



Permian Trilobites from Antalya Province, Turkey, and Enrollment in Late Palaeozoic Trilobites

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Abstract: Trilobites are a minor component of Permian benthic marine faunas, which explains why they remain poorly known. For example, only two specimens have been found in the highly fossiliferous and extensively studied Middle-Upper Permian Pamucak Formation (Antalya Province, Turkey). These two complete enrolled trilobites of Wordian age are described herein. The diagnosis of the subgenus *Pseudophillipsia* (*Nodiphillipsia*) Kobayashi & Hamada 1984a is emended and its occurrence outside of eastern Asia is reported for the first time. The second specimen represents a new species, *Pseudophillipsia* (*Carniphillipsia*) *kemerensis* sp. nov. Its discovery in the Wordian of Turkey suggests that *Pseudophillipsia* (*Carniphillipsia*) is no less diversified in the Middle Permian than in the Early Permian. Both specimens exhibit a particular enrollment posture, with the anterior part of the pygidium located within the cephalic cavity, while its posterior part is adpressed against the anterior cephalic doublure. The advantages of this style of enrollment are discussed, especially with regards to resistance of the enrolled body to external pressures, and rare examples of similar postures in older trilobites are reported. These two specimens are the first Permian trilobites from Turkey to be described, thus complementing the poor fossil record of these organisms in the Permian of southwestern Asia.

Key Words: Trilobita, Ditomopyginae, Permian, Wordian, Turkey, Pamucak Formation, enrollment

Antalya Bölgesinden (Türkiye) Permiyen Trilobitleri, ve Geç Paleozoyik Trilobitlerindeki Kayıtları

Özet: Trilobitler Permiyen bentik deniz faunasının minör bileşenlerinden biridir ve bu özellikleri trilobitler hakkındaki bilgilerin neden sınırlı olduğunu da açıklamaktadır. Örneğin, ayrıntılı Orta-Geç Permiyen yaşlı Pamucak Formasyonu'nun (Antalya Bölgesi, Türkiye) bol fosilli seviyelerinden derlenen örneklerden sadece iki numune trilobit bulunmuştur. Bu makalede Wordiyen yaşlı bu iki trilobit örneği tanımlanacaktır. Sub cins *Pseudophillipsia* (*Nodiphillipsia*) Kobayashi & Hamada 1984a nim tanımı yeniden düzenlenmiş ve doğu Asya dışında ilk kez tanımlanmıştır. İkinci örnek yeni bir tür olan *Pseudophillipsia* (*Carniphillipsia*) *kemerensis* sp. nov. yı temsil etmektedir. Türkiye Wordiyen'inde *Pseudophillipsia* (*Carniphillipsia*) bulgusu bu türün Orta Permiyende de Erken Permiyende olduğu kadar çeşitlendiği izlemine bırakmaktadır.

Her iki numune özel bir durumu kayıt etmektedir; şöyleki, pygidium'un ön bölümü cephalic oyuğun içine yerleşmişken geri bölümü öndeki cephalic doublure karşı dayanmıştır. Bu stilin avantajları, özellikle dışardan gelen baskılara karşı gelişen direniş, tartışılmış, yaşlı trilobitlerdeki benzer konumlar rapor edilmiştir. Bu iki form Türkiye'de tanımlanan ilk Permiyen trilobitleri olurken, güneybatı Asya'nın Permiye'nindeki zayıf fosil kayıtlarını da tamamlayıcı niteliktedir.

Anahtar Sözcükler: Trilobita, Ditomopyginae, Permiyen, Wordiyen, Türkiye, Pamucak Formasyonu, kaydetme

Introduction

Little attention has been paid to trilobites with reference to the Permian extinction events. As stated by Owens (2003), this probably stems from the fact they represent a minor component of benthic marine faunas at that time. However, detailed studies (Brezinski 1999; Owens 2003) have demonstrated that the evolution of trilobite diversity during the Permian followed a more complex pattern than the general rather simplistic view of a slow and steady decrease, ending with the 'coup de grace' of the Permo-Triassic biocrisis and the extinction of the group. The complexity of this pattern suggests that it may mirror, at least to some extent, diversity patterns of more abundant marine taxa (e.g., corals, fusulinids and brachiopods) and, more generally, the pattern of evolution of biodiversity during this period. It has been shown, for example, that a significant decrease of trilobite diversity occurred at the end-Guadalupian (Owens 2003). A similar abrupt decline of diversity at this time has been observed in major Permian marine taxa, such as corals (Wang & Sugiyama 2000), fusulinids (Stanley & Yang 1994) and brachiopods (Shi & Shen 1999), which led to the claim that a sixth mass extinction, besides the 'big five', marked the end of the Guadalupian (Stanley & Yang 1994; Wang *et al.* 2004; Retallack *et al.* 2006). Thus, it appears that trilobites may contribute, to some extent, to the investigation of the origin and modalities of the main changes in biodiversity during the Permian. This stresses the need for a precise description of the evolution of their diversity during this period, and Permian trilobites being rare, each newly discovered specimen is of particular importance in order to achieve this objective.

This contribution constitutes the second report but the first description of Permian trilobites from Turkey. Previously, the discovery of a single pygidium in the Hazro region (Diyarbakır Province) indicated that Permian trilobites occurred in this country (Canuti *et al.* 1970). However, the specimen was too poorly preserved to be properly described and therefore was only figured and assigned tentatively to *Pseudophillipsia*. The faunule described herein is composed of one, probably two new species, *P. (Carniphillipsia) kemerensis* sp. nov. and

Pseudophillipsia (Nodiphillipsia) aff. obtusicauda, this latter subgenus being reported for the first time outside eastern Asia. Both species exhibit a particular enrollment posture, the efficiency of which is discussed in detail.

Geological Setting

The trilobites were collected from the Middle–Upper Permian Pamucak Formation (Lys & Marcoux 1978), a 400–600-metre-thick succession of inner to outer platform well-bedded bioclastic wackestones and packstones, cherty limestones and marlstones, belonging to the Upper Antalya Nappes (Western Taurus), a system of thrust sheets cropping out along Antalya Bay (Marcoux *et al.* 1989) (Figure 1a). The Pamucak Formation is rich in calcareous algae, foraminifers, brachiopods, ostracods, conodonts, echinoderms, and bryozoans, most of which have been described in recent papers (Crasquin-Soleau *et al.* 2002, 2004a, b; Angiolini *et al.* 2007).

The trilobites were collected in marlstones and marly limestones from a four-metre-thick outcrop at Kemer Gorge (36°37'08"N, 30°29'12"E; Figure 1b). These beds are very rich in fusulinids (*Polydiexodina bythinica*, *P. afghanensis*) and correspond to unit III of Lys & Marcoux (1978) of Wordian (Guadalupian) age (Figure 1c). Moreover, they yielded a brachiopod fauna dominated by semi-infaunal concavo-convex spiny productids, interpreted as usually having thrived on quiet water, muddy bottoms with low or moderate nutrient supply. Pedunculate spiriferids and large photozoan fusulinids are also present. The latter are considered to have had photosymbionts and therefore their occurrence may indicate low nutrient supply and clear, shallow water. In summary, the setting was probably a quiet, protected shallow water embayment.

The described and figured specimens are housed in the collection of the Museum of Palaeontology, Department of Earth Sciences 'A. Desio', University of Milan (MPUM 9734, 9735).

Systematic Palaeontology

Terminology. Morphological terms and abbreviations used herein follow those defined by Whittington *et*

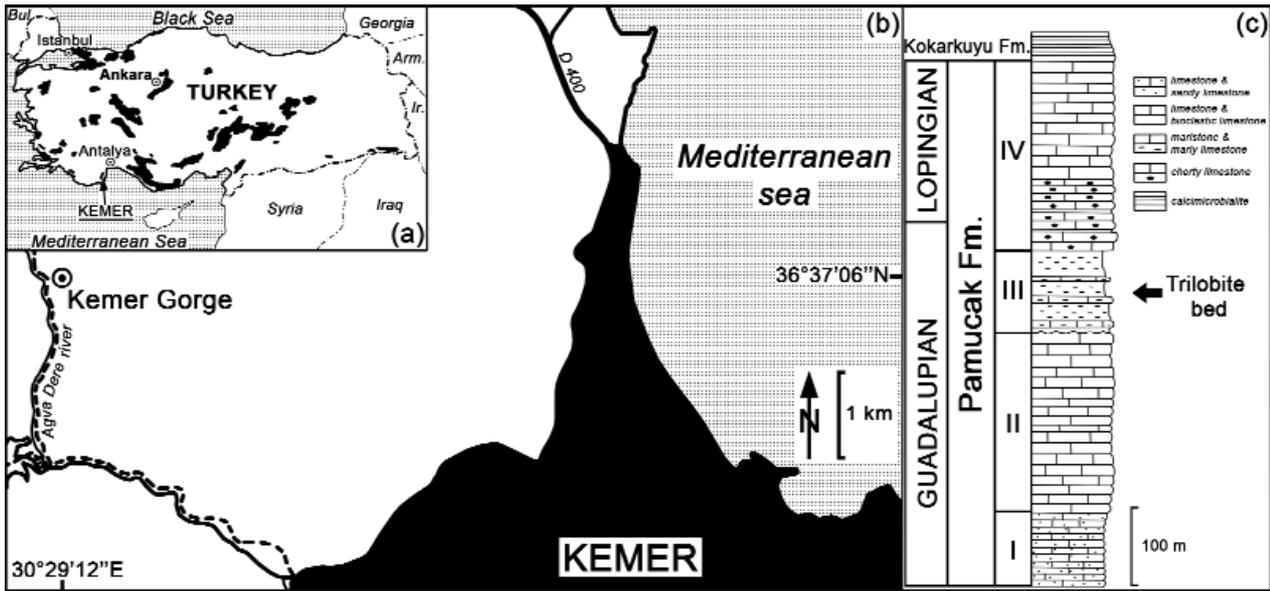


Figure 1. Location of the trilobite bed. (a) Palaeozoic (undivided) outcrops in Turkey (black areas) and location of the city of Kemer, Antalya province (simplified after Dean 2005). (b) Location of the Kemer Gorge, about five kilometres northwest of Kemer. (c) Vertical section across the Pamucak Formation showing the level of the trilobite bed (modified after Lys & Marcoux 1978).

al. (1997). ‘Main glabellar lobe’ designates that part of the glabella in front of preoccipital lobes. ‘Anterior glabellar furrows’ refers to glabellar furrows S2 to S4.

Order Proetida Fortey & Owens 1975

Family Phillipsiidae Oehlert 1886

Subfamily Ditomopyginae Hupé 1953

Genus *Pseudophillipsia* Gemmellaro 1892

Subgenus *Pseudophillipsia* (*Carniphillipsia*) Hahn & Brauckmann 1975.

Type Species. *Pseudophillipsia ogivalis* Gauri 1965, from the Lower Kasimovian (Pennsylvanian) of the Zoellner Ridge near Waidegger-Alm, Carnic Alps, Austria.

Diagnosis. See Hahn & Hahn 1987, p. 588.

***Pseudophillipsia* (*Carniphillipsia*)**

kemerensis sp. nov.

Figures 2a–f

Derivatio Nominis. After the type locality.

Holotypus (*Monotypus*). Complete enrolled specimen, slightly deformed anteriorly, more severely distorted in the pygidial region (Figure 2a–f), MPUM 9734.

Locus Typicus. Kemer Gorge, Taurus Mountains, about five kilometres west of Kemer, Antalya province, Turkey (Figure 1a, b).

Stratum Typicum. Marlstones and marly limestones, middle part of the Pamucak Formation, Wordian (Guadalupian) (Figure 1c).

Diagnosis. A species of *Pseudophillipsia* (*Carniphillipsia*) displaying the following combination of characters: cephalic border convex forwards and short (sag.) medially, and in lateral view rather narrow anteriorly but significantly and abruptly increasing in height posteriorly; main glabellar lobe especially convex forwards, relatively narrow (tr.) anteriorly but wide (tr.) and inflated posteriorly, bearing three pairs of faint and narrow glabellar furrows (S2–S4); subparallel-sided and rather narrow (tr.) posterior glabella; median preoccipital lobe short (sag.), wide (tr.), very low, and

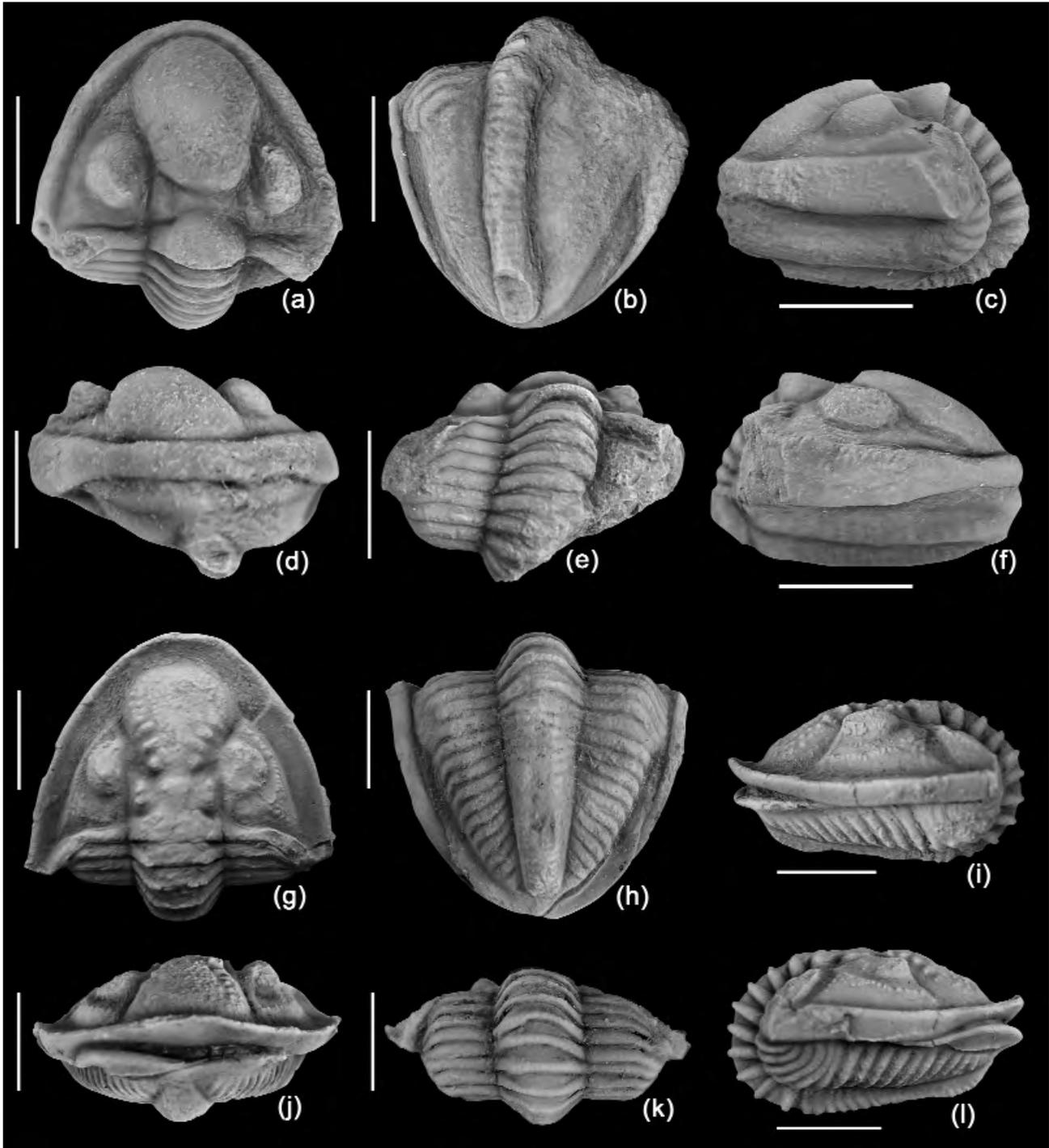


Figure 2. (a)–(f) *Pseudophillipsia (Carniphillipsia) kemerensis* sp. nov., holotype, enrolled specimen with severely distorted pygidial region, Pamucak Formation, Wordian, Kemer Gorge, MPUM9734, (a) cephalon, (b) pygidium, (c) left lateral view, (d) frontal view, (e) thorax, (f) right lateral view. (g)–(l), *Pseudophillipsia (Nodiphillipsia)* aff. *obtusicauda*, enrolled, partially exfoliated specimen with posterior part of the glabella and pygidial axis weathered, Pamucak Formation, Wordian, Kemer Gorge, MPUM9735, (g) cephalon, (h) pygidium, (i) left lateral view, (j) frontal view, (k) thorax, (l) right lateral view. Scale bars 5 mm.

poorly separated from low and narrow (tr.) L1; SO strongly convex forwards; occipital ring long (sag.), distinctly narrowing abaxially, and lacking occipital node; palpebral lobes wide (tr.) and rather anteriorly located; genal spine with a particularly wide base; pygidium with 21 ± 1 axial rings.

Description. Cephalon of strongly parabolic outline (Figure 2a). Glabella rather slender, long (sag.), and almost parallel-sided posteriorly; dorsal furrow broad and rather deep, slightly shallowing anteriorly; SO deep abaxially, strongly shallowing and curving forwards medially; occipital ring long (sag.), distinctly narrowing (exs.) abaxially, and lacking median node; lateral and median preoccipital lobes delimited by furrows running obliquely from axial furrows, where they are broad and deep, toward SO, then rapidly splitting into very weak anterior and posterior branches; lateral preoccipital lobe (L1) narrow (tr.), slightly longer than palpebral lobe (exs.); median preoccipital lobe short (sag.), wide (tr.), and only weakly inflated; main glabellar lobe rather wide (tr.) posteriorly, only moderately widening (tr.) anteriorly, with strongly forwardly convex anterior margin, and bearing three short and shallow furrows along left postero-lateral margin (not discernible on the right side). α located roughly in line (exsag.) with γ and ϵ , α - β and β - γ long and respectively diverging and converging (c. 40° for both), γ - δ and δ - ϵ respectively diverging and converging (c. 40° for both) defining wide (tr.) and rather anteriorly located palpebral lobes, ϵ - ζ rather long and sub-parallel, ζ - ω rather short and strongly diverging (c. 60°). Anterior and especially posterior fixigenal fields narrow (tr.). Eye rather narrow (tr.) and kidney-shaped. Librigenal field narrow (tr.) except posterior to eye, where it widens. Posterior border furrow deep, shallowing adaxially, and rather narrow; posterior border narrow (exs.) adaxially, abruptly and strongly widening abaxially from about mid-length (tr.), and inflated. Cephalic border rather narrow in dorsal view, slightly narrowing anteriorly due to forward protrusion of glabella, separated from this latter and librigenal field by broad but rather deep furrow; genal spine broken but apparently provided with a wide base. In lateral view (Figures 2c, f), cranidium vaulted. Occipital ring high

posteriorly and sloping forwards; glabella moderately inflated, higher than occipital ring posteriorly, increasingly sloping forwards; modest height of median preoccipital lobe obvious; visual area rather low (Figure 2c), provided with a narrow socle lying in a subvertical plane (Figure 2f). Posterior two-thirds of cephalic border especially high while anterior third narrows markedly (Figure 2f). In anterior view (Figure 2d), glabella particularly high, exceeding height of palpebral lobes. Lateral cephalic border almost vertical. Cephalic doublure only partially visible around the pygidium but apparently convex (Figure 2b). Sculpture: numerous thin terrace ridges are visible in lateral view on the base and possibly at the top of the posterior part of lateral cephalic border and on the corresponding doublure; otherwise, cephalon entirely smooth.

Nine thoracic segments of roughly similar proportions (Figure 2e). Axial rings rather wide [c. about a third of the maximum width of segments (tr.)], rather short (sag.) but widening slightly (exs.) abaxially, and apparently devoid of preannulus; articulating half-rings long [c. roughly the length of axial rings (sag.)]. Pleurae divided into a horizontal, straight inner part [about one-third of pleural width (tr.)] and an almost straight outer part – this latter is backwardly and ventrally flexed in anterior segments (Figure 2e) but progressively becomes more convex backwards and ventrally flexed in posteriormost segments (Figure 2c); no pleural furrows discernible. In lateral view (Figure 2c, f), axial rings rather low. Sculpture: thorax entirely smooth.

Pygidium deformed but apparently of strongly parabolic outline (Figure 2b). Axis long (c. ninety five percent of the sagittal length of the pygidium), reaching posterior border, and apparently rounded in section (tr.); 21 ± 1 axial rings, decreasing in width (sag.) from anterior to posterior, and delimited by very weak furrows. Pleural field subdivided in a horizontal inner and strongly downwardly flexed outer parts (Figure 2d); inconspicuous pleural furrows discernible along right pleural field (Figure 2f). Pygidial border separated from pleural field by a moderate break in slope and apparently gradually decreasing in width from front to rear in dorsal view, as it progressively lies in a more vertical plane and slightly inflates. Sculpture: few thin and

amalgamated terrace ridges occur on pygidial border along its posterior margin.

Comparisons. The distinction between *Pseudophillipsia* (*Pseudophillipsia*) and *Pseudophillipsia* (*Carniphillipsia*) is clear when cephalic characters are known, but is difficult to make on pygidial features alone. Indeed, *Pseudophillipsia* (*Pseudophillipsia*) is supposed to exhibit a more-segmented pygidial axis (i.e. 20-27 axial rings; Hahn & Brauckmann 1975), but many species of *Pseudophillipsia* (*Carniphillipsia*), including *P. (C.) kemerensis* sp. nov., possess 20 or more axial rings. Thus, only species assigned with certainty (i.e. with known cephalic morphology) to *Pseudophillipsia* (*Carniphillipsia*) are considered here. The pygidium discovered in the Permian of the Hazro region (Canuti *et al.* 1970) is too poorly preserved to be compared with the specimens described herein and consequently will not be considered further.

According to Hahn & Hahn (1987), three different groups can be recognized within the seventeen species that they assigned confidently to *Pseudophillipsia* (*Carniphillipsia*). The *ogivalis*-group [i.e. *P. (C.) collendiaulensis* Hahn & Hahn 1987, *P. (C.) ogivalis* Gauri 1965, *P. (C.) savensis* Hahn & Hahn in Hahn *et al.* 1977, *P. (C.) semicircularis* Gauri 1965 (later recognized as a synonym of *P. (C.) ogivalis*; see Hahn *et al.* 1989), and *P. (C.) triangulata* Ju in Zhang 1982] is characterized by the occurrence of laterally depressed areas on the main glabellar lobe. This feature is not apparent in *P. (C.) kemerensis* sp. nov., which differentiates it from all species of the *ogivalis*-group.

The second group of Hahn & Hahn (1987), the *rakoveci*-group, comprises species with the main glabellar lobe devoid of laterally depressed areas or furrows. Accordingly, the presence of anterior glabellar furrows in *P. (C.) kemerensis* sp. nov. should be sufficient to differentiate this species from members of this group. However, the anterior glabellar furrows are especially weak in the new species and consequently, they may be hardly discernible or absent in a poorly preserved specimen, possibly leading to its misassignment. Also, some

additional characters distinguishing *P. (C.) kemerensis* sp. nov. from the members of the *rakoveci*-group are noted in Table 1.

The characteristic of the third group of Hahn & Hahn (1987), i.e. the *lipara*-group, is the occurrence of anterior glabellar furrows. As this feature is present in *P. (C.) kemerensis* sp. nov. (Figure 2a, c), it should be regarded as a member of this group. With the exception of *P. (C.) praepermica* (Weber 1933), a geographically widespread and possibly polyphyletic (see Haas *et al.* 1980, p. 106) taxon from the Donetz Basin in the western part of the former USSR, the representatives of this group are all of Early to Middle Permian age. Like *P. (C.) schoeningi*, *P. (C.) praepermica* exhibits a particularly short (sag.) median preoccipital lobe, which easily differentiates it from *P. (C.) kemerensis* sp. nov. The characters distinguishing the new species from the members of the *lipara*-group (i.e. as originally defined; Hahn & Hahn 1987) are listed in Table 1.

Hahn *et al.* (1989) described *P. (C.) lepta*, and reassigned five species to *Pseudophillipsia* (*Carniphillipsia*): *Ditomopyge emilianensis* Gandl 1987, *Ditomopyge kunlunensis* Zhang 1983, *Jinia liulinensis* Zhang & Wang 1985, *Jinia longmentaensis* Zhang & Wang 1985, and *Pseudophillipsia pyriformis* Qian 1977. *D. emilianensis* and especially '*P. (C.) lepta*' exhibit a strongly inflated glabella that overhangs the cephalic anterior border (Gandl 1987, pl. 6, figs 90-91; Hahn *et al.* 1989, pl. 3, figs 1-3). In our opinion, this character precludes their attribution to *Pseudophillipsia* but indicates closer affinities with *Ditomopyge*, the genus to which these two species are here assigned. The holotype cranidium of '*Ditomopyge kunlunensis*' figured by Zhang (1983, pl. 187, fig. 12) is too poorly preserved to be properly attributed to a genus, and *a fortiori* to be compared at a specific level. In our opinion, its general aspect does not favour the reassignment to *P. (Carniphillipsia)*, although the associated pygidium (Zhang 1983, pl. 187, fig. 13) may belong to this subgenus. Hahn *et al.* (1989, p. 135) considered that the holotype cephalon and a pygidium of the type species *Jinia liulinensis* figured by Zhang & Wang (1985, pl. 147, figs 1, 6) represent a species of *Pseudophillipsia* (*Carniphillipsia*). This should consequently lead *Jinia* being considered a junior

synonym of *P. (Carniphillipsia)*. However, this assumption stems from the fact the holotype cephalon may display a median preoccipital lobe, which is not obvious on the figures of Zhang & Wang (1985, pl. 147, figs 1, 1a), especially on their figure 1a, where a median lobe located behind the main glabellar lobe may represent either a preoccipital median lobe or the occipital ring. The absence of glabellar furrows was considered by Zhang & Wang (1985, p. 483) an important diagnostic character of the genus *Jinia*. In addition, a preoccipital median lobe is nowhere mentioned in the diagnosis or the descriptions of *Jinia* and its type species, and its absence is obvious on the two of the three cranidia figured by Zhang & Wang (1985, pl. 147, figs 2, 3). Accordingly, we do not believe these authors have erroneously associated specimens with a difference as important as the presence/absence of a median preoccipital lobe, as suspected by Hahn *et al.* (1989). We do not, however, exclude the possibility that they overlooked small and only faintly inflated lateral preoccipital lobes in *J. liulinensis*, especially when we consider that at least two of the three specimens figured have obviously not been prepared in the region where these lobes would be located (Zhang & Wang 1985, pl. 147, figs 2, 3). We also agree with Hahn *et al.* (1989) that these two specimens belong to a species of *Paladin* (*s.l.*), probably morphologically close to species such as *Paladin eichwaldi shunnerensis* (King 1914), with a similar shape of the main glabellar lobe, as well as short (exsag.) and rather low L1 (e.g., Clarkson & Zhang 1991, figs 12d,e). We also suspect the holotype cephalon to be similar to the other two specimens figured by Zhang & Wang (1985) and to represent the same taxon. Recent phylogenetic analysis of the genus *Paladin* (*s.l.*) suggested that *P. eichwaldi* should be reassigned to *Weberides*, a genus morphologically close to *Paladin* (*s.s.*) but restricted to Europe (Brezinski 2003, 2005). Consequently, *Jinia liulinensis* and *J. longmentaensis* are here tentatively reassigned to *Weberides* and *Jinia* considered a subjective junior synonym of this latter genus. Lastly, we agree with the assignment by Hahn *et al.* (1989) of *Pseudophillipsia pyriformis* to *P. (Carniphillipsia)* and even advocate its inclusion within the *lipara*-group as it exhibits two pairs of anterior glabellar furrows. In so far as it can be determined from the

single partial cephalon (Qian 1977, pl. 1, fig. 6) known from this species, it differs from *P. (C.) kernerensis* sp. nov. in having a longer (sag.) cranial anterior border, an anteriorly less convex and posteriorly narrower (tr.) main glabellar lobe, and more inflated median and lateral preoccipital lobes, differentiated by deeper furrows (Table 1).

An undetermined species of *P. (Carniphillipsia)* was described recently from the Permian of Central Iran by Feist, Yazdi, and Ghobadi Pour (in Mistiaen *et al.* 2000, pl. 8, figs 2, 3). This species is here reassigned with caution to *P. (Carniphillipsia)* as a photograph of the only known and badly altered specimen shows strong anterior glabellar furrows and the occurrence of structures that may represent originally raised, but secondarily weathered L2-L4 (Mistiaen *et al.* 2000, pl. 8, fig. 2). Additional differences are summarized in Table 1.

Lastly, we here assign to *Pseudophillipsia (Carniphillipsia)* five previously described species: *P. chongqingensis* Lu 1974 (following Owens 1983), *P. heshanensis* Qian 1977 (following Owens 1983), *P. lui* Kobayashi & Hamada 1984b (originally described as '*P. obtusicauda* in Lu 1974), *P. reggorcakaensis* Qian 1981 (misnamed? *P. raggyorcakaensis* in the English summary of the original publication) and *Pseudophillipsia* sp. of Brezinski (1992). Among them, *P. (C.) lui* is included within the *lipara*-group, while the undetermined species of *Pseudophillipsia (Carniphillipsia)* described by Brezinski (1992) is considered a member of the *rakoveci*-group. Table 1 summarizes the characters displayed by *P. (C.) kernerensis* sp. nov. that enable its differentiation from all these taxa.

Genus *Pseudophillipsia* Gemmellaro 1892

Subgenus *Pseudophillipsia (Nodiphillipsia)*
Kobayashi & Hamada 1984a

Type Species. *Pseudophillipsia (Pseudophillipsia) spatulifera* Kobayashi & Hamada 1980, from the Middle Permian of Japan.

Assigned Species. *Pseudophillipsia (Pseudophillipsia) spatulifera* Kobayashi & Hamada 1980,

Table 1. Summary of the characters differentiating *Pseudophilipsia kernerensis* sp. nov. from all the other species attributed to *Pseudophilipsia* (*Carniophilipsia*), except the members of the *ogivalis*-group of Hahn & Hahn (1987). Remark: (1) Assigned herein to one of the groups defined by Hahn & Hahn (1987).

Taxa compared	Anterior margin of cranium	Cranial anterior border	Posterior glabella	Main glabella lobe	L1	Median prooccipital lobe	Occipital ring	Palpebral lobes	Genal spine	Librigenal border	Pygidial axial rings
<i>P. (C.) intermedia</i>	more forwardly convex	***	parallel-sided	- anteriorly narrower (tr.) - extending farther forwards	***	***	longer (sag.)	***	***	***	***
<i>P. (C.) javornikensis</i>	more forwardly convex	***	parallel-sided	- anteriorly narrower (tr.) - extending farther forwards	***	***	***	wider (tr.)	wider base	***	more
<i>P. (C.) mengshanensis</i>	more forwardly convex	***	parallel-sided	- anteriorly narrower (tr.) - extending farther forwards	***	***	***	wider (tr.)	wider base	***	***
<i>P. (C.) liparoides</i>	***	***	parallel-sided	- anteriorly narrower (tr.) - posteriorly wider (tr.) - more inflated	***	wider (tr.)	***	wider (tr.)	wider base	much higher	***
<i>P. (C.) rikoveci</i>	more forwardly convex	***	parallel-sided	- anteriorly narrower (tr.) - lacks median posterior sulcus	***	wider (tr.) shorter (sag.)	markedly shortens (exs.) axially	***	***	***	***
<i>P. (C.) schoeningi</i>	***	***	parallel-sided	***	***	longer (sag.)	- longer (sag.) - markedly shortens (exs.) axially	wider (tr.)	***	***	more
<i>P. (C.)</i> sp. from USA ⁽¹⁾	***	***	***	- anterior glabella furrows visible - smooth	***	***	- convex forwards SO	- more anteriorly located	***	***	***
<i>rvkoveci</i> Group											
<i>P. (C.) cooperationis</i>	more forwardly convex	***	***	- anteriorly narrower (tr.) - more forwardly convex - fainter anterior glabella furrows	- lower - longer (exs.)	- lower - shorter (sag.)	longer (sag.)	***	***	***	***
<i>P. (C.) lipara</i>	more forwardly convex	***	parallel-sided	- anteriorly narrower (tr.) - more forwardly convex - higher posteriorly	lower	- lower - shorter (sag.)	- longer (sag.) - no node	***	***	***	***
<i>P. (C.) loricata</i>	***	- shorter (sag.) - higher	***	- anteriorly narrower (tr.) - more forwardly convex - higher posteriorly	lower	lower	- shorter (sag.) - less convex backwards - no node	***	wider base	***	less
<i>P. (C.) lai</i> ⁽¹⁾	more forwardly convex	shorter (sag.)	***	- anteriorly narrower (tr.) - more forwardly convex	narrower (tr.)	lower	*** *** - shorter (exs.) - more anteriorly located	***	***	***	***
<i>P. (C.) praeparmitica</i>	***	***	***	***	***	longer (sag.)	***	***	***	***	***
<i>P. (C.) pyriformis</i> ⁽¹⁾	***	shorter (sag.)	***	- more forwardly convex - wider posteriorly (tr.)	more inflated	more inflated	***	***	***	***	***
<i>P. (C.) steatopyga</i>	***	***	***	***	***	lower	- less convex backwards	***	***	***	***
<i>lipara</i> Group											
<i>P. (C.) chongqingensis</i>	more forwardly convex	***	narrower (tr.)	narrower (tr.)	- lower - narrower (tr.)	- wider (tr.) - shorter (sag.)	longer (sag.)	***	wider base	***	***
<i>P. (C.) heshanensis</i>	more forwardly convex	shorter (sag.)	***	- more forwardly convex	***	shorter (sag.)	- longer (sag.) - more convex backwards	***	***	***	***
<i>P. (C.?)</i> sp. from Iran	***	***	***	- more forwardly convex - narrower (tr.) posteriorly	***	***	- longer (sag.) - more convex backwards	***	***	***	***
<i>P. (C.) reggocakensis</i>	***	shorter (sag.)	***	- anteriorly narrower (tr.) - posteriorly wider (tr.)	narrower (tr.)	- lower? - wider (tr.)	longer (sag.)	***	***	***	***
Others											

Pseudophillipsia (*Nodiphillipsia*) aff. *obtusicauda* herein. Tentatively assigned: *Pseudophillipsia* (*Nodiphillipsia*?) *obtusicauda* (Kayser 1883).

Emended Diagnosis. A subgenus of *Pseudophillipsia* characterized by the following features: cephalic border composed of a flat and rather wide rim with a crest at its margin, cephalic doublure partially upturned and V-shaped in cross section, genal spine blade-like.

Remarks. Hahn *et al.* (2001) pointed out that the occurrence of three small nodes instead of three lobes ('festooning') along the postero-lateral margin of the main glabellar lobe is only the result of preservation (nodes being present on internal moulds). As a consequence, they concluded that the subgenus *Pseudophillipsia* (*Nodiphillipsia*), initially based on this characteristic, should be restricted to the sole type species, *P. (N.) spatulifera*, this latter having peculiar, blade-like genal spines. The Turkish specimen of *P. (N.)* aff. *obtusicauda*, like *P. (N.) spatulifera*, exhibits a flat cephalic border somewhat curving dorsally along the margin and an outer part of the cephalic doublure lying in a plane increasingly inclined posteriorly relative to the horizontal plane. Also, although genal spines are broken in our specimen, it is highly probable they were very similar to that of *P. (N.) spatulifera*. We believe that this justifies our assignment of the Turkish taxon to the subgenus *P. (Nodiphillipsia)* and that we emend the diagnosis of this latter, so that it includes the characteristics of the cephalic border. To remain logical, we also tentatively reassign *P. (P.) obtusicauda* to *P. (Nodiphillipsia*?), although the fragmentary nature of the holotype of this species precludes the diagnostic features of the subgenus to be observed.

Pseudophillipsia (*Nodiphillipsia*) aff. *obtusicauda*

Figures 2g–l

Material. A complete, enrolled, and largely exfoliated specimen, with weathered posterior part of the glabella and pygidial axis (Figures 2g–l), MPUM9735.

Locality. Kemer Gorge, Taurus Mountains, about five kilometres west of the city of Kemer, Antalya province, Turkey (Figure 1a, b).

Horizon. Marlstones and marly limestones, middle part of the Pamucak Formation, Wordian (Guadalupian) (Figure 1c).

Description. Cephalon of strongly parabolic outline (Figure 2g). Glabella long (sag.), parallel-sided posteriorly, moderately broadening (tr.) and protruding forwards without reaching anterior margin medially; axial furrow broad and rather deep except opposite anterior half of palpebral lobe where it shallows and slightly curves outwards; SO broad, deep at the limits between medial and lateral thirds but shallows abaxially and particularly medially where, despite evidence of weathering, it seems to be faint and curves forwards; occipital ring broad (sag.), strongly narrowing (exs.) abaxially, no median node visible; lateral and median preoccipital lobes delimited by deep and broad furrows, running obliquely from depressed areas near axial furrows towards SO, then rapidly splitting into broad and shallow anterior branches that join medially, and broad and faint posterior branches; L1 triangular, roughly as long as palpebral lobe (exs.), and divided into two small nodes by a transverse furrow at mid-length (exs.); median preoccipital lobe somewhat trapezoidal and slightly inflated; main glabellar lobe bears three pairs of node-like lateral lobes (L2–L4) along its postero-lateral margins delimited by three pairs of deep and wide glabellar furrows (S2–S4), with L2 discoidal and L3 and L4 somewhat transversally elongated; another tubercle roughly similar in size and shape to L2 but not separated from the frontal lobe by a furrow anteriorly situated in front of L4 (Figure 2g). Facial suture with α located beyond δ , α - β very short, β - γ long and converging (c. 35°), γ - δ and δ - ϵ respectively diverging (c. 40°) and converging (c. 30°) defining rather large palpebral lobe, ϵ - ζ long and subparallel, ζ - η long and strongly diverging (c. 70°), η - ω short and diverging (c. 35°) with ω located as far abaxially as α ; anterior and posterior fixigenal fields narrow (tr.). Eye narrow (tr.) and kidney-shaped; eye-socle narrow (tr.) near δ but moderately widening anteriorly and posteriorly where it reaches γ and ϵ ; librigenal field narrow (tr.), except between eye-socle

and posterior border where it widens. Posterior border furrow broad, deep, and slightly shallowing and curving backwards adaxially; posterior border inflated, composed of a narrow (exs.) adaxial part running laterally and a moderately widening abaxial part running laterally and posteriorly. Cephalic border flat and wide, somewhat upturned near margin, although narrowing anteriorly due to anterior protrusion of glabella, separated from librigenal field and glabella by a strong break in slope rather than a distinct furrow; genal spines broken but obviously present. In lateral view (Figure 2i, l) cranidium moderately vaulted. Occipital ring rather flat, although this may be due to weathering; glabella slightly inflated and rather gently sloping forwards. Eye low. Doublure folded and apparently v-shaped in section (tr.), with only the wide outer part visible anteriorly, laterally, and ventrally (Figure 2h–j, l); this latter lays in a plane increasingly inclined posteriorly relative to the horizontal plane (from c. 35° to c. 50°; Figure 2j, l) and bears numerous very fine terrace ridges where cuticle has been preserved (not visible on Figure 2). Sculpture: glabella almost completely covered by heterogeneous tubercles that increase slightly in size laterally (Figure 2g); a row of similar coarse tubercles surrounds eye-socket and posterior border adaxially, while smaller tubercles cover postero-adaxial corner of librigenal field (Figure 2l).

Nine, very similar thoracic segments (Figure 2l). Axis rather wide [c. 40% of the maximum length of segments (tr.)], moderately and gently narrowing (tr.) from sixth to ninth segments, and composed of especially short (sag.) rings that lengthen (exs.) abaxially (Figure 2h, k); articulating half-rings particularly long [c. twice the length of axial rings (sag.); Figure 2k]. Pleurae composed of a straight, horizontal inner portion [about two-thirds of pleural width (tr.)] and a backwardly convex outer portion that flexes ventrally, the convexity of which increases in the posteriormost segments (Figure 2h, k, l); no pleural furrows discernible. In lateral view (Figure 2i, l), axial rings crest-like and relatively high compared with half-rings. Pleurae of the four anteriormost segments are hidden behind the posterior librigena, but those of the five posteriormost segments gently increasing in height from front to rear (representing two-thirds and three-quarters of the maximum height of respectively the fifth and the ninth

segments; Figure 2l). Sculpture: a row of inconspicuous tubercles runs along posterior margin of each axial ring.

Pygidium very slightly wider (tr.) than long (sag.) (width/length ratio: 1.1) and displaying concave lateral margins (Figure 2h). Axis long (c. ninety percent of the sagittal length of the pygidium), reaching posterior border furrow, narrow [c. one-third of the maximum width (tr.) of the pygidium anteriorly], gently narrowing rearwards, rounded posteriorly, and likely elliptical in transverse section; 20 ± 1 short (sag.) axial rings, delimited by shallow (anteriorly) to inconspicuous (posteriorly) inter-ring furrows, and shortening (sag.) from front to rear, especially in posterior two-fifths of axis. Pleural field subdivided into roughly horizontal inner two-thirds and a strongly downwards flexing outer third; twelve inflated pleural ribs; pleural furrows broad, increasing in depth abaxially, running in a straight line backwards adaxially then strongly curving backwards abaxially on the four anteriormost and the two posteriormost segments, but having a peculiar sigmoidal shape on segments five to ten (particularly obvious on the left side on Figure 2h); interpleural furrows probably superimposed on pleural furrows adaxially and thus hardly discernible from them - they are visible abaxially on some rare pleurae in the form of shallow and narrow lines located just behind pleural furrow of preceding segment, which demonstrates that the posterior band of a segment is represented mainly by pleural furrow. Pygidial border narrow and slightly upturned anteriorly, abruptly increasing in width just behind mid-length (sag.) of the pygidium, then constant in width and bearing very fine terrace ridges on its marginal edge (not discernible on Figure 2h). In lateral view, pygidium moderately vaulted. Although partially weathered, axis seems to be relatively low (e.g., hardly one-third of pygidial height anteriorly) and to progressively decrease in height rearwards (Figure 2i, l); in so far as it can be observed, pygidial border flat. No sculptural features discernible on the specimen.

Remarks. Hahn & Brauckmann (1975) redescribed *P. (N.?) obtusicauda* and refigured its holotype specimen. Unfortunately, this latter was not whitened and as a result, some details remain hardly

visible on the dark photographs. New illustrations of this specimen (Figure 3) show that it is similar to the specimen from the Wordian of Turkey, sharing with this latter the following characters: a flat glabella that is roughly parallel-sided posteriorly and rather moderately expanded (tr.) forwards, raised L2–L4, a short (sag.) and narrow (tr.) median preoccipital lobe, a particularly long (sag.) occipital ring, and pygidial pleural ribs of sigmoidal shape. However, compared with *P. (N.?) obtusicauda*, the Turkish specimen differs in having a narrower (tr.) posterior glabella, a slightly more inflated main glabellar lobe covered with heterogeneous tubercles, a wider (sag.) cephalic anterior border, L1 divided into two nodes, a flatter preoccipital lobe, and a flatter occipital ring. These latter two differences likely stem from an abrasion of the posterior glabella in the Turkish specimen. Likewise, only internal moulds of L1 are visible in this latter specimen, which may explain the presence of two nodes. The sculpture of the main glabellar lobe of *P. (N.?) obtusicauda* is also not known, as this part is exfoliated on the holotype (Figure 3a, b). Lastly, the cranidium of this latter is larger by *c.* 35 percent than that of the Turkish specimen, both in length and in width (see Hahn & Brauckmann 1975 for measurements of the holotype specimen). This suggests that the Turkish specimen most likely represents a younger holaspid stage, which may explain the moderate difference in glabellar height in lateral view. Alternatively, this difference may be a consequence of the deformation affecting the holotype specimen (Hahn &

Brauckmann 1975, p. 119). However, the new photographs of the holotype of *P. (N.?) obtusicauda* clearly show that, although exfoliated anteriorly, it has a shorter (sag. and exs.) anterior cephalic border than the Turkish specimen, indicating that the two specimens obviously belong to different species. Thus, the Turkish specimen likely represents a new species, but awaiting more and better preserved material, it is attributed to *P. (N.)* aff. *obtusicauda*.

The original material of *P. (N.?) obtusicauda* consists of a single specimen found in the Upper Permian (Lopingian) of South-East China (Jiangxi Province). Discoveries of *P. (N.?) obtusicauda* have been reported from other Chinese localities of Late Permian age, as well as from the Middle Permian of Japan. In China, Lu (1974) and Zhou (1977) attributed to this species specimens found respectively in the Sichuan and the Guangxi Provinces. Both attributions were incorrect, as already pointed out by Kobayashi & Hamada (1984b, p. 52). The material described by Lu (1974) was even used by these authors to create, in a somewhat peculiar way, *P. (C.) lui* (Kobayashi & Hamada 1984b, p. 52), that we here assign to the subgenus *P. (Carniphillipsia)* (see above). The pygidium described by Zhou (1977) is particularly acuminate posteriorly, unlike in *P. (N.?) obtusicauda*, which indicates that it has been misassigned (Kobayashi & Hamada 1984b, p. 52). We therefore propose to attribute this isolated pygidium to an undetermined species of *Pseudophillipsia*. Several authors have

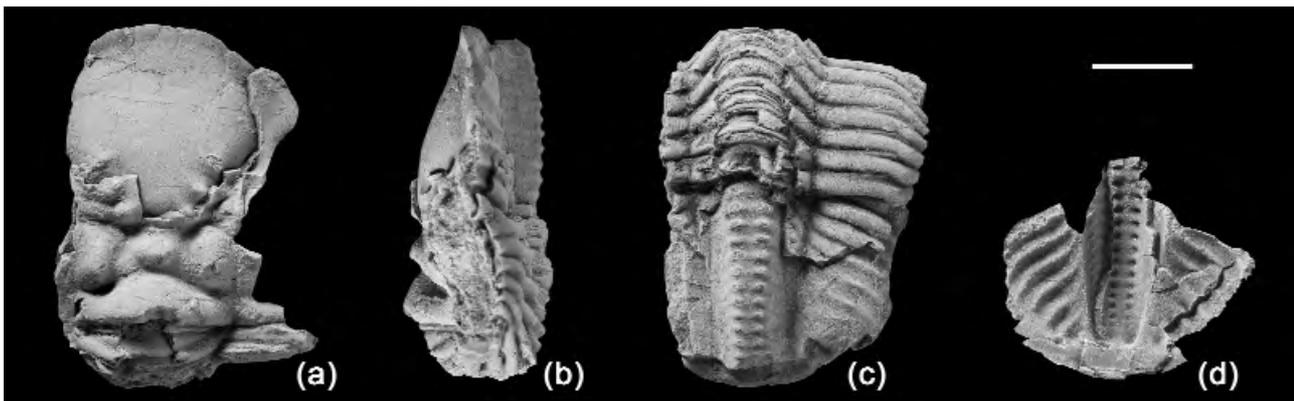


Figure 3. (a)–(d) *Pseudophillipsia (Nodiphillipsia?) obtusicauda* (Kayser 1883), holotype, Lopingian, Jiangxi Province (South-East China), MB.T.5103 (Museum für Naturkunde, Berlin), (a) cranidium in dorsal view, (b) right-lateral view, (c) posterior thorax and exfoliated pygidium in dorsal view, (d) external mould and separated part of posterior pygidium in ventral view. Scale bar 5 mm. Photographs courtesy Carola Radke (Museum für Naturkunde, Berlin).

reported the presence of *P. (N.?) obtusicauda* in the Middle Permian of Japan (for a list of references, see Kobayashi & Hamada 1980, p. 198). Interestingly, according to Kobayashi & Hamada (1984b, p. 52, 59, 62; see also Hahn & Brauckmann 1975), the Japanese specimens belong to *P. (Nodiphillipsia) sasakii* Kobayashi & Hamada 1984b or more likely *P. (N.) spatulifera* Kobayashi & Hamada 1980.

Lastly, *Iranaspidion* has been defined as a ditomopygine genus exhibiting three particularities: a sagittal sulcus on the posterior part of the main glabellar lobe, bilobate L1, and a small median slit at the posterior end of the pygidial axis (Kobayashi & Hamada 1978). As discussed by Goldring (1957), this latter feature can also be observed on internal moulds of various species within the genus *Pseudophillipsia*. Likewise, a sagittal sulcus on the posterior part of the main glabellar lobe can be observed in another Permian ditomopygine, *Hentigia bulbops* Haas *et al.* 1980 (see text-fig. 5a and pl. 1, fig. 1b therein). In this latter species, the occurrence of this character represents an intraspecific variation, suggesting it may be less constant in adults of *Iranaspidion* than thought by Kobayashi & Hamada (1978). Some specimens of *P. (C.) rakoveci* also display a similar structure but in the form of a sagittal depression instead of a true sulcus (Hahn & Hahn 1987, p. 591, text-fig. 18, pl. 4, fig. 7). Finally, in the Turkish specimen of *P. (N.)* aff. *obtusicauda*, the exoskeleton is so weathered at the level of L1 that these lobes appear bilobate. This observation leads to questioning to what extent the peculiar aspect of the L1 in *Iranaspidion* is not a consequence of a similar preservation. Kobayashi & Hamada (1978) did not mention if their specimens were preserved as internal moulds, but we can suspect that at least some of them were. Indeed, the median slit at the posterior end of the pygidial axis, for example, is known to occur on internal moulds only in *Pseudophillipsia*, suggesting the presence of a septum on the internal side of the exoskeleton. In summary, it can be demonstrated that the three characteristics of the genus *Iranaspidion* are features present within the genus *Pseudophillipsia*. Both genera being similar in every other aspects, we reassign *Iranaspidion sagittalis* Kobayashi & Hamada 1978 to the subgenus *Pseudophillipsia*

(*Carniphillipsia*) (for a similar view, see Owens 1983). The association of these three features in a species remains unique, which justify the maintaining of the species *P. (C.) sagittalis* as an independent taxon.

Comments on Some Particular Features Related to Enrollment in Some Late Palaeozoic Trilobites

When stressed, most trilobites were able to enroll their body so that only the dorsal mineralized exoskeleton was exposed to the threat, the ventral soft parts (including appendages) remaining encapsulated. This defensive strategy might have largely contributed to the success of trilobites throughout their 275-million-year evolutionary history. On the other hand, it has also undoubtedly represented a major constraint on the evolution of their body plan (e.g., Hughes 2007). In the Cambrian, some of the earliest representatives of the clade could already enroll, as exemplified by *Paradoxides* (Gil Cid 1985) and agnostid trilobites. Since then, it seems major evolutionary trends, such as the reduction in the number of thoracic segments and the phenomenon of caudalization, have chiefly led to improve enrollment in trilobites (e.g., Hughes *et al.* 1999; see also Hughes 2007 for a somewhat different view). Many studies (see Clarkson & Whittington in Whittington *et al.* 1997 and references therein) have emphasized the great diversity of structures that evolved more or less independently within virtually all trilobite groups to facilitate the process of enrolling (e.g., articulating surfaces, processes and sockets, etc...), to avoid 'over-enrollment' (for a list of enrollment stopping devices, see Chatterton & Campbell 1993), to create a perfectly closed capsule or to prevent lateral shearing (e.g., Clarkson & Henry 1973). Among these structures, coaptative devices, such as the vincular notches and furrows of phacopid trilobites, could be particularly complex.

In the Permian, enrollment likely remained an important constraint on the morphological evolution of trilobites. Despite their relative rarity, it seems Permian trilobites continued to develop particular structures to improve enrollment.

The Sagittal Arching of the Pygidial Axis

Goldring (1957) pointed out that, in contrast to most trilobites, the highest part of the pygidial axis does not correspond with the first axial ring, but with a more posterior one (usually axial rings 3 to 6) in some representatives of the genera *Anisopyge*, *Delaria*, and *Pseudophillipsia*. Additional examples of this particular pygidial morphology can be found within the Permian genera *Acropyge*, *Ditomopyge*, 'Iranaspidion' (reassigned above to *Pseudophillipsia*), and *Hentigia* (Table 2). In these ditomopygines, the pygidial axis thus forms an arch in sagittal section, instead of progressively declining from front to rear, as in most trilobites. A rapid overview of the main monographs on proetoid trilobites revealed that within this superfamily, this sagittal arching of the pygidial axis may be specific to the Permian genera listed above, with the exception of the Carboniferous *Kaskia chesterensis* and *Tripuroetus roemeri* (see Brezinski 2003 for a recent reassignment of these two taxa) and of few Devonian members of the genus *Crassiproetus* (Table 2). The examination of figures of all known proetoids with this characteristic enables us to conclude that its occurrence is independent of the general shape (outline, height) of the pygidium and of the relative height of its axis. However, all these species share a long (sag.) pygidial axis composed of a large number of rings (minimum 13, generally much more), but the reciprocal is not true (i.e. not all proetoids with a long and highly segmented pygidial axis display this characteristic), as already noticed by Goldring (1957). Within a single genus (or subgenus), some species may display a sagittally arched pygidial axis whilst others do not. It seems the species having a 'normal' pygidial axis are usually those with fewer axial rings, as exemplified by *Crassiproetus neoturgis*, *C. stummi*, *Delaria brevis*, *Pseudophillipsia (Carniphillipsia) schoeningi*, and *P. (Pseudophillipsia) kiriuensis* (Table 2). The pattern is not clear in *Ditomopyge*, especially if '*P. (C.) lept*a' is reassigned to this genus as proposed above, but this only stresses the need for a review of the concept of this taxon. Thus, not only the arching of the pygidial axis in these proetoids may be related to its degree of segmentation, but it seems that the restricted number of axial rings over which this character appears varies from one genus

to another. Moreover, this feature also changes during ontogeny. In *A. perannulata* (Brezinski 1992, figs. 10.13 and 10.16) and *Hentigia bulbops* (Haas *et al.* 1980, pl. 4, figs. 11, 12, 14), for example, the earliest growth stages display a 'normal' pygidial axis but in larger specimens, the axis increasingly slopes downwards anteriorly. It is noteworthy that in *Hentigia bulbops* at least, this trend is accompanied by an increase in the number of axial rings (Haas *et al.* 1980).

The exact functional advantage for a trilobite of having a sagittally arched pygidial axis is not clear, but it is likely related to enrollment. Goldring (1957) tentatively argued that this feature might have facilitated enrollment in those forms which, according to him, had pygidia slightly longer than their cranidia. It is rather hard to precisely measure relative sizes of exoskeletal parts on figures, which explains we are not able to provide new data supporting or refuting Goldring's claim. However, the difference (10–20%) between pygidial and cranidial lengths in trilobites with a sagittally arched pygidial axis, according to Goldring (1957), should be considered with caution, especially given the difficulty in making proper measurements from published illustrations. In all cases, where articulated specimens are available, this arching enables the pygidial axis to perfectly continue the curvature of the enrolled thoracic axis. Also, we believe it enabled a better redistribution of any forces exerted along the sagittal axis of the body, in particular on the weaker thoracic region. In the absence of this structure, it can be speculated that, in the enrolled position, the contact between the last thoracic segment and the pygidium might have been sharper, and therefore more prone to breakage, in those trilobites with relatively few thoracic segments. This assumption complements than conflicts with Goldring's explanation. That this particular pygidial axis configuration is displayed only by species having a pygidium with a relatively large number of axial rings, but of very different shapes, may stem from the fact that it is easier to slightly vary the height of numerous rings than to create few rings of significantly different heights, especially from a developmental perspective. Whatever the exact functional role of this feature, its development in

Table 2. Presence or absence of a sagittally arched pygidial axis and number of axial rings in some proetoid species. Within a single genus, some species may display a sagittally arched pygidial axis and others (underlined> do not. These latter are generally those with fewer rings in their pygidial axis (numbers in bold). Remarks: (1) According to Brezinski (pers. com. 2007), the current concept of *Ditomopyge decurtata* consists of an unnamed Pennsylvanian species with a shorter pygidial axis and *D. decurtata* sensu stricto of Cisuralian (Asselian-Sakmarian) age; (2) Reassigned herein, see text; (3) Specimens attributed to *Anisopyge* aff. *mckeei* by Cisne (1971) have been reassigned to an unnamed species of *Ditomopyge* by Brezinski (1991, p. 481); (4) According to Brezinski (pers. com. 2007), '*Ditomopyge fatmii*', displaying a distinct cephalic anterior border, should be reassigned to *Pseudophillipsia (Carniphillipsia)*; (5) Kobayashi & Hamada (1984b) assigned three pygidia to a new form of *P. (C.) kiriuensis*, *P. (C.) kiriuensis forma subtrigonalis*, which in our opinion belongs to a different species - consequently, we here refer to *P. (C.) kiriuensis* sensu stricto, i.e. as originally defined by Kobayashi & Hamada (1984a).

Taxa	Sagittally arched axis	Number of axial rings	Examples
<i>Acropyge</i>			
<i>A. lanceolata</i>	+++	20+	Kobayashi & Hamada 1978, fig. 5b
<i>A. weggeni</i>	+++	28	Hahn & Hahn 1981, fig. 1d
<i>Anisopyge</i>			
<i>A. inornata</i>	+++	19-24	Cisne 1971, pl. 68, fig. 13
<i>A. perannulata</i>	+++	28-30	Brezinski 1992, figs. 10.19, 22
<i>Crassiproetus</i>			
<i>C. neoturgis</i>	---	13	Lieberman 1994, fig. 21.4
<i>C. stummi</i>	---	13	Lieberman 1994, fig. 20.11
<i>C. halliturgidus</i>	+++	15	Lieberman 1994, fig. 21.7
<i>C. sibleyensis</i>	+++	16	Lieberman 1994, fig. 20.6
<i>C. crassimarginatus</i>	+++	16-18	Lieberman 1994, figs. 17.10, 11, 18.3
<i>C. traversensis</i>	+++	17-18	Lieberman 1994, fig. 16.3
<i>Delaria</i>			
<i>D. brevis</i>	---	9-10	Brezinski 1992, fig. 7.25
<i>D. granti</i>	+++	13-14	Brezinski 1992, fig. 7.19
<i>D. antiqua</i>	+++	15	Brezinski 1992, fig. 7.3
<i>D. westexensis</i>	+++	15-16	Brezinski 1992, figs. 9.2, 5, 17
<i>D. sevilloidea</i>	+++	16-17	Brezinski 1991, fig. 2.22
<i>Ditomopyge</i>			
<i>D. emilianensis</i>	---	13-14	Gandl 1987, pl. 7, fig. 94c
<i>D. decurtata</i> (s.s.) ⁽¹⁾	+++	c. 14+	Grant 1966, pl. 13, fig. 2c
<i>D. lept</i> ⁽²⁾	---	15-17	Hahn <i>et al.</i> 1989, pl. 4, figs. 8b, 9b
<i>D. undetermined</i> ⁽³⁾	+++	c. 24	Cisne 1971, pl. 68, fig. 23
<i>Hentigia</i>			
<i>H. planops</i>	+++	18-19	Haas <i>et al.</i> 1980, pl. 5, figs. 7-9
<i>H. bulbops</i>	+++	19-21	Haas <i>et al.</i> 1980, pl. 3, figs. 1-8
<i>Kaskia</i>			
<i>K. chesterensis</i>	+++	14-19	Weller 1936, pl. 85 fig. 4c
<i>Pseudophillipsia</i>			
<i>P. (Carniphillipsia)</i>			
<i>P. (C.) schoeningi</i>	---	16	Hahn & Hahn 1987, text-fig. 27b, pl. 3, fig. 11b
<i>P. (C.) fatmii</i> ⁽⁴⁾	+++	17	Grant 1966, pl. 13, fig. 4c
<i>P. (C.) rakoveci</i>	+++	19-21	Gauri 1965, text-fig. 8b, pl. 1, fig. 16
<i>P. (C.) lipara</i>	+++	20	Goldring 1957, pl. 1, figs. 2b, 3b
<i>P. (C.) cooperationis</i>	+++	21-23	Haas <i>et al.</i> 1980, pl. 7, figs. 3c, 4c, 5b
<i>P. (C.) sagittalis</i> ⁽²⁾	+++	23	Kobayashi & Hamada 1978, fig. 4b
<i>P. (C.) loricata</i>	+++	24	Haas <i>et al.</i> 1980, pl. 6, fig. 4b
<i>Pseudophillipsia</i>			
<i>P. (Nodiphillipsia)</i>			
<i>P. (N.) spatulifera</i>	+++	24-25	Kobayashi & Hamada 1984b, pl. 5, figs. 1b, 2d
<i>Pseudophillipsia</i>			
<i>P. (Pseudophillipsia)</i>			
<i>P. (P.) kiriuensis</i> (s.s.) ⁽⁵⁾	---	22	Kobayashi & Hamada 1984b, pl. 7, fig. 3b
<i>P. (P.) borissiaki</i>	+++	25+	Toumanskaya 1935, pl. 1, figs. 4-7
<i>P. (P.) sumatrensis</i>	+++	27	Owens 1983, pl. 4, fig. 6
<i>P. (P.) azzouzi</i>	+++	31	Termier & Termier 1974, pl. 40, figs. 3, 5
<i>Tripuroetus</i>			
<i>T. roemeri</i>	+++	14	Chamberlain 1970, pl. 140, fig. 32

several ditomopygines in the Permian demonstrates that a selective pressure towards an improved enrollment still existed at that time.

An Original Posture of Enrollment

It is hard to determine whether sagittal arching of the pygidial axis occurs in the two specimens described above, as their pygidial axis are either deformed or weathered. However, both of them display a morphological characteristic that may be interpreted as an adaptation for improved enrollment. Indeed, the pygidium is narrower (tr.) than the cranidium in these two specimens and therefore the lateral margins of the anterior part of the pygidium adpress against the inner part of the cephalic doublure (Figure 2b, h). The ventral part of the anterior cephalic doublure, however, directly abuts the ventral part of the posterior pygidial doublure. We believe this relative disposition of the cranidium and the pygidium in our two specimens is original and not induced by post-mortem pressure exerted along a dorso-ventral axis on the posterior and anterior parts of respectively the cranidium and the pygidium. This assumption is supported by (1) the fact there is no abrupt change in width (tr.) between the most posterior thoracic segments and the anterior part of the pygidium in the two species, (2) the morphology of the cephalic border, especially in *P. (C.) kemerensis* sp. nov. (e.g., Figure 2f), and (3) the somewhat sigmoidal outline of pygidial lateral margins of *P. (N.)* aff. *obtusicauda* (Figure 2h).

It can be speculated that this particular disposition of the pygidium relative to the cranidium enabled the trilobite to combine the advantages of both the spiral and the sphaeroidal types of enrollment, as defined by Bergström (1973). The sphaeroidal enrollment designates a functional type 'in which the pygidium rests with its ventral side more or less on the cephalic marginal doublure, not inside it, and in which the pleurae close the exoskeletal basket laterally' (Bergström 1973). It is conceivable that this kind of configuration was particularly efficient when pressure was exerted along a dorsal-ventral axis on the cranidium and/or the pygidium of an enrolled specimen. Indeed, the vault of the cranidium (/pygidium) might have led to

a redistribution of the pressure from the top of the sclerite towards its margins, and from there to the pygidium (/cranidium) without affecting the soft parts (organs, appendages, etc...) encapsulated within the two sclerites. However, a trilobite with a sphaeroidal enrollment was particularly prone to lateral shearing, unlike a spirally enrolled trilobite. This latter type is defined by Bergström (1973) as 'an enrollment in which at least part of the tergal (*i.e. dorsal*) side of the pygidium abuts against the ventral side of the cephalon or thorax or the appendages of this region (...) irrespective of the amount of doubling'. In this position, the rigidity of the pygidium, and sometimes of the thoracic segments as well, prevented lateral movements of the posterior part of the body relative to the anterior part. Nevertheless, this configuration could not prevent the soft parts being compressed if pressure was exerted along a dorso-ventral axis on the cranidium and/or the pygidium. In *P. (C.) kemerensis* sp. nov. and *P. (N.)* aff. *obtusicauda*, the posterior thoracic segments and the anterior part of the pygidium are enclosed within the cephalic cavity, their margins abutting the inner part of the cephalic doublure (Figure 2b, h). This disposition enabled the enrolled body to be particularly resistant to lateral shearing as in a classical spiral enrollment (Figure 4a, b). However, the contact between the ventral parts of the anterior cephalic doublure and the posterior pygidial doublure permitted, at least to some extent, the internal soft parts to be protected from pressure exerted along a dorsal-ventral axis on the cephalon and/or the pygidium, as in a typical sphaeroidal enrollment (Figure 4c, d). This system might have also been efficient against a pressure exerted dorsally on the three and the six posteriormost segments of respectively *P. (C.) kemerensis* sp. nov. and *P. (N.)* aff. *obtusicauda*, or on the anterior part of the cephalon of both species, the wider (tr.) anterior part of the pygidium being stopped by the anterior cephalic doublure (Figure 4e, f). However, the relationships between the cranidium and the pygidium could not prevent them from being separated, leading to the exposure of the ventral soft parts to the threat, if a pressure was exerted dorsally on more anterior thoracic segments or on the posterior part of the pygidium (situation not represented on Figure 4). It is noteworthy that robust genal spines were possibly

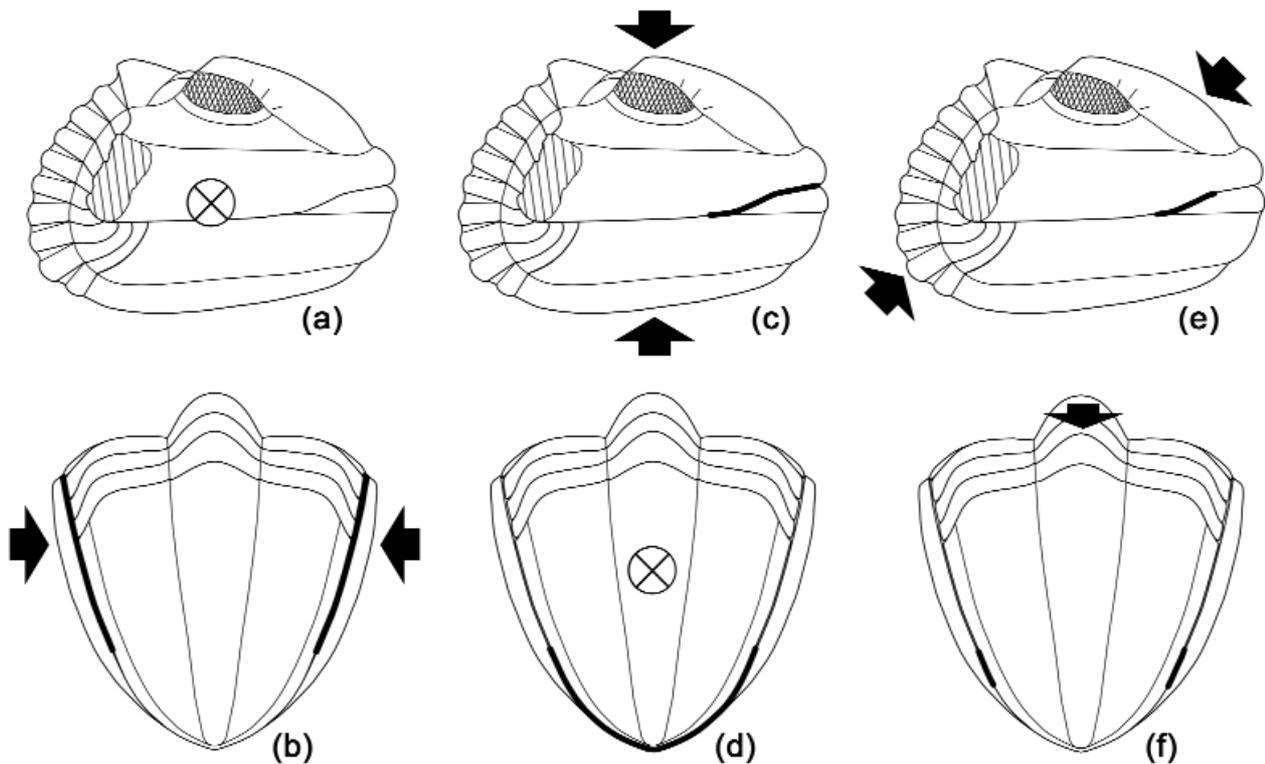


Figure 4. Main contact zones (bold black lines) between the cephalon and the pygidium of an enrolled specimen of *P. (C.) kemerensis* when pressures are exerted along different directions (arrows and crossed circles). The enrolled specimen is represented in right lateral view in (a), (c), (e) and in pygidial view in (b), (d), (f). (a, b) If pressure is exerted laterally on the cranidium or on the pygidium, lateral shearing is prevented by the contact between the inner part of cephalic doublure and the lateral margins of most posterior thoracic segments and pygidium. (c, d) If pressure is exerted along a dorsal-ventral axis on the cranidium and/or the pygidium, compression of internal soft parts is avoided by the contact between ventral parts of the anterior cephalic doublure and the posterior pygidial doublure. (e, f) If pressure is exerted dorsally on the anterior part of the cephalon or on the three most posterior thoracic segments, the posterior part of the pygidium is too wide (tr.) to slide forwards between anterior parts of librigenal doublures, and the trilobite remains enrolled.

important in dissuading predators from attacking the thorax (i.e. the weakest zone) of an enrolled trilobite. Our two specimens probably had well-developed genal spines, as suggested by the remains of large bases (Figures 2 & 5a, b). Thus, if our view of the redistribution of forces along the dorsal exoskeleton of our enrolled specimens is correct, it might have been particularly hard for a predator to gain access to the ventral soft parts of these trilobites without breaking the whole structure.

The distribution of this particular type of enrollment within the Trilobita is unknown. A specimen of the Devonian *Parahomalonotus calvus* figured by Chatterton *et al.* (2006, pl. 33, figs. 4, 5) suggests that it is not restricted to the Proetida, but it

is not clear from their figures whether the most posterior thoracic segments and the anterior part of the pygidium are effectively bordered laterally by the librigenal doublures. Likewise, it has been hypothesized that another homalonotid, *Trimerus delphinocephalus*, might have enrolled in this way, but unfortunately no completely enrolled specimen supports this view (Whittington 1993, fig. 9A). However, it is certain that this kind of enrollment is not unique to the Ditomopyginae, as a similar system occurs in the dechenelline *Camsellia truncata* from the Middle Devonian of northwestern Canada (Ormiston 1976, pl. 1, figs. 1–3). In this species, most of the thoracic segments and the anterior half of the pygidium are bordered laterally by the cephalic doublure (Figure 5c). In contrast, the posterior part

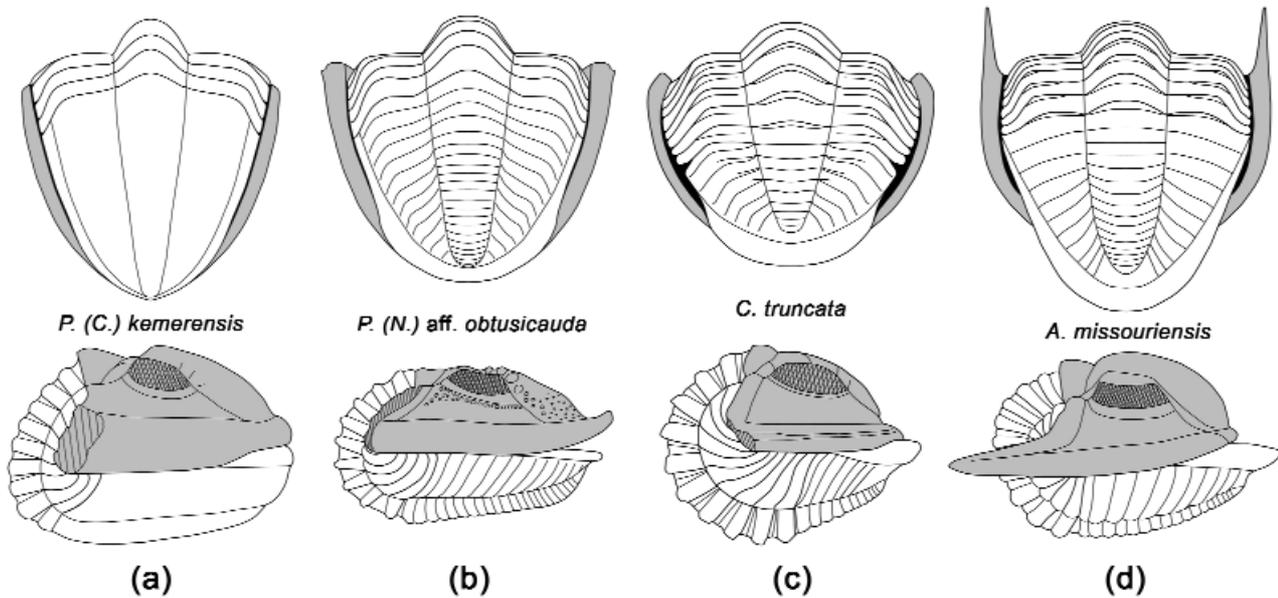


Figure 5. Reconstructions of the enrolled posture in four proetid trilobites: (a) *Pseudophillipsia* (*C.*) *kemerensis* sp. nov.; (b) *P. (N.)* aff. *obtusicauda*; (c) *Camsellia truncata* Ormiston 1976, and (d) *Ameura missouriensis* (Shumard 1858). The pygidial views (top row) show that in these species, the posterior thoracic segments and the anterior part of the pygidium are flanked laterally by the cephalic doublure (shaded) when enrolled. Emerging from the cephalic capsule (shaded), only the posterior part of the pygidial border can be seen on the right lateral views (bottom row).

of the pygidium distinctly protrudes beyond the anterior margin of the cephalic border, of which it is separated by a narrow (sag. and exs.) space. The lateral margins of the pygidium are concave (Ormiston 1976, pl. 1, figs. 3, 5, 7, 12) and sufficiently separated from the cephalic doublure to enable circulation of water between inner and outer capsule regions, with the opening at the rear of the pygidium (Ormiston 1976, p. 1164). However, we believe that the particular shape of the pygidial lateral margins in this species is primary to prevent lateral shearing, such as in *P. (C.) kemerensis* sp. nov. and *P. (N.)* aff. *obtusicauda*. A comparable result might have been obtained, although in a different way, in another dechenelline, *Fuscinipyge yolcini* (Ormiston 1972, pl. 1, figs. 1–4). In this species, lateral tips of the most posterior thoracic segments abut against the ventral part of the posterior cephalic doublure, but the anterior cephalic margin is bordered by the inner part of the pygidial doublure in an ‘inverted spiral’ type of enrollment (Bergström 1973). Being partially enclosed within the pygidial cavity, the anterior part of the cranium prevented

lateral shearing, while its posterior part enabled it to avoid the compression of soft parts when a dorsal-ventral pressure was exerted, such as in the pygidium of the two Turkish trilobites and of *C. truncata*. Within the Permian Ditomopyginae, the thoracic segments and the anterior part of the pygidium of *Ameura missouriensis* display a similar disposition relative to the cranium as *P. (C.) kemerensis* sp. nov. and *P. (N.)* aff. *obtusicauda* (see Owens 2003, pl. 1, fig. 6), and therefore probably prevented lateral shearing in an enrolled position (Figure 5d). However, the posterior part of the pygidium not only abuts against the cephalic anterior doublure like in the two Turkish specimens, but it protrudes beyond its anterior margin, as in *C. truncata*, so probably allowing the water to be renewed within the capsule.

Although the systems displayed by *P. (C.) kemerensis* sp. nov., *P. (N.)* aff. *obtusicauda*, *C. truncata*, and *A. missouriensis* represent similar morphological responses to ensure comparable functions (i.e. they probably combined the qualities of both spiral and sphaeroidal types of enrollment), it seems likely when studied in detail that they arose

independently in these four species. In *C. truncata*, the thorax consists in ten segments, the pygidium is short (tr.) and its lateral margins are concave, so fitting particularly well to the anterior cephalic doublure (Figure 5c). By contrast, *A. missouriensis* has only nine thoracic segments but it possesses an especially long (sag.) pygidium with straight lateral margins (Figure 5d). These important morphological differences evidently resulted in different functional constraints on the structure of the enrolled body. They also demonstrate that the similarities shared in terms of relative disposition of the different body parts are homoplastic in these two species, as they are separated by at least seventy millions years. The two Turkish trilobites also display clear evidence of independent acquisition of their similar enrolled posture. In *P. (C.) kemerensis* sp. nov., the cephalic border is particularly high laterally, which explains the posterior thorax and anterior pygidium can readily abut against it. But opposite γ abaxially, it strongly and abruptly lowers anteriorly and therefore the posterior pygidium can emerge out of the cephalic capsule and its doublure can abut against the anterior cephalic doublure (Figures 2f & 5a). In *P. (N.)* aff. *obtusicauda*, the posterior thoracic segments and the anterior pygidium are maintained within the cephalic capsule by the high outer part of the doublure, which is apparently v-shaped in transverse section. Indeed, the border in this species is almost flat and it mainly lies in a horizontal plane (Figure 2g). The adpression of the doublure of the posterior pygidium against the doublure of the anterior cephalon is made possible by an anterior shift in the inclination of the plane of the cephalic doublure (from c. 50° to 35° relative to the horizontal plane), and not by a decrease in its height. It seems that this adpression was only partial and that the cephalic and pygidial doublures remained separated medially, possibly enabling exchange of water between the inner and outer capsule regions. Lastly, despite their inclusion within the same genus, these two species exhibit distinctive and dissimilar appearances, as demonstrated by their assignment to two distinct subgenera. As a consequence, it is particularly unlikely that their apparently similar enrollment posture was inherited from a common ancestor.

Thus, we believe that this particular enrollment posture exhibited by these four species probably

arose independently several times during the evolutionary history of proetoids. This phenomenon probably benefited from a certain degree of flexibility in the method of enrollment that pre-existed within the Proetida, as exemplified by the otarionine *Harpidella* (Fortey & Owens 1979, fig. 2). Consequently, following Fortey & Owens (1979), morphological features related to enrollment should not be considered as characters that are better than others for the systematics of the Proetida. Rather, they should be used with caution. The occurrence of comparable complex innovations of the enrollment in three different Permo–Carboniferous ditomopygines is nevertheless remarkable in so far as it demonstrates that enrollment has remained a major constraint on the evolution of trilobite body until the end of the group.

Geographical, Palaeobiogeographical, and Stratigraphical Considerations

The present work represents the first description but the second report of Permian trilobites found in Turkey. Although poorly preserved, the pygidium from the Hazro region obviously belongs to an undetermined species of *Pseudophillipsia*, as proposed by Canuti *et al.* (1970). Only few discoveries of Permian specimens have been reported in the neighbouring countries. In his thorough review of the stratigraphical and geographical distributions of Permian trilobites, Owens (2003) mentions the occurrence of representatives of *Pseudophillipsia* and *Acropyge* in the Wordian of Armenia, described and figured by Weber (1944). The presence of *Acropyge* in Armenia had also been mentioned by Owens & Hahn (1993, p. 195). In Iran, Hahn & Hahn (1981) described four pygidia from the Late Permian of the Alborz Mountains, which they assigned to two species of *Acropyge* and one species of *Iranaspidion*. As discussed above (section 3), we do not believe *Iranaspidion* represents an independent taxon and consequently, the two pygidia from Northern Iran attributed to *Iranaspidion* are here reassigned to *Pseudophillipsia*. From Central Iran, *P. (C.) sagittalis* and *Acropyge lanceolata* were described by Kobayashi & Hamada (1978) from specimens collected in the Middle Permian of the region of Abadeh. Still in Central Iran, Feist *et al.* (in Mistiaen

et al. 2000) recently figured a weathered enrolled specimen of 'Permian' age from the Chahriseh area (Esfahan Province), which they attributed to an undetermined species of *P. (Carniphillipsia)*. On the other side of the Black Sea, a more diversified trilobite fauna of Wordian age has been described by Toumanskaya (1935; also known as 'Toumansky', see Owens 2003, p. 379) from Ukraine (Crimea). This fauna is composed of the genera *Kathwaia*, *Neogriffithides*, *Paraphillipsia*, *Permoproetus*, and once again *Pseudophillipsia* (Owens 2003). Thus, the material found in Turkey complements our knowledge of the presence of Permian trilobites in this part of Asia, in particular in suggesting a possible occurrence of the subgenus *P. (Nodiphillipsia)* in this region.

The description of *P. (C.) kemerensis* sp. nov. also confirms that the subgenus *P. (Carniphillipsia)* continued to diversify in the Middle Permian. In addition to this species, *P. (C.) intermedia* in Japan, *P. (C.) lipara* and *P. (C.) steatopyga* in Oman (work in progress), and *P. (C.) sagittalis* from Iran are also present at this time, which challenges the recent claim of Hahn *et al.* (2001) that the subgenus 'has its main distribution in the Upper Carboniferous and in the Lower Permian'. According to our data, it appears that the diversity of this subgenus remained roughly unchanged throughout the Permian. In contrast, *P. (Nodiphillipsia)* only occurs with certainty in the Middle Permian, while *P. (Pseudophillipsia)* is present in Middle to Upper Permian strata.

Lastly, *Pseudophillipsia* is one of the most diversified and widespread trilobite genera of the Permian (Lerosey-Aubril 2008). In the Wordian, the subgenus *P. (Pseudophillipsia)* occurs in all likelihood in Ukraine (Crimea) and Italy (Sicily), probably also in Tunisia and Indonesia (Sumatra), and possibly in Japan. In addition to the new report in Turkey, *P. (Carniphillipsia)* is known with certainty in the

Wordian of Oman (work in progress), and possibly in the Wordian of Iran and Japan. Lastly, if the attribution of the second Turkish specimen to *P. (Nodiphillipsia)* is correct, this subgenus occurs in the Wordian of Turkey and possibly also of Japan. Isolated pygidia of Wordian age and attributed to *Pseudophillipsia* confidently extends the palaeobiogeographic distribution of the genus to Timor (Indonesia), and possibly also to Hungary and Laos. Thus, it appears that *Pseudophillipsia* in the Wordian, as for most of its history, is particularly widespread within the Tethyan Realm, precluding its use for testing palaeogeographical models. Even taken separately, its subgenera confirm this view, from which the question arises as to which aspects of the life-history of this trilobite have given rise to such wide dispersion.

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