Systematic relationships of the blind phacopine trilobite *Trimerocephalus*, with a new species from Causses-et-Veyran, Montagne Noire

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The paper describes a new species of blind trilobite from the lower Fammenian of Concours-le-Haut at Causses-et-Veyran, Montagne Noire (France). *Trimerocephalus (Trifoliops) nigritus* subgen. et sp. nov. is assigned to a new subgenus together with *Tr.* (*Trif.*) *trifolius* (Osmólska, 1958). This grouping is supported by the results of phylogenetic analysis of thirteen species attributed to the Fammenian genus *Trimerocephalus* McCoy, 1849; of 16 previously known species attributed to this genus, only 12 were represented by data of quality sufficient to be included in the analysis, using 23 morphological characters. The Frasnian phacopine *Acuticryphops acuticeps* (Kayser, 1889) is used as the outgroup. The three most parsimonious trees have a length of 51 steps and a consistency index of 0.82. The new subgenus *Trifoliops* forms a clade together with *Trimerocephalus*? *steinachensis* (Richter and Richter, 1926), supported by an exclusive synapomorphy: widening of the cephalic antero-lateral border. *Tr.*? *steinachensis* seems to be more closely related to *Tr.* (*Trif.*) *trifolius* (sharing two synapomorphies) and may represent a more derived taxon (possibly deserving a separate subgeneric status). The remanig *Trimerocephalus* species are not formally assigned to subgeneric taxa, pending further studies (their relationships are shown in cladograms). The results do not confirm the classification suggested by Chlupač (1966) for *Trimerocephalus*.

Key words: Trilobita, Phacopinae, Upper Devonian, Famennian, Montagne Noire, France.

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Introduction

In Upper Devonian strata, blind phacopine trilobites are relatively diverse and abundant throughout the world, particularly in calcareous facies. In particular, the blind genus *Trimerocephalus* McCoy, 1849, which ranges throughout Famennian, includes 16 species, and is widely distributed in the world (except America). The monophyly of the genus would be confirmed by several distinct features, especially both the absence of eyes and the course of the submarginal facial suture cutting the anterior ends of the cheeks. The medially continuous S1 and the wide (tr.), short (sag.), and sharply segmented pygidium, are analogous to those of *Acuticryphops* Crônier and Feist, 2000, which differs mainly in the presence of an eye lobe with a small number of lenses. *Trimerocephalus* is also close to the other blind genus *Dianops* Richter and Richter, 1923. *Dianops* differs in having an interrupted (tr.) S1, a facial suture restricted to the border (not transecting border furrow), and a longer (sag.), strongly convex and indistinctly segmented pygidium.

The discovery of new calcareous material assigned to the genus *Trimerocephalus* from the Famennian of the Montagne Noire (France) gives us the opportunity to investigate the systematic relationships between species and to determine their affinities. It permits us to redefine the species *Trimerocephalus*? *trifolius* and to create the new species *Trimerocephalus* (*Trifoliops*) *nigritus* subgen. et sp. nov. These two species, characterized by a trilobed cephalic outline, are attributed to *Trimerocephalus* (*Trifoliops*) subgen. nov.

The new material from the old quarry of Concours-le-Haut near Causses-et-Veyran in the Montagne Noire (Fig. 1), comprises a few fragmentary pygidia and several hardly damaged cephala of different sizes. The lower Famennian series exhibits thin beds, never exceeding 30 cm in thickness, of reddish calcilutites (cephalopod limestones). A few proetids and blind phacopids occur throughout these beds. The presence of intraclastic masses, which have slid by gravity and evidence of rotation in goniatite bioclasts indicate a sedimentary domain from external platform to slope.

The material described and figured in this work is housed in the collection USTL/CC of the Laboratory of Paleontology of Montpellier (France).

Systematic paleontology

Terminology.—The most useful terminology for describing the different morphological parts of the exoskeleton of

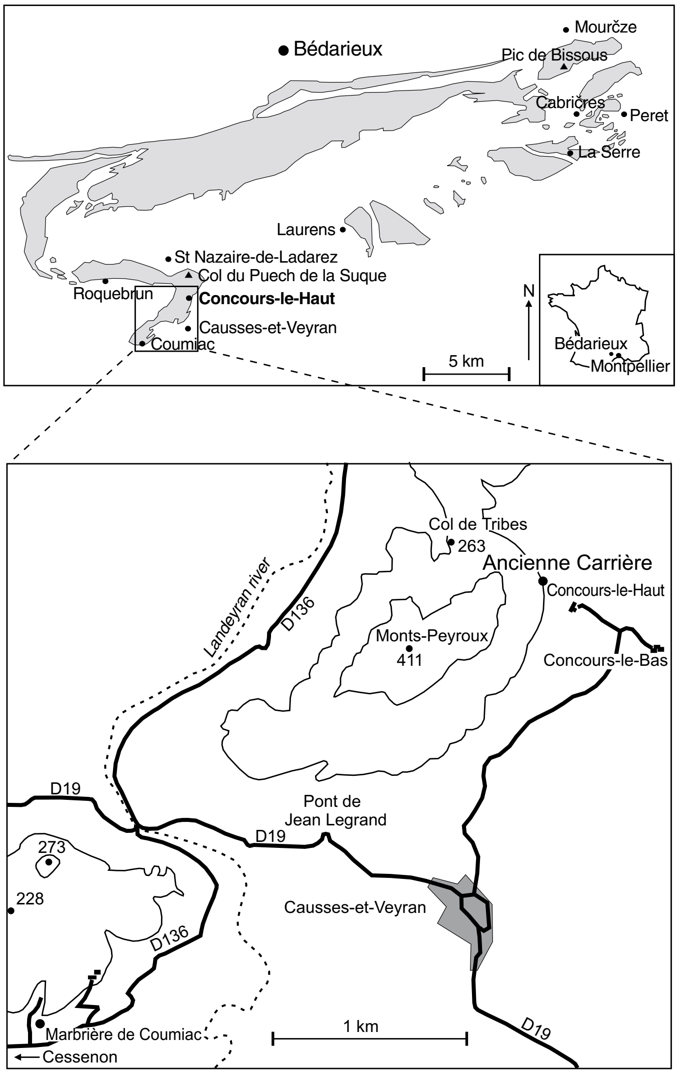

Fig. 1. Location map of the old quarry of Concours-le-Haut at Causses-et-Veyran, in Montagne Noire, southern of the France.

phacopid trilobites depends on the works of Whittington et al. (1997) and Clarkson (1998). Some common abbreviations of directions and symbol are used: sag., sagittal; tr., transversal; L, length; w, width; C, cephalon; G, glabella; R, rachis; P, pygidium.

Family Phacopidae Hawle and Corda, 1847
Subfamily Phacopinae Hawle and Corda, 1847
Genus *Trimerocephalus* McCoy, 1849

Type species: *Phacops mastophthalmus* Richter, 1856 (= *Trinucleus*? *laevis* Münster, 1842); Upper Devonian (Famennian); Thuringia.

Species.—*Trimerocephalus mastophthalmus* (Richter, 1856): Lower Famennian (do II, III?), Rhineland, Harz Mts., Thuringia, Holy Cross Mts., England, South-Western Asia, Kazakhstan; *Trimerocephalus caecus* (Gürich, 1896): Lower Famennian (do II–III), Holy Cross Mts., Harz Mts., Rhineland, Thuringia, Urals Mts., North Africa, Armorican Massif; *Trimerocephalus*? *steinachensis* (Richter and Richter, 1926): Famennian (do II), Thuringia, Harz Mts.; *Trimerocephalus cryptophthalmoides* (Maksimova, 1955): Lower Famennian, South Urals Mts., Kazakhstan; *Trimerocephalus vodorezovi* (Maksimova, 1955): Famennian (do II), Kazakhstan; *Trimerocephalus sponsor* Chlupač, 1966: Famennian (do III), Moravia, Cantabrian Mts.; *Trimerocephalus lentiginosus* (Maksimova, 1955): Famennian (do V), South Urals Mts.; *Trimerocephalus polonicus* Osmólska, 1958: Famennian (do III), Holy Cross Mts.; *Trimerocephalus*? *trifolius* (Osmólska, 1958): Famennian (do II, III?), Holy Cross Mts.; *Trimerocephalus lacunosus* (Pfeiffer, 1959): Famennian (do II), Thuringia; *Trimerocephalus dianopsoides* Osmólska, 1963: Famennian (do II?, do III), Holy Cross Mts.; *Trimerocephalus procurvus* Arbizu, 1985: Famennian (do III), Cantabrian Mts., Germany; *Trimerocephalus interruptus* Berkowski, 1991: Famennian (do III), Holy Cross Mts.; *Trimerocephalus lelievrei* Crônier and Feist, 1997: Famennian (do III), Tafilalt (Morocco); *Trimerocephalus tardispinosus* Feist and Becker, 1997: Famennian (do II, *Palmatolepis rhomboidea* Zone), Australia; *Trimerocephalus shotoriensis* Feist, Yasdi, and Becker, in press: Famennian (lower *P. marginifera* to upper *P. trachytera* Zone), Eastern Iran (Shotori-Range).

Trimerocephalus? *steinachensis* displays a massive border, which is not covered by the glabella in dorsal view. This is analogous to *Cryphops*? *latilimbatus* (Maksimova, 1955) which has well developed eyes.

The discovery of new material with a trilobed cephalic outline allows redefinition of *Trimerocephalus*? *trifolius* and creation of a new species: both are attributed to *Trimerocephalus* (*Trifoliops*) subgen. nov.

Stratigraphic and geographic distribution.—The range of all species falls within the late Upper Devonian: Famennian do II–IV (acme in Lower Famennian); Europe, South-Western Asia, Kazakhstan, North-East China, North Africa and Australia.

The diversity of Upper Devonian blind phacopids coincides with the expansion of off-shore environments of external platforms (Chlupač 1975).

These different species are widely represented in Europe: *P. rhomboidea* Zone in the Montagne Noire, Upper *P. crepida* Zone in the Harz Mts.

Besides *Trimerocephalus lelievrei*, only one individual belonging to the species *Trimerocephalus caecus* has been cited, but not figured, from North Africa (Alberti 1970). This species is still of problematical status.

Few studies have been undertaken in South-Western Asia and Kazakhstan. *Trimerocephalus lentiginosus* has been discovered from the Urals Mts., in the upper Famennian (V); but this age has not been confirmed by conodont data.

Subgenus *Trimerocephalus* (*Trifoliops*) subgen. nov.

Fig. 2A–D.

Type species: *Trimerocephalus* (*Trifoliops*) *trifolius* (Osmólska, 1958); Upper Devonian (Famennian); Holy Cross Mts., Poland.

Derivation of the name: After the clover-shaped cephalic outline; subgenus being distinguished from other species representative of genus

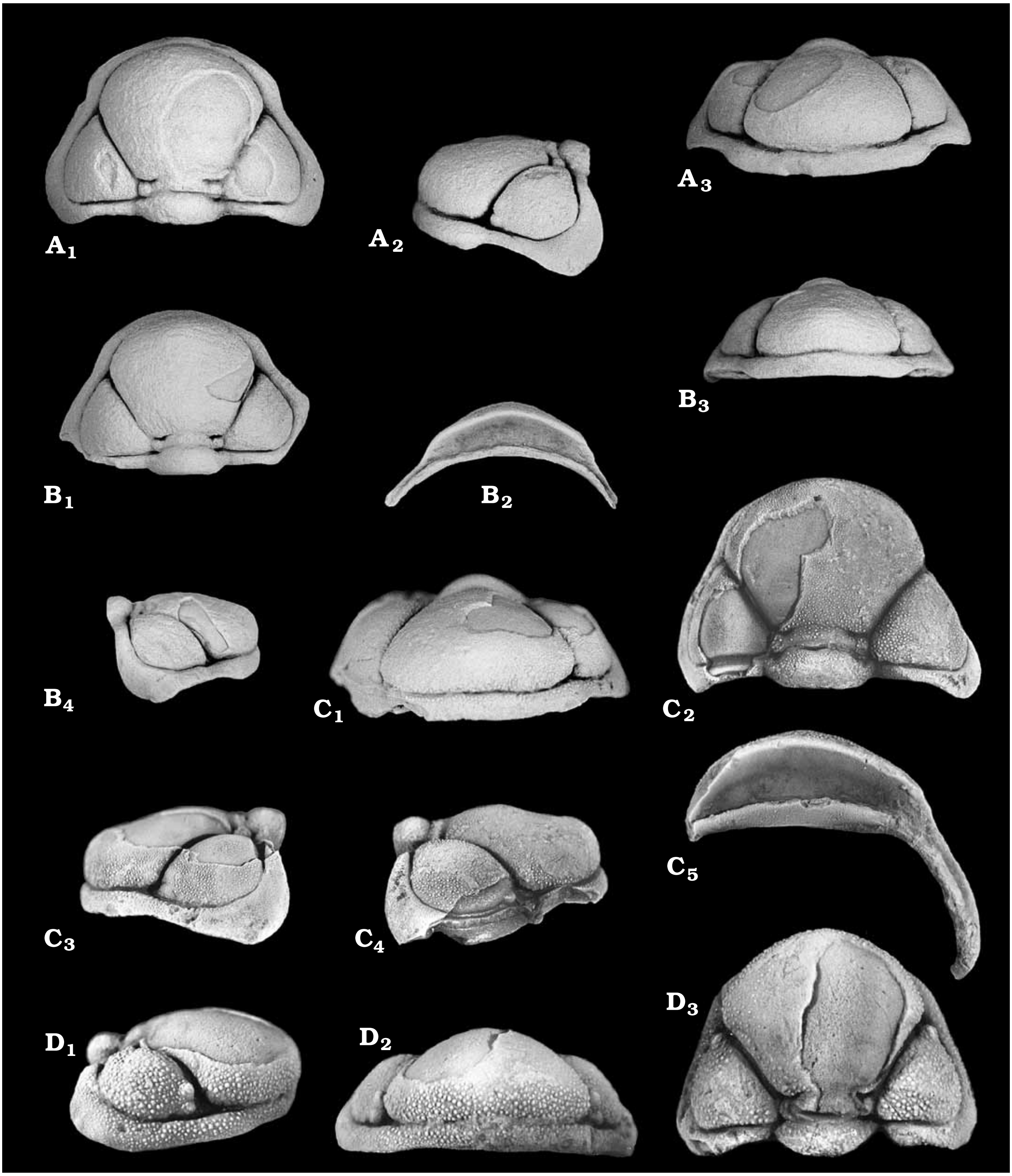

Fig. 2. *Trimerocephalus* (*Trifoliops*) *trifolius* (Osmólska, 1958) subgen. nov. Concours-le-Haut, Causses-et-Veyran, Montagne Noire, Famennian, Upper Devonian. Samples housed in the collection USTL/CC of the Laboratory of Paleontology of Montpellier (France). Photographs of calcareous shells. **A**. Cephalon, USTL/CC014, in dorsal (A_1), lateral (A_2), and frontal (A_3) views; × 3. **B**. Cephalon, USTL/CC015, in dorsal (B_1), ventral (B_2), frontal (B_3), and lateral (B_4) views; × 3. **C**. Cephalon, USTL/CC016, in frontal (C_1), dorsal (C_2), left lateral (C_3), right lateral (C_4), and ventral (C_5) views; × 5. **D**. Cephalon, USTL/CC017, in lateral (D_1), frontal (D_2), and dorsal (D_3) views, × 10.

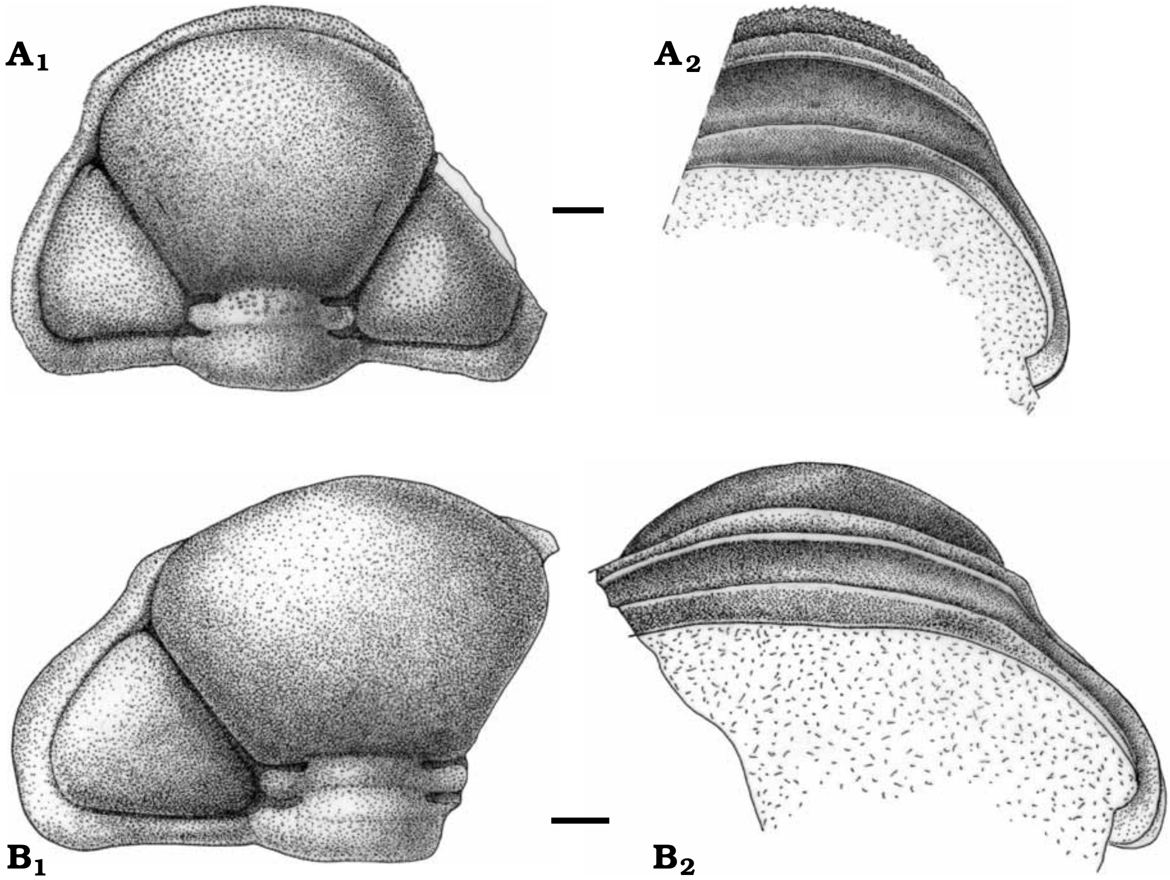

Fig. 3. **A**. *Trimerocephalus* (*Trifoliops*) *trifolius* (Osmólska, 1958) subgen. nov. Montagne Noire, France, Famennian, Upper Devonian. Reconstruction of the cephalon, in dorsal (A_1) and in ventral (A_2) views. **B**. *Trimerocephalus* (*Trifoliops*) *nigritus* subgen. et sp. nov. Montagne Noire, France, Famennian, Upper Devonian. Reconstruction of the cephalon, in dorsal (B_1) and in ventral (B_2) views. Scale bars 1 mm.

Trimerocephalus by a clover-shaped cephalic outline: the frontal border widens distally close to antero-lateral angles.

Diagnosis.—Subgenus of *Trimerocephalus* McCoy exhibiting the following characteristics: clover-shaped cephalic outline; subpentagonal glabella with parabolic frontal outline; S1 continuous; facial suture cutting the cheeks. Vincular furrow very broad (tr.) and deep with an angular curve; posterior band of the cephalic doublure narrow (sag.). Dense and fine granulation. Pygidium with a posterior margin strongly widened transversally.

Species included.—*Trimerocephalus* (*Trifoliops*) *trifolius* (Osmólska, 1958) subgen. nov. and *Trimerocephalus* (*Trifoliops*) *nigritus* subgen. et sp. nov.

Trimerocephalus (*Trifoliops*) *trifolius* (Osmólska, 1958) subgen. nov.

Figs. 2A–D, 3A, 4A, B.

?*Dianops trifolius* Osmólska; Osmólska 1958: 136–138, pl. 4: 2, 3, text-fig. 6.

Trimerocephalus trifolius (Osmólska); Osmólska 1963: 507–509, pl. 4: 1–3, 6.

Trimerocephalus? *trifolius* (Osmólska); Chlupač 1977: 123.

Emended diagnosis.—Species belonging to *Trimerocephalus* (*Trifoliops*) subgen. nov., showing the following characteristics: cephalon with a narrow, trilobed outline; frontal lobe plumbs above the frontal border; S2 and S3 present; presence of ocular protuberances; marked elongation (sag.) of the vincular furrow.

New material.—The calcareous material is composed of six cephala, from the Concours-le-Haut old quarry at Causses-et-Veyran, in the Montagne Noire, France (Fig. 1).

Remarks.—The trilobed cephalon, corresponding to the distal widening of the frontal border at the level of the genal angles, with a sagittal and transverse elongation of the vincular furrow, is similar to the configuration of *Trimerocephalus*? *trifolius* (Osmólska 1958, 1963). In addition to previous descriptions, it may be noted that deep slightly outwardly concave dorsal furrows diverge about 60º and widen just before and close to the antero-lateral angle making indentations; the frontal lobe does not overhang the wide frontal border; the glabellar furrows S3 and S2, well marked on internal moulds, are visible on the surface of exoskeletons; ocular protuberances (relics of ancestral ocular lobe) are present at the level of the anterior genal angle; the submarginal facial suture, detectable from the mid-length of the lateral border, traverses the border obliquely and comes back up on the cheeks, forming a

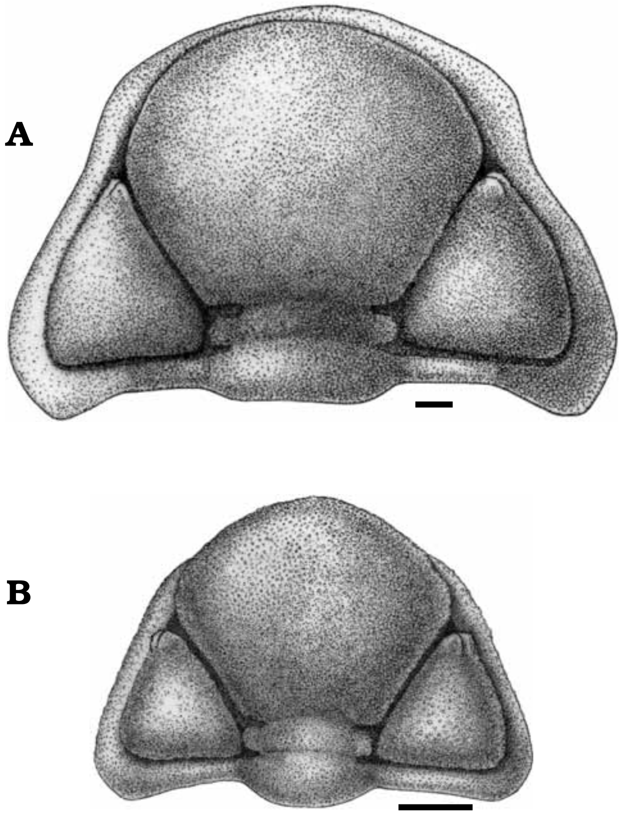

Fig. 4. *Trimerocephalus* (*Trifoliops*) *trifolius* (Osmólska, 1958) subgen. nov. Montagne Noire, France, Famennian, Upper Devonian. **A**. Reconstruction of a mature cephalon, in dorsal view. **B**. Reconstruction of a young cephalon, in dorsal view. Scale bars 1 mm.

crescent only slightly narrower than the lateral border, and continuing into the dorsal furrow, elongated at this level, and cutting through the ocular protuberance; the lateral border at the anterior angle is inclined strongly backward; the vincular furrow is very broad (tr.), deep, constant, simple, delimited by sharp ridges and abnormally widened (sag.); the curve of the vincular furrow rearwards is about 115º, the posterior band of the doublure is narrow (sag.) and flat; the ratio between the maximum width of the vincular furrow/ posterior band is about 0.32. The ventral view (ZPAL Tr. D. I/39) figured by Osmólska in 1963, has nearly the same ratio (0.33).

Osmólska (1958) mentioned that S2 and S3 are indistinct, S1 is discontinuous and the antero-lateral angles are gently truncated. But remarks added by Osmólska in 1963 from new material demonstrate opposite features. According to her (H. Osmólska personal communication 2002), (1) the left glabellar angle on the holotype (Osmólska 1958: pl. 4: 2) is less "slightly truncated" than the right one on the paratype (Osmólska 1958: pl. 4: 3); thus it seems, that this character may be either preservation-dependent, or just due to an intraspecific variability; (2) glabellar furrow S1 is rather continuous, although the mesial sections are shallower than the distal ones. This difference is clearly due to preservation; (3) glabellar furrows S2 and S3 are not clearly perceptible; the surface of the glabellar exoskeleton is poorly preserved. Thus, it may be another taxonomically worthless character.

This species differs from other species of the genus *Trimerocephalus* in possessing the trilobed cephalic outline: the frontal border widens distally near the antero-lateral angles; the configuration of the vincular furrow shows sagittal and transverse elongation. The specimens here described probably belong to a separate genus.

Developmental instars.—The material includes a few ontogenetic instars, from the early holaspid period. This has allowed at least partial description of the morphogenesis of *Trimerocephalus* (*Trifoliops*) *trifolius* subgen. nov. In order to establish the size distribution in *Trimerocephalus* (*Trifoliops*) *trifolius* subgen. nov., the widths as a function of length of 6 cephala in dorsal view, have been measured with a Nikon mesuroscope (0.001 mm), and have been plotted on a bivariate diagram (Fig. 5). Relative proportions of cephalon and glabella remain constant ($y = ax + b$; cephalon: $r = 0.996$, $p < 0.001$***; glabella: $r = 0.995$, $p < 0.001$***) whatever the degree of development of individuals. Nevertheless, it is not possible to distinguish many instars; the sample is too poor for this.

The complete individual (ZPAL Tr. D. I/16) described by Osmólska (1963) agrees well with these specimens from the Montagne Noire (Fig. 5).

Early post-larval instars.—The cephalon, 0.43 cm long is narrower with a ratios L/w about 0.77 than in older stages. The L/w ratios of the hardly inflated glabella is about 0.90. The frontal outline is more closely parabolic and more pointed anteriorly than in older stages. The frontal lobe hides the anterior border that is slightly bent backwards by contrast with older stages where the anterior border is no longer bent backwards. Slightly outward concave dorsal furrows diverge about 60º. The glabella widens anteriorly from S1. The base of the glabella corresponds to 45% of the total width (tr.). The ratios wG/wC is about 0.68. The glabellar furrows S2 and S3 are faint. The narrow cheeks show more marked ocular protuberances. The facial suture is no longer functional: the librigenae are linked to the cephalic doublure. At the level of the dorsal furrows and the anterior genal angles, there is a widening in front of ocular protuberance.

Trimerocephalus (*Trifoliops*) *nigritus* subgen. et sp. nov.

Figs. 3B, 6A–H.

Holotype: Cephalon USTL-CC018, Fig. 6A.

Type locality: Old quarry of Concours-le-Haut near Causses-et-Veyran. Montagne Noire, France (Fig. 1).

Type horizon: Red cephalopod limestones, lower member of "griottes" limestones formation, Lower *rhomboidea* Subzone, lower Famennian.

Derivation of the name: After Latin equivalent of "Noire" (black): niger. The name refers to the Montagne Noire where specimens have been sampled.

Material.—The calcareous material is composed of 10 cephala and 3 fragmentary pygidia, from the Concours-le-

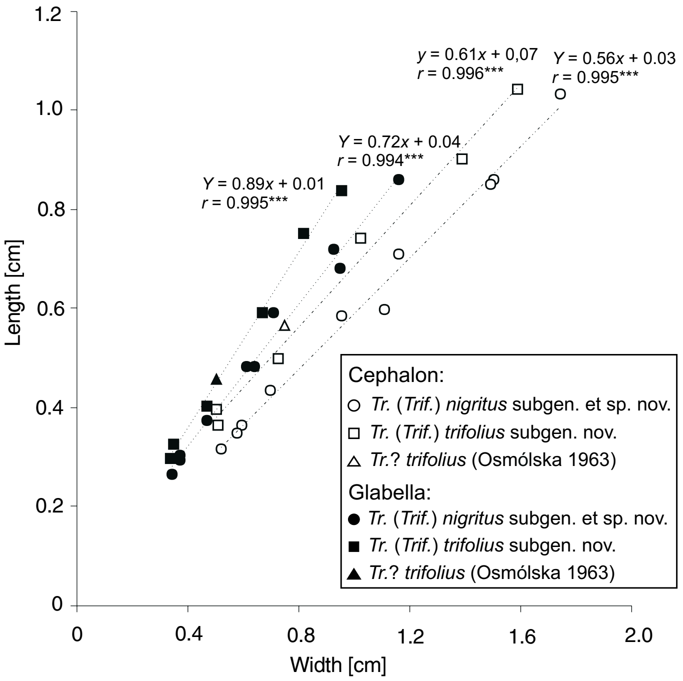

Fig. 5. Scatter diagram of length (cm) *versus* width (cm) of cephalon and glabella in specimens of *Trimerocephalus* (*Trifoliops*) *trifolius* (Osmólska, 1958) subgen. nov, *Trimerocephalus* (*Trifoliops*) *nigritus* subgen. et sp. nov. and *Trimerocephalus*? *trifolius*, the specimen ilustrated (ZPAL Tr. D. I/16) by Osmólska in 1963.

Haut near Causses-et-Veyran old quarry, in the Montagne Noire, France (Fig. 1).

Diagnosis.—Species belonging to *Trimerocephalus* (*Trifoliops*) subgen. nov., showing the following characteristics: cephalic outline wide and trilobed; glabella with a broadly parabolic frontal outline; frontal lobe overhanging the frontal border; S2 and S3 absent. Slight thickening along the whole length (tr.) of the posterior pygidial margin.

Description.—Cephalon with a wide and trilobed outline. Ratios L/w about 0.55.

In dorsal view, the ratio L/w of the poorly inflated glabella is about 0.73. The frontal outline is broadly parabolic. Deep, slightly outwardly concave dorsal furrows diverge at about 55º and widen slightly just before the anterolateral angle. The frontal lobe overhangs the uninflated frontal border. Glabellar furrows S3 and S2 are very faint and often indistinct. The median portion of the preoccipital furrow is shallow. The preoccipital ring is not inflated. The lateral preoccipital lobes are slightly differentiated, whereas the occipital furrow is more clearly differentiated. The strongly inflated occipital ring is almost twice as broad (sag.) as the preoccipital ring. Lateral occipital lobes are not differentiated. No ocular protuberance and no visual area are developed at the level of the anterior genal angle. The submarginal facial suture cuts the cheeks forming a crescent narrower than the lateral border, and continuing along the dorsal furrow. The cheeks are uniformly and poorly inflated. The frontal furrow is well defined but clearly shallower than the lateral and posterior furrows. The lateral and posterior furrows are not interrupted at the level of the genal angle, only reduced in depth. The lateral border at the anterior angle is inclined strongly backward. Lateral and posterior borders widen at their junction and are inclined slightly backward. The genal angle is rounded.

In lateral view, the frontal outline of the glabella is moderately arched and posteriorly is slightly convex dorsally. The outline of the preoccipital ring is straight. The strongly convex occipital ring is as high as the glabella at its maximum of convexity. The uninflated frontal border is oriented inward.

In frontal view, the glabella outline is semicircular.

In ventral view, transversally, the vincular furrow is very broad (tr.), fairly deep, constant, simple, delimited by sharp ridges and slightly widened (sag.) in comparison with the genus *Trimerocephalus* sensu stricto. The curve of the vincular furrow backwards is about 135º. The posterior band of the doublure is narrow (sag.) and flat. The ratio between the maximum width of the vincular furrow/posterior band is about 0.47.

Pygidium with a transverse and lenticular shape.

In dorsal view, the anterior margin is straight (tr.). Dorsal furrows are wide and more or less deep. The rachis, arched in relief, shows a convexity decreasing progressively backwards. The rachis is short (sag.) and wide (tr.). Its posterior extremity is rounded. It has 4 well differentiated rings, well delimited by wide axial furrows. The terminal piece is delimited by less marked furrows. Pleural and interpleural furrows sharply distinct anteriorly, becoming a little less distinct at the posterior portion of the pygidium. They delimit distinct, moderately inflated half-ribs. These furrows do not reach the posterior border, delimiting a laterally widening limbus. The limbus is twice as broad (sag.) as the terminal piece of the rachis. The posterior margin, lacking a pleural spine, shows a very slight forward inflection in its median portion and a thickening along all its length (tr.). Angles of lateral and posterior border are about 70º.

In frontal view, the posterior margin is strongly widened transversally and moderately elongated sagittally, and its ends are inclined posteriorly.

Sculpture—Both cephalon and pygidium show a fine and dense granulation, except on the doublure of the vincular furrow that is smooth.

Remarks.—The dorsal view of this form may be compared to that of *Trimerocephalus*? *trifolius* (Osmólska 1958, 1963). Nevertheless, the frontal lobe overhangs the inwardly oriented frontal border, the configuration of the vincular furrow showing only a moderate elongation (sag.) and differing from those of the genus *Trimerocephalus* sensu stricto.

Developmental instars.—The material collected includes a few ontogenetic instars, from the early holaspid period. This has allowed to a partial description of the morphogenesis of *Trimerocephalus* (*Trifoliops*) *nigritus* subgen. et sp. nov. In

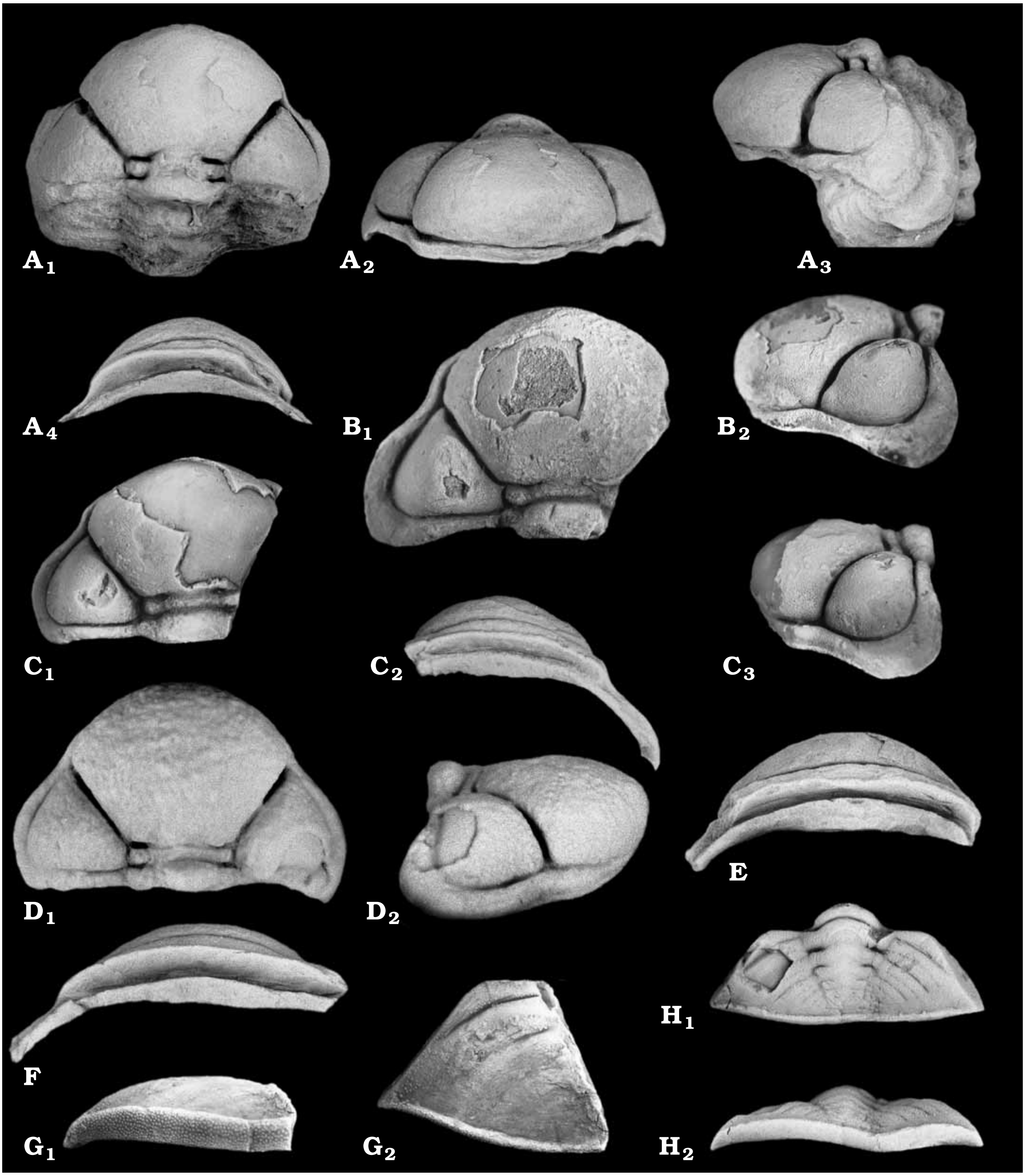

Fig. 6. *Trimerocephalus* (*Trifoliops*) *nigritus* subgen. et sp. nov. Concours-le-Haut, Causses-et-Veyran, Montagne Noire, Famennian, Upper Devonian. Samples housed in the collection USTL/CC of the Laboratory of Paleontology of Montpellier (France). Photographs of calcareous shells. **A**. Cephalon, USTL/CC018, in dorsal (A_1), frontal (A_2), lateral (A_3), and ventral (A_4) views; × 3. **B**. Cephalon, USTL/CC019, in dorsal (B_1) and lateral (B_2) views; × 5. **C**. Cephalon, USTL/CC020, in dorsal (C_1), ventral (C_2), and lateral (C_3) views; × 5. **D**. Cephalon, USTL/CC021, in dorsal (D_1) and lateral (D_2) views; × 10. **E**. Cephalon, USTL/CC022, in ventral view, × 5. **F**. Cephalon, USTL/CC023, in ventral view, × 5. **G**. Pygidium, USTL/CC024, in frontal (G_1) and dorsal (G_2) views; × 7. **H**. Pygidium, USTL/CC025, in dorsal (H_1) and frontal (H_2) views; × 5.

order to establish the size distribution in *Trimerocephalus* (*Trifoliops*) *nigritus* subgen. et sp. nov., the width as a function of length of 10 cephala in dorsal view, has been measured with a Nikon mesuroscope (0.001 mm), and plotted on a bivariate diagram (Fig. 5). Whatever the degree of development, relative proportions of cephalon and glabella remain constant ($y = ax + b$; cephalon: $r = 0.995$, $p < 0.001$***; glabella: $r = 0.995$, $p < 0.001$***). Nevertheless, it is not possible to distinguish many instars; the sample is insuficuent for this.

Early post-larval instars.—The cephalon, 0.38 cm long, is moderately broad with a L/w ratios about 0.58. The L/w ratios of the moderately inflated glabella is about 0.76. The frontal outline is more closely parabolic and more pointed anteriorly. Slightly outwardly concave dorsal furrows diverge at about 55–60°. The glabella widens anteriorly from S1. The base of the glabella corresponds to 46% of the total width (tr.). The ratios wG/wC is about 0.64. Glabellar furrows S2 and S3 are indistinct. The narrow cheeks show no ocular protuberances. The facial suture is no longer functional: the librigenae are linked to the cephalic doublure.

Conclusion and discussion.—The dimensions and the principal morphologic traits that differ between these two species *Trimerocephalus* (*Trifoliops*) *trifolius* subgen. nov. and *Trimerocephalus* (*Trifoliops*) *nigritus* subgen. et sp. nov. are given in Appendix 1.

Morphological changes which obviously took place between the early and late post-larval instars include: (1) cephalon relatively wider in older stages due to convexity change and lateral extension of the glabella; (2) decrease of the length/width ratios of the cephalon and the glabella, whereas the base/width ratios of the glabella increase; (3) decrease of the ocular protuberances (testimony to a relic of an ancestral ocular lobe) in a mature stage of *Trimerocephalus* (*Trifoliops*) *trifolius* subgen. nov.; (4) orientation of the anterior border slightly bent backwards in larval becomes and no longer bent backward in older stages.

These ontogenetic shape changes, notably including the widening (tr.) of the glabella, have also been observed in *Phacops spedeni* Chatterton, 1971 and *Trimerocephalus lelievrei* Crônier and Feist, 1997, thus emphasizing the close phylogenetic relationship between these taxa. However, whereas in the ancestral *Phacops* the visual complex enlarges and migrates posteriorly, a real eye is never developed in the descendant *Trimerocephalus*. An ocular protuberance, without any visual area, develops and decreases during the ontogenetic development of *Trimerocephalus* (*Trifoliops*) *trifolius* subgen. nov. This delay in development results from the effects of paedomorphosis (Feist 1995; Crônier and Feist 1997).

Within the assemblage from the Upper Devonian of Montagne Noire, two distinct morphotypes have been identified in the same bed, depending on two important cephalic characters: absence/presence of ocular protuberances and a vincular furrow moderately or strongly elongated sagittally. These two morphotypes seem to have no intermediary forms and show a morphological differentiation comparable to all development instars. The main shape difference manifested in the youngest specimen and maintained during ontogenetic development is a structural difference.

The occurrence of *Trimerocephalus* (*Trifoliops*) *trifolius* subgen. nov. in Holy Cross Mts. (Osmólska 1958, 1963) and Montagne Noire (France), underlines the close geographic relationship.

Phylogenetic analysis

Few cladistic analyses have concerned phacopid trilobites from Silurian and Devonian strata: Campbell (1975), Ramsköld (1988), Ramsköld and Werdelin (1991). The cladistic study of Ramsköld and Werdelin (1991) showed evidence of several evolutionary trends that allow palaeobiogeographic discrimination in early phacopid trilobites. Nevertheless, any cladistic analysis has been restricted to a single genus.

Within the genus *Trimerocephalus*, Chlupač (1966) distinguished 2 major groups of closely related species: a group of *Trimerocephalus caecus* characterised by an anteriorly rounded glabellar outline and a group of *Trimerocephalus sponsor* characterised by an anteriorly pointed glabellar outline; a third independent group is represented by *Trimerocephalus*? *steinachensis* and *Trimerocephalus*? *trifolius*.

The proposed classification for *Trimerocephalus* is here tested by investigating the systematic relationships between taxa belonging to the genus *Trimerocephalus*. Phylogenetic analysis using parsimony should allow the analysis of the evolution of morphological characters whether participating or not towards the phylogenetic reconstruction.

Additionally, the revised species and the new one from the Upper Devonian of Montagne Noire (South-East France), attributed to *Trimerocephalus* (*Trifoliops*) subgen. nov., have been included in this analysis in order to determine their affinities.

Material and methods

A cladistic approach using the morphologic data has been chosen. Such morphological data are based on the one hand on the literature and illustrations of different authors and on the other hand on personal observations. Thus, of the 17 species constituting the genus *Trimerocephalus*, 13 have been analysed. For the 4 species not included the literature was inappropriate or insufficient. The selected species for the reconstruction of the data matrix are reported in Appendix 2. The species *Trimerocephalus*? *steinachensis* (Richter and Richter, 1926), although its affiliation to the genus *Trimerocephalus* is still uncertain, and the 2 species constituting the *Trimerocephalus* (*Trifoliops*) subgen. nov. have also been included.

We regard the genus *Trimerocephalus* as a monophyletic group. The Frasnian *Acuticryphops acuticeps* species is the oldest phacopine taxon to share a narrow posterior band of the cephalic doublure with an angular outline with the spe-

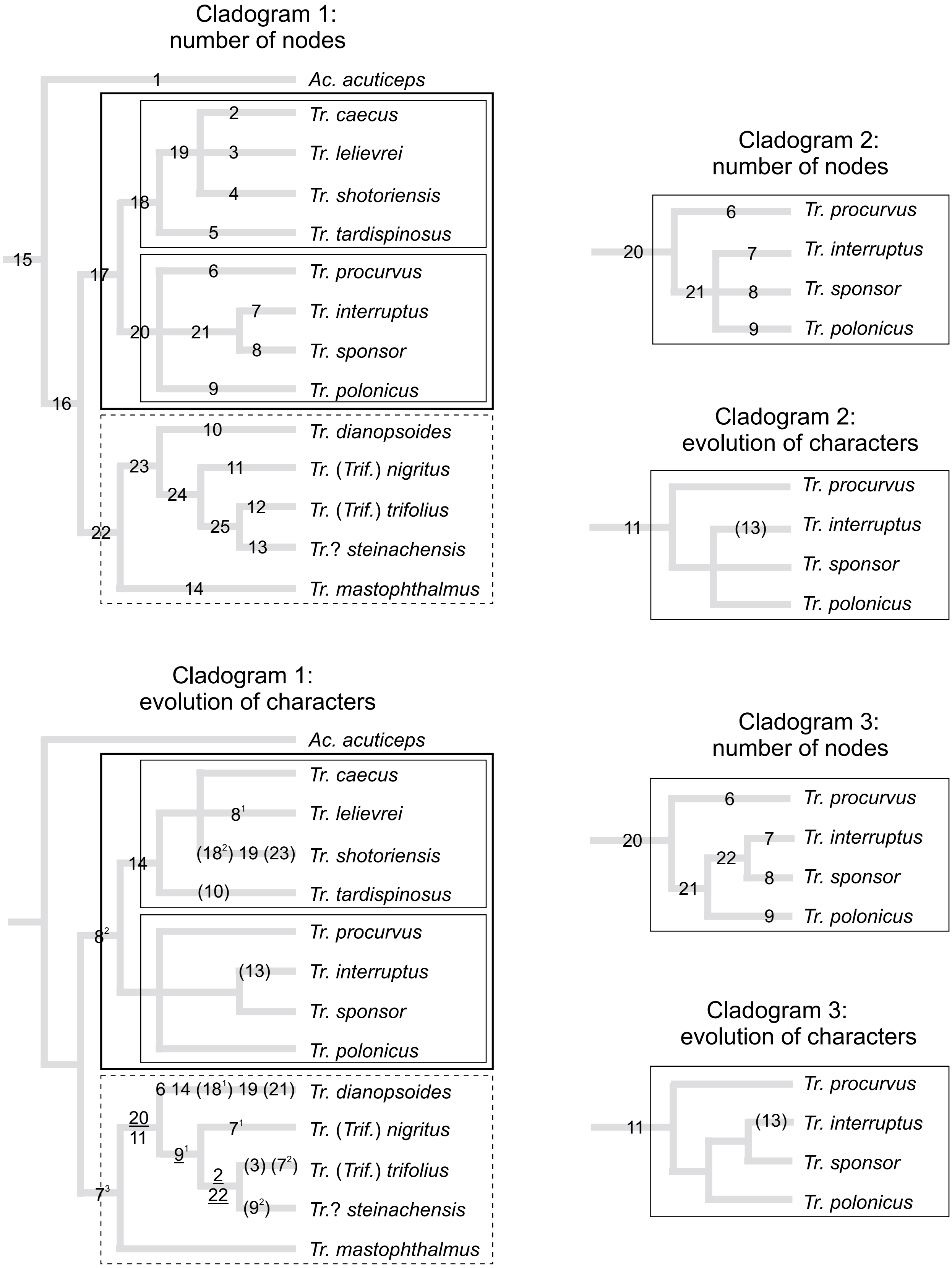

Fig. 7. Cladograms representing relationships among the species of the genus *Trimerocephalus*: 3 trees of length 50 steps; I.C. = 0.82; I.R. = 0.73. 1^2: state 2 of character 1; 1: homoplasic apomorphic character; <u>1</u>: exclusive apomorphic character; (1): autapomorphic character; the tree is rooted with an outgroup (here *Acuticryphops acuticeps*). The evolution of characters is also detailed in Appendix 5. Taxonomic abbreviations are used: *Ac.*, *Acuticryphops*; *Tr.*, *Trimerocephalus*; *Trif.*, *Trifoliops*.

cies of the genus *Trimerocephalus* (Crônier 1999; Crônier and Feist 2000). In this phylogenetic analysis, this phacopine is used as outgroup to the *Trimerocephalus*, and allows rooting ancestral states by an extra-group comparison.

Phylogenetic studies require the establishment of relationships between taxa based on phylogenetic reconstruction. This method is based on the concept of "descent with modification" (Darlu and Tassy 1993), after identification of the primitive state (plesiomorphic) and derived state (apomorphic) of homologous characters. The relationships between taxa are identified on the basis of derived states shared by each taxon. Thus, 23 characters, sufficiently variable morphologically, have been selected. Characters, coding polarity of states *a priori* for each characters, are detailed in Appendix 3.

The selection of characters is an important step in a cladistic study. All characters selected are situated on the outer face of the exoskeleton, except for the character 3 in ventral view. Of the 23 characters selected, 18 are from the cephalon and 5 are from the pygidium. Both concentration of suitable cephalic characters, and availability of material and illustrations bring a strong bias towards this morphologically complex part. The hypostome and the thorax are known in only few species and thus have been excluded from this study. Due to the nature of characters, it is inevitable that the coding is not strict enough to permit inclusion of true homologies. A maximum of characters was selected for their supposed ability to retrace an evolutionary history. However, several characters have states defined according to entirely subjective definitions, but all species have been compared with a reference set of standard states for each character. Therefore, the states of characters are objective as far as possible. The coding of taxa with multiple states interpreted as polymorphism has also been considered.

The data matrix (Appendix 4) used for the cladistic analysis was performed using the software PAUP ver. 3.1.1. (Swofford 1993).

The parsimony analysis performed on this data matrix produces trees (the nodes of the cladograms are defined by all apomorphies shared by all taxa). The maximum parsimony Branch and Bound searches were selected. All characters were assumed to be of equal weight, and multistate characters were treated as unordered *a priori*, to minimize assumptions of evolutionary process in the cladistic analysis (Lee 1999). The trees were rooted using an outgroup that seems to be *Acuticryphops acuticeps*, which is the oldest species to share the same cephalic doublure with the species of the genus *Trimerocephalus* (for more details see Crônier and Feist 2000).

The cladograms produced have been analysed with MacClade ver. 3.04. (Maddison and Maddison 1992) in order to analyse *a posteriori* the estimates of polarity and evolution of the characters.

Results

Topology.—The analysis of the data matrix (Appendix 4) produced 3 most parsimonious trees of 51 steps (consistency

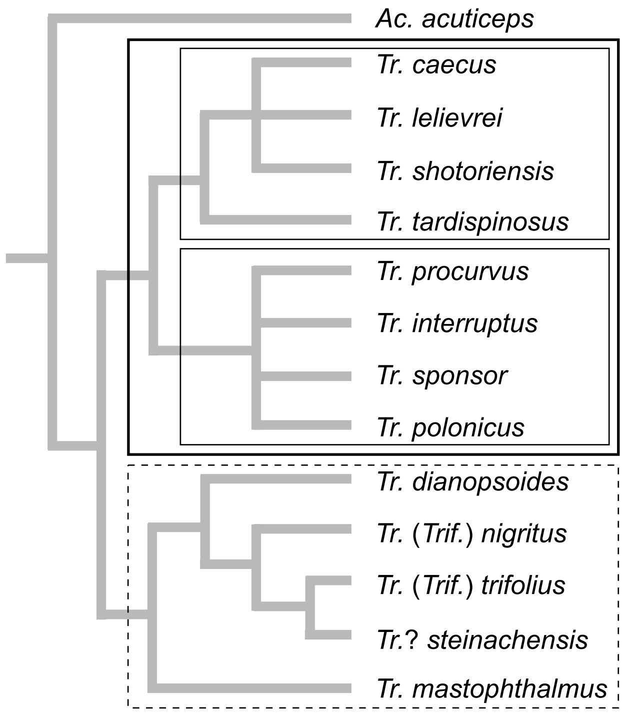

Fig. 8. Strict consensus tree of 3 most parsimonious cladograms. Taxonomic abbreviations are used: *Ac.*, *Acuticryphops*; *Tr.*, *Trimerocephalus*; *Trif.*, *Trifoliops*.

index, 0.82; retention index, 0.72), shown in Fig. 7. Consistency Index appraises the robustness of the tree by the number of synapomorphies (a tree with a C.I. = 1 comprises no homoplasy). Retention Index represents the ratios number of observable homoplasies/number of observed homoplasies (a tree with a R.I. = 1 comprises no homoplasy) (Darlu and Tassy 1993).

Three most parsimonious trees are congruent except in the relationships within the clade "*sponsor*". The conflict between these 3 most parsimonious trees is represented in the strict consensus tree by the polytomy (Fig. 8). According to this strict consensus tree, the genus *Trimerocephalus* is constituted of 2 major groups: a group comprising *Trimerocephalus mastophthalmus* (Fig. 8, dotted outline), and another comprising *Trimerocephalus caecus* on the one hand and *Trimerocephalus sponsor* on the other (Fig. 8, continuous outline).

Evolution of characters.—The states and status of characters at the nodes were analysed under MacClade, for each most parsimonious tree (Appendix 5). The polarity and status *a posteriori* for each character are also detailed in Appendix 5. The synapomorphies at each node are indicated (shared derived states). Out of 23 characters without *a priori* ancestral state, 5 remain *a posteriori* unoriented. Out of 10 informative and oriented characters, 6 are homoplasic, implying a relatively important rate of convergence. Character 3 is autapomorphic in *Trimerocephalus* (*Trifoliops*) *trifolius* subgen. nov., character 10 in *Trimerocephalus tardispinosus*, character 13 in *Trimerocephalus interruptus*, character 21 in *Trimerocephalus dianopsoides*, character 23 in *Trimerocephalus shotoriensis*. State 2 of character 7 is autapomorphic in *Trimerocephalus* (*Trifoliops*) *trifolius* subgen. nov., state 2 of character 9 in *Trimerocephalus*? *steinachensis*, state 1 of character 18 in *Trimerocephalus dianopsoides* and state 2 of character 18 in *Trimerocephalus shotoriensis*.

Within the genus *Trimerocephalus*, some nodes of cladograms are robust. The clade "*dianopsoides/nigritus/trifolius/steinachensis*" is supported by one exclusive synapomorphy (character 20) which is the presence of shallow interpleural furrows, and by one homoplasic apomorphy (character 11) which is the absence of glabellar furrows S2 and S3 (apomorphic character occurring independently in the group "*sponsor*" in cladograms 2 and 3, Fig. 7). The clade comprising *Trimerocephalus*? *steinachensis* and *Trimerocephalus* (*Trifoliops*) *trifolius* subgen. nov. *and Trimerocephalus* (*Trifoliops*) *nigritus* subgen. et sp. nov. is supported by 1 exclusive synapomorphy (characters 9^1) which is a widening of the antero-lateral border. The clade comprising *Trimerocephalus*? *steinachensis* and *Trimerocephalus* (*Trifoliops*) *trifolius* subgen. nov. is supported by 2 exclusive synapomorphies (characters 2 and 22) which are the swelling of the frontal border and the disposition of the frontal lobe in comparison with the anterior border.

The group comprising *Trimerocephalus mastophthalmus* (Fig. 7; dotted outline) is supported by one homoplasy (state 3 of character 7) which is the rounded and broad glabellar outline. The group comprising *Trimerocephalus caecus* on the one hand and *Trimerocephalus sponsor* on the other hand (Fig. 7; continuous outline) is likewise supported by one homoplasy (state 2 of character 8) which is the narrow cephalon.

The group "*caecus*" is supported by one homoplasy (character 14) which is the presence of a median nodule (apomorphic character occurring independently in *Trimerocephalus dianopsoides*).

Conclusion and discussion

The classification suggested by Chlupač in 1966 is not confirmed here. Within the genus *Trimerocephalus*, Chlupač distinguished 3 groups of species on morphological characters: (1) "*mastophthalmus/caecus/dianopsoides*" characterised by an anteriorly rounded glabellar outline and an often transverse cephalon, (2) "*sponsor/polonicus/interruptus*", probably younger, characterised by a pentagonal glabella, pointed anteriorly, and a narrow cephalon, and (3) an independent group: *Trimerocephalus*? *steinachensis* (Richter and Richter, 1926) where the frontal border is not overhung by the frontal lobe and *Trimerocephalus*? *trifolius* (Osmólska, 1958) where the frontal border is widened strongly laterally.

The 3 clades obtained with this cladistic analysis differ from the traditional classification: *Trimerocephalus mastophthalmus* and *Trimerocephalus dianopsoides* occupy a marginal position with regard to traditional systematics. Chlupač integrated these 2 species in the group "*caecus*". The present study indicates a marginal position as sister-group of the clades "*caecus/sponsor*" with *Trimerocephalus* (*Trifoliops*) *trifolius* subgen. nov., *Trimerocephalus*? *steinachensis*, and *Trimerocephalus* (*Trifoliops*) *nigritus* subgen. et sp. nov. The observations showed that *Trimerocephalus mastophthalmus* differs essentially from the group "*caecus*" by the outline of the facial suture cutting the cheek, the absence of the median nodule and the presence of a fine granulation. *Trimerocephalus dianopsoides* differs by a hardly defined segmentation of the pygidium, the absence of S2 and S3 and the presence of the ocular protuberances.

A strong relationship exists between *Trimerocephalus sponsor*, *Trimerocephalus interruptus*, *Trimerocephalus procurvus* and *Trimerocephalus polonicus*. The general aspect of *Trimerocephalus interruptus* Berkowski, 1991, from Poland resambles the specimen of the Cantabrian mountain *Trimerocephalus procurvus* Arbizu, 1985. The only differences are the configuration of S1 and the ornamentation: interrupted S1 and ornamentation constituted of fine and condensed granules in *Trimerocephalus interruptus*; continuous S1 and ornamentation less visible, constituted of dispersed granules in *Trimerocephalus procurvus*. Otherwise, *Trimerocephalus interruptus* shows also some similitudes with *Trimerocephalus polonicus*. Nevertheless, *Trimerocephalus polonicus*, that is twice as small has a more pronounced ornamentation constituted of big granules hardly dispersed. *Trimerocephalus polonicus*, represented only by a few cephala of very young individuals, remains insufficiently known. *Trimerocephalus interruptus* is also closely related to *Trimerocephalus sponsor* in possessing a pentagonal glabellar outline, pointed anteriorly, a similar outline of the facial suture, a fine and condensed granulation, but a less inflated glabella, an S1 medially continuous, almost straight and a less convex genal field. In *Trimerocephalus interruptus*, the pygidium is not so well segmented and is less lenticular. Moreover, *Trimerocephalus sponsor* occupies a somewhat more recent stratigraphic position. It is probable that these differences result from geographic variation. Becker and Schreiber (1994) have already expressed this hypothesis. Possibly, that these specimens represent different populations of the same species.

Trimerocephalus (*Trifoliops*) *trifolius* subgen. nov., *Trimerocephalus* (*Trifoliops*) *nigritus* subgen. et sp. nov. and *Trimerocephalus*? *steinachensis* integrated within the group of "*mastophthalmus*" differ notably from the genus *Trimerocephalus*: the vincular furrow is widened (tr.) in *Trimerocephalus* (*Trifoliops*) *trifolius* subgen. nov. and *Trimerocephalus* (*Trifoliops*) *nigritus* subgen. et sp. nov.; the frontal border is inflated, wide and oriented forward in *Trimerocephalus* (*Trifoliops*) *trifolius* subgen. nov. and *Trimerocephalus*? *steinachensis*. *Trimerocephalus* (*Trifoliops*) *trifolius* subgen. nov. is probably a more derived species in comparison with *Trimerocephalus* (*Trifoliops*) *nigritus* subgen. et sp. nov. In early ontogenetic stages, the frontal

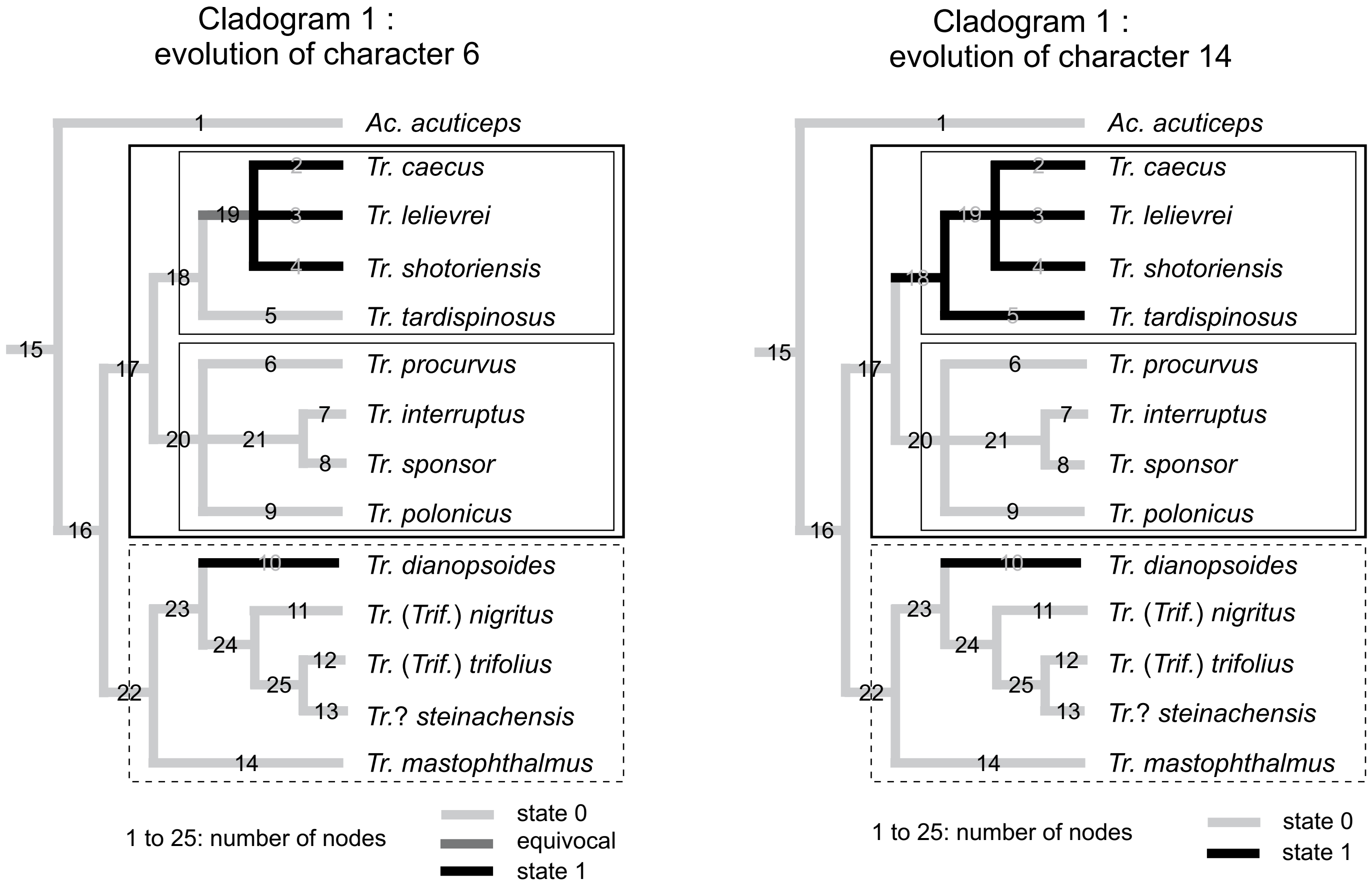

Fig. 9. Tree 1 representing the evolution of characters 6 and 14 analysed under MacClade ver. 3.04. (Maddison and Maddison 1992). Each node is numbered (1 to 25). States of characters are represented by different colors. Details of characters 6 and 14 and coding are discussed in appendix 5. Taxonomic abbreviations are used: *Ac.*, *Acuticryphops*; *Tr.*, *Trimerocephalus*; *Trif.*, *Trifoliops*.

lobe overhangs the frontal border in these two species. However, in later stages, whereas in *Trimerocephalus* (*Trifoliops*) *nigritus* subgen. et sp. nov., the frontal lobe still overhangs the frontal border, in *Trimerocephalus* (*Trifoliops*) *trifolius* subgen. nov., the frontal lobe no longer overhangs the frontal border any more. The frontal lobe hides the anterior border that is slightly bent backward by contrast with later stages where the anterior border is no longer bent backwards.

Trimerocephalus? *steinachensis* may represent a separate taxon. Further material would be necessary for erection of a new taxon of subgeneric rank for *Trimerocephalus*? *steinachensis*, which would also enable an objective characterisation of the pygidium.

The group *mastophthalmus*, possessing the majority of the derived characters, is the oldest stratigraphically and occurs essentially in Poland and Germany. The groups "*caecus/ sponsor*" constituting the second main branch of this genus is scattered mostly in the south of Europe (Spain for the group "*sponsor*"), the north of Africa (Morocco for the group "*caecus*"), the Australian continent (for *Trimerocephalus tardispinosus*) and Iran (for *Trimerocephalus shotoriensis*), thus occupying a more extensive territory.

This study has allowed to trace the phylogeny of the genus *Trimerocephalus* and also the position of the new genus, and to determine evolutionary trends. Within the observed trends, the acquisition of a marginal facial suture which does not cut the cheeks (character 6) and the acquisition of a median nodule (character 14) are apparent (Fig. 9).

In all respects, the topology of resulting tree is dependent upon the starting hypothesis, i.e., on the choice of characters and their changes, on the choice of the outgroup linked to the ancestry of character states; the cladistic analysis being an hypothetico-deductive analysis (see Darlu and Tassy 1993).

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Appendix 1

Dimensions and main cephalic features of *Trimerocephalus* (*Trifoliops*) *trifolius* (Osmólska, 1958) subgen. nov. and *Trimerocephalus* (*Trifoliops*) *nigritus* subgen. et sp. nov.

	Tr. (*Trif.*) *trifolius* (Osmólska, 1958) subgen. nov.	*Tr.* (*Trif.*) *nigritus* subgen. et sp. nov.
L/l of the cephalon	0.63 (0.77 in early instar)	0.55 (0.58 in early instar)
Outline of the cephalon	trilobed	trilobed
Swelling of the cephalon	moderate	moderate
L/l of the glabella	0.88 (0.90 in early instar)	0.73 (0.76 in early instar)
lM/lm of the glabella	0.49 (0.45 in early instar)	0.48 (0.46 in early instar)
GL/Cl	0.58 (0.68 in early instar)	0.55 (0.64 in early instar)
Anterior outline of the glabella	parabolic	widely parabolic, more or less sharp anteriorly
Swelling of the glabella	moderate	moderate
Axial furrows	deep, widening just before the antero-lateral angle	deep, widening just before the antero-lateral angle
Divergence forwards of axial furrows with an angle about	60º	55º
Glabellar furrows S2 and S3	faint	often indistinct
S1	moderately curved forwards, continuous (tr.) but a little marked	moderately curved forwards, continuous (tr.) but a little marked
Preoccipital ring	uninflated, nearly twice shorter (sag.) than occipital ring	uninflated, nearly twice shorter (sag.) than occipital ring
Lateral preoccipital lobes	discernible	discernible
Visual complex	absent but presence of ocular protuberance	absent
Facial suture	cuts the cheek, in forming a crescent narrower than the lateral border	cuts the cheek, in forming a crescent narrower than the lateral border
Swelling of the cheeks	moderate	moderate
Sculpture of the cephalon	fine and dense granulation	fine and dense granulation
Vincular furrow	broad (tr.), strongly elongated (sag.), deep	broad (tr.), moderately elongated (sag.), deep
Length (sag.) of the posterior band/length of the vincular furrow	0.32 cm	0.47 cm

Appendix 2

Stratigraphic and geographic distribution of selected species of the genus *Trimerocephalus* and the probable ancestor *Acuticryphops acuticeps*, selected for the reconstruction of the data matrix.

Species	Etage	Geographic distribution
Trimerocephalus mastophthalmus (Richter, 1856)	Lower Famennian	Rhineland, Harz Mts., Thuringia, Holy Cross Mts., England, South-Western Asia, Kazakhstan
Trimerocephalus caecus (Gürich, 1896)	Lower Famennian	Holy Cross Mts., Harz Mts., Rhineland, Thuringia, Urals, North Africa, Armorican Massif
Trimerocephalus? *steinachensis* (Richter and Richter, 1926)	Lower Famennian	Thuringia, Harz Mts.
Trimerocephalus polonicus Osmólska, 1958	Lower Famennian	Holy Cross Mts.
Trimerocephalus (*Trifoliops*) *trifolius* (Osmólska, 1958) subgen. nov.	Lower Famennian	Holy Cross Mts., Montagne Noire
Trimerocephalus dianopsoides Osmólska, 1963	Lower Famennian	Holy Cross Mts.
Trimerocephalus sponsor Chlupač, 1966	Lower Famennian	Moravia, Cantabrian Mts.
Trimerocephalus procurvus Arbizu, 1985	Lower Famennian	Cantabrian Mts., Germany
Trimerocephalus interruptus Berkowski, 1991	Lower Famennian	Holy Cross Mts.
Trimerocephalus lelievrei Crônier and Feist, 1997	Lower Famennian	Morocco
Trimerocephalus tardispinosus Feist and Becker, 1997	Lower Famennian	Australia
Trimerocephalus shotoriensis Feist, Yasdi, and Becker, in press	Lower Famennian	Eastern Iran
Trimerocephalus (*Trifoliops*) *nigritus* sp. nov.	Lower Famennian	Montagne Noire
Acuticryphops acuticeps (Kayser, 1889)	Upper Frasnien	Rhineland, Thuringia, Harz Mts., Moravia, North Africa, Montagne Noire, England, Carnic Alps Mts.?, Southwestern Asia?

Appendix 3

Morphological characters used in cladistic analysis of genus *Trimerocephalus* with character states. The ancestral state "0" is determined *a priori* by an outgroup comparison with *Acuticryphops acuticeps*. The data matrix is given appendix 4.

Character:

1. *Length and orientation of anterior border*: (0) short, oriented backward, (1) wide, oriented forward, (2) wide, oriented hardly forward.
2. *Swelling of the anterior border*: (0) not inflated, flat, (1) inflated, curved.
3. *Sagittal length of the vincular furrow*: (0) wide, (1) very wide.
4. *Visual surface*: (0) kidney-shaped to elliptic, (1) protuberance, (2) absent.
5. *Ocular lenses*: (0) present, (1) absent.
6. *Outline of facial suture*: (0) cutting the check, (1) running in the lateral furrow.
7. *Shape of glabella*: (0) pentagonal, pointed anteriorly, (1) pentagonal, wide, pointed anteriorly, (2) pentagonal, rounded anteriorly, (3) pentagonal, wide, rounded anteriorly.
8. *Width of cephalon*: (0) wide, (1) very wide, (2) narrow.
9. *Shape of antero-lateral border*: (0) not widened laterally, (1) strongly widened laterally, (2) widened on all outline.
10. *Shape of genal angle*: (0) rounded, (1) with genal spine.
11. *S2 and S3*: (0) present, (1) absent.
12. *Ornamentation on cephalon*: (0) large dense granules, (1) small dense tubercles, (2) large sparse granules, (3) sparse granules, (4) fine and dense granulation.
13. *Shape of S1*: (0) continuous, (1) interrupted.
14. *Occipital median node*: (0) absent, (1) present.
15. *Shape of preoccipital ring*: (0) inflated, (1) depressed.
16. *Preoccipital lateral lobes*: (0) differentiated, convex (1) hardly differentiated.
17. *Shape of rachis*: (0) less prominent, (1) prominent.
18. *Shape of pygidium*: (0) lenticular, (1) trapezoidal.
19. *Shape of limbus*: (0) narrow, (1) wide.
20. *Interpleural furrows*: (0) weak to distinct, (1) indistinct to weak.
21. *Pleural furrows*: (0) deep, (1) shallow.
22. *Disposition of the frontal lobe in comparison with the anterior border*: (0) overhanging, (1) not overhanging.
23. *Shape of postero-lateral angle*: (0) curve, (1) angular.

Appendix 4

Data matrix with ancestral states and status of states of 23 characters used for the cladistic analysis, using the software PAUP ver. 3.1.1. and an optimal procedure. Details of characters and coding are discussed in appendix 5. The sign "?" indicates a missing datum.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Ac. acuticeps	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tr. caecus	0	0	0	2	1	1	0.2	0.2	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0
Tr. lelievrei	0	0	0	2	1	1	1.3	1	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0
Tr. shotoriensis	0	0	0	2	1	1	0.2	0.2	0	0	0	1	0	1	1	1	0	2	1	0	0	0	1
Tr. dianopsoides	0	0	0	1	1	1	2.3	0	0	0	1	3	0	1	1	1	0	1	1	1	1	0	0
Tr. tardispinosus	0	0	0	2	1	0	0	2	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0
Tr. procurvus	0	0	0	2	1	0	0	2	0	0	1	3	0	0	1	1	0	0	0	0	0	0	0
Tr. interruptus	0	0	0	2	1	0	0	2	0	0	1	4	1	0	1	1	0	0	0	0	0	0	0
Tr. sponsor	0	0	0	2	1	0	0	2	0	0	1	4	0	0	1	1	0	0	0	0	0	0	0
Tr. polonicus	0	0	0	2	1	0	0	2	0	0	1	2	0	0	1	1	?	?	?	?	?	0	0
Tr. mastophthalmus	0	0	0	1	1	0	1.3	0.1	0	0	0	3	0	0	1	1	0	0	0	0	0	0	0
Tr. (*Trif.*) *nigritus*	0	0	0	2	1	0	1	0.1	1	0	1	4	0	0	1	1	1	0	0	1	0	0	0
Tr. (*Trif.*) *trifolius*	1	1	1	1	1	0	2	2	1	0	1	4	0	0	1	1	?	0	?	?	?	1	0
Tr.? *steinachensis*	2	1	0	1	1	0	3	1	2	0	1	4	0	0	1	1	?	?	?	?	?	1	0
status of characters	N	I	N	I	N	I	I	I	I	N	I	I	N	I	N	N	N	N	I	I	N	I	N

Appendix 5

Polarity *a posteriori* and status of states of characters *via* the analysis of characters under MacClade (Maddison and Maddison 1992).

Cladogram 1

Character	Polarity *a posteriori* and status of states of characters	Nodes
1	0 → 1, 2 (0, 1, 2 are equivocal at node 25)	
2	0 → 1 (1 is apomorphic, S.E.)	(1): 25
3	0 → 1 (1 is autapomorphy of *Tr.* (*Trif.*) *trifolius* subgen. nov.)	(1): 12
4	not oriented	
5	not oriented	
6	0 → 1 (1 is homoplasic and equivocal at node 19)	(1): 10
7	0 → 3 → 1, 2 (1 is apomorphic and equivocal at node 3 (homoplasic); 2 is autapomorphy of *Tr. (Trif.) trifolius* subgen. nov.; 3 is apomorphic and equivocal at node 3 (homoplasic))	(1): 11; (2): 12; (3): 22
8	0 → 1, 2 (1 is apomorphic and equivocal at node 24 (homoplasic); 2 is apomorphic and equivocal at node 25 (homoplasic))	(1): 3; (2): 17
9	0 → 1 → 2 (1 is apomorphic; 2 is autapomorphy of *Tr.*? *steinachensis*)	(1): 24; (2): 13
10	0 → 1 (1 is autapomorphy of *Tr. tardispinosus)*	(1): 5
11	0 → 1 (1 is apomorphic and equivocal at node 20 (homoplasic))	(1): 23
12	not oriented	
13	0 → 1 (1 is autapomorphy of *Tr. interruptus*)	(1): 7
14	0 → 1 (1 is homoplasic)	(1): 10, 18
15	not oriented	
16	not oriented	
17	0 → 1 (1 is equivocal at node 24)	
18	0 → 1 (1 is autapomorphy of *Tr. dianopsoides*; 2 is autapomorphy of *Tr. shotoriensis*)	(1): 10; (2): 4
19	0 → 1 (1 is homoplasic)	(1): 4, 10
20	0 → 1 (1 is apomorphic, S.E.)	(1): 23
21	0 → 1 (1 is autapomorphy of *Tr. dianopsoides*)	(1): 10
22	0 → 1 (1 is apomorphic, S.E.)	(1): 25
23	0 → 1 (1 is autapomorphy of *Tr. shotoriensis*)	(1): 4

Cladogram 2 (only the character 11 differs from the cladogram 1)

Character	Polarity *a posteriori* and status of states of characters	Nodes
11	0 → 1 (1 apomorphic)	(1): 20, 23

Cladogram 3 (with an additional node; only the character 11 differs from the cladogram 1)

Character	Polarity *a posteriori* and status of states of characters	Nodes
11	0 → 1 (1 apomorphic)	(1): 20, 24