

A unified Lower – Middle Cambrian chronostratigraphy for West Gondwana

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ABSTRACT:

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Similarities in biotic successions support a unified, composite chronostratigraphy for the Lower-Middle Cambrian of the Iberian and Moroccan margins of West Gondwana. The Cordubian Series (emended from an Iberian stage-level unit) comprises the sub-trilobitic Lower Cambrian of West Gondwana. This series represents ca. half of the Cambrian (ca. 25 m.y.), has a base defined at the lowest occurrence of diagnostic Cambrian ichnogenera in central Spain, and is comparable to the Placentian Series of Avalon. The overlying trilobite-bearing Lower Cambrian (ca. 9 m.y. duration), or Atlasian Series (new), of West Gondwana consists of two stages originally defined in highly fossiliferous (trilobites and archaeocyaths) Moroccan sections where they have great potential for precise U-Pb geochronology. The penultimate Lower Cambrian stage, the Issendalenian, with the near-joint lowest occurrence of trilobites and archaeocyaths, is approximately comparable with the sparsely fossiliferous, Iberian “Ovetian Stage” (designation abandoned). The “Ovetian” as currently revised is invalid because it is an objective homonym of Sdzuy’s original “Ovetian.” The “Ovetian” is not a practically applicable unit as its basal stratotype horizon lacks any identified fossils, and its trilobites are so rare that it cannot serve as a standard for interregional correlation. By contrast, the Banian Stage as defined in Morocco is suitable as the terminal Lower Cambrian stage of West Gondwana. It is based on very fossiliferous successions that allow recognition of three successive trilobite zones and is similar in concept to the Iberian “Marianian Stage” (designation abandoned). The “Marianian” lacks a designated lower boundary stratotype locality, lacks a biostratigraphically defined base at a stratotype, and is so sparsely fossiliferous that no biostratigraphic zonation exists.

Long-term problems involving regional definition of the West Gondwanan Lower–Middle Cambrian boundary are resolved. The lowest occurrence of paradoxid trilobites, the classic index for the base of the Middle Cambrian, is diachronous in West Gondwana and other regions, with the group showing a delayed appearance in Iberia, Sweden, and Bohemia, by comparison with Morocco. Taxonomic revision of Iberian trilobites and new documentation of their ranges in Morocco show that the Iberian terminal “Lower Cambrian” “Bilbilian Stage” (designation abandoned) correlates with the Moroccan upper Banian and lower and middle “Tissafinian” Stages and with the Siberian upper Toyonian (traditionally assigned to the Lower Cambrian in Siberia) and lower Amgan (assigned to the Middle Cambrian in Siberia) Stages. The “Bilbilian” thus includes Middle Cambrian strata in a traditional international concept. Faunas from the base of the Iberian “lowest” Middle Cambrian “Leonian Stage” (designation abandoned) correlate largely into the second trilobite zone of the “Tissafinian” and are now understood to appear above an intra-Middle Cambrian faunal break. This faunal break is still poorly understood and may be an artifact of collection failure immediately above the sparsely fossiliferous, problematical “Valdemiedes event” interval. The base of this “Middle Cambrian”, now termed Celtiberian Series (new designation), in West Gondwana is best defined by the base of the lower Middle Cambrian Agdzian Stage (new designation). The Agdzian includes the “Tissafinian” and overlying lower “Toushamian Stage” (designations abandoned) of Morocco,

and has its top defined by the base of the middle Middle Cambrian Caesaraugustian Stage, as defined in Spain at the lowest occurrence of *Badulesia tenera*. The Languedocian, originally defined at the lowest occurrence of *Solenopleuropsis (Manublesia) thoralis* in the southern Montagne Noire of France comprises the third, and terminal stage of the Celtiberian Series. We suggest that the designations “Lower Cambrian” and “Middle Cambrian” be regarded as descriptive and non-chronostratigraphic terms in discussions of the Cambrian.

New taxa or taxonomic combinations include *Myopsolenites altus* (LIÑÁN & GOZALO, 1986), *M. boutiouiti* sp. nov., *M. kielciensis* (BEDNARCZYK, 1970), and *Hamatolenus (Hamatolenus) vincenti* sp. nov.

Key words: Cambrian, chronostratigraphy, Cordubian Series, Atlasian Series, Celtiberian Series, Agdzian Stage, Trilobita, Spain, Morocco, Poland, Israel, Jordan, Australia, South China, Siberia.

INTRODUCTION

Biostratigraphic zonation summarizes biotic changes that are a consequence of immigration, extermination, and extinction events through time, and are the basis of regional chronostratigraphic stages and series within faunal provinces (e.g. VALENTINE 1973). Regional chronostratigraphic units are particularly important as they serve as the bases for intercontinental, and even worldwide, correlations. In the latter part of the 20th century, some

regional stages and series have been proposed and accepted as global chronostratigraphic units (e.g. MITCHELL & *al.* 1997). Because regional chronostratigraphic units are so important in relative time correlation, they must be based on well-established biostratigraphic successions and allow precise regional correlatability of their boundaries, within the limits of biostratigraphic resolution. West Gondwana, with richly fossiliferous successions and diverse biotic assemblages, is one of the biostratigraphically best-known areas for the Lower

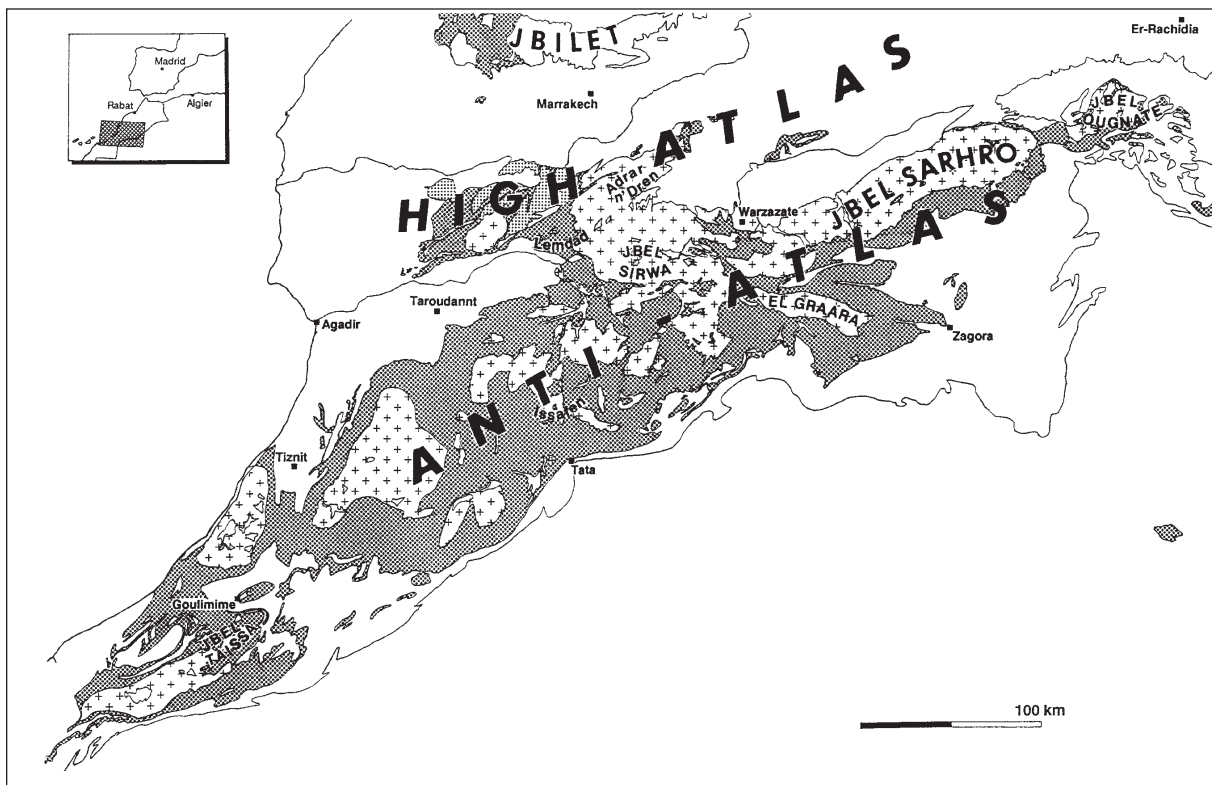


Fig. 1. Sketch map of the southern Moroccan Atlas regions showing outcrops of latest Terminal Neoproterozoic(?)–Cambrian strata (densely stippled), areas presumed or known to include Cambrian strata (small stippling) and outcrops of older Neoproterozoic rocks and crystalline basement (crosses). Location of Tarhoucht in the Jbel Ougnate area, eastern Anti-Atlas, indicated

Cambrian and most of the Middle Cambrian. The best known and most complete Gondwanan successions are in Spain and Morocco, although successions in the Montagne Noire, southern France; Sardinia; Bohemia; Germany; Turkey; Israel; and Jordan offer additional information on biostratigraphy and the role of dynamic lithostratigraphy (e.g. changes of depositional environments and their relationships to eustasy and epeirogeny) on biotic successions (e.g. GEYER & LANDING, 1995; GEYER & *al.* 1995; ÁLVARO & VENNIN 1998; ÁLVARO & *al.* 2000a, 2000b).

More favorable lithologies for body-fossil preservation, exceptionally complete outcrops across and along an immense depositional strike (Text-fig. 1), and limited Hercynian and Alpine deformation all mean that the Lower Cambrian biotas and lithostratigraphy of Morocco are better understood than those of Iberia (e.g. GEYER & *al.* 1995, LIÑÁN & *al.* 1996a; Text-fig. 2). In turn, long-term study focused on the successions in northern Spain has led a more complete and refined biostratigraphic scheme of the higher parts of the Middle Cambrian (e.g. LIÑÁN & *al.* 1993b). We propose that the current understanding of the Cambrian biostratigraphy of Morocco and Spain suggests that the Lower and lower Middle Cambrian regional stages of Morocco are appropriate for use as a standard for West Gondwana. On the other hand, the Iberian middle and upper Middle Cambrian is more fossiliferous and probably more complete than that of Morocco, and is especially useful for regional (Gondwanan paleocontinent) and interregional correlations. Thus, its potential to provide a chronostratigraphic standard should be considered. However, the focus of this report is on a unified chronostratigraphy for lower strata of the Lower Cambrian and Lower–Middle Cambrian boundary interval.

IBERIAN LOWER CAMBRIAN STAGES

Historical development

Two schemes for Lower Cambrian stage nomenclature exist on the Iberian and Moroccan margins of West Gondwana (Text-fig. 2). The Iberian Lower Cambrian stage succession was primarily established by SDZUY (1971a), who proposed three successive stages: 1) Ovetian, an interval with dolerolenids *s.l.* but without olenellids and inclusive of an underlying, non-trilobite-bearing interval down to the base of the Cambrian; 2) Marianian, with olenellids, ellipsocephalids, protolenids, and a few eodiscoids [e.g. *Delgadella*, *Triangulaspis*]; and 3) Bilbilian, a sub-paradoxidid (and thus sub-Middle

Cambrian; see discussion below of Lower–Middle Cambrian boundary) interval without olenelloids but with protolenines and ellipsocephalines) for the Iberian Lower Cambrian. Subsequently, LIÑÁN & *al.* (1984) proposed a sub-trilobitic Cordubian Stage that corresponded to the lowest Cambrian. Only the Cordubian–Marianian interval is discussed in this section. As discussed below in the section on the West Gondwanan Lower–Middle Cambrian boundary, taxonomic re-evaluations and new work in Morocco indicate that a larger part of the Bilbilian is better referred to the lowest Middle Cambrian.

Applicability

Of the Iberian Lower Cambrian stages, the Cordubian has the most satisfactory definition and constitutes an interval with potential for interregional correlation. It was defined in central Spain in an apparently continuous, unrestricted marine, uppermost Proterozoic–Lower Cambrian succession. Its base is defined, as is the global stratotype for the base of the Cambrian in eastern Newfoundland (LANDING, 1994), at the lowest occurrence of assemblages with characteristic Cambrian ichnogenera (see LIÑÁN & *al.* 1996c, pp. 33–34). One consequence of the proposal of the Cordubian was that LIÑÁN & *al.* (1984) restricted SDZUY's (1971a) Ovetian Stage by subtracting off the sub-trilobitic part of the original Ovetian and terming this lower part the Cordubian Stage (Text-fig. 2). Unfortunately, they retained “Ovetian Stage” for the trilobite-bearing upper part. This practice made “Ovetian” an objective homonym of itself. They should have abandoned the chronostratigraphic term “Ovetian,” and proposed a new stage name for the remnant interval that constitutes the lowest part of the trilobite-bearing Lower Cambrian of Iberia (i.e., HEDBERG 1976). For this reason, Ovetian is not regarded as a legitimate stage name, and the designation “Ovetian” is used below.

SDZUY's definitions of the Ovetian, Marianian, and Bilbilian were relatively informal and did not follow the rigorous procedures required for establishing chronostratigraphic units (e.g. HEDBERG 1976, compare North American Stratigraphic Commission 1983). SDZUY's article provided generalized comments about the characteristic trilobites of each stage. However, the stratigraphic ranges of the trilobites were not recorded; biostratigraphic zones were not proposed; stratotypes and reference sections were not specified, and the lower boundaries of the stages were not precisely defined at these sections.

Unfortunately, even after their revision and the designation of a number of type and reference sections (LIÑÁN

WEST GONDWANAN COMPOSITE		MOROCCO		IBERIA				
CELTIBERIAN	LANGUEDOCIAN	no zone established ?		"MIDDLE CAMBRIAN"	LANGUEDOCIAN	"Solenopleuroopsis-free"		
		Bailiella cf. Jevyi interval ?				S. thorali + marginata		
	CAESARAUGUSTIAN	no zone established ?			CAESARAUGUSTIAN	Solenopleuroopsis		
		Pardailhania				Pardailhania multispinosa		
		Badulesia tenera				Pardailhania hispanica		
		Kymataspis arenosa				Pardailhania hispida		
AGDZIAN	"TOUSHAMIAN STAGE"	Ornamentaspis frequens		"LEONIAN"	Eccaparadoxides asturianus			
		Cephalopyge notabilis			Eccaparadoxides szuyi			
	"TISSAFINIAN"	Hupeolenus *		"BILIBILIAN"	Acadoparadoxides mureoensis *			
		Sectigena			Hamatolenus (H.) ibericus			
ATLASIAN	BANIAN	BANIAN	Antatlasia guttapliviae	"MARIANIAN"	Protolenus (Hupeolenus)			
			Antatlasia hollardi		Realaspis			
			Daguinaspis		Serrodiscus			
	ISSENDALENIAN	ISSENDALENIAN	Choubertella	Andalusiana				
			Fallotaspis tazemmourtensis	"Strenuaeva"				
			Eofallotaspis ?	"Strenuella" ? Archaeo. zones VIII-IX				
CORDUBIAN	CORDUBIAN	"LOWER CAMBRIAN"	zones and stages not established		"LOWER CAMBRIAN"	CORDUBIAN		
			Granolenus				"OVETIAN"	Archaeo-cyathan zones I-VII
			Lemdadella					Rusophycus avalonensis
			Bigotina					"Phycodes" pedum - Monomorphichus lineatus
			Serrania					Anabarella
"Bigotiniidae" ?		Sabellidites (pars)						

Fig. 2. Chronostratigraphic schemes for Iberia and Morocco and unified chronostratigraphy for West Gondwana. Scheme for Iberia according to the latest modifications by GOZALO & al. (2003). Asterisks (*) indicate bases of Middle Cambrian as defined in Morocco (GEYER 1989, 1990a and this report) and Spain (LIÑAN & al. 1996). Re-evaluation of Lower-Middle Cambrian biotic events and proposal of a West Gondwanan standard based on that of Morocco (GEYER 1990a, 1998; GEYER & LANDING 1995 and this report) requires a qualified use of "Lower Cambrian" and "Middle Cambrian" in Iberia in this figure. Black interval below "Acadoparadoxides mureoensis Zone" is the Valdemiedes interval. Moroccan and Iberian chronostratigraphic terms that are abandoned in this report are placed within quotation marks. In addition, the existing Iberian concepts of Lower and Middle Cambrian are placed in quotation marks as they must be modified by comparison with the proposed West Gondwana Standard for the Lower Cambrian (Cordubian and Atlasian Series) and Middle Cambrian (Celtiberian Series). The diagonal line at the top of the Cordubian shows the differences between the original and the later concepts of the Cordubian in Iberia. The approach in this report is to regard the Cordubian Series as the sub-trilobitic Lower Cambrian of West Gondwana

& *al.* 1993b), SDZUY's Lower Cambrian stages remain poorly defined in terms of their faunal components. Indeed, trilobites are rare and local in distribution in the "Ovetian"-Bilbilian. The complex zonal succession proposed through the interval (Text-fig. 2) is largely based on local occurrences that were united into a biostratigraphic succession partly based on lithostratigraphic arguments. PEREJÓN's (1986, 1994) nine archaeocyathan zones for the "Ovetian"-lower Marianian are actually a composite succession of assemblages developed from localities across Spain. The assemblage zones show relatively little change through this interval. Indeed, all Marianian archaeocyathans persist from the "Ovetian;" most Marianian forms originate in the lower "Ovetian," and the suggestion is that the key differences between successive archaeocyathan zones are an artifact of collection bias, with genera "appearing" or "disappearing" from the zones with changes in the diversity of successive assemblages.

LIÑÁN & *al.* (1993b, 1996a) provided somewhat clearer definitions of the "Ovetian"-Bilbilian Stages by defining their bases with available range data on trilobites and the Iberian composite archaeocyathan zonation. Thus, the base of the "Ovetian" is stated to be defined by the joint lowest occurrence of archaeocyathans (Zone I of PEREJÓN) and trilobites (unidentified bigotinids). The lowest occurrence of archaeocyathans and trilobites define the base of the "Ovetian" at its stratotype at the La Tierna section (LIÑÁN & *al.* 1993b), but the only published record of identified fossils from La Tierna are trace fossils from the underlying Cordubian Stage (FEDONKIN & *al.* 1985). It should be noted that this joint lowest occurrence of trilobites and archaeocyathans in the type area of the "Ovetian" in southern Spain is interpretable as a biofacies shift because it nearly corresponds to a lithofacies change from siliciclastic- to carbonate-rich facies (LIÑÁN & *al.* 1993b). The shallow, restricted marine conditions represented by most sections in the "Ovetian," as well as the Marianian and Bilbilian, mean that biotas are of low diversity and frequently endemic. The mixed carbonate-siliciclastic units of the Ossa-Morena Zone where PEREJÓN (1986, 1994) defined the "Ovetian" archaeocyathan zonation feature oolites, calcimicrobe-dominated archaeocyathan build-ups, stromatolites and thrombolites, and low-diversity trilobites. The rarity of trilobites in these southern Iberian successions is not unexpected, as the early evolution and diversification of Early Cambrian trilobites was in more off-shore facies (LANDING & WESTROP 1999), and trilobite diversities remained low in near-shore/restricted marine habitats through the Early Paleozoic (WESTROP & *al.* 1995). The relatively few trilobites, such as *Bigotina* COBBOLD, 1935; *Pararedlichia* HUPÉ, 1953a; and *Lemdadella* SDZUY, 1978, that appear in the "Ovetian" Stage of the Ossa-Morena Zone occur

elsewhere but only allow tentative correlations in West Gondwana with comparable near-shore carbonate facies exposed in Normandy and the southern slopes of the Moroccan High Atlas (PILLOLA 1993, GEYER & *al.* 1995, pp. 74-81), and are not useful in precise correlations even into West Gondwanan open-shelf facies of southern Morocco. Further north in the Iberian Chains, the trilobite-poor southern "Ovetian" carbonates are replaced by shallow siliciclastics that not only lack archaeocyathans, but have trilobites limited to several endemic dolerolenids (SDZUY 1986, ÁLVARO & *al.* 1993).

The distinctive faunal changes reported at Iberian higher Lower Cambrian stage boundaries reflect, in part, limited exposures and lithologies not conducive to the preservation of relatively continuous, fossiliferous successions that allow detailed correlations even within Iberia. This is seen in the revised definitions of the Marianian and Bilbilian Stages. No appropriately fossiliferous section is known that can be designated as a stratotype for the base of the Marianian, and the Marianian base remains an imprecise biostratigraphic, not chronostratigraphic, concept at "the first record of *Delgadella*, which coincides with one of the archaeocyaths of Zone VIII." However, this biostratigraphic horizon is not recorded in the revision of the Marianian Stage at any section, and no section has been designated the stratotype (LIÑÁN & *al.* 1993b, p. 827). Similarly, the small number of sections with Bilbilian-aspect faunas and the relatively sparse trilobite faunas of the lower Bilbilian have led to comparable problems. A revised base of the Bilbilian has been defined at a stratotype in the Alconera 3 section of southwest Spain (LIÑÁN & PEREJÓN 1981). This stage boundary is at the highest occurrence of olenelloids (*Andalusiana* SDZUY 1961) and *Serrodiscus* RICHTER & RICHTER 1941 of the Marianian Stage at the top of the Alconera Formation (LIÑÁN & *al.* 1993b). However, chronostratigraphic units are defined by biostratigraphic or other features that define the base of the chronostratigraphic unit, and not by the top of an underlying chronostratigraphic unit (HEDBERG 1976). At Alconera 3, the overlying, supposedly "type Bilbilian" La Lapa Formation lacks any biostratigraphically useful macrofossils, and this further detracts from the concept and utility of the Bilbilian as a terminal Lower Cambrian stage even at its type section. The existing definitions of the Marianian and Bilbilian Stages further help illustrate the limited utility of the Spanish Lower Cambrian stages for precise interregional correlation, even within West Gondwana. The eodiscoid-rich faunas of the Marianian and the protolenids and ellipsocephalids of the higher Bilbilian are significant aids in interregional correlation, but the non-standard definitions of these stages and their relatively poorly fossiliferous successions are not appro-

priate as West Gondwanan standards for the Lower Cambrian.

MOROCCAN LOWER CAMBRIAN STAGES

Historical development

Two stages (Issendalenian and Banian) were introduced for the trilobite-bearing Lower Cambrian of the Moroccan margin of West Gondwana (GEYER 1990a). These stages replaced HUPÉ's (1960) ill-defined five stages for this interval (i.e., Assadasien, Amouslekien, Timghitien, Tasousektien, and lowest Aguilizien), which had come to be arbitrarily used as litho- and biostratigraphic units and were described on the basis of incomplete and/or incorrect faunal ranges and taxa that have remained as *nomina nuda* (GEYER 1990a). The Issendalenian and Banian are based on well-exposed successions in the Atlas ranges and feature abundant body fossils dominated by diverse trilobites with locally common archaeocyathan build-ups. The two stages have shown a high potential for regional correlation, and have biostratigraphically well-defined stage boundaries recognizable across southern Morocco (GEYER 1990a, GEYER & LANDING 1995, GEYER & *al.* 1995). The fact that a large percentage of the Moroccan Lower Cambrian trilobite faunas remain incompletely known or inadequately studied means that the well-established utility of these stages for correlation will only grow with further work. Indeed, their suitability for intercontinental correlation is additionally enhanced by a developing geochronologic framework based on precise U-Pb zircon dating of volcanic ashes which can be cross-correlated with exact biostratigraphic data (e.g. LANDING & *al.* 1998).

Issendalenian Stage

The Issendalenian Stage consists of a vertical succession of four trilobite-based zones (*Eofallotaspis*, *Fallotaspis tazemmourtensis*, *Choubertella*, and *Daguinaspis*). These zones are best known in the Anti-Atlas from the carbonate-dominated uppermost Igoudine Formation and mixed siliciclastic-carbonate facies of the overlying Amouslek Formation of GEYER (1990b). The characteristic trilobites associated in each of these zones are outlined in GEYER (1990b). More detailed, bed-by-bed information on faunas through the Issendalenian that lists trilobites, archaeocyathans, brachiopods, hyoliths, small shelly fossils, and calcimicrobes is available for the well-studied sections at Amouslek, Oued Boutergui,

Tazemmourt, and Tiout (HUPÉ 1953a, 1959; BERNEKER & GEYER 1990; GEYER & *al.* 1995). These lists help illustrate that the Issendalenian regularly exhibits abundant and diverse fossil assemblages in the western and central Anti-Atlas.

The only feature lacking for the Issendalenian Stage to be a formal chronostratigraphic unit has been the designation of its lower boundary at a stratotype section. In this report, we define the stratotype base of the Issendalenian Stage to be the base of the *Eofallotaspis* Zone in the lower Tiout Member of the Igoudine Formation at the Tiout section in the western Anti-Atlas. At Tiout, the base of the *Eofallotaspis* Zone is at SDZUY's (1978, 1981) sample T1, which yielded the oldest-identifiable trilobites, e.g. the bigotinid *Hupetina antiqua* SDZUY, 1978 (see columnar sections in GEYER & *al.* 1995, figs 2, 3). The lowest archaeocyathans in Morocco appear ca. 13 m above sample T1 (DEBRENNE & DEBRENNE 1978), and archaeocyathans occur in the shallower carbonate facies through the mixed siliciclastic and carbonate strata of the higher Issendalenian. The abrupt and nearly joint appearance of trilobites and archaeocyathans in the lower Tiout Member is related to deepening and appearance of the more open-marine oolitic facies of the Tiout Member above lower-energy calcareous mudstones with thrombolites (see MONNINGER 1979, GEYER, 1989). In addition to the wealth of biostratigraphic data available through the stage, aquagene volcanic ashes are abundant. We have sampled them for U-Pb zircon geochronology immediately below, within, and above the *Eofallotaspis* Zone through the top of the Issendalenian (E. LANDING, G. GEYER, and S.A. BOWRING, unpublished data).

Banian Stage

Faunas of the uppermost Lower Cambrian Banian Stage appear in the uppermost Amouslek Formation and are best documented through the mixed siliciclastic – (minor) carbonate facies of the overlying Issafen Formation in the central and western Anti-Atlas and southern slopes of the High Atlas. The Banian consists of three successive trilobite-based zones (*Antatlasia hollardi*, *A. guttapliviae*, *Sectigena*). The characteristic trilobites of these zones are outlined in GEYER (1990b), and detailed, bed-by-bed information is available on trilobites, archaeocyathans, brachiopods, hyoliths, and small shelly fossils for the well-studied sections at Amouslek, Oued Boutergui, and Imighz in the Anti-Atlas and the Lemdad section in the foothills of the High Atlas (BERNEKER & GEYER 1990, GEYER & *al.* 1995, GEYER & LANDING 2002 and unpubl.). As with the fossiliferous sequences through the Issendalenian listed above, Banian successions in the

central and western Anti-Atlas and foothills of the High Atlas regularly exhibit diverse and abundant faunas. Ellipsocephaloid, saukiandiid, and eodiscoid trilobites are characteristic elements of Banian faunas, and these geographically widespread forms allow detailed interregional correlation through the stage.

The only feature lacking for the Banian Stage to be a formal chronostratigraphic zone has been the designation of its lower boundary at a stratotype section. In this report, we define the stratotype base of the Banian Stage to be the base of the *Antatlasia hollardi* Zone in the upper Amouslek Formation at Amouslek village. This horizon is immediately below the base of the lowest bed of *Calcaire scoriacé* lithology at ca. 303 m above the base of the Amouslek Formation at the northeastern slope of the Amouslek “amphitheater” (see GEYER & *al.* 1995, pp. 63-73).

As in the Issendalenian, aquagene volcanic ashes are abundant through the Banian Stage, and we are in the process of developing a U-Pb geochronology through the stage (E. LANDING, G. GEYER, and S.A. BOWRING, unpublished data). One of these ashes gives an age of 517 ± 1.5 m.y. on the upper *Antatlasia guttaphuviae* Zone (LANDING & *al.* 1998).

A UNIFIED LOWER-MIDDLE CAMBRIAN CHRONOSTRATIGRAPHY FOR WEST GONDWANA

The similar biotic and lithostratigraphic successions on the Iberian and Moroccan margins of West Gondwana do not support maintenance of distinct chronostratigraphic schemes. A unified chronostratigraphy would allow precise interregional correlations between the relatively fossiliferous successions of Iberia and Morocco and provide a standard for other West Gondwanan regions. A unified Lower Cambrian stage-level chronostratigraphy for West Gondwana should not be based on simple nomenclatural priority for somewhat similar and roughly coeval stages, but should feature their utility and potential for interregional correlation, and the adequacy of the definitions of existing stages.

Cordubian Series

The Iberian Cordubian Stage is appropriate for the sub-trilobitic Lower Cambrian of West Gondwana. No equivalent stage has been named for the non- to sparsely fossiliferous, evaporitic to restricted marine, sub-trilobitic Lower Cambrian of Morocco (i.e., Adoudou, Lie-de-vin, and lower Igoudine Formations of the Anti-Atlas). The

lower boundary of the Cordubian has been appropriately defined in an apparently continuous upper Proterozoic–Lower Cambrian open-marine succession (discussed above). With a lower boundary defined on the basis of trace fossils, the sub-trilobitic Cordubian is comparable to the Placentian Series of the Avalon continent (LANDING & *al.* 1989). With the sub-trilobitic Lower Cambrian representing ca. 25 m.y., and almost half of the Cambrian and the majority of the Lower Cambrian (LANDING & *al.* 1998, 2000), the Cordubian is the chronostratigraphic unit with the longest duration of those discussed in this report. Because of its exceptional duration, which is significantly longer than any of the other stage-level units, individually or in aggregate in this report – indeed, a duration which is longer than such geological periods as the Silurian – the Cordubian is emended herein as a series-level unit. This revision in rank does not change the definition, lower boundaries, stratotype section, or biostratigraphic content of the Cordubian, and brings the Cordubian into the same rank as the approximately coeval and broadly equivalent Placentian Series.

Issendalenian Stage

The trilobite bearing Lower Cambrian is relatively brief (ca. 9 m.y., LANDING & *al.* 1998). The trilobite-bearing Lower Cambrian of Iberia and Morocco has been divided into two stages that have somewhat similar lower boundaries. The “Ovetian” (as presently restricted) and Issendalenian Stages both feature the abrupt and nearly joint appearance of the oldest trilobites and archaeocyaths in Iberia and Morocco – suggesting that the biostratigraphic events at these stage boundaries reflect coordinated bio- and lithofacies changes. The bases of the “Ovetian” and Issendalenian may prove to be approximately coeval. Indeed, they have similar archaeocyathan faunas (e.g. *Afiacyathus*, *Archaeopharetra*, *Erisma-coscinus*, *Nochoroicyathus*, *Protophareta*, *Rotundocyathus* from Tiout [DEBRENNE & DEBRENNE 1978] appear in PEREJÓN’s [1986] Zone I), but these genera persist through the Issendalenian and “Ovetian” and into higher strata in Morocco and Spain and do not assist in precise correlations. Similarly, the majority of the trilobites in the Tiout Member are bigotinines (SDZUY 1978, 1981), with unidentified specimens of this group characteristic of the base of the “Ovetian” and present at the La Tierna stratotype (E. LIÑÁN, personal commun. to E.L., September 1996). However, these trilobites do not aid in correlation of the Tiout and La Tierna sequences with each other or into other Cambrian regions.

An evaluation of available data indicates that the Moroccan Issendalenian Stage provides more criteria for

detailed inter-regional and global correlation and should be the West Gondwanan standard for the penultimate Lower Cambrian stage. Unlike the Iberian “Ovetian” Stage, identifiable trilobites occur from the base of the Issendalenian Stage and allow a four-fold zonal subdivision that complements an abundant archaeocyathan record. The eponymous fallotaspid trilobite genera that are the basis of the Issendalenian zonation are closely related phylogenetically and may form a series of possible ancestors and descendents (GEYER, 1996); thus the vertical succession of these genera and their species likely has important biostratigraphic potential in other regions. The greater biostratigraphic potential of the Issendalenian is complemented by the presence of numerous volcanic ashes through the stage that offer the potential for precise geochronologic correlations into faunal provinces, such as the Avalon continent, that have very dissimilar biotas but also have an extensive record of marine aquagene ashes (e.g. LANDING & *al.* 1998).

Banian Stage

A comparable conclusion based on available data is that the Moroccan Banian Stage provides more criteria for detailed inter-regional and global correlation and should be the West Gondwanan standard for the terminal Lower Cambrian stage. Although both the Banian and Iberian Marianian Stage have abundant eodiscoids, ellipsocephaloids, and archaeocyathans that provide a biostratigraphic basis for inter-regional and global correlations, only the Banian has 1) an established trilobite-based zonation that allows detailed correlations within the stage and 2) a lower boundary definition that is tied to the lowest occurrence of a taxon in a designated stratotype section. Trilobites are abundant and diverse throughout the Banian, and its trilobite zonation can be recognized across a particularly wide area that includes the central and western Anti-Atlas and southern foothills of the High Atlas. In addition to the wealth of biostratigraphic data, volcanic ashes that bracket and occur through the Banian have the potential for precise geochronologic correlations into faunal provinces that have very dissimilar biotas, but also have an extensive record of marine aquagene ashes. The first such use of volcanic ashes to improve and resolve biostratigraphic correlations between the Banian and the Branchian Series of the Avalon continent has already been published (LANDING & *al.* 1998). The replacement of the Marianian Stage by the Banian has relatively few consequences for paleontologic and geologic syntheses in Iberia. The lowest occurrence of the eodiscoid *Delgadella*, originally proposed as the base of the Marianian, is with-

in the lower Banian *Antatlasia hollardi* Zone in Morocco (e.g. GEYER & *al.* 1995, p. 72). LIÑÁN & *al.* (1996a) subsequently changed the concept of the Marianian and declared its base as defined “by the appearance of the trilobites *Strenuella* and by the archaeocyathan zones VIII and IX of PEREJÓN (1994)” (LIÑÁN & *al.* 1996a, p. 11); a definition that does not satisfy mandatory rules. In addition, it remained unclear what species is represented by “*Strenuella*” because this genus does not occur in Spain according to modern taxonomic concepts. In any case, application of the Banian in Iberia would mean lowering the base of the terminal Lower Cambrian stage in the few sections that expose this interval in southern and north-central Spain (LIÑÁN & *al.* 1993a, p. 827).

Atlasian Series (new)

The terminal Lower Cambrian stages of West Gondwana comprise a “natural” chronostratigraphic unit that is above the sub-trilobitic Lower Cambrian. These two stages constitute an interval defined by relatively gradual upward changes in trilobite- and archaeocyathan assemblages, and underlie the classic paradoxidid-bearing (at least locally in Morocco) lowest Middle Cambrian. This interval (estimated 9 m.y.) that forms the top of the Lower Cambrian is roughly comparable in concept and duration to such series-level units as the Waucoban Series of Laurentia (PALMER 1998) and Branchian Series of the Avalon continent (LANDING 1996). For this chronostratigraphic interval in West Gondwana, we propose the term Atlasian Series (new). The Atlasian Series, named for the distribution of the trilobite- and archaeocyathan-bearing Lower Cambrian in the Atlas ranges of southern Morocco, has its stratotype base defined at the base of the Issendalenian Stage (discussed above). “Atlasian” is not preoccupied by any chrono- or lithostratigraphic interval.

WEST GONDWANAN LOWER-MIDDLE CAMBRIAN BOUNDARY DEFINITIONS

Historical development

One of the basic problems in establishing a composite chronostratigraphic standard for West Gondwana is the definition of the Lower-Middle Cambrian boundary. Different aspects and definitions of this boundary in Iberia and Morocco have been discussed (SDZUY 1971b; GEYER 1990a, b, 1998; GOZALO & *al.* 1993b; ÁLVARO & LIÑÁN 1997; DIES & *al.* 2000, 2001). These contrasting definitions derive from differences in: 1) interpretation of

tolenine-dominated assemblages of the *Hupeolenus* Zone of GEYER (1990a). These paradoxidine specimens give a Middle Cambrian faunal aspect to the *Hupeolenus* Zone, and the *Hupeolenus* Zone was defined to be the lowest part of the lowest Middle Cambrian Tissafinian Stage of Morocco, although the earliest paradoxidine skeletal fragments occur somewhat above the base of the zone (GEYER 1990a). These paradoxidine remains include those of *Paradoxides* (*Acadoparadoxides*) *nobilis* GEYER, 1998, from the *Hupeolenus* Zone, which ranges up into the *Cephalopyge notabilis* Zone. *Protolenus* (*Hupeolenus*) *hupei* GEYER, 1990d and *P. (H.) termierelloides* GEYER, 1990d, with nearly identical stratigraphic ranges, are used as the index fossils of the Moroccan *Hupeolenus* Zone. The base of this zone marks the distinct faunal turnover from antatlasine-strenuelline-saukiandine-dominated trilobite faunas of the Banian Stage to the protolenine-ellipsocephaline-dominated faunas of the Tissafinian Stage (GEYER 1990b). This faunal turnover marks a better characterized stratigraphic interval than the diachronous lowest occurrences of paradoxidines, and it is clearly not dependant on facies changes.

Application of the Moroccan Lower–Middle Cambrian boundary standard

Proposal of the base of the *Hupeolenus* Zone as the standard for definition of the Lower–Middle Cambrian boundary in West Gondwana helps emphasize that the lowest occurrence of paradoxidines is diachronous within West Gondwana, as well as on a number of Cambrian continents. *Paradoxides* (*Acadoparadoxides*) *mureoensis* SDZUY, 1958, is the oldest paradoxidine and the index of the “lowest Middle” Cambrian Leonian Stage in Spain. However, *P. (A.) mureoensis* is now known to have a lowest occurrence in the Moroccan *Cephalopyge notabilis* Zone. Indeed, our field work in Morocco during the last two decades has led to recovery of only few specimens attributable to *P. (A.) mureoensis* as low as the *Cephalopyge notabilis* Zone of the Lemdad syncline in the southern foothills of the High Atlas. The stratigraphic range of *P. (A.) mureoensis* begins only above that of *P. (A.) nobilis* in the lowest Middle Cambrian *Hupeolenus* Zone in Morocco (GEYER 1998; Fig. 3). Thus, the base of *P. (A.) mureoensis*’ range is within, and not at the base of, the lower Middle Cambrian of Morocco. Earlier correlations of the base of the Iberian Leonian Stage with the base of the Moroccan Tissafinian Stage were based on the partly erroneous identifications of *Paradoxides* (*A.*) *nobilis* and similar, unidentified forms of *Paradoxides* as *P. (A.) mureoensis* in the Atlas ranges by GOZALO & al. (1993b) or SDZUY (1995) that led to the conclusion that

this species is the earliest *Paradoxides* species in Morocco. GEYER (1998) subsequently distinguished the earlier-appearing form as *P. (A.) nobilis*.

Use of the base of the *Hupeolenus* Zone to define the base of the West Gondwanan Middle Cambrian necessarily leads to a re-evaluation of the “uppermost Lower” Cambrian Bilbilian Stage of Iberia. It is important to note that the lower Bilbilian has sparse body fossils. It includes regressive, sandstone-dominated units (e.g. Daroca Formation and equivalents) from which *Hupeolenus* species are reported (ÁLVARO & LIÑÁN 1997, DIES & al. 2001). No biostratigraphically useful, zone-level divisions have been proposed for the lower part of the Bilbilian. Its base was initially not formally defined on the basis of its fossils but rather by the top of the ranges of Marianian Stage species. More recently, the base of the Bilbilian has been defined at the lowest appearance of the problematical trilobite genus *Realaspis* SDZUY, 1961, whereas the lower-upper Bilbilian boundary is within the Iberian *Hupeolenus* Zone (GOZALO & al. 2003) and cannot be defined by trilobite ranges. The presence of the true *Hupeolenus* specimens identified by GOZALO & al. (2003) indicates that at least part of the lower Bilbilian is correlative with the *Hupeolenus* Zone of the lowest Middle Cambrian (lower Tissafinian Stage) of Morocco. Simply stated, the Bilbilian is herein interpreted to refer to a paradoxidid-free facies apparently referable to the uppermost Lower Cambrian and lower Middle Cambrian on the Iberian margin of West Gondwana. As noted above, paradoxidids appear in Bilbilian-equivalent strata in Morocco (i.e. *Hupeolenus*–lower *Cephalopyge notabilis* Zones) of the lower Tissafinian Stage. Interestingly, *Peronopsis* has been recorded from the Bilbilian of the Iberian Chains, where it co-occurs with such species as *Ahueva undulata* and *A. hastata* (LIÑÁN & GOZALO 1986, p. 23, pl. 2, fig. 18) that give this traditional Iberian “Lower” Cambrian fauna a Middle Cambrian aspect.

Higher Bilbilian Stage strata referred to the Iberian *Hamatolenus* (*H.*) *ibericus* Zone by GOZALO & al. (1997) and DIES & al. (2001, pl. 1, figs 1, 3) feature *Protolenus* (*Hupeolenus*) *dimarginatus* GEYER, 1990d, from the Bilbilian at Jarque in the Iberian Chains, along with specimens identified as *P. (H.)* cf. *termierelloides*. Although the material is imperfectly preserved, the identifications appear to be correct. *Protolenus* (*Hupeolenus*) *dimarginatus* ranges in the Moroccan High Atlas and Anti-Atlas ranges from the upper *Hupeolenus* well into the *Cephalopyge notabilis* Zone and is even found associated with *Cephalopyge* in the Tarihoucht section (GEYER & al. 1995, p. 117).

Briefly summarized, trilobite faunas from northern Spain indicate that the “middle” Bilbilian of Iberia correlates with the Moroccan *Hupeolenus* Zone. According to

the occurrence of the newly described trilobites dealt with below, faunas of the sub-paradoxidid upper Bilbilian (*Hamatolenus ibericus* Zone) of Iberia do *not* correlate into the older *Hupeolenus* Zone, as suggested by GEYER (1983, 1998) and GEYER & SHERGOLD (2000), but correlate unmistakably into the Moroccan *Paradoxides*-bearing Middle Cambrian *Cephalopyge notabilis* Zone. Indeed, SDZUY's (1995) and GEYER's (1998, fig. 2) earlier correlation of the upper Bilbilian Stage into the Moroccan lower Tissafinian Stage must now be revised in favor of a lower-middle Tissafinian Stage correlation. This "stratigraphically high" correlation of the Bilbilian is further strengthened below in the section "Improved Lower-Middle Cambrian boundary correlation" with taxonomic revisions of species earlier reported from Spain and elsewhere across Gondwana and new data on the stratigraphic ranges of rarer trilobite species in Morocco.

MIDDLE CAMBRIAN CHRONOSTRATIGRAPHY IN GONDWANA

Tissafinian, "Bilbilian," and "Leonian" Stages

In contrast to the published successions from the Iberian Peninsula, the coeval Lower-Middle Cambrian boundary interval in the Atlas ranges of southern Morocco preserves a more transitional and complete lithologic succession and more diverse faunal assemblages. The Moroccan boundary interval succession is particularly significant for two reasons. The first is that the Moroccan lowest Middle Cambrian Tissafinian Stage preserves a record of the overlap of typical Lower Cambrian Redlichiina and Olenellina (e.g. *Cambropallas telesto* GEYER, 1993) with characteristic Middle Cambrian paradoxidids (GEYER 1993, GEYER & PALMER 1995). Secondly, the Moroccan Tissafinian Stage shows the co-occurrence of paradoxidids with a fairly rich assemblage of protolenine trilobites. Such protolenine trilobites, however, are typically considered uppermost Lower Cambrian not only in Spain but also in other regions (GEYER 1990a, 1990b, 1998; GEYER & LANDING 1995). The Tissafinian Stage of Morocco is crucial to understanding the biotic history through the Lower–Middle Cambrian boundary interval. It represents a highly fossiliferous (trilobites, brachiopods, helcionelloids, pelecypods, hyoliths, "small shelly fossils", echinoderms) interval that is widespread and well documented in the foothills of the High Atlas and much of the Anti-Atlas (GEYER & *al.* 1995, pp. 65-71, 81-117). Volcanic ashes occur through the lower and middle Tissafinian Stage in the foothills of the High Atlas and across the Anti-Atlas.

However, Tissafinian volcanism seems to have been exclusively basaltic, and we have only recovered zircons reworked from the late Proterozoic Pan-African orogen (E. LANDING & S.A. BOWRING, unpub. data). In this report, we designate the lower boundary stratotype of the Tissafinian Stage at the lowest occurrence of *Protolenus* (*Hupeolenus*) *termierelloides* in the lowermost Tazlaft Formation (level 9B, 0.05 m above base of formation) at the Le IV section in the Lemdad syncline, west-central High Atlas (see GEYER & *al.* 1995, fig. 14).

By comparison, the largely coeval Bilbilian Stage of Iberia is a far less practical unit for regional and inter-regional correlation of the West Gondwanan lowest Middle Cambrian. As noted above, the definition of the (traditionally terminal Lower Cambrian) Bilbilian Stage (SDZUY 1971a) was never adequate for its application as a useful chronostratigraphic unit. Indeed, its base was first defined by the top of the range of "Marianian Stage" (designation abandoned) trilobites, and its stratotype section lacks biostratigraphically useful fossils. For these reasons, "Bilbilian Stage" should be abandoned as the existing Tissafinian Stage provides a far more useful chronostratigraphic standard for the lowest Middle Cambrian of West Gondwana.

The Iberian "Leonian Stage" of SDZUY (1971b) is an older designation than the Moroccan Tissafinian Stage (GEYER 1983) for the lower Middle Cambrian of West Gondwana. However, the formally defined base of the "Leonian Stage" as proposed by SDZUY & *al.* (1998, 1999) correlates into a biostratigraphically undiagnostic interval in the second zone (*Cephalopyge notabilis* Zone) of the Moroccan Middle Cambrian. Rather than emend "Leonian" by assigning a significant amount of Iberian sub-paradoxidine Middle Cambrian (i.e., the "Bilbilian Stage") to the "Leonian" and thus creating a confusing objective homonym, "Leonian" must be abandoned as an Iberian and West Gondwanan designation for the lowest Middle Cambrian.

Agdzian Stage of the Celtiberian Series (new designations)

The designation of a reference standard for the base of the West Gondwanan Middle Cambrian at the base of the existing Tissafinian Stage is appropriate. However, the Tissafinian Stage is not the lateral equivalent of the "Leonian," and the chronostratigraphically longer and higher ranging "Leonian" is succeeded in Iberia by the highly fossiliferous, finely biostratigraphically subdivisible Caesaraugustian Stage (e.g. SDZUY 1971b; LIÑÁN & *al.* 1993b). The base of the middle Middle Cambrian Caesaraugustian Stage is defined by the lowest occur-

rence of *Badulesia tenera*, a horizon recognizable within the Moroccan Touthamian Stage above the Tissafinian Stage (GEYER & *al.* 1995). Rather than create an objective homonym of “Tissafinian” as a term for the West Gondwanan lower Middle Cambrian by revising it so that it extends upward to the base of the *B. tenera* Zone in the Touthamian, both “Tissafinian Stage” and “Touthamian Stage” must be abandoned in favor of a new stage-level unit. The Agdzian Stage (new) is proposed herein for the lower Middle Cambrian of West Gondwana. The Agdzian Stage consists of the *Hupeolenus*, *Cephalopyge notabilis*, and *Ornamentaspis frequens* Zones of the “Tissafinian Stage” (designation abandoned) and *Kymataspis arenosa* Zone of the lower “Touthamian Stage” (designation abandoned). The basal stratotype locality and horizon of the Agdzian corresponds to those of the Moroccan “Tissafinian” (discussed above), and its top is defined by the base of the Caesaraugustian Stage in West Gondwana. The designation “Agdzian” is unoccupied as a lithostratigraphic or chronostratigraphic term. “Agdzian” derives from the town of Agdz, central Anti-Atlas, which lies in an area with particularly vast and important outcrops of Middle Cambrian rocks.

The Agdzian is succeeded by the middle Middle Cambrian Caesaraugustian Stage, which, in turn, is succeeded by comparatively sparsely fossiliferous, dominantly siliciclastic terminal Middle Cambrian successions in West Gondwanan successions in Morocco, Iberia, southern France, and Sardinia (e.g. GEYER & *al.* 1995). ÁLVARO & VIZCAÍNO (1998) proposed the Languedocian Stage for this upper Middle Cambrian interval, and defined the base of the stage at Ferrals-les-Montagnes in the southern Montagne Noire at the lowest occurrence of *Solenopleuropsis* (*Manublesia*) *thorali* SDZUY, 1958. The Agdzian–Languedocian Stages are regarded as comprising the Middle Cambrian chronostratigraphic reference succession for West Gondwana, and are referred to the Celtiberian Series (new designation; name derives from the “Celtiberian Chains” of northern Spain, where important Middle Cambrian sections are distributed and studied).

“Celtiberian” is regarded as a particularly useful term for the Gondwanan Middle Cambrian because the series is a composite of three successive stages based on stratotypes in widely separated regions (southern Morocco, northern Spain, southern France) of West Gondwana. The lower stratotype locality and horizon of the Celtiberian Series are those of the Agdzian Stage, and lie at the base of the *Hupeolenus* Zone at the Le I section in the Lemdad syncline, southern Atlas Range (GEYER & *al.* 1995). “Celtiberian” is previously unused and is available as a chronostratigraphic term. The duration of the

Celtiberian Epoch is likely approximately equivalent to that of the Middle Cambrian as currently defined on other Early Paleozoic paleocontinents and its top (as well as the top of the Languedocian Stage) defined by the base of the recently introduced Furongian Series. An estimated at 9–10 m.y. duration of the Middle Cambrian (LANDING & *al.* 2000) is comparable to that of the Atlasian Epoch, the trilobitic Early Cambrian.

IMPROVED LOWEST MIDDLE CAMBRIAN CORRELATIONS

Scattered occurrences of ellipsocephaline, protolenine, and other trilobites in the Lower–Middle Cambrian boundary interval of Spain have been used in recent publications to corroborate earlier proposed correlations from Iberia with other areas and to further strengthen the potential of the Iberian faunal successions and stages for use elsewhere in West Gondwana (GOZALO & *al.* 1993a, 1993b, 1997; GOZALO & LIÑÁN 1997, 1998; DIES & *al.* 2000, 2001). The caveat to these latter proposals is these correlations are useful only if they rely on correctly identified specimens and accurate stratigraphic information. As discussed below, our contention is that even if these caveats are satisfied, the Iberian stages in the Lower–Middle Cambrian boundary interval do not provide an adequate basis for highly resolved intra-regional (West Gondwanan) and interprovincial correlations. In the following sections, we summarize available data on the taxonomy and stratigraphic ranges of trilobites from Gondwana, Baltica, and South China that serve to improve and modify correlations in the Lower–Middle Cambrian boundary interval. Of particular concern are comparisons and improved correlations of West Gondwanan lower Middle Cambrian faunas with the Ordian Stage of Australia and Amgan Stage of Siberia.

Onaraspis and the Ordian

ÖPIK (1968) proposed the trilobite genus *Onaraspis*. This genus, with two new species (*Onaraspis somniura* and *O. adusta*) and a form kept in open nomenclature by ÖPIK (1968), was found in the Australian Northern Territory region of East Gondwana with fossils that comprised a characteristic faunal association. This fauna, first informally termed the “*Redlichia* fauna,” was used by ÖPIK to define the Ordian Stage as the lowest Middle Cambrian chronostratigraphic unit in Australia. It includes Australian species of the redlichiid genus *Redlichia* COSSMANN, 1902; several species of *Xystridura* WHITEHOUSE, 1936; generalized corynexochids brought

to *Kootenia* WALCOTT, 1888; the enigmatic trilobite genus *Bathynotus* HALL, 1860; and archaeocyathans. This Ordian fauna, with its mixture of “Lower Cambrian” redlichoids and “Middle Cambrian” paradoxidoid-type and corynexochoid trilobites underlies and predates the “typical” Middle Cambrian Templetonian Stage faunas of Australia.

ÖPIK (1968, 1975) recognized that the Ordian provided a key role in intercontinental correlation and used it in proposing more highly resolved correlations of Australia with South China, Siberia, and other Cambrian areas. Particularly important in his synthesis is the fact that the fauna provides a strong link for a correlation of the Ordian with intervals in China traditionally assigned to the uppermost Lower Cambrian. These include the *Redlichia*-dominated Lungwangmiaoan Stage of the North China Platform (XIANG 1981, CHANG 1988) and most of the Duyunian Stage of the South China Platform together with its slightly younger terminal *Bathynotus* Zone (PENG & *al.* 1999, PENG 2003).

Although ÖPIK (1968), obviously correctly, correlated the Ordian with intervals worldwide with “*Protolenus* faunas,” he considered it to post-date olenellid/redlichiid-bearing (= “Early Cambrian”) and predate paradoxid-bearing (= “Middle Cambrian”) strata elsewhere. However, the state of knowledge on trilobite faunas in the Lower-Middle Cambrian boundary interval was too limited at that time to permit sufficiently plausible and precise correlations.

One of the key Ordian taxa is *Onaraspis*, which in 1968 was an endemic East Gondwanan genus known only from Australia. ÖPIK (1968) assigned it to the family Metadoxididae, which is based on the Sardinian genus *Metadoxides* BORNEMANN, 1891. *Metadoxides* has some resemblance to *Onaraspis* in cephalic morphology (e.g. a comparable shape of the glabella with three simple pairs of glabellar furrows and the front reaching almost to the anterior border, comparatively small eyes, rhachis with nodes, etc.). However, clear suprageneric differences can be seen between these genera in the thorax and the pygidium (e.g. with a macropleurale segment and a much larger, multisegmented, shield-like pygidium in *Onaraspis*).

***Onaraspis* clade in North Gondwana**

PARNES (1971) proposed *Myopsolenus palmeri* from the supposed upper Lower Cambrian of southern Israel. Although the type specimens from the Hakhilil Member of the Timna Formation are poorly preserved, this species shows the same type of thorax and pygidium as the Australian *Onaraspis somniurna* ÖPIK, 1968. ÖPIK (1975) commented on PARNES’ publication, recognized clear

generic differences, and proposed the new genus *Myopsolenites* on the basis of the Israeli material (ÖPIK 1975, p. 8, table caption; see also comments in GEYER 1990d, p. 175). Although a precise correlation of *Myopsolenites palmeri*-bearing interval is unknown, the presence of the genus in northwestern Gondwana significantly expanded the geographic distribution of *Onaraspis*-clade trilobites. Over the last decades this geographic range became even larger. Together with recent findings in Morocco the clade now even appears to have had its maximum diversity and geographic range in West Gondwana.

***Onaraspis* clade in West Gondwana (Iberia)**

A species of the *Onaraspis* clade was described in West Gondwana as *Perrector? altus* LIÑÁN & GOZALO, 1986, from the lower Valdemiedes Formation. This species came from the “terminal Lower Cambrian” upper “Bilbilian Stage” (SDZUY 1971a) in the Iberian Chains of northern Spain, where it occurs with *Hamatolenus* (*H.*) *ibericus*, *H.* (*Lotzeia*) *lotzei*, *Alueva undulata*, *A. hastata*, and other trilobites. GOZALO & LIÑÁN (1997) and GOZALO & *al.* (1997) revised *P.? altus* and assigned it to *Onaraspis*. In addition, they also assigned *Myopsolenites palmeri* from Israel to *Onaraspis*. It should be noted that the type material from the Iberian Chains is distorted in such a way that delicate morphological details cannot be identified with certainty. However, it is interesting that GOZALO & *al.* (1997) assigned the Iberian species to *Onaraspis*, and used this assignment to suggest a correlation of the lower part of the Valdemiedes Formation, and thus the “Bilbilian Stage,” with the Australian Ordian and with strata in Israel that yielded *Myopsolenites*. The significance of this Iberian report is that the “upper Bilbilian” occurrence of an apparent *Onaraspis* is in strata correlative with the Moroccan lower, but not lowermost, Middle Cambrian *Cephalopyge notabilis* Zone (discussed above, and further below). As detailed below in the Systematic Paleontology, we share ÖPIK’s (1975) opinion and regard *Myopsolenites*, as well as the Iberian forms, as species separate from, but closely related to *Onaraspis*.

Taxonomic considerations aside, an important concern remains. It is neither practical nor justifiable to use the scattered occurrences of a rare genus *per se* for highly resolved inter-regional and inter-provincial correlations at the stage level, particularly when problems exist with the definition of the boundaries of series-level chronostratigraphic units (e.g. the Lower-Middle Cambrian boundary). The distribution of associated additional taxa must be used for refined correlations.

Onaraspis clade in West Gondwana (Morocco)

A new species of the *Onaraspis* clade, described below as *Myopsolenites boutiouiti* sp. nov., has been recently discovered at a locality in the Jbel Ougnate uplift of the Moroccan eastern Anti-Atlas. The locality is on the northern slope of Bou Tiouit close to the reknowned village of Tarhoucht. This is the site where the Moroccan “giant trilobites” *Paradoxides (Acadoparadoxides) briareus* GEYER, 1993, and *Cambropallas telesto* GEYER 1993, are quarried for sale to fossil collectors (GEYER 1993; see GEYER & al. 1995, pp. 112-117, for details of the Tarhoucht section).

These specimens of *Myopsolenites boutiouiti* sp. nov. come from the lower half of the *Cephalopyge notabilis* Zone (Text-fig. 1). They are found in the lower 10 m of the Jbel Wawmast Formation, with a first occurrence ca. 2-3 m above the base of the formation (T. VINCENT, written communications, April and May 2002). The known material consists of six complete exoskeletons and a very fragmentary cranidium, but the morphology is well preserved. Due to the imperfect preservation of the Spanish material earlier described as *Perrector? altus*, a precise comparison is difficult, but characters detailed in the systematic section below indicate that the new species from Morocco is very similar to *Myopsolenites altus* (LIÑÁN & GOZALO, 1986).

Hamatolenus (H.) vincenti sp. nov. is associated in this interval with *Myopsolenites boutiouiti* and occurs with various trilobites typical of the lower part of the *Cephalopyge notabilis* Zone (see GEYER & al. 1995, pp. 112-117). These trilobites include *C. notabilis* GEYER, 1988; *Protolenus (P.) densigranulatus* GEYER, 1990d; *Latoucheia (L.) epichara* GEYER, 1990d; *Kingaspidoidea* cf. *K. laetus* GEYER, 1990d; *K. neglectus* GEYER, 1990d; *Ornamentaspis usitata* GEYER, 1990d; *O. angustigena* GEYER, 1990d; *Paradoxides (Acadoparadoxides)* sp. nov. A; *P. (A.) nobilis* GEYER, 1998, *P. (A.) briareus* GEYER, 1993; and *Parasolenopleura* sp. nov. A. Non-trilobite taxa include the obolellid brachiopod *Trematobolus splendidus* GEYER & MERGL, 1995; various mollusks; and eocrinoid ossicles. These data prove that *Onaraspis*-type trilobites occur in the West Gondwanan lower Middle Cambrian in Morocco and Iberia.

Onaraspis clade in Poland

A previously neglected occurrence of an *Onaraspis*-type trilobite was described by BEDNARCZYK (1970) from the Brzechów area in the Świętokrzyskie (Holy Cross) Mountains of southern Poland. BEDNARCZYK (1970) assigned three incomplete large cranidia and a pygidium

to the new species “*Jakutus kielciensis*” (*Jakutus kielciensis* in ORŁOWSKI 1985a). The morphological similarities with jakutid trilobites is superficial, or homoplastic, and include a tapered glabella with a subtruncate front, short palpebral lobes, absence of a preglabellar field, and a multisegmented pygidium. The specimens agree well with the Spanish material described as *Perrector? altus*, and the Polish and Spanish forms are assigned herein to the genus *Myopsolenites* (see Systematic Paleontology).

It is interesting that the fauna with the *Onaraspis*-type trilobite *Myopsolenites kielciensis* includes the ellipsocephaline *Germaropyge sanctacrucensis* (CZARNOCKI, 1927) (which probably is a species of the genus *Kingaspidoidea* that frequently occurs in the Moroccan lower and middle “Tissafinian”; see GEYER, 1990d), with species described as *Strenuaeva orlowinensis* SAMSONOWICZ, 1959; *Protolenus bodzanti* BEDNARCZYK, 1970; *P. medius* BEDNARCZYK, 1970; and *Paradoxides oelandicus* SJÖGREN, 1872 (BEDNARCZYK, 1970). The trilobite described as “*Protolenus bodzanti* CZARNOCKI, 1927” in BEDNARCZYK (1970) is in reality a small palaeolenid trilobite. Its comparatively poor preservation as internal molds in relatively coarse-grained siliciclastic deposits does not permit recognition of fine details of the glabella. However, the convex cephalon with the slightly forward expanding glabella and the narrow anterior border resemble these features in *Palaeolenus*, and particularly some of the material described as *Palaeolenus lantenoisi* MANSUY, 1912. However, the specimens from Poland have very inconspicuous anterior pairs (S3 and S4) of lateral glabellar furrows. The second species described as “*Protolenus medius*” appears to fall within the intraspecific variability of “*Protolenus bodzanti*” and could be regarded as a junior synonym of this species.

Strenuaeva orlowinensis is also known only from internal molds in relatively coarse-grained siliciclastics that are too imperfectly preserved to allow a precise determination. It shows similarities with species described from Scandinavia as *Strenuaeva*, but has distinct differences with *Strenuaeva primaeva* (BRÖGGER, 1879), the genotype species. The precise definition of *Strenuaeva* and its differences with more-or-less coeval species described from Scandinavia and referred to *Proampyx* is problematical, and goes beyond the scope of this report. However, it should be noted that these species occur in the (traditional) uppermost Lower Cambrian “*Ornamentaspis*” *linnarssoni* Zone of Baltica, but not in the overlying lower Middle Cambrian *Paradoxides oelandicus* Stage (BERGSTRÖM & AHLBERG 1981). Roughly similar specimens are also known under the name *Comluella* sp. from the southern Negev, Israel (PARNES 1971), where they occur with *Myopsolenites palmeri* (PARNES 1971, GEYER & LANDING, unpub. data).

The identification of *Paradoxides oelandicus* SJÖGREN, 1872 (consistently spelled “Sjörger” by BEDNARCZYK 1970) in the fauna of the Świętokrzyskie Mountains is based partly on ORŁOWSKI’S (1957, 1959, 1964) earlier determinations, and has been used to correlate the fauna with those of the *Paradoxides oelandicus* “Zone” of Sweden. However, the single immature cranidium illustrated by BEDNARCZYK (1970, pl. 1, fig. 1) is insufficient for a precise identification or highly resolved biostratigraphic correlation, and even BEDNARCZYK (1970, p. 34) listed some differences with the Swedish toptype material of *P. oelandicus*.

The overall composition of the fauna of the Świętokrzyskie Mountains is “Ordian” in that it shows the “mixed” assemblage of uppermost Lower Cambrian-type with Middle Cambrian-type faunal elements and includes *Onaraspis*- and palaeolenid-type trilobites that apparently share a stratigraphically limited occurrence. In its composition, the assemblage from the Świętokrzyskie Mountains resembles the faunas of the Iberian and Moroccan lower, but not lowest, Middle Cambrian *Cephalopyge notabilis* Zone, as well as Gondwanan faunas from Israel and Jordan.

Possible *Onaraspis* clade in South China

Pygidia with *Onaraspis*-type morphology were described and figured from Sichuan Province in South China and attributed to *Chengkouaspis longioculus* [sic!] ZHANG & LIN, 1980 (in ZHANG & al. 1980, pl. 70, figs 4–10), a genus and species on which the Family Chengkouaspididae ZHANG & LIN, 1980 was based. It should be mentioned that the family name is incorrectly compounded (correctly Chengkouaspididae). This family originally included a number of late Early to earliest Middle Cambrian trilobite genera. However, it obviously includes phylogenetically distantly related genera, and it seems appropriate to limit it to the eponymous genus *Chengkouaspis*. Furthermore, more and better preserved material of this genus may indicate that the family will prove to be a junior synonym. The size of the associated pygidia, however, apparently does not fit with the associated cranidia of *Chengkouaspis longioculus* and it remains uncertain whether the species is correctly referred to this genus. The material comes from the Yingzuiyan Formation. This formation correlates with the Shipai Formation that yields *Palaeolenus* (or, more probably, *Megapalaeolenus*; according to PENG SHANCHI, written comm., January 2003), and thus would be referable to the “uppermost Lower” Cambrian *Megapalaeolenus* Zone of the Yangtze Platform. However, examination of Mansuy’s material of *Palaeolenus* from Yunnan and western Hubei

brought LIN & PENG (in press) to regard *Megapalaeolenus* as a junior synonym of *Palaeolenus*. This affects primarily the concept of the genus and still leaves an evolutionary trend. However, it would lead to a revised stratigraphic scheme for the Yangtze Platform with a *Palaeolenus* Zone extended upward to include the *Megapalaeolenus* Zone (PENG, written comm., March 2004).

“*Kingaspis campbelli*” and West Gondwanan correlations

Correlation of the Lower–Middle Cambrian boundary interval from Iberia into other Cambrian areas of the Mediterranean realm recently has also been based on additional trilobites from Spain identified as *Kingaspis* spp. and *Kingaspidoides* spp. Particularly important for the correlations are trilobites identified as “*Kingaspis campbelli* (KING, 1923)” (LIÑÁN & al. 2003) from the upper “Bilbilian” of the Valdemiedes Formation at Jarque and the Rambla de Valdemiedes in the Iberian Chains. In the Jarque 1 section, the reported “*Kingaspis campbelli* (KING, 1923)” specimens overlap in stratigraphic range with “*Protolenus (Hupeolenus)* cf. *termiereloides* GEYER, 1990”, *P. (H.) jilocanus* LIÑÁN & GOZALO, 1986, and *P. (H.) dimarginatus* GEYER, 1990a. The highest occurrence of this “*Kingaspis campbelli*” is interpreted to lie at the lower limit of the “Valdemiedes event,” and thus forms part of the highest non-paradoxidid faunal horizon in Iberia.

Kingaspis campbelli was originally described from the limestone- and dolostone-rich Burj Formation on the eastern shore of the Dead Sea in Jordan (KING 1923). Therefore, the report of *K. campbelli* from Spain, if confirmed, would indeed enhance correlations from Iberia into the Cambrian successions of Jordan and Israel and assist in interregional correlation of the Lower–Middle Cambrian boundary interval. RUSHTON & POWELL (1998) re-examined the Jordanian succession and showed that *K. campbelli* occurs with *Schistocephalus antiquus* ČERNYŠEVA, 1956. The latter species is significant for inter-provincial correlation as it is an index fossil of the basal Amgan Stage (lowest Middle Cambrian) of the Siberian Platform. Although RUSHTON & POWELL (1998) preferred assignment of *S. antiquus* to *Palaeolenus* MANSUY, 1912, we follow the Russian convention (e.g. EGOROVA & SAVICKIJ 1969, ČERNYŠEVA 1971) in assigning the species to *Schistocephalus* on the basis of morphologic features. It should also be noted that *Palaeolenus* occurs in the (momentary) *Megapalaeolenus* Zone (see remarks above), or the coeval *Protoryctocephalus* Zone of the Duyunian Stage, on the South China Platform. This zone underlies the terminal Duyunian *Bathynotus* Zone that is supposed to correlate with the Ordian *Onaraspis*

faunule, and therefore an assignment to *Schistocephalus* appears to be more logical from a phylogenetic viewpoint.

The Siberian lower Amgan can be shown to be generally coeval with the Moroccan lower, but not lowest, Middle Cambrian *Cephalopyge notabilis* Zone. A key reason for this inter-provincial correlation is the fact that the *Cephalopyge notabilis* Zone has a species of the *Schistocephalus* clade that has been described as *Schistocephalus? ornatus* GEYER, 1998. Precisely determinable specimens of *Kingaspis campbelli* have also been found in Morocco, but are known only at a single horizon in the Jbel Wawrmast Formation at Abdallah/Najim east of Bou Kaïs, south of the Tamlelt area in easternmost Morocco (GEYER 1990d). Unfortunately, the complete stratigraphic range of the species is incompletely known in Morocco, and the specimens cannot be unequivocally assigned to a biostratigraphic zone. However, it can be shown that these Moroccan occurrences are lower, but not lowest, Middle Cambrian, and belong either to the *Cephalopyge notabilis* Zone or to the overlying *Ornamentaspis frequens* Zone (GEYER 1990a).

In contrast, the specimens identified from Spain as *Kingaspis campbelli* occur, according to LIÑÁN & al. (2003), with such species of *Hupeolenus* as *H. termierelloides* that would indicate a somewhat lower correlation with the lowest Middle Cambrian *Hupeolenus* Zone of Morocco. This apparent difference in the reported range of *K. campbelli* between Spain and Morocco can be explained by the fact that all of the reported Spanish specimens of *Kingaspis*, *Kingaspidoidea*, and *Hupeolenus* are considerably deformed and usually do not show the precise morphology of the external surface. As detailed by GEYER (1990b), kingaspidooid genera such as *Kingaspis* KOBAYASHI, 1935; *Kingaspidoidea* HUPÉ, 1953a; and *Ornamentaspis* GEYER, 1990d; and particularly their species, can be identified with certainty and used in precise correlations only if the detailed morphology of the external and internal surfaces is known. For this reason, the Spanish material is not precisely determinable. However, the internal molds of the specimens identified as *Kingaspis (K.) campbelli* from Spain represent a species different from *K. campbelli*. One principal character of *K. campbelli* is that the anterior facial suture meets the margin exsagittally posterior to the anterolateral corners of the glabella – a character that is not shown in the Spanish material. In addition, the Spanish specimens have a more elevated glabella and show palpebral lobes in a more anterior position.

Significance of *Hamatolenus (H.) vincenti* sp. nov.

Additional evidence for improved Lower – Middle Cambrian correlation between northern Spain and the

Moroccan Atlas ranges comes from the stratigraphic range of a species of *Hamatolenus* HUPÉ, 1953a. Specimens from the Iberian Chains of northern Spain were recently identified by DIES & al. (2001, pl. 1, figs 4–5) as *Protolenus (Hupeolenus)* cf. *termierelloides* GEYER, 1990. *Protolenus (H.) termierelloides* is characteristic of the *Hupeolenus* Zone, the lowermost Middle Cambrian zone in southern Morocco (e.g. GEYER 1990a, 1998).

However, the Spanish specimens of *Protolenus (H.)* cf. *termierelloides* described by DIEZ & al. (2001) from the upper “Bilbilian Stage” (abandoned designation) are herein referred to *Hamatolenus (Hamatolenus) vincenti* sp. nov. Additional specimens of this species from the Iberian Chains have been described and figured by LIÑÁN & GOZALO (1986, pl. 5, figs 9, 14) as “*Hamatolenus (Myopsolenus)?* sp.”

Interestingly, a large number of specimens of this new *Hamatolenus* species recently became available by sales to fossil collectors. The specimens usually come from the vicinity of Tarhoucht village in the eastern Anti-Atlas. Our work at Tarhoucht and additional data from Mr. Tony VINCENT of Oued Zem, Morocco, has served to define the stratigraphic range of *Hamatolenus (Hamatolenus) vincenti* sp. nov. Specifically, the species’ range can be documented in the nearly flat-lying section on the north-facing slope of Bou Tiouit. This slope just south of Tarhoucht has a number of small quarries that yield *Paradoxides (Acadoparadoxides) briareus* and *Cambropallas telesto*. The lowest occurrence of *Hamatolenus (H.) vincenti* in a measured section is approximately 4.3 m above the base of the Jbel Wawrmast Formation. T. VINCENT (written communication, April 2002) observed a lowest occurrence of this species about 3 meters above the base of the Jbel Wawrmast Formation. Confirmed frequent occurrences end with the top of HELDMAIER’s (1997) “Color Cycle 4”, which has an upper boundary in the Tarhoucht section at 5.9 m. However, specimens have also been found at 10.5, 10.6 and 14.6 m above the base of the Jbel Wawrmast Formation. All these occurrences belong to the lower *Cephalopyge notabilis* Zone, which starts immediately at the unconformable base of the Jbel Wawrmast Formation at Bou Tiouit and extends there through at least 93 m (GEYER & al. 1995, pp. 112–117).

The relative abundance of *Hamatolenus (H.) vincenti* sp. nov. in the lower *Cephalopyge notabilis* Zone in the Tarhoucht area helps emphasize the significance of this new species for lower, but not lowest, Middle Cambrian correlations. The species’ presence in Iberia provides further evidence for correlation of the traditional “terminal Lower” Cambrian (upper “Bilbilian Stage,” designation abandoned) of Iberia into the lower, but not lowest, Middle Cambrian and well into the Agdzian Stage. Both *H. (H.) vincenti* and the *Onaraspis*-type trilobite *Myopsolenites*

boutioui (discussed above) co-occur with *Protolenus* (*P. densigranulatus*), a more geographically widespread trilobite limited to the *Cephalopyge notabilis* Zone. *Protolenus* (*P. densigranulatus*) occurs in sections of the Lemdad area, where no facies change across the *Hupeolenus-Cephalopyge* zonal boundary can be determined which could be responsible for limiting its stratigraphic range.

Correlation of the *Hamatolenus* (*H. vincenti* sp. nov.-bearing, upper “Bilbilian” (designation abandoned) fauna described by DIES & al. (2001) with the Moroccan lower *Cephalopyge notabilis* Zone, rather than with the *Hupeolenus* Zone, marks an improvement in West Gondwanan lower Middle Cambrian correlation. It also means an improvement in interprovincial correlations in this interval. Although earlier correlations of the upper “Bilbilian” have been with the Siberian uppermost Lower Cambrian Toyonian Stage (SDZUY 1995), correlation of the upper “Bilbilian” with the *Schistocephalus*?-bearing *C. notabilis* Zone (discussed above) further supports earlier and higher correlations with the Siberian lower Middle Cambrian Amgan Stage (GEYER 1990c, GEYER & PALMER 1995, GEYER & al. in GEYER & SHERGOLD 2000).

These improved correlations further emphasize the significance of our re-evaluation of Lower–Middle Cambrian boundary correlations by stressing the temporally delayed appearance of *Paradoxides* (*Acadoparadoxides*) *mureroensis* in Iberia, by comparison with the earlier occurrences of paradoxidines in Morocco.

Intercontinental significance of the *Cephalopyge notabilis* Zone and its fossils

The *Cephalopyge* Chron was the period during which the maximum transgression of the early Middle Cambrian took place on a global scale. Thus, this interval should be detectable with some certainty by means of sedimentologic and sequence stratigraphic techniques even if index fossils cannot be found. Despite the notorious level of endemism, the interval bears a number of fossils with intercontinental distribution. These include the trilobite genera *Cephalopyge*, *Cobboldites*, *Protolenus*, and *Ovatoryctocara*. *Cephalopyge notabilis*, introduced as an endemic species from southern Morocco (GEYER 1988) was recently described from southeastern (Avalonian) Newfoundland by FLETCHER (2003), directly confirming the earlier proposed correlation between the western Avalonian and West Gondwanan successions (GEYER 1990c, 1998; GEYER & PALMER 1995; GEYER & al. in GEYER & SHERGOLD 2000). However, a caveat remains: Some of the specimens figured by FLETCHER (2003) as *Cephalopyge notabilis* do not belong to this species and genus because they show pronounced ventrally directed

spines on the pygidium (FLETCHER 2003, pl. 2, figs 23-24) whereas *Cephalopyge* has a smooth pygidial margin. It seems possible that these specimens with an apparently very low convexity could be specimens of *Kerberodiscus*; a genus described from the Hell’s Mouth Grits of North Wales where it co-occurs with *Hamatolenus* (*Myopsolenus*) *douglasi* (BASSETT & al. 1976).

Nevertheless, FLETCHER (2003) illustrated additional species which permit an unimpeachable correlation into the Moroccan *Cephalopyge notabilis* Zone. These taxa include *Condylopyge eli* GEYER, 1998. FLETCHER (2003) also identified *Hupeolenus* in his Avalonian faunas and recognized the Moroccan *Hupeolenus* and *Cephalopyge* zones in southeastern Newfoundland. However, we regard recognition of the *Hupeolenus* Zone in southeastern Newfoundland as tentative, at best. Indeed, the zone appears to be based on a single internal mold of an incompletely preserved cranidium from the Long Cove section, Trinity Bay, southeastern Newfoundland, on which FLETCHER’S (2003) species *Protolenus* (*Hupeolenus*) *mckillopi* is based. Indeed, the characters of *Protolenus* (*Hupeolenus*) *mckillopi* suggest that it in fact represents a species of *Protolenus* (*Protolenus*). Particularly puzzling is that FLETCHER (2003) lists *P.* (*Hupeolenus*) from his Redland section, Cape St. Mary’s peninsula, where it occurs above such typical *Cephalopyge* and post-*Cephalopyge* Zone trilobites as *Cobboldites* and *Condylopyge*. In this case, an identification as *P.* (*Protolenus*) is more consistent with the new species’ occurrence. Regardless, the identification of a *Hupeolenus* Zone in Newfoundland awaits further scrutiny.

A further problem exists with the occurrence of *Strenuaeva nefanda* GEYER, 1990d, which FLETCHER (2003) reports from the *Cephalopyge* Zone of southwestern Newfoundland. This species is known only from the significantly older *Sectigena* Zone in Morocco, where it occurs with other typical species of *Strenuaeva* and *Issafeniella*; genera which are as well known from equivalent Banian strata in Iberia, Poland, and Scandinavia (see GEYER 1990d).

The occurrence in southeastern Newfoundland of *Cephalopyge* at a relatively short stratigraphic distance below *Ovatoryctocara granulata* ČERNÝŠEVA, 1962 (a species first described from Siberia) is an important guide to global correlation because it allows correlation with the lowermost Amgan Stage (FLETCHER 2003). In addition, it sheds some light on the correlation with strata bearing *Arthricocephalus*, which was suggested as an important faunal element in the correlation of South China and Laurentian Greenland sequences described by BLAKER & PEEL (1997; see FLETCHER 2001, 2003; PENG 2003).

Finally, it should be noted that oryctocephalaceans presently show little potential for improved correlations

of the West Gondwanan and Siberian successions with Laurentia because of their extremely sparse and scattered occurrence in West Gondwana. In this context, we would like to report that the first oryctocephalacean specimens of Morocco were recently discovered from *Myopsolenites*-bearing strata of the *Cephalopyge notabilis* Zone in the eastern Anti-Atlas by Mr. T. VINCENT.

AGDZIAN STAGE TRILOBITE SUCCESSIONS AND THE “VALDEMEIDES EVENT”

The proposal of the Agdzian Stage as the lowest Middle Cambrian standard for West Gondwana permits a new synthesis of changes in trilobite faunas through the Lower–Middle Cambrian boundary interval. As discussed above, the standard for the base of the Gondwanan Middle Cambrian is best defined in southern Morocco, where the lowest Middle Cambrian is particularly fossiliferous by comparison with approximately coeval strata of the Iberian lower “Bilbilian Stage” (designation abandoned). The Moroccan lowest Agdzian trilobite faunas are dominated by the earliest protolenines [such as *Protolenus* (*Hupeolenus*)] and ellipsocephalines (such as *Kingaspidoidea* or *Latikingaspis*). The oldest paradoxinines [e.g. *Paradoxides* (*Acadoparadoxides*) *nobilis*] appear locally in this fauna and emphasize that it is “Middle” Cambrian in the traditional sense (discussed above). This lowest Middle Cambrian trilobite assemblage is replaced upward by a second assemblage with abundant and more diverse ellipsocephalines (such as *Kingaspis*, *Ornamentaspis*, *Ellipsocephalus*, and featuring the acme of *Kingaspidoidea*), the lowest occurrence of abundant *Paradoxides* s.l. [including *Paradoxides* (*A.*) *mureroensis* in Iberia and Morocco], and *Onaraspis*-type trilobites such as *Myopsolenites*. This second lower Middle Cambrian interval features horizons in which palaeolenid trilobites show up in West Gondwana. The overlying third lower Middle Cambrian (and Agdzian Stage) fauna is not dramatically different from the second fauna, but includes ptychopariaceans, solenopleuraceans (e.g. *Parasolenopleura*, *Conocoryphe* s.l.), and agraulids (*Agraulos*, *Skrejaspis*) with ellipsocephalines. These newly appearing groups in the third assemblage even tend to dominate the ellipsocephalines in siliciclastic deposits, and *Paradoxides* s.l. becomes abundant. The gradual increase of Ptychopariida and *Paradoxides* s.l. serves to define the fourth trilobite association of the upper Agdzian Stage; this fourth fauna represents the typical Mediterranean-type Middle Cambrian trilobite association. These four successive associations correspond to the four zones of the Moroccan Tissafinian and lower Touthamian Stages (*Hupeolenus*, *Cephalopyge notabilis*, *Ornamentaspis frequens*, and *Kymataspis arenosa* Zones). Although these successive changes in trilobite fau-

nas cannot be proven to have taken place simultaneously across West Gondwana, they likely provide a level of biostratigraphic resolution appropriate to regional and inter-provincial correlations comparable to that of trilobite zonations elsewhere in the Cambrian.

The reason for the diachronous local appearance of paradoxidids remains problematical. As discussed above, the diachronous local occurrence of representatives of this trilobite group even between Moroccan and Iberian sections and differences in the frequency of characteristic trilobite species has led us to abandon the “Leonian” in favor of the reference standard for the Agdzian.

The lowest occurrence of *Paradoxides* (*Acadoparadoxides*) *mureroensis* in Iberia immediately succeeds a several meter-thick interval in the Iberian Chains (West Asturian-Leonese Zone) that has been interpreted as the record of a “Valdemiedes event” (GOZALO & al. 1993a, 2003; LIÑÁN & al. 1993a, 1993b, 1996a). This sparsely fossiliferous interval separates underlying protolenid-rich from overlying paradoxidid-bearing trilobite assemblages (LIÑÁN & al. 1993a). The “Valdemiedes event” remains a problematical interval in Iberia. It has been interpreted to record an “event” of abrupt faunal turnover, or extinction, related to climate changes (LIÑÁN & al. 1993a) or simply as a replacement of benthic communities (ÁLVARO & al. 1999). The problem remains that the “event” character is based on the stratigraphic distribution of trilobites and their local absence, and thus, may be simply an artifact of sampling in a low diversity/low specimen occurrence interval. Careful study of additional fossil groups is necessary to clarify its character (e.g. CLAUSEN 2001). Although of regional extent, the “event” may also include significant stratigraphic condensation/cut-outs at the bases of sandstones in the “event” interval (see GOZALO & al. 1996, figs 33–34).

What is evident from this review of the successive changes in lower Middle Cambrian trilobite faunas in West Gondwana is that the “Valdemiedes event” is best regarded as having “occurred” within the early Middle Cambrian. Obviously, the “Valdemiedes event” corresponds to an interval (of ca. ten metres in thickness in the Jarque 1 section) within the *Cephalopyge notabilis* Chron in which little happened in other coeval West Gondwanan (Moroccan) successions. Thus, the “Valdemiedes event” may represent nothing more significant than collection bias in a low diversity bio- and/or lithofacies. If the “Valdemiedes event” marks a real biotic event, the “event” is presently restricted to the Iberian Chains. Explanation of the “event” notwithstanding, the base of the Leonian Stage [and base of the *Paradoxides* (*Acadoparadoxides*) *mureroensis* Zone] correlates into the Moroccan *Cephalopyge notabilis* Zone, and its correlation is not differentiable biostratigraphically from the correlation of the upper “Bilbilian Stage” into the *C. notabilis* Zone (see GEYER 1998, pp. 376–377).

Unified Lower–Middle Cambrian boundary chronostratigraphy

Known Moroccan stratigraphic ranges and revised identifications of key trilobite taxa indicate that specimens from the lower part of the Valdemiedes Formation of the Iberian Chains earlier identified as *Onaraspis altus*, *Kingaspis campbelli*, *Protolenus (Hupeolenus) cf. termierelloides*, and *P. (H.) dimarginatus* (GOZALO & LIÑÁN 1997, GOZALO & al. 1997, DIES & al. 2001, LIÑÁN & al. 2003) and referred to the Iberian upper “Bilbilian Stage” [or *Hamatolenus (H.) iberica* Zone] actually indicate a correlation with the Moroccan *Cephalopyge notabilis* Zone. Indeed, *Onaraspis altus* and *P. (H.) cf. termierelloides*, respectively revised to *Myopsolenites altus* and *Hamatolenus (H.) vincenti* sp. nov. herein, are characteristic of the *Cephalopyge notabilis* Zone of Morocco. These taxonomic revisions of species earlier reported from Spain and new data on the stratigraphic range of these species in Morocco indicate that correlation of the sub-paradoxidid upper “Bilbilian” of Iberia is *not* with the older *Hupeolenus* Zone as suggested earlier by SDZUY (1995). This correlation detailed herein corroborates correlations of the supposedly “Lower Cambrian” “Bilbilian Stage” (e.g. LIÑÁN & al. 1993b) higher into the Middle Cambrian as suggested by GEYER (1983, 1998) and GEYER & SHERGOLD (2000). Indeed, SDZUY’s (1995) and GEYER’s (1998, fig. 2) earlier correlation of the upper “Bilbilian Stage” into the Moroccan lower “Tissafinian Stage” must now be revised in favor of a lower middle Agdzian Stage correlation. Re-examination of species-level identifications also confirms the earlier proposal that the identification of *Kingaspis campbelli* from the Iberian Chains and the suggested correlation of the Spanish interval in which the material was found with the Burj Formation in Jordan are not correct.

If the upper “Bilbilian Stage” is definitely Middle Cambrian by correlation into Morocco, then how is the Lower–Middle Cambrian boundary to be defined in Iberia? In addition, what is the status of the Iberian Lower–Middle Cambrian boundary-interval stages?

CONCLUSIVE REMARKS

Nomenclatural consequences of a unified Lower–Middle Cambrian chronostratigraphy (i.e., Cordubian Series; new formulation) for the sub-trilobitic Lower Cambrian, Issendalenian and Banian Stages of the Atlasian Series for the trilobite-bearing Lower Cambrian, and a new Agdzian and existing Caesaraugustian Stages for the lower and middle Middle Cambrian of the Iberian and Moroccan regions of West

Gondwana are of minor significance to local, regional, and interregional stratigraphy and geological syntheses. None of the existing biostratigraphic zonations or lithostratigraphic schemes for Morocco or Iberia have to be altered because they are appropriate in providing a local summary of biotic and depositional history. In addition, use of this unified chronostratigraphy as a regional standard will allow an easy reference standard for the developing U-Pb zircon geochronology that is being developed for this interval.

The Cordubian Series provides a practical term for the non- to sparsely fossiliferous, sub-trilobitic Lower Cambrian when extended into Morocco, and provides a basis for worldwide correlation into lowest Cambrian successions with trace fossil-dominated assemblages. The Cordubian has the longest duration of all named Cambrian chronostratigraphic units in West Gondwana. The Issendalenian and Banian Stages are appropriate as the penultimate and terminal Lower Cambrian stages of West Gondwana. They are approximately equivalent in concept to the Iberian “revised Ovetian” and “Marianian” Stages, respectively, but have formally defined basal stratotypes and feature highly fossiliferous successions with greater potential for trilobite-, archaeocyathan-, and geochronologic-based correlations across and out of West Gondwana. A unified stage-level chronostratigraphy for the Lower-lower Middle Cambrian of West Gondwana does mean that the position of the Lower–Middle Cambrian boundary has to be lowered in Spain. However, the supposedly “upper Lower” Cambrian “Bilbilian Stage” (abandoned term) must be partly referred to the Middle Cambrian, a necessary revision based on the Middle Cambrian aspect of its faunas. Indeed, the “Bilbilian” proves to be correlative with units with Middle Cambrian faunas both within West Gondwana (Morocco, Israel, Jordan) and worldwide (e.g. the Siberian Amgan Stage).

The proposal of the Agdzian Stage and abandoning of the Moroccan “Tissafinian–Toushamian” Stages and Iberian “Leonian Stage” for the lower Middle Cambrian of West Gondwana helps emphasize that unresolved factors (biofacies barriers/regional unconformity/sedimentary condensation in the “Bilbilian”-“Valdemiedes” interval) were responsible for the late first-occurrence of paradoxidids in Iberia. The consequence of these factors is that “Leonian” (designation abandoned) proves not to be a lowest Middle Cambrian stage in West Gondwana, and that inter-regional correlation of its base [i.e., the lowest occurrence of the index species *Paradoxides (Acadoparadoxides) mureoensis*] can only provide a tie line within the lower Middle Cambrian.

One consequence of a unified chronostratigraphic nomenclature is that it helps relate biotic and geological events to a regional standard and contributes significant-

ly, for example, to an understanding of the sequence stratigraphy in West Gondwana. Indeed, the unified chronostratigraphy helps evaluate the effect of eustatic and epeirogenic sea-level changes. One important regressive–transgressive interval created a complicated pattern of coarse siliciclastic deposition that marks the Lower–Middle Cambrian boundary interval in the Moroccan Atlas region (see GEYER & LANDING 1995 for stratigraphic overview). A blanket of shallow marine, tidalite-dominated sandstone in Morocco is termed the Tazlaft Formation. This formation can be shown to belong to the upper *Sectigena* and lowermost *Hupeolenus* Zones, and is lithologically comparable with and correlative with the Daroca Formation and coeval sandstone-dominated units in Iberia. Thus, the Tazlaft and Daroca Formations reflect a major regression in the Lower–Middle Cambrian boundary interval (see ÁLVARO & VENNIN 1998) that LANDING & *al.* (2002) have recognized in coeval shallow- and deep-water sequences on the Laurentian continent and referred to the Hawke Bay regression. The Tazlaft Formation is overlain unconformably by similar siliciclastics, which, however, were deposited under a transgressive regime. This thin formation (usually only several tens of meters in thickness) is termed the “Tatelt Formation.” Its biostratigraphic position largely depends on local and regional epeirogenic events and pre-onlap topography – features that controlled the time of local onlap and marine submergence (E. LANDING, W. HELDMAIER, and G. GEYER, unpublished data). The Tatelt Formation usually represents the upper *Hupeolenus* and lower *Cephalopyge notabilis* Zones. The Tatelt Formation is then overlain at a cryptic unconformity by the usually thick, siliciclastic mudstone-dominated Jbel Wawrmast Formation. This mudstone deposition persisted into the *Ornamentaspis frequens* Zone, which overlies the *Cephalopyge notabilis* Zone.

The important unconformity between the Tazlaft and the Tatelt Formations can be precisely timed in regions such as the Lemdad syncline in the southern foothills of the High Atlas. In areas of the Moroccan Anti-Atlas, erosion and resulting cut-out locally created a larger gap underneath the Tatelt Formation. The subsequent Middle Cambrian transgression inundated areas in which Lower Cambrian deposits were not developed so that the Jbel Wawrmast Formation (which succeeded the Tatelt Formation) rests unconformably on older late Proterozoic (Pan-African) basement. A consequence of the revised and unified Cambrian chronostratigraphy proposed herein is that it provides a standard for inter-regional correlation and the potential recognition of such complex Lower–Middle Cambrian boundary interval events across West Gondwana.

Further benefits follow from this proposal and adop-

tion of a unified Lower–Middle Cambrian series- and stage-level chronostratigraphic nomenclature for West Gondwana. The proposal in this report establishes, for the first time, chronostratigraphic divisions for the West Gondwanan Lower and Middle Cambrian that meet all the requirements (e.g. precisely defined lower boundaries in designated stratotype sections) mandatory for their formal definition (e.g. HEDBERG 1976). In addition, the sequence of series and stages proposed herein derive from an improved and more fully understood biostratigraphic succession, and more adequately reflect the biotic history of immigration, evolutionary, and extinction events in Iberia and Morocco. For this reason, this province-appropriate chronostratigraphic scheme allows the most highly resolved correlations across the West Gondwanan faunal province (e.g. VALENTINE 1973, pp. 357–358). Although no consensus yet exists on globally appropriate chronostratigraphic subdivisions of the Lower and Middle Cambrian, this report provides a basis for global correlations within this interval. Finally, the lower boundary definitions of a number of the Cambrian subdivisions proposed herein are available for consideration as global chronostratigraphic standards.

It should be noted that the traditional subdivision of the Cambrian, as has been the practice for many other eras and periods, into “Lower,” “Middle,” and “Upper” divisions may not be deemed appropriate in future decisions by the *International Subcommittee on Cambrian Stratigraphy* and the *International Commission on Stratigraphy*. For the Cambrian, the Furongian Series has recently replaced the traditional term “Upper Cambrian” for worldwide use. As shown in this report and in earlier discussions (e.g., LANDING & *al.* 1989), the “Lower Cambrian” is better regarded as two series-level divisions (sub-trilobitic and trilobite-bearing) in a number of faunal provinces, and thus “Lower Cambrian” is better regarded as a descriptive, and not chronostratigraphic, unit. Similarly, the widely differing concepts and definitions of the base of the Middle Cambrian even within West Gondwana means that “Middle Cambrian” has previously been used subjectively.

SYSTEMATIC PALEONTOLOGY

Material

The new material described below all comes from the area in the vicinity of the small village of Tārhoucht in the Jbel Ougnat uplift of the Moroccan eastern Anti-Atlas. Most of the material was collected in the reknowned section on the northern slope of Bou Tiouit just south of

Tarhoucht. This section was studied earlier in detail and is generally known as the “Tarhoucht section” (GEYER 1993; see GEYER & *al.* 1995, pp. 112–117, and HELDMAIER 1997, pp. 135–141, for details of the section). Sample numbers below refer to the distance (in meters) of the stratum from the base of the Jbel Wawrmast Formation. This section is the site where the Moroccan “giant trilobites” *Paradoxides (Acadoparadoxides) briareus* GEYER, 1993, and *Cambropallas telesto* GEYER, 1993, are quarried for sale to fossil collectors. The majority of the material described below was collected by T. VINCENT (of Oued Zem) in this section, mostly without precise measurement of the stratum. However, Mr. VINCENT was able to confidently assign the material to HELDMAIER’s (1997) color cycle scheme so that the stratigraphic position of the specimens is well defined.

A new quarry was opened by the local fossil collectors on the western side of the dirt road from Tarhoucht to Tarhia, roughly 1.5 km north of Tarhoucht close to Jbel Tazderout (5°1.30’W, 31°23.65’N), termed below the “Tarhia track quarry”. This site also exposes the lowest meters of the Jbel Wawrmast Formation. The material from this locality studied herein was exclusively collected by T. VINCENT, who also prepared a preliminary map and section.

Family uncertain

DISCUSSION: ÖPIK (1968) assigned his newly introduced genus *Onaraspis* to the family Metadoxididae. The Sardinian genus *Metadoxides* BORNEMANN, 1891, has some resemblance to *Onaraspis* in its cephalic morphology (e.g. the shape of the glabella with three simple pairs of glabellar furrows and the front reaching almost to the anterior border, comparatively small eyes, axis with nodes). Clear suprageneric differences can be seen in the thorax and the pygidium: *Onaraspis* has a prominent, posteriorly located macropleural segment and a much larger, multisegmented and shield-like pygidium, whereas the pygidium of *Metadoxides* is triangular with relatively small, pleural fields that have distinct furrows (see PILLOLA 1991, pl. 8, fig. 7, and pl. 9, fig. 2). The pygidial axis in *Metadoxides* has a wide terminal axial piece that tends to be faintly bilobate. In addition, the thoracic segments of *Metadoxides* are articulated in a different style than those of *Onaraspis* and *Myopsolenites*, as described below. Finally, the thoracic axis in *Metadoxides* has conspicuous swellings at the axial furrows. These swellings mark the locations where the muscles for the appendages inserted from the ventral side. These differences indicate a distinctly different systematic position of the *Onaraspis* clade.

ÖPIK’s (1968) viewpoint may have been directed by

HUPÉ’s (1953b, fig. 168) reconstruction of *Metadoxides*. This reconstruction showed *Metadoxides armatus* (MENEHINI, 1881) with a pygidium that has much larger pleural areas, more gently curved lateral margins, and a clearly tapered pygidial axis.

In this respect, the pygidium of *Onaraspis* is more similar to that known from typical species of the *Resserops* group. The similarities with the *Resserops* group and related genera are so homoplastic that it remains questionable whether *Onaraspis* should be grouped together with such genera. Despite these considerations, the *Resserops* clade was earlier assigned to the Neoredlichiiidae (HARRINGTON 1959), but re-evaluated as a distinct subfamily Resseropinae by ZHANG (“CHANG” 1966) and re-assigned to the family Saukiandidae by ZHANG & *al.* (“CHANG” & *al.* 1997). The latter placement appears to be inappropriate as *Saukianda* and closely related genera have a characteristic glabella with a distinct pattern of the lateral glabellar furrows, a rounded frontal lobe, and medium-sized pygidia, all distinctly different from *Resserops* and related genera as well as *Onaraspis* and the closely related *Myopsolenites*.

Genus *Myopsolenites* ÖPIK, 1975

TYPE SPECIES: *Myopsolenus palmeri* PARNES, 1971; Timna Formation, Timna area, southern Israel.

EMENDED DIAGNOSIS: Redlichiiine genus characterized by a cephalon with low overall convexity; glabella tapering forward, front subtruncate, reaches to anterior border; three pairs of lateral glabellar furrows, S1 longer than S2 and S3, and with a tendency to be connected medially; anterior border relatively shallow, slightly sloping rearward from anterior rim, poorly defined, anterior border furrow weakly impressed; thorax in adult individuals with twelve to fourteen segments, with tenth, eleventh or twelfth segment conspicuously macropleural and thoracic tergites posterior to the macropleural segment reduced in size; pygidium shield-like, with long, multisegmented axis; pleural fields with shallow to modestly developed furrows; lateral and posterior border obsolete, lateral and posterior margins smooth, usually gently curved.

DISCUSSION: The genus *Myopsolenites* ÖPIK, 1975, is based on a species described by PARNES (1971) as *Myopsolenus palmeri* from the supposed upper Lower Cambrian Timna Formation of southern Israel. One of the principal reasons to assign these strata to the Lower Cambrian was the identification of this form as a species of *Myopsolenus* HUPÉ, 1953a; a genus which at that time

was regarded as characteristic for the latest Early Cambrian age. *Myopsolenus* is now regarded as a subgenus of the protolenoid genus *Hamatolenus* HUPÉ, 1953a (see GEYER, 1990d and below). ÖPIK (1975) recognized significant generic (and supra-generic) differences, and proposed the new genus *Myopsolenites* for the Israeli species (ÖPIK 1975, p. 8, table caption; see GEYER 1990d, p. 175).

The type specimens of *Myopsolenites palmeri* (PARNES, 1971) from the Hakhilil Member of the Timna Formation was based on incomplete and poorly preserved material. However, the species shows the same type of thorax and pygidium as the Australian *Onaraspis somniurna* ÖPIK, 1968. Although a precise correlation of the strata with *M. palmeri* is unknown, the presence of the genus in northwestern Gondwana significantly expanded the geographic distribution of *Onaraspis*-clade trilobites. Over the last decades the known geographic range became even larger. Together with recent finds in Morocco, the clade now appears to have had its maximum diversity in West Gondwana.

We studied the type material of *Myopsolenites palmeri*, now housed in the Geological Survey of Israel. However, it does not unequivocally preserve the species' morphology. What can be seen is that the glabella progressively tapers forward to a subtruncate front. The eye ridges commence at S3 and run more-or-less straight posteriorly and abaxially. The well-elevated palpebral lobes are oblique to the axis and moderately long. The occipital ring carries a stout terminal node. The anterior border is slightly elevated anteriorly, but weakly defined towards the preglabellar field. The holotype (PARNES 1971, pl. 3) is a fairly complete but slightly disarticulated specimen (due to the molting process) that is more than 120 mm in length. Due to the cranidium being dislocated from the thorax, the exact number of thoracic segments cannot be counted with certainty. However, the specimen's taphonomically modified condition suggests that the thoracic segments are all preserved, with only the anteriormost tergite disconnected from the rest of the thorax. Therefore, the thorax would have twelve segments, with a macropleural tenth followed by two tergites of reduced size between it and the pygidium. The pygidium is quite well known from additional material. It has relatively gently curved lateral margins, shallow interpleural furrows only on the anterior parts of the pleural fields, and successively shallower furrows across the axis. An additional small specimen from the same locality at Har 'Amram (PARNES 1971, pl. 4, figs 35-36) also has twelve thoracic segments.

The best preserved type specimens were collected at Har 'Amram and have been considered to come from the Mikhrot Member of the Timna Formation. Additional

material of the type lot comes from the overlying Hakhilil Member of the Timna Formation in Timna National Park. Our investigations (GEYER and LANDING, unpub. data) suggest that the geological situation at Har 'Amram has been incorrectly evaluated, and the specimens may indeed come from the Hakhilil Member. We collected additional material at Timna, and this material for the first time clearly shows the cranial features. These include a stout terminal occipital node; a relatively straight, well impressed occipital furrow with a shallower part medially; posterior lateral glabellar furrows (S1) that are not clearly deeper than S2 or S3; low, almost straight eye ridges that are connected with and progressing into a parafrontal band; and moderately curved, medium sized palpebral lobes, the posterior ends of which are clearly distant from the posterior border furrow.

In summary, the small number of thoracic segments, the comparatively short (exsag.) palpebral lobes, and the shallow lateral glabellar furrows S1 serve to distinguish *Myopsolenites palmeri* from the three other species assigned to this genus (Table 1).

Perrector? altus LIÑÁN & GOZALO, 1986 from the "Bilbilian Stage" (abandoned designation) of the Iberian Chains, northern Spain, is difficult to characterize on the basis of the type material from the Valdemedes Formation at the Rambla de Valdemedes. This material is so strongly deformed that the exact morphology of the lateral glabellar furrows and details of the pygidium cannot be determined. However, it appears that the morphology of this Iberian form is very similar to that from the Anti-Atlas described below. Differences may be seen in the more robust genal spines and the somewhat less curved palpebral lobes of the Anti-Atlas specimens. Taking into consideration the large intraspecific variation seen in *M. boutiouti* sp. nov., these differences would not be regarded as sufficient to distinguish the Iberian and Moroccan material on a species level. Nevertheless, LIÑÁN & GOZALO (1986, p. 44) describe *M. altus* as having a thorax consistently with fourteen segments, and with three segments posterior to the macropleural eleventh segment. This feature is visible in specimens on their pl. 3, figs 3-4. By contrast, exoskeletons of adult individuals of *M. boutiouti* larger than the specimens of *M. altus* show no more than thirteen thoracic segments, and with only two posterior to the macropleural eleventh segment. These features are interpreted to mean that the Moroccan material represents another very closely related species. Additional, better preserved material of *M. altus* will probably reveal additional characters that distinguish the species.

Although *Myopsolenites boutiouti* sp. nov. shows unusually large variability, it can be distinguished unequivocally from *M. kielciensis* (BEDNARCZYK, 1970).

This species, now known only from the lowermost Middle Cambrian of the Brzechów area in the Świętokrzyskie (Holy Cross) Mountains and described as *Jakutus? kielciensis*, is known only from incomplete, large cranidia and a single pygidium. This species from southern Poland differs from *M. boutiouiti* in having distinctly shorter eye ridges and, as a result, narrower fixigenae and palpebral lobes that are somewhat more oblique to the axis. The anterior border appears to be narrower and more upturned, but this may be a result of the preservation. Nevertheless, the pygidium of *M. kielciensis* is narrower, with distinctly less curved lateral margins, so that the outline is more-or-less “heart-shaped,” in contrast to the subrounded to subparabolic pygidium of *M. boutiouiti*. In addition, the almost smooth lateral border is much narrower (tr.) in the pygidium of *M. kielciensis* than that in *M. boutiouiti*. The same characters that distinguish *M. kielciensis* from *M. boutiouiti* are also useful to differentiate it from *M. altus*.

It should be noted that according to our observations (GG, unpubl. data) additional species of this or a closely related genus are found in a section at Tierga in the Iberian Chains, which is comparable stratigraphically with the sections in the Rambla de Valdemiedes where the type material of *Myopsolenites altus* was found. These undescribed species, some with two macropleurale thoracic segments, contribute to the notion that this stratigraphic interval represents a brief bloom of this *Onaraspis* clade.

Character	S1	palpebral lobes	number of thoracic segments	pygidial outline
<i>M. palmeri</i>	shallow, disconnected	rel. short	12	subparabolic
<i>M. altus</i>	well impressed, connected	mod. long	14	subparabolic
<i>M. boutiouiti</i>	well impressed, connected	mod. long	13	subparabolic
<i>M. kielciensis</i>	well impressed, connected	rel. short	unknown	heart-shaped

Table 1. Comparative morphologies of four *Myopsolenites* species

Myopsolenites boutiouiti sp. nov.
(Text-figs 4, 5, 7.3)

ETYMOLOGY: Named for Bou Tiouit, the mountain on the south side of the village of Tarhoucht where the type material was found.

HOLOTYPE: Specimen PIW 2003III23a (Text-figs 4.10 and 4.11).

LOCUS TYPICUS: Tarhoucht-Bou Tiouit section, Jbel Ougnat area, eastern Anti-Atlas.

STRATUM TYPICUM: Horizon ca. 3m above the base of the Jbel Wawrmast Formation, Brèche à *Micmacca* Member, *Cephalopyge notabilis* Zone, Agdzian Stage.

OCCURRENCE: All material (except specimen EF-01; precise locality and stratum unknown) comes from the *Cephalopyge notabilis* Zone, middle Agdzian Stage; Jbel Wawrmast Formation, Brèche à *Micmacca* Member, at or close to Tarhoucht, Jbel Ougnat area. The material known so far comes from HELDMAIER's (1997) Color Cycle 4, a stratigraphic interval ca. 2.1 to 5.9 m above the base of the Jbel Wawrmast Formation. More and better preserved material was found in the basal yellowish fine-grained sandstones, but specimens also occur higher in this interval (T. VINCENT, written comm., Dec. 2002).

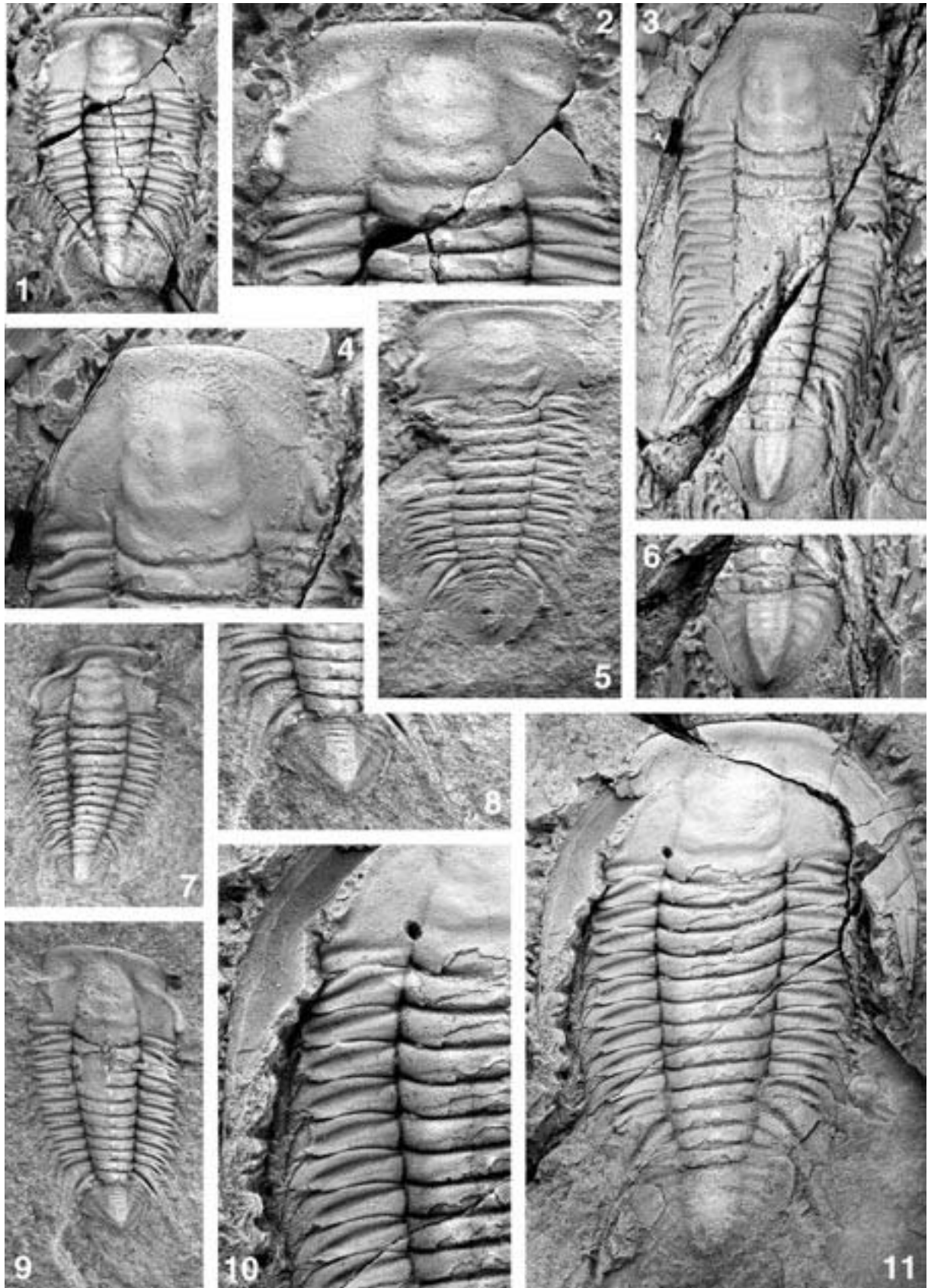
REPOSITED MATERIAL: Six almost complete exoskeletons; PIW 2003III19, PIW 2003III20, and PIW 2003III21 all without librigenae; PIW 2003III23a with librigenae slightly attached; PIW 2003III22 with dextral librigena disarticulated next to exoskeleton; two isolated cranidia, PIW 2003III24 and 2003III25a; one incomplete thorax with articulated pygidium, PIW 2003III25b; one isolated partial librigena, PIW 2003III25c. PIW 2003III19, 2003III20, 2003III22 and 2003III23a from Tarhoucht-Bou Tiouit, PIW 2003III21, 2003III24 and 2003III25a-c from Tarhia track quarry.

Collection of Patrick BOMMEL, St.-Julien-aux-Bois, France: EF-01/ No. 1403, articulated exoskeleton without librigenae.

DIAGNOSIS: Species of *Myopsolenites* with moderately tapering glabella with well developed, transglabellar S1 and truncate front; moderately long palpebral lobes; thorax with thirteen segments; pygidium with with gently curved lateral and posterior margins, subparabolic in outline.

DESCRIPTION: Medium- to large-sized (large complete holaspis up to 9.5 cm in the studied material) trilobites.

Cranidium transversely subrectangular, overall convexity modest, length about 65 to 75 percent maximum width across center of palpebral lobes. Glabella moderately convex, length in adult specimens slightly more than 80 percent cephalic length and 1.3 times width across occipital ring; continuously tapers forward. Frontal lobe sagittally short, with shallow curvature in juvenile individuals, subtruncate in large specimens. Three pairs of lateral furrows developed, all shallow and progressively indis-



tinct from S1 to S3. S1 commences at dorsal furrows, backward directed, separated medially on glabella, but with tendency to bifurcate. S2 somewhat distant from dorsal furrows, shallow, transverse or slightly backward directed. S3 short and indistinct but narrower than S1 and S2, somewhat forward directed. Occipital furrow moderately wide but relatively shallow in median sagittal section, lateral sections deeper and slightly backward-directed from axial furrows, median portion almost straight. Occipital ring up to 15 percent cephalic length, posterior rim gently curved in large individuals, with subterminal occipital node or short spine. Dorsal furrows moderately narrow and very shallow, weakly defined from fixigenae.

Fixigenae faintly convex, subtriangular, exsagittally about 45 percent maximum cephalic length and transversely about 35 percent maximum cranial width (across center of palpebral lobes). With small baculae opposite anterior part of occipital ring. Posterolateral projections of fixigenae small and narrow, slope somewhat ventrally. Palpebral lobes slightly convex, with moderate curvature in juvenile specimens, faintly bent in adults, about 5 percent cranial width and ca. 15 percent glabellar width across occipital lobe, ca. 30 to 35 percent maximum cephalic length, slightly oblique to exsagittal axis, posterior tips distant from posterior border furrow. Palpebral furrows narrower (tr.) than palpebral lobes, shallow, but relatively well defined. Eye ridges oblique to axes, directed ca. 25 degrees anteriorly from anterior tips of palpebral lobes, obscure in adult individuals, merely slight swellings marked posteriorly by shallow furrows that develop from the palpebral furrow. Eye ridges curve forward adaxially into narrow bands that terminate at or in front of the anterolateral corners of the glabella.

Anterior branches of facial suture short, diverge relatively strongly to meet anterolateral border and curve forward to meet anterolateral margin. Posterior branches also diverge strongly, curve gently from posterior tips of palpebral lobes. Preglabellar field narrow, forms more-or-less a sunken area between glabella and anterior border furrow. Preocular fields shallow and slope faintly ventrally from eye ridges. Anterior border moderately wide, about 10 percent cephalic length in front of glabella, fairly low, slightly ascend from preglabellar field to attain

highest point close to anterior rim. Anterior border shallow and indistinct. Posterior border moderately wide and moderately convex, adaxial section normal to axis up to a small socket that corresponds to fulcral process at first thoracic segment, then runs somewhat backward and is dorsally deflected. Posterior border furrow moderately wide close to dorsal furrows, deepens from midway the fixigenal width.

Thorax of adults consists of thirteen segments; one immature specimens has eleven segments. Thorax subdivided by a macropleural segment which always appears to be the third from the rear. Greatest width in normal segments at about third segment, progressively tapering backward. Rhachis conical, widest at second or third tergite, progressively tapering rearward to less than ca. 40 percent of thoracic width, with axial ring at first segment slightly wider than occipital ring.

Axial rings about 40 to 45 percent width of the tergite in segment 3. Moderately convex transversely; consist of wide median portion and fairly indistinct narrow (tr.) lateral portions. Median portion sagittally weakly convex, with large median node which is slightly extended sagittally to form a short ridge. Anterior margin of axial ring generally straight, but with distinct rearward bend in segments 1, 2, and the terminal segment. Posterior margin generally almost straight. Doublure often visible due to compression, consists of a moderately wide lenticular strip at the posterior rim of the axial ring. Articulating half-ring moderately wide (sag.) and distinctly convex. Axial ring of first thoracic segment modified, consists of a narrower median portion with a strongly backward curved anterior and a slightly backward-curved posterior margin due to the rearward extension of the occipital ring.

Normal pleurae of anterior tergites with anterior margin straight and normal to axis up to a stout fulcral process about half way between dorsal furrows and pleural tips, curves slightly to rear abaxial to the fulcral process. Anterolateral portion forms strongly deflected facet abaxial to fulcral socket. Posterior margin of pleurae faintly S-shaped, distal portion slightly bent forward to form shallow concave area close to the pleural spine, with small dorsoventral flexure half way between dorsal furrow and pleural tip that forms an indistinct socket that

Fig. 4. 1-11 – *Myopsolenites boutiouti* sp. nov. 1, 2 – PIW 2003III20, medium-sized dorsal exoskeleton (without librigenae); 1 – entire specimen; $\times 1.5$; 2 – cephalon, $\times 3$. 3-4, 6 – PIW 2003III19, dorsal exoskeleton (without librigenae) of large individual; 3 – entire specimen, natural size; 4 – cranium and articulated anterior thoracic tergites; $\times 2.5$; 6 – posterior thorax with attached largely exfoliated pygidium; $\times 2$. 5 – Coll. P. Bommel no. 1403, medium sized dorsal exoskeleton (without librigenae), $\times 1.5$. 7 – PIW 2003III22, dorsal exoskeleton (without librigenae) of small individual. Note convex eye ridges and indistinct anterior end of palpebral lobes, $\times 2.5$. 8-9 – PIW 2003III21, dorsal exoskeleton (without librigenae) of small individual; 8 – detail of posterior thorax and pygidium. Note convex pygidial border and numerous interpleural furrows, $\times 5$; 9, entire specimen, $\times 2.5$. 10-11 – Holotype, PIW 2003III23a, large individual with slightly detached librigenae; 10 – enlarged view of left side with posterior cephalon and anterior and median thorax. Note posterior doublure of pleurae and different style of articulation as suggested by fulcral processes, $\times 1.5$; 11 – entire specimen with small cranium of *Latoucheia epichara* GEYER, 1990 to the right of thoracic segment 9, natural size

corresponds to the fulcral process of the adjacent tergite. Except for tergite 1, fulcral sockets and corresponding processes are in a progressively adaxial position in posterior tergites. Pleural furrows moderately deep, well defined, widest medially, with progressively lenticular shape posteriorly, abaxial tip reaches base of pleural spine. Pleural tip formed by a relatively strong posterior curvature of the anterolateral margin and a slight concave curvature of the distal part of the posterior margin which produce a moderately long, strongly backward-directed pleural spine that grows progressively rearward.

Pleurae of first tergite modified, with short abaxial portions terminated by fulcral processes corresponding to posterior border furrows. Abaxial part of pleurae at first thoracic tergite with strong posterior curvature of anterior margin to form strongly deflected, large facet, rearward curvature of distal posterior margin and a relatively small pleural spine. Pleural furrow with wider area adaxially and distal curvature (Text-figs 4.2 and 4.10).

Macroleural (tenth or eleventh) segment with axial ring more-or-less comparable in morphology to that in other thoracic segments, distal portions strongly modified: pleurae greatly expanded, with anterior margin of pleurae similar to normal pleurae and posterior margin

directed backward from axial furrows. Mid-pleural areas attain double (exsag.) width of normal pleurae. Pleural spines extend outward and rearward beyond posterior tip of pygidium.

Presence of a macroleural segment affects shape of adjacent posteriormost one or two tergites. Pleurae in first tergite behind macroleural segment reduced to small subtriangular or slightly falcate areas with the anterior margins strongly truncate and posterior margins slightly rearward directed; pleural spine absent. Pleurae of posteriormost tergite (of two present) with S-shaped anterior margin; pleural spine absent.

Pygidium large, subsemicircular to heart-shaped in outline, length from articulating furrow to posterior margin slightly more than two-thirds maximum width (tr.). Lateral margins smooth, diverge from anterolateral corners to reach maximum width about one-fourth distance from anterior margin, the swing gently inward and merge posteriorly in a slightly sharper curvature behind the axis.

Articulating half-ring narrow (sag.). Axis of about 90 percent pygidial length, consists of semi-fused axial rings, with five to six relatively distinctive rings recognizable in the juvenile specimen PIW 2003III21, four to five ill-defined rings recognizable in the adult specimen PIW

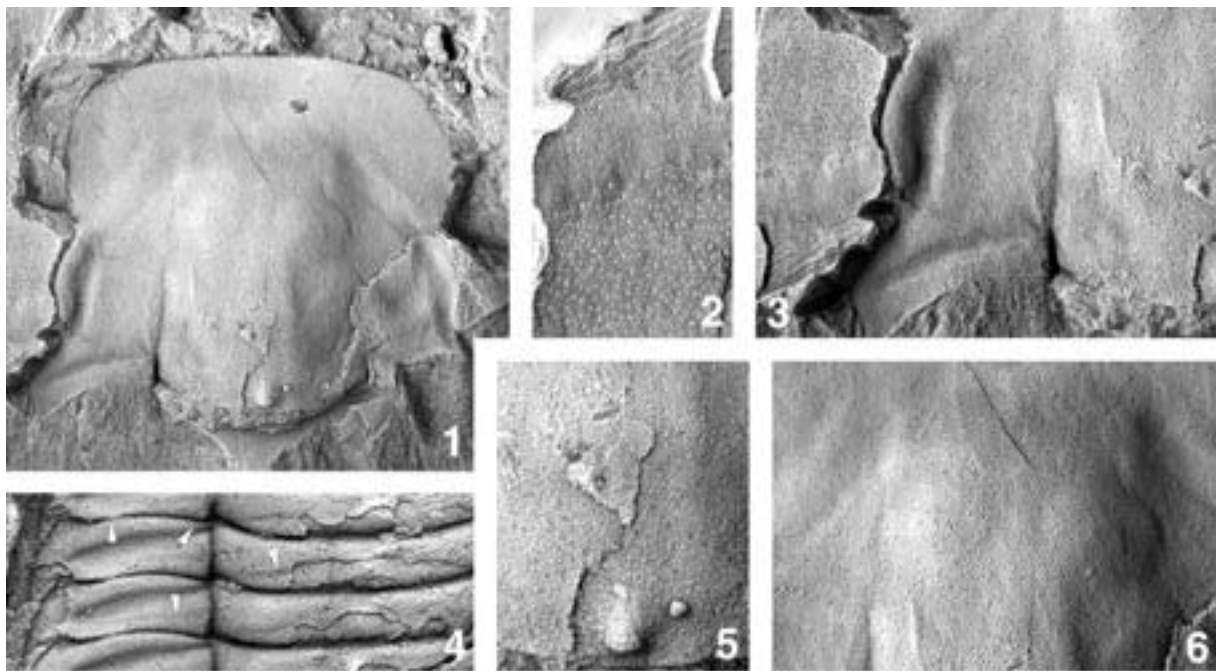


Fig. 5. *Myopsolenites boutiouiti* sp. nov. 1, 3, 5-6 – PIW 2003II24a, from Tarhia track quarry; medium-sized cranidium, internal mold; $\times 1.5$; 3 – detail of left fixigena, left palpebral lobe and posterior glabella; $\times 3$; 5 – detail of posterior glabella with occipital node and different granulation; $\times 4$. 6 – detail showing anterior glabella and granulated surface; $\times 3$. 2 – PIW 2003II24b, from Tarhia track quarry; detail of fragmentary librigena (electronically inverted), showing terrace ridges and small granules; $\times 4$; note that granules on exterior are smaller and more acute than those on internal molds (see 3, 5, 6). 4 – PIW 2003III23a, from Tarhoucht-Bou Tiouit section; detail of anterior thorax; $\times 2.5$; note posterior double of pleurae and style of articulation as suggested by fulcral processes (arrows)

2003III19, followed by a large terminal axial piece. Pleural areas fused to form a relatively homogenous, weakly convex platform. Five to six weakly defined interpleural furrows recognizable. Border furrow poorly defined in PIW 2003III19 by a subtle change in convexity. Border low, relatively narrow. Very wide doublure visible in PIW 2003III19, covered by terrace lines arranged subparallel to pygidial margin.

Surface of test covered with low but relatively large, densely spaced granules (best recognizable at PIW 2003III24a and PIW 2003III24b; Text-figs 5.2 and 5.3).

ONTOGENETIC VARIABILITY: Judging from the available material, the ontogenetic variability of *Myopsolenites boutiouiti* sp. nov. is enormous, and features some of the most dramatic developmental changes known in trilobites. The early glabella has a clearly tapering outline and relatively strongly impressed lateral glabellar furrows. With growth, the glabella appears to become less elevated, less tapering, and increasingly smooth. Eye ridges and palpebral lobes are similarly elevated in small specimens and only distinguishable by a slight change in their direction. In the large specimens, however, the eye ridges are less elevated than the palpebral lobes, which then are bound adaxially by a much better defined palpebral furrow. The anterior border is ribbon-like in small individuals, but shows a clear tendency to broaden into a rearward sloping and weakly defined band with increasing size. The glabellar front, which reaches just to the anterior border in small specimens, protrudes slightly into this band, so that the shallow border furrow delineates a faint curvature in front of the glabella.

The thorax in the available specimens consists of eleven and thirteen segments, respectively. Remarkably, it is not necessarily the smallest specimen that has only eleven thoracic segments, but EF-01/no. 1403 and PIW 2003III21 (Text-figs 4.5 and 4.9). In these specimens, there is only one segment posterior to the macropleural (tenth) tergite, whereas the other specimens have a macropleural eleventh tergite with two thoracic segments posterior to it.

Family Ellipsocephalidae MATTHEW, 1887

Subfamily Protoleninae RICHTER & RICHTER, 1948

DISCUSSION: The Subfamily Protoleninae was revised by GEYER (1990d), largely based on characters found in the unusually diverse Cambrian members of this group in the Moroccan High Atlas and Anti-Atlas ranges. The Moroccan material included some 2000 specimens, referable to 23 genera, 64 species, and 41 forms kept in open

nomenclature. However, the taxonomic recommendations made by GEYER (1990d) were not readily utilizable by students of protolenoid trilobites for several reasons. A very important consideration is that ellipsocephalide trilobite identification usually requires almost undeformed specimens with information on the external and internal morphology of the exoskeleton. In addition, a purely morphologic approach to the group's systematics will not lead to unequivocal results because of a mosaic pattern of character evolution and frequent convergence in morphological details between the relatively similar lower-level taxa of the group.

The systematics in GEYER (1990d) have been considered to represent a cladistic approach by WESTROP & LANDING (2000), who tried to designate apomorphic characters in similar ellipsocephalide species from New Brunswick. Their criticism focused on the notion that “there do not appear to be any apomorphies in GEYER's [...] diagnosis” (WESTROP & LANDING 2000, p. 873). Of course, this remark shows confusion between the concept of a diagnosis and the recognizability of true apomorphy in fossil material. That apomorphies are not identical with and do not involve characters which can be used to define, typify, and recognize fossil arthropods is emphasized by the identification of the proximal endite as the principal apomorphy of stem-group eucrustaceans (WALOSSEK & MÜLLER 1998). Trilobite taxonomy in general has to work with recognizable features, which are usually not true apomorphies. The tendency to evolve effaced morphology creates taxonomic problems, but such shared morphologies may also be a clue to systematic relationships and cannot be simply ignored or labelled as worthless plesiomorphy.

Nevertheless, the new material from Morocco, which is described below, largely confirms GEYER's (1990d) conclusions about the mosaic of characters that developed in the clade of protolenine (and also antatlasine and ellipsocephaline) genera and subgenera that include *Protolenus*, *Hupeolenus*, *Latoucheia*, and *Hamatolenus*. *Hamatolenus* (*H.*) *vincenti* sp. nov. is a species with a macropleural second (!) segment with extremely long pleural spines. This feature is unique among *Hamatolenus* species and is not known from any other species of the *Protolenus* clade. It would count as an autapomorphy. However, all other characters in this species are typical of *Hamatolenus* (*Hamatolenus*), and it is even difficult to distinguish this new species from other species of the genus when the individuals are of similar size. This includes the typical subquadrate pygidium of *Hamatolenus*, which clearly differentiates the genus from the other Protoleninae (GEYER 1990d).

A species of *Protolenus* (*Protolenus*) which co-occurs with *Hamatolenus* (*H.*) *vincenti* sp. nov. has an almost identical thorax except for the macropleural segment.

Slightly deformed cranidia of *P. (P.) densigranulatus* (see below) are also difficult to distinguish from those of *H. (H.) vincenti* sp. nov. However, the transverse pygidium with the small axis clearly characterizes this species of *Protolenus* (*Protolenus*).

Hamatolenus HUPÉ, 1953a

TYPE SPECIES: *Hamatolenus continuus* HUPÉ, 1953a (= *Protolenus elegans* var. *marocana* NELTNER, 1938); from unidentified strata in the Wirgane area, High Atlas, Morocco.

DISCUSSION: *Hamatolenus* HUPÉ, 1953a, once believed to represent a typical Moroccan faunal element, has been identified subsequently from Spain, Wales, and south-eastern Newfoundland, and is probably also present in faunas from Poland. It is indeed a genus that is important for intercontinental correlations. However, identification of specimens of this genus may be challenging because slightly deformed cranidia of *Protolenus* are often difficult to distinguish from those of *Hamatolenus*, as noted above. Among the characters that were noted to be particularly characteristic of *Hamatolenus* by GEYER (1990d) was the separation of the eye ridges and palpebral lobes. This was noted to be incorrect by WESTROP & LANDING (2000). In response, this report emphasizes that eye ridges and palpebral lobes in *Hamatolenus* are indeed clearly separated. A precise analysis shows that the eye ridges are merely elongated swellings in *Hamatolenus*, so that the connection with the palpebral lobes has the form of a small, tapered bottleneck. In *Protolenus*, the eye ridges are typically parallel-sided bars, and the connection to the palpebral lobes is defined by a dorsoventral depression.

Subgenus *Hamatolenus* (*Hamatolenus*) HUPÉ, 1953

Hamatolenus (*Hamatolenus*) *vincenti* sp. nov.
(Text-figs 6.1-6.17)

?1986. *Hamatolenus* (*Myopsolenus*)? sp.; LIÑÁN & GOZALO, p. 47, pl. 5, figs 9, 14 (only).

1995. *Protolenus*? sp.; GEYER & al., p. 116.

2001. *Protolenus* (*Hupeolenus*) cf. *termierelloides*; DIES & al., p. 303, pl. 1, figs 2, 4, 5 (only).

?2001. *Protolenus* (*Hupeolenus*) cf. *termierelloides*; DIES & al., pl. 2, fig. 1 (only).

ETYMOLOGY: Named after Mr. Tony VINCENT, now of Tinerhir, Morocco, who collected and donated most of the specimens used for this study.

HOLOTYPE: Specimen PIW 2003III27 (Text-fig. 7.17).

LOCUS TYPICUS: Tarhoucht-Bou Tiouit section, Jbel Ougnate area, eastern Anti-Atlas.

STRATUM TYPICUM: TAR-10.5, Jbel Wawrmast Formation, Brèche à *Micmacca* Member, *Cephalopyge notabilis* Zone, Agdzian Stage.

REPOSITED MATERIAL: Fourteen complete dorsal exoskeletons, some with librigena(e) split off the cephalon (PIW 2003III2, 2003III3a,b, 2003III4a, 2003III5, 2003III6, 2003III8, 2003III9, 2003III10a,b, 2003III11, 2003III12, 2003III14, 2003III24, 2003III25a, 2003III26a, 2003III27), one complete cephalon with articulated thorax (PIW 2003III1), five cranidia with articulated incomplete thorax (PIW 2003III4a, 2003III13a,b, 2003III17a, 2003III18a), one almost complete thorax with articulated pygidium (2003III6), one juvenile specimen with pygidium and incomplete thorax (PIW2003III16); all specimens from Bou Tiouit section except PIW 2003III25a, and 2003III26a (from Tarhia track quarry). All from *Cephalopyge notabilis* Zone, Agdzian Stage, Jbel Wawrmast Formation, Brèche à *Micmacca* Member.

DIAGNOSIS: Species of *Hamatolenus* (*Hamatolenus*) with glabella faintly tapering forward in the posterior third, progressively tapering anteriorly; occipital ring with median node; parafrontal band relatively narrow; eye ridges almost straight, slightly thinner and more elevated than palpebral lobes; palpebral lobes clearly longer (>1.2 times) than anterior branches of facial suture, but posterior tips clearly distant from posterior border furrow; preglabellar field moderately narrow; anterior border barely wider than preglabellar field, modestly elevated.

DESCRIPTION: Medium-sized trilobites (maximum length in the available material slightly exceeds 50 mm). Cranidium transversely subrectangular, overall convexity modest, length about 70 percent maximum width across center of palpebral lobes. Glabella relatively strongly convex, length in adult specimens about 81 to 84 percent cephalic length and 1.35 times width across occipital ring; posterior section in small and medium-sized specimens subparallel to slightly tapering forward, anterior part of glabella (anterior to L3) clearly tapering forward. Frontal lobe clearly narrower than L3, tending to develop a semi-acute front in some specimens. Three pairs of lateral furrows developed, S1 and S2 commence at dorsal furrows, slightly curved, moderately backward directed, separated medially on glabella, but with tendency to develop a shallow depression medially on the glabella. S1 barely longer

than S2, sometimes more strongly curved. S3 shorter, commences short distance from dorsal furrows, almost straight, directed obliquely backward. Occipital furrow moderately wide in sagittal section, deeper and slightly backward directed laterally, medially straight or with slight forward bend. Occipital ring about 10 percent cephalic length, sagittally almost twice width at dorsal furrows, posterior rim curved, with median occipital node. Dorsal furrows moderately wide, relatively shallow, deeper opposite L1 and L3, and more distinctly defined there from fixigenae.

Fixigenae with shallow convexity, exsagittally 41 to 44 percent maximum cephalic length and transversely about 16 percent maximum cranial width (across center of palpebral lobes). With small baculae opposite occipital furrow, traversed by shallow and wide diagonal depression. Posterolateral projections of fixigenae small, slope somewhat ventrally. Palpebral lobes slightly convex; moderately bent; ca. 7.5 percent of cranial width, 17 to 18 percent of glabellar width across occipital lobe, and ca. 30 percent maximum cephalic length; posterior end teardrop-shaped, tapering towards the anterior end, slightly oblique to exsagittal axis; posterior tips reach to broadened posterior border furrow. Palpebral furrows slightly narrower (tr.) than palpebral lobes, shallow. Eye ridges oblique to axes, directed ca. 20 degrees anteriorly from anterior tips of palpebral lobes, straight or almost so, slightly to markedly prominent, defined from palpebral lobes by a short narrower section. Eye ridges taper adaxially to meet glabella slightly posterior to S3, curve forward to form a complete but relatively narrow parafrontal band which slightly tapers in front of the glabella.

Anterior branches of facial suture diverge moderately, with straight portion across preocular areas and strong adaxial curvature at anterior border furrow to cut anterior border on a comparatively long section; about 1.5 times length of posterior branches. Posterior branches diverge moderately, straight from posterior tips of palpebral lobes, curved adaxially a short distance from posterior border. Preglabellar field moderately wide, faintly convex, with narrow, low, moderately curved ridge directly anterior to parafrontal ridge. Preocular fields slightly convex, slope somewhat ventrally from eye ridges. Anterior border moderately wide, about 6 percent cephalic length in front of glabella, moderately convex, slightly tapering abaxially. Anterior border furrow narrow, shallow, but well recognizable. Posterior border narrow, strongly upturned, adaxial section normal to axis up to a small socket that corresponds to fulcral process at first thoracic segment, increasing in width from two-thirds the distance from dorsal furrows to palpebral lobes, posterior margin curved posterior to palpebral

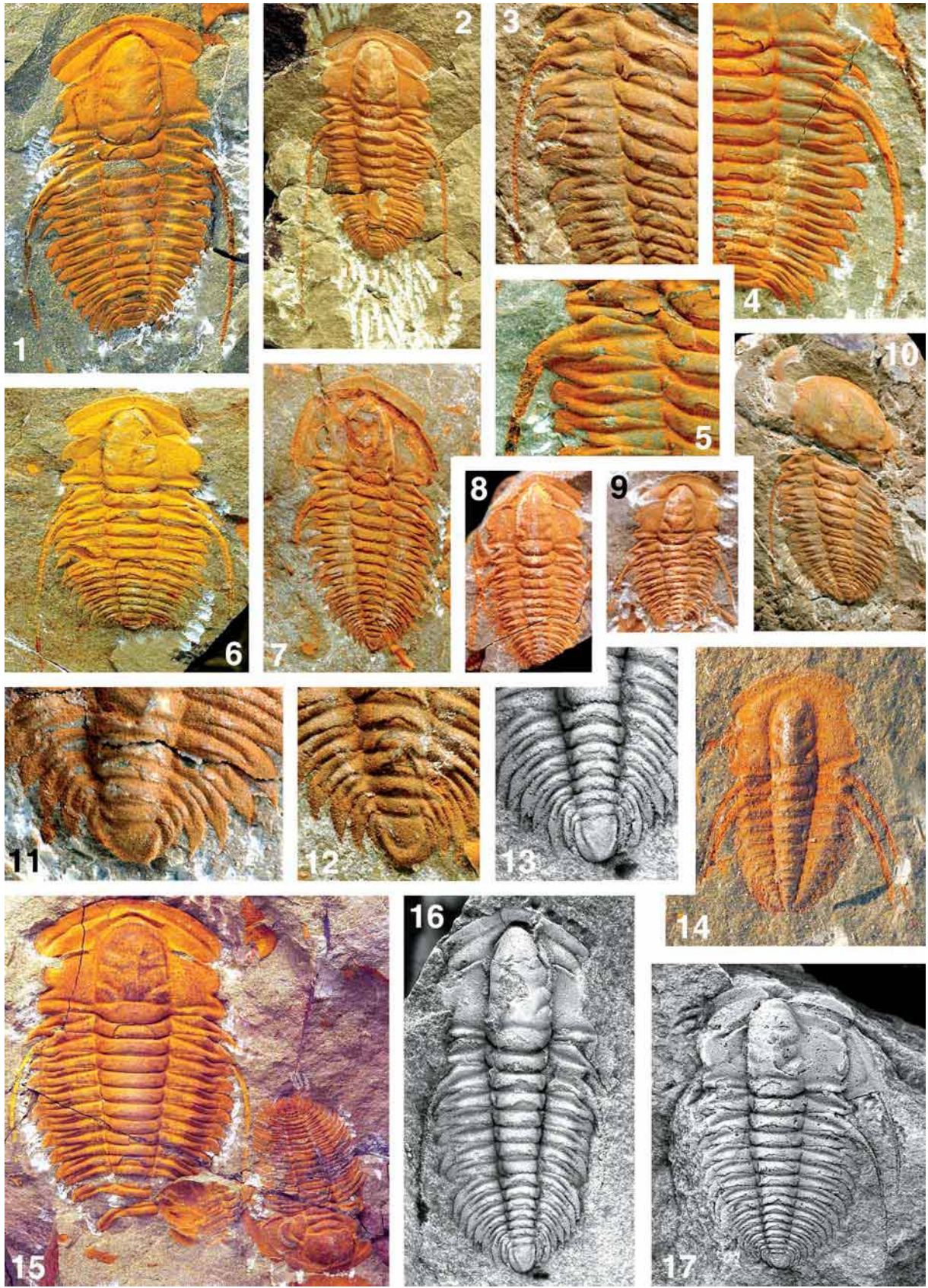
lobes. Posterior border furrow moderately wide close to dorsal furrows, growing distinctly in exsagittal width from half distance to suture.

Surface generally smooth, but glabella in some specimens with widely spaced, fine- to medium-sized granules. Abaxial portion of fixigenae, preglabellar field, and preocular fields covered with irregular network of faint, centrifugal caeca.

Holaspid thorax with fourteen to fifteen segments (a minimum of twelve segments observed in the smallest known specimens). Greatest width in normal segments at third segment, progressively tapering backward. Rhachis conical, progressively tapers rearward to less than 45 percent of thoracic width in anterior tergites, with axial ring of first segment about the width of the occipital ring and almost double the width at posteriormost segment.

Axial rings ca. 45 percent width of the tergite in segment 3 or 4. Moderately convex transversely; consists of wide median portion and distinctly narrower (tr.) lateral portions. Median portion sagittally with steeply sloping anterior and posterior rim, slightly convex between rims, anterior margin with slight forward bend, posterior margin almost straight. Lateral portions consist of transversely elongate, slightly swollen anterolateral nodes and narrow (exsag.) posterior strip which increases in width adaxially to coalesce with medial portion of the axial ring. Medial and lateral portions separated by a shallow depression and obliquely directed anterior and posterior margins of the axial ring. Doublure regularly visible due to compression, consists of a narrow, lenticular strip at the posterior rim of the axial ring that reaches up to 40 percent total width (sag.) of the axial ring and tapers towards the dorsal furrows. Articulating half-ring narrow (sag.), but highly convex. Axial ring of first thoracic segment modified, consists of a narrower median portion with a strongly backward curvature anteriorly and a slightly backward curvature to posterior margin due to the posterior extension of the occipital ring.

Normal pleurae of anterior tergites with anterior margin straight and normal to axis up to a stout fulcral process about half way between dorsal furrows and pleural tips, abaxially of the fulcral process anterior margin curves slightly rearward. Posterior margin of pleurae slightly S-shaped, with distal portion slightly bent forward to form a gentle concave curve close to the pleural spine followed by another gentle dorsoventral flexure half way between the dorsal furrows and pleural tips; this second curve forms an indistinct socket that corresponds to the fulcral process of the adjacent tergite. Fulcral sockets and corresponding processes become progressively adaxial in rear tergites. Pleural furrows moderately deep, resulting from the confluence of sloping areas; anterior and posterior margins ill-defined, widest medially, progressively S-



shaped posteriorly; abaxial tip reaches base of pleural spine. Pleural tip shows a gentle rearward curvature of the anterolateral margin and a gentle concave curvature of the distal part of the posterior margin; the small, obliquely backward-directed pleural spines become progressively directed to posterior from about the seventh tergite and progressively curved backward.

Macropleural second segment with adaxial part more-or-less comparable in morphology to other thoracic segments, distal portion is strongly modified with pleural spine extended in a gentle arc backward and inward (Text-fig. 6.4). Pleural tip extends beyond end of pygidium. Base of spine develops from regularly shaped pleura, but pleural furrow extends into the proximal one-fourth of the pleural spine. Posterior half of distal pleura slightly swollen.

Presence of a macropleural segment affects the shape of adjacent first and third tergites (Text-figs 6.4 and 6.5). Pleural tip in the first segment extended into a comparatively long, slender, pointed end that varies in shape between specimens. Pleurae of first thoracic segment modified, short, with a strong ventral deflection of the distal portions of the pleurae and with an anterior margin which curves strongly backward from fulcral process to allow strong deflection of the tergite underneath the posterior part of cephalon during enrollment.

Distal parts of pleurae in third segments reduced in size anterolaterally to allow movement of second tergite during inclination. Anterior border of distant pleural portion inclined in dorsal view, pleural tip acute.

Posteriormost segment also strongly modified, consists of axial ring which extends into pleurae that are strongly backward directed to swing around the anterior half of the pygidium. Anterior margin of pleura normal to axis for a short distance, then strongly arched backward and inward. Pleural furrow directed backward from origination at anterior part of dorsal furrow in this segment, curved. Pleurae slightly twisted and ventrally deflected so that the proximal part of the posterior pleural rib has highest elevation.

Pygidium roundish in outline, length from articulating furrow to posterior margin about two-thirds maximum width (tr.). Lateral margins diverge from articulating furrow to reach maximum width about two-thirds from posterior end, then swing gently inward and merge in a small, more-or-less straight posterior margin (Text-figs 6.11-6.12).

Articulating half-ring narrow (sag.). Axis consists of fused rings, and thus defines a large terminal axial piece of about 80 percent pygidial length. This piece is surrounded laterally and posteriorly by a collar-like lobe, which anteriorly decreases in elevation and is fused with the anterolateral tips of the axis. Distinct pleural areas absent. Lateral and posterior border forms low platform that surrounds axis and collar-shaped lobe. Border furrows ill-defined by a change in convexity.

VARIABILITY AND DIMORPHISM: *Hamatolenus (H.) vincenti* sp. nov. displays a comparatively wide phenotypic variability. This variation involves such features as the degree of inclination of the lateral glabellar furrows with respect to the axis, the relative width of the frontal lobe, and the width of the palpebral lobes.

Ontogenetic differences are mainly an effect of allometric growth of the cephalic parts so that the most conspicuous changes involve the width of the fixigenal and preocular fields, the distance between the frontal lobe and the anterior border, and the relative width and length of the glabella. One of the typical ontogenetic variations involves a relative decrease in eye length as expressed by the length of the palpebral lobes. This feature shows a development normal for protolenoid trilobites. In addition, the overall relief of the cephalon decreases slightly with size and, thus, with age.

Two macropleural segments are conspicuous in the smallest observed specimens (total length 7.8 mm, twelve thoracic segments). In these specimens, both anterior thoracic tergites have a long pleural spine which turns strongly outward (Text-fig. 6.14). This feature might have been an aid to extend swimming peri-

Fig. 6. 1-17 – *Hamatolenus (Hamatolenus) vincenti* sp. nov., dorsal views unless otherwise stated. 1 – PIW 2003III18a, dorsal exoskeleton without librigenae and pygidium, $\times 1.5$. 2, 11 – PIW 2003III6, almost complete dorsal exoskeleton with extremely long spines; 2 – entire specimen; $\times 1.5$; 11 – posterior thorax with pygidium, $\times 5$. 3, 10 – PIW 2003III3a, b; 3 – detail of thorax, anterior and medial region on left side; $\times 2.5$; 10 – thorax and pygidium of *Hamatolenus (Hamatolenus) vincenti* sp. nov., artificially mounted with cranium and disarticulated left librigena of *Kingaspidoides* cf. *K. laetus*, $\times 1.5$. 4-5 – PIW 2003III1a, almost complete dorsal exoskeleton. 4 – detail of posterior cephalon and thorax, $\times 2$; 5 – detail of macropleural thoracic region, $\times 4$. 6 – PIW 2003III8a, dorsal exoskeleton without librigenae, $\times 1.5$. 7, 12 – PIW 2003III2a, almost complete dorsal exoskeleton; 7 – entire specimen; natural size; 12 – posterior thorax with pygidium, $\times 5$. 8 – PIW 2003III5, dorsal exoskeleton without librigenae of immature specimen, $\times 2$. 9 – PIW 2003III4a, dorsal exoskeleton without librigenae and pygidium of immature specimen, $\times 2$. 13, 16 – PIW 2003III9, dorsal exoskeleton; 13 – detail showing posterior thorax and pygidium in three-dimensional preservation; $\times 3.5$; 16 – entire specimen; $\times 2.5$. 14 – PIW 2003III26a, immature specimen without librigenae showing two macropleural segments; Tarhia track quarry; $\times 6$. 15 – PIW 2003III17a, large individual, incomplete carcasse after molting with disarticulated posterior thoracic tergites and librigenae detached; remains of additional specimen of *H. (H.) vincenti* and *Paradoxides (Acadoparadoxides)* sp. nov. in vicinity; natural size. 17 – Holotype, PIW 2003III27, Tarhoucht-Bou Tiout section, sample horizon TAR 10.5; $\times 2.5$

ods. In these specimens, the glabella is narrow and almost parallel sided, but has short and clearly impressed lateral glabellar furrows.

COMPARISON WITH OTHER SPECIES: *Hamatolenus* (*H.*) *vincenti* sp. nov. is a very distinct species of the nominal subgenus as shown by its long palpebral lobes (exsag. longer than the anterior branches of the facial suture). In addition to *H.* (*H.*) *vincenti*, the thorax is known for *H.* (*H.*) *maroccanus* (NELTNER, 1938) and *H.* (*H.*) *ibericus* SDZUY, 1958, but the latter two species do not have a macropleural segment.

Hamatolenus (*H.*) *maroccanus* (NELTNER, 1938), the type species of the genus, is known from the *Cephalopyge notabilis* Zone of the western Anti-Atlas and the west-central High Atlas ranges where it occurs primarily in greenish shales. *H.* (*H.*) *maroccanus* is distinguished from *H.* (*H.*) *vincenti* sp. nov. by an occipital ring with a strong spine and by a (sag.) wider, more elevated anterior border (preglabellar band less than one-third the anterior border in *H.* (*H.*) *maroccanus*, at least more than half the width of the anterior border in *H.* (*H.*) *vincenti*; compare GEYER, 1990d, pl. 41, figs 1-10). In addition, adult specimens of *H.* (*H.*) *maroccanus* are usually distinctly larger than those of *H.* (*H.*) *vincenti*.

Hamatolenus (*H.*) *draensis* (HUPÉ, 1953a) has even longer palpebral lobes than *H.* (*H.*) *vincenti* sp. nov., and the tips of the palpebral lobes reach the posterior border furrow. The former species also has a clearly narrower (tr.) frontal lobe, a complete parafrontal band, and slightly S-shaped eye ridges. *H.* (*H.*) *draensis* was previously known only from the *Cephalopyge notabilis* Zone of the central Anti-Atlas in calcareous layers of the Brèche à *Micmacca* facies, but was later recovered from the Tarhoucht section, partly in association with *H.* (*H.*) *vincenti* sp. nov.

Hamatolenus (*H.*) *meridionalis* GEYER, 1990d, like *H.* (*H.*) *draensis*, has palpebral lobes that reach backward to the posterior border furrow. Furthermore, it differs from *H.* (*H.*) *vincenti* sp. nov. by having both a small occipital spine that originates close to the posterior margin of the occipital ring and a complete and relatively thick parafrontal band. *H.* (*H.*) *meridionalis* is known only from shales and fine-grained volcanoclastics of the western Anti-Atlas, where it first appears in the *Hupeolenus* Zone and ranges into the *Cephalopyge notabilis* Zone.

Hamatolenus (*H.*) *ibericus* SDZUY, 1958, from the upper "Bilbilian Stage" (designation abandoned) of the Iberian Chains in northern Spain also has longer palpebral lobes that reach backward to the posterior border furrow. The anterior border of this species is elevated and wider (sag.) than in *H.* (*H.*) *vincenti* sp. nov.

Protolenus MATTHEW, 1892

TYPE SPECIES: *Protolenus elegans* MATTHEW, 1892; Hanford Brook Formation, Branchian, southern New Brunswick, Canada.

DISCUSSION: Cranidia of *Protolenus*, particularly those of the eponymous subgenus *Protolenus*, are often difficult to distinguish from those of *Hamatolenus*, as exemplified by erroneous identifications of material from the Iberian Peninsula and also by incorrect identifications of Moroccan specimens sold on the global fossil market. The correct identification is indeed problematical if the specimens are preserved as internal molds, and even more difficult if they are dorsoventally flattened. Clear distinguishing characters between these two genera include: 1) the relatively strongly convex anterior border of most *Protolenus* species; 2) the shorter, quasi-nodular eye ridges of *Protolenus*; 3) the parafrontal band of *Protolenus* which curves into the extension of the eye ridges clearly in front of L3; and 4) the palpebral lobes in *Protolenus* which clearly increase in width posteriorly.

The pygidium is not a criterion to reliably distinguish *Protolenus* from *Hamatolenus*. *Protolenus* tends to have a transversely subrectangular pygidium with an almost straight posterior margin, a large axis, and moderately wide pleural areas divided by a clearly visible interpleural furrow (Text-fig. 6.13). *Hamatolenus*, in contrast, tends to be characterized by a pygidium with a somewhat curved posterior margin, strongly developed axis, and narrow (tr.) pleural portions (Text-figs 6.11-6.12). However, these general rules are often difficult to apply because of the morphologic variations shown in taxa such as *Hamatolenus* (*H.*) *draensis* (HUPÉ, 1953a) (GEYER, 1990d, pl. 42, fig. 6a-c) or *Protolenus* (*P.*) *interscriptus* GEYER, 1990 (GEYER, 1990d, pl. 45, fig. 3).

Subgenus *Protolenus* (*Protolenus*) MATTHEW, 1892

TYPE SPECIES: As for *Protolenus*.

Protolenus (*Protolenus*) *densigranulatus* GEYER, 1990d
(Text-figs 7.1, 7.2, 7.4)

1995. *Protolenus* (*Protolenus*) sp.; GEYER & al., p. 116

ADDITIONAL REPOSITED MATERIAL: From Bou Tiouit section near Tarhoucht, Jbel Ougnate area, eastern Anti-Atlas: PIW 2003III7, 2003III15. From Tarhia track quarry close to Jbel Tazderout: PIW 2003III27-2003III29. All from *Cephalopyge notabilis* Zone, Agdzian

Stage, Jbel Wawmast Formation, Brèche à *Micmacca* Member.

DESCRIPTION: Medium-sized trilobites (maximum length in the available material slightly exceeds 45 mm). Cranidium transversely rectangular, overall convexity modest, length about 70 to 75 percent maximum width across center of palpebral lobes. Glabella relatively strongly convex, length in adult specimens ca. 80 to 83 percent cephalic length and 40 to 43 percent width across occipital ring; posterior section of glabella in small- and medium-sized specimens subparallel to slightly tapering forward; anterior part of glabella (anterior to L3) clearly tapers forward. Frontal lobe narrower than L3. Three pairs of lateral furrows developed, S1 and S2 commence at dorsal furrows, slightly curved, moderately backward directed, connected medially on glabella by shallow depression. S3

shorter, commences short distance from dorsal furrows, almost straight, directed obliquely backward. Occipital furrow moderately wide in sagittal section, deeper and slightly backward directed laterally, medially straight or with slight forward bend. Occipital ring ca. 15 percent cephalic length, sagittally almost twice width at dorsal furrows, posterior rim curved medially, almost straight laterally, medial occipital node present. Dorsal furrows moderately wide, relatively shallow, deeper opposite L1 and L3, and more distinctly defined there from fixigenae.

Fixigenae with shallow convexity, exsagittally 40 to 44 percent maximum cephalic length and transversely ca. 18 to 20 percent maximum cranial width (across center of palpebral lobes). With small baculae opposite occipital furrow, traversed by shallow and wide diagonal depression stretching from near L3 to posterior tips of palpebral lobe. Posterolateral projections of fixigenae small, slope

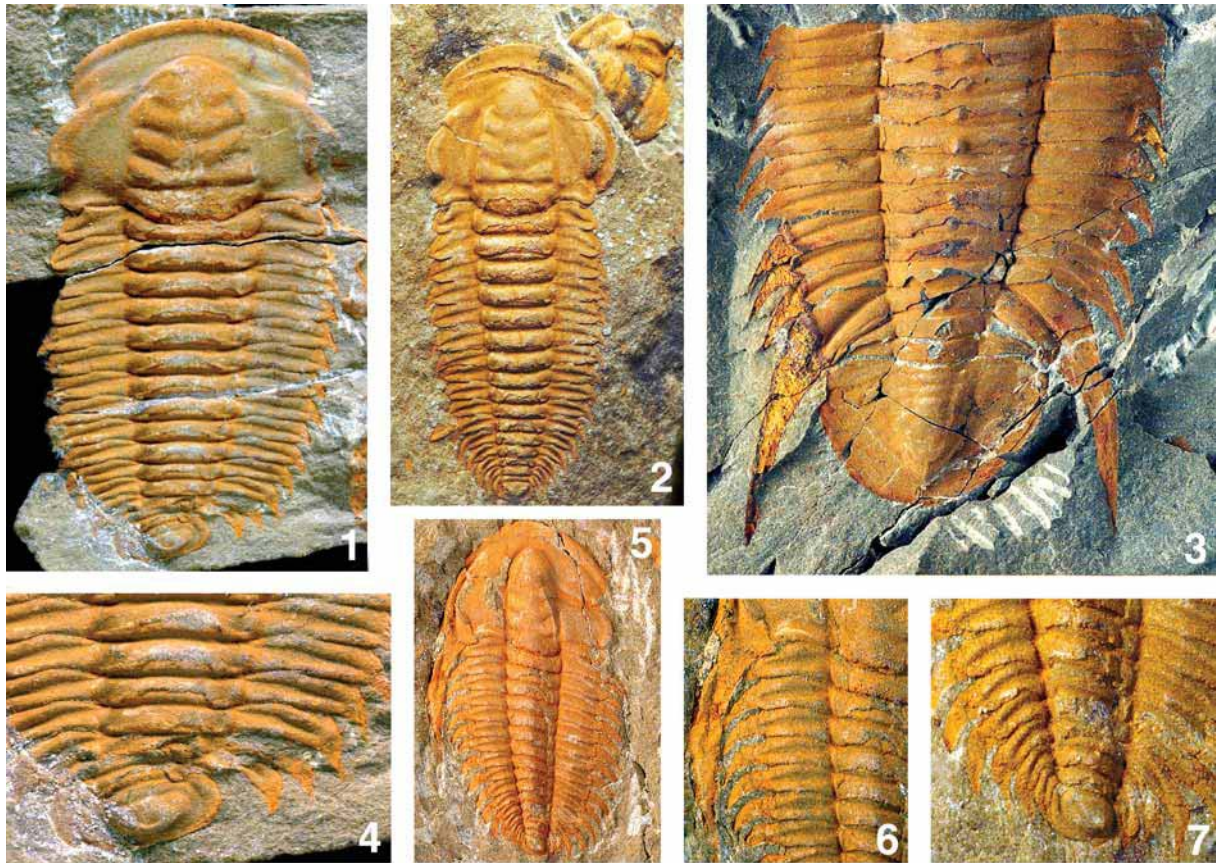


Fig. 7. 1, 2, 4 – *Protolenus (Protolenus) densigranulatus* GEYER, 1990. 1, 4 – PIW 2003III7, dorsal exoskeleton without librigenae; 1 – entire specimen, $\times 1.5$; 4 – posterior thorax with slightly detached pygidium, $\times 3$; 2 – PIW 2003III15a, b, dorsal exoskeleton without librigenae and isolated cranidium. Note impression of dorsally detached rostral plate and different type of dorsal prosopon (coarse granules in isolated cranidium); $\times 1.5$. 3 – *Myopsolenites boutiouti* sp. nov. PIW 2003III28, Tarhia track quarry; articulated thorax and pygidium of large individual; pygidium preserved as internal mold (showing ventral double with terrace ridges); distal pleurae usually exfoliated; $\times 1.4$. 5-7 – *Protolenus (Protolenus)* sp. PIW 2033III29. Dorsal exoskeleton of small specimen, right librigena absent, left librigena slightly detached; Tarhia track quarry; 5 – complete specimen, $\times 3$; 6 – detail showing posterior cranidium and anterior thorax on left side; $\times 5$; 7 – posterior thorax and pygidium; $\times 5$

somewhat ventrally. Palpebral lobes slightly convex, moderately to relatively strongly curved, ca. 6.5 to 7 percent cranial width, ca. 15 percent glabellar width across occipital lobe and ca. 35 percent maximum cephalic length, posterior end tear drop-shaped, tapers toward the anterior end, slightly oblique to exsagittal axis, posterior tips reach broadened posterior border furrow. Palpebral furrows slightly narrower (tr.) than palpebral lobes, shallow, poorly defined abaxially. Eye ridges somewhat oblique to axes, directed ca. 10 degrees anteriorly from anterior tips of palpebral lobes, straight or almost so, slightly to markedly prominent, defined from palpebral lobes by a short narrower section. Eye ridges taper adaxially to extend into a relatively narrow, low ridge that meets glabella at S3. This band curves forward to form a complete, well defined parafrontal band.

Anterior branches of facial suture diverge moderately, with straight portion across preocular areas and strong adaxial curvature at anterior border furrow so that they cut anterior border on a comparatively long section; about 1.5 times length of posterior branches. Posterior branches diverge moderately, straight from posterior tips of palpebral lobes, curved adaxially a short distance from posterior border. Preglabellar field moderately wide (almost 10 percent cephalic length), weakly convex, with narrow, low, moderately curved ridge directly anterior to parafrontal ridge. Preocular fields slightly convex, slope somewhat ventrally from eye ridges. Anterior border moderately wide, ca. 7 to 7.5 percent cephalic length in front of glabella, markedly convex. Anterior border furrow narrow, shallow, but well defined. Posterior border narrow, strongly upturned in adaxial section, which is normal to axis; external section defined by a small socket that corresponds to fulcral process at first thoracic segment, increases in width from two-thirds the distance from dorsal furrows to palpebral lobes, posterior margin curved posterior to palpebral lobes. Posterior border furrow moderately wide close to dorsal furrows, becomes distinctly wider exsagittally half-distance to palpebral lobes.

Surface densely covered with small to moderately large granules, which are not recognizable on internal molds. Fixigenae, preglabellar field, and preocular fields covered with irregular network of faint or moderately sized, centrifugal caeca on internal molds.

Holaspid thorax with 15 segments. Greatest width at about fourth segment, progressively tapers backward. Rhachis conical, progressively tapers rearward to less than 45 percent of thoracic width in anterior tergites, with axial ring at first segment about the width of the occipital ring and almost double width at posteriormost segment.

Axial rings ca. 45 percent width of the tergite in segment 3 or 4. Moderately convex transversely; consist of

wide median portion and narrower (tr.) lateral portions. Median portion sagittally with steeply sloping anterior and posterior rim, slightly convex between, anterior margin and with slight forward bend, posterior margin almost straight. Lateral portions consist of transversely elongate, slightly swollen anterolateral nodes and narrow (exsag.) posterior strip which increases in width adaxially to coalesce with medial portion of the axial ring. Median and lateral portions separated by shallow depression and obliquely directed anterior and posterior margins of the axial ring. Doublure regularly visible due to compression, consists of a narrow, lenticular strip at posterior rim of axial ring that reaches 40 percent total width (sag.) of the axial ring and tapers towards the dorsal furrows. Articulating half-ring narrow (sag.), but highly convex. Axial ring of first thoracic segment modified, consists of a narrower median portion with a strongly backward swinging anterior and a slightly backward swinging posterior margin due to the rearward extension of the occipital ring.

Pleurae of anterior tergites with anterior margin straight and normal to axis up to a stout fulcral process roughly half way between dorsal furrows and pleural tips, curve rearward abaxially of the fulcral process. Posterior margin of pleurae slightly S-shaped, distal portion slightly bent forward to coalesce into shallow indentation close to the pleural spine, with small dorsoventral flexure half way between dorsal furrows and pleural tips that forms a small socket that corresponds to the fulcral process of the adjacent tergite. Fulcral sockets and corresponding processes progressively more adaxial in rearward tergites. Pleural furrows moderately deep, posterior margin weakly defined, formed by slope of posterior lobe; widest medially, progressively S-shaped rearward, abaxial tip reaches base of pleural spine. Pleural tips in anterior tergites usually show gentle rearward curvature of the anterolateral margin and slight concave curvature of the distal part of the posterior margin; the intersection of these curves produces a small, obliquely backward directed pleural spine. Pleural tips in mid-thoracic segments similar, but obliquely truncated. Pleural spines grow progressively rearward from about the seventh tergite and are progressively curved backward.

Posteriormost segment strongly modified, consists of axial ring which extends into pleurae that are strongly backward directed and swing around the anterior half of the pygidium. Anterior margin of pleura normal to axis for a short distance, then strongly arched backward and inward. Pleural furrow directed backward from its origination in the anterior part of the dorsal furrow in this segment, curved. Pleurae slightly twisted and ventrally deflected so that the proximal part of the posterior pleural rib has the highest elevation.

Pygidium subsemicircular in outline, length from articulating furrow to posterior margin about two-thirds maximum width (tr.). Lateral margins diverge from articulating furrow to reach maximum width about two-thirds from posterior end, then swing gently inward and merge in a small, more-or-less straight posterior margin.

Articulating half-ring narrow (sag.). Axis consists of fused rings and thus defines a large terminal axial piece about 80 percent of pygidial length. This piece is surrounded laterally and posteriorly by a collar-like lobe, which anteriorly decreases in elevation and is fused with the anterolateral tips of the axis. Distinct pleural areas absent. Lateral and posterior border forms low platform that surrounds axis and collar-shaped lobe. Border furrows weakly defined by subtle change in convexity.

DISCUSSION: *Protolenus (Protolenus) densigranulatus* was proposed by GEYER (1990d) on the basis of material from sections in the Lemdad syncline in the west-central High Atlas. Additional material was tentatively assigned by GEYER (1990d) to this same species from the Tizi n'Tichka (central High Atlas), Tadakoust (western Anti-Atlas), and Tizi n'Izem and Tinifift in the Jbel Ougnat area, eastern Anti-Atlas. The provisional species-level assignments resulted from differences in taphonomy and preservation which did not allow adequate morphologic comparisons. However, supplemental material from the Tarhoucht section suggests that all of these specimens indeed belong to this species, and that the species has one of the widest occurrences in the Moroccan Cambrian, although it is generally a relatively rare faunal element.

Protolenus (P.) densigranulatus is similar to *P. (P.) interscriptus* GEYER, 1990d, a second species from the Moroccan Atlas ranges. However, the two species are easily distinguished by the occipital ring, which features a stout spine in *P. (P.) interscriptus*, whereas the posterior margin of the occipital ring in *P. (P.) densigranulatus* forms a gentle curve. A partial pygidium of *P. (P.) interscriptus* was available for the original description of this species (GEYER, 1990d, pl. 45, fig. 3), but not for *P. (P.) densigranulatus*. The new material from the Tarhoucht area shows that the pygidium of *P. (P.) densigranulatus* differs distinctly from that of *P. (P.) interscriptus* in being wider and thus more transverse, having a slightly better defined (although very weak) posterior median border, and having a wider and more elevated pleural ridge.

Both Moroccan species are distinguished from the Avalonian species *Protolenus (P.) elegans* MATTHEW, 1892, and *P. (P.) articephalus* (MATTHEW, 1895) from New Brunswick (see GEYER, 1990d; WESTROP & LANDING, 2000) in having a preglabellar field which slopes at only a low angle toward the anterior border. *Protolenus (P.)*

paradoxoides MATTHEW, 1892, also from New Brunswick, is morphologically similar to *P. (P.) densigranulatus* in having a less steeply sloping preglabellar field. Nevertheless, the dip of the preglabellar field in *P. (P.) paradoxoides* is still clearly steeper than that in *P. (P.) densigranulatus* and *P. (P.) interscriptus*. *P. (P.) paradoxoides* does not show caeca on internal molds of the preglabellar field; it has a less prominent and slightly thinner (sagittally) anterior border and a slightly expanded glabella across L1.

Poorly preserved specimens of *P. (P.) densigranulatus* can be misidentified as specimens of *Hamatolenus (H.) vincenti* sp. nov. Additional problems in identification result from the fact that isolated or partial thoraxes collected by local fossil hunters at Tarhoucht are sometimes glued together with cephalons of other trilobites of comparable size. In some of these specimens, thoraxes of *P. (P.) densigranulatus* are associated with cephalons of *H. (H.) vincenti*. These “chimera” show an artificial dimorphism, with *H. (H.) vincenti* appearing to include individuals with and without a macropleural second segment.

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