south-west of Girvan, in beds containing an unusual facies fauna dominated by blind and large-eyed trilobites (Ingham pers. comm.). The cephalon is of the *parabola sensu lato* species group type and is most like topotype specimens of *P. parabola*. However, the Girvan specimen occurs below strata with *Dicellograptus complanatus* and above those with *Pleurograptus linearis* and is thus older than *Phillipsinella parabola*.

*Acknowledgements.* I am most grateful to Professor H. B. Whittington, Dr. J. K. Ingham, and Dr. V. Jaanusson for access to specimens in their care as well as their own collections, and to Dr. L. Marek for sending me topotype material of *Phillipsinella parabola*. Dr. J. K. Ingham has kindly read a draft of the manuscript and offered valuable suggestions for its improvement. Mr. G. McTurk kindly took the photographs on Plate 106, figs. 3 and 4. Material belongs to Palaeontological Museum, University of Oslo (PMO), Palaeontological Institute, Uppsala (UM), Swedish Museum of Natural History, Stockholm (RM), Palaeontological Institute, Lund (LO), and Hunterian Museum, Glasgow (HM).

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