

CLASSIFICATION AND PHYLOGENY OF HOMALONOTID TRILOBITES

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ABSTRACT. The composition, classification, and phylogeny of the Homalonotidae are discussed, and new family and subfamily diagnoses given. *Plaesiacomia hughesi* sp. nov. and *P. vacuvertis* sp. nov. from the Llanvirn of Wales and Saudi Arabia respectively, and *Platycoryphe dyaulax* sp. nov. from the Llandovery of Saudi Arabia, are described.

SOME of the problems involved in classifying homalonotid trilobites have arisen because the Silurian and Devonian genera are known principally from old, inadequate descriptions. The difficulties are increased by the rarity of Ashgill and Llandovery forms which has emphasized the apparent morphological gap between post-Ordovician and older genera. Study of the species described here, together with work on middle and upper Silurian homalonotines to be published elsewhere, has shed new light on the classification and phylogeny of the family.

Repositories. The following abbreviations are used herein: BM—British Museum (Natural History), London; GSM—The Geological Museum, Institute of Geological Sciences, London; SM—Sedgwick Museum, Cambridge.

SYSTEMATIC PALAEOLOGY

Family HOMALONOTIDAE Chapman, 1890
[= Portaginidae Lespérance, 1968]

Diagnosis. The following diagnosis is based on that of Sdzuy (*in* Moore 1959, pp. 0454–0455) and incorporates the correction and emendation noted by Whittington (1965, p. 488).

Cephalic border rarely well defined, often absent. Glabella narrowing forwards, with four or fewer pairs of lateral glabellar furrows. Paraglabellar area usually present. Genal angle generally rounded with facial suture displaying gonatoparian condition; opisthoparian or proparian sutures and genal spine rarely occur. Palpebral lobe small, eye ridge present in some early forms. Rostral plate narrows posteriorly. Rostral suture ventral or marginal in early genera, dorsal in later forms. Hypostome subquadrate, with small anterior wing and weakly developed lateral notch; posterior margin rarely rounded, usually bifurcate. Thorax of thirteen segments; axis moderately wide in early genera, indistinct and very broad in later ones. Pleural tips blunt. Pygidium subsemicircular to triangular in outline.

Discussion. *Brongniartella* Reed, 1918; *Burmeisterella* Reed, 1918; *Burmeisteria* Salter, 1865; *Calymenella* Bergeron, 1890; *Colpocoryphe* Novák *in* Perner 1918;

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Digonus Gürich, 1909; *Dipleura* Green, 1832; *Eohomalonotus* Reed, 1918; *Parahomalonotus* Reed, 1918; *Plaesiacomia* Hawle and Corda, 1847; and *Trimerus* Green, 1832 are sufficiently well known for no doubt to arise concerning their membership of the family.

Henningsmoen (*in* Moore 1959, p. 0524) regarded *Platycoryphe* Foerste, 1919 as of uncertain affinities but I agree with Whittington (1965) that it is a homalonotid. Přibyl (1953, p. 16) placed *Bavarilla* Barrande, 1868 in the Olenidae but it was excluded therefrom by Henningsmoen (1957, p. 20). *Bavarilla* is accepted as a homalonotid and its systematic position is discussed further below. No good illustrations are available of *Leiostegina* Kobayashi, 1937 but the anteriorly narrowing glabella and transversely straight, apparently dorsal, rostral suture (see Kobayashi 1937, pl. 6, fig. 18) suggest that it is a homalonotid. Professor S. Kuss (Paläontologisches Institut, Freiburg) informed me (*pers. comm.*, 8 October 1975) that the type material of *L. inexpectans*, the only known species, seems to be lost. A more detailed appraisal of *Leiostegina* must therefore await the availability of topotype material.

The available illustrations of *Pamirotellus* Balashova, 1968 (= *Pamirites* Balashova, 1966; *non* Toumansky, 1938) are poor but what can be seen suggests that it is a synonym of *Brongniartella*. In particular, the pygidium is longer than wide, well segmented, and obtusely pointed posteriorly (Balashova 1966, pl. 2, fig. 6; 1968, pl. 52, fig. 5c). The glabella (Balashova 1966, pl. 2, fig. 7; 1968, pl. 52, fig. 5d) is constricted (*tr.*) anteriorly, a feature typical of many *Brongniartella* species. Balashova gives the horizon of *Pamirotellus* as Wenlock whereas *Brongniartella* is not known elsewhere after the lower Llandovery. Possibly a relic species is represented or the horizon given may be incorrect. Since no other faunal elements are listed from this horizon the reasons for suggesting a Wenlock age are unclear. *Portaginus* Lespérance, 1968, from the upper Ashgill of Quebec, is also synonymous with *Brongniartella* (see Dean 1976, pp. 238-239). *Liangshanaspis* Chang, 1974 shows no major differences from *Platycoryphe*. Apollonov (1974, pp. 59-61, pl. 11, figs. 1-11; pl. 12, figs. 1-6, 8) recently redescribed the type species, and referred it to that genus.

Neseuretus Hicks, 1873 (see Whittard 1960, p. 139 for use of this name rather than *Synhomalonotus* Novák *in* Perner 1918) has been regarded as a homalonotid by various authors but I agree with Whittington (1966a, pp. 499-500) that it is a calymenid. *Lakaspis* Kobayashi, 1937 was provisionally assigned to the Homalonotidae by both Kobayashi and Hupé (1953). The available illustrations (Kobayashi 1937, pl. 2, figs. 27, 28; Lake 1906, pl. 11, figs. 2, 3) are poor but it is clear that the glabella expands (*tr.*) in its anterior half. This indicates that *Lakaspis* is not a homalonotid and Jaanusson (*in* Moore 1959, p. 0358) questionably assigned it to the Nileidae. Clarke (1913) erected *Homalonotus* (*Schizopyge*) *parana* for a pygidium from the lower Devonian of Brazil. The specimen displays no homalonotid features and Struve (1958) erected the calmoniid genus *Tibagya* to receive it (see also Struve *in* Moore 1959, p. 0486).

Classification of the Homalonotidae. Hupé (1953, 1955) placed the Homalonotidae in the superfamily Calymenoidea (which he attributed to Swinnerton 1915). He

proposed three subfamilies based on cephalic and pygidial shape, form of the rostral suture, and distinctness of trilobation:

EOHOMALONOTINAE	<i>Eohomalonotus</i> , <i>Calymenella</i> , <i>Plaesiacomia</i>
HOMALONOTINAE	<i>Homalonotus</i> , <i>Burmeisterella</i> , <i>Brongniartella</i> , <i>Parahomalonotus</i> , <i>Digonus</i> , ? <i>Lakaspis</i> , ? <i>Leiostegina</i>
TRIMERINAE	<i>Trimerus</i> , <i>Burmeisteria</i> , <i>Dipleura</i>

Hupé (1953, p. 232) included *Neseuretus* in the Calymenidae but in 1955 erected the calymenid subfamily Colpocoryphinae to include *Neseuretus*, *Colpocoryphe*, and the non-papillate calymenids.

In Sdzuy's (1957; in Moore 1959, pp. 0454-0461) revision, *Bavarilla* was accepted as a homalonotid and placed in its own subfamily. Sdzuy's other subfamilies are as follows:

EOHOMALONOTINAE	<i>Calymenella</i> (<i>Calymenella</i>), <i>C.</i> (<i>Eohomalonotus</i>), <i>Brongniartella</i> , <i>Neseuretus</i> (this was simultaneously classified as a calymenid, p. 0453; and listed as <i>incertae sedis</i> , p. 0523)
COLPOCORYPHINAE	<i>Colpocoryphe</i> , <i>Plaesiacomia</i> , ? <i>Leiostegina</i>
HOMALONOTINAE	<i>Homalonotus</i> , <i>Burmeisterella</i> , <i>Burmeisteria</i> (<i>Burmeisteria</i>), <i>B.</i> (<i>Digonus</i>), <i>Parahomalonotus</i> , <i>Trimerus</i> (<i>Trimerus</i>), <i>T.</i> (<i>Dipleura</i>)

Hupé's Trimerinae was not recognized. Přibyl (1957, p. 92) had pointed to the close similarities between trimerines and homalonotines—especially the tendency to ill-defined trilobation, broad thoracic axis, and similar length to breadth proportions of the cephalon and pygidium.

Kobayashi (1960) erected the Synhomalonotinae to include *Neseuretus* and the calymenid *Vietnamia*. Having accepted Whittard's (1960) arguments for regarding *Synhomalonotus* as a junior synonym of *Neseuretus*, Kobayashi (1969, p. 243) proposed 'Neseuretinae' as a replacement subfamily name. This procedure contravenes Article 40 of the ICZN and 'Synhomalonotinae' must be retained. As *Neseuretus* is regarded as a calymenid, this subfamily is referred to the Calymenidae (see also Whittington 1971).

Subsequent workers have viewed the suprageneric classification of calymenaceans in different ways. Some authors (Dean 1966a; Hughes 1969; Henry 1971; Sadler 1974) favour several different families, others (Whittington 1966a, 1971; Dean 1971) utilize a number of different subfamilies assigned to either the Calymenidae or Homalonotidae.

A number of genera are present in the Tremadoc and Arenig from which younger calymenids and homalonotids arose (see Whittington 1966a, p. 500). While accepting that such early genera may not be easily accommodated in either group, I consider that the familial classification should reflect this essentially bipartite pattern. Within the Homalonotidae, three subfamilies are recognized for post-Tremadoc forms. The Cambrian ancestors of homalonotids are unknown but *Bavarilla* seems to be related. Hence the Bavarillinae Sdzuy, 1957 (as diagnosed by Sdzuy in Moore 1959, p. 0455) is retained.

Subfamily EOHOMALONOTINAE Hupé, 1953

Diagnosis. Cephalon subtriangular, rounded anteriorly; with anteriorly widened border. Glabella trapezoidal to parabolic; three or fewer pairs of lateral glabellar furrows, 1p sigmoidal. Paraglabellar area defined. Rostral suture is marginal or nearly so and describes a wide, forwardly convex curve. Facial suture gonatoparian. Thorax with distinct, moderately wide axis. Pygidium triangular, wider than long, with distinct trilobation.

Genera. *Eohomalonotus*, *Calymenella*.

Remarks. Reed (1918, p. 321) erected *Eohomalonotus* (*pro Brongniartia* Salter, 1865 (*pars*); *non* Leach, 1824, *nec* Eaton, 1832) as one of his subgenera of *Homalonotus*. Reed included a number of forms now referable to *Platycoryphe* as well as species of *Eohomalonotus* as presently understood, and distinguished it from *Calymenella* by the lack of a projecting frontal area. Sdzuy (*in* Moore 1959, pp. 0455-0456) regarded *Eohomalonotus* as a subgenus of *Calymenella*, the two being distinguished by the position of the rostral suture and degree of development of pygidial interpleural furrows, as well as the structure of the frontal area. Little recent information is available and whether two distinct genera are represented is a matter which must await further research.

Many authors have placed *Platycoryphe* and *Brongniartella* in the Eohomalonotinae. I regard them as homalonotines and reasons for doing so are given in the discussion of that subfamily.

Subfamily COLPOCORYPHINAE Hupé, 1955

Diagnosis. Cephalon subcircular; convex (tr. and sag.), sometimes highly so. Frontal area short (sag.), no anterior or lateral border. Rostral suture marginal. Glabella clearly defined. Palpebral lobe anteriorly placed. Cheek strongly declined laterally; genal angle well rounded, facial suture gonatoparian. Thoracic axis well defined. Pygidial axis wide and well defined. Border furrow deep; border flexed strongly downwards.

Genera. *Colpocoryphe*, *Plaesiacomia*.

Remarks. Vaněk (1965), like Hupé (1955) and Dean (1971), excluded the Colpocoryphinae from the Homalonotidae and considered them to be calymenids close to *Neseuretus*. The cephalic and glabellar shape, presence of paraglabellar areas (in many species), lack of anterior and lateral cephalic border, marginal rostral suture, moderately wide thoracic axis, thoracic structure, and the poorly segmented pygidium (which lacks interpleural furrows) suggest that colpocoryphines are homalonotids.

Sdzuy (*in* Moore 1959) questionably assigned *Leiostrigina* to this subfamily. The genus is poorly known but shows no obvious features suggestive of a colpocoryphine relationship and I regard it as of uncertain subfamilial position.

Genus PLAESIACOMIA Hawle and Corda, 1847

Type species. *P. rara* Hawle and Corda, 1847, p. 55, pl. 3, fig. 30; from the Caradoc of Bohemia; by monotypy.

Other species. *P. hughesi* sp. nov.; *P. oehlerti* (Kerforne, 1900); *P. vacuvertis* sp. nov.; ?*P. brevicaudata* (Deslongchamps, 1825).

Diagnosis. Colpocoryphine with weakly impressed lateral glabellar furrows, glabella tapering rapidly forwards. Paraglabellar areas usually present; eye ridges absent. Pygidial axis with up to four (?five) weakly defined rings.

Discussion. Vaněk's (1965) view that *Colpocoryphe* and *Plaesiacomia* were synonymous was questioned by Dean (1966b, pp. 140-141) who listed nine distinguishing characters. Five of these—cephalic convexity, depth of anterior arch, and height of the pygidial axis (all greater in *Colpocoryphe*), position of pygidial border furrows, and degree of divergence of the pygidial margins—are interdependent characters connected with enrolment (see Clarkson and Henry 1973). Two more, the development of glabellar furrows and eye ridges, are too variable to be reliable discriminatory characters. Glabellar furrows are usually strongly developed in *Colpocoryphe*, but in a few cases are as weak as in *Plaesiacomia* (see Whittington 1953). Paraglabellar areas occur in all *Plaesiacomia* species known to Dean, but are absent in *P. hughesi*. Two of the features listed by Dean can be reliably used to distinguish between the genera: the glabella in *Colpocoryphe* species is bell-shaped, slightly tapering, with an inflated frontal lobe, while that of *Plaesiacomia* tapers more rapidly to a low frontal lobe and the pygidial axis lacks the clear segmentation of *Colpocoryphe*. *Colpocoryphe* species are poorly known and a revision is necessary before a decision concerning its status can be reached.

Plaesiacomia hughesi sp. nov.

Plate 23, figs. 1-5, 7

v. 1969 *Plaesiacomia* sp.; Hughes, pp. 95-96, pl. 13, figs. 4-8; pl. 14, figs. 1-2.

. 1972 *Plaesiacomia* sp.; Robardet *et al.*, p. 122.

Name. After Dr. C. P. Hughes, who first described this species and made additional material available for study.

Holotype. BM It3024, incomplete internal mould of cranidium, from Ordovician, lower Llanvirn, exposure on the left bank in the ravine in the upper reaches of Camnant Brook immediately north of the S bend 230 yd (207 m) S. 13° W. of the fence crossing the stream source, Builth district, Powys (Radnorshire) (SO 088 575).

Paratypes. BM It13815ab, incomplete cephalon; It13816-13819, It13821ab, It13823ab, cranidia; It3025, external mould of cranidium; It13822ab, It13824ab, It13825ab, It13826-13827, It3023, It3026ab-3027, pygidia; It13820, external mould of pygidium.

Diagnosis. *Plaesiacomia* species with palpebral lobe placed two-thirds the way along the cephalon from the posterior margin. Glabellar furrows absent or very weak; paraglabellar areas absent. Pygidial axis with four (?five) ring furrows on the internal mould.

Description. The following points supplement the description given by Hughes (1969, pp. 95-96). Three pairs of very faint glabellar furrows are developed in the holotype

(Pl. 23, fig. 3a-b), but these are not clearly seen in other specimens. The pygidial border is broad, almost vertically inclined, and narrows somewhat beneath the posterior tip of the axis.

Discussion. Hughes (1969, p. 96) referred this species to *Plaesiacomia* because of the glabellar outline, poor development of lateral glabellar furrows, lack of prominent eye ridges, and shallow anterior arch. I accept this assignation but in the lack of paraglabellar areas, *P. hughesi* is reminiscent of *Colpocoryphe* species. The pygidial axis has more ring furrows than any other *Plaesiacomia* species but, unlike the situation in *Colpocoryphe*, these are shallow and faint.

P. hughesi differs from other *Plaesiacomia* species in lacking paraglabellar areas and having the glabellar furrows very faint or absent, as well as by the relatively large number of pygidial axial rings.

Plaesiacomia vacuvertis sp. nov.

Plate 23, figs. 6, 8-11; Plate 24, figs. 1-6

Name. From Latin *vacuus*, empty and *vertis*, top of the head; alluding to the absence of lateral glabellar furrows in the later growth stages.

Holotype. SM A87322, internal mould of complete specimen, from Ordovician, Llanvirn, type locality of the Hanadir Shale Member of the Tabuk Formation, Jebel Hanadir, Saudi Arabia (25° 28' 00" N. Lat., 43° 27' 30" E. Long.).

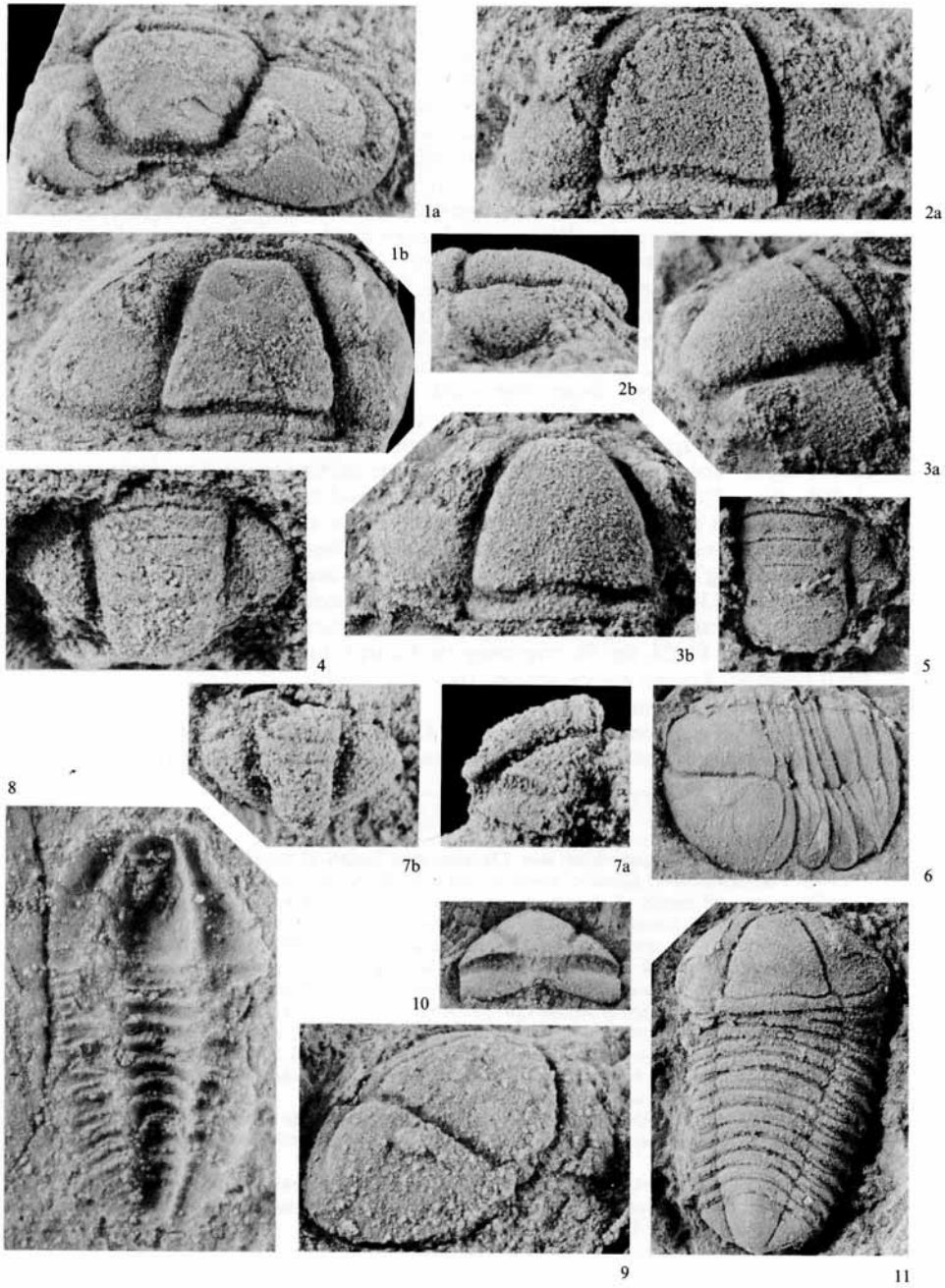
Paratypes. SM A87353, external mould of complete specimen; A87243ab, A87349, A87355, cephalon; A87244, A87321, A87350, partial thoraces and cephalon; A87163ab-A87178ab, A87237ab, A87365, A87294, A87306, A87352, cranidia; A87351, internal mould of incomplete thorax; A87162ab, thoracic segment; A87354, internal mould of pygidium and part of thorax; A87179ab, A87295, pygidia. All from locality and horizon of holotype.

Diagnosis. *Plaesiacomia* species with palpebral lobe placed about half-way along the cephalon. Paraglabellar areas well developed; lateral glabellar furrows weak in smaller individuals, absent in larger ones. Pygidial axis with up to three ring furrows.

EXPLANATION OF PLATE 23

Figs. 1-5, 7. *Plaesiacomia hughesi* sp. nov. Lower Llanvirn, exposure on the left bank in the ravine in the upper reaches of Camnant Brook immediately north of the S bend 230 yd (207 m) S. 13° W. of the fence crossing the stream source, Builth district, Powys (SO 088 575). 1a-b, BM It13815a, internal mould of cephalon, oblique anterior and dorsal views, ×6. 2a-b, BM It13821a, internal mould of cranidium, dorsal and right lateral views, ×8. 3a-b, BM It3024, holotype, internal mould of cranidium, oblique anterolateral and dorsal views, ×8. 4, BM It13820, latex cast from external mould of pygidium, dorsal view, ×6. 5, BM It3026b, latex cast from external mould of pygidium, dorsal view, ×8. 7a-b, BM It13824a, internal mould of pygidium, right lateral and dorsal views, ×8.

Figs. 6, 8-11. *Plaesiacomia vacuvertis* sp. nov. Llanvirn, type locality of the Hanadir Shale Member of the Tabuk Formation, Jebel Hanadir, Saudi Arabia (25° 28' 00" N. Lat., 43° 27' 30" E. Long.). 6, SM A87350, internal mould of incomplete cephalon and thorax, oblique lateral view, ×6. 8, SM A87353, external mould of degree 9? meraspid, ventral view, ×20. 9, SM A87243, internal mould of cephalon, oblique anterolateral view, ×8. 10, SM A87295, internal mould of pygidium, posterior view, ×6. 11, SM A87322, holotype, internal mould of complete specimen, dorsal view, ×4.



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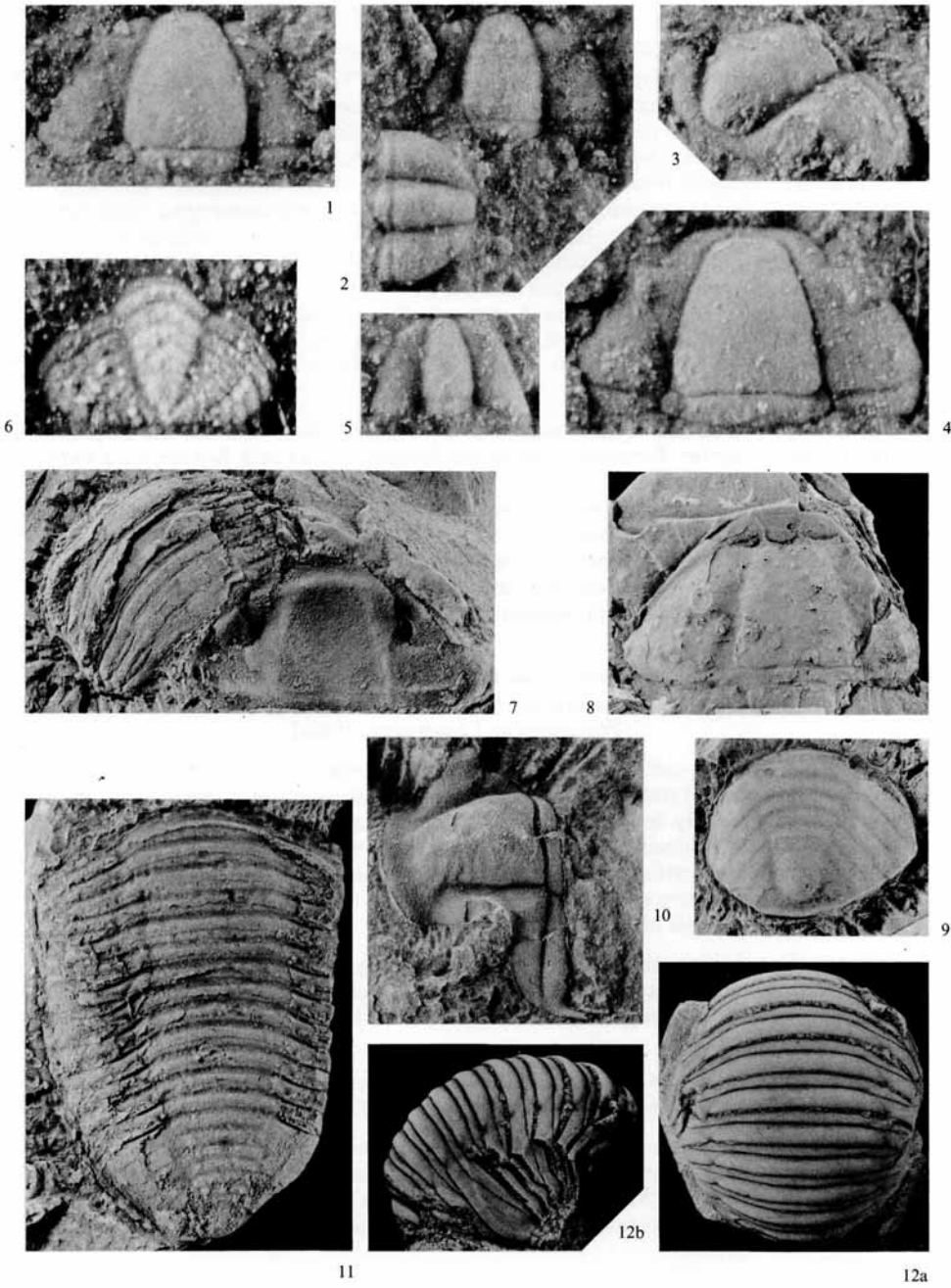
Description. Dorsal exoskeleton more than one and one-half times as long as wide, the maximum width (tr.) situated slightly less than one-third the cephalic length forwards from the posterior cephalic margin. Cephalon semicircular, steeply declined anteriorly and laterally. Occipital ring wide (tr.), trapezoidal, clearly demarcated anteriorly by the occipital furrow. Median occipital tubercle present in some meraspid specimens (Pl. 24, figs. 1, 2, 5). Axial furrows deep and well defined, shallowing posteriorly. Initially they converge at 45° then, anterior to the occipital ring, converge more gently. Preglabellar furrow similar in form to axial furrow and is almost straight (tr.). Glabella tapering forwards to about one-third the width of the occipital ring in larger specimens (Pl. 23, fig. 11). In small meraspid the glabella is subparallel sided, the glabella widening posteriorly during growth (Pl. 24, figs. 5, 2, 1, 4). Up to three pairs of short, faint lateral glabellar furrows are seen in some meraspid (e.g. Pl. 24, fig. 3) but these become effaced in later growth stages. Paraglabellar areas oval, not deeply impressed, their length (exsag.) about one-quarter that of the glabella. Paraglabellar areas are not clearly seen in meraspid but are marked in larger specimens by a distinct flexure in the axial furrow (Pl. 23, fig. 11; Pl. 24, fig. 4). Anterior arch shallow, frontal area narrow (sag.), broadening (exsag.) slightly abaxially. Immediately adjacent to the axial furrow the posterior border is the same width (exsag.) as the occipital ring but it expands somewhat abaxially. Posterior border deep on adaxial two-thirds of fixed cheek, becoming fainter abaxially and terminating near the lateral margin. Posterior branch of facial suture strongly curved, normal to axial furrow at first, then backwardly flexed. Anterior branch of facial suture straight. Palpebral lobe placed near anterior end of glabella in smallest specimens (e.g. Pl. 24, fig. 5), migrating backwards through ontogeny to assume its adult position. Rostral suture straight (tr.).

Hypostome and rostral plate unknown.

Thorax with well-defined trilobation. Axis comprising two-thirds the anterior width (in large specimens), tapering to about half posteriorly. Axis rather narrower

EXPLANATION OF PLATE 24

- Figs. 1-6. *Plaesiacomia vacuvertis* sp. nov. Llanvirn, type locality of the Hanadir Shale Member of the Tabuk Formation, Jebel Hanadir, Saudi Arabia (25° 28' 00" N. Lat., 43° 27' 30" E. Long.). 1, SM A87166a, internal mould of cranium, dorsal view, ×20. 2, SM A87167a and A87168a, internal moulds of crania, dorsal views, ×20. 3, SM A87163a, internal mould of cranium, dorsal view, ×20. 4, SM A87172a, internal mould of cranium, dorsal view, ×20. 5, SM A87170a, internal mould of cranium, dorsal view, ×20. 6, SM A87179a, internal mould of pygidium, dorsal view, ×30.
- Figs. 7-9, 11. *Platycoryphe dyaulax* sp. nov. 7-9, from *convolutus* Zone, Idwian, Llandoverly, Qusayba Shale, Qusayba district, Saudi Arabia (26° 53' 54" N. Lat., 43° 32' 15" E. Long.). 11, from Qusayba Shale, Qusayba district (exact locality unknown). 7, SM A87542, external mould of cephalon and internal mould of incomplete thorax, ventral and dorsal views, ×2. 8, SM A81820, holotype, cranium, dorsal view, ×2. 9, SM A87541, pygidium, slightly oblique posterodorsal view, ×3. 11, SM A89859, internal mould of thorax and pygidium, dorsal view, ×3.
- Fig. 10. *Brongniartella* sp. Dufton Shale, lower Longvillian, south side of valley 780 yd (702 m) at 142° from Dufton Pike, British Lake District (NY 7042 2605). GSM PJ4549, cranium, oblique lateral view, ×4.
- Fig. 12a-b. *Trimerus cylindricus* Salter, 1865. Woolhope Limestone (lower Wenlock), Little Hope, Woolhope district, Hereford and Worcester (Herefordshire). BM I5308, incomplete enrolled thorax, dorsal and right lateral views, ×1.



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in meraspids (compare Pl. 23, figs. 8 and 11). Pleural furrow directed slightly posteriorly and becomes progressively fainter abaxially. The pleura is thus divided into two portions of subequal size. Pleural furrow becomes forwardly directed at the fulcrum, portion of furrow on articulating facet shallower and narrower than that on the more proximal part of the pleura (Pl. 23, fig. 6).

Holaspid pygidium about one-third as long (sag.) as the cranidium. Axis constituting almost half the pygidial width, defined by posteriorly converging, deep axial furrows. Ring furrows faint, barely extending to axial furrow in holaspids; much more distinct in meraspids (compare Pl. 23, fig. 11 with Pl. 24, fig. 6). Larger specimens have unfurrowed pleural areas but at least four pairs of pleural ribs are present in meraspids (Pl. 24, fig. 6). Pleural areas small and triangular in holaspids, with deep border furrow. Latter widest and deepest anteriorly, becoming narrower and shallower as it nears the axis (Pl. 23, fig. 10). Border not developed in meraspid individuals.

Discussion. *P. vacuvertis* is most similar to *P. oehlerti* and *P. rara* but the palpebral lobe is placed further forwards than in the former species and further backwards than in the latter. The lateral glabellar furrows are weaker than in either species.

The only previous descriptions of juvenile homalonotids have been of homalonotines (Cooper 1935; Morzadec 1969; Saul 1967; Sheng 1964). It is interesting to note that no border is developed in *P. vacuvertis* meraspids. The deep border furrow in colpocoryphines is associated with enrolment and overlap of the pygidium by the cephalon in holaspids; no such overlap is possible in meraspids.

Subfamily HOMALONOTINAE

[= Portagininae Lespérance, 1968 (*nom. transl.* Bergström, 1973;
ex Portaginidae Lespérance, 1968)]

Diagnosis. Cephalon subtriangular or semicircular, usually without border. Glabella trapezoidal, often ill defined. Glabellar furrows indistinct, may be absent. Paraglabellar areas usually defined. Posterior branch of facial suture intersecting margin at, or anterior of, rounded genal angle; genal spine very rarely developed. Trilobation often indistinct with very wide axis, though axis may be only moderately wide in Ordovician representatives. Pygidium triangular to semicircular, with tendency to reduced distinctness of trilobation.

Remarks. Genal spines in members of this subfamily are known only in two specimens of *Brongniartella* (e.g. Pl. 24, fig. 10). In contrast to the condition in *Bavarilla*, the facial sutures are proparian. Some Devonian homalonotines may also have proparian sutures.

Genera. *Homalonotus* König, 1825, *Brongniartella*, *Burmeisteria*, *Burmeisterella*, *Digonus*, *Dipleura*, *Parahomalonotus*, *Platycoryphe*, *Trimerus*.

Discussion. *Platycoryphe* was placed in the Eohomalonotinae by various authors (e.g. Hughes 1969; Henry 1971; Apollonov 1974) and *Brongniartella* in the same subfamily by Sdzuy (*in* Moore 1959). These genera show few close similarities to *Calymenella* or *Eohomalonotus* but differ from younger genera only in the more

pronounced trilobation and presence of distinct lateral glabellar furrows in some species. Consequently I regard them as homalonotines.

Genus PLATYCORYPHE Foerste, 1919

Type species. *Calymene platycephala* Foerste, 1910, pp. 81-82, pl. 2, fig. 7; pl. 3, fig. 21; from the Trenton (middle Ordovician) of Clifton, Tennessee; by monotypy.

Other species. *P. barroisi* (Lebesconte, 1887); *P. bohemicus* (Barrande, 1852); *P. christyi* (Hall, 1860); *P. dangeardi* Henry, 1971; *P. dentatus* Dean, 1961; *P. dubius* Savage, 1913; *P. dyaulax* sp. nov.; *P. herberti* (Lebesconte, 1887); *P. sinensis* (Lu, 1963); *P. vulcani* (Murchison, 1839); ?*P. convergens* Dean, 1966a.

Diagnosis. Glabella elongate, trapezoidal in outline, with two to three pairs of glabellar furrows. Frontal area relatively short (sag. and exsag.). Cephalic axial furrows straight or with slightly convex-outwards curvature. Thoracic axis wide or moderately wide. Pygidium wider than long; rounded posteriorly; with eight or fewer ring furrows and six or fewer pleural furrows which become fainter posteriorly.

Platycoryphe dyaulax sp. nov.

Plate 24, figs. 7-9, 11

Name. From Greek *dyo*, two and *aulax*, furrow; alluding to the number of lateral glabellar furrows.

Holotype. SM A81820, cephalon, from *convolutus* Zone, Idwian Stage, Llandovery Series, Qusayba Shale Member of the Tabuk Formation, Qusayba district, Saudi Arabia (26° 53' 54" N. Lat., 43° 32' 15" E. Long.).

Paratypes. From the type locality: SM A87542, internal mould of incomplete thorax and external mould of cephalon; A87541, A87543ab, A87754ab, pygidia. From Qusayba district, 22 m below top of Qusayba Shale (26° 53' 30" N. Lat., 43° 32' 30" E. Long.): A87117ab, cephalon. From Qusayba district, 8 m below top of Qusayba Shale (26° 50' 30" N. Lat., 43° 35' 15" E. Long.): A87772, incomplete cephalon; A87920, cranidium. From Qusayba Shale, Qusayba district (exact locality unknown): A87859, internal mould of thorax and pygidium.

Diagnosis. *Platycoryphe* species with two pairs of broad, shallow glabellar furrows. Thoracic axis broad (tr.). Pygidium with six axial rings and five pairs of pleural ribs.

Description. Cephalon subtriangular, slightly less than twice as wide as long, rounded anteriorly. Breadth (tr.) of occipital ring slightly less than half the maximum cephalic width and slightly greater than the glabellar length. Occipital ring trapezoidal, narrowing forwards, bounded anteriorly by well-defined occipital furrow. Occipital furrow narrow abaxially but broader and shallow along the sagittal line. Axial furrows broad and shallow, strongly convergent at first (at approximately 45° to the posterior margin), then converging more gently. Glabella narrows anteriorly to slightly more than half its posterior width, median raised area present along the sagittal line. 1p broad and shallow, posteriorly directed, not confluent with axial furrow. 2p arises opposite the anterior end of the palpebral lobe, is broad and shallow and orientated parallel to 1p. Adaxially posterior border is the same width (exsag.) as the occipital ring, broadening slightly abaxially. Posterior border furrow broad, shallow, terminating near the rounded genal angle. Paraglabellar area very faint, oval, about one-quarter the glabellar length. Frontal area flat and wide (tr.). Anterior branches of facial suture diverge backwards at first then, behind the frontal area, lie subparallel to an exsagittal line. Posterior branch of facial suture strongly curved at

first, running normal to the sagittal line; then sharply recurved. Free cheek triangular in plan view, steeply sloping to lateral border. Lateral border narrows posteriorly, defined by broad, shallow lateral border furrow.

Hypostome unknown. Rostral plate only known from narrow (sag. and exsag.) dorsal portion (Pl. 24, fig. 8).

Thorax with indistinct trilobation. Axis broad, about half the thoracic width. Pleural furrow deep and narrow; posteriorly directed adaxially, becoming parallel to the segment margins abaxially, then directed forwards on the expanded pleural tip.

Pygidium slightly wider than long, rounded posteriorly. Axis infundibular, poorly defined. Ring furrows become shallower on margins of the axis. Pleural furrows directed only slightly backwards, terminating close to the pygidial margin.

Discussion. Most *Platycoryphe* species have three pairs of distinct lateral glabellar furrows—but these are variably developed in some species (see Whittington 1965, p. 488; Henry 1971, p. 70), especially *P. vulcani* (see Whittard 1961, pl. 22, figs. 12, 16; Hughes 1969, p. 97, pl. 14, figs. 3, 6). *P. dyaulax* is most similar to the latter species but differs in having a much wider thoracic axis and less deeply impressed axial furrows. The pygidium of *dyaulax* is more rounded in outline and the axial, ring, and pleural furrows are much shallower than those of *vulcani* (see Whittard 1961, pl. 22, figs. 8–19).

P. dyaulax is closely comparable with *Brongniartella* and *Trimerus* species, as well as with other species of *Platycoryphe*. From species of *Brongniartella* the cephalon differs principally in lacking indented axial furrows. The *Brongniartella* pygidium is distinguished by being longer than wide with a well-defined axis and nine to twelve axial rings. With other species of *Platycoryphe*, *P. dyaulax* shares the straight cephalic axial furrows, posteriorly rounded pygidium (similar to that of *Brongniartella* but with fewer segments) and a similar occipital ring. The cephalon of *P. dyaulax* is similar to that of some *Trimerus* species, the principal differences being in the pygidium—that of *Trimerus* being characteristically longer than wide and pointed posteriorly. With *Trimerus*, and Silurian–Devonian homalonotids in general, *P. dyaulax* shares the wide thoracic axis.

The mosaic of characters seen in *P. dyaulax* is taken to imply a phyletic relationship between *Brongniartella*/*Platycoryphe* and later homalonotines. Because of this mosaic of characters, reference of *dyaulax* to an existing genus is to some extent both arbitrary and subjective. It has been placed in *Platycoryphe* rather than either *Brongniartella* or *Trimerus* because in this way the minimum disruption is caused to the present concept of these genera.

It is likely that the previously apparently well-defined morphological discontinuity between Ordovician and Silurian–Devonian homalonotids was due to the rarity of Llandovery representatives. Apart from *P. dyaulax* I am aware of only seven records of possible Llandovery homalonotids. *Brongniartella* is known from the lower Llandovery of South Wales (Temple 1975) and from beds of questionable Llandovery age in southern Jordan (Wolfart *et al.* 1968). Wolfart (1961) described a Llandovery *Trimerus* species from Paraguay. The specimens (SM A65437–65438) of '*Homalonotus*' recorded by Jones (1925, p. 370) from the Fronian and Telychian of the Llandovery area are poorly preserved but probably represent a *Trimerus* species.

Yin (1966, p. 297) listed '*Homalonotus* sp.' from the *persculptus* Zone of the Upper Yangtze Province—the genus *Liangshanaspis* was later proposed for this material (see discussion p. 160). The specimen (SM A38734ab) from the British Lake District, listed as '*Homalonotus?*' by Marr and Nicholson (1888, p. 664), is not homalonotid. The record of '*Homalonotus* sp.' by Pocock *et al.* (1938, p. 269) rests on a fragment of a thoracic segment (GSM D34473) which is not homalonotid.

PHYLOGENY OF THE HOMALONOTIDAE

The Cambrian ancestors of homalonotids are unknown but a number of Cambrian genera occur in which the over-all morphology, especially the forwardly narrowing glabella and opisthoparian sutures, is similar to that of early calymenids and homalonotids. Warburg (1925, p. 69) noted the similarity of the Calymenacea to *Ptychoparia* and its allies, while Shirley (1931, pp. 8–9) pointed to the similarities shared with ptychopariids in general and *Alokistocare* and *Acrocephalites* in particular. The resemblance of *Lobocephalina* (Conocephaloninae; see Moore 1959, pp. 0237–0238, fig. 176.2c) and *Modocia* (Marjumiidae; see Moore 1959, p. 0306, fig. 228.2a–d) to early homalonotids, especially *Bavarilla*, is also striking. Apart from the glabellar shape and sutural morphology these forms display the tendency to reduced distinctness of glabellar furrows, relatively short genal spines, small eyes (in *Modocia*), thorax of fourteen segments with rounded pleural tips, and a posteriorly rounded pygidium which possesses an ill-defined border.

By the Tremadoc/Arenig a number of genera occur from which evolutionary lines lead to younger calymenids and homalonotids. The difficulty of classifying these early genera has been discussed and is indicative of their common origin.

In the Arenig representatives of the Colpocoryphinae, Eohomalonotinae, and Homalonotinae are present, the colpocoryphines and eohomalonotines becoming extinct in the Caradoc and Ashgill respectively. Homalonotines persist until the middle Devonian though they are rare in the Ashgill and even more so in the Llandovery (see pp. 170–171). *Trimerus* first appears in the upper Llandovery and seems to have given rise to younger genera. A new radiation began in the upper Silurian (three genera) and continued in the lower Devonian (six genera). The stratigraphical ranges of the Devonian genera are imprecisely known but on present evidence *Trimerus* disappears in the Siegenian while *Parahomalonotus*, *Burmeisterella*, *Burmeisteria*, and *Digonus* are restricted to the interval Gedinnian to Emsian. Only *Dipleura* is certainly known from the middle Devonian. These genera are in need of revision but show many similarities to *Trimerus* and *Dipleura* and were probably derived from one or both of these genera. The cephalon of *Burmeisteria*, for instance, shares many features with juvenile specimens of *Dipleura* (compare Morzadec 1969, pl. 2, fig. 6a with Moore 1959, p. 0460, fig. 361.1a). The form of the glabella and lateral glabellar furrows are exceedingly similar and *Burmeisteria* may be a neotenus descendant of *Dipleura*.

As far as Ordovician forms are concerned, *Colpocoryphe* and *Plaesiacomia* share many common characters, some of which are due to the presence of coaptative structures associated with enrolment. Many of the features of *Colpocoryphe* are present in a more extreme form in *Plaesiacomia*—the tendency to efface glabellar

furrows and loss of distinct pygidial segmentation, for instance—and I regard *Plaesiacomia* as being derived from early *Colpocoryphe* species. *Colpocoryphe* displays some 'primitive' features concordant with this view in that strong eye ridges are often developed and paraglabellar areas absent (Dean 1966b, p. 141). The evidence is inconclusive, however, since the oldest *Plaesiacomia* species have smooth cephalae without eye ridges and resemble *Colpocoryphe* mainly in having a relatively large number of pygidial axial rings.

Fortey (1974, pp. 61–65, pl. 20, figs. 1–12) described the unusual olenid *Svalbardites hamus*, from the Arenig of Spitsbergen, and noted (p. 64) the similarity of its pygidium to those of *Plaesiacomia* species, although he doubted a direct relationship. The form of the colpocoryphine pygidium is largely determined by its role in enrolment, and the lack of a deep border furrow in *Svalbardites* suggests that the resemblance is superficial. There is also some cephalic similarity, notably in eye position and general effacement, but the *Svalbardites* glabella is completely unlike the forwardly tapering form characteristic of homalonotids. Homalonotids have a well-developed rostral plate, olenids commonly have no rostral plate and the free cheeks are united by a narrow strip of doublure. I consider an olenid-homalonotid relationship unlikely and the similarities between *Plaesiacomia* and *Svalbardites* to be superficial.

Eohomalonotus and *Calymenella* form a distinct group. Some early species of *Platycoryphe* resemble *Calymenella* in having distinct eye ridges and a sigmoidal 1p furrow (see Henry 1971). In other respects (no distinct cephalic border; pygidial form; no prominent pygidial interpleural furrows), however, they are closer to later species of *Platycoryphe*. Such forms seem to be close to the point of divergence of homalonotines and eohomalonotines.

Platycoryphe and *Brongniartella* are similar genera and the difficulty of discriminating between them when the glabellar furrows are weak has often been noted (Dean 1961, p. 344; Whittington 1965, p. 488; Hughes 1969, p. 98). The resemblances are unsurprising since *Brongniartella* may have been derived from *Platycoryphe* (Whittington 1966b, p. 723, text-fig. 13). The Llandovery homalonotine, *P. dyaulax*, shows features in common with both younger homalonotids and with *Platycoryphe* and *Brongniartella*. I consider that post-Ordovician homalonotines were derived from this stock. Sdzuy (1957, p. 284) suggested that the pygidial morphology of *Brongniartella* indicated that it did not give rise to younger genera. He did not develop this theme, and *Platycoryphe* was not discussed. Sdzuy (p. 286, fig. 3) derived *Trimerus* from *Eohomalonotus* but, because of the morphological differences discussed above, this view is considered untenable.

Silurian–Devonian homalonotines comprise a closely related, morphologically homogeneous group (for a summary of their relationships see Tomczykowa 1975). The Ludlow genus *Homalonotus* may have evolved from an upper Wenlock form like *T. johannis* by the loss of glabellar lobation together with a reduction in length, and folding, of the frontal area. Other features of the exoskeleton are very similar (compare Salter 1865, pl. 12, figs. 2–10 and pl. 13, fig. 8 with pl. 12, fig. 11 and pl. 13, figs. 1–7). Tomczykowa (1975, p. 14) suggested that *T. johannis* might also be ancestral to *Digonus*. Such a relationship is plausible but a substantial stratigraphical gap exists between the occurrence of *T. johannis* and the earliest record of *Digonus* in the

Gedinnian. *Dipleura* first appears in the Ludlow and may have been derived from *Trimerus* through a form similar to *T. lobatus* Tomczykowa, 1975.

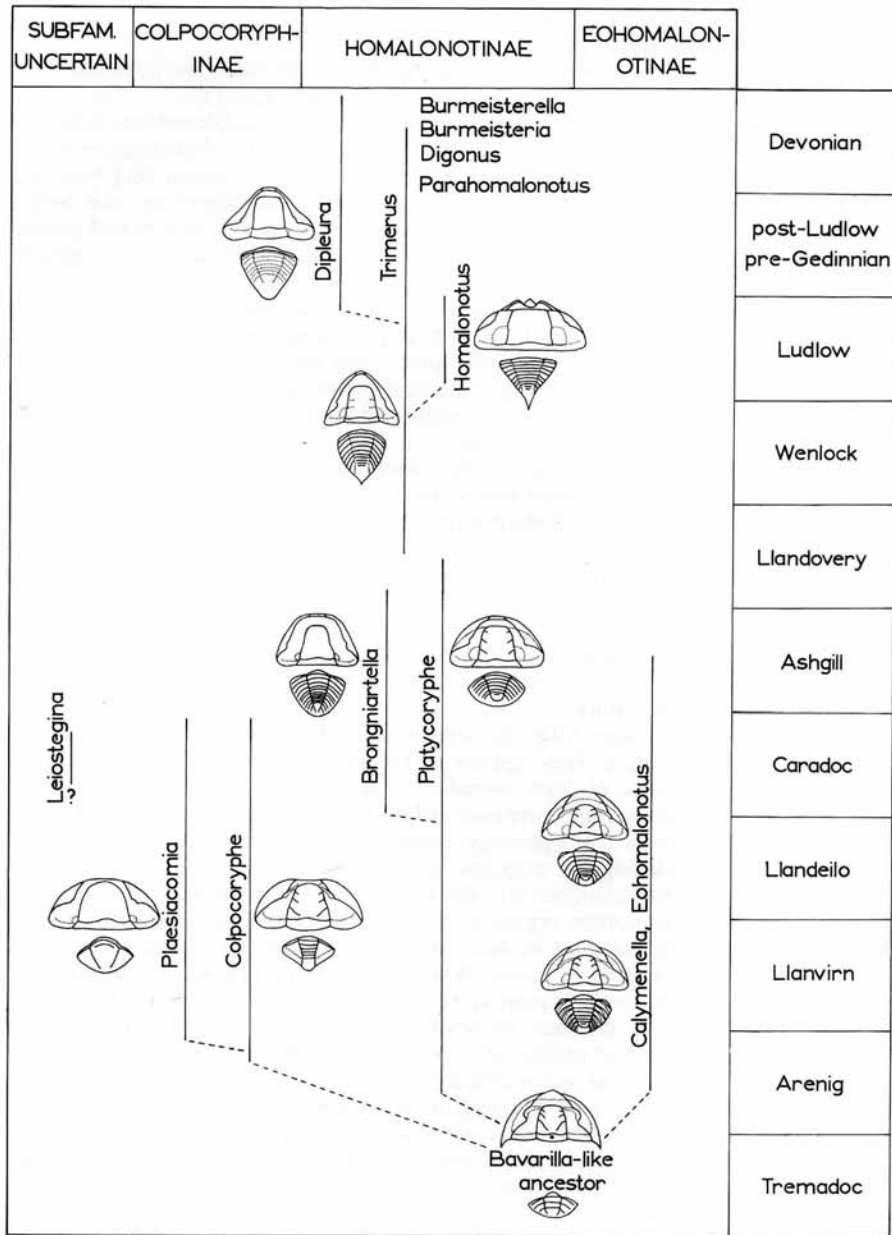
Throughout the Ordovician, and in the early Silurian, homalonotines display a progressive increase in the width (tr.) of the thoracic axis and a tendency to reduced distinctness of trilobation. By the middle Silurian the thoracic axis is very wide and trilobation quite indistinct. The thoracic segments of homalonotines and colpocoryphines differ from those of all other trilobites in that the articulating and pleural furrows merge and the articulating half ring becomes fused with the anterior pleural band. Hence the articulating half ring becomes greatly enlarged (tr.) and comes to occupy much of the width of the segment (see Pl. 24, fig. 12a-b). Material of *Calymenella* loaned to me by Professor H. B. Whittington indicates that eohomalonotines differ from other homalonotids in this respect. They have a more 'normal' type of articulation, the articulating half rings not extending outside the axis (see also Szalay 1957, pl. 1, fig. 8). This phenomenon is associated with the retention of a relatively narrow thoracic axis in eohomalonotines.

The selective forces responsible for the evolutionary changes outlined above are unknown. The adoption of a rather specialized mode of life may explain the morphological contrasts between the Colpocoryphinae/Homalonotinae and their inferred ancestor, *Bavarilla*.

The similarity of Silurian-Devonian genera suggests that the post-Ordovician homalonotine radiation was connected with the exploitation of a number of closely related niches, the general mode of life being broadly similar. *Homalonotus* is the most unusual post-Ordovician homalonotine. The complex structure of the anterior part of the cephalon (see Salter 1865, pl. 12, fig. 2) may indicate that this genus had somewhat different life habits.

Eohomalonotines change little throughout their history and show few major differences from *Bavarilla*. They appear to represent a group whose way of life changed little from that of their ancestors. The retention of several 'primitive' characters (e.g. eye ridges, anteriorly widened border, sigmoidal 1p furrow, relatively small rostral plate, thoracic morphology) accords with this view. A case could therefore be argued for placing the colpocoryphines and homalonotines in a separate family from the Eohomalonotinae and *Bavarilla*. This reflects the inferred phylogeny in which the eohomalonotines represent a relatively unchanged conservative stock while the Colpocoryphinae and Homalonotinae are 'progressive' groups united, in particular, by their thoracic structure. While such an arrangement is in some ways appealing, its adoption would be premature. The pattern outlined may need modification when relationships between homalonotids and calymenids in general, and between *Bavarilla* and older genera, are better understood.

What is known of homalonotid distribution supports the proposed phylogeny. Whittington (1966b, 1972) and Whittington and Hughes (1972, 1973) have demonstrated the existence of discrete faunal provinces in which different trilobite groups evolved in relative isolation through much of Ordovician time. In the Arenig-Llandeilo *Colpocoryphe*, *Plaesiacomia*, *Eohomalonotus*, *Calymenella*, and *Platycoryphe* are restricted to the Florida/west-central Europe/North Africa region (the Selenopeltis province), a part of which *Bavarilla* inhabited in the Tremadoc. The upper Ordovician decay of faunal provincialism is reflected in homalonotid



TEXT-FIG. 1. Phylogeny of the Homalonotidae. Solid lines represent known ranges of genera, broken ones their inferred relationship.

distribution with *Brongniartella* and *Platycoryphe* extending their range into North America and Kazakhstan during the Caradoc and Ashgill. In the Ashgill *Brongniartella* is widespread in northern Europe, *Calymenella* being present in central China (Whittington 1966b, p. 728) and possibly Argentina (Baldis and Blasco 1975).

Some of the unusual features of *Leiostegina*, from the Caradoc of Bolivia, may be due to its having evolved in relative isolation. According to Whittington and Hughes's (1972, p. 257, fig. 9) palaeogeographical map Bolivia lay on the opposite side of Gondwanaland to the *Selenopeltis* fauna, although at a similar latitude.

No marked provincialism is developed in the Silurian. *Platycoryphe* occurs in the Llandovery of Saudi Arabia and China and *Brongniartella* in the low Llandovery of South Wales. *Trimerus* first occurs in the upper Llandovery of South Wales and Paraguay and extends its range in the later Silurian and lower Devonian, being known from North America, Europe, Mongolia, and Australia. *Homalonotus* first appears in the lower Ludlow of South Wales and throughout its short range was restricted to Nova Scotia, Britain, Scandinavia, and Poland. On a pre-drift map these areas lie close together some 10°–20° south of the equator. *Dipleura* is first known from the upper Ludlow of Britain and Poland and was probably derived from one of the *Trimerus* species found in this area. Homalonotids are widespread in the Devonian but it is not possible to discuss the distribution of individual genera since the taxonomy is poorly known.

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Note on orientation. Dorsal view refers to the orientation in which cephalae are placed with the occipital ring in a vertical plane and pygidia placed with the anterior margin of the axis vertical.

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