

Post-Kellwasser event recovery and diversification of phacopid trilobites in the early Famennian (Late Devonian)

RAIMUND FEIST



While no Frasnian phacopid genera are known to survive the terminal Frasnian Kellwasser extinction event, recovery of phacopids in the early Famennian is characterised by one of the highest origination rates of the clade. In this study species and subspecies currently known are updated with regard to their age distribution according to conodont-based bio-zonation. They occur in representative sites including Sessacker (Rhenish Slate Mountains), Wieda (Harz), McWhae Ridge (Canning Basin, Western Australia), Beni Abbès (Algerian Sahara) and Montagne Noire (Southern France). More than two-thirds of the taxa are reduced-eyed or blind, which might indicate adaptation to deep offshore habitats. A few taxa with *Phacops*-like kidney-shaped eyes with many lenses represent shallower environments in the photic zone. The fauna is characterised by different features of the ventral cephalic doublure due to the presence or absence of individualized anterior border, vincular furrow and postvincular doublure. Phyletic affiliation to Frasnian taxa remains difficult to assess until these are better known for their diversity in various habitats. *Chlupacops* may be a possible ancestor of taxa with cephalic anterior border such as *Nephranops* and *Houseops*, while *Cryphops* and *Trimerocephalus* may be rooted in *Acuticryphops* as previously thought. The systematic part is devoted to diagnoses and descriptions that are completed by new morphological criteria leading to some taxonomic re-assignments. The following taxa are new: *Nephranops* (*Nephranops*) *angerae* sp. nov., *Nephranops* (*Maternia*) *occitanicus* subgen. et sp. nov., *Pulvinocephalus* gen. nov., *P.* (*Pulvinocephalus*) *steinachensis triangulus* subgen. et subsp. nov., *P.* (*Cryphopsides*) *ovatus* subgen. et sp. nov., *P.* (?*Cryphopsides*) *walliseri* ?subgen. et sp. nov., *Trifoliops septimanicus* sp. nov., *Struveops wiedaensis* sp. nov. • Key words: phacopid trilobites, Famennian, biostratigraphy, phylogeny, morphology, systematics.

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Raimund Feist, Institut des Sciences de l'Evolution, Laboratoire de Paléontologie, Université Montpellier, pl. E. Bataillon, F 34095 Montpellier, France; raimund.feist@umontpellier.fr

The Frasnian was an age of severe restriction in trilobite diversity triggering one of the highest extinction rates in the Late Palaeozoic (Lerosey-Aubril & Feist 2012). This is essentially due to the terminal Frasnian global Kellwasser crises (Feist 1991, McNamara & Feist 2016). The peak of the main level of mass extinction, *i.e.* the Upper Kellwasser Horizon, coincides with the Frasnian–Famennian boundary as defined in 1993 by IUGS at the base of the Lower *triangularis* Zone (Klapper *et al.* 1993). The Famennian starts now much earlier than at the first appearance of the goniatite *Cheiloceras* (Ziegler 1971) in the Late *triangularis* Zone which was previously used to define the boundary. Accordingly, and after restriction of both *Nephranops* and *Cryphops* to the early Famennian (Crônier & Feist 2000; Feist *et al.* 2009, p. 16), phacopids lost all remaining three genera recognized to date from the late Frasnian: *Chlupacops* at the base of the

Lower Kellwasser Horizon, and *Trimerocephaloides* and *Acuticryphops* at the base of the Upper Kellwasser Horizon (Feist *et al.* 2009, McNamara & Feist 2016). Thus, and in contrast to previous thinking (Alberti 1970, Feist 1991), phacopids were severely affected by the Kellwasser crises. Elucidation of phylogenetic relationships between taxa prior to and following the terminal Frasnian global biocrises is hindered by the scarcity of recorded trilobite taxa, in particular from shallow near-shore environments. Further difficulties lie in the fact that age attribution of phacopids previously followed ammonoid-based chronology and that modern biostratigraphical assignments of taxa to conodont zones have been achieved only locally (*e.g.* Ziegler 1962; Lütke 1968; Feist *et al.* 2009, 2016). For instance, important Uralian taxa close to the Frasnian–Famennian boundary, such as “*Phacops* (*Cryphops*)” *latilimbatus* Maximova, 1955 [assigned herein to the new

taxon *Pulvinocephalus* (*Cryphopsides*) gen. and subgen. nov.] and “*Phacops* (*Phacops*)” *pronini* Maximova, 1955 [assigned with question to *Houseops* by Feist *et al.* (2009)] were recovered from the *Crickites* Zone and were considered of Frasnian age (Maximova 1955, p. 192). However, these taxa possibly occur in the topmost part of this zone that, devoid of *Crickites* and preceding the first occurrence of *Cheiloceras* (“post dolδ” interval; Ziegler 1971), has now become basal Famennian. This is proven at least for *latilimbatus* from the Barma horizon in the SW Uralian Bol’shaya Barma section that yields conodonts from the Early and Middle *triangularis* Zones (Abramova & Artyushkova 2004, Tagarieva 2013). In this context, an attempt is made to update and revise both known and new post-event early Famennian phacopids, with respect to their systematic definition and their temporal occurrence within the conodont zonation (Fig. 1). In addition to the description of new taxa, systematic palaeontology focusses on previously unconsidered or newly observed criteria that necessitate taxonomic re-assignments.

Distribution in time and space

Post-event recovery and diversification of phacopids during the early Famennian (Early *triangularis* through Early *marginifera* Zones), while stepwise, is rather important: at the present state of knowledge 11 genera (+2 subgenera) with 38 species (+3 subspecies) successively appear within the time interval of some 6 m.y. (Kaufmann 2006) *versus* only 6 genera with 12 species during the entire Frasnian of 7 m.y. duration. Currently known taxa and their attribution to conodont zones are shown in Fig. 1 (some attributions remain tentative).

While Famennian phacopids are distributed worldwide with the exception of the Americas (Chlupáč 1975, Crônier & François 2014), fewer than half of the genera (i.e. *Trimerocephalus*, *Houseops*, *Nephranops*, *Pulvinocephalus* and *Trifoliops*) have intercontinental significance. The others are virtually restricted to a single cratonic margin. However, other discoveries in unexploited areas may reveal a wider distribution of currently known taxa. The most significant phacopid assemblages that occur in some representative conodont-dated sites are as follows.

On the Avalonian margin of the Old Red continent early Famennian phacopids are best represented in the Rhenish Slate Mountains though they are dated by conodonts only in a few localities. Many taxa occur in red cephalopod-bearing calcilitites at the famous Sessacker locality near Oberscheld, SE Rhenish Slate Mountains (Emmrich 1844; Richter & Richter 1926; Matern 1927, 1931). The specimens were recovered from trenched sections and their stratigraphical position was dated according to associated

ammonoids. More recently, several new trenches have been investigated to establish conodont biozonations across the Frasnian–Famennian boundary and in the lower Famennian (Ziegler 1962, Feist & Schindler 1994, Schülke 1995). In particular, conodonts from Matern’s and Lippert’s trilobite samples (Senckenberg collections) were determined by Ziegler (1962) and, in addition, those of my own collections by Corradini and Girard (contributions herein). These investigations made it possible to assign occurrences of diversified phacopid faunas to conodont zones. It should be noted that, with the exception of the Early *triangularis* Zone, all other early Famennian conodont zones can be recognised by phacopids: Early *marginifera* – *Struveops wiedaensis* sp. nov.; *rhomboidea* – *Dienstina diensti* (Richter & Richter, 1923); Late *crepida* to *marginifera* – *Trimerocephalus mastophthalmus* (Richter, 1856); Middle *crepida* to Late *crepida* – *Cryphops cryptophthalmus* (Emmrich, 1844); Early *crepida* to Early *marginifera* – *Ductina ductifrons* (Richter & Richter, 1923); Early *crepida* to *rhomboidea* – *Pulvinocephalus* (*P.*) *steinachensis triangulus* gen., subgen. et subsp. nov.; Late *triangularis* to Late *crepida* – *Pulvinocephalus* (*Cryphopsides*) *ovatus* gen., subgen. et sp. nov.; Middle *triangularis* to Early *crepida* – *Nephranops* (*Maternia*) *dillanus* Richter & Richter, 1926; Middle to Late *triangularis* – *Nephranops* (*Nephranops*) *incisus* (Roemer, 1866).

In the Harz Mountains several localities near Wieda, in particular the Stöberhaifahrweg, yield well preserved phacopids that were dated by conodonts (Lütke 1968): Early *marginifera* – *Struveops wiedaensis* sp. nov.; Early *marginifera* – *Pulvinocephalus* (*Pulvinocephalus*) cf. *steinachensis* (Richter & Richter, 1926); Late *crepida* – *Trimerocephalus mastophthalmus* (Richter, 1856); Late *crepida* – *Ductina ductifrons* (Richter & Richter, 1923); Late *crepida* – *Houseops miserrimus wiedensis* (Lütke, 1968).

On the southeastern margin of Gondwana, the McWhae Ridge area in the Canning Basin, Western Australia, offered a diverse fauna of phacopids from reef-slope environments (Feist *et al.* 2009). These characterise several conodont zones (det. G. Klapper): *rhomboidea* – *Trimerocephalus mimbi* Feist, 2009 in Feist *et al.* (2009); *rhomboidea* – *Trimerocephalus tardispinosus* Feist & Becker, 1997; Uppermost *crepida* to Lower *rhomboidea* – *Babinops planiventer* Feist & Becker, 1997; Upper *crepida* – *Babinops minor* Feist, 2009 in Feist *et al.* (2009); Lower to Middle *crepida* – *Houseops canningensis* Feist, 2009 in Feist *et al.* (2009); Upper *triangularis* – *Houseops beckeri* Feist, 2009 in Feist *et al.* (2009); Upper *triangularis* – *Houseops* sp. A Feist, 2009 in Feist *et al.* (2009).

On the north-western margin of Gondwana, in the Beni Abbès area of the Algerian Sahara, numerous phacopids recently brought to light (Crônier *et al.* 2013, Feist *et al.*

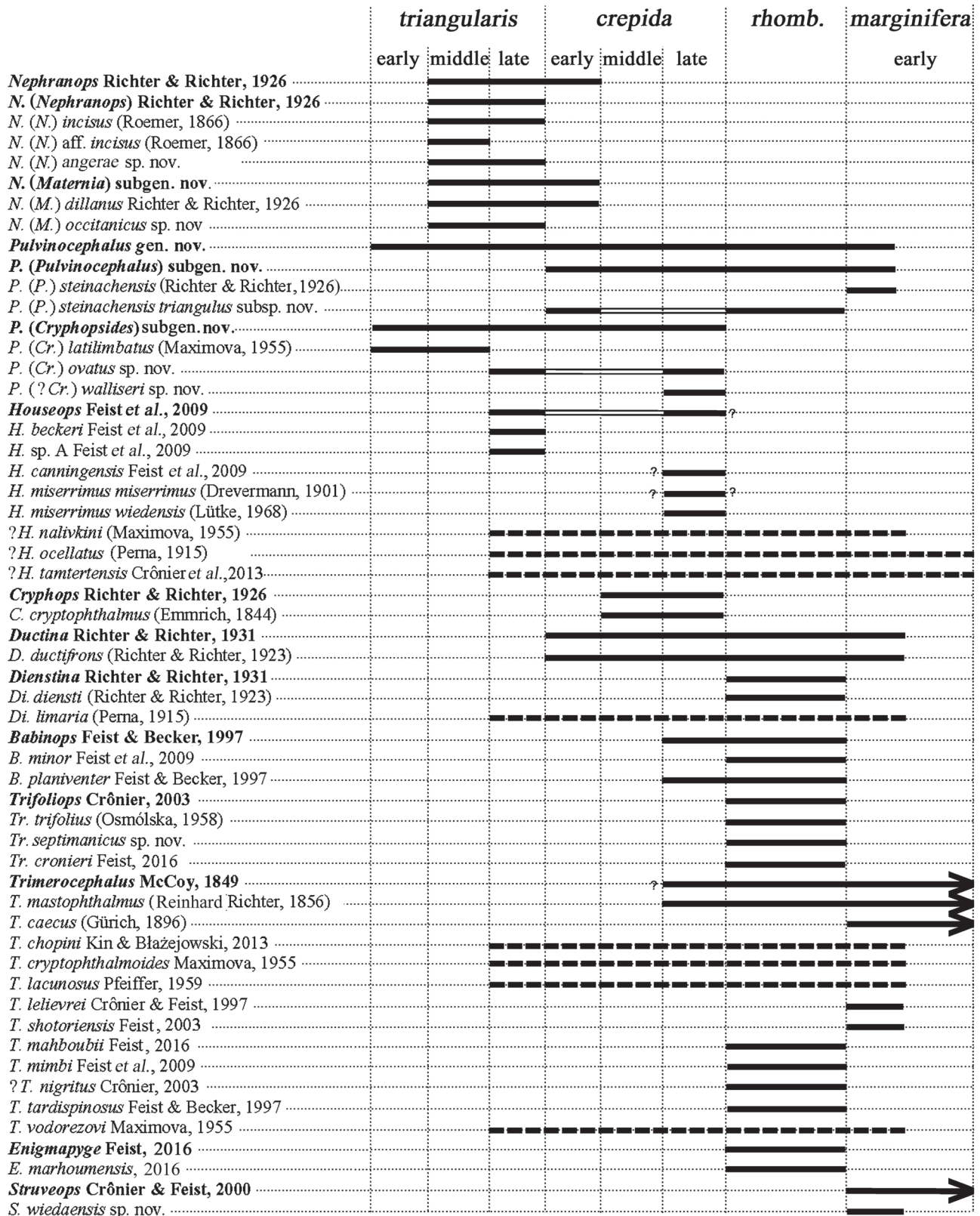


Figure 1. Range chart of early Famennian phacopids according to conodont biozonation (Late/Latest *crepida* Zones and *rhomboidea* Zones undifferentiated). Explanation: full lines – known ranges; empty lines – inferred occurrences; dashed lines – undifferentiated ranges; question marks – possible extensions; arrows – extensions beyond early Famennian.

2016) have been dated by conodonts (det. C. Corradini & C. Girard): Early *marginifera* – *Trimerocephalus caecus* (Gürich, 1896); Early ?*marginifera* – ?*Houseops tamertensis* Crônier, 2013 in Crônier *et al.* (2013); *rhomboidea* – ?*Houseops cryphoides* (Richter & Richter, 1926) (= *Houseops* aff. *miserrimus* Drevermann, 1901); *rhomboidea* – ?*Trimerocephalus nigrinus* Crônier, 2003; Early *rhomboidea* – *Trimerocephalus mahboubii* Feist, 2016 in Feist *et al.* (2016); Early *rhomboidea* – *Trifoliops trifolius* (Osmólska, 1958); Early *rhomboidea* – *Trifoliops cronierae* Feist, 2016 in Feist *et al.* (2016); Early *rhomboidea* – *Enigmatopyge marhoumensis* Feist, 2016 in Feist *et al.* (2016).

In the Montagne Noire the following taxa were dated by conodonts (Girard *et al.* 2014): Late *rhomboidea* – *Trifoliops septimanicus* sp. nov.; Middle to Late *triangularis* – *Nephranops* (*Nephranops*) *angerae* sp. nov.; Middle to Late *triangularis* – *Nephranops* (*Maternia*) *occitanicus* sp. nov.

In conclusion, according to known occurrences, most early Famennian conodont zones are characterised by phacopid associations.

Characteristic morphological features

Evolutionary trends in early Famennian phacopids include the reduction of the visual complex, *i.e.* forward migration and lowering of the palpebral lobes, as well as regression of the visual surface and optical devices until their complete effacement in blind taxa. In this regard, three groups can be distinguished. Firstly, there are “normally” sighted taxa that exhibit the ancestral phacopid configuration of the palpebral area with visual surfaces carrying numerous lenses. They attain up to 27% of the total number of species and sub-species considered. The earliest representatives of *Pulvinocephalus* (*Cryphopsides*) that are characterised by kidney-shaped eyes occur in shallow brachiopod-rich bioclastic limestones in the South Urals (Maximova 1955). Australian taxa from reef-slope environments of the Canning Basin such as *Babinops* and *Houseops* exhibit kidney-shaped palpebral lobes and eyes, though those of the latter are smaller and advanced in comparison to *Phacops*. Uralian taxa assigned with question to *Houseops* occur in shallower brachiopod-yielding environments. A particular case is represented by *Nephranops*, inhabitant of deeper offshore cephalopod limestones and marls. The palpebral lobes have become low kidney-shaped swells and the wide visual surface, generally without lenses, is defined by dorsally convex palpebral sutures in lateral view. This is an outstanding case of *in situ* disappearance of functional optic devices likely due to adaptation to level-bottom environments below the photic zone. The second category comprises sighted taxa with advanced reduction

of the palpebral lobe. This has become a small bulged area close to the antero-lateral edge of the genal field with small elliptical or circular visual surfaces exhibiting few lenses. This “cryptophthalmus” configuration (Richter & Richter 1926) occurs in 12% of early Famennian taxa, exemplified by *Cryphops*, *Dienstina* and late forms of *Pulvinocephalus* (*Cryphopsides*) that lived in offshore cephalopod limestone habitats in moderate water depth within light penetration. *Struveops* is outstanding in the presence of a far-forward shifted, tiny bulged palpebral area without lenses. A majority (56%) of the remaining early Famennian species and subspecies of which the genal fields are known (*i.e.* *Ductina*, *Trifoliops*, *Trimerocephalus* and *Pulvinocephalus* (*Pulvinocephalus*)) are blind. Palpebral lobes and visual surfaces are absent on the vaulted genal field, and minute crescent-shaped dorsal librigenae are defined by facial sutures running onto the anteriormost genal field, in the border furrow (*Trimerocephalus*) or along the outer antero-lateral border (*Ductina*). These taxa might have adopted a semi-endobenthic lifestyle under muddy substrate conditions at the limits of light-penetration.

In earlier epochs, singular cases of blindness in phacopids are known [*e.g.* in the late Silurian *Denckmannites* (Schränk 1973) or in the Middle Devonian *Illaeonula* (Chlupáč 1977, Basse & Müller 2000)]. But a general trend of eye-reduction leading to a majority of blind taxa that cohabit with sighted ones in the same offshore environment is outstanding, and characterises the early Famennian phacopid communities. In this regard, the occurrence of demonstrably 23 blind taxa out of 41 species and sub-species marks a peak period of eye-reduction within the evolutionary history of phacopids.

The ventral side of the ankylosed librigenae (*i.e.* the ventral doublure), in particular the inner parts anteriorly and below the frontal suture, also underwent considerable morphological variations. These are related to the presence or absence of a protruding anterior cephalic border which, in case of its regression, is replaced by a backwardly oriented flat pre-vincular doublure, and, additionally, the presence or absence of both the vincular furrow and the postvincular doublure (Fig. 2). In most early Famennian taxa (*i.e.* *Babinops*, *Houseops*, *Nephranops*, *Pulvinocephalus*, *Trifoliops* and *Dienstina*) a convex anterior border is differentiated from the front of the glabella by its own vault and forward extension (Fig. 3A–D, F–H). It is defined ventrally by an edge or break in slope against the vincular furrow when the latter is present. In *Babinops*, *Nephranops* (*Nephranops*) and *Dienstina* no vincular furrow is developed adaxially and there is an undivided ventral doublure between the posterior edge of the cephalic border and the hypostomal suture (Fig. 3A, D). In *Cryphops*, *Trimerocephalus*, *Struveops* and *Ductina* no anterior cephalic border can be defined as the

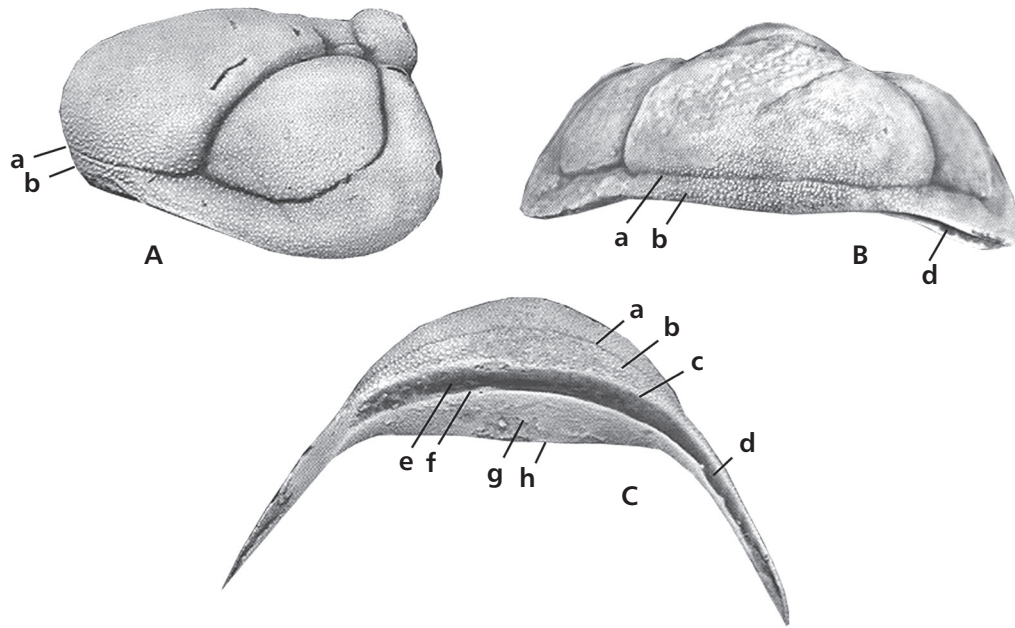


Figure 2. Terminology of lateral (A), anterior (B) and ventral (C) views of *Trimerocephalus mahboubii* Feist, 2016 in Feist *et al.* (2016) – anterior suture (a); pre-vincular doublure (b) corresponding to anterior border; posterior edge of pre-vincular doublure (c); lateral notches of vincular furrow (d); vincular furrow (e); anterior edge of postvincular doublure (f); postvincular doublure (g); hypostomal suture (h).

profile of the anterior glabellar vault extends continuously downwards across the suture; the pre-vincular doublure is backwardly directed (Fig. 3E, I, J) until reaching the vincular furrow. The latter is absent in *Struveops* and *Ductina* where the ventral doublure remains undivided (Fig. 3E). The vincular furrow varies in depth and sagittal length: it is deep and narrow (sag.) in *Houseops*, *Nephranops* (*Maternia*), *Pulvinocephalus* (*Cryphopsides*), *Cryphops* and *Trimerocephalus*, very wide and profound

in *Trifoliops* (Fig. 3H). The postvincular doublure is generally as long as or up to three times longer (sag.) than the vincular furrow. In *Trifoliops* and *Pulvinocephalus* (*Cryphopsides*) it is shorter (Fig. 3G, H), and it is absent in *Cryphops* (Fig. 3I).

Apparently, features of the ventral doublure are not related to evolutionary changes that concern eye-reduction and the course of the suture on the dorsal side of the librigenae. This is obvious when comparing normally-

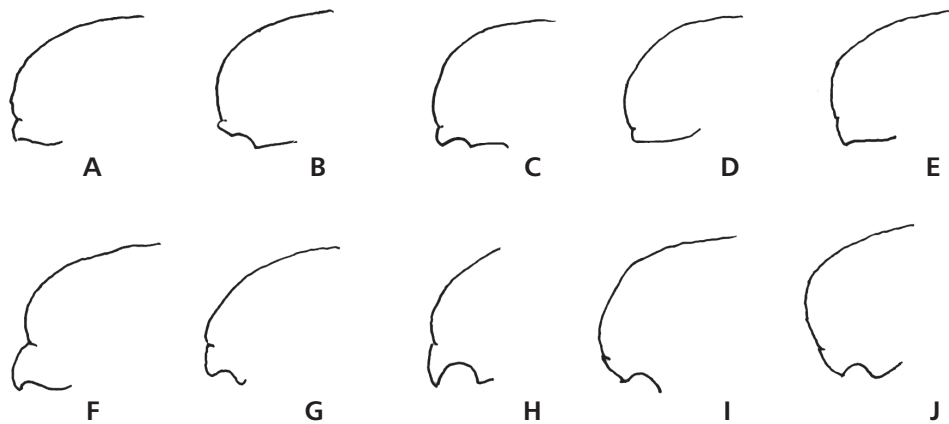


Figure 3. Diagrammatic representation of sagittal profiles of anterior part of cephalon in representative early Famennian phacopid taxa. • A – *Babinops planiventer* Feist & Becker, 1997. • B – *Houseops canningensis* Feist, 2009 in Feist *et al.* (2009). • C – *Nephranops* (*Maternia*) *dillanus* Richter & Richter, 1926. • D – *Nephranops* (*Nephranops*) *incisus* (Roemer, 1866). • E – *Struveops wiedaensis* sp. nov. • F – *Pulvinocephalus* (*Pulvinocephalus*) *steinachensis triangulus* gen. et sp. nov. • G – *Pulvinocephalus* (?*Cryphopsides*) *walliseri* gen., subgen. et sp. nov. • H – *Trifoliops septimanicus* sp. nov. • I – *Cryphops cryptophthalmus* (Emmrich, 1844). • J – *Trimerocephalus mimbi* Feist, 2009 in Feist *et al.* (2009).

sighted taxa of *Houseops* and *Babinops*, the former having deep vincular furrows that are absent in the latter. Presence or absence of the vincular furrow might reflect a different life-style: tighter fit of the pygidial edge during enrolment is reached in the first case. It is difficult to explain at this stage the co-occurrence of species of *Nephranops* (*Maternia*) that exhibit deep vincular furrows with those of *Nephranops* (*Nephranops*), in which these structures are almost effaced. Indeed, both taxa are associated at Sessacker (Rhenish Slate Mountains), Rübeland (Harz Mountains) and Montagne Noire (southern France) in similar offshore cephalopod-yielding limestones.

Questions about phyletic affiliations

The earliest Famennian phacopids, *Pulvinocephalus* (*Cryphopsides*) and *Nephranops*, appeared shortly after the Kellwasser Extinction Event. They must have been derived from ancestral pre-Kellwasser lines, but their origin remains cryptic. Indeed, the cushion-like advanced configuration of the cephalic anterior border that characterises the former is unknown in any earlier phacopid. Likewise, *Nephranops*-type eye reduction with maintenance of a wide visual field without lenses is not known from earlier periods. However, other general cephalic traits are shared with diagnostic features of Frasnian taxa of *Chlupacops*, especially with *C. cryphoides* (Richter & Richter, 1926) and *C. aff. cryphoides* (in Feist *et al.* 2016). These traits are in particular advanced, reduced palpebral lobes and, in *Nephranops* (*Maternia*), concave postvincular doublures as well as the outline of the multi-segmented pygidium. Despite the absence of transitional forms between both entities that might have existed shortly before or contemporaneously with the Kellwasser events, an origin of *Nephranops* from *Chlupacops*-derived taxa might best be envisaged. On the other hand, as stated earlier (Feist *et al.* 2009, p. 16), *Nephranops* and *Houseops* are closely related and may have had a common ancestry to be searched for among late representatives of *Chlupacops*.

In contrast to phacopids with a differentiated anterior cephalic border that are the first to appear after the Kellwasser events, Famennian representatives with a backwardly directed pre-vincular doublure do not occur earlier than in the Middle *crepida* Zone. The late appearance of *Trimerocephalus* in particular leaves a considerable gap of record after the morphologically closest *Acuticryphops* that is last present in the terminal Frasnian *linguiformis* Zone preceding the Upper Kellwasser Extinction. Nevertheless, a direct phyletic lineage between both taxa has been suggested (Chlupáč 1977, Feist 1995). Richter & Richter (1926, 1955) considered *Cryphops* the direct ancestor of the slightly younger *Trimerocephalus*, but this

view is contradicted by different features of the pygidium (unknown to the Richters) and of the ventral postvincular doublure. On the other hand, the virtual absence of morphologically intermediate evolutionary states of eye-regression between the sighted *Acuticryphops* and the blind *Trimerocephalus* during a long period of some 2 m.y. calls in question the existence of direct links between both taxa. Alternatively, both *Cryphops* and *Trimerocephalus* may have resulted from iterative evolution, descending from unknown survivors of the Kellwasser crises. In both scenarios the question of ancestry remains problematic and currently unsolved.

In conclusion, the Late Kellwasser Event accelerated the general decline of phacopids that characterised their evolution during the Frasnian. It is striking that no species and no genera are recognised to cross the Frasnian–Famennian boundary. In contrast, phacopids experienced the highest origination rate during the early Famennian.

Systematic Palaeontology

Terminology follows Whittington & Kelly (1997) and Feist *et al.* (2016).

Depository: SMF – Senckenberg Museum Frankfurt; UM-IP – University of Montpellier, Invertebrate Palaeontology; BGRB – Bundesanstalt für Geologie und Rohstoffe Spandau (former Zentral Geologisches Institut Berlin); MB.T – Naturkunde Museum Berlin.

Genus *Nephranops* Richter & Richter, 1926

Type species. – *Phacops* (*Trimerocephalus*) *incisus* Roemer, 1866; Rübeland (Harz Mountains), Germany.

Diagnosis. – phacopid with low kidney-shaped palpebral lobes; wide visual surface, generally without lenses, defined by dorsally convex palpebral sutures in lateral view; vincular structure un-notched distally; pygidium with narrow, long axis composed of 7–9 rings, not reaching posterior margin.

Remarks. – After reassignment of *Phacops* (*Trimerocephalus*) *miserrimus* Drevermann, 1901 and, tentatively, *Trimerocephalus* *ocellatus* Perna, 1915 to *Houseops* Feist, 2009 in Feist *et al.* (2009), the definition of *Nephranops* by Richter *et al.* (1959) is emended. Taxa here included in *Nephranops* are characterised by kidney-shaped visual surfaces, generally devoid of lenses. Only the holotype specimen of the type-species and one specimen of the new taxon *N. (Maternia) occitanicus* sp. nov. have two residual lenses on the right side only (Fig. 4F). As pointed out by Richter & Richter (1926, p. 127), the posterior edge of the

vincular furrow in *Nephranops*, though rather smooth in the type species, and as high as the anterior edge in lateral view, is situated far back. In comparison, the vincular structure is more forwardly projected in *Phacops*. Taking into account the distinct diagnostic characters, both the configuration of the ventral side of the cephalon and the outline and shape of the pygidial axis, two subgenera are discriminated: *N. (Nephranops)* and *N. (Maternia)* subgen. nov.

Subgenera included. – *N. (Nephranops)*, *N. (Maternia)* subgen. nov.

Subgenus *Nephranops* (*Nephranops*) Richter & Richter, 1926

Diagnosis. – Anterior glabellar lobe not overhanging upturned anterior border; antero-lateral borders of cephalon flat with sharp edges; vincular furrow almost inconspicuous adaxially with poorly defined posterior edge; postvincular doublure very long (sag.), slightly vaulted with straight hypostomal suture; pygidial length equals half width, axis low, narrow with 9 rings and long terminal piece, pointed behind with crested tip, separated from posterior edge by shallow marginal depression; wide pleural field with 7 ribs composed of markedly distinct bands, the anterior almost reaching antero-lateral margins; posterior margin sharp-edged without rim.

Occurrence. – Rhenish Slate Mountains, Harz, Thuringia, Montagne Noire, Morocco.

Species included. – *N. (Nephranops) incisus* (Roemer, 1866), Harz Mountains, Rhenish and Thuringian Slate Mountains, Holy Cross Mountains, *N. (N.) sigmoidalis* sp. nov., Montagne Noire; *N. (N.)* aff. *sigmoidalis*, central Hercynian Morocco; all from early Famennian Middle and Late *triangularis* zones.

***Nephranops* (*Nephranops*) *incisus* (Roemer, 1866)**

Figures 3D; 4A–L, S–U

- 1866 *Phacops* (*Trimericephalus*) *incisus*; Roemer, p. 212, pl. 35, fig. 4.
- 1869 *Proetus Münsteri*. – Richter (Reinhard), p. 391.
- 1926 *Phacops* (*Nephranops*) *incisus incisus*. – Richter & Richter, p. 149, pl. 8, fig. 48, pl. 9, figs 49, 50 (see earlier synonymies here).
- 1954 *Perliproetus? münsteri*. – Pfeiffer, p. 33, pl. 1, figs 1, 2.
- 1954 *Phacops* (*Nephranops*) *incisus incisus*. – Pfeiffer, p. 39, pl. 2, fig. 1.
- 1970 *Nephranops incisus incisus*. – Alberti, p. 153, fig. 3.
- 2007 *Nephranops incisus incisus*. – Crônier, p. 685, figs 2–5.
- 2009 *Nephranops incisus*. – Feist et al., p. 14.
- 2018 *Nephranops incisus*. – Feist & Weyer, p. 204, fig. 2a–h.

Material. – Cephalon from Sessacker figured by Richter & Richter (1926, pl. 9, fig. 49), SMF RX 565a1, refigured herein; new material from Sessacker: coll. Lippert in Ziegler (1962), cephalon SMF 97026, pygidium SMF 97027, trench II, bed 25, Middle *triangularis* Zone; cephalon SMF 97028, pygidium SMF 97029, trench VI, bed 28a, Late *triangularis* Zone (after Schülke 1995); cephalon SMF 97030, coll. Denckmann, Marburg.

Diagnosis. – Cephalic axial furrows straight, frontal lobe of glabella not overhanging anterior border, of semicircular outline; anterior border furrow deep; pygidium of semicircular to sub-pentagonal outline, slightly truncated behind, axis with straight axial rings; pleural ribs not extending to lateral edges; postero-lateral border region defined against pleural field by break in slope, circumscribing inconspicuous border depression. Sculpture: low tiny granules.

Description. – The outer edge of anterior border coincides with anterior edge of vincular furrow. The latter represents a rather faint depression with flat bottom that extends abaxially without deepening, being framed by slightly thickened anterior and posterior edges. Distally, the flat bottom of the vincular furrow is provided with faint, oblique, almost inconspicuous ridges that join the edges of the furrow. They may delimit relicts of notches of the vincular structure. Pygidium sub-pentagonal, length (including articulating halfring) equal to half width. Posterior outline slightly truncated. Posterolateral edges are flat and sharp. Axis narrow, of moderate height with slightly depressed lateral profile, 9 + 1 straight axial rings of equal length, the anterior ones with sigmoidal pseudo-articulating halfrings that encroach on preceding ring; terminal piece long, triangular, conspicuously crested, pointed behind, remaining distant from posterior edge of pygidium. Axial furrows markedly divergent anteriorly, thereafter straight with weak taper as far as terminal piece, converging more strongly around terminal piece as far as the tip. Pleural field moderately and uniformly vaulted; 7 pleurae discernible, posterior pleural bands being higher and longer than anterior pleural bands, not reaching lateral edge; they terminate at slight break in slope that defines flat, lesser inclined, sharp-edged border region. Sculpture: densely granulose; postvincular doublure smooth.

Remarks. – ?*Perliproetus münsteri* Richter, 1869 from Saalfeld, Thuringia, based on pygidia alone, was recognised representing the pygidium of *N. incisus*, and as such constitutes a junior synonym of the latter (Feist & Weyer 2018). New features of the ventral side of the cephalon, notably the vincular structure, only known from immature specimens (Crônier 2007), are described, and further traits

of the pygidium are added to the original description provided by Richter & Richter (1926, p. 151).

Nephranops (Nephranops) aff. incisus (Roemer, 1866)
Figure 4V, W

Material. – Pygidium UM-IP 820 from locality Bou-Ounebdou, 5 km SE of Mrirt, Central Moroccan Meseta, from first 20 cm above Upper Kellwasser Horizon, Middle *triangularis* Zone (after Lazreq 1992).

Remarks. – The single specimen shares with *incisus* the general outline of the pygidium with sharp posterolateral edges, and the long, narrow axis with a post-axial crest-like prolongation that does not reach the posterior edge. In contrast, anterior and posterior pleural bands are almost equal in height and length. In lateral view the profile of the axis is straight, without median depression. Further material is necessary to assess the assignment of the specimen. This is the first evidence of *Nephranops* in North Africa.

***Nephranops (Nephranops) angerae* sp. nov.**
Figure 4M–R

Holotype. – Cephalon, UM-IP 821, Fig. 4M–O, from Coumiac, Montagne Noire, Middle *triangularis* Zone.

Type horizon and locality. – Coumiac marble quarry, near Cessenon, Hérault, S France; upper quarry, bed 32c, hematite-rich, dark red calcilutite (Klapper *et al.* 1993).

Material. – Paratypes: 2 cephalon UM-IP 822, 823 from type horizon.

Etymology. – After Jana Anger, Senckenberg Museum Frankfurt, in recognition of her assistance and help.

Diagnosis. – Cephalon semicircular with glabella in front of intercalating ring wide, covering anterior border, laterally defined by slightly sigmoidal axial furrows; narrow intercalating ring with backwards protruding lateral lobes; junction between posterior and lateral border furrows blunt; sculpture: dense tuberculation of elongated fused nodules forming wavy alignments.

Description. – Cephalon of semicircular outline anterolaterally. Genal field of half glabellar width, slightly truncated in anterior outline, covering anterior border. Axial furrow deep, slightly sigmoidal between S1 and lateral corners of frontal lobe. Lateral glabellar furrows rather deeply impressed, S2 small triangular, posterior branch of S3 crescent-shaped. Glabellar furrow S1 straight, becoming very shallow medially. Intercalating ring straight, narrow, inflated medially with less inflated, low lateral lobes, anteriorly separated from median lobe by deep notches connected with S1, extending rearwards beyond median portion of occipital furrow. Occipital ring more than twice as long (sag.) as intercalating ring, sub-rectangular, higher than glabella in front of intercalating ring, evenly vaulted, abruptly narrowing distally behind lateral lobes of intercalating ring. Genal field sub-triangular, posterior and lateral border furrows very shallow, merging in an obtuse angle. Palpebral lobe an oblique, low swelling differentiated from posterior genal field by indistinct palpebral furrow. Visual surface slightly swollen, without lenses, sharply differentiated from palpebral lobe by markedly incised facial suture. Antero-lateral margins sharp-edged, carrying a thin rim. Anterior border discrete, not protruding, remaining below anterior glabellar lobe, and slightly upturned on its anterior side. Vincular furrow very shallow, almost imperceptible medially, merging with postvincular doublure, becoming conspicuous abaxially in the form of a narrow, un-notched groove below lateral border. Sculpture: dense elongated nodules tending to form alignments of fused nodules across glabella that curve backwards abaxially. Vincular doublure with dense, wavy lines of fused elongated tubercles; distal vincular furrows smooth.

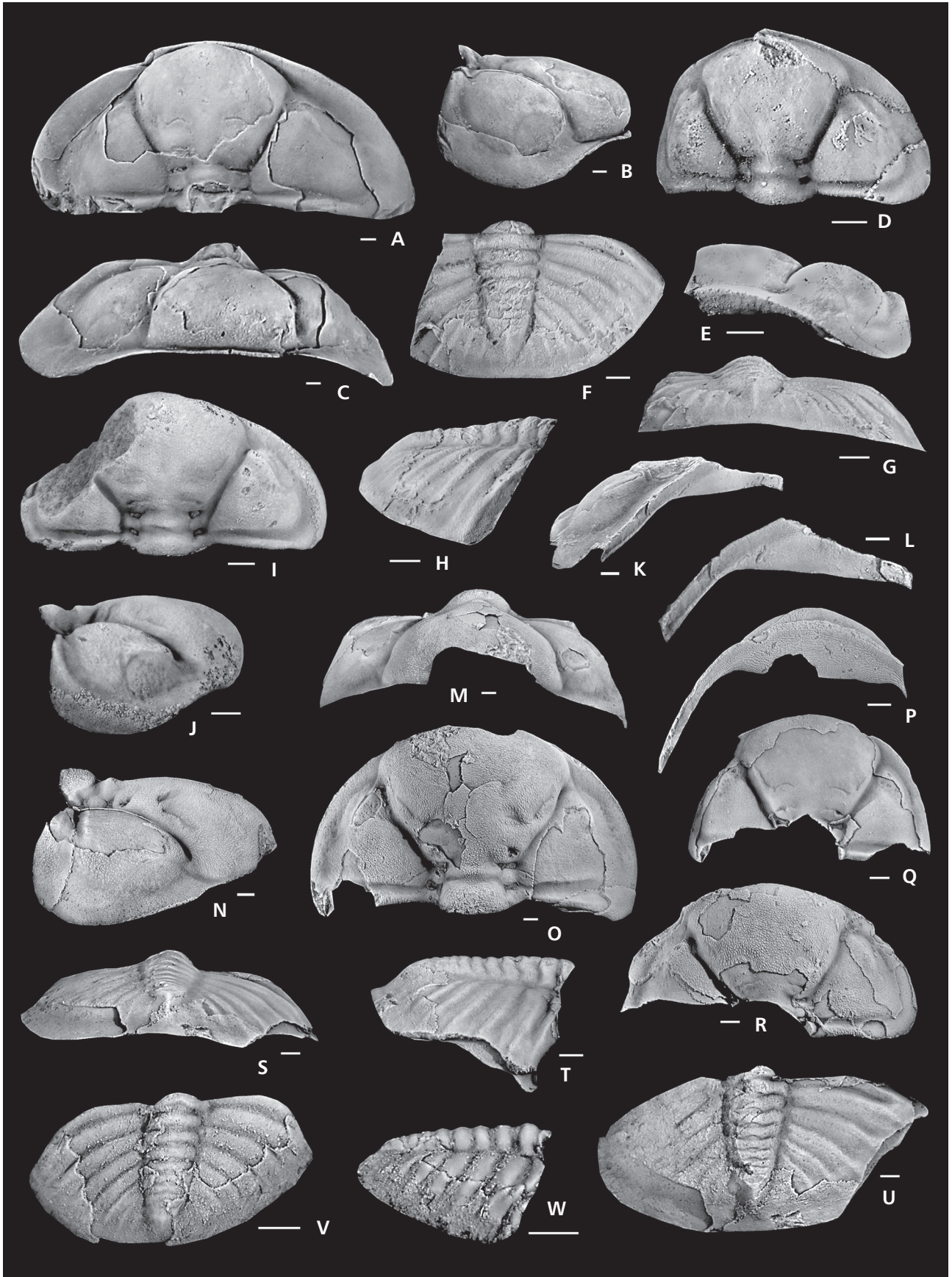
Remarks. – The new species differs from *Nephranops (Nephranops) dillanus* in its anteriorly wider glabella that covers the anterior border, the backwardly extending lateral lobes of the intercalating ring, and the typically wavy alignments of nodules on the entire cephalon.

Subgenus *Nephranops (Maternia)* subgen. nov.

Type species. – *Nephranops incisus dillanus* Richter & Richter, 1926.

Etymology. – After Hans Matern who investigated the

Figure 4. A–L, S–U – *Nephranops (Nephranops) incisus* (Roemer, 1866), Sessacker near Oberscheld, Eastern Rhenish Slate Mountains, Germany; A–C – cephalon SMF X565a, latex cast of original specimen figured by Richter & Richter (1926, pl. 9, fig. 49), dorsal (A), lateral (B), anterior (C) views; D, E – cephalon SMF 97026, almost entirely exfoliated, dorsal (D), oblique antero-lateral (E) views; F–H – pygidium SMF 97027, dorsal (F), posterior (G), lateral (H) views; I, J – cephalon SMF 97028, dorsal (I), lateral (J) views; K, L – fragment of anterior cephalon SMF 97030 showing ventral doublure, antero-lateral (K), ventral (L) views; S–U – pygidium SMF 97029, posterior (S), lateral (T), dorsal (U) views. • M–R – *Nephranops (Nephranops) angerae* sp. nov., Coumiac, Montagne Noire, Southern France; M–O – holotype cephalon UM-IP 821, anterior (M), lateral (N), dorsal (O) views; P, Q – cephalon UM-IP 822 partially exfoliated, ventral (P), dorsal (Q) views; R – cephalon UM-IP 823, dorsal view. • V, W – *Nephranops (Nephranops) aff. incisus*, Mrirt, Central Hercynian Meseta, Morocco. Pygidium UM-IP 820 dorsal (V), lateral (W) views. Scale = 1 mm.



Late Devonian faunas of the Dill region and especially trilobites from several trenced sections at Sessacker near Oberscheld.

Diagnosis. – Antero-lateral borders of cephalon slightly vaulted with blunt edges; inflated anterior border, anteriorly pitted; vincular furrow rather deep, with well defined posterior edge of same height as anterior edge in lateral view; long postvincular doublure, anteriorly flat, concave behind with backwards convex hypostomal suture; pygidium more than twice as wide as long, axis obtusely rounded behind with 8–9 rings and short terminal piece, post-axis region very short, deeply inclined; pleural region with 5–6 ribs, equal in height and length; pleural furrows rather deep remaining distant from pygidial margins, postero-lateral margin slightly downturned, blunt, edge with marginal rim. Sculpture: dense nodules.

Occurrence. – Rhenish Slate Mountains, Harz, Montagne Noire; Middle *triangularis* through Early *crepida* zones.

Species included. – *N. (Maternia) dillanus* Richter & Richter, 1926, Rhenish Slate Mountains, Harz Mountains; *N. (M.) franconicus* Alberti, 1970, Franconia; *N. (M.) occitanicus* sp. nov.

***Nephranops (Maternia) dillanus* Richter & Richter, 1926**

Figures 3C; 5J–Q

*v 1926 *Phacops (Nephranops) incisus dillanus*; Richter & Richter, p. 180, pl. 10, figs 76–79.

non 1927 *Phacops (Nephranops) incisus dillanus*. – Matern, p. 255, [= *Pulvinoccephalus (Pulvinoccephalus) steinachensis triangulus* subsp. nov.].

2009 *Nephranops dillanus*. – Feist et al., p. 14.

Material. – Holotype cephalon, SMF RX 566b figured by Richter & Richter (1926), pl. 9, fig. 51, refigured herein; cephalon, SMF X 566h, Matern (1927), Sessacker trench 2, bed 7, Early *crepida* Zone; new material from Sessacker, coll. Lippert in Ziegler (1962): 2 cephalons, SMF 97032, SMF 97033, trench I, bed 20, 1 pygidium, SMF 97031 trench II, bed 23, Late *triangularis* Z.; cephalon NKMB-T1017 from Sessacker; slab with dissociated sclerites of

same specimen comprising cephalon, hypostome, thoracic segment and pygidium, Weilburg/Lahn, MB.T 8258.1.

Diagnosis. – Anterior outline of glabella widely elliptical; frontal glabellar lobe slightly overhanging medially without overhanging anterior border; hypostome with straight converging posterior edges, pointed behind; vincular furrow deep with wide parabolic curvature, slightly widening distally, postvincular doublure concave, three times longer than vincular furrow (sag.); thoracic axial rings with swollen lateral lobes; pygidium transverse, short, evenly curved behind, axis with narrow parabolic posterior outline, pleural region moderately vaulted with thin marginal rim present antero-laterally.

***Nephranops (Maternia) occitanicus* sp. nov.**

Figure 5A–I

non 1989 *Nephranops incisus*. – Becker et al., p. 262, fig. 3.

non 1993 *Nephranops dillanus*. – Klapper et al., p. 483, fig. 7.

Holotype. – Cephalon, UM-IP 824, Fig. 5A–C, from Causse-et-Veyran, Montagne Noire, Middle *triangularis* Zone.

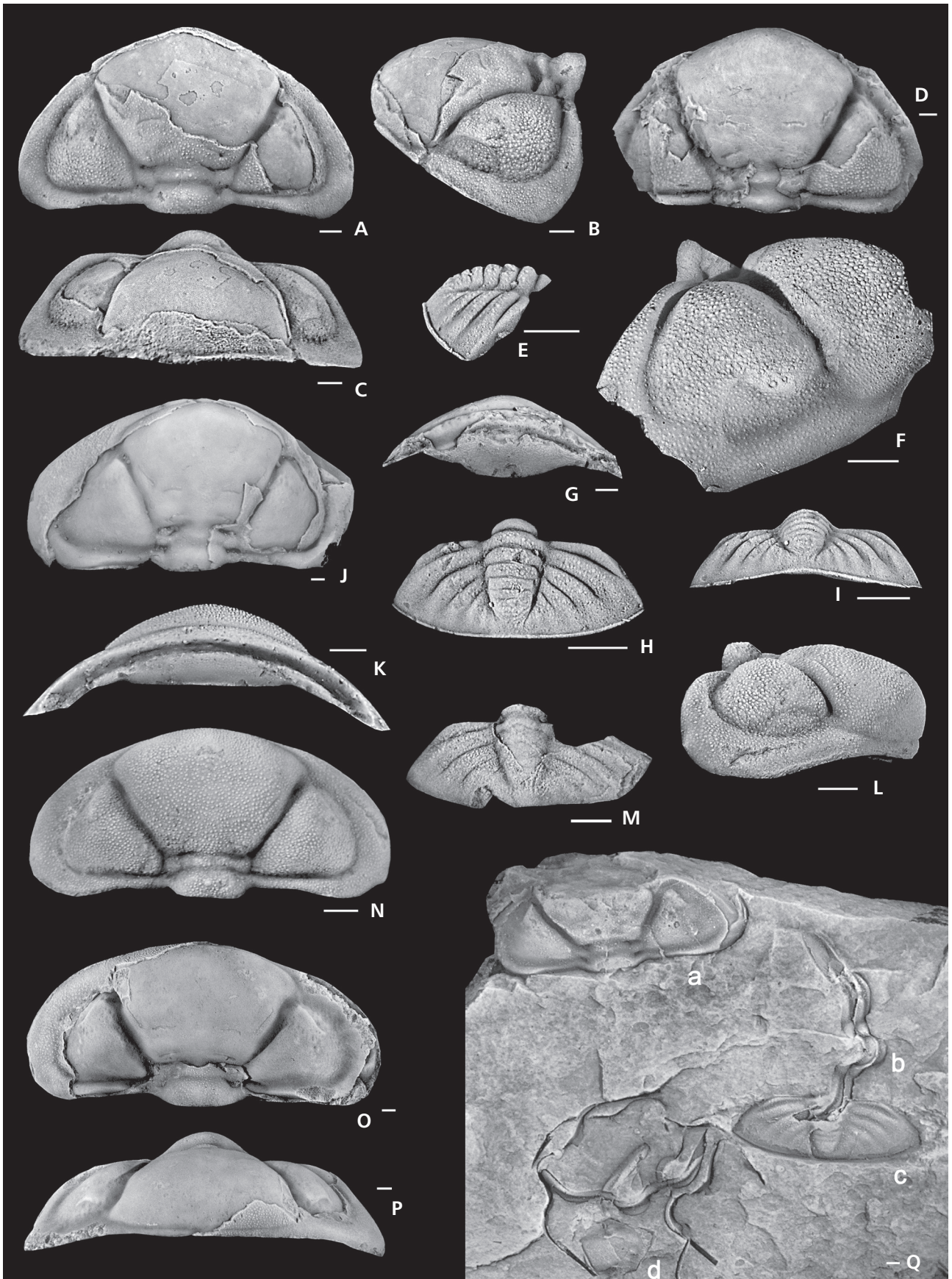
Type horizon and locality. – Causse-et-Veyran, Hérault, Southern France, 400 m W of village; CV-S section, bed 35 (Feist 1990, p. 25, fig. 11), hematite-rich, brick-red calcilutite.

Material. – Paratypes: 2 cephalons UM-IP 825–826, from type horizon, 1 cephalon with residual lenses UM-IP 827, from CV-S section, bed 33, cephalon UM-IP 828 from Coumiac UQ, bed 36 (Upper *triangularis* Zone, Feist 1990), 2 pygidia UM-IP 829–830, from type horizon.

Etymology. – From *Occitania* [Latin], Roman Province in Southern France.

Diagnosis. – Glabella highly vaulted, sub-pentagonal, pointed medially, overhanging frontal border; lateral glabellar furrows forwardly curved adaxially; intercalating ring with flat lateral lobes expanding forwards distally; postvincular doublure very long (sag.). Pygidium slightly truncated behind; axis high, weakly tapering; strong marginal rim at postero-lateral edges.

Figure 5. A–I – *Nephranops (Maternia) occitanicus* sp. nov., Causse-et-Veyran, Montagne Noire, Southern France; A–C – holotype cephalon UM-IP 824, dorsal (A), lateral (B), anterior (C) views; D, G – cephalon UM-IP 828, dorsal (D), ventral (G) views; E, H, I – pygidium UM-IP 829, lateral (E), dorsal (H), posterior (I) views; F – cephalon UM-IP 827, latex cast of internal mould, antero-lateral view showing visual surface with two residual lenses. • J–Q – *Nephranops (Maternia) dillanus* Richter & Richter, 1926, Sessacker near Oberscheld (J–P), Weilburg/Lahn (Q), Eastern Rhenish Slate Mountains, Germany; J – holotype cephalon SMF-X566b, latex cast of original specimen, dorsal view; K, L, N – cephalon SMF-X566h, ventral (K), lateral (L), dorsal (N) views; M – pygidium SMF 97031, dorsal view; O, P – cephalon NKMB-T1017, dorsal (O), anterior (P) views; Q – dissociated sclerites of same individual on same slab MB. T 8258.1, cephalon (a), thoracic segment (b), pygidium (c), hypostome (d). Scale = 1 mm.



Description. – Cephalon almost twice as wide as long, of evenly curved anterior outline. Glabella sub-pentagonal, as long as wide, pointed anteriorly with obtusely angular antero-lateral corners, of high, continuously vaulted lateral and frontal profiles, overhanging anterior border adaxially. Axial furrows straight anteriorly, slightly outwardly curved behind. Lateral glabellar furrows markedly impressed. S1 narrow and deep distally, not reaching axial furrow, forwardly curved adaxially where merging with very shallow median portion. Intercalating ring straight, slightly vaulted in its median part (sag.) carrying two tubercles, with less vaulted sub-quadrangular lateral lobes that are projected forwards distally. Occipital ring strongly vaulted (sag., tr.), higher and wider (tr.) than base of glabella in front of L1, twice as long as intercalating ring (sag.), carrying flat, pitted median tubercle. Anterior border protruding from border furrow, moderately vaulted (sag.) medially, continuously narrowing distally until merging with slightly vaulted, sharply edged antero-lateral border. Vincular furrow deep, anteriorly merging with frontal slope of anterior border, as long as anterior border (sag.), well defined by sharp edge against very long (sag.) postvincular doublure, that is anteriorly flat and slightly downwardly curved posteriorly. Genal field strongly vaulted throughout, circumscribed by homogeneously deep border furrows. Eye lobe in advanced position, very low with slightly swollen oblique palpebral lobe. Visual surface is rather small, slightly sunken against palpebral lobe, well defined by crescent-shaped facial suture, generally without lenses with the exception of a single case, where two residual tiny lenses of different sizes seem to be developed (Fig. 5F). Sculpture: densely set nodules throughout including visual surface.

Early holaspide pygidium transverse sub-pentagonal with slightly truncated posterior outline, shorter (sag.) than half width (length/width index = 1:2.4), strongly curved lateral profile, kinked posterior border in posterior view. Axis is highly vaulted, weakly tapering, long with undefined posterior outline, not reaching posterior edge. Eight vaulted axial rings, markedly separated by straight ring furrows that reach axial furrows where slightly backwardly curved. Pleural region horizontal adaxially, strongly downwardly curved distally in posterior view, with 5 ribs markedly separated by deep pleural furrows that terminate far distant from postero-lateral margin. Interpleural furrows are inconspicuous. Strong marginal rim runs along antero-lateral edges. Sculpture: dense nodules becoming finer peripherally, outer margins smooth.

Remarks. – The new species shares with *Nephranops (Maternia) dillanus* the position and outline of the palpebral lobes and the small librigenae. It is distinct mainly in the markedly pointed anterior outline of the

glabella, its higher transverse vault, the larger, anteriorly expanding lateral lobes of the intercalating ring and the much longer postvincular doublure. The pygidium is relatively longer and has a pronounced marginal rim. The new species shares the anteriorly protruding frontal glabellar lobe and the long postvincular doublure with *N. (M.) franconicus*. The main difference is seen in the shape of the palpebral lobe, which in *franconicus* extends significantly farther backwards, is more prominent and situated almost equidistant from the sagittal line anteriorly and posteriorly.

Genus *Pulvinocephalus* gen. nov.

Type species. – *Phacops (Trimeroccephalus) steinachensis* Richter & Richter, 1926.

Etymology. – *pulvinus* [Latin] = cushion, referring to the cushion-like protruding anterior border of cephalon.

Diagnosis. – Reduced-eyed or blind with palpebral suture running onto cheek; anterior border cushion-like inflated, protruding beyond front of glabella, vincular furrow rather long (sag.) and shallow; pygidium transverse, axis high, narrow, almost reaching posterior edge.

Remarks. – The new genus regroups phacopine taxa with anterior cephalic border forwardly extending beyond anterior outline of glabella. The nominotypical subgenus is characterised by blind species whereas the new subgenus *P. (Cryphopsides)* comprises oculated species.

Occurrence. – Early Famennian: Early *triangularis* to Early *marginifera* zones.

Subgenera included. – *P. (Pulvinocephalus)* subgen. nov., *P. (Cryphopsides)* subgen. nov.

Subgenus *Pulvinocephalus (Pulvinocephalus)* gen. et subgen. nov.

Type species. – *Phacops (Trimeroccephalus) steinachensis* Richter & Richter, 1926.

Diagnosis. – Glabella low, with flat median profile, not overhanging anterior border furrow; anterior border inflated, protruding, widest opposite anterior axial furrows (exsag.), genal field without eyes, suture running onto cheek anteriorly; vincular furrow very shallow and long, with ill-defined posterior edge; postvincular doublure short, flat; pygidium transverse with evenly rounded posterior outline, narrow axis with 5 flat rings, inclined behind, merging with postaxial region; pleural field with 4 ribs not reaching margin.

Occurrence. – Rhenish and Thuringian Slate Mountains, Harz Mountains, Germany; Early *crepida* to Early *marginifera* zones.

Species included. – *Phacops* (*Trimerocephalus*) *steinachensis* Richter & Richter, 1926; *Pulvinocephalus* (*Pulvinocephalus*) *steinachensis* *triangulus* subsp. nov.; *Pulvinocephalus* sp. [= *Phacops* (*Nephranops*?) sp., Maximova (1955), p. 149, pl. 12, fig. 13].

***Pulvinocephalus* (*Pulvinocephalus*) *steinachensis* (Richter & Richter, 1926)**

Subspecies included. – *P. (P.) steinachensis steinachensis* (Richter & Richter, 1926), *P. (P.) steinachensis triangulus* subsp. nov.

***Pulvinocephalus* (*Pulvinocephalus*) *steinachensis steinachensis* (Richter & Richter, 1926)**

Figure 6D–F, J, K, R, S

- *v 1926 *Phacops* (*Trimerocephalus*) *steinachensis* n. sp.; Richter & Richter, p. 180, pl. 10, figs 76–79.
- non 1927 *Phacops* (*Trimerocephalus*) *steinachensis*. – Matern, p. 255 (= *triangulus* subsp. nov.).
- non 1931 *Phacops* (*Trimerocephalus*) *steinachensis*. – Matern, p. 106 (= *triangulus* subsp. nov.).
- 1939 *Phacops* (*Trimerocephalus*) *steinachensis*. – Volk, p. 215.
- 1954 *Phacops* (*Trimerocephalus*) *steinachensis*. – Pfeiffer, p. 43, pl. 2, fig. 12.
- 1955 *Trimerocephalus steinachensis*. – Maximova, p. 154.
- 1959 *Phacops* (*Trimerocephalus*) *mastophthalmus*. – Pfeiffer, pl. 4, fig. 5.
- cf. 1968 *Trimerocephalus* sp. cf. *steinachensis*. – Lütke, p. 165, pl. 8, fig. 8.
- 2003 *Trimerocephalus* ? *steinachensis*. – Crônier, pp. 63–66.

Material. – Cephalon SMF-X 540b figured by Richter & Richter (1926, pl. 10, fig. 78), refigured herein; coll. Volk (1939) from type-locality Steinach, Thuringia: cephalon SMF 540 h, 1, pygidium SMF-540 c; cephalon BGRB – BD 2534/1, coll. Reuter, Bohlen section, Thuringia, Plattenbruch Member, bed 4, late early Famennian.

Diagnosis. – Cephalon with evenly rounded anterior outline. Maximum width of cephalon opposite two-thirds cephalic length (sag.) from anterior; with remnant eye-protuberances crossed by facial suture; pygidium with axis having rounded posterior outline and relatively long postaxial region.

Remarks. – In addition to the description of Richter & Richter (1926): the anterior axial furrows of the cephalon are deeply impressed slightly before reaching the border

furrow. At this point the adaxial anterior cheek is markedly notched by the passage of facial suture that partly separates a minute swollen portion of anterior-most cheek. The entire exoskeleton is covered with tiny tubercles that become coarser on frontal parts of glabella and on anterior border. The hitherto un-described pygidium is elongated transversely. The axis has 5 slightly vaulted (sag.) rings, the first of which has a pseudo-articulating half-ring. First 2 inter-ring furrows reaching axial furrows, very shallow medially, deepening abaxially and forming deep oval pits distally. Posterior rings fused medially and separated abaxially by thin inter-ring furrows that do not reach axial furrows.

Occurrence. – Thuringia; Harz Mountains (cf. *steinachensis* after Lütke 1968); Early *marginifera* Zone after Lütke (1968).

***Pulvinocephalus* (*Pulvinocephalus*) *steinachensis triangulus* subsp. nov.**

Figures 3F; 6A–C, G, H

Holotype. – Cephalon SMF-X 540 d, coll. Matern, Sessacker trench II, bed 4, *rhomboidea* Zone, Fig. 6A–C.

Type horizon and locality. – Sessacker near Oberscheld, eastern Rhenish Slate Mountains, Germany; trench II, bed 4 of Matern (1927), red calcilutite with *Palmatolepis* cf. *rhomboidea*, *Pa. quadrantinodosalobata*, *Icriodus alternatus alternatus*: *rhomboidea* Zone.

Material. – Holotype specimen SMF-X 540 d; paratypes: pygidium SMF-X 566g, trench II, bed 4 of Matern (1927), pygidium SMF-X 540e, associated to poorly preserved cephalon, trench II bed 5 of Matern (1927), red calcilutite with *Pa. rhomboidea*: *rhomboidea* Zone; 1 fragment of cephalon showing vincular furrow, SMF 97034, trench VI, 29 b, Early *crepida* Zone, after Schülke (1995).

Etymology. – After the triangular anterior outline of cephalon.

Diagnosis. – Outline of cephalon truncated antero-laterally, widest opposite to occipital furrow; anterior angle of cheek without protuberances; facial suture cutting small recessed crescent into anterior cheek; pygidial axis narrow anteriorly, with obtusely pointed posterior outline; postaxial region short.

Description. – The cephalon with a sub-cylindrical anterior border that is truncated antero-laterally, i.e. longer adaxially and in line with course of axial furrows; at the latter position it is markedly swollen, a little uplifted, and causes a slight backwards deflection of the border furrow. Crescent-shaped anteriormost portion of genal field between border furrow and suture is markedly lowered. Border furrow remains

continuously deep around genal angles. Genal angles shifted far behind to a position opposite occipital furrow. In lateral view, profile of glabella flat-topped, strongly down-curved anteriorly, slightly overhanging anterior border furrow. Axial furrows straight and deep; anterior corners of glabella sub-angular, not extending outwards. Anterior outline of glabella is sub-circular. Pygidium transverse, length/width ratio = 0.43, posterior outline widely rounded; axis narrow, nearly half as wide as pleural region, with 5 + 1 indistinct, low, straight rings, obtusely pointed behind, not reaching posterior edge. Pleural region slightly vaulted, more strongly at posterior margin, with 4 undivided ribs separated by relatively deep pleural furrows that die out far from lateral border. No border; edges with narrow rim. In lateral view, profile of axis evenly curved with very low axial rings, effaced behind, the posterior end merging with vaulted postaxial region. Sculpture: dense small-sized tuberculation throughout.

Remarks. – Differences from nominate subspecies: cephalon with triangular anterior outline, anterior outline of glabella sub-circular (elliptical in *steinachensis*) smaller area of genal field cut by suture, absence of ocular protuberances on anterior gena, border furrow continuously deep at genal angles (shallower in *steinachensis*), maximum width farther behind. First axial ring in the pygidium as wide transversely as second (in *steinachensis* it is wider). Ring furrows shallow but continuous (in *steinachensis* only first one continuous, the following impressed only distally and effaced medially). Posterior end of axis obtusely pointed (in *steinachensis* vaguely rounded, largely merging with postaxial area, remaining more distant from posterior edge). Pleural ribs slightly vaulted (exsag.) (in *steinachensis* almost flat-topped).

Occurrence. – Type-locality only; Early *crepida* to *rhomboidea* zones.

Subgenus *Pulvinocephalus* (*Cryphopsides*) gen. et subgen. nov.

Type species. – *P. (Cryphopsides) ovatus* sp. nov.

Etymology. – Resembling *Cryphops*.

Diagnosis. – Anterior border of cephalon convex, very high (sag.); anterior outline of glabella wide, with obtusely rounded corners; axial furrows abaxially convex in front of S1; S2 and S3 indiscernable; genal field with ocular lobe bearing visual surface with lenses.

Remarks. – *P. (Cr.) latilimbatus* (Maximova, 1955) was recovered from the Barma horizon in the SW Uralian Bol'shaya Barma section with the brachiopod *Pugnoides triaequalis* Goss. [= *Parapugnax markowskii* (Yud.)]. Previously considered late Frasnian this horizon is now referred to the basal Famennian Early and Middle *triangularis* Zones by conodonts (Abramova & Artyushkova 2004, Tagarieva 2013).

Occurrence. – Rhenish Slate Montians, Southern Urals; Early Famennian *triangularis* through *crepida* zones.

Species included. – *P. (Cryphopsides) ovatus* sp. nov., Late *triangularis*–Latest *crepida* Zones, Sessacker, Germany; *P. (Cr.) latilimbatus* (Maximova, 1955), Early and Middle *triangularis* zones, SW Urals; tentatively assigned: *P. (?Cr.) walliseri* sp. nov., Late *crepida* Zone, Sessacker, Germany.

***Pulvinocephalus* (*Cryphopsides*) *ovatus* sp. nov.**

Figure 6P

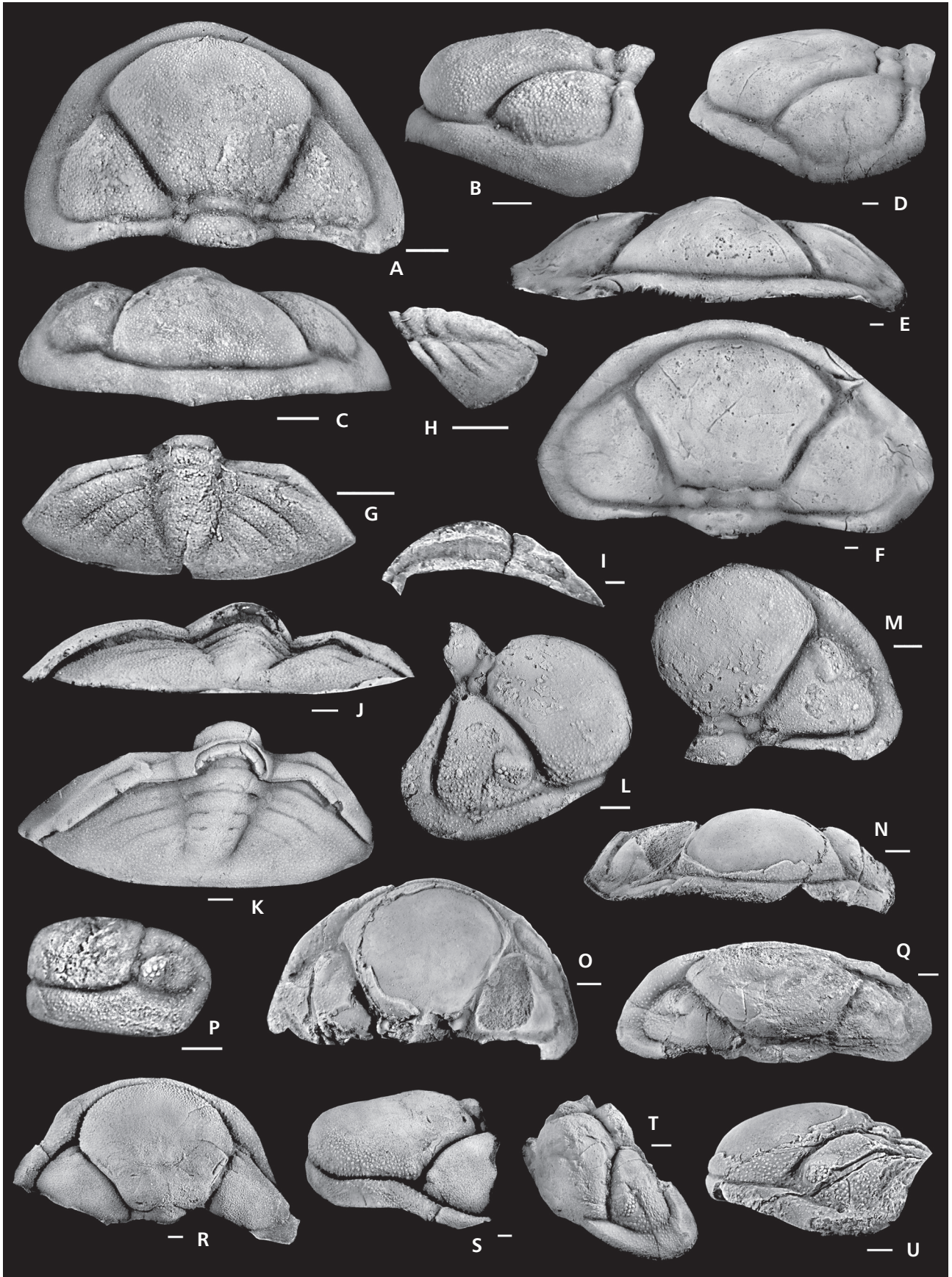
- v 1927 *Phacops* (*Cryphops*) *cryptophthalmus*. – Matern, p. 255.
- 2000 *Cryphops* cf. *latilimbatus*. – Crônier & Feist, p. 505, pl. 1, fig. 10a–d.

Holotype. – Cephalon SMF-X 563 b, Sessacker, coll. Matern, trench II, bed 5, figured in Crônier & Feist (2000, pl. 1, fig. 10a–d).

Type horizon and locality. – Sessacker near Oberscheld, eastern Rhenish Slate Mountains, Germany; trench II, bed 5 of Matern (1927), red calcilutite with *Palmatolepis quadrantinodosalobata*, *Icriodus alternatus alternatus*: Latest *crepida* Zone.

Material. – Paratype: fragmentary cephalon SMF 97035, Sessacker, coll. Lippert, trench II, bed 23, Late *triangularis* Zone.

Figure 6. A–C, G, H – *Pulvinocephalus* (*Pulvinocephalus*) *steinachensis triangularis* subsp. nov., Sessacker near Oberscheld, Eastern Rhenish Slate Mountains, Germany; A–C – holotype cephalon SMF-X540d, dorsal (A), lateral (B), anterior (C) views; G, H – pygidium SMF-X540e, dorsal (G), lateral (H) views. • D–F, J, K, R, S – *Pulvinocephalus* (*Pulvinocephalus*) *steinachensis steinachensis* (Richter & Richter, 1926), Steinach, Thuringia; D–F – cephalon SMF-X540b, plaster cast of original specimen, lateral (D), anterior (E), dorsal (F) views; J, K, R, S – pygidium and cephalon SMF-X540c, latex casts of original specimens, posterior (J), dorsal (K) views of pygidium, dorsal (R), lateral (S) views of cephalon. • I, L–O, Q, T, U – *Pulvinocephalus* (?*Cryphopsides*) *walliseri* ?subgen. et sp. nov., Sessacker near Oberscheld, Eastern Rhenish Slate Mountains, Germany; I, L–O – holotype cephalon SMF 97036 ventral (I), antero-lateral (L, latex cast of internal mould), dorsal (M, latex cast of internal mould), anterior (N), dorsal (O) views; Q, T, U – cephalon SMF 97037, dorsal (Q), oblique antero-lateral (T), lateral (U) views. • P – *Pulvinocephalus* (*Cryphopsides*) *ovatus* subgen. and sp. nov., Sessacker near Oberscheld, Eastern Rhenish Slate Mountains, Germany, cephalon SMF 97035, lateral view. Scale = 1 mm.



Etymology. – *ovatus* [Latin] = oval, referring to shape of visual surface.

Diagnosis. – Anterior border as high as front of glabella in anterior view; anterior outline of glabella widely parabolic; posterior axial furrows inwardly curved; eye lobes small, ovoid, situated far forward with lower edge in border furrow; palpebral furrows oblique, adaxially convex; visual surface oval, with 5–6 lenses; antero-lateral border enlarged at junction between axial and border furrows.

Description. – See Crônier & Feist (2000, p. 505).

Remarks. – The new species differs from *latilimbatus* mainly in the form and position of the eye, which, in the latter, is kidney-shaped and extends farther to the rear.

Occurrence. – Rhenish Slate Mountains (Sessacker only); Late *triangularis* through latest *crepida* zones.

***Pulvinocephalus* (?*Cryphopsides*) *walliseri* sp. nov.**

Figures 3G; 6I, L–O, Q, T, U

Holotype. – Cephalon SMF 97036 Sessacker trench VI, Late *crepida* Zone, Fig. 3G; 6I, L–O.

Type horizon and locality. – Sessacker near Oberscheld, eastern Rhenish Slate Mts., Germany; Sessacker trench VI, red calcilutite, loose sample, Late *crepida* Zone.

Material. – Cephalon SMF 97037, Sessacker trench VI, same slab as holotype.

Etymology. – After the late Prof. O. Walliser who discovered the holotype specimen.

Diagnosis. – Frontal glabellar lobe low semi-circular, not overhanging anterior border of moderate height; axial furrows straight in front of S1; ocular lobe on anterior genal field, close to border furrow, with crescent-shaped, oblique palpebral lobes, straight palpebral furrows, kidney-shaped visual surface carrying numerous lenses; vincular furrow deep, postvincular doublure very short, swollen.

Description. – Anterior outline of glabella semi-circular, of even curvature and high transverse vault, moderately strongly vaulted in lateral view. Frontal glabellar lobe descends moderately steeply anteriorly, not overhanging border furrow. Anterior border is of moderate vertical height adaxially. Axial furrows straight in front of S1, meeting border furrow in an obtuse angle at glabella corners. Anterior genal field exhibits small elevated triangular area between facial suture and axial furrow adjacent to glabellar corners. Eye lobe situated far forward

but remains distant from antero-lateral border furrow leaving an interval equivalent to half width of adjacent border. Palpebral lobes elongated crescent-shaped, flat, adaxially inclined, with abaxially convex palpebral suture and straight, obliquely diverging palpebral furrows. Visual surface is kidney-shaped with about 17 lenses. Vincular furrow is rather deep and wide (sag.), and sharply delimited against lower edge of anterior border and postvincular doublure. Postvincular doublure is rather short, markedly lower than anterior edge of vincular furrow, crest-like, swollen, and shorter than half length of vincular furrow. Sculpture: densely tuberculated, coarser nodules on anterior slope of glabella, genal fields including pre-ocular genal field, and antero-lateral borders.

Remarks. – The configuration of the vincular structure resembles *Cryphops cryptophthalmus* (Emmrich, 1844) in the deep position of the posterior edge of the vincular furrow and the reduction of the postvincular doublure. However, in contrast to *cryptophthalmus* where the vincular furrow terminates posteriorly with a sharp edge without postvincular doublure, in the new species there is a marked swollen rim representing an enrolled, rather short postvincular doublure. The main differences from *Cryphops* include the slightly forwardly protruding anterior border (compare Figs 3G and 6I) and the eye remaining distant from border and exhibiting kidney-shaped visual surfaces.

Genus *Cryphops* Richter & Richter, 1926

Type species. – *Phacops cryptophthalmus* Emmrich, 1844.

Diagnosis. – See Crônier & Feist (2000).

Remarks. – *Phacops* (*Cryphops*) *latilimbatus* Maximova, 1955 and *Cryphops* cf. *latilimbatus* Maximova, 1955 (in Crônier & Feist 2000) are reassigned to *Pulvinocephalus* (*Cryphopsides*).

Species included. – Type species only.

***Cryphops cryptophthalmus* (Emmrich, 1844)**

Figures 3I; 7A–H

Synonymy. – See Crônier & Feist (2000).

Material. – New material from Sessacker: cephalon SMF 97038, trench II R, collected Matern, latest *crepida* Zone; cephalon SMF 97039, collected Lippert, trench I, bed 25–26, Middle *crepida* Zone; pygidium SMF 97040, trench II R, collected Matern, on same slab as cephalon SMF 97038.

Diagnosis. – Glabella in front of L1 pentagonal with

medially acute, anteriorly protruding anterior outline, antero-lateral border wide, moderately inflated, slightly kinked opposite axial furrows, ovoid eye-lobe on anterior-most genal field reaching border furrow, with elliptical visual surface carrying 7–11 lenses. Pre-vincular doublure very broad (sag.), slightly vaulted, inclined postero-ventrally; vincular furrow deep, long (sag.), bordered by sharp edges, postvincular doublure absent. Pygidium transverse with narrow, long axis containing 7 + 1 rings, pleural region with 5 ribs.

Remarks. – The hitherto un-recognized pygidium has the following characteristic traits: Pygidium transverse, length/width ratio = 0.54; axis robust, high, with continuously down-curved profile, with 7 + 1 narrow, straight rings, separated by deep inter-ring-furrows; axial furrows weakly and uniformly converging backwards, posterior end of axis obtusely rounded, almost reaching posterior edge, merging with elevated post-axial region. Pleural region moderately vaulted, with 5 ribs whose anterior bands are longer than posterior ones but do not reach lateral edges. Latero-posterior margin has no border furrow, edge with tiny elevated rim.

Genus *Trifoliops* Crônier, 2003

Type species. – *Dianops? trifolius* Osmólska, 1958.

Diagnosis. – See Crônier (2003).

Remarks. – The species *nigritus* originally included by Crônier (2003) exhibits different diagnostic features including the short and wide glabella, the protruding anterior cephalic outline and relatively short (sag.) vincular furrow. It is excluded from *Trifoliops* here and assigned to *Trimercephalus* with question.

Species included. – *Dianops? trifolius* Osmólska, 1958, Holy Cross Mountains., SW Algeria, Early *rhomboidea* Zone; *T. cronierae* Feist, 2016 in Feist *et al.* (2016), Marhouma, SW Algeria, Early *rhomboidea* Z.; *T. septimanicus* sp. nov., Causses-et-Veyran, Montagne Noire, Southern France, Late *rhomboidea* Zone.

Trifoliops septimanicus sp. nov.

Figures 3H, 7I–M

2003 *Trimercephalus* (*Trifoliops*) *trifolius*. – Crônier, pp. 58, 59, figs 2a–d, 3a, 4a, b.

2003 *Trimercephalus* (*Trifoliops*) *nigritus*. – Crônier, pp. 59–62, fig. 6g, h.

2013 *Trimercephalus* (*Trifoliops*) *trifolius*. – Crônier *et al.*, p. 1012.

2016 *Trifoliops trifolius*. – Feist *et al.*, p. 254.

Holotype. – Cephalon USTL/CC014 in Crônier (2003, fig. 2a), from Causses-et-Veyran, Southern France.

Type horizon and locality. – Causses-et-Veyran Village, Hérault, Southern France, Concours-le-Haut quarry; red nodular calcilutites with marly interstices, Bed 43 (in Girard *et al.* 2014, fig. 5), Late *rhomboidea* Zone.

Material. – Collection Crônier 2003 (USTL/CC014-017, 024-025), new material: 3 cephalons UM-IP 831–833.

Etymology. – After *Septimania* [Latin], province of Southern France (Languedoc region).

Diagnosis. – Glabella slightly longer than wide, antero-lateral border furrows straight; anterior cheek with ocular protuberances cut by facial suture; vincular furrow more than twice as long as postvincular doublure, widest medially, with continuously curved anterior and posterior edges, the anterior more highly arched than the posterior in ventral view; pygidium trapezoidal with framed pleural fields, and granulated, rather long vertical portion (sag.) of doublure.

Description. – Pygidium transverse trapezoidal with 4 axial rings. Terminal piece triangular with elevated sagittal ridge and lower abaxial parts; articulating half-ring longer than first axial ring, very long pseudo-articulating half-ring in front of second axial ring, bearing tubercles on its posterior part, pseudo-articulating half-rings developed on third and fourth axial rings; axial rings inflated abaxially where flexed forward and separated by rather deep, transversely elongated muscle scars, axial rings moderately inflated medially. Post-axial region is half as long as terminal piece of axis. Four pleural ribs not extending to postero-lateral edges. Pleural fields are framed by thick, elevated marginal rim merging, on its external side, with vertical portion of doublure. Pleural furrows are deeper but shorter than inter-pleural furrows. Profile of axis evenly curved, pleural fields modestly vaulted. Sculpture: dense granules except on distal parts of pleural region which are smooth.

Comparison: The anterior border protrudes slightly beyond the anterior glabellar lobe, whereas it does not protrude in *trifolius* (*cf.* Osmólska 1963, pl. 4, fig.1). In the latter, the anterior edge of the vincular furrow is straight transversely, and both the vincular furrow and the postvincular doublure are less strongly curved than in *septimanicus*. The pygidium of the new species is closest to *T. cronieri* Feist, 2016 (see comparisons in Feist *et al.* 2016, p. 254).

Remarks. – The new species from the Montagne Noire was earlier assigned to *Trimercephalus* (*Trifoliops*) *trifolius* (Osmólska, 1958) by Crônier 2003. Feist in Feist

et al. (2016, p. 254) pointed out that the Montagne Noire material exhibits diagnostic features such as the presence of ocular protuberances that are absent in the Polish originals. Other distinct diagnostic characters, the outline of the vincular structure in particular, justify the specific differentiation of the Montagne Noire material. The pygidium was originally assigned to *?Trimerorcephalus nigrinus* Crônier, 2003 before being reassigned by Crônier *et al.* (2013) to *Trimerorcephalus (Trifoliops) trifolius* (Osmólska, 1958). It is here considered to belong to the new species *Trifoliops septimanicus*. A few morphological features are added to Crônier's description.

Genus *Trimerorcephalus* McCoy, 1849

Type species. – *Trinucleus? laevis* Münster, 1842 = *Phacops (Trimerorcephalus) mastophthalmus* Reinhard Richter, 1856, Gattendorf, Thuringian Slate Mountains, Germany, early Famennian.

?Trimerorcephalus nigrinus Crônier, 2003

Figure 7N–R

v. 2003 *Trimerorcephalus (Trifoliops) nigrinus* n. sp.; Crônier, pp. 59–62, figs 3b, 6a–f.

non 2003 *Trimerorcephalus (Trifoliops) nigrinus*; Crônier, pp. 59–62, fig. 6g, h.

2013 *Trimerorcephalus (Trifoliops) nigrinus*. – Crônier *et al.*, pp. 10, 11, fig. 3d–h, s–v.

2016 *Trifoliops nigrinus*. – Feist *et al.*, p. 253.

Material. – Collection Crônier 2003 (USTL/CC018-023); new material: 2 cephalon UM-IP 834, 835; 1 pygidium UM-IP 836.

Diagnosis. – Glabella wider than long, overhanging anterior border furrow, antero-lateral border compressed, incurved, elevated opposite axial furrow; vincular furrow deep, shorter than postvincular doublure; pygidium transverse, lens-shaped; axis low with wide posterior end not reaching margin, four uniformly forwardly arched rings and continuous inter-ring furrows.

Description. – Features of the cranidium were described in detail by Crônier (2003). The newly discovered pygidium is lens-shaped. It has a wide, moderately vaulted axis with 4 + 1 forwardly curved rings of even length (sag. exsag.) from the middle to their distal ends. Inter-ring furrows are well marked, deepening abaxially where reaching axial furrows. Posterior end of axis widely rounded, low, not reaching posterior margin. Pleural field moderately vaulted, with 4 ribs; pleural furrows as wide (tr.) as inter-pleural furrows but deeper than them; both vanishing far before reaching postero-lateral margin.

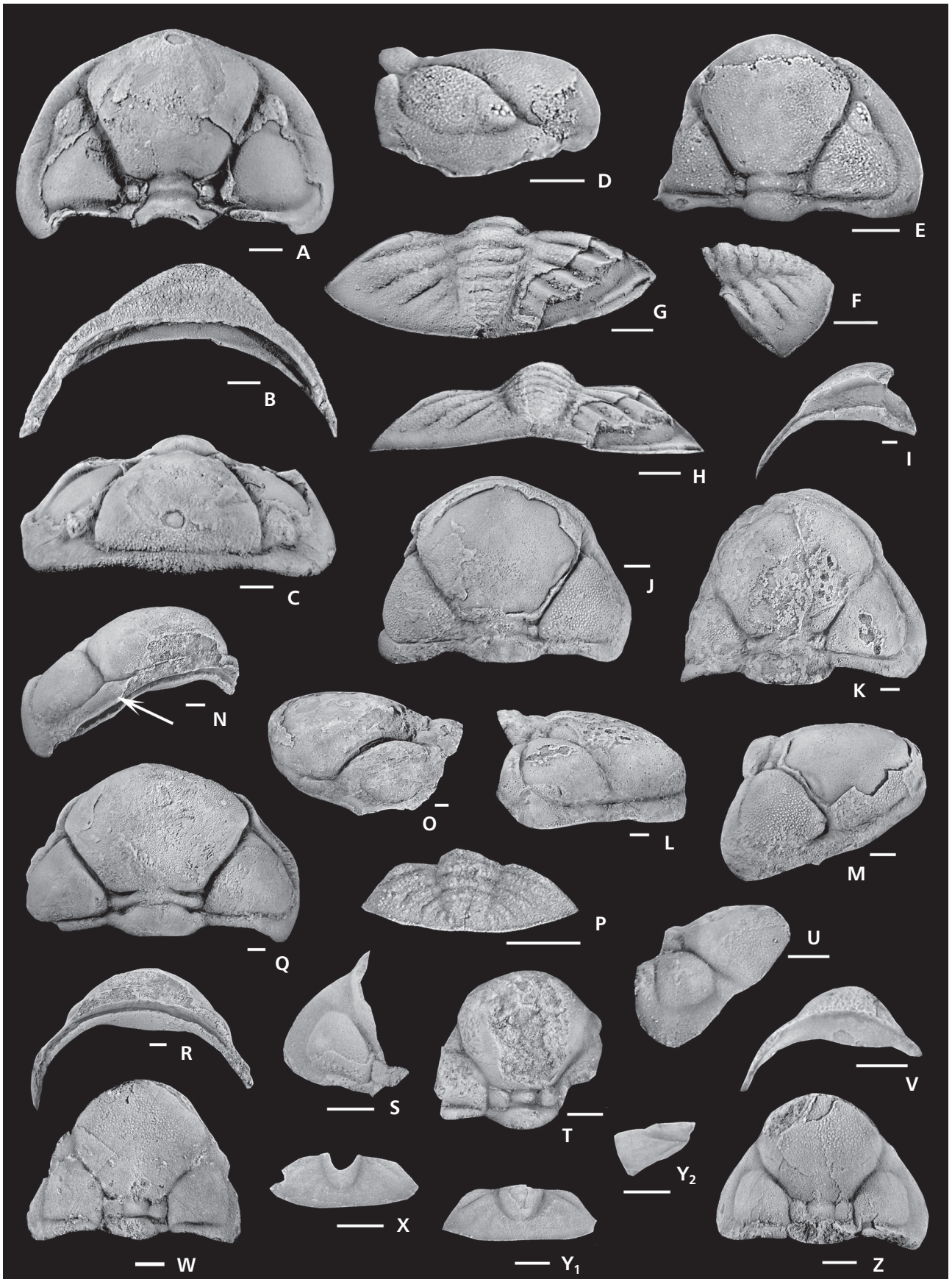
Remarks. – The species was hitherto assigned to *Trifoliops* on account of the inwardly curved antero-lateral cephalic borders that characterise *T. trifolius* and allies. In the latter the inward curvature results from the sudden increase in width (exsag.) and forward projection of the swollen border in front of the junction between antero-lateral border furrow and axial furrow. In antero-lateral view the border remains at the same level at this point and the antero-lateral border furrow is straight. In *nigrinus* the inward curvature results from the antero-lateral compression of the border which is elevated to a triangular, narrow structure surrounding the corners of the anterior glabella lobe (Fig. 7N). Unlike *Trifoliops* and *Trimerorcephalus*, the ventral edge of the anterior border has a forwardly protruding rim. This rim extends abaxially along the antero-lateral border where it defines an elongated depression in the vertical outer slope of the border, which is upraised opposite the axial furrow (see arrow in Fig. 7N).

Genus *Struveops* Crônier & Feist, 2000

Type species. – *Phacops (Cryphops) schlosseri* Richter & Richter, 1955.

Diagnosis. – Cephalon eyeless, with functional marginal sutures; triangular, swollen palpebral lobe on border, separated from genal field by continuous border furrow reaching axial furrow far behind point of maximum lateral extension of glabella; pre-vincular doublure high, crescent-shaped, backward oriented; vincular furrow with

Figure 7. A–H – *Cryphops cryptophthalmus* (Emmrich, 1844), Sessacker near Oberscheld, Eastern Rhenish Slate Mountains, Germany; A–C – cephalon SMF 97038, dorsal (A), antero-ventral (B), anterior (C) views; D, E – cephalon SMF 97039, lateral (D), dorsal (E) views; F–H – pygidium SMF 97040, lateral (F), dorsal (G), posterior (H) views. • I–M – *Trifoliops septimanicus* sp. nov., Concours-le-Haut near Causses-et-Veyran, Montagne Noire, Southern France; I, K, L – cephalon UM-IP 831, ventral (I), dorsal (K), lateral (M) views; J, M – cephalon UM-IP 832, dorsal (J), lateral (M) views. • N–R – *?Trimerorcephalus nigrinus* Crônier, 2003, Concours-le-Haut near Causses-et-Veyran, Montagne Noire, Southern France; N, O, Q, R – cephalon UM-IP 834, oblique antero-lateral view (N) showing elevated antero-lateral border exhibiting longitudinal depression and marginal rim (arrow), lateral (O), dorsal (Q), ventral (R) views; P – pygidium UM-IP 836, dorsal view. • S–Z – *Struveops wiedaensis* sp. nov., Sessacker near Oberscheld, Rhenish Slate Mountains (S–T) and Stöberhaifahrtweg near Wieda, Harz (U–Z), Germany; S – fragment of cranidium SMF 97055, dorsal view; T – cranidium SMF 97056, dorsal view; U – cranidium SMF 97043, oblique antero-lateral view; V – cephalic doublure showing vincular furrow SMF 97044, ventral view; W – cranidium SMF 97042, dorsal view; X – pygidium SMF 97045, dorsal view; Y – pygidium SMF 97046, dorsal (Y1), lateral (Y2) views; Z – holotype cranidium SMF 97041, dorsal view. Scale = 1 mm.



sharp anterior edge, devoid of posterior edge, merging with postvincular area of doublure; pygidium transverse with slightly truncated posterior edge; axis short and plump, furrows of axial rings and pleural fields almost effaced.

Species included. – *Phacops (Cryphops) schlosseri* Richter & Richter, 1955 from Talnitz near Plauen, do III, *Phacops (Trimerocephalus) pulvinifer* Matern, 1927 from Sessacker, do III; *Struveops wiedaensis* sp. nov. from Stöberhaifahrweg near Wieda, Early *marginifera* Zone.

***Struveops wiedaensis* sp. nov.**

Figures 3E, 7S–Z

1968 *Cryphops schlosseri*. – Lütke, p. 161, pl. 8, fig. 2a, b.
p 2000 *Struveops schlosseri*. – Crônier & Feist, pp. 509, 510,
pl. 2, figs 13–17, non 18.

Holotype. – *Cranidium* SMF 97041, Fig. 7Z, Wieda, Harz Mountains, Early *marginifera* Zone.

Type horizon and locality. – Stöberhaifahrweg, north of Wieda, Harz Mountains; section Stöberhaifahrweg, bed 9 (Lütke 1968, fig. 3), Early *marginifera* Zone.

Material. – Paratypes: fragmentary *cranidium* SMF 97042, *cranidium* SMF 97043, cephalic doublure showing vincular furrow, SMF 97044, pygidia SMF 97045–46; additional material: 2 *cranidia* SMF 97047–48, 5 cephalic doublures SMF 97049–53, 1 fragmentary pygidium SMF 97054, all from type locality and horizon; coll. Lütke (SMF 20561b, 20568a–h); coll. Crônier & Feist (SMF 57520–57524) from Wieda; fragmentary *cranidia* SMF 97055–56, Sessacker near Oberscheld, section Lippert SI 13, Early *marginifera* Zone.

Etymology. – After Wieda Township in the Harz Mountains.

Diagnosis. – Contour of *cranidium* parabolic with semi-circular anterior outline of glabella, glabella in front of L1 shorter than wide, outer genal field and lateral border moderately sloping and not inflated, lateral border furrow evenly curved inward where merging with palpebral furrow, lateral lobes of intercalating ring markedly separated from median lobe by continuous longitudinal furrows.

Description. – Glabella in front of L1 wider than long (length/width ratio = 0.84), inconspicuously truncated antero-laterally, evenly curved anteriorly, of moderate longitudinal and transverse vault, flattened behind, without discernible S2 and S3. Intercalating ring tripartite, with un-inflated quadrangular lateral lobes, longer and lower than swollen median lobe (exsag.) and separated from the latter by continuous ex-sagittal furrows, running from

S1 to occipital furrow. S1 is deeper in front of lateral occipital lobes, shallowing medially. Occipital furrow is continuously deep. Occipital ring, as high as median lobe of intercalating ring, extends forward medially to become slightly longer than intercalating ring (sag.); it is markedly reduced in length laterally, provided with tiny, inconspicuously separated lateral lobes. Genae as wide as occipital ring (tr.), moderately vaulted adaxially, flattened and modestly sloping abaxially. Genal field short (exsag.), sub-pentagonal, defined by uniformly deep border furrow that turns inwards anteriorly in a parabolic curve to merge with palpebral furrow, and to meet axial furrow in an acute angle. This junction lies in the posterior third of glabella in front of L1. Lateral border scarcely vaulted (tr.), moderately inclined, very wide at genal angle, narrowing forward, expanded anteriorly to form a triangular, inflated palpebral area. Extremely narrow strip devoid of visual surface remains beyond suture. Functional suture runs sub-marginally along genae before meeting anterior glabella lobe just in front of its maximum width (tr.). Frontal portion of suture separates a vaulted, sigmoidal pre-vascular doublure below remainder of frontal glabella that, in anterior view, is almost as high as the latter. The pre-vascular doublure is backwardly inclined, and sharply bordered by semi-circular anterior edge of vincular furrow. The latter is deep with steep anterior slope and a gently concave posterior area lacking a distinct edge and merging with flat postvincular doublure. Vincular furrows become narrow below genae in the form of marked groves devoid of pits. The dorsal exoskeleton provided with sculpture of dense, minute tuberculation throughout; the anterior half of glabella in front of L1 exhibits coarser tubercles. Pygidium transverse, short trapezoidal, with posterior outline widely curved, slightly truncated medially; axis rather short, a little longer than half length of pygidium (sag.), surrounded by continuous axial furrows, of parabolic posterior outline, high in lateral view, moderately inclined at posterior end, with 3 almost effaced axial rings of which the anterior-most is higher and medially narrower (sag.) than the others; pleural region modestly vaulted, with almost effaced 2–3 ribs, first pleural furrow well marked. Pygidium without sculpture except top of axial rings which display tiny tubercles.

Remarks. – The material from Wieda is very close to the younger *Struveops schlosseri* (do III from Plauen, Thuringia), to which it has hitherto been assigned. The main difference characterizing the new species is the markedly rounded anterior outline of the glabella which is therefore relatively shorter. The triangular palpebral area extends farther backward at the expense of the length of the genal field (exsag.); the maximum length of the palpebral area to the length of the genal field is 0.67 *versus* 0.43 in *schlosseri*. The intercalating ring of *wiedaensis*

has a more prominent median lobe and the separation of the lateral lobes is strongly marked.

Struveops pulvinifer (do III from Sessacker, Oberscheld, Rhenish Slate Mountains.) shares with the new species the rounded anterior outline of the glabella, but the genal fields are much more strongly vaulted and, in anterior view, the genal fields and lateral borders exhibit a marked break in slope whereas they are evenly sloping in *wiedaensis*.

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