RADNORIA, A NEW SILURIAN PROETACEAN TRILOBITE, AND THE ORIGINS OF THE BRACHYMETOPIDAE

by R. M. OWENS *and* A. T. THOMAS

ABSTRACT. The new trilobite genus *Radnoria* is proposed to include the type, *R. syrphetodes* sp. nov., and two other species, *R. triquetra* sp. nov. and *R. humillima* (Barrande, 1852), from the Silurian of Britain and Czechoslovakia. Its morphology includes features typical of both the Brachymetopidae and Warburgellinae, suggesting a phyletic link between the two groups. The composition of the Brachymetopidae is discussed, and new family and subfamily diagnoses are given.

RECENT collecting from the Dolyhir Limestone (Silurian, Wenlock Series) in the Old Radnor district, Powys (Radnorshire), the Much Wenlock Limestone Formation of Wren's Nest Hill, Dudley, West Midlands, and from a limestone of Wenlock age near Llandeilo, Dyfed (Carmarthenshire) has furnished large numbers of dissociated exoskeletal parts of two undescribed proetacean trilobite species, here placed in a new genus. *Cyphaspis humillima* Barrande, 1852 from the late Wenlock of the Prague district, Czechoslovakia also belongs to the same genus. The significance of this new genus lies in its similarities both to members of the proetid subfamily Warburgellinae and to the family Brachymetopidae, and in the consequent implications for the origins of the latter.

Terminology. Terms used in the descriptions are those defined by Harrington *et al.* (*in* Moore 1959, pp. 0117-0126) and Owens (1973, pp. 3, 5; text-fig. 1A, p. 4).

Repositories. The following abbreviations are used herein: GSM—The Geological Museum, Institute of Geological Sciences, London; NMW—National Museum of Wales, Cardiff; NMP—National Museum, Prague.

SYSTEMATIC PALAEONTOLOGY

Family BRACHYMETOPIDAE Prantl and Přibyl, 1951

Diagnosis. The following diagnosis is based on that of Whittington (1960, p. 407), modified to include the Warburgellinae and other slight amendments. Cephalon with preglabellar field; tropidium or tropidial ridges may be present; glabella narrows forwards, commonly with well defined 1p lobe; 2p and 3p furrows may be present; palpebral lobe far back and close to glabella; anterior branches of facial sutures divergent; connective sutures diverge backwards; thorax of 8-10 segments; no preannulus; pygidium relatively large; axis with ?6-14 rings, pleural ribs with flat-topped profile, or with posterior band elevated above anterior; pygidial margin entire or with short spines; external surface smooth, granular, tuberculate, rugulose, pitted, or spinose, or combination of these.

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Stratigraphical range. Silurian (Llandovery) to uppermost Carboniferous, possibly to Permian.

Subfamily WARBURGELLINAE Owens, 1973

[= Warburgellinae Yolkin, 1974]

Diagnosis. 1p furrow deep; tropidium or tropidial ridges may be present; occipital ring with lateral lobes; thorax of 8–10 segments; pygidium with narrow axis with ?6–14 rings; pleural areas with ?5–7 pairs of ribs with flat-topped profile; pygidial border may be present; sculpture granular or rugulose, or exoskeleton smooth.

Genera and subgenera. Warburgella (*Warburgella*) Reed, 1931; *W.* (*Tetinia*) Chlupáč, 1971; *Prantlia* Přibyl, 1946; *Tropidocare* Chlupáč, 1971; ?*Koneprusites* Přibyl, 1964.

Stratigraphical range. Silurian (Llandovery) to Devonian (Gedinnian), possibly to Middle Devonian.

Remarks. Yolkin (1974, p. 64) included *Warburgella*, *Astroproetus* Begg, 1939, *Tetinia*, *Cyphoproetus* Kegel, 1927, and *Paleodechenella* Maximova, 1970 in the Warburgellinae. Of these genera, Owens (1973, p. 8) placed *Cyphoproetus* in the Proetinae and *Astroproetus* in the Tropidocoryphinae (ibid., p. 40), and reasons for doing so are discussed therein. Without having seen original material of *Paleodechenella*, we cannot comment on its subfamilial affinities.

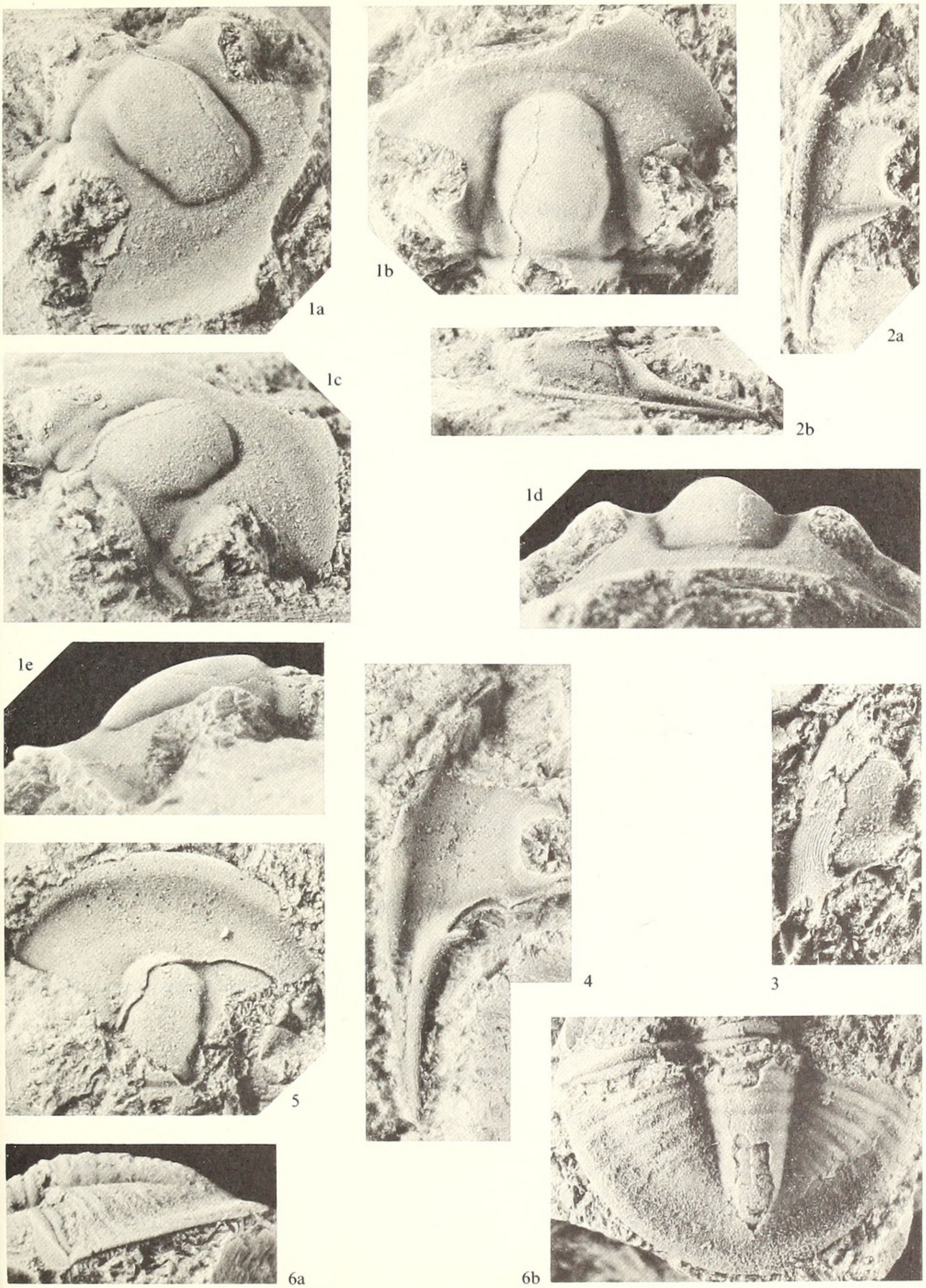
Yolkin (1974, p. 64) referred the Warburgellinae to the Dechenellidae. Members of this family (which we consider to be a proetid subfamily) do show a broad resemblance to warburgellines, but possess a preannulus, and the pygidial pleural rib structure is like that of the Proetinae. On the basis of the thoracic and pygidial differences, and also because dechenellines are almost certainly phyletically linked with proetines (Owens 1973, p. 84), we consider that their general similarity to warburgellines is due to homoeomorphy.

Subfamily BRACHYMETOPINAE Prantl and Přibyl, 1951

Diagnosis. Preglabellar field broad, concave or weakly convex in longitudinal section; 1p lobe isolated except in *Brachymetopus*; 2p and 3p commonly absent or ill defined; anterior branches of facial sutures widely divergent (ankylosed in *Brachymetopus*); tropidium absent; occipital ring without lateral lobes; rostral plate large, may extend as far back as genal angle; thorax of nine segments; pygidial axis with 10–13 axial rings; pleural ribs commonly with posterior band elevated above anterior, but

EXPLANATION OF PLATE 95

Figs. 1–6. *Radnoria syrphetodes* gen. et sp. nov. 1*a–e*, Limestone of probable Wenlock age, old quarry opposite Ty-newydd Farm, 1·3 km at 127° from Llanarthney church, Dyfed (SN 5442 1951): GSM 103744, cranidium, anterolateral oblique, dorsal, posterolateral oblique, anterior, and left lateral views, ×8. 2–6, Wenlock Series, Dolyhir Limestone, disused quarry 475 m W. of Dolyhir Bridge, Old Radnor, Powys (SO 2409 5812): 2*a–b*, NMW 74.30G.12a, left free cheek, dorsal and left lateral views, ×8. 3, NMW 74.30G.62b, right free cheek, ventral view, ×8. 4, NMW 74.30G.15, left free cheek, oblique dorsal view, ×8. Note course of connective suture. 5, NMW 72.18G.177, holotype cranidium, dorsal view, ×8. 6*a–b*, NMW 74.30G.23, pygidium and thoracic segment, left lateral and dorsal views, ×8.



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rarely with flat-topped profile; pygidial margin entire or with short spines; external surface tuberculate, pitted, spinose, or smooth.

Stratigraphical range. Silurian (Wenlock Series) to Carboniferous, possibly to Permian.

Genera. Australosutura Campbell and Goldring, 1960; *Brachymetopus* M'Coy, 1847; *Cordania* Clarke, 1892; *Mystrocephala* Whittington, 1960; *Proetides* Walter, 1924; *Radnoria* gen. nov.; *Tschernyshewiella* Toll, 1899; ?*Cheiropyge* Diener, 1897.

Discussion. Brachymetopus, Cordania, Mystrocephala and *Australosutura* are well known and there is no doubt as to their membership of the family. We agree with Hessler (1962, p. 812) that *Proetides* is a brachymetopid. No good illustrations are available for *Tschernyshewiella*, but we accept Whittington's (1960, p. 407) observations on its close similarity to *Cordania*, and include it in the family. We consider that *Piltonia* Goldring, 1955 should be excluded; both Hahn (1964, p. 362) and Osmólska (1970, pp. 12, 13) considered it to be closely allied to 'phillipsiid' genera, in particular to *Eocyphinium* Reed, 1942, a view supported by Owens's unpublished work. *Cheiropyge*, from the Permian of the Himalayas, was excluded from the family by Whittington (1960, p. 408). His reasons for doing so were not discussed, except to state that the pygidium on which the genus is based did not, in his view, resemble those of other brachymetopids. Schmidt (*in* Moore 1959, p. 0408) questionably included *Cheiropyge* in the Brachymetopidae, and although existing illustrations (Diener 1897, pl. 1, fig. 2*a–c*; Moore 1959, fig. 310.4, p. 0407) are poor, they do show that the pygidium resembles spinose *Brachymetopus* pygidia. Until this genus can be revised, we follow Schmidt, and provisionally assign it to the Brachymetopidae. *Namuropyge* R. and E. Richter, 1939 was included with question in the Brachymetopidae by Schmidt (*in* Moore 1959, p. 0408), but we agree with Whittington (1960, p. 408) that it should be excluded; we also agree with Schmidt (*in* Moore 1959, p. 0408, footnote) and Whittington (1960, p. 408) that *Panarchaeogonus* Öpik, 1937 is not a brachymetopid, and Owens (1974, p. 687) and Fortey and Owens (1975, p. 231) considered it to be an otarionid.

Genus RADNORIA gen. nov.

Derivation of name. From Old Radnor, Powys, from where most of the material of the type species originates.

Type species. Radnoria syrphetodes sp. nov.

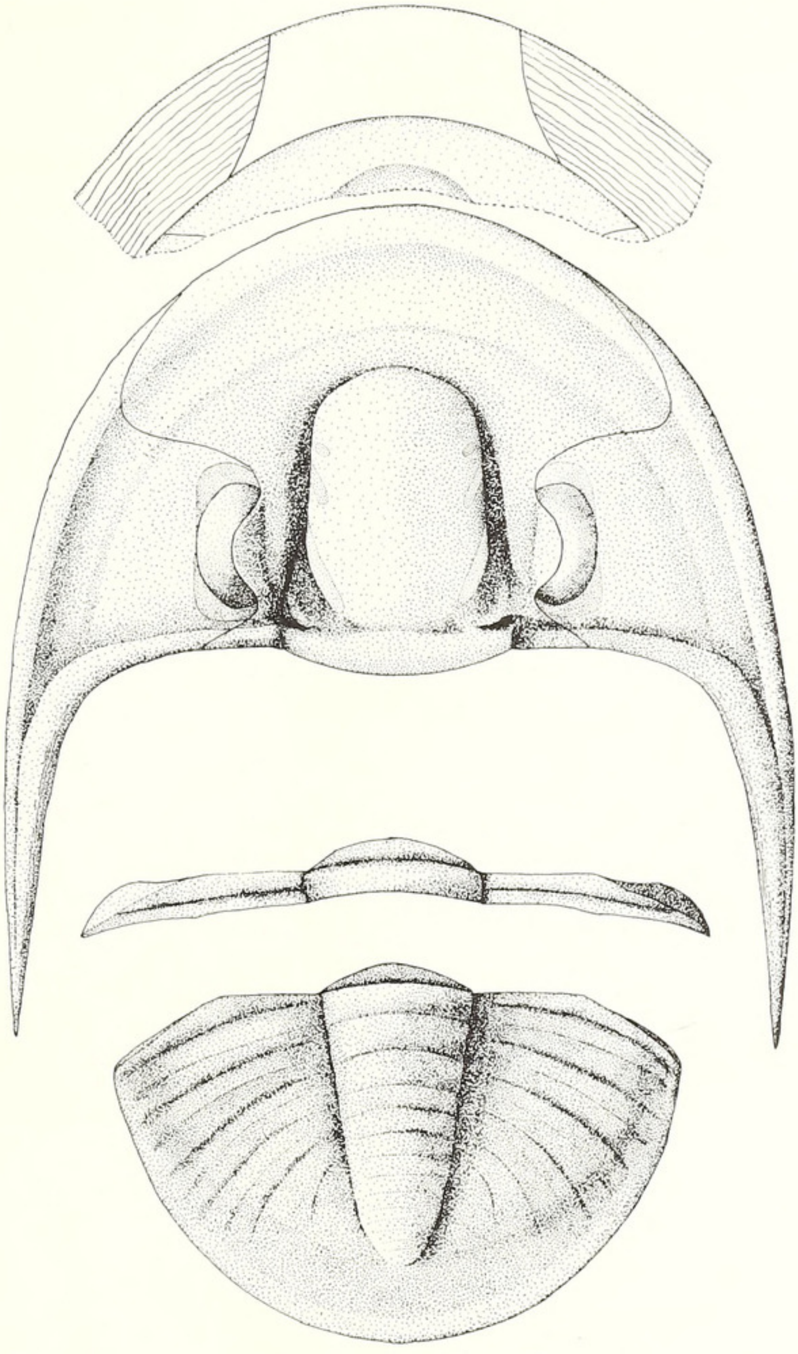
Other species. R. triquetra sp. nov., *R. humillima* (Barrande, 1852).

Diagnosis. Preglabellar field concave or flat in longitudinal section; shallow depression traverses its posterior part and inner part of fixed and free cheeks, running parallel to margin; anterior branch of facial suture diverges at 60–70° from an exsagittal line through γ; pygidial axis with 10–13 rings, pleural areas with 6–7 pairs of ribs; latter with flat-topped profile or with posterior pleural band elevated above anterior; dorsal surface smooth or with fine pits and sporadic granules.

Radnoria syrphetodes sp. nov.

Plate 95, figs. 1–6; Plate 96, figs. 1, 2; text-fig. 1

v. 1972 *Warburgella* cf. *stokesii* (Murchison); Bassett, p. 31.
v. 1973 *Warburgella* (*Warburgella*) *stokesii* (Murchison); Owens, p. 67 *pars*. [reference only to single specimen from Ty-newydd Farm].
v. 1974 ?*Prantlia* sp.; Bassett, p. 759.



TEXT-FIG. 1. Reconstruction of *Radnoria syrphetodes* gen. et sp. nov. Topmost illustration represents the ventral aspect of the anterior part of the cephalon to show the inferred shape of the rostral plate (blank area). All ×11 approx.

Derivation of name. Greek *syrphetodes*, jumbled together; reference to the mosaic of characters of various genera seen in *Radnoria*.

Holotype. Cranidium NMW 72.18G.177, from Wenlock Series, Dolyhir Limestone (lower Wenlock); disused quarry 475 m W. of Dolyhir Bridge, Old Radnor, Powys (SO 2409 5812) (Quarry 'D' of Garwood and Goodyear 1918, pl. 7).

Paratypes. Cranidia NMW 72.18G.178, 74.30G.4a–b, c, 10b–c, 13c–d, 18–19, 68, 73a, free cheeks NMW 74.30G.8–9, 10a, 11–13, 15–17, 62b, pygidia NMW 72.18G.179–180, 74.30G.3e–f, 10d, 14, 20–61, 62c–d, 67, 69–72, 73b, 74 from the type locality; pygidium NMW 74.30G.77 from shale band in Dolyhir Limestone, type locality; cranidia GSM 103744, NMW 74.30G.93a–b, pygidia GSM DEX2927, NMW 74.30G.94–98 from limestone of probable lower-middle Wenlock age, old quarry opposite Ty-newydd Farm, 1·3 km at 127° from Llanarthney church, Dyfed (SN 5442 1951). An ill-preserved cranidium, NMW 74.30G.99 from the Much Wenlock Limestone Formation (*lundgreni* Zone) of Wren's Nest Hill, Dudley, may also belong to this species.

Diagnosis. Glabella with weak forward taper; 1p furrows broad and shallow, 1p lobes reduced; pygidium with 10–13 axial rings and six pairs of pleural ribs with flat-topped profile.

Description. Cranidium moderately vaulted, palpebral width about two-thirds sagittal length. Glabella about as wide as long, defined laterally by deep axial furrows; these shallow and narrow at 1p lobes, and at anterolateral corner of glabella run into shallower preglabellar furrow, which is shallowest at sagittal line. From its posterolateral corners, glabella tapers gently forwards to bluntly rounded frontal lobe. In lateral profile it is gently convex, with the posterior end elevated well above the occipital ring (Pl. 95, fig. 1*e*). In transverse section it is strongly convex (Pl. 95, fig. 1*d*). 1p furrow runs into axial furrow opposite anterior part of palpebral lobe, and is directed inwards and backwards at about 25° to an exsagittal line, with steep adaxial slope and shallow abaxial slope. 1p furrow defines partially isolated, reduced, roughly triangular 1p lobe, which is fused with remainder of glabella at its inner end. 2p furrow a smooth area, not impressed, meeting axial furrow about two-thirds of way along glabella from its posterior end, directed backwards at about same angle as 1p. 3p small, not reaching axial furrow, placed a short distance in front of 2p, directed backwards at about 40°.

Occipital furrow rather broad and shallow in its median section, deepening markedly behind 1p lobes, and arched forwards very weakly sagittally. Occipital ring about as wide (trans.) as base of glabella, its sagittal length about one-third that of preglabellar area. No lateral lobes; presence or absence of occipital node unknown. Preglabellar field about half sagittal length of glabella, weakly concave in longitudinal section, anteriorly merges almost imperceptibly into gently upturned, weakly convex anterior border, which is between one-third and one-half the sagittal length of preglabellar field. Preglabellar field traversed on its posterior portion by shallow depression running parallel with margin, and which continues on to

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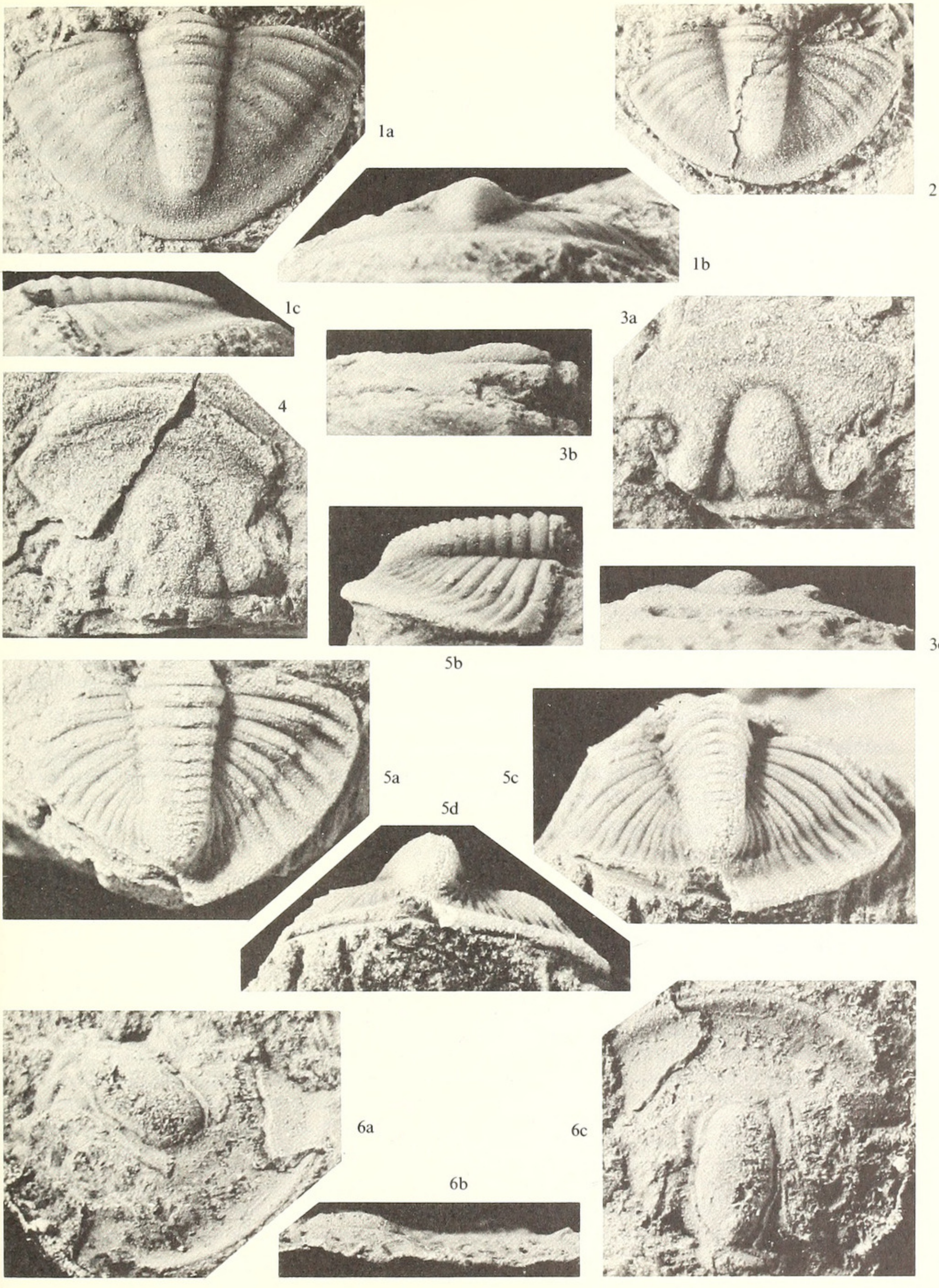
EXPLANATION OF PLATE 96

Figs. 1–2. *Radnoria syrphetodes* gen. et sp. nov. Wenlock Series, Dolyhir Limestone, disused quarry 475 m W. of Dolyhir Bridge, Old Radnor, Powys (SO 2409 5812). 1*a–c*, NMW 74.30G.33a, pygidium, dorsal, posterior, and left lateral views, ×8. 2, NMW 72.18G.179, pygidium, dorsal view, ×8.

Figs. 3–5. *Radnoria triquetra* gen. et sp. nov. Wenlock Series, Much Wenlock Limestone Formation, Nodular Beds, large bedding plane exposure on west side of Wren's Nest Hill, Dudley, West Midlands (SO 9350 9210). 3*a–c*, NMW 71.6G.239, holotype, internal mould of cranidium, dorsal, left lateral, and anterior views, ×10. 4, NMW 71.6G.260, internal mould of cranidium, dorsal view, ×8. 5*a–d*, NMW 71.6G.240, pygidium, dorsal, right lateral, oblique posterodorsal, and posterior views, ×12.

Fig. 6. *Radnoria humillima* (Barrande, 1852). Wenlock Series, Liteň Formation, Loděnice, near Beroun, Czechoslovakia. NMP 215/68, latex cast of cranidium, oblique anterolateral, right lateral, and dorsal views, ×12. Original of Horný, Prantl and Vaněk 1958, pl. 2, fig. 6.



OWENS and THOMAS, *Radnoria*

field of free cheek. This depression appears to correspond roughly with the inner edge of the cephalic doublure (Pl. 95, figs. 2*a*, 3).

Anterior branch of facial suture diverges at 60–70° from an exsagittal line through γ. γ a broad curve, a little way out from axial furrow. Palpebral lobe backwardly placed, subsemicircular and about one-third sagittal length of glabella. ϵ and ξ a single angle, a short distance in front of posterior border furrow. Section $\epsilon+\xi$ to ω short, nearly straight, defining minute, triangular posterior portion of fixed cheek. Visual surface unknown. Distinct eye socle, the lower margin of which is not incised and which diverges strongly from the upper margin at either end; median section directed almost exsagittally. Field of free cheek broad, lateral border more upturned and a little narrower than anterior. Posterior border furrow shallow, comparable to lateral. Long genal spine with deep median groove, which dies out before reaching posterior end. Cephalic doublure broad (Pl. 95, fig. 3); connective sutures of rostral plate backwardly divergent (Pl. 95, fig. 4). Hypostome unknown. Thorax known only from one incomplete segment (Pl. 95, fig. 6*a*–*b*).

Pygidium rather weakly vaulted, about two-thirds as long as wide. Axis about one-quarter greatest transverse pygidial width, tapering gently backwards, not reaching posterior margin; axial rings defined by shallow ring furrows which become progressively shallower posteriorly. No postaxial ridge. Pleural areas broad, weakly convex with six pairs of pleural ribs of flat-topped profile whose anterior and posterior pleural bands are of approximately equal width (exsag.). Pleural furrows rather shallow, of constant depth along their length, much deeper than ill-defined interpleural furrows, which become deeper at their abaxial ends. Both pleural and interpleural furrows reach close to pygidial margin. No border, but marginal area of pygidium flattened. Sculpture of fine pits (on preglabellar field, cheeks and 1p lobe) and granules (on glabella, anterior border, and palpebral lobe) seen on some cranidia (Pl. 95, fig. 1), and some pygidia have very fine granulation (Pl. 96, fig. 1) or pits (e.g. GSM DEX2927). The apparent absence of these sculptural elements on some specimens (Pl. 95, figs. 5, 6) may be a product of preservation or of variation. The similarity of other features of all the material included in this species suggest that the presence or absence of fine sculptural details is not of taxonomic significance.

Radnoria triquetra sp. nov.

Plate 96, figs. 3–5

Derivation of name. Latin *triquetrus*, triangular; with reference to the shape of the glabella.

Holotype. Cranidium NMW 71.6G.239, from Wenlock Series, Much Wenlock Limestone Formation, Nodular Beds (*lundgreni* Zone), large bedding plane exposure on west side of Wren's Nest Hill, 200 m SW. of 'Caves' public house, Dudley, West Midlands (SO 9350 9210).

Paratypes. Cranidium NMW 71.6G.260 and pygidia NMW 71.6G.240, 72.18G.181; horizon and locality of holotype.

Diagnosis. Glabella triangular with distinct 1p lobes; pygidium with thirteen axial rings, each with a posteriorly placed median node, and seven pairs of pleural ribs in which posterior pleural band is elevated above anterior.

Description. Cranidium weakly vaulted, with palpebral width three-quarters of sagittal length. Glabella as wide posteriorly as long, defined by deep axial furrows which merge anteriorly with shallow preglabellar furrow. In lateral profile glabella gently convex, more strongly so in transverse section, with posterior end elevated above occipital ring. 1p furrow runs from axial furrow backwards and inwards at 60° from an exsagittal line, curved adaxially, into the occipital furrow, widening and shallowing at its posterior end. 1p lobe isolated, semi-oval, about one-third glabellar length. 2p and 3p furrows not seen on available material. Occipital furrow broad and shallow, arched very weakly forwards sagittally, deepening laterally behind 1p lobes. Occipital ring nearly one-third length (sag.) of preglabellar field, and marginally wider (trans.) than widest part of glabella. No lateral lobes. Preglabellar field approximately two-thirds sagittal length of glabella, nearly flat in longitudinal section, traversed on its posterior portion by a shallow depression. Anterior border furrow weak, anterior border about half sagittal length of preglabellar field. Anterior branches of facial sutures strongly divergent, each branch diverging at about 70° from an exsagittal line through γ, which is some distance out from axial furrow. Palpebral lobe crescentic, about half sagittal length of glabella. Posterior section of facial suture unknown. Hypostome, rostral plate, free cheek, and thorax unknown.

Pygidium about two-thirds as long (sag.) as wide (trans.). Axis anteriorly one-quarter greatest pygidial width, tapering gently backwards, not reaching posterior margin and with thirteen rings defined by moderately distinct ring furrows which become progressively shallower towards posterior. Median node on posterior edge of each ring. No postaxial ridge. Pleural areas broad, adaxial part horizontal in transverse section, abaxial part rather steeply declined. Seven pairs of pleural ribs, with the posterior pleural bands elevated above the anterior. Pleural furrows deeper and wider than the interpleural adaxially, but abaxial ends of latter are deeper than corresponding sections of pleural furrows. Interpleural furrows reach pygidial margin, pleural do not. Anterior and posterior pleural bands of approximately equal width (exsag.), abaxial ends of latter distinctly elevated and crest-like. No border. Section of pygidial doublure seen (Pl. 96, fig. 5*a*, *c*) shows that it has fine, parallel, terrace lines. Dorsal exoskeleton smooth.

Radnoria humillima (Barrande, 1852)

Plate 96, fig. 6*a*–*c*

- *1852 *Cyphaspis humillima* Barrande, p. 492, pl. 18, figs. 57–58.
- 1868 *Cyphaspis humillimus* Barrande; Bigsby, p. 47.
- 1951 *Otarion* (?) *humillimum* (Barrande); Prantl and Přibyl, pl. 1, figs. 27, 28.
- v. 1958 *Otarion*? *humillimum* (Barrande); Horný, Prantl and Vaněk, pl. 2, fig. 6.
- v. 1970 *Otarion*? *humillimum* (Barrande); Horný and Bastl, p. 169.

Type specimens. Barrande (1852, p. 492) states that he had several specimens (all cranidia) at hand when he erected this species. Therefore the statement by Horný and Bastl (1970, p. 169) that specimen NMP IT309 is the holotype by monotypy is incorrect, and it is here designated lectotype. It is from high Liteň Formation (late Wenlock), Lištice, near Beroun, Czechoslovakia. Barrande's other syntypes are also from this locality.

Other material. One cranidium NMP 215/68, Liteň Formation, Loděnice, near Beroun. Figured Horný, Prantl and Vaněk 1958, pl. 2, fig. 6.

We have only had the opportunity to examine the specimen figured by Horný, Prantl, and Vaněk. This is poorly preserved and no preparation has been possible. A full description and comparison must await revision of Barrande's material, but a latex cast is figured for comparison with the British species. Although *R. humillimum* shows certain similarities to *R. syrphetodes*, it is distinguished by the relatively longer, narrower, and more ovate glabella, while the anterior border is relatively narrower (sag. and exsag.).

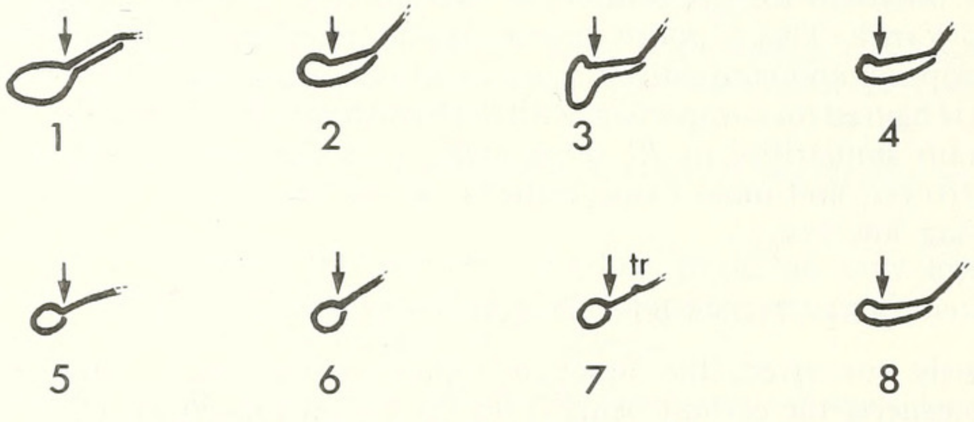
RELATIONSHIPS OF THE BRACHYMETOPIDAE

As previously conceived, the Brachymetopidae comprised a number of Upper Palaeozoic genera, the earliest being from the Lower Devonian. Different authors have classified these trilobites in different ways: Prantl and Přibyl (1951, p. 439) proposed the Brachymetopinae as a subfamily of the Otarionidae; Hupé (1953, p. 220; 1955, p. 210) elevated them to family status, and believed that they were allied to proetids rather than to otarionids; Maximova (1957, pp. 60–61) and Whittington (1960, p. 407) considered their morphology to suggest relationship with the phillipsiids; Whittington and Campbell (1967, pp. 450–451) and Fortey and Owens (1975, p. 231) surmised that they could have evolved from otarionids; the latter also suggested (1975, p. 231) a possible origin in the proetid subfamily Warburgellinae. So far, however, no convincing evidence has been advanced in support of either a proetid or an otarionid ancestry.

In an attempt to trace brachymetopid relationships and ancestry, we have considered the following morphological characters: rostral plate, cephalic doublure, lateral occipital lobes, preannulus, outline of pygidium, and structure of pygidial pleural ribs. We have selected these features since they show the greatest variation in the groups considered, and we believe that, taken together, they are of phylogenetic significance.

Rostral plate. The Warburgellinae is the only proetid (*sensu* Owens 1973, p. 6) subfamily in which the connective sutures diverge backwards. The connective sutures also diverge backwards in *Mystrocephala* (Whittington 1960, pl. 54, fig. 3), *Brachymetopus* (Hahn 1964, pl. 32, fig. 3), and *Australosutura* (Amos, Campbell and Goldring 1960, pl. 39, figs. 10, 11; pl. 40, figs. 1, 5, 6) (although in the last two genera the posterolateral corners of the greatly expanded rostral plate extend to the base of the genal spine). The only species of *Cordania* in which any part of the rostral plate is known is *C. falcata* Whittington (1960, p. 411, pl. 51, fig. 16), one specimen showing the anterior part of the left-hand connective suture. Whittington points out that the connective sutures converge backwards. He also figured free cheeks of *C. macrobius* (Billings, 1869) and one of these (ibid., pl. 53, fig. 10) shows a very broad doublure. If the doublure of *C. falcata* is similar, only part of the connective suture is seen on the specimen mentioned above. It may therefore be that the connective sutures of *C. falcata* (and presumably other *Cordania* species) do diverge, after initially converging. As all other known brachymetopids have backwardly diverging connective sutures it would be surprising if the same condition did not obtain in *Cordania*. *R. syrphetodes* has backwardly diverging connective sutures (Pl. 95, fig. 4).

In otarionids, and typical proetids, the rostral plate is small and triangular or



TEXT-FIG. 2. Schematic sections through doublures of free cheeks of: 1, *Cordania macrobius* (Billings, 1869) (based on Whittington 1960, pl. 53, figs. 1, 10); 2, *Australosutura gardneri* Campbell and Goldring, 1960 (based on Amos, Campbell and Goldring 1960, pl. 39, figs. 1, 10); 3, *Proetides insignis* (Winchell, 1863) (after Hessler 1962, fig. 1A, p. 812); 4, *Radnoria syrphetodes* sp. nov. (based on Pl. 95, figs. 3, 4); 5, *Proetus pluteus* Whittington and Campbell, 1967 (based on Whittington and Campbell 1967, pl. 1, fig. 11; pl. 2, fig. 2); 6, *Otarion plautum* Whittington and Campbell, 1967 (based on Whittington and Campbell 1967, pl. 7, figs. 1, 6); 7, *Warburgella rugulosa canadensis* Ormiston, 1967 (based on Ormiston 1971, pl. 21, figs. 4, 5); 8, *Prantlia grindrodi* Owens, 1973 (based on Owens 1973, pl. 15, figs. 3, 5). Arrows indicate position of lateral border furrow, 'tr' the tropidium.

trapezoidal with backwardly converging connective sutures (see Whittington and Campbell 1967, pl. 6, figs. 2, 9; pl. 7, fig. 6; pl. 10, fig. 15).

Cephalic doublure. In many Proetacea (see Owens 1973; Whittington and Campbell, 1967; Ormiston 1971) the cephalic border and doublure form a 'tube' (Fortey and Owens 1975, p. 236) (see text-fig. 2), where the inner margin of the doublure coincides with the border furrow, which in all these cases tends to be well defined. In some genera, as Hessler (1962, p. 811) has observed, the doublure extends well inside the border furrow (which in these cases tends to be ill-defined), and its inner section runs more or less parallel with the dorsal surface of the corresponding part of the cephalon (see text-fig. 2). In such cases a nearly flat 'trough' is commonly developed which crosses the cheeks and preglabellar field parallel to the cephalic margins. The inner edge of this 'trough' corresponds with the inner edge of the doublure, and is represented by an abrupt change in slope. This structure is found in *R. syrphetodes* (Pl. 95, fig. 2*a*), *Prantlia grindrodi* Owens (1973, pl. 15, fig. 3), *Proetides insignis* (Winchell, 1863) and *P. colemani* Hessler, 1962 (see Hessler 1962, text-fig. 1, p. 812), *Cordania macrobius* (Billings, 1869) (see Whittington 1960, pl. 53, figs. 10–12), *Mystrocephala pulchra* (Cooper and Cloud, 1938) (see Whittington 1960, pl. 53, fig. 15), and *Australosutura gardneri* (Mitchell, 1922) (see Amos, Campbell and Goldring 1960, pl. 39, figs. 1, 6, 10, 11).

Lateral occipital lobes. These are of common occurrence in the Proetacea, but are lacking in the Otarionidae, Brachymetopidae, and many Tropidocoryphinae. Lateral occipital lobes are well developed in Silurian Proetinae (but absent in later members of the subfamily), present in most Warburgellinae (but suppressed in some species of *Warburgella*), and have evidently been repeatedly acquired and lost at various times in different proetacean lineages.

Preannulus. This feature is found in the Proetinae and their derivatives—e.g. Dechenellinae and 'phillipsiids', but is lacking in Tropidocoryphinae, Warburgellinae, Brachymetopinae, and Otarionidae.

Structure and shape of the pygidium. Owens (1973, pp. 5–6; text-fig. 2, p. 5) has recognized three types of pygidial pleural rib structure in Lower Palaeozoic Proetidae, with different kinds characterizing the Tropidocoryphinae, Warburgellinae, and the Proetinae and their derivatives. *R. syrphetodes* has pleural ribs like those found in Warburgellinae. *R. triquetra* and other Brachymetopinae, however, have a different type, in which the posterior pleural bands are elevated above the anterior; this type of structure appears to be a modification of that typical of Warburgellinae. In Otarionidae the structure is similar to that found in Proetinae.

Proetinae, Tropidocoryphinae, Warburgellinae, and Brachymetopinae normally have a pygidium of subparabolic outline with five (or commonly many more) axial rings. Within any one lineage there is commonly an increase in number of rings in successively younger genera; less commonly there is a decrease. Otarionidae differ from all the above groups in that the pygidium is short (sag.), with its width (trans.) commonly over twice its sagittal length, and the number of axial rings never exceeds seven, and is most commonly in the range three to four.

Inferred relationships. Brachymetopinae and *Prantlia* have in common the shape of the rostral plate, type of cephalic doublure, lack of preannulus, pygidial outline, and large number of pygidial axial rings. Other Warburgellinae share these characters, but have a different kind of cephalic doublure structure. Proetinae and Otarionidae have less in common with the above groups and, in particular, are distinguished by the type of rostral plate and pygidium, and the possession of the preannulus in the former. The Proetinae and their 'phillipsiid' derivatives, therefore, do not seem to be closely related to the Brachymetopinae. Otarionidae bear a close general resemblance to certain Brachymetopinae, especially to *Cordania* species, in general cephalic morphology. There are marked contrasts, however, in the structure of the cephalic doublure, and probably also in the rostral plate. The similarity between otarionids and *Cordania* is therefore considered to be due to homoeomorphy.

It would seem to be too great a coincidence for so many common features to be independently acquired in brachymetopines and warburgellines and we consider *Radnoria* and later brachymetopines to be derived from warburgellines along the paths outlined below. The earliest known warburgellines are *Warburgella* species from the mid-Llandovery (Owens 1973, p. 72). *Warburgella* has a backwardly widening rostral plate, a tropidium or tropidial ridges, lateral occipital lobes, and the pygidial pleural ribs are flat-topped in profile; the cephalic border and doublure together form a 'tube'. The earliest known *Prantlia* species is *P. grindrodi* Owens, 1973 from the highest Llandovery and Wenlock. The stratigraphical occurrence and morphology of *Prantlia* suggest that it is derived from *Warburgella* through secondary loss of the tropidium and by modification and widening of the cephalic doublure. *W. scutterdinensis* Owens, 1973 from the early Wenlock is more similar to *P. grindrodi* than is any other *Warburgella* species. In particular, it has a flat-bottomed 'trough' running parallel to the margin, similar to that typical of *P. grindrodi.* The presence of this structure suggests that the doublure may be widened, but it is still unknown in this species.

The pygidium of *R. syrphetodes* is similar to those of *Prantlia* species, particularly that of *P. longula* (Hawle and Corda, 1847) (see Chlupáč 1971, pl. 20, fig. 10). The cephalon is also similar in its broad 'trough' and lack of tropidium but lateral occipital lobes are absent, the 1p lobes reduced, and the anterior branches of the facial sutures much more strongly divergent. *R. triquetra* is additionally distinguished by the structure of the pygidial pleural ribs. The range of characters of *Radnoria* species include some found in *Prantlia* (see above) and others—especially the strongly divergent anterior branches of the facial sutures, lack of lateral occipital lobes, and the pygidial pleural rib structure (of *R. triquetra*)—found in *Cordania. Radnoria* thus has a mosaic of *Prantlia* and *Cordania* characters, implying a close relationship between the three genera.

Systematic position of the Warburgellinae and of Radnoria. Hitherto, warburgellines and brachymetopines have been classified in different families but, because of their inferred relationships, we consider such a division to be artificial. Because warburgellines have more characters in common with brachymetopines than their presumed proetid ancestors, the tropidocoryphines, we classify them with the former.

All three *Radnoria* species possess highly divergent anterior branches of the facial sutures and lack occipital lobes—features typical of brachymetopines. The pygidial pleural rib structure of *R. triquetra* is also similar to members of this subfamily, although that of *R. syrphetodes* is more like that of warburgellines. We consider that brachymetopine characters outweigh warburgelline ones, and place *Radnoria* in the Brachymetopinae.

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