The type species of *Cyrtosymbole* and the oldest (Famennian) cyrtosymboline trilobites

RAIMUND FEIST and RUDY LEROSEY-AUBRIL

Feist, R. and Lerosey-Aubril, R. 2005. The type species of *Cyrtosymbole* and the oldest (Famennian) cyrtosymboline trilobites. *Acta Palaeontologica Polonica* 50 (3): 465–475.

The hitherto poorly known type species of *Cyrtosymbole*, i.e., *Dechenella escoti*, is redescribed on the basis of an abundant new material recovered from the early Famennian Lower Griotte Limestone Formation at La Tourière, near Cabrières, southern France. It includes sclerites (hypostome, librigenae, thoracic segments and external surface of the pygidium) that previously were either unknown, or represented by poorly preserved and incomplete specimens, together with a full suite of post-protaspid growth stages. The latter has revealed that certain characters, in particular the preglabellar region and postocular facial sutures, show marked changes between the early and late holaspid stages. In the past, some species have been based on immature specimens; for example the lectotype of *C. escoti* is an early holaspis, and the characters that it displays have been regarded as diagnostic of the genus. For confident specific assignments in cyrtosymboline trilobites it is important, therefore, to have to hand sufficient material, including late holaspids. A revised diagnosis of *Cyrtosymbole* is given, and only those species that share diagnostic adult characters with *C. escoti* are assigned to it. Insights into early growth development exemplified by *C. escoti* and allies corroborate the attribution of the Cyrtosymbolinae to the Proetidae.

Key words: Trilobita, Proetidae, Cyrtosymbolinae, ontogeny, Devonian, Famennian.

Raimund Feist [rfeist@isem.univ-montp2.fr] and Rudy Lerosey-Aubril [lerosey@isem.univ-montp2.fr], Laboratoire de Paléontologie, Paléobiologie et Phylogénie, Institut des Sciences de l'Evolution de Montpellier, 34095 Montpellier Cedex 05, France.

Introduction

Following the reduction in diversity and extinctions that trilobites suffered during the late mid-Devonian Taghanic onlap proetids were again severely affected during the mid– Late Devonian global biocrisis but survived into the Famennian. However, there is no record of recovery and speciation of proetids immediately after the terminal Frasnian Kellwasser event. The earliest known proetid in the lower Famennian is the blind taxon *Formonia* Richter and Richter, 1913 that occurs within the middle *Palmatolepis crepida* sub-biozone at Sessacker (Rhenish Slate Mts., Germany) (Ziegler 1962: 133), which is five conodont sub-biozones above the Upper Kellwasser extinction level. Shortly afterwards, in the Late *Palmatolepis crepida* sub-biozone and *Palmatolepis rhomboidea* biozone, the first normally oculated proetids appear; these belong to *Cyrtosymbole* Richter, 1913, and include its type species, *C. escoti* (von Koenen, 1886). In his original concept of *Cyrtosymbole*, Richter (1913) included Famennian and early Carboniferous proetids with an anteriorly tapering glabella, pronounced glabellar furrows, sigmoidal, anteriorly strongly diverging sutures and a semicircular pygidium with a high, multisegmented axis and a narrow border. Many species lineages originally recognised and defined by Richter and Richter (1926), Osmólska (1962), and Chlupáč (1966) as subgenera of *Cyrtosymbole* (such as *Calybole* Richter and Richter,

1926, *Waribole* Richter and Richter, 1926, and *Mirabole* Osmólska, 1962) have subsequently been elevated to generic status. Other species, especially from the late Famennian have been assigned to new genera, e.g., *Pseudowaribole* Hahn and Hahn, 1967, *Haasia* Yuan, 1988 and *Sinosymbole* Yuan and Xiang, 1998. Conversely, a group of species sharing a triangular, anteriorly pointed glabella, rather large palpebral lobes and eyes, and a characteristic reticulate sculpture was placed by Alberti (1976) in the subgenus *Cyrtosymbole (Franconicabole)*. We recognize this as a monophyletic group that is distinct from *Cyrtosymbole*, and regard it as an independent genus; however it needs to be redefined, since the available material of the type species, *Cyrtosymbole dillensis* (Drevermann, 1901), is inadequate to properly characterise this taxon.

By restricting *Cyrtosymbole* to a group of species closely related to *C. escoti*, it is necessary to revise its diagnosis. Descriptions of the type species by von Koenen (1886), Richter (1913), and Alberti (1975) are all based on the small number of incomplete, mostly exfoliated cranidia and pygidia that were collected by de Rouville in 1886, and it has thus remained inadequately known. The abundant new material recovered by us is well preserved, and includes the previously unknown hypostome and thoracic segments, and so it is now possible to give a full description of all sclerites (with the exception of the still unrecognized rostral plate), together with the post-protaspid ontogenetic stages. The latter are particu-
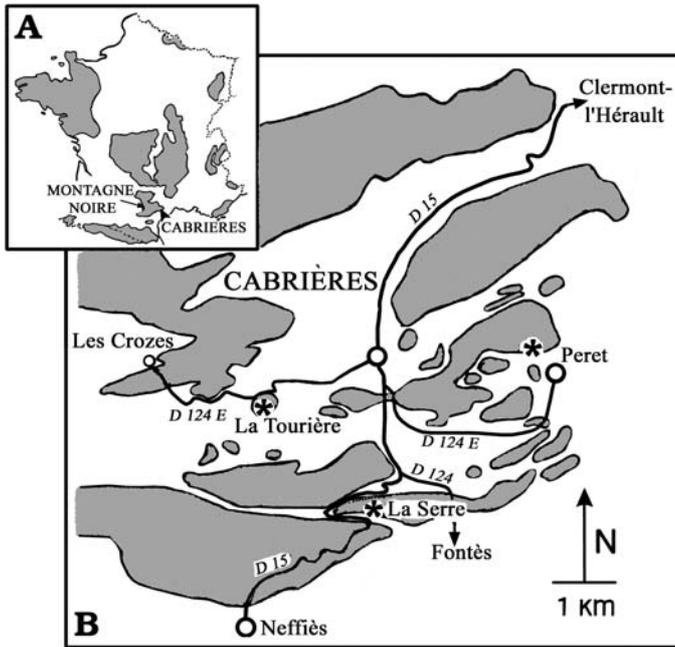
Acta Palaeontol. Pol. 50 (3): 465–475, 2005

http://app.pan.pl/acta50/app50-465.pdf

Fig. 1. **A**. Location of Cabrières village in the southeastern Montagne Noire, southern France; shaded areas indicate outcropping pre-Mesozoic massifs. **B**. *Cyrtosymbole escoti* bearing localities (La Tourière, La Serre and Peret) in the vicinity of Cabrières village; shaded areas indicate Devonian outcrops; solid lines indicate roads.

larly important, and analysis of the development of diagnostic features has elucidated of the role of heterochrony in phylogenetic links within cyrtosymboline trilobites. Unfortunately we failed to discover a complete adult specimen that would have confirmed the possible progenetic reduction in number of thoracic segments, as seen in other cyrtosymbolines, such as *Calybole* and *Helioproetus* (Hahn and Brauckmann 1984; Brauckmann 1985; Feist et al. 2000).

Material and occurrence

Species of *Cyrtosymbole* occur in the cephalopod biofacies, which is interpreted as having been deposited as lime-mud substrates on submarine rises, within the photic zone in an offshore, subtropical environment. They are widely distributed in this biofacies in Morocco (Tafilalet and Central Hercynian Meseta), southern France (Montagne Noire), western Germany (Rhenish Slate Mts), Poland (Holy Cross Mts), Russia (eastern slope of southern Urals and Mugodjar), Iran (Shotori Range) and Western Australia (Canning Basin). By contrast, the genus has not been found in the Americas, or in eastern and southeast Asia.

The type species of *Cyrtosymbole*, *C. escoti* occurs in early Famennian cephalopod-bearing limestones that characterize the lower member of the Griotte Limestone Formation (Feist 1985), which is exposed in several localities such as La Tourière, Peret and La Serre, all in the vicinity of Cabrières, in the southeastern part of the Montagne Noire, southern

France (cf. location map, Fig. 1). It is most abundant at La Tourière Hill, 1.7 km W of Cabrières village, from where most of the material studied by von Koenen (1886) originated. The trilobites are from a small, abandoned marble quarry situated on the southeastern foothill, which is the site of Becker's (1993) detailed investigations into the cephalopod and conodont based biostratigraphy. From this site and from La Boissière, 500 m NNW of Peret village, new material of *C. escoti*, comprising more than 200 isolated sclerites of various sizes, was recovered by us from red cheiloceratid-rich calcilutites, which immediately overlie black limestones and marls of the underlying upper member of the La Serre Formation. All the trilobites are from the *Palmatolepis rhomboidea* Biozone.

Repositories and institutional abbreviations.—The specimens described and figured by von Koenen (1886), Richter (1913) and Alberti (1975) (lectotype and syntypes from de Rouville's collection) are housed in the collections of the Palaeontological Institute of the University Göttingen (Gö). Our new material is housed in the Invertebrate Palaeontology collections at the University of Montpellier (UMC-IP: Université de Montpellier, Collections—Invertébrés, Paléontologie).

Other abbreviations.—exsag., exsagittal; sag., sagittal; tr., transversal

Systematic paleontology

Family Proetidae Hawle and Corda, 1847
Subfamily Cyrtosymbolinae Hupé, 1953

Remarks.—Hahn et al. (1980) regarded the Cyrtosymbolinae as belonging to the Phillipsiidae Oehlert, 1886, of which they considered them to be the ancestral rootstock, giving rise to a series of evolutionary lineages that together make up what they presumed to be a monophyletic family. However, in their concept of the Phillipsiidae, they included lineages that have characters that we regard as contradictory. This is the case in particular in cyrtosymbolines, of which fundamental traits such as the generally forwardly tapering glabella, the thorax (where known) with only seven or eight segments, and the semicircular pygidium with relatively few axial rings are not shared by the presumed "derived" younger descendants. Another, perhaps more fundamental difference concerns the early development. In phillipsiids the frontal glabellar lobe reaches as far as, or close to the anterior border, and is parallel-sided (e.g., *Paladin shunnerensis* (King, 1914) (Clarkson and Zhang Xi-guang 1991); *Ditomopyge scitula* (Meek and Worthen 1865) (Pabian et al. 1993: fig. 3: 1, 2, 5, 7); *Liobole* aff. *glabra erdbachensis* Hahn and Hahn, 1971 (Gröning 1986: pl. 1: 1) and *Liobole glabra proxima* Chlupáč, 1966 (Owens and Tilsley 1995: pl. 4u) or forwardly expanding (e.g., *Hentigia bulbops* Haas, Hahn and Hahn 1980: pl. 4: 7a). In equivalent growth stages of cyrtosymbolines (including the type species of *Cyrtosymbole*) the frontal

lobe of the glabella is narrow and anteriorly pointed, and there is a long preglabellar field bearing a plectrum-like median groove (e.g., Fig. 2A, B herein). These features are shared by the Proetidae, for example *Proetus talenti* Chatterton, 1971, and especially dechenellines (Chatterton et al. 1999: figs. 1–22), of which the last known representative is the early Late Devonian *Clavibole* Hahn et al. (1982) assigned by these authors to the Cyrtosymbolinae. We believe, therefore, that it is more appropriate to consider the cyrtosymbolines as proetids rather than phillipsiids, although we do not exclude the possibility that some at least of the latter might originate in certain cyrtosymbolines (e.g., by adaptation to a particular feeding mode).

Genus *Cyrtosymbole* Richter, 1912

Type species: *Dechenella escoti* von Koenen, 1886; La Serre near Cabrières, Montagne Noire, France, early Famennian, Devonian.

Emended diagnosis.—Small, oculated Cyrtosymbolinae with conical glabella with subparabolic frontal lobe; lateral glabellar furrows incised; S1 bifurcated; preglabellar field extremely narrow or absent; pronounced antero-lateral cephalic border and border furrow; well defined palpebral lobe, placed towards anterior part of preoccipital glabella, close to axial furrow; postocular sutures with ε-ζ straight; genal spines short; pygidium semicircular, with narrow, high axis; narrow border furrow and border, well defined axial rings and pleural furrows that extend as far as border furrow.

Differentiated from *Calybole* Richter and Richter, 1926 by the following features: glabella relatively longer with anterior outline largely parabolic, anterior sutures modestly divergent, α-α distant to each other, preglabellar field absent or extremely narrow (sag.), pygidial axis robust with wide posterior outline and higher number of axial rings. Differentiated from *Haasia* Yuan, 1988 by: glabella wider and unconstricted anterolaterally, librigenal spines present, pygidial axis longer with postaxial field absent or rather narrow (sag.), nodular sculpture.

Cyrtosymbole escoti (von Koenen, 1886)
Figs. 2, 3.

Dechenella Escoti sp. nov.; von Koenen 1886: 164.
Dechenella sp. nov.; von Koenen 1886: 164.
Dechenella Escoti von Koenen, 1886; Frech 1887: 438.
Cyrtosymbole Escoti von Koenen, 1886; Richter 1913: 381, pl. 22: 17, 18.
Cyrtosymbole escoti von Koenen, 1886; Perna 1915: 45.
Cyrtosymbole (*Cyrtosymbole*) *escoti* von Koenen, 1886; Richter and Richter 1926: 31.
Cyrtosymbole (*Cyrtosymbole*) *escoti* von Koenen, 1886; Richter, Richter and Struve 1959: O389–O391
Cyrtosymbole (*Cyrtosymbole*) *escoti* von Koenen, 1886; Osmólska 1962 : 70.
Cyrtosymbole (*Cyrtosymbole*) *escoti* von Koenen, 1886; Chlupáč 1966: 22.
Cyrtosymbole (*Cyrtosymbole*) *escoti* von Koenen, 1886; Alberti 1975: 209, fig. 1: 1–9.
Cyrtosymbole (*Cyrtosymbole*) *escoti* von Koenen, 1886; Alberti 1976: 40.
Cyrtosymbole (*Cyrtosymbole*) *escoti* von Koenen, 1886; Feist 1977: 64, pl. 6: 15, 16.

Cyrtosymbole (*Cyrtosymbole*) *escoti* von Koenen, 1886; Yuan 1988: 16.

Lectotype.—Selected Alberti 1975: 209; cranidium, Gö 420-1, Fig. 2F (herein), from Famennian, lower member of Griotte Limestone Formation, La Serre Hill at 2.5 km SW of Cabrières, southeastern Montagne Noire. Paralectotypes (syntypes from de Rouville's collection): cranidia—Gö 420-2, Gö 420-3, Gö 420-4; librigena—Gö-11; pygidia—Gö 420-5, Gö 420-6/7, Gö 420-8, Gö 420-9/10, from Famennian, lower member of Griotte Limestone Formation, La Tourière Hill, 1.7 km W of Cabrières.

Material.—Comprises from La Tourière: cranidia—UMC-IP320 (Fig. 2A), UMC-IP321 (Fig. 2B), UMC-IP322 (Fig. 2C), UMC-IP323 (Fig. 2D), UMC-IP324 (Fig. 2E), UMC-IP325 (Fig. 2F), UMC-IP326 (Fig. 2G), UMC-IP328 (Fig. 2I), UMC-IP329 (Fig. 2J), UMC-IP330 (Fig. 2K), UMC-IP331 (Fig. 2L), UMC-IP332 (unfigured); cephala—UMC-IP333 (Fig. 3A), UMC-IP334 (unfigured); hypostomes—UMC-IP335 (Fig. 3B), UMC-IP336 (Fig. 3C), UMC-IP337 (Fig. 3D), UMC-IP338 (unfigured); librigenae—UMC-IP339 (Fig. 3E), UMC-IP340 (Fig. 3F), UMC-IP341 (Fig. 3G), UMC-IP342 (Fig. 3H), UMC-IP343 (unfigured); pygidia—UMC-IP344 (Fig. 3I), UMC-IP345 (Fig. 3K), UMC-IP346 (Fig. 3L), UMC-IP347 (Fig. 3M), UMC-IP348 (Fig. 3N), UMC-IP349 (Fig. 3O), UMC-IP350 (Fig. 3P), UMC-IP351 (Fig. 3Q), UMC-IP353 (Fig. 3S), UMC-IP354 (Fig. 3T), UMC-IP355 (Fig. 3U), UMC-IP357 (unfigured). From Peret: cranidia—UMC-IP327 (Fig. 2H), UMC-IP358 (unfigured); librigenae—UMC-IP359 (unfigured); pygidia—UMC-IP352 (Fig. 3R), UMC-IP356 (Fig. 3V), UMC-360 (unfigured).

Revised diagnosis.—Type-species of *Cyrtosymbole*, with anterior part of cranidium strongly declined; long glabella, widest (tr.) at base, with frontal lobe extending as far as deep border furrow in late holaspids; weakly convex, flat lying, modestly arched border; palpebral lobes of moderate size; postocular sutures with ε-ζ long, extending from opposite anterior third of L1 to occipital furrow, parallel to axial furrows in late holaspids; low, reniform visual field; genal spines outwardly directed, with broad bases; hypostome narrow, with low posterior lobe and narrow postero-lateral borders; thoracic segments with low pre-annulus; pygidium with strongly vaulted pleural fields, moderately long axis with 7 + 1 low axial rings, well delimited by continuous, deep ring furrows; 7 pleural ribs with distinct pleural bands; border furrow tends to be progressively effaced from anterior to posterior from early to late growth stages; in latter, posterior border is continuously declined behind axis.

Differentiated from *C. gotica* Richter and Richter, 1926, *C. crebra* Perna, 1915, and *C. playfordi* Feist and Becker, 1997 by: anteriorly strongly downwards flexed cranidium with relatively flat anterior border and narrower, more anteriorwards placed palpebral lobes; from *C. vates* Alberti, 1976 by: preglabellar field absent; from *C. pusilla* (Gürich, 1896), *C. nana* Richter, 1913, and *C. niazensis* Feist, 2003 by: glabella widest at base and fewer number of pygidial axial rings.

Description.—Based on largest holaspid exoskeletons (sagittal length of cranidia > 4 mm; pygidia > 3mm). Glabella long, subconical (length/width ratio of preoccipital glabella: 1.27), frontal lobe narrow, parabolic in outline, non-constricted antero-laterally, moderately vaulted transversely, more so antero-medially than laterally in anterior view; in longitudinal profile strongly downturned anteriorly, terminating opposite γ, less vaulted to the rear; circumscribed by axial furrows of even depth that run parallel from occipital furrow to S1, then converge slightly towards anterior. Glabellar furrows narrow, moderately deep, slightly curved backwards; S1 markedly impressed, bifurcated with transversely directed anterior branch half as long as posterior; posterior branch obliquely curved backwards with narrowing distal ends that do not extend to occipital furrow; S2 and S3 narrow and shallow; S4 not discernable. Lateral glabellar lobes not inflated; L1 markedly longer (exsag.) than wide (tr.) at base. Occipital furrow deep, medially widened and curved forward. Occipital ring not inflated, slightly vaulted (sag.), higher than base of preoccipital glabella, narrowing laterally (exsag.), narrowed (tr.) behind posterior border furrow (exsag.) by inward curvature of axial furrows; anterior margin slightly notched opposite posterior ends of S1; lateral occipital lobes absent.

Deep, narrow anterior border furrow and broad, upturned, weakly convex border which is flexed evenly backwards laterally; border weakly vaulted (sag.) with two narrow terrace ridges on its anterior part. Palpebral lobes relatively narrow and short, forwardly placed (ε a short distance behind S1), a little lower than glabella and slightly inclined from axial furrows in longitudinal profile, provided with thickened margins; anterior part of palpebral suture (δ-γ) longer and of lesser curvature than posterior (δ-ε). Preocular facial sutures (γ-β) shorter than postocular (ε-ζ), straight and moderately divergent, then sharply adaxially incurved on anterior border into long β-α portion. Posterior sutures with long ε-ζ portion parallel to axial furrows, which turns strongly abaxially on posterior cephalic border. Posterior fixigenae rather narrow, ε being situated closer to axial furrow than γ; anterior fixigenae strongly declined, weakly vaulted. Posterior cephalic border narrow, subcylindrical in section (exsag.).

Librigenae broad, with field weakly convex, defined by deep border furrows and wide, semicylindrical border with four continuous terrace ridges. Lateral and posterior borders merging at genal angle and continue onto broad, relatively short genal spine. Eye semicircular, relatively low, with visual surface inclined laterally at 45° in life position, carrying less than 150 lenses; eye-socle absent; eye circumscribed by broad, shallow sub-ocular furrow, with tiny, ovoid weakly inflated sub-ocular platforms adjacent to the facial suture in front of and behind the eye-lobe.

Hypostome narrow subrectangular; middle body well defined by deep furrows around it, anterior lobe ovoid, inflated, merging medially with low, weakly vaulted posterior lobe; middle furrows straight, well marked, directed towards posterior, and lack maculae; anterior margin straight, with narrow upturned anterior rim, markedly separated from middle body by straight anterior furrow; declined, broadly rounded anterior wings; lateral border narrows at lateral notch; shoulder narrow, only modestly outwardly curved; lateral borders flat, of even width, straight, convergent, before merging with curved posterior border; tiny spines protruding below postero-lateral corners.

Sculpture of minute, dense granules on axial parts of the cranidium; granules increasing in size towards posterior, being present on anterior fixigenae but absent on palpebral lobes, posterior fixigenae and borders. Granules present over entire librigenal field, becoming coarser adaxially, and form an obvious single row, where they are slightly enlarged, along the margin of the otherwise smooth sub-ocular groove. Anterior fixigenal and abaxial librigenal fields pitted. Terrace ridges on hypostomal margins and around centre of anterior lobe; posterior lobe smooth.

Thoracic segment with high axial ring in transverse profile, moderately vaulted sagittally, less so laterally, subdivided into antero-laterally enlarged (exsag.) postannulus and rather narrow, short (tr.), depressed preannulus; articulating half ring flat-topped, markedly shorter (tr.) than axial ring. Pleura as broad (tr.) as axial ring, displaying a horizontal inner portion that is broader (tr.) than declined, abaxially pointed outer portion.

Pygidium with relatively narrow, elliptical postero-lateral outline (mean length/width index = 0.63), evenly curved postero-lateral margin, high in posterior and lateral views. Maximum breadth of axis slightly less than that of pleural area; axis strongly vaulted in transverse profile, gently declined in lateral view, but with terminal piece remaining elevated above postaxial area; well defined by straight, slowly converging axial furrows and narrow parabolic postaxial furrow; 7+1 low, moderately inflated axial rings, well defined by anteriorly curved, continuously and evenly marked ring furrows, diminishing in depth from front to rear. Pleural area slightly vaulted adaxially, strongly declined abaxial of fulcrum, considerably higher than axis in lateral view; broad border sloping strongly downwards, separated from inner pleural area by weak border furrow that shallows towards

Fig. 2. Cranidia of *Cyrtosymbole escoti* (von Koenen, 1886). **A**. Early meraspis, UMC-IP320, in dorsal (A₁) and frontal (A₂) views. **B**. Early meraspis, →
UMC-IP321, in dorsal (B₁) and lateral (B₂) views. **C**. Late meraspis, UMC-IP322, in dorsal view. **D**. Late meraspis, UMC-IP324, in dorsal (D₁) and lateral (D₂) views. **E**. Early holaspis, UMC-IP325, in dorsal (E₁), lateral (E₂), and frontal (E₃) views. **F**. Lectotype, early holaspis, Gö 420-1, in dorsal (F₁) and lateral (F₂) views. **G**. Early holaspis, UMC-IP326, in dorsal (G₁), lateral (G₂), and frontal (G₃) views. **H**. Early holaspis, UMC-IP327, in dorsal (H₁), lateral (H₂), and frontal (H₃) views. **I**. Early holaspis, UMC-IP328, in dorsal (I₁), lateral (I₂), and frontal (I₃) views. **J**. Late holaspis, UMC-IP329, in dorsal (J₁), lateral (J₂), and frontal (J₃) views. **K**. Late holaspis, UMC-IP330, in dorsal (K₁), lateral (K₂), and frontal (K₃) views. **L**. Late holaspis, UMC-IP331, in dorsal (L₁), lateral (L₂), and frontal (L₃) views. The specimens are coated with MgO. A–G, I–L from La Tourière, H from Peret, both vicinity of Cabrières, southern France, early Famennian, Devonian. Scale bars 0.5 mm.
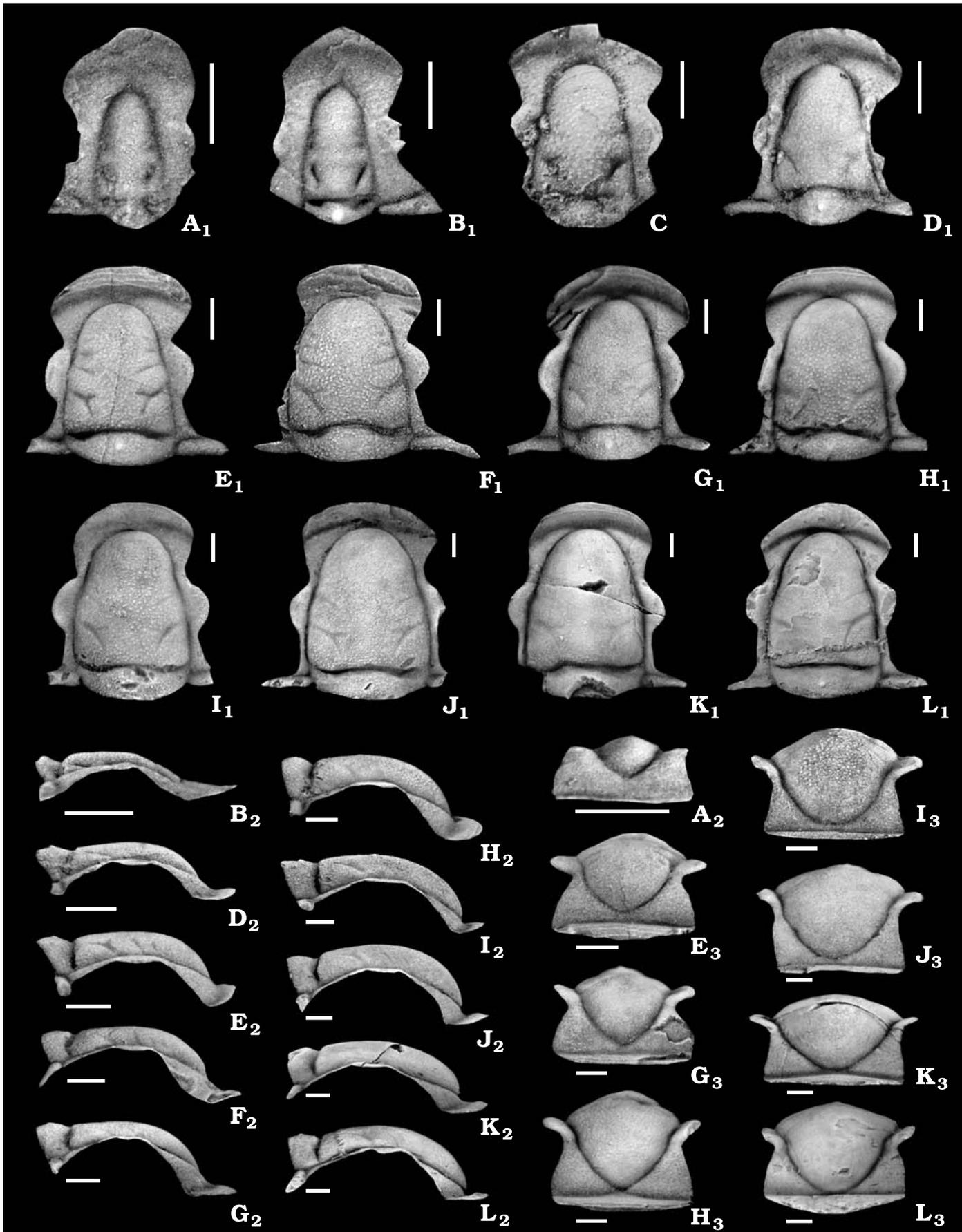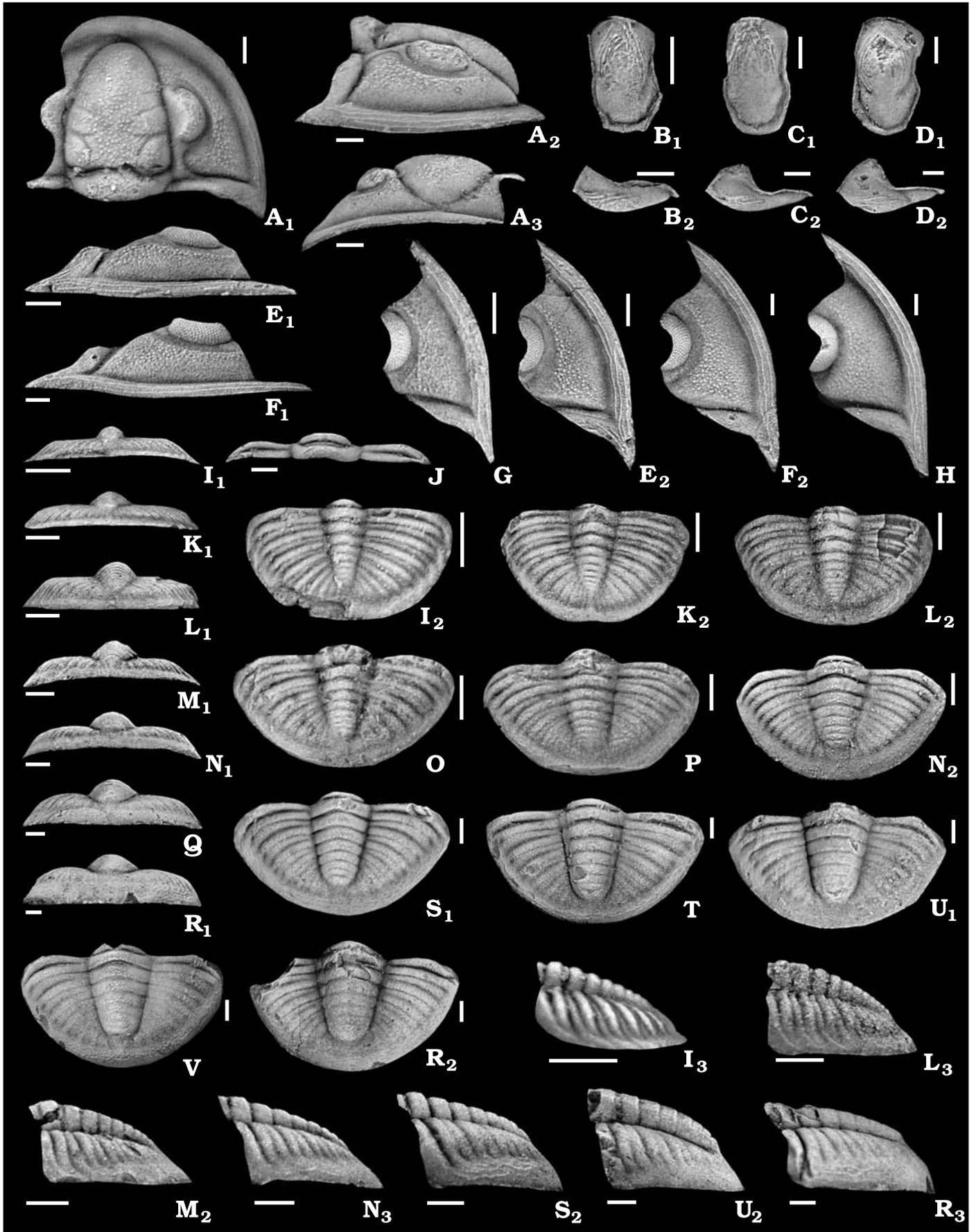
posterior; postaxial area vaulted with short, triangular, weakly inflated, post axial ridge. 6+1 pleurae, slightly curved towards posterior, extending as far as border furrow, markedly separated from each other by narrow interpleural furrows that widen abaxially at border furrow, and subdivided by deeper and wider pleural furrows into weakly vaulted bands, the posterior of which are adaxially twice as wide (exsag.) as anterior ones. Pygidial sculpture of fine, dense granulation on entire exoskeleton, with anastomosing terrace ridges along border.

Comparisons and discussion

Only a restricted number of species are sufficiently well known, and demonstrably closely related to *Cyrtosymbole escoti* for them to be assigned with confidence to *Cyrtosymbole* (Fig. 4).

Other species, such as *C.? incerta* Perna, 1915 (a single incomplete cranidium), *C.? plenifrons* Perna, 1915 (synonymised with *C. crebra* by Chlupáč 1966: 19), *C.? planilimbata* Richter and Richter, 1919 (a single incomplete cranidium), *C.? guembeli* (Richter, 1913) (based only on pygidia) must await additional material to provide definitive evidence that they belong to *Cyrtosymbole*. *C. fluctu-*

osus Maksimova, 1955 has a parallel-sided anterior glabellar lobe and strongly inflated lateral glabellar lobes, with L1 apparently completely isolated by deep posterior branches of S1 that meet the occipital furrow. These characters are not present in any species assigned here to the genus, so despite similarities in the pygidium, we follow Alberti (1976: 41) and exclude this species. Likewise, we do not consider *C. varica* Alberti, 1976 to be a species of *Cyrtosymbole*, because it has a comparatively long (sag.) preglabellar field, strongly divergent postocular branches of the facial suture and a flat pleural field without a defined pygidial border. These features, which characterise adults of "*C.*" *varica*, occur only in early growth stages in *Cyrtosymbole* species, before changing in shape during the holaspis period. This case of paedomorphosis is an apparently genetically fixed character state, which distinguishes this taxon from Cy*rtosymbole* species.

Among those species assigned here to *Cyrtosymbole*, two groups can be distinguished. An older one comprising *C. gotica*, *C. crebra*, *C. playfordi*, and *C. vates*, is that which is most closely related to the type species, and is restricted to the early Famennian (to II, Late *Palmatolepis crepida* subbiozone to *Palmatolepis rhomboidea* biozone). This group is characterized by slightly converging posterior axial furrows, the preoccipital glabella therefore reaching its maximum

Early Famennian (to II, Late *Palmatolepis crepida* sub-biozone to *Palmatolepis rhomboidea* biozone)	
C. escoti (von Koenen, 1886)	Montagne Noire (Southern France; von Koenen 1886)
C. gotica Richter and Richter, 1926	Langenaubach (Rheinisches Schiefergebirge; Richter and Richter 1926) Holy Cross Mountains (Poland; Osmólska 1962)
C. crebra Perna, 1915	Urals (eastern slope of southern Urals; Perna 1915)
C. playfordi Feist and Becker, 1997	Canning Basin (NW Australia; Feist and Becker 1997)
C. vates Alberti, 1976	Bou Keziam (Moroccan Central Meseta; Alberti 1976) ? Letmathe (Rheinisches Schiefergebirge; Becker et al. 1994)
Mid- to late Famennian (to III-V, *Palmatolepis marginifera* to *Palmatolepis expansa* biozones)	
C. pusilla (Gürich, 1896)	Holy Cross Mountains (Poland; Osmólska 1962) Shotori Range (Iran; Feist et al. 2003)
C. nana Richter, 1913	to III, Hady near Brno (Czech Republic; Richter 1913; Chlupáč 1966)
C. niazensis Feist, 2003	Shotori Range (Iran; Feist et al. 2003)

Fig. 4. Stratigraphic and geographic distribution of species attributed to *Cyrtosymbole* Richter, 1912.

← Fig. 3. Cephalon, hypostomes, librigenae, transitory pygidia and pygidia of *Cyrtosymbole escoti* (von Koenen, 1886). **A**. Cephalon, early holaspis, UMC-IP333, in dorsal (A_1), lateral (A_2), and frontal (A_3) views. **B**. Hypostome, meraspid?, UMC-IP335, in dorsal (B_1) and lateral (B_2) views. **C**. Hypostome, early holaspis, UMC-IP336, in dorsal (C_1) and lateral (C_2) views. **D**. Hypostome, late holaspis, UMC-IP337, in dorsal (D_1) and lateral (D_2) views. **E**. Librigena, UMC-IP339, in dorsal (E_1) and lateral (E_2) views. **F**. Librigena, UMC-IP340, in lateral (F_1) and dorsal (F_2) views. **G**. Librigena, early holaspis, UMC-IP341, in dorsal view. **H**. Librigena, late holaspis, UMC-IP342, in dorsal view. **I**. Transitory pygidium, early meraspis, UMC-IP344, in posterior (1_1), dorsal (I_2), and lateral (I_3) views. **K**. Transitory pygidium, early meraspis, UMC-IP345, in posterior (K_1), and dorsal (K) views. **L**. Transitory pygidium, UMC-IP346, in posterior (L_1), dorsal (L_2), and lateral (L_3) views. **M**. Transitory pygidium, UMC-IP347, in posterior (M_1) and lateral (M_2) views. **N**. Pygidium, early holaspis, UMC-IP348, in posterior (N_1), dorsal (N_2), and lateral (N_3) views. **O**. Transitory pygidium, late meraspis, UMC-IP349, in dorsal view. **P**. Transitory pygidium, late meraspis, UMC-IP350, in dorsal view. **Q**. Transitory pygidium, late meraspis, UMC-IP351, in posterior view. **R**. Pygidium, late holaspis, UMC-IP352, in posterior (R_1), dorsal (R_2), and lateral (R_3) views. **S**. Pygidium, early holaspis, UMC-IP353, in dorsal (S_1) and lateral (S_2) views. **T**. Pygidium, UMC-IP354, in dorsal view. **U**. Pygidium, late holaspis, UMC-IP355, n dorsal (U_1) and lateral (U_2) views. **V**. Pygidium, late holaspis, UMC-IP356, in dorsal view. The specimens are coated with MgO. A–Q, S–U La Tourière, R, V Perret, both vicinity of Cabrières, southern France, early Famennian, Devonian. Scale bars 0.5 mm.

width posterior to the middle of the palpebral lobes. Whereas in late holaspids of *C. escoti* the adaxial anterior fixigenae are separated by the sagittally merged preglabellar and anterior border furrows, there remains a very narrow preglabellar field in the other species when similar growth stages are compared. The typically strong downward flexure of the anterior part of the cranidium in *C. escoti* is less pronounced in the other species. Unlike *C. escoti*, *C. gotica*, and *C. crebra* have an upturned, thickened anterior cranidial border, wider and more backwardly placed palpebral lobes, and a greater number of pygidial segments. *C. playfordi* has less divergent anterior sutures, thickened border and, besides the same number of axial rings in the pygidium, a continuous, inflated postero-lateral border. *C. vates* is the most similar to *C. escoti*, especially with regards to the long straight portion of sub-parallel posterior suture, the outline of the preoccipital glabella and the continuously downturned posterior margin in the pygidium. On the basis of the specimens assigned to this species by Alberti (1976), it has a wide variability, but whether they all belong to the same taxon is not certain. A feature that differs consistently from *C. escoti* is the less pronounced bifurcation of S1, with a reduced anterior branch, and the maintenance of a preglabellar field up to late holaspid growth stage (see Alberti 1976: figs. 3–7 and 8), with the frontal lobe of the glabella apparently remaining separated from the border furrow by a short distance.

The second group, that comprises *C. pusilla*, *C. nana*, and *C. niazensis*, ranges from the mid-to late Famennian (to III–V, early *Palmatolepis marginifera* to *Palmatolepis expansa* biozones). It is characterized by the maximum glabellar width being located farther forward, due to the slight outward extension of L2; the slight lateral constriction of the anterior glabella; the reduction of the anterior branch of S1; and an increase in number of pygidial axial rings and pleural ribs.

Trends in ontogeny

Aspects of the early ontogeny of cyrtosymboline trilobites have been described by Osmólska (1962), Chlupáč (1966) and Alberti (1976) and are partially known in *Cyrtosymbole pusilla*, *C. gotica*, *C. nana*, and *C. vates*. Lerosey-Aubril and Feist (2005b, this volume) described the ontogeny of a cyrtosymboline *Osmolskabole prima* (Osmólska, 1962). General trends were summarized by Chlupáč (1966: 118) and these have been confirmed in the nearly complete growth series from the early meraspid to the late holaspid periods of *C. escoti* (Figs. 1, 2) described here. The ways that specific features of the preglabellar area and the postocular sutures change with size increase in *C. gotica* Richter and Richter, 1926 are corroborated.

The smallest known cranidia of *C. escoti*, of 1.24 and 1.45 mm in sagittal length (Figs. 2A, B, 5), are early meraspids. Contemporaneous meraspids of similar sizes are known from *C. vates* and *C. gotica*. In all these specimens the
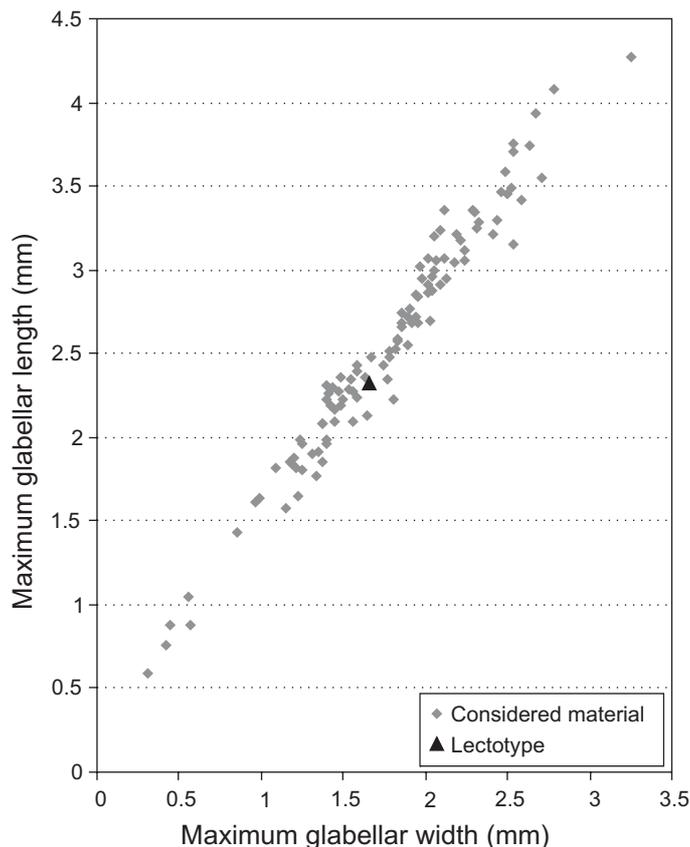

Fig. 5. Scatter plot of maximum length *versus* maximum width of the glabella (glabellar lobe + occipital lobe) for 105 undistorted individuals. The lectotype is marked with a black triangle.

glabellar lobe is individually vaulted, narrow, elongate, gradually tapering forward to an anteriorly pointed frontal lobe that is connected to a conspicuous axial groove-like plectrum, subdividing a rather broad (sag.) preglabellar field and dying out before reaching the broad border furrow. Four glabellar furrows are discernable, the posterior ones rather deeply impressed; S1 not yet bifurcated. The occipital ring is relatively narrow (sag.) and high, backwardly projected, provided with a rather large, prominent median node. The anterior border, only medially developed, remains flat; the anterior margin projects adaxially forwards as a result of closely approaching α-α suture points. The most striking character in this stage concerns the rather broad fixigenae with palpebral lobes and ocular ridges discernable to a variable degree, and with straight backwardly and outwardly directed postocular sutures, defining a triangular posterior portion. Among early cyrtosymbolines, the latter trait is retained up to the adult stage in two species hitherto assigned to *Cyrtosymbole varica* Alberti, 1976, and "*C*". *dillensis* (Drevermann, 1901), whereas in others it is generally subjected to major transformation during ontogeny. Indeed, in all other species, including the type, a turning point at ζ appears rapidly and migrates inwards during the meraspid period until reaching a position in later holaspids where the proximal postocular portion of the suture runs subparallel to the axial

furrow. The length of this portion is affected by specific variation as it relies largely on the position and size of the palpebral lobe. In *C. escoti* this portion of the suture is particularly long, the palpebral lobe remaining relatively short and in a likewise far anterior position.

Other cranidial traits that undergo major changes during late meraspid and early holaspid ontogeny concern the preglabellar field, the relative length, vaulting and outline of the glabella, the form and degree of impression of the glabellar furrows and the expression of sculpture. Whereas the preglabellar and anterior border furrows are separated from each other by a plectrum throughout the meraspid and early holaspid periods, this progressively narrows with increasing growth until the complete merger of the preglabellar and border furrows in larger holaspids.

The longitudinal vault of the cranidium, and especially that of the glabella, remains weak in early meraspids; thereafter it increases considerably anteriorly. In late meraspids and early holaspids the anterior cranidium is strongly downturned when the anterior border is horizontally positioned. In this posture the occipital lobe rises backwards whereas the posterior two-thirds of the preoccipital glabella remain horizontal in lateral view, the anterior part being strongly declined. The point of strongest flexure lies in front of the projection γ-γ (tr.) in early holaspis specimens, including the lectotype (Fig. 2F$_2$), the curvature extending backwards in older stages at the expense of the progressively shortening horizontal profile of the posterior preoccipital glabella; in the largest specimens the preoccipital glabella is evenly vaulted from posterior to anterior, with the modestly elevated occipital ring only slightly interrupting the lateral profile. The proportional overall glabellar length increases in late ontogeny by the protrusion of the anterior lobe, whereas the transverse vaulting diminishes slightly. In young holaspids the occipital furrow is typically strongly sigmoidally curved forwards sagittally, so that the occipital ring impinges into the base of the preoccipital glabella (see original description by Richter and Richter 1913: 381), but this feature is less obvious in the largest specimens, where the occipital furrow is only slightly and evenly curved forwards with the L1 lobes shifted backwards to a relatively small extent. Glabellar furrows, especially the posterior ones, are particularly deeply impressed during the meraspis period, though becoming progressively shallower with growth. Four pairs of glabellar furrows are discernable in early meraspids, whereas bifurcation of S1 furrows starts in late meraspids. In the early holaspis stage four pairs of furrows are deeply impressed and both branches of the bifurcated S1 reach approximately the same length, the anterior branch being slightly anteriorly directed (Fig. 2E$_1$ and F$_1$). In later holaspis stages the glabellar furrows become progressively shallower, S4 becomes effaced, and the anterior branch of S1 reduces in length and becomes directed backwards.

Granulose sculpture appears in late meraspid specimens and becomes the relatively coarse granulation of the entire exoskeleton during the early holaspis stage. The granulation
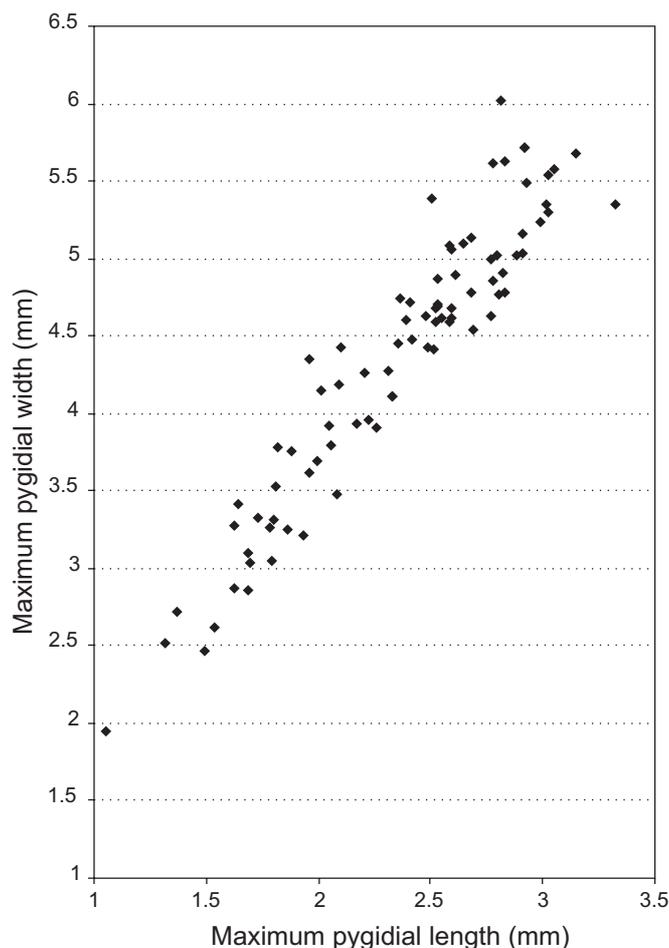

Fig. 6. Scatter plot of maximum sagittal length *versus* maximum width of the pygidium (excluding articulating half-ring) for 81 undistorted individuals.

decreases in size but increases in density thereafter. The median occipital node is large in early meraspids where it occupies most of the medial occipital ring; it decreases rapidly thereafter to become a tiny tubercle in the holaspis stage.

The shape of the librigena does not change markedly; the height of the eye increases slightly with growth, whereas the length of the genal spine diminishes. In the hypostome the posterior lobe elongates and becomes slightly flatter in older specimens whereas the anterior lobe concomitantly inflates.

Changes in shape particularly affect the meraspid transitory pygidium. These are due essentially to the generation of new pleural segments and continuous release of segments into the thorax after establishment of functional articulations. The youngest transitory pygidium of our sample measures 1.95 mm in width and 1.06 mm in length (Fig. 6), and has a narrow, parabolic posterior outline, with a faint postero-medial notch. In posterior view, the shield is relatively low, trapezoidal, with wide, flat inner pleural fields that only flex downwards close to the border. It has a high, rather long and narrow, posteriorly pointed axis with 9 axial rings and a fused end-piece. The anterior four segments may constitute future thoracic segments as their pleural

bands continue distinctly onto the border where they flex backwards in the border furrow before merging into a set of prominent crests that anticipate thoracic pleural spines. At this stage the posterior pleural bands dominate by far the anterior ones, both in height and breadth; however they are overridden in the border furrow by the backwardly curving anterior bands. These features, especially the well defined border and border furrow, the pointed axis that is connected to the border by a postaxial ridge and the faint postero-medial notch, characterize the early meraspid period. Thereafter the overall height and vault of the transitory pygidium increases and the axis continuously broadens whereas the postero-lateral borders enlarge considerably and the larval notch disappears. During the holaspid period the pygidium becomes highly vaulted. Related to this, its relative width diminishes and its posterior outline becomes parabolic or even semicircular. The axis broadens to become hyperbolic, with a broadly rounded posterior that approaches the border. The pleural fields progressively become more vaulted, whereas the border furrows, still well defined in young specimens, tend to vanish; some of the oldest specimens exhibit an unbroken curvature from the axial furrow down to the edge of the border. The pleural bands become equal in length and height, tending to form ribs defined by continuously deeper pleural furrows. Tiny terrace ridges appear on the external border in young holaspids, and these become numerous and much coarser in older specimens.

Conclusions

Evidence from the ontogenetic development of *Cyrtosymbole escoti* described here shows that the specimen described and figured by Richter (1913), erroneously represented by R. Richter, E. Richter, and Struve in the *Treatise* (1959: O391) as lacking an anterior border, and refigured by Alberti (1975) (Fig. 2F herein), is an early holaspis. Particular characters that demonstrate this include the presence of a preglabellar field bearing a plectrum-like depression, four deeply impressed glabellar furrows, marked sagittal widening of the occipital ring, strong downward flexure of the anterior part of the cranidium, and a sculpture of coarse granulation. Notwithstanding the fact that following numerical comparison, Alberti (1976: 40) was aware of the juvenile character of this specimen, he unfortunately designated it as the lectotype. Indeed, late holaspids of *C. escoti* differ from early ones to such an extent that they could be regarded as belonging to a different species. We thus agree entirely with Chlupáč's (1966: 119) statement that "single growth stages would necessarily be taken for independent species" when the necessary amount of material including morphs of different growth are unavailable.

In this regard it is important to give due consideration to the postlarval growth in *C. escoti*, a species that belongs to the ancestral group of a highly diversified clade of the Cyrto-

symbolinae, in order to recognize heterochronic processes that have operated in descendent lineages.

Acknowledgements

References

Alberti, H. 1975. Neue Trilobiten (*Waribole*) aus dem Ober-Devon IV–V (Nord-Afrika und Mittel-Europa) – Beitrag 4 – Revision einiger Typus-Spezies der Proetidae Salter, 1864, aus dem Ober-Devon II–V. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 150: 207–226.

Alberti, H. 1976. Neue Trilobiten (*Cyrtosymbole*) aus dem Ober-Devon II (Nord-Afrika und Mittel-Europa) – Beitrag 5. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 152: 19–50.

Becker, R.T. 1993. Stratigraphische Gliederung und Ammonoideen-Faunen im Nehdenium (Oberdevon II) von Europa und Nord-Afrika. *Courier Forschungsinstitut Senckenberg* 155: 1–405.

Becker, R.T. and Schreiber, G. 1994. Zur Trilobiten-Stratigraphie im Letmather Famennium (nördliches Rheinisches Schiefergebirge). *Berliner Geowissenschaftliche Abhandlungen E* 13: 369–387.

Brauckmann, C. 1985. Eine weitere Art der Cyrtosymbolinae mit vollständig erhaltenem Thorax (Trilobita, Ober-Devon). *Jahresberichte des naturwissenschaftlichen Vereins von Wuppertal* 38: 150–153.

Chatterton, B.D.E. 1971. Taxonomy and ontogeny of Siluro-Devonian trilobites from near Yass, New South Wales. *Palaeontographica A* 137: 1–108.

Chatterton, B.D.E., Edgecombe, G.D., Vaccari, N.E., and Waisfeld, B.G. 1999. Ontogenies of some Ordovician Telephinidae from Argentina, and larval patterns in the Proetida (Trilobita). *Journal of Paleontology* 73: 219–239.

Chlupáč, I. 1966. The Upper Devonian and Lower Carboniferous Trilobites of the Moravian Karst. *Sborník geologických věd* P, 7: 5–143.

Clarkson, E.N.K. and Zhang Xi-guang 1991. Ontogeny of the Carboniferous trilobite *Paladin eichwaldi shunnerensis* (King 1914). *Transactions of the Royal Society of Edinburgh: Earth Sciences* 82: 277–295.

Drevermann, F. 1901. Die Fauna der oberdevonischen Tuffbreccie von Langenaubach bei Haiger. *Jahrbuch der königlich preussischen geologischen Landes-Anstalt und Bergakademie* 21: 99–207.

Feist, R. 1977. *Le Siluro-Dévonien du Sud-Est de la Montagne Noire (Hérault, France) et ses faunes de Trilobites*. 251 pp. Unpublished Ph.D. thesis, University of Montpellier, Montpellier.

Feist, R. 1985. Devonian Stratigraphy of the Southeastern Montagne Noire (France). *Courier Forschungsinstitut Senckenberg* 75: 331–352.

Feist, R. and Becker, R.T. 1997. Discovery of Famennian Trilobites in Australia (Late Devonian, Canning Basin, NW Australia). *Geobios, Mémoire Spécial* 20: 231–242.

Feist, R., Lemke, U., and Korn, D. 2000. Trilobiten aus der *Wocklumeria*-Stufe des höchsten Oberdevon von Apricke, Sauerland. *Senckenbergiana lethaea* 79: 517–539.

Feist, R., Yasdi, M., and Becker, T. 2003. Famennian trilobites from the Shotori Range, E-Iran. *Annales de la Société Géologique du Nord* 10: 285–295.

Frech, F. 1887. Die paläozoischen Bildungen von Cabrières. *Zeitschrift der deutschen geologischen Gesellschaft* 39: 360–485.

Gröning, E. 1986. Revision der Gattung *Liobole* (Trilobita, Unter-Karbon). *Courier Forschungsinstitut Senckenberg* 80: 1–216.

Gürich, G. 1896. Das Palaeozoicum im Polnischen Mittelgebirge. *Verhandlungen der Russisch Kaiserlichen Mineralogischen Gesellschaft, St. Petersburg* 32 (2): 1–539.

Haas, W., Hahn, G., and Hahn, R. 1980. Perm-Trilobiten aus Afghanistan. *Palaeontographica A* 169: 73–127.

Hahn, G. and Brauckmann, C. 1984. Zur Kenntnis ober-devonischer Trilobiten aus dem Bergischen Land. *Jahresberichte des naturwissenschaftlichen Vereins Wuppertal* 37: 116–124.

Hahn, G. and Hahn, R. 1967. Zur Phylogenie der Proetidae (Trilobita) des Karbons und Perms. *Zoologische Beiträge, neue Folge* 13: 303–349.

Hahn, G. and Hahn, R. 1971. Trilobiten aus dem unteren Teil der *crenistria*-Zone (Unter-Karbon, cu IIIα$_{1–2}$) des Rheinischen Schiefer-Gebirges. *Senckenbergiana Lethaea* 52: 457–499.

Hahn, G. and Hahn, R. 1975. Die Trilobiten des Ober-Devon, Karbon und Perm. *In*: K. Krömmelbein (ed.), *Leitfossilien 1*, 1–127. Gebrüder Borntraeger, Berlin.

Hahn, G., Hahn, R., and Brauckmann, C. 1980. Die Trilobiten des belgischen Kohlenkalkes (Unter-Karbon). 1. Proetinae, Cyrtosymbolinae und Aulacopleuridae. *Geologica et Palaeontologica* 14: 163–188.

Hahn, G., Hahn, R., and Brauckmann, C. 1982. *Catalogus Fossilium Austriae. Heft VII/a Trilobita*. 148 pp. Österreichische Akademie der Wissenschaften, Wien.

Hawle, I. and Corda, A.J.C. 1847. Prodrom einer Monographie der böhmischen Trilobiten. *Abhandlungen der königlichen böhmischen Gesellschaft der Wissenschaften* 5 (5): 1–176.

Hupé, P. 1953. Classe des Trilobites. *In*: J. Piveteau (ed.), *Traité de Paléontologie III*, 44–246. Masson, Paris.

King, W.B.R. 1914. A new trilobite from the Millstone Grit of North Yorkshire. *Geological Magazine* 63: 390–394.

Koenen, A. von 1886. Ueber Clymenienkalk und Mitteldevon resp. Hercynkalk? Bei Montpellier. *Neues Jahrbuch für Mineralogie* 1: 163–167.

Lerosey-Aubril, R. and Feist, R. 2005a. First Carboniferous protaspid larvae (Trilobita). *Journal of Paleontology* 79: 702–718.

Lerosey-Aubril, R. and Feist, R. 2005b. Ontogeny of a new cyrtosymboline trilobite from the Famennian of Morocco. *Acta Palaeontologica Polonica* 50: 449–464.

Maksimova, Z.A. 1955. Trilobites from the Middle and Upper Devonian of the Urals and northern Mugodjar [in Russian]. *Trudy Vsesoúznogo Naučno-Issledovatel'skogo Geologičeskogo Instituto* 3: 1–263.

Meek, F.B. and Worthen, A.H. 1865. Contributions to the paleontology of Illinois and other western states. *Academy of Natural Sciences of Philadelphia, Proceedings* 1865: 245–273.

Oehlert, M.D. 1886. Étude sur quelques trilobites du groupe de Proetidae. *Bulletin de la Société d'Études Scientifiques d'Angers, n. s.* 15 (1885): 121–143.

Osmólska, H. 1962. Famennian and Lower Carboniferous Cyrtosymbolinae (Trilobita) from the Holy Cross Mountains, Poland. *Acta Palaeontologica Polonica* 7: 53–222.

Owens, R.M. and Tilsley, J.W. 1995. An atheloptic trilobite assemblage from the Carboniferous of North Devon. *Geological Magazine* 132: 713–728.

Pabian, R.K., Borovich, J., and Mapes, R.H. 1993. Growth stages of the Middle and Late Pennsylvanian Trilobite *Ditomopyge scitula* from the North American Midcontinent. *Journal of Paleontology* 67: 230–240.

Perna, A. 1915. Upper Devonian Trilobites from the environ of the Town Vierkhnie-Uralsk, Government Orenburg [in Russian with abridged English version]. *Mémoires du Comité Géologique. Nouvelle série* 138: 1–58.

Richter, R. 1912. Beiträge zur Kenntnis devonischer Trilobiten. I. Die Gattung *Dechenella* und einige verwandte Formen. *Abhandlungen der senckenbergischen naturforschenden Gesellschaft* 31: 241–340.

Richter, R. 1913. Beiträge zur Kenntnis devonischer Trilobiten. II. Oberdevonische Proetiden. *Abhandlungen der senckenbergischen naturforschenden Gesellschaft* 31: 341–393.

Richter, R. and Richter, E. 1919. Proetiden aus neueren Aufsammlungen im vogtländischen und sudetischen Oberdevon. *Senckenbergiana* 1 (4): 97–130.

Richter, R. and Richter, E. 1926. Die Trilobiten des Oberdevon. Beiträge zur Kenntnis devonischer Trilobiten 4. *Abhandlungen der Preussischen Geologischen Landes-Anstalt, neue Folge* 99: 1–314.

Richter, R., Richter, E., and Struve, W. 1959. Proetidae. *In*: R.C. Moore (ed.), *Treatise on Invertebrate Paleontology, part O, Arthropoda 1*, O389–O391. Geological Society of America and University of Kansas Press, Lawrence.

Rouville, P.-G. de 1886. Monographie géologique de la commune de Cabrières. *Mémoires de l'Académie de Montpellier, section Sciences* 11: 75–132.

Yuan, J.L. 1988. Proetiden aus dem jüngeren Oberdevon von Süd-China. *Palaeontographica A* 201: 1–102.

Yuan, J.L. and Xiang, L. 1998. Trilobite fauna at the Devonian-Carboniferous boundary in South China (S-Guizhou and N-Guangxi). *National Museum of Natural Science, Taiwan, Special publication* 8: 1–281.

Ziegler, W. 1962. Taxonomie und Phylogenie Oberdevonischer Conodonten und ihre stratigraphische Bedeutung. *Abhandlungen des hessischen Landesamtes für Bodenforschung* 38: 1–166.