University of Alberta

Select Lower and Middle Devonian Phacopidae (Trilobita) of southern Morocco.

by

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A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of

Master of Science

Department of Earth and Atmospheric Sciences

Edmonton, Alberta
Fall 2006

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Your file Votre référence
ISBN: 978-0-494-22319-2
Our file Notre référence
ISBN: 978-0-494-22319-2

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ABSTRACT

Trilobites of the family Phacopidae occur throughout the Lower and Middle Devonian strata of southern Morocco. This region is renowned for its large numbers of articulated trilobites with preservation matched by few other localities. In this study, select phacopids from a number of lithologies are described, and subjected to cladistic analyses in order to assess their relationships. New species or subspecies are named within *Phacops* and two proposed new genera, including: *Phacops araw,* New genus A *kermiti*, N. g. A *salamandar*, N. g. A *speculator punctatus*, New genus B *ovatus*, and N. g. B *forteyi*. Additionally, the new species *Boeckops stelcki* and *Reedops pembertoni* are described, and considered alongside recently published taxa including N. g. B *granulops*, N. g. A *smoothops*, and N. g. B *lebesus* (CHATTERTON *et al.*, 2006). The cladistic analyses performed here impact many of the genera and subgenera of Devonian phacopids, and their higher-level taxonomy.

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ACKNOWLEDGEMENTS

This work would not have been possible without the help of many people, and stands upon the work and support of many other individuals. If I overlook anyone, it is unintentional. It is likely that half of the people that read these acknowledgements have helped in some way or form, and it is all appreciated.

First and foremost, Dr. Brian D.E. Chatterton has provided both the academic and financial support required for this project, and an unending sense of humour. I owe him a great deal for welcoming me into the invertebrate palaeontology program, and providing me with the tools to begin my career. No one could hope for a better supervisor.

The other members of the invertebrate palaeontology team also deserve a lot of credit: Stacey Gibb was an invaluable source of assistance, in terms of fieldwork, data sharing, and support; Al Lindoe helped in the field, prepared specimens, and taught me how to prepare my own material; and Kevin Brett supplied some of the original stratigraphic data, and some prepared specimens. All funding for our team's work was provided by the NSERC grants of B.D.E. Chatterton.

In Morocco, Hammi and Amur Ait H'ssaine provided excellent field support, large numbers of specimens, and more food than anyone should consume. This family, their friends, and the Berber miners deserve the credit for discovering most of the productive trilobite localities, and for furnishing us with, or helping us to collect, the bulk of the specimens seen in this thesis. The Moroccan geological survey was also quite accommodating in providing the permits and background geological information necessary for this work.

At the University of Alberta, I would like to thank Dr. M.W. Caldwell and Dr. M.V.H. Wilson for participating in my committee, reviewing this thesis, and providing useful feedback. I would also like to thank Dr. S.G. Pemberton, Dr. M.W. Caldwell, and Dr. B.D.E. Chatterton for providing graduate courses that exposed me to a wide range of palaeontological topics. Administrative and technical staff from the Department of Earth and Atmospheric Sciences have also been invaluable in keeping me on the right track, and providing me with supplies or advice needed for side-projects related to the main thesis. The EAS department has also provided me with study-related employment and volunteer opportunities.

Last, but in no way least, I cannot extend enough thanks to my wife and family for their support throughout this process: their patience and understanding has been limitless.

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LIST OF SYMBOLS, NOMENCLATURE, OR ABBREVIATIONS:

Institutions:

UA – University of Alberta
CGMTA – Service de la Carte géologique du Maroc, Rabat (Alberti collection)
CGMT – Service de la Carte géologique du Maroc, Rabat
SMF – Sammlung des Forschungsinstituts Senckenberg
NM IT – National Museum, Prague
NYSM – New York State Museum
ICSR – Institute Scientifique Chérifien, Rabat

Nomenclature:

The anatomical terminology used here follows that employed by the Treatise on Invertebrate Paleontology (WHITTINGTON, in KAESLER, 1997). Any deviations from this terminology follow that of CHLUPÁČ (1977), including references to the palpebral lobe (region of cephalon between palpebral furrow and palpebral rim), the palpebral area (region of cephalon between palpebral furrow and axial furrow), and the intercalating ring (L1 medial lobe). Anatomical directions or planes are often abbreviated (e.g. transverse = tr.), but these are all standard terms. Eye lens formula diagrams are adapted from the works of CAMPBELL (1967; 1977), and indicate the occurrence of miniscule lenses in smaller fonts.

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CHAPTER 1: INTRODUCTION

Introduction:

Phacopid trilobites are almost ubiquitous fossils within the Lower and Middle Devonian strata of Morocco, and display a diversity of form seen at no other point in the history of the family. The southern and southeastern margins of Morocco make ideal field areas for studying the Phacopidae through this time interval, because rock units of this age are present in long, continuous exposures that are traceable for many kilometers along strike and affected only by very low amplitude folding and minor faulting. Furthermore, the fossils themselves show articulation and preservation matched in few other localities (making complete, definitive descriptions possible), and are commercially mined by the local Berbers (making specimens available in large numbers). This study depicts the phacopids as they appear in correlatable strata from the three major Devonian basins in southern Morocco, the Tindouf, Tafilalt, and Ma'der basins (see Text Fig. 1), and shows that their presence is useful for correlation within and between these basins, as well as farther abroad. In the process, 11 new taxa of the specific or subspecific rank are described[1], including: *Reedops pembertoni*, New Genus A *smoothops*, New Genus A *speculator punctatus*, New Genus A *kermiti*, New Genus A *salamandar*, *Boeckops stelcki*, New Genus B *granulops*, New Genus B *lebesus*, New Genus B *ovatus*, New Genus B *forteyi*, and *P. araw*; additionally, new information is provided for *Reedops bronni* (BARRANDE, 1846), *R. cephalotes hamlagdadianus* ALBERTI, 1983, *Pedinopariops* (*Hypsipariops*) *vagabundus* STRUVE, 1990, *Drotops megalomanicus megalomanicus* STRUVE, 1990, and *D. armatus* STRUVE, 1995. Cladistic analysis of these taxa and other select phacopids suggests the relationships of the new taxa, and has implications for their higher-level placement.

Previous Work:

The study of phacopid trilobite taxonomy and systematics had its true beginnings in the Rhenish-Bohemian faunal subprovince of the Old World Realm. This subprovince

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[1] Three of these taxa, *Phacops granulops*, *Phacops smoothops*, and *Phacops lebesus*, have already been included in a published work (see CHATTERTON *et al.*, 2006).

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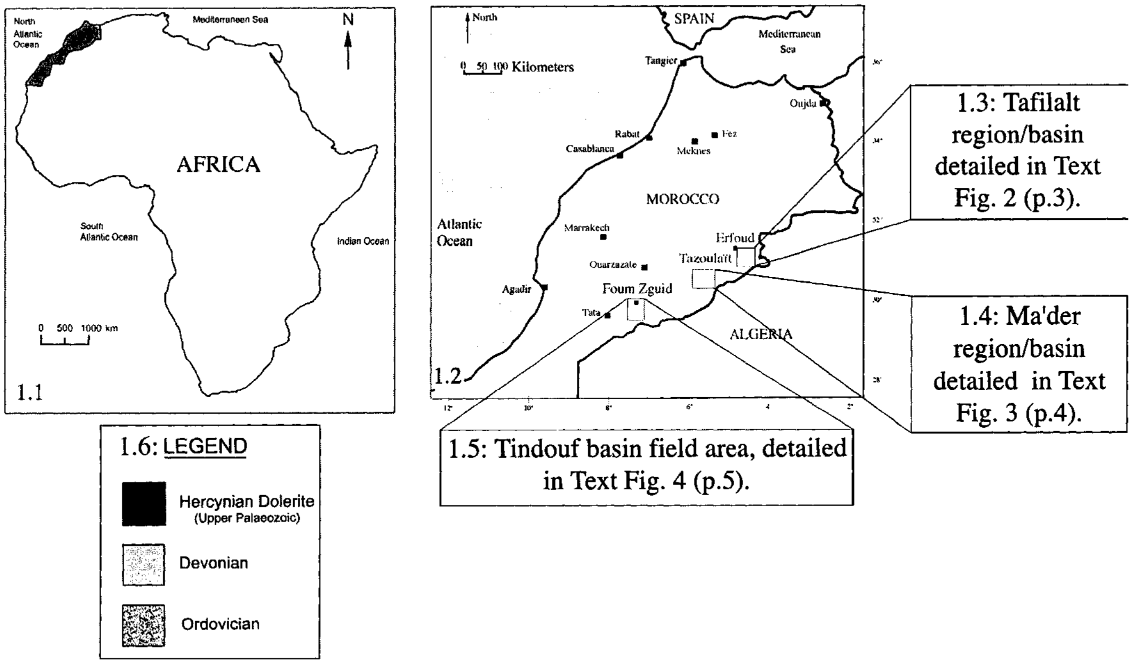

Text Fig. 1: Generalized locality maps for field areas within Morocco (detailed outcrop maps of individual basins are presented on subsequent pages, and keyed to this diagram).
1.1: Overview map of Africa, showing position of Morocco (modified from Phillip, 1991; reproduced from Gibb, 2005).
1.2: Overview map of Morocco, showing three main study regions in three separate Devonian basins (reproduced with permission from Gibb, 2005).
1.3-1.5: Key to study area outcrop maps (presented as Text Figs. 2-4, on pages 3-5).
1.6: Legend for all subsequent outcrop maps.

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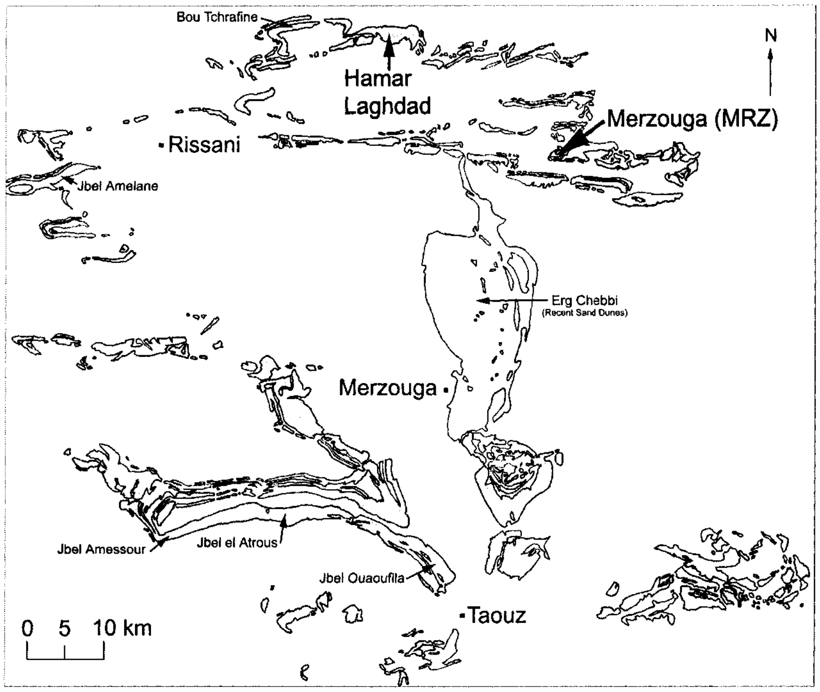

Text Fig. 2: Overview map of Devonian outcrop (shaded) within the Tafilalt basin. Individual mountains are indicated with their Moroccan titles (e.g. Jbel Amelane or Hamar Laghdad). (Diagram modified from Fetah *et al.*, 1988, and reproduced with permission from Gibb, 2005).

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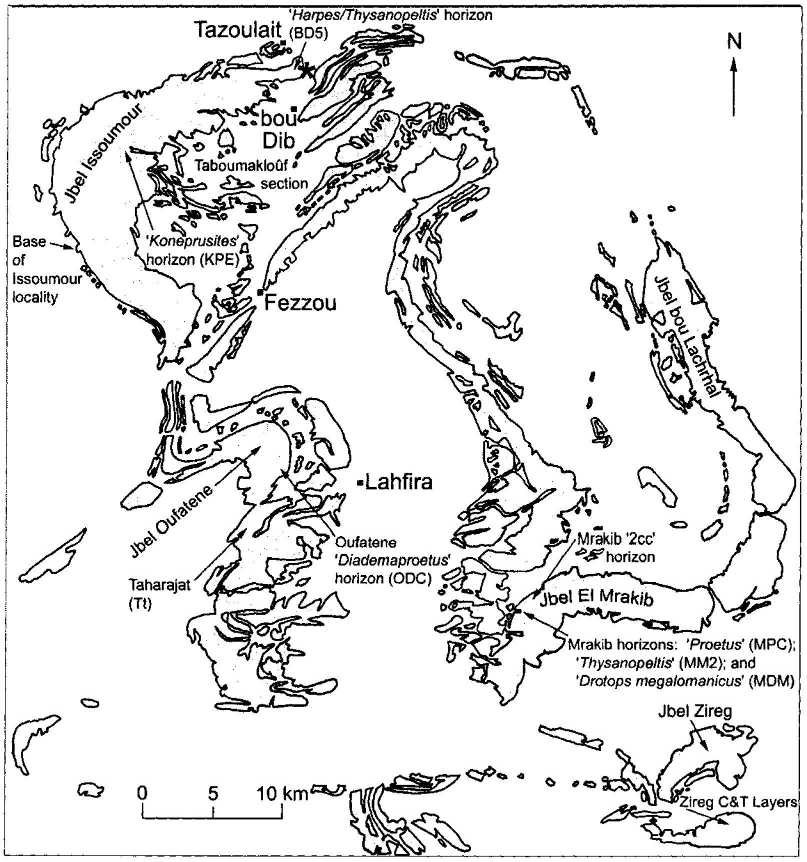

Text Fig. 3: Overview map of Devonian outcrop (shaded) within the Ma'der basin. Individual mountains are indicated with their Moroccan titles (e.g. Jbel El Mrakib). Section at bou Dib has been indicated with asterisk on map. (Diagram modified from Fetah *et al.*, 1988, and reproduced with permission from Gibb, 2005).

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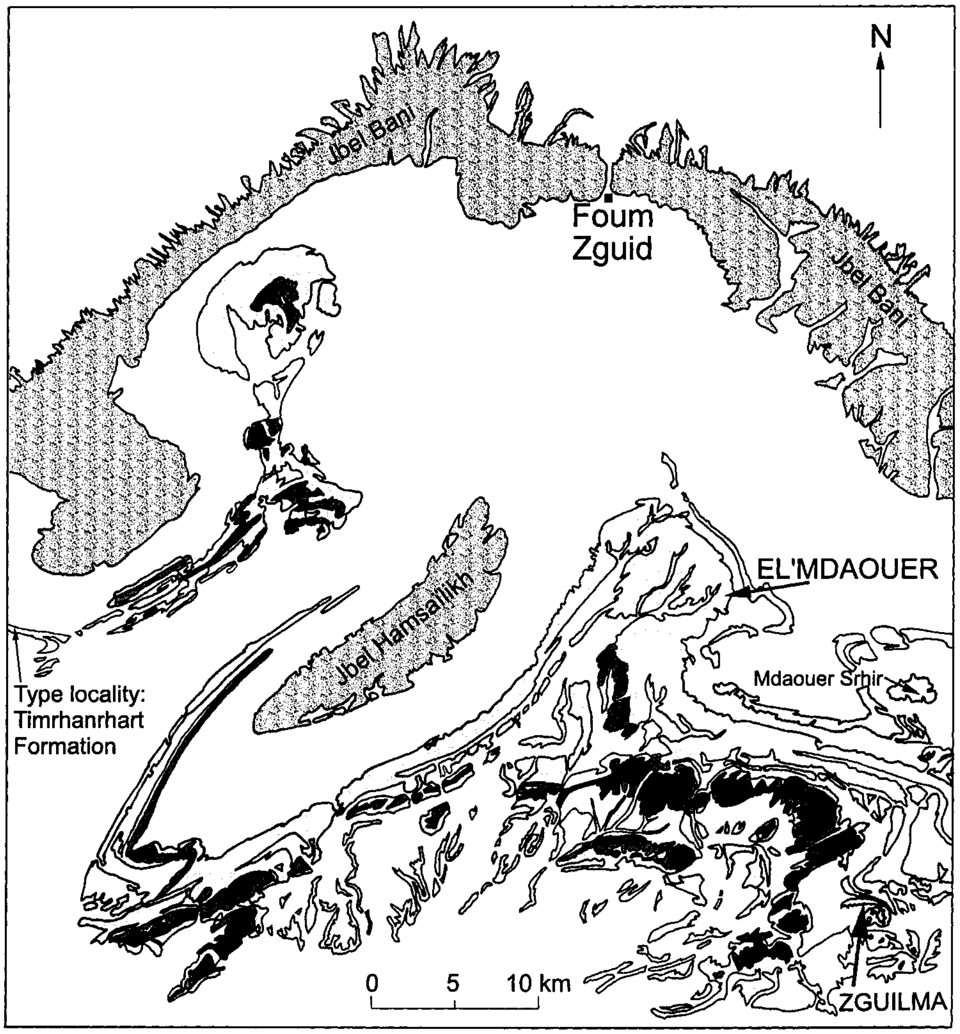

Text Fig. 4: Overview map of Devonian outcrop (shaded medium gray) within part of the Tindouf basin. Individual mountains are indicated with their Moroccan titles (e.g. Jbel Bani). Zquilma and El'Mdaouer sections have been indicated with arrows on map. (Diagram modified from Fetah *et al.*, 1988, and reproduced in secondarily modified form, with permission from Gibb, 2005).

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encompasses Germany, North Africa, France, and the Czech Republic, and has at times extended to encompass portions of northern Europe and even portions of Nova Scotia and Quebec (in the Emsian) (BOUCOT AND GRAY, 1976). Work on phacopids began in earnest with German and Czech studies like those of BARRANDE (1846; 1852; 1872), and HAWLE AND CORDA (1847), building largely upon the work of EMMRICH (1839). This labour was carried through the early 20th century and expanded farther abroad by workers such as RUDOLPH AND EMMA RICHTER (1933; 1939; 1942; 1943; 1955), ERBEN (1952), KIELAN (1954), STUMM (1954), and DELO (1935; 1940).

A peak in work on the Phacopidae occurred between the late 1960's and early 1980's. Thorough and large works were completed on North American phacopids by researchers such as CAMPBELL (1967; 1977) and ELDREDGE (1972; 1973), and Bohemian material was similarly covered by CHLUPÁČ (1971; 1977). German researchers, like G.K.B. ALBERTI (1969; 1970; 1981; 1983), completed large amounts of work on Moroccan material (mostly from localities far to the North or West of the study area of this work), and tried to connect it to faunal contents from the remainder of the Rhenish-Bohemian faunal subprovince. Other workers, such as STRUVE, had more of a Rhenish focus to their labours (1970; 1972; 1976; 1982; 1989; 1990; 1992), but could not resist the allure of Moroccan specimens (1995), using them for comparative purposes in many works. Additional, smaller contributions were made by workers such as MAKSIMOVA (1972; 1978), HAAS (1968; 1998), SCHRAUT (1998; 2000a,b), KOWALSKI (1989, 1990), PŘIBYL AND VANĚK (1970), MORZADEC (1983), CRONIER AND FEIST (2000), PILLET (1972), for example, but few have made phacopid taxonomy or systematics the focal point of entire research programs.

Throughout all of the aforementioned work on phacopids, the bulk of the specimens studied have been disarticulated, and were often poorly preserved. This has forced some researchers to name taxa based upon loosely associations of sclerites or cephala only, and these were often purchased with little or no stratigraphic information available. This situation makes any putative connections between Moroccan specimens and those from other localities tenuous at best, and has resulted in some questionably included materials within almost all species described from the region. Unfortunately, there has been little work done on articulated phacopids from Morocco to address this

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problem, because most of the recent research attention has been directed at more ornate groups of trilobites.

A revival of interest in phacopid systematics began in 1991, with the cladistic analysis of RAMSKÖLD AND WERDELIN paving the way for future work by revising the relationships among many of the Silurian members of the family (and including some Devonian North American taxa as well). There has also been a relatively recent increase in our understanding of this group's fine-scale morphology (including ventral appendages and soft tissue), due to works such as that of BRUTON AND HAAS (1999), as well as the numerous studies performed on musculature patterns (ELDREDGE, 1971), eye structures (CLARKSON, 1997), and ontogeny within this family (CRONIER AND FEIST, 1997). These studies provide us with many new characters, and a better understanding of character state polarity for future work.

Morocco has a fairly extensive history of geological exploration and description, which is discussed below (under that heading) to avoid repetition.

Purpose and scope of thesis:

The main goal of this study is to collect, describe, and classify select Lower and Middle Devonian phacopids from a number of southern Moroccan localities, in order to further our understanding of their morphology, relationships, and distribution. It is by no means an exhaustive work on this topic, as most of the specimens available were obtained from mined trilobite-rich beds, with little or no sampling between beds; and the sections where these beds were sampled represent a small sample of the massive Devonian outcrop in southern Morocco. The selective nature of this study is a trade-off for the ability to describe thoroughly and accurately taxa that either have previously received cursory treatments in the literature, have been incorrectly described based on poor collections, or have received no coverage to date. The aim is to repair some problematic existing work, while providing solid descriptions for use in future studies of both old and new taxa.

In the most basic sense, this thesis picks up where RAMSKÖLD AND WERDELIN (1991) left off, and tries to lay the groundwork for a continuation of phylogenetic (cladistic) analyses of the Phacopidae throughout the Devonian, while describing any

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new species encountered. To this end, complete, articulated individuals were collected and coded for a large suite of morphological characters from all regions of the dorsal exoskeleton. Comparison was made to the type species of all pertinent phacopid genera (but many of these genera themselves are poorly known), in an attempt to place the new Moroccan species among existing taxa systematically, and to assess some supraspecific taxa at the same time. In order to avoid all preconceptions of the group's phylogeny, the analysis tries to incorporate a broad spectrum of phacopids, and makes no assumptions as to character polarity.

Additional goals of this project include the establishment of alternative index macrofossils for the strata involved in the study. Phacopid trilobites are remarkably common within the Devonian strata of Morocco, are easily identified, and have widespread biogeographic distributions that stretch throughout the Rhenish-Bohemian faunal subprovince and farther abroad. This makes them potentially ideal index fossils within Morocco and neighbouring North African countries, and suggests that they may have useful affinities to German, Czech, French, and Spanish taxa, as well as those found in the rest of Eurasia and North America. Previous works such as those of SCHRAUT (1998), FEIST (1991) and CHLUPAC *et al.* (2000) have already shown that phacopid trilobites can be used to correlate strata from many of these regions, but they have typically resorted to using extreme morphologies (like that of *Reedops cephalotes*) in preference to more subtle variations on the phacopid bauplan: this study aims to consider other species and subspecies as potential high-resolution biostratigraphic indicators.

Methods and materials:

The specimens encompassed in this thesis are the collective product of 6 trips to southern Morocco over the last 11 years. There were many workers involved in the collection and generation of the data used in this thesis. Most of the initial stratigraphic and collecting work was completed by KEVIN BRETT and DR. BRIAN CHATTERTON, and much of this has been refined through the work of STACEY GIBB. The author assisted in the 2003 and 2004 fieldwork, contributing slightly to stratigraphic measurements, but mostly in collecting and purchasing trilobites with an emphasis on members of the Phacopidae. Specimens were collected from mined trilobite-rich horizons (known locally

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as 'couches'). Most specimens were collected from the spoil heaps around the mined trenches, where there were large numbers of partial or complete phacopid trilobites (because they are commercially less desirable than other faunal elements), and their stratigraphic origins are certain. Often these specimens were supplemented by purchased material mined (and occasionally prepared) by the local Berber miners working at a couche. This allowed large numbers of additional specimens to be procured with a high degree of stratigraphic control, and this was verified by comparing matrix material, as well as the specimens from the appropriate beds themselves.

Specimens were prepared using mechanical preparation techniques, which consisted mainly of 'MicroJack' pneumatic chisels, or hand-preparation using a pin-vise. The bulk of the specimens used in this study were prepared by the author, with some material prepared by either DR. CHATTERTON or AL LINDOE (a professional preparator at the University of Alberta). KEVIN BRETT also prepared a few individuals using air abrasive techniques. Supplementary silicified material and alternative faunal elements (such as conodonts, ostracods, and brachiopods) were used in this study for index purposes, and these were prepared through acid dissolution techniques involving dilute hydrochloric or acetic acid. Most of the acid work was completed by STACEY GIBB, with some help from the author.

Specimens were photographed using a Nikon D100 digital camera, after ammonium chloride whitening. Most specimens were photographed by the author, but some were also photographed and edited by DR. CHATTERTON. Once all species had been photographed and described, a cladistic analysis was performed, and a detailed account of its methodology is presented in Chapter 2.

Systematic background:

Currently, Phacopid systematics is in a mild state of disarray. The existing taxonomy for this family does not reflect relationship, and very little of the necessary work has been done to bring the group out of its grade-based taxonomy. ELDREDGE (1973) best articulated this problem when he stated that higher-level taxa were founded on the basis of their distribution, as opposed to their actual phylogeny. This is unacceptable with the current emphasis on holophyletic taxa, and must be rectified.

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Before one can go about rearranging the systematics within the Phacopidae, one must understand how the current situation came to be, and what exactly the systematic arrangement looks like in its current form. This is not easily accomplished, because there are very few comprehensive sources for information on the family, and the current (post 1970's) taxonomy is largely cobbled together from the efforts of various workers who are often in disagreement with one another. The major sources of disagreement are the degree to which taxonomic 'lumping' or 'splitting' should exist within the family, the presence of polymorphic/dimorphic species, and whether or not it is actually possible to gain information on relationships within this family of trilobites through cladistic analyses.

After the major burst of work in the 1970's and 1980's, there was a great deal of indecision regarding the hierarchical levels to which the divisions within the Phacopidae should be assigned. Phacopid workers spanned a spectrum ranging from those that treated most large-scale divisions as subgeneric in nature (CHLUPÁČ and others), to those that recognized all of the potential genera, as well as additional genera that were not widely accepted (STRUVE and others). Over time, the latter interpretation seems to have won more widespread acceptance, but there is still much variability in which taxa are recognized and how they are arranged by different researchers. Below is an approximation of the current systematic structure within the family Phacopidae (see Table 1).

- Tribe Phacopini Flick and STRUVE, 1984 (HAWLE AND CORDA, 1847 *nom. transl.*)
  - *Phacops (Phacops)* EMMRICH, 1839*
  - *Phacops (Cultrops)* STRUVE, 1995
- Tribe Ananaspini (informal grouping of HAAS, 1998)
  - *Ananaspis* CAMPBELL, 1967
  - *Kainops* RAMSKÖLD AND WERDELIN, 1991
  - *Paciphacops* MAKSIMOVA, 1972*
  - *Viaphacops* MAKSIMOVA, 1972*
  - *Denkmannites* WEDEKIND, 1914
  - *Lochkovella* CHLUPÁČ, 1972
- Tribe Geesopini FLICK AND STRUVE, 1984
  - *Geesops* STRUVE, 1972*
  - *Pedinopariops (Pedinopariops)* STRUVE, 1972*
  - *Pedinopariops (Hypsipariops)* STRUVE, 1982*
  - *Nyterops* STRUVE, 1972
  - *Omegops* STRUVE, 1976
  - *Arduennops* STRUVE, 1972
  - *Eldredgeops* STRUVE, 1990*
  - *Burtonops* STRUVE, 1990*

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- *Drotops* STRUVE, 1990*
- *Teichertops* STRUVE, 1992

Tribe Reedopini STRUVE, 1989
- *Reedops* R. AND E. RICHTER, 1925*

Tribe Cordapeltini STRUVE, 1989
- *Cordapeltis* PŘIBYL AND VANĚK, 1971
- *Chotecops* CHLUPÁČ, 1971*
- *Liolophops* STRUVE, 1972
- *Rabienops* STRUVE, 1989
- ?*Boeckops* CHLUPÁČ, 1971*
- ?*Signatops* PŘIBYL AND VANĚK, 1971

Tribe Cryphopini STRUVE, 1989
- *Cryphops* R. AND E. RICHTER, 1926
- *Eocryphops* R. AND E. RICHTER, 1931
- *Plagiolaria* KEGEL, 1952
- *Trimerocephalus* M'COY, 1849
- *Dianops* R. AND E. RICHTER, 1923
- ?*Prokops* CHLUPÁČ, 1971
- ?*Nephranops* R. AND E. RICHTER, 1926

Incertae sedis:
Eophacops DELO, 1935
Acernaspis CAMPBELL, 1967
Phacopidella REED, 1905
Rhinoreedops MAKSIMOVA, 1978
Other unmentioned genera.

Table 1: Current (1998) systematics of the family Phacopidae (largely according to STRUVE, 1970; 1972; 1976; 1982; 1989; 1990; 1992; 1995; FLICK AND STRUVE, 1984; and HAAS, 1998). This interpretation is slightly at odds with that presented in the most recent Treatise coverage of the phacopids (in MOORE, 1959), because it ignores the subfamily divisions used therein, and assigns many of the members usually in the Phacopidellinae to the same tribe as members of the Phacopinae (e.g. *Denckmannites*). It also does not show all of the available genera provided by JELL AND ADRAIN (2003).
* Denotes taxa pertinent to research on Devonian Moroccan phacopids, due to similarity in morphology and temporal distribution.
? Denotes uncertain placement in the classification scheme of STRUVE.

Further complicating matters is the overall similarity of many members of the Phacopidae, and the problem this creates in assigning any given specimen to one taxon in preference to another. Many of the subgeneric, generic, or tribal divisions are based upon diagnostic characteristics that are not strictly exclusive to the group delimited, or are gradational in nature. To place individuals within a taxon often becomes a question of which set of characteristics one chooses to emphasize, and becomes questionable in cases of poor preservation or partial representation. Many species within the Phacopidae have 'bounced around' in their systematic positioning, and few higher-level taxa are truly stable within the family, as a result of this problem. This has created a situation in which no systematic account is widely accepted without dispute, few workers question

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contradictions to previous work, and it is exceedingly difficult to obtain a cohesive and comprehensive account of phacopid systematics.

The two largest single contributors to the existing work on Moroccan phacopid trilobites are G.K.B. ALBERTI and STRUVE. The works of each author are surrounded by their own particular circumstances, and these are a necessary preface that must be taken into account when dealing with the taxa or systematic groupings they generated. Some of the minor taxonomic pitfalls created in their works are discussed here.

STRUVE was quite possibly the most prolific 'splitter' among phacopid systematic workers. He single-handedly generated over 1/3rd of the currently used phacopine genera, is the individual responsible for the wholesale elevation of most phacopine subgenera to the generic rank, and developed most of the group's higher-level taxonomic divisions. He dealt with Moroccan material on a rather limited basis, but had a huge impact on how it was viewed. STRUVE worked largely with Moroccan specimens with pronounced sculpture, and complained that many of the phacopid species in Morocco had been incorrectly assigned to *Phacops rana africanus* BURTON AND ELDREDGE, 1974 (in his 1990 work). He observed much more diversity among the Moroccan phacopids than some previous workers had, and felt that their taxonomy should reflect this diversity. Unfortunately, he decided to erect the genus *Burtonops* STRUVE, 1990 as a wastebasket taxon to encompass this diversity and contain most of the species that did not fit into his research surrounding *Drotops* and other members of his tribe Geesopini. At the same time, he also erected the genus *Eldredgeops* STRUVE, 1990 to encompass *Phacops rana* and its subspecies, because he felt its group of subspecies fit better in the Geesopini than the Phacopini (which is basically stating that these specimens are closer in morphology to *Geesops schlotheimi* than to *Phacops latifrons*).

One concern when dealing with North African phacopids is the use of *Burtonops,* as it is a problematic taxon. Its type species is *Phacops cristatus* HALL, 1861, a taxon ELDREDGE (1973) deemed a senior subjective synonym for *Phacops pipa* HALL AND CLARKE, 1888. Complicating matters is the fact that *Phacops pipa* had been previously used by MAKSIMOVA (1972) as the type for her new subgenus *Viaphacops* (a subgenus subsequently raised to generic rank by RAMSKÖLD AND WERDELIN, 1991). This means *Burtonops* is a junior subjective synonym of *Viaphacops.* STRUVE did not explicitly

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specify which species belong within the bounds of *Burtonops* in either of his publications in which the taxon appears (1990, 1992), and to the best of the author's knowledge, he was the only person to use this monospecific taxon in print, so it is easily suppressed.

G. ALBERTI, on the other hand, dealt largely with many Moroccan specimens possessing reduced sculpture, and was much more conservative in his taxonomy. He worked almost exclusively with disarticulated remains. The main problem associated with his work is that it resulted in many new species being described from rather limited material (often only the cephalon was described), and with little certainty as to whether or not the individual sclerites he associated actually belonged to members of the same species. The uncertainty this created hinders the definitive assignment of some of his species to higher-level taxa, and creates a demand for verification of his species by comparison with articulated, whole-exoskeleton material.

Geological background:

In the Early and Middle Devonian, Morocco was part of the continental shelf of Gondwana, and was usually submerged beneath epicontinental seas. The field area of this study is perhaps best represented as the "Moroccan Meseta" of ROBARDET *et al.* (1990) – a submerged mass positioned about midway between 30° and 60° South latitude, with the bulk of Gondwana to its South and West, other portions of the Bohemian, Armorican, and Rhenish regions sharing the same epeiric sea to its North/North-East, and a slowly closing Rheic Ocean separating these regions from Laurentia and Baltica further to the North (see Fig. 6 of ROBARDET *et al.*, 1990). The Middle Devonian saw the Rheic Ocean shrink even further, closing completely in the Upper Devonian, but leaving Morocco in warm temperate waters below 30° South latitude throughout the process (SCOTESE, *et al.*, 1999).

Among the most significant influences upon deposition and the biota within the study area were water depth and currents within the region. Epicontinental seas seem to have been most widespread in the Givetian (DINELEY, 1984), but they were fairly persistent in the vicinity of Morocco throughout the Devonian. There were many regional transgressive and regressive events during the Early and Middle Devonian, some of which are tied to major regional biotic events. LUBESEDER *et al.*, (2003) stated that there

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are 6 transgressive/regressive cycles that occur within the Early Devonian of Morocco, and an additional 6 cycles in the Middle and Late Devonian. The Early Devonian is generally considered to be a time of relative lowstand, while the Middle and Late Devonian are typically viewed as times of increased relative sea level, predominantly due to changes in mid-oceanic ridges (ZIEGLER, 1989). Of importance to this study are: the earliest Emsian Basal Zlichov Event, associated with a major transgression and the first global distribution of ammonoids, as well as some diversification within the phacopids; the mid-Emsian Daleje Event, associated with a sharp rise in eustatic sea level followed by the deposition of numerous tentaculite-rich shales across the Old World faunal province and minor faunal impacts; the early Eifelian Choteč Event, associated with lower sea levels and a burst of shallower-water carbonate production, followed by a series of transgressive events producing widespread black shales, and resulting in a faunal explosion within the Phacopidae – largely composed of coarsely sculpted species and gigantic forms – while other groups of trilobites slowly declined; the late Eifelian Kačák Event, associated with a large eustatic sea level rise and widespread anoxic conditions, that produced a huge downturn in trilobite diversity including minor effects within the phacopids; and the mid-Givetian Taghanic Event, associated with more widespread extinctions and yet another major transgression (CHLUPÁČ, 1994; HOUSE 1985; 2000). Many of the regressive deposits (between the events mentioned above) are represented in Morocco by thick, resistant sandstone intervals referred to as a series of numbered 'Rich' units (BECKER *et al.*, 2004), and the Zquilma locality appears to straddle the Choteč Event within its section (CHATTERTON *et al.*, 2006), although its position has not been pinpointed.

General oceanic currents during the Devonian place the shallow seas of Morocco along the southern margin of a warm eastward flow between North Africa and Bohemia-Armorica (HECKEL AND WITZKE, 1979). This flow was the southern margin of what HECKEL AND WITZKE (1979) called the "Subtropical Gyre", a warm counterclockwise loop that circled the rims of Euramerica and Gondwana, between these two masses and the smaller continental blocks of Bohemia-Armorica and fragments of Asia. Where the current passed between North Africa and Bohemia-Armorica, it could have either been strong (a boundary current along the 45th parallel, as stated by HECKEL AND WITZKE,

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1979), or fairly weak. The weaker current is much more likely, as there are great faunal affinities shared between Morocco and the Rhenish-Bohemian subprovince. Based on slight (species-level) differences between this region and the Rhenish-Bohemian subprovince in general, there is a slight degree of isolation between these two faunal suites, but Morocco displays faunal contents that are mostly on par with the surrounding depositional areas. There is no true isolation or provincialism evident, and what little differences do exist appear to fade through the Middle Devonian.

Deposition in Morocco has been characterized as "a thick, carbonate-dominated succession that accumulated in a series of platforms and actively subsiding grabens" (HALLAM AND WIGNALL, 1999; citing WENDT AND BELKA, 1991). These platforms were the Ma'der and Tafilalt, while the basins of interest to this work are the Ma'der, Tafilalt, and Tindouf (see Text Fig. 1). Deposition within these basins is best depicted as a Bohemian (carbonate dominated) facies pattern, based on the taxa present, but there is a lot of (variable) clastic input as well. The three basins have been subject to fairly intensive study, since the Middle and Late Devonian are well represented and exposed in Morocco. The bulk of the pre-existing geological work in Morocco has been completed by workers of the country's own Geological Survey, most notably within the works of HOLLARD (1967; 1974; 1978; 1981). This work had been built upon and had its coverage of the Lower and Middle Devonian improved by KAUFMANN (1998), BECKER *et al.* (2004), JANSEN *et al.*, (2004), PLODOWSKI *et al.* (1999), BULTYNCK AND WALLISER (2000), and too many other workers to cite. These basins have been studied to the point of determining palaeocurrents through the basins at specific time intervals (e.g. WENDT, 1995), but most of the rock units themselves have not been analyzed as thoroughly as their fossil contents, and the taphonomy of these fossils.

The field area for this study consisted of a number of discrete sections from each of the three Devonian depositional basins in the Anti-Atlas region of Morocco. These sections focused mainly on the Ma'der basin (Text Fig. 3), which outcrops as an oblong ring of mountains with the villages of Lahfira and Fezzou at its centre. There is a single section at bou Dib (Text Fig. 5), located at N 31° 05' 16.6" and W 04° 52' 32.2" ±6m. Two sections were studied at Jbel Issoumour (Text Fig. 6), the base of which is at N 30° 58' 15.9" and W 05° 02' 42.7" ±4m, with an additional section along the mountain's dip

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slope – often referred to as the Taboumakhloûf section – at N 30° 02' 0.8" and W 05° 00' 36" (CAMPBELL *et al.*, 2002; STRUVE, 1995). A number of connected sections through Jbel Oufatene (Text Fig. 7), were sampled, focussing mainly on the '*Diademaproetus* couche' located at N 30° 50' 21.3" and W 04° 52' 58.7" ±5m, and also at the Taharajat d'Oufatene section, located farther southwest along the mountain's curvature, at N 30° 47' 48.0" and W 04° 54' 20.3". The 'Mrakib' section is a composite of many collection localities along Jbel El Mrakib (Text Fig. 8), most of which are located at approximately N 30° 45' 48.6" and W 04° 40' 42.7", ±5m, along the southern rim of the Ma'der basin, with the main collections in this study taken from horizons at Aferdou de Mrakib, an outcrop located near N 30° 46' 03.3" and W 04° 37' 38.0". Passing mention is also made to specimens originating from Jbel Zireg, a portion of the Ma'der basin outcrop located to the S-SE of the other localites, at about N 30° 36' 41.6" and W 04° 32' 22.7" (GIBB, 2005).

The Tindouf basin (in particular the Dra Valley region) (Text Fig. 4) was explored through a section at Jbel Gara El Zquilma, hereafter referred to as 'Zquilma' (Text Fig. 9), at N 29° 42' 35.2" and W 06° 42' 10.2", 53Km southeast of the town of Foum Zquid. Limited collections were also made from a single horizon near the base of the El'Mdoauer section, located at N 29° 53' 30.4" and W 06° 47' 43.4", approximately 20Km to the NE of the Zquilma section (GIBB, 2005).

The Tafilalt basin (Text Fig. 2) was also explored through sections near Merzouga (Text Fig. 10), located at N 31° 16' 28.5" and W 03° 53' 29.4" ±7m (but only the basal portion of this section is included in this work as the higher portions are to be included in future publications); and spot-collecting at the Hamar Laghdad bioherms located near N 31° 22' 56.7" and W 04° 04' 41.0", which again takes the form of collection from a single interval, as stratigraphy within the crevasse fills between the bioherms is not fully resolved.

For many of the sections mentioned above, the names have been shortened to just the central word (i.e. Taharajat d'Oufatene is called Taharajat, and Jbel El Mrakib is called Mrakib) in the remainder of this thesis, for the sake of brevity. All phacopid trilobites described in this thesis have their stratigraphic occurrences plotted on the

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section diagrams at the end of this chapter (Text Fig. 5-10). Section diagrams were provided courtesy of STACEY GIBB.

Strata encompassed in this study include portions of the Ihandar, Bou Tiskaouine, Tazouläit, El Otfal, Taboumakhloûf and Bou Dib formations in the Ma'der basin; Assa, and Timrhanrhart formations in the Tindouf basin; and Kess-Kess Formation and Amerboh Group in the Tafilalt basin (formations are listed from oldest to youngest, see BULTYNCK AND WALLISER, 2000, for a full depiction of formations within these regions and their correlations, and GIBB, 2005, for authorship and background information on individual formations). These units are often difficult to recognize in the field, as they mostly consist of repetitive, resistant mud-rich limestones interbedded with recessive calcareous shales. The resistant layers vary in thickness and number, in lateral extent, making them hard to trace with certainty without relying heavily upon their fossil contents. Many previous works have avoided trying to attach formation names to studied units, instead opting for the conodont or ammonoid zonation schemes used widely throughout Europe, but every attempt has been made to provide formation names here.

The genesis of many of these rock units has been tied to repetitive event deposits, such as tempestites (CHATTERTON *et al.*, 2006; CHLUPÁČ, 1994), with some specific layers explained as the product of Tsunamis or other catastrophic events (BULTYNCK AND WALLISER, 2000; citing LOTTMAN, 1990). In any case, the bulk of the strata surveyed in this study represent deposits in relatively low energy settings, most likely in neritic to upper bathyal positions near the slope, with mixed clastic and carbonate inputs. Noteworthy exceptions are those deposits from sections such as the Hamar Laghdad bioherms, which likely represent a shallow setting with much purer carbonate deposition, and some of the upper Ma'der basin horizons containing *Drotops* species, which often contain high concentrations of brachiopods and large solitary rugose corals – suggesting a shallower depositional setting.

Format of thesis:

The thesis has been presented in chapter format, and has been formatted to match the editorial standards of Palaeontographica Abteilung A, the journal to which a slightly modified version of this work will eventually be submitted. The use of bold and italics in

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headings has been retained (against submission demands) for ease of reading, while small capitals are used for author's names (to meet submission demands). Figure sets (Plates or Figures) have been included at the end of the appropriate chapters, and Text Figures included within the body of the text, also for ease of reading. A single list of works cited is provided at the end of the thesis to reduce repetition. Portions of this thesis have already been published (see CHATTERTON *et al.*, 2006).

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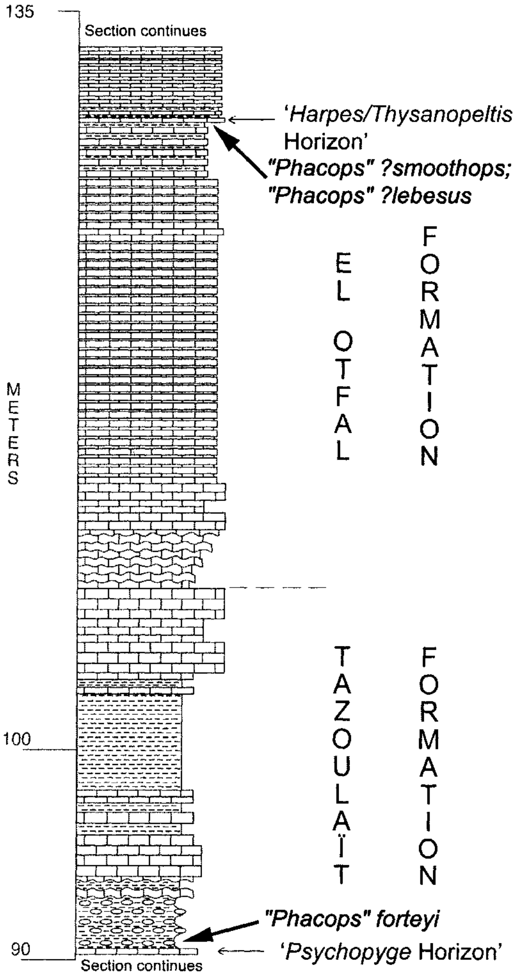
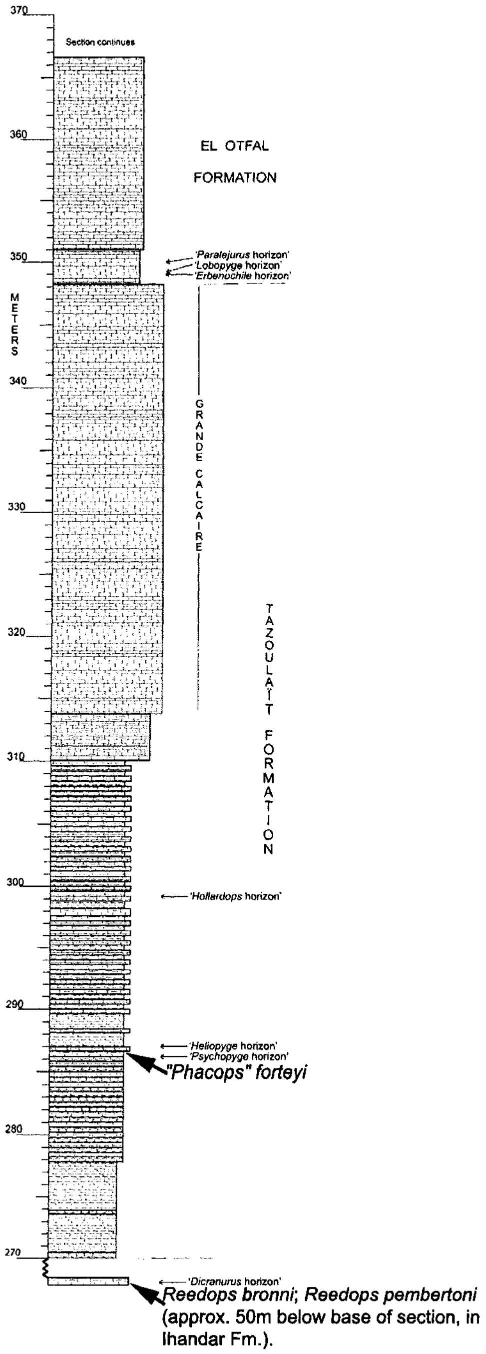


Text Fig. 5: Bou Dib stratigraphic column (based upon the measured section of Kevin Brett). Phacopid trilobite occurrences are indicated with thick arrows and taxa present are listed. (Courtesy of Gibb, 2005)



Text Fig.6: Issoumour stratigraphic column (based upon the measured section of B.D.E. Chatterton). Phacopid trilobite occurrences are indicated with thick arrows and taxa present are listed. (Courtesy of Gibb)

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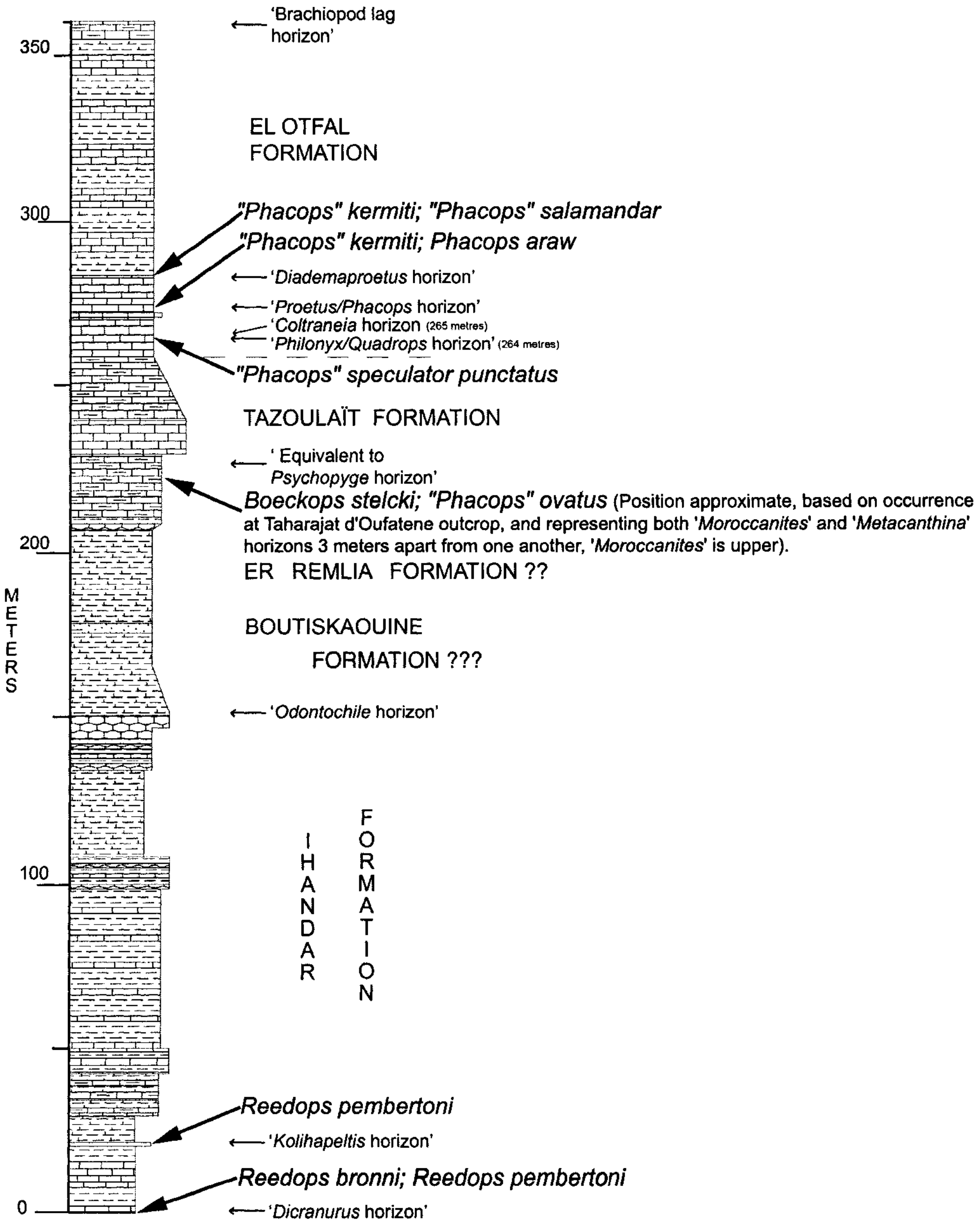

Text Fig. 7: Oufatene composite stratigraphic column (based upon the measured sections of S. Gibb and B.D.E. Chatterton). Boundaries between the formations in the middle of the section were still undecided at the time the diagram was prepared.
Phacopid trilobite occurrences are indicated with thick arrows and taxa present are listed. (Courtesy of Gibb, 2005)

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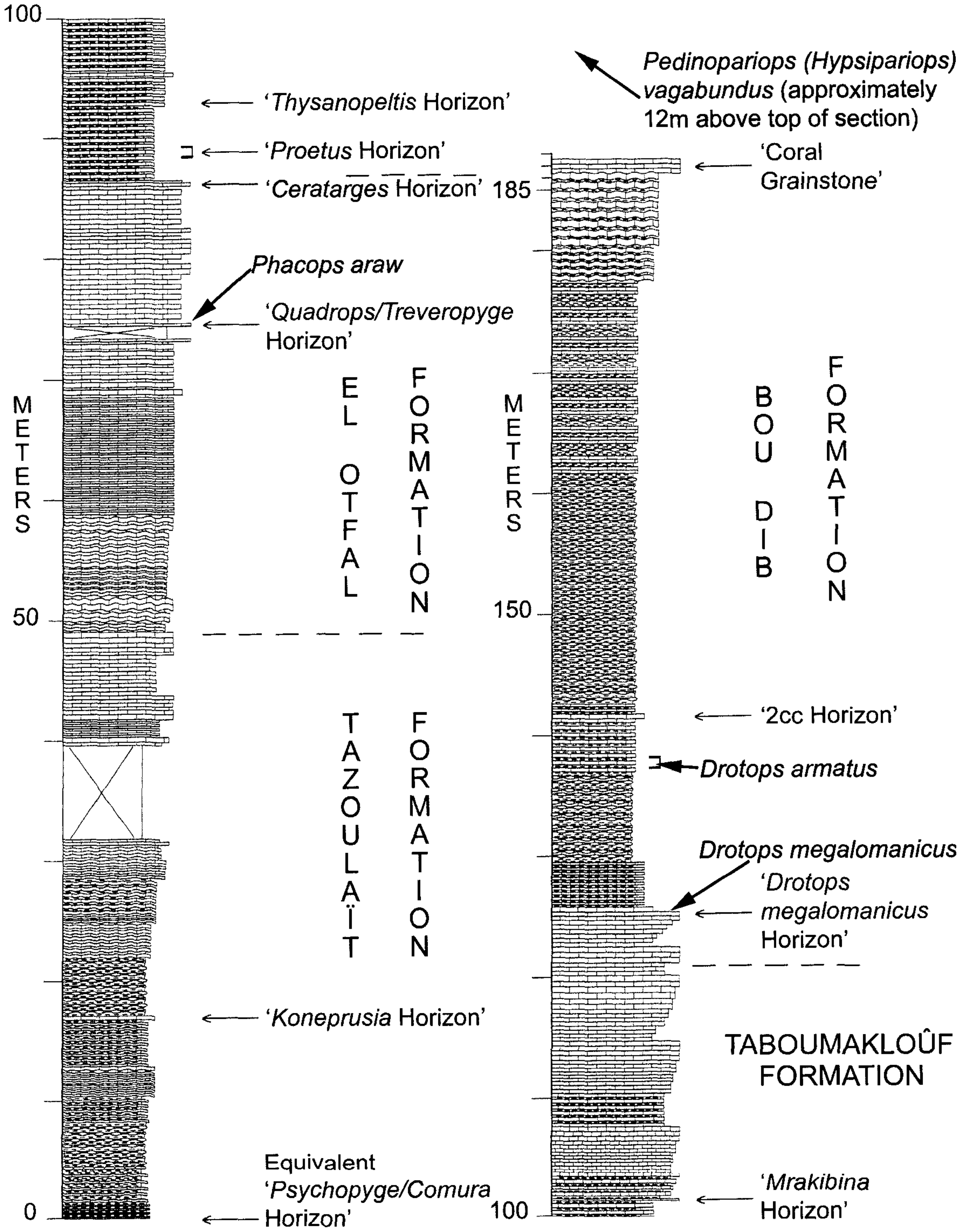

Text Fig. 8: Mrakib stratigraphic column (based upon the measured sections of B.D.E.C, S.G., and R.C.M.). Phacopid trilobite occurrences are indicated with thick arrows and taxa present are listed. (Courtesy of Gibb, 2005).

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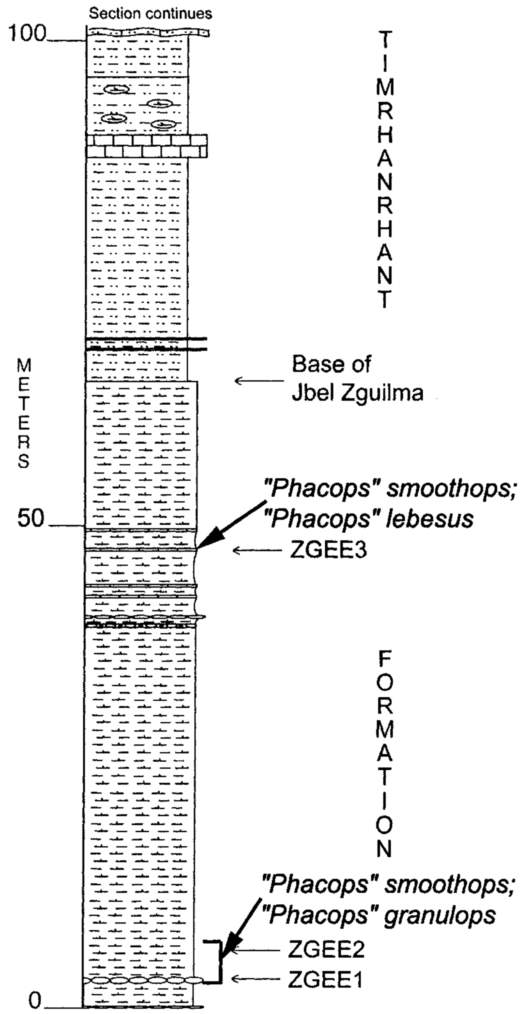
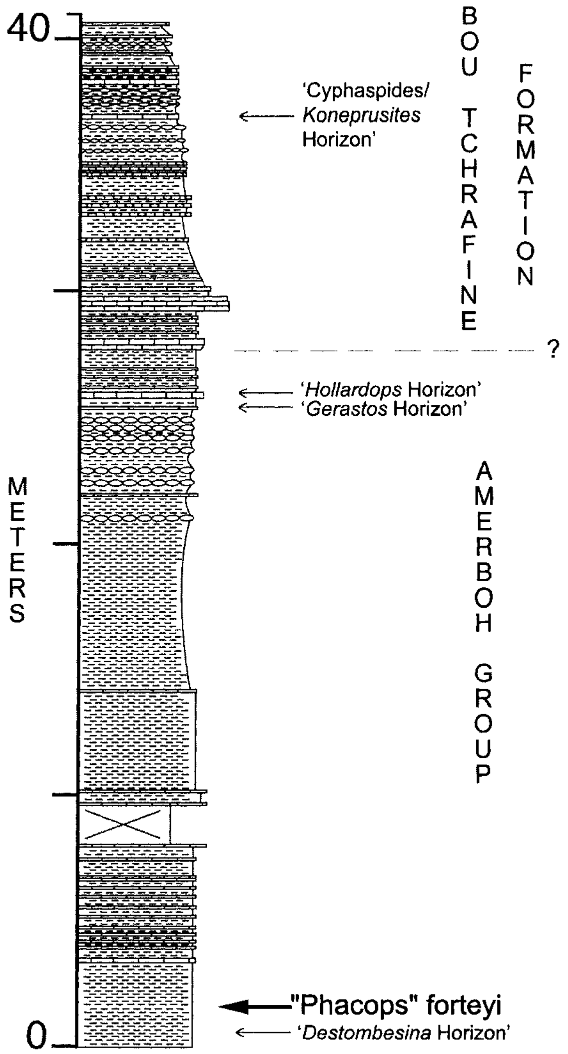


Text Fig. 9: Zquilma stratigraphic column, measured by B.D.E.C., S.G., and R.C.M.
Phacopid trilobite occurrences are indicated with thick arrows and taxa present are listed. (Courtesy of Gibb, 2005).



Text Fig. 10: Merzouga stratigraphic column, measured by R.C.M. Phacopid trilobite occurrences are indicated with thick arrows and taxa present are listed. (Courtesy of Gibb, 2005).

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CHAPTER 2: PHYLOGENETIC ANALYSIS

The main goal of this analysis is to assess the relationships of the Moroccan species encountered in this study in the context of their contemporaries, and to provide the basis for a Devonian continuation of the cladistic work completed by RAMSKÖLD AND WERDELIN (1991) (involving mainly Silurian taxa). Unfortunately, the Phacopidae are plagued by many genera (or subgenera, depending on opinion), most of which are based on as little as one or two distinctive characters, and almost all of which are currently defined in a gradational context (making the majority of superspecific taxa likely to be paraphyletic or polyphyletic). This problem is extreme among the Early and Middle Devonian taxa encountered here.

Taxa included in the analysis:

Due to the problematic and abundant genera available for the time interval of this study, only the type species of most commonly accepted genera have been included. This is in an attempt to observe the placement of the Moroccan specimens amongst these genera, and to some extent, an attempt to assess the validity (monophyly) of the existing higher-level taxa. Also, by including just type species, this work has avoided expanding into an evaluation of all Devonian phacopid genera.

Two outgroup taxa were chosen. *Calyptaulax glabella* COOPER, 1930, is the first, because it is the well-documented type species of *Calyptaulax*, and is a Late Ordovician (Ashgill) member of the family Pterygometopidae, which has been suggested as a putative sister group to the Phacopidae by works such as LUDVIGSEN AND CHATTERTON (1982). *Acernaspis orestes* (BILLINGS, 1860), is the second, because it is the exceptionally well-documented type species of *Acernaspis* CAMPBELL, 1967, is an Early Silurian member of the family Phacopidae, and is commonly viewed as an 'ancestor' to *Phacops* and its close relatives (CAMPBELL, 1977; CHLUPÁČ, 1977). Coding of characters for *Calyptaulax glabella* was based on the work of LUDVIGSEN AND CHATTERTON (1982) and MOORE (1959), and for *Acernaspis orestes* it was based on the work of CHATTERTON AND LUDVIGSEN (2004). Two outgroup taxa were used because there appeared to be some dispute as to whether the lineage containing *Reedops* had broken off from that containing

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Phacops before or after the occurrence of *Acernaspis* (compare Fig. 4 of CAMPBELL, 1977; Fig. 26 of CHLUPÁČ, 1977; Fig. 1 of PŘIBYL AND VANĚK, 1970; and Fig. 1 of HAAS, 1998), and the fact that *Calyptaulax* is distant (in age and morphology) from the taxa being analyzed.

Ingroup taxa consist of the Moroccan taxa encountered (both new and previously described species), and the type species of most genera to which they could potentially belong. The additional genera chosen are basically a cross-section through the common phacopids of the Early and Middle Devonian, excluding seriously disparate morphologies like those found in members of many taxa with reduced eyes, and distant, geographically restricted, genera.

Eldredgeops rana rana (GREEN, 1832) is used here because it is the nominate subspecies for the type species of the genus, and is much better known than *Eldredgeops rana africanus* (BURTON AND ELDREDGE, 1974) or *Eldredgeops rana tindoufensis* (BURTON AND ELDREDGE, 1974) from the Spanish Sahara. Furthermore, the author has serious reservations about placing the latter two taxa within *Eldredgeops rana*, but an assessment of this grouping is beyond the scope of this study. Coding was completed based on the works of ELDREDGE (1972) and BURTON AND ELDREDGE (1974).

Paciphacops logani (HALL, 1861) and *Viaphacops cristatus* (HALL, 1861) were included because these genera are both Early to earliest Middle Devonian in age, and have wide distributions (including North America, South America, Europe, Australia and central and eastern regions of Asia) (CHLUPÁČ, 1977; CAMPBELL, 1977). CAMPBELL considered the genus *Paciphacops* to be "part of the main 'stem' from *Acernaspis* to *Phacops*" and fairly similar in overall morphology to *Boeckops*. The type species of *Boeckops,* in turn, shares much in common with *Boeckops stelcki* new species. This combination of connections and putative position in the phylogeny of the Devonian phacopids makes *Paciphacops* a necessary inclusion to assess its relationship to *Boeckops stelcki* and other Moroccan species. *Viaphacops cristatus* must also be included, as it was originally a subgenus of *Paciphacops*, and its existence and level of recognition have been widely disputed. ELDREDGE (1973) and CHLUPÁČ (1977) did not regard *Viaphacops* as a valid taxon, while CAMPBELL (1977) regarded it valid at the

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subgeneric level, and RAMSKÖLD AND WERDELIN (1991) regarded it as a valid full genus based on their cladistic analysis.

Chotecops auspex CHLUPÁČ, 1971 and *Boeckops boecki* (HAWLE AND CORDA, 1847) have both been suggested as intermediate morphologies between *Reedops* and *Phacops* (with *Boeckops* closer in general) (CHLUPÁČ, 1977). The Moroccan specimens described here meet many of the diagnostic restrictions placed upon the members of these mainly Early and Middle Devonian genera, and species such as *Boeckops stelcki* n. sp. are close in overall morphology to members of both genera, making the inclusion of these two genera necessary. They were both coded from the work of CHLUPÁČ (1977).

Geesops schlotheimi (BRONN, 1825) is the type species for its genus, and also for the Geesopini, a tribe that STRUVE erected to contain most of the old world phacopids. As such, its relationship to the Moroccan species is crucial, because it dictates their large-scale classification. There is also significant doubt surrounding the validity (monophyly) of this tribe, and the generic rank of its nominate genus. This species was coded mainly from the works of STRUVE (1982), KOWALSKI (1989; 1990), and MOORE (1959).

Pedinopariops (Pedinopariops) lentigifer STRUVE, 1970 is the type species for this Eifelian genus, and is included in this analysis to observe its relationship to both *Pedinopariops (Hypsipariops)* and *Drotops*, since distinctions between these two genera appear insubstantial in the Moroccan material available. This species was coded from the works of STRUVE (1970; 1972). Both species of *Drotops* used in this analysis were also coded partially from the work of STRUVE (1995), wherever the condition or quantity of material available made coding impossible, topotypic specimens at hand were used.

Last but not least, *Phacops latifrons* (BRONN, 1825) must be included, to assess the relationships of the taxa involved relative to the strictest definition of the genus (since this is its type) and its potential subgenera. Furthermore, the relationship between *P. latifrons* and *P. araw* n. sp. is of interest, because they are very similar in morphology. *Phacops latifrons* was coded mainly from the works of KOWALSKI (1989; 1990), and MOORE (1959).

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Taxa not included in the analysis:

A major hurdle for this study was limiting the number of taxa analyzed. In the subgenus *Phacops (Phacops)* alone, CHLUPÁČ (1977) included 41 species (with a fairly restrictive set of diagnostic characters). Since 1977, many of these species have subsequently been transferred to other subgenera (many of which were later raised to genera), but most of these new higher taxa are grade-based and questionably monophyletic. The Moroccan material encompassed here comes from at least 4 of the currently accepted genera. To test the monophyly of all of these genera thoroughly is something beyond the scope of this thesis. Here, only type species for each of the potential genera are used, in order to see if the Moroccan phacopids share any close relationships with them. Resolving the contents of the individual genera involved is a much larger problem for future studies.

The main foreseeable complaint with this study is the omission from the analysis of other Moroccan phacopid species generated by workers such as G. ALBERTI, HAAS, and others. This is an unfortunate side-affect of the fact that these species are known almost exclusively from cephala, while pygidia are often unknown or only loosely associated with other exoskeletal elements, and most material is substantially weathered (G. ALBERTI, 1981; 1983; HAAS, 1968). This is also another reason for the general limits placed on the number of taxa analyzed here, as most are not represented as completely as the Moroccan specimens, and would result in many states coded as "?". From a cladistic standpoint, their inclusion would be problematic, both because coding is difficult, and because partial coding may introduce unnecessary uncertainty into the analysis.

Explanation of characters and character states:

This analysis is an attempt to continue the cladistic work of RAMSKÖLD AND WERDELIN (1991), and as such, makes use of many of their characters and character states. Where their characters have been used, the corresponding character number has been included in square brackets behind the character name, and any changes to coding specified. Of the 39 characters used in this study 10 are binary and 29 are multistate in nature. Just as in most phacopid work, there is a significant bias towards cephalic characters (c. 16), and those relating to ornament (c. 9) and aspects of the eye (c. 5);

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every effort has been made to include pygidial characters (c. 8), and thoracic characters (c. 2), but for many species these sclerites are poorly known or poorly represented in the literature. The characters used are summarized in Appendix 1, and the complete data matrix for this analysis is included as Appendix 2.

A full explanation of the characters and their states is included below, as well as a justification for their use here, explanation of any modifications made to characters used in other studies, and examples for difficult qualitative character states. Any new numerical or measurement-based characters introduced here were constructed by measuring 3 or more specimens (if available) from a range of holaspid sizes, plotting their distribution, and coding based on gaps in this distribution. An interpretation of characters and their states in terms of ontogenetic development and broader outgroup comparison is provided by RAMSKÖLD AND WERDELIN (1991) for their characters, and is not repeated here for the sake of brevity.

1. *Glabellar width* [1 modified] – transverse width of frontal lobe adjacent to anteroventral corner of eye, expressed as percentage of total cephalic width (tr.).

Remarks: This character is a continuation of [1], with the addition of the larger (4) and (5) character states to accommodate new taxa. It has been retained because it seemed that it would form synapomorphic states at low taxonomic levels, but after analysis, most of these appear to be homoplastic in a broader context. An extremely narrow glabella is characteristic of some upper Middle Devonian taxa found in Morocco (but not included in this study due to limited material available), so this character will likely be more useful in future studies, but probably would benefit from wider ranges in its character states.

States: (0) 51-55.9%; (1) 56.0-60.9%; (2) 61.0-65.9%; (3) 66.0-70.9%; (4) 71.0-75.9%

2. *Occipital ring width* [3 modified] – transverse width of occipital ring, measured from axial furrow to axial furrow, and expressed as percentage of total cephalic width (tr.).

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Remarks: This is an unaltered continuation of [3], a character that suffered from the same problem of broader-scale homoplasy as [1] in both this study and that of RAMSKÖLD AND WERDELIN (1991). It was retained because, in most cases, it also accurately depicts the percentage of the anterior thoracic segments width (tr.) that is occupied by the axial ring, without the problems of deformation or missing sclerites seen in that region, and thoracic characters are scarce.

States: (0) ≥38%; (1) 36.0-37.9%; (2) 34.0-35.9%; (3) 32.0-33.9%; (4) 0-31.9%

3. *Intercalating ring* [4 modified] – shape and position of intercalating ring (L1), relative to surrounding glabella and L1 lateral lobes.

Remarks: As long ago as 1933, workers like R. AND E. RICHTER realized the importance of the intercalating ring to the classification of phacopids. This feature has figured prominently in most phacopid descriptions and diagnoses since. The only significant modification to this character was to replace the #1 "other" state of RAMSKÖLD AND WERDELIN (1991) with the character states (1) and (3) seen below. The only difficulty in using this character comes from judging degree of prominence or size in cases where the intercalating ring is very close to level with the back of the glabella, or bears a concentration of tubercles that locally boosts its prominence.

States: (0) small, subtriangular, displaying independent inflation, and typically barren of sculpture (e.g. *Reedops bronni*, Pl. 1.9); (1) mid-sized to large, raised pad with sculpture (e.g. New Genus B *forteyi*, Pl. 24.2); (2) small, circumscribed by furrows, set anterior to L1 lateral lobes (e.g. *Phacops araw*, Pl. 26.4); (3) faint or absent with no sculpture (e.g. New Genus A *kermiti*, Pl. 12.9).

4. *L1 lateral lobe size* [5] – relative size of each lobe and its distinction from intercalating ring by obvious furrow.

Remarks: [5] is retained unchanged, because it appears to be a fairly reliable synapomorphy at the species level, and perhaps a little higher. Some caution should be used with this character, as was mentioned by RAMSKÖLD AND WERDELIN (1991), because photographic representation can be somewhat variable.

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States: (0) L1 lateral very small (e.g. *Acernaspis orestes*, see CHATTERTON AND LUDVIGSEN, 2004, Pl. 28); (1) L1 lateral medium-sized (e.g. *Phacops araw*, Pl. 26.4); (2) L1 lateral large, with distinct adaxial edge (e.g. New Genus B *ovatus*, Pl. 20.5); (3) L1 lateral large, with indistinct adaxial edge (e.g. New Genus A *kermiti*, Pl. 12.6)

5. *Length of L2 versus length of L3* [6 modified] – exsaggital length of L2 across its long axis, expressed as percentage of same measure for L3.

Remarks: Although none of the highest states used by RAMSKÖLD AND WERDELIN (1991) are present in the specimens encompassed in this study, those states that are used appear to act as fairly consistent synapomorphies for the groups involved. This should be accepted with some hesitancy, because many of the specimens involved were not possible to code from photographs, or had coarse tubercles that totally obscured the paths of the S2 and S3 furrows involved.
States: (0) 40-49%; (1) 50-59%; (2) 60-69%; (3) ≥70%

6. *Granules on glabella* [7 modified] – presence and concentration of granules on various surfaces and sculpture of glabellar surface.

Remarks: This has been commonly used as a measure of how 'primitive' or 'advanced' any given phacopid is, since most early forms show pervasive granulation, and there seems to be a general reduction through time (CAMPBELL, 1977; RAMSKÖLD AND WERDELIN, 1991). Unfortunately, there also seems to be no rigid definition as to what constitutes a true granule, as opposed to a very fine tubercle, especially within *Reedops* (see Systematic Palaeontology, Discussion section of *Reedops bronni* for further discussion there). CAMPBELL'S (1977) view of *Reedops* sculpture as being of fine tubercles is used here.
States: (0) granules present on all convex surfaces (e.g. *Acernaspis orestes*, CHATTERTON AND LUDVIGSEN, 2004, Pl. 33); (1) granules reduced between tubercles (e.g. *Paciphacops logani*, CAMPBELL, 1977; Pl. 12-13); (2) granules absent between tubercles (e.g. New Genus A *speculator punctatus*, Pl. 10.9)

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7. *Tubercles on glabella* [8 modified] – generalized class of large sculpture elements and their distribution upon glabella.

Remarks: Sculpture elements and their density are used in almost all phacopid diagnoses and have been considered important aspects of classification at all levels. The character states of RAMSKÖLD AND WERDELIN (1991) have been repeated here, with some modification to accommodate forms with reduced sculpture, and some added states to accommodate more specialized tubercle forms.

States: (0) tubercles absent or bordering on granule-size (e.g. *Reedops pembertoni*, Pl. 4.10); (1) tubercles weak, sparse (e.g. *Boeckops stelcki*, Pl. 15.8); (2) tubercles distinct, medium density (e.g. New Genus B *lebesus*, see CHATTERTON *et al.*, 2004, Pl. 3); (3) tubercles distinct to coarse, high density (e.g. New Genus B *forteyi*, Pl. 18.8); (4) tubercles pustular, dense (e.g. *Eldredgeops rana rana*, see ELDREDGE, 1972, Fig. 4); (5) tubercles pustular, relatively sparse (e.g. *Phacops araw*, Pl. 26.2); (6) tubercles tall, conical or spinose (e.g. *Drotops megalomanicus*, see STUVE, 1995, Pl. 1)

8. *Postocular area length* [11] – exsaggital length of area between back of eye and posterior border furrow, measured at posterior-most extreme of eye when specimen is viewed dorsally, and expressed as fraction of posterior border length (exsag.), directly behind first measurement.

Remarks: This character encompasses aspects of both the positioning of the eye relative to the glabella and cephalic margin, and the width (exsag.) of the postocular pad. RAMSKÖLD AND WERDELIN (1991) stated that the posterior border itself has a very neutral allometry throughout holaspid growth, making this an ideal point for comparision. Problems arise when one tries to locate a point along the back of the eye for measuring (the posterior border and postocular pad both widen distally, and not at the same rate, and the back of the eye usually presents a rounded margin): this necessitates measuring from a dorsal view, along the exsagittal plane, directly behind the most posterior portion of the eye. This measurement can also be compromised by variable lighting conditions in photographs, or angled dorsal views.

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States: (0) less than half the length of posterior border; (1) half to equal length of posterior border; (2) longer than posterior border

9. *Lateral border furrow* [12 modified] – definition and shape of lateral border furrow behind posterior branch of facial suture (in other words, posterior border furrow where it swings anteriorly below tip of postocular pad), and resulting effect this has upon definition of postocular pad.

Remarks: STRUVE (1976) and many other workers have commented upon the variations in the postocular pad of phacopids, and this feature is essentially coded for in the work of RAMSKÖLD AND WERDELIN (1991), by commenting upon the furrow at its distal tip. The only significant addition to [12] was to take note of the corresponding pad condition.

States: (0) absence or hint of furrow, pad fades distally (e.g. *Reedops pembertoni*, Pl. 4.11); (1) narrow, weak furrow, pad has poorly defined tip (e.g. *Phacops araw*, Pl. 26.6); (2) narrow, deep furrow, pad has sharply defined tip (e.g. New Genus B *forteyi*, Pl. 24.12); (3) wide, distinct furrow, pad has rounded tip (e.g. New Genus B *ovatus*, Pl. 21.10); (4) wide, shallow furrow, pad has gently sloping tip (e.g. *Pedinopariops (Hypsipariops) vagabundus*, Pl. 28.12)

10. *Palpebral area height* [13 modified] – in true frontal view, height of palpebral lobe relative to dorsal surface of palpebral area, and glabella.

Remarks: 'True frontal view' refers to an anterior view with the cephalon held so that the tops of the palpebral lobes are horizontal, and lens rows near the middle of the eye are usually vertical. In coding this character, there often was some degree of interpretation necessary, based on a lateral picture for specimens, where this view was missing or imperfect, but in most cases the coding is fairly obvious.

States: (0) regions are about level; (1) palpebral area lower than palpebral lobe; (2) palpebral area markedly higher than lobe

11. *Lateral L1 definition and shape* [14 modified] – distinction of L1 lateral lobe from adjacent (abaxial) palpebral area, and its general shape and sculpture.

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Remarks: Besides the overall size of the L1 lateral lobes mentioned previously, these lobes have distinctive combinations of shape ornament, and separation from their surroundings. To some extent, this character also shows how pronounced the axial furrows are (between the palpebral areas and the back of the glabella).

States: (0) distinct, globular, unornamented; (1) distinct, globular, unornamented; (2) indistinct, nearly flat, unornamented

12. *Palpebral furrow definition* [15] – depth of palpebral furrow in median 1/3rd of its course.

Remarks: States (2) and (3) may not be possible to consistently discern based on photographs, and (3) may have been treated as too extreme of a difference here, so the number of taxa coded as (2) may be slightly high. In future work, (2) and (3) may be treated as a single state to avoid this problem. Even with the problems in coding, this character seemed to delimit some groups quite well, and would be a reasonable addition to future analyses. Outgroup taxa are atypical in their lack of a 'primitive' genal spine.

States: (0) faint to absent (e.g. New Genus A *kermiti*, Pl. 12.6); (1) weak (e.g. New Genus B *ovatus*, Pl. 20.5); (2) distinct (e.g. New Genus B *forteyi*, Pl. 25.5); (3) deep (e.g. *Paciphacops birdsongensis,* see CAMPBELL, 1977, Pl. 11)

13. *Genal angle* [16] – shape of genal angle and any prominences it may bear.

Remarks: Genal spines are seen in many similar outgroups (slightly outside this study), are often associated with early members of the Phacopidae, and are seen in many juvenile forms of the ingroup, making their remnants focal points in many classification schemes (RAMSKÖLD AND WERDELIN, 1991; ELDREDGE, 1973). Additionally, the degree of elongation (posteroventrally) changes the shape of the genae into a more angular form, which has also been viewed as important in classification. Here only the three most obvious conditions are recognized, but there is still some difficulty in distinguishing states (2) and (3).

States: (0) drawn out, with acute tip or large spine (e.g. *Viaphacops cristatus,* see ELDREDGE, 1973, Fig. 20); (1) drawn out, with small spine (e.g. *Reedops pembertoni,*

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Pl. 4.11); (2) rounded angular, with distinct node at corner (e.g. *Boeckops stelcki*, Pl. 16.3); (3) rounded, with or without hint of node (e.g. New Genus B *forteyi*, Pl. 25.9)

14. *Palpebral sculpture* [19 modified] – presence of pitting on palpebral lobe and palpebral area (which shows some correspondence to pitting in genal field), and other sculpture elements present.

Remarks: RAMSKÖLD AND WERDELIN (1991) observed the sculpture on the palpebral area only, but the specimens in this study showed fairly uniform sculpture across the palpebral lobe as well (as long as the broad depressions adjacent to the palpebral rim were not mistaken for pits). In addition, the correlation between pronounced pitting in the genal field and that in the palpebral region (noted by these authors) was seen here, and used as an additional indicator for this character in cases of doubt.

States: (0) even surface; (1) pitted surface; (2) perforated appearance, with deep, wide pits; (3) smooth between tubercles

15. *Terrace lines* – presence of terrace lines or generally elongate sculpture (either fragmentary or continuous) on various regions of dorsal surfaces of cephalon.

Remarks: The presence and extent of terrace lines or their fragments, upon the dorsal or laterally facing regions of the cephalon is often mentioned in species descriptions, but seldom used as a diagnostic character. STRUVE (1982) used the presence of elongate sculpture across the cheek as an indicator of 'marginulation' being incomplete (see below), but there is more to the distribution of elongate sculpture than this. Some species show strong terrace lines or keeled tubercles across the anterior face of their glabella, and some entire groups, like the genus *Reedops*, seem to have relatively equidimensional granules along their ventral margins, instead of the slightly elongate ones seen in most other taxa at this level of analysis.

States: (0) absent or nearly so; (1) on ventral margin only; (2) on glabella, cheek, and ventral margin

16. *Definition of lateral axial lobes* [21 modified] – definition of lateral axial lobes of occipital ring (as delimited by furrow arising from apodemal pit directly ahead of

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it), and definition of lateral axial lobes in thoracic segments, (which seem to be controlled by same factors).

Remarks: CAMPBELL (1977) used lateral 'notching' of the axial rings as a thoracic characteristic in his discussion of phacopid classification, and other authors have made note of it in their descriptions. Here it is combined with the impact apodemes have on the occipital ring – previously character [21] – since this is essentially a metameric repetition caused by similar apodemal impingements.

States: (0) lobes are strongly defined, furrow runs halfway across occipital ring; (1) lobes are weak to distinctly inflated, moderately defined; (2) distinct lobes are absent or effaced, poorly defined

17. *Sclera in eyes* [23 modified] – nature of interlensar sclera within visual surface of eye.

Remarks: Distinctive scleral surfaces have often been overlooked in the classification of phacopids, because workers such as ELDREDGE have portrayed them as something that can vary intraspecifically. RAMSKÖLD AND WERDELIN (1991) used the varying degrees of thickness seen in the interlensar sclera as a character in their analysis, and this study simply takes this a step further, using the various forms of sculpture seen in the sclera of Devonian phacopids as well.

States: (0) thin sclera throughout; (1) sclera slightly thickened, dorsally only; (2) sclera considerably thickened dorsally, only weakly ventrally; (3) entire sclera surface thickened; (4) tubercles on thickened sclera, lenses in cruciform arrangement; (5) tubercles on thickened sclera, lenses in hexagonal arrangement

18. *Vincular furrow* [24 modified] – course and depth of medial part of vincular furrow.

Remarks: Whether or not the vincular furrow is continuous medially has been one of the most consistently used characteristics for classifying phacopids (MOORE, 1959). Unfortunately, it has also been one of the most problematic. The type species of *Reedops* shows a fairly well impressed vincular furrow throughout its course, while the lack thereof is supposed to be the main defining characteristic for the genus. It has

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been included here without some of the inapplicable character states used in previous work, and with slight modifications to match better the specimens in this study.

States: (0) wide, shallow furrow; (1) deep, distinct furrow; (2) completely absent medially, or only shown through ornament

19. *Width of pygidial axis* [26 modified] – width (tr.) of pygidial axis across its first axial ring, expressed as percentage of total pygidial width (tr.) excluding articulating facets.

Remarks: The only modification made to this character was to enlarge the ranges encompassed by the character states, because most sets of specimens had a range of variation well outside 2-3% originally allowed, and categories this narrow could easily fall within the range of measurement error.

States: (0) 25-29.9%; (1) 30-34.9%; (2) 35-39.9%

20. *Closure of pygidial axis* – degree of closure of axial furrows behind terminus of pygidial axis, and attendant postaxial ridge this sometimes creates.

Remarks: CHLUPÁČ (1977) mentioned this character in many of his species descriptions, but was uncertain as to whether it was of use in classification, because he had lingering doubts as to whether or not it was a product of sexual dimorphism. This feature has been noted in many taxa, and is fairly easy to see in both specimens and photographs (with occasional lighting complications in the latter). In the species encompassed here, it seems to be a rather stable characteristic within each species, so it has been included.

States: (0) nearly complete closure, leaving mild postaxial ridge (e.g. New Genus B *forteyi*, Pl. 24.8); (1) minor closure, often leaving strong postaxial ridge (e.g. New Genus A *kermiti*, Pl. 12.3)

21. *Interannular rings* [27 modified] – presence or absence of interannular rings behind anteriormost axial rings of pygidium, and their general appearance.

Remarks: Interannular rings are common in the apodemal sector of the tail (*sensu* LUDVIGSEN AND CHATTERTON, 1982) for most phacopids. These rings may vary

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slightly in their expression from specimen to specimen, but on the whole, are fall into one of the states proposed by RAMSKÖLD AND WERDELIN (1991) at the species level and beyond. In this study, those specimens with pronounced interannular rings often had strong ring furrows, which left well-impressed depressions within the axial furrow (distally) as well.

States: (0) widened furrow or hint of ring (e.g. *Phacops forteyi*, Pl. 23.6); (1) distinct ring present (e.g. *Phacops kermiti*, Pl. 12.3); (2) strong ring, near level with axial ring in front, and ornamented (e.g. *Calyptaulax glabella*, see LUDVIGSEN AND CHATTERTON, 1982, Pl. 4)

22. *Number of axial rings* – generalized number of axial rings in pygidial axis, roughly corresponding to use of 'richly' or 'poorly' segmented as axis descriptors.

Remarks: Most descriptions of phacopids include a range for the number of axial rings borne by the pygidial axis, but most diagnoses for larger groupings rely on vague terms like 'richly' or 'poorly' segmented (CHLUPÁČ, 1977). Here there was an attempt to make use of this generalized statement (and avoid the "numbers trap" that worried RAMSKÖLD AND WERDELIN in their 1991 work). Ranges were charted for each taxon, and a natural gap in the number of segments was taken advantage of here. Future studies may choose to add more character states at the extreme ends of the spectrum, but this was not attempted here.

States: (0) 7-11 well defined rings, relatively numerous; (1) 4-6 well defined rings, relatively few

23. *Number of clear pleural ribs* – generalized number of clear pleural ribs in pygidium, based on independent inflation, and roughly corresponding to use of 'richly' or 'poorly' segmented pleural field descriptions.

Remarks: Character states were constructed as they were for the preceding character, and with the same reasoning. With this character, there is also the additional problem of defining what a 'clear' rib was. In this context, a clearly defined rib was judged to be one that displayed independent convexity, and was typically bound by a set of observable pleural furrows. Sometimes lateral views were used to help in this

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assessment with hand-specimens, meaning that specimens coded from pictures could potentially have more pleural ribs than indicated here. (The descriptive work of others was taken into account, as well as their figures, and the author feels that he was conservative in the number of ribs coded for in each taxon.)

States: (0) 2-5 clear pleural ribs, comparatively few; (1) 6-10 clear pleural ribs, comparatively many

24. *Depth of pleural furrows* [31] – depth and profile shape of pleural furrows in pygidium.

Remarks: This character remains unchanged from the work of RAMSKÖLD AND WERDELIN (1991). It should be noted that this character also speaks to the nature of the ribbing on the tail (its profile in cross-section), and gives some indication of how far the furrows travel distally before fading into the pleural field.

States: (0) weak, thin pleural furrows (e.g. *Reedops pembertoni*, Pl. 4.6); (1) deep, thin pleural furrows (e.g. *Phacops kermiti*, Pl. 12.3); (2) deep, steep-sided to medium-wide pleural furrows (e.g. *Phacops ovatus*, Pl. 21.9); (3) deep, wide pleural furrows, usually with circular profiles (e.g. *Phacops araw*, Pl. 26.10)

25. *Number of vertical rows in eye* – typical number of vertical rows of lenses within visual surface of relatively large holaspid, excluding specimens showing teratological or atypical features.

Remarks: Aside from injured or atypical specimens, those encompassed in this study have shown remarkable intraspecific consistency in the number of vertical rows within their eyes. This feature has been used as a diagnostic character in most phacopid studies, but is usually restricted to species-level diagnoses. In an attempt to circumvent the 'numbers trap' that kept RAMSKÖLD AND WERDELIN (1991) from using this character, the character states have been kept narrow, so that they are not taken as large-scale synapomorphies in this study. Instead, they are meant to unite

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taxa just above the species level, in a study that spans a huge array of disparate morphologies.[1]

States: (0) 14-16; (1) 17; (2) 18; (3) 19; (4) 21; (5) 25

26. *Maximum number of lenses per vertical row* – typical maximum number of lenses found within single vertical row of visual surface of fairly large holaspid free from teratological or otherwise atypical features.

Remarks: In most cases (without scleral spacers or reduced lens sizes), this character reflects the height of the visual surface. Aside from potential cases of sexual dimorphism, this character appears to be relatively stable at the species level, with the potential to act as a synapomorphy for small species groups. With the sheer variety of scleral types and eye sizes in this study, this character is almost guaranteed to show a lot of homoplasy, but it is worth using for its finer resolution. It may be worthwhile to amalgamate the many states into a binary character for future work.

States: (0) 4; (1) 5; (2) 6; (3) 7; (4) 8: (5) 9

27. *Subocular pad* – presence and relative inflation of raised pad beneath eye and dorsal to genal field.

Remarks: CAMPBELL (1977) and MAKSIMOVA (1972), as well as STRUVe (1982) and HAAS (1968) have all commented on the presence or absence of a convex pad beneath the eye, or a largely concave region existing there. In most cases, this feature has been used in the description of species, but MAKSIMOVA and CAMPBELL disputed whether or not it could be used as a diagnostic characteristic at the genus level, distinguishing between *Paciphacops* and *Phacops*. Here, it appears to be more of a matter of whether or not the lower margin of the eye has extended ventrally to crowd this feature out; whether the visual surface is raised away from that of the cheek, leaving a sort of column with a weak pad below the eye; or if the eye is in an intermediate

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[1] Removal of this character only seems to affect the position of *Boeckops boecki* in the resulting cladogram – with no other change in topology – which seems a bit odd, as this taxon is autapomorphic for state (4), and the characters are not ordered in the analysis (see Results for further discussion).

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position, with some room for independent inflation below it. In all cases, sculpture emphasizes the pad itself, and in many cases is limited to the surface of the pad.
States: (0) pad absent (e.g. New Genus A *kermiti*, Pl. 13.7); (1) pad weak (e.g. *Phacops araw*, Pl. 26.6); (2) pad strong (e.g. New Genus B *forteyi*, Pl. 23.5)

28. *Pygidial axis length* [29 modified]– length (sag.) of pygidial axis from base of first axial ring to tip of its terminal piece, expressed as percent of total pygidial length (sag.), from base of first axial ring to pygidial margin.

Remarks: Instead of measuring the length of the first 5 axial rings, this character attempts to indicate how long the axis is by showing how close to the pygidial margin it extends. Natural breaks in the measured ranges for each taxon have again been used for this character, and the two extreme states are those that are obvious to even the most casual observer.
States: (0) short, <84%; (1) long, >84%; (2) exceptionally short, <78%; (3) exceptionally long, >89%

29. *Thorax shape* – backwards taper of thorax, measured by observing total width (tr.) of first and last thoracic segments, and expressed as percentage of first that last segment comprises.

Remarks: Again, plotting ranges and taking advantage of a gap in distribution allowed this character to quantify something that has been observed in many works. This feature has not really been used in phacopid classification, but it is used in the classification of other groups of trilobites. Effort was made to take this measurement from enrolled specimens, where distortion of the thoracic segments becomes fairly obvious and can be avoided.
States: (0) strong taper, last segment <80% of first segment's total width; (1) weak taper, last segment >80% of first segment's total width

30. *Degree of glabellar overhang* – a qualitative judgement of how much glabella overhangs anterior border furrow and adjacent anterior border, usually taking into account position of vincular furrow as well.

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Remarks: This has been one of the two key features used in just about every diagnosis for *Reedops*, and like the vincular furrow, it has created some minor problems. The degree of glabellar overhang seen in some *Phacops* species approaches that of the type species of *Reedops*, but one must also take into account the position of the vincular furrow. In most specimens with high glabellar overhang, this is well back of the anterior tip, when the cephalon is positioned with the palpebral lobes horizontal. Roughly speaking, this measure also corresponds with whether or not the glabella appears long, relative to the rest of the cephalon.

States: (0) no overhang; (1) frontal face of glabella vertical or with mild overhang; (2) high degree of overhang

31. *Degree of glabellar divergence* – angle of divergence found between two axial furrows, as they spread anteriorly around sides of glabella, in front of S1.

Remarks: This is yet another character that has been used in most species descriptions but never really extended to a role in classification. Extremely broad categories are used for each character state, because this character is most easily measured from a photograph. As such, the angle of the cephalon plays a major role in the final measurement, so care must be taken that the palpebral lobes are horizontal when measuring this angle.

States: (0) low, <60°; (1) moderate, 60-70°; (2) high, >70°

32. *'Marginulation'* – presence of raised (laterally) bead along ventral margin of cephalon, to position behind that of eye and usually extending to genal angle, without disappearing into gena or disintegrating into component sculpture elements.

Remarks: "Marginulation" was a diagnostic feature used by FLICK AND STRUVE for their tribe Geesopini, which was meant to encompass most of the old world phacopid genera (1984). This may be identical to [17] of RAMSKÖLD AND WERDELIN (1991), but they made no mention of duration of their "ridge" behind the eye, which was fundamental to its use by STRUVE (1984). CAMPBELL (1977) also made mention of "ropy" ornament along the cephalic margin of some North American taxa, but

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judging from the figures he cited, his useage was far from that of STRUVE. On the whole, this feature has never really been evaluated from a phylogenetic standpoint.

States: (0) rim incomplete or absent; (1) rim complete, reaching almost or fully to genal angle

33. *Posterior border spines or tubercle row* – presence of locally prominent concentration of coarse tubercles or spines along posterolateral margin of posterior border.

Remarks: This character seems to be a synapomorphy shared by many of the taxa STRUVE allocated to his tribe Geesopini. In many instances where cephalic ornament is reduced or pustular, there still appears to be a distinct row of tubercles in this position.

States: (0) absent; (1) present

34. *S1 medial continuity* – whether or not medial portion of S1 furrow is continuous and easily traceable between intercalating ring and back of more anterior portions of glabella.

Remarks: This character tries to encompass the trend within the Phacopidae, in which the intercalating ring merges into the back of the frontal part of the glabella. This is something termed "basisolution" of the glabella by R. AND E. RICHTER (1939), and has since been observed by most phacopid workers. It has was to separate the genera *Paciphacops* and *Viaphacops* (MAKSIMOVA, 1972; CAMPBELL, 1977), but has been applied to very few broad classification schemes.

States: (0) discontinuous or effaced furrow; (1) continuous furrow

35. *Doublure sculpture* – nature of sculpture elements upon doublure, especially its medial portion beneath glabella.

Remarks: CHLUPÁČ (1977) was the first to use this character as a diagnostic feature for the genus *Reedops*, after the importance of a complete vincular furrow had been questioned. Researchers such as ELDREDGE and CAMPBELL have mentioned an intermediate condition (1), but never really used it in classification schemes.

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States: (0) relatively equidimensional granules dominant; (1) short, broken terrace lines, or granules severely elongated transversely; (2) fully developed, largely continuous terrace lines dominant

36. *Base of visual surface with tubercles* – presence or absence of row of coarse tubercles along ventral margin of visual surface, often these have become broad and rounded in nature.

Remarks: Occasionally termed a 'socle' (a feature found in other groups of trilobites, to which this is unlikely to be homologous), there exists a row of tubercles along the base of the visual surface within many phacopid taxa. This feature is particularly common and prominent in the Turkish species described by HAAS (1968) and Rheno-Bohemian species described by CHLUPÁČ (1977), and takes on a much more subdued (almost pustular) appearance in the Middle Devonian species in the works of ELDREDGE and STRUVE.

States: (0) absence of strong tubercles; (1) presence of strong tubercles

37. *Sculpture on pygidium* – nature and extent of tuberculation upon various regions of pygidium.

Remarks: Many works comment upon the presence of tubercles on the pygidium, but comparatively few look at their distribution. Here, tuberculation is characterized by its extent and prominence across the three major regions of the pygidium, which to some degree also corresponds with the extent and prominence of ornament on the thoracic segments.

States: (0) tubercles absent; (1) tubercles restricted to axis only; (2) tubercles faintly present on pleural ribs; (3) tubercles moderately to strongly present on pleural ribs, and also upon marginal field

38. *Accessory lens row* – presence of single additional horizontal row of lenses, beginning near middle of visual surface and continuing posteriorly – which is usually composed of diminutive lenses – as opposed to consistently level top row proceeding from anterior corner of eye.

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Remarks: CLARKSON (in KAESLER, 1997, p.122) termed this feature the "accessory lens row". It appears consistently in species placed within the genus *Acernaspis* (CHATTERTON AND LUDVIGSEN, 2004), and can also be found within members of *Paciphacops* and *Viaphacops* (CAMPBELL, 1977).

States: (0) accessory lens row absent; (1) accessory lens row present

39. *Interpleural furrow strength* [32 modified]– depth of impression found in interpleural furrows of pygidium.

Remarks: Almost all phacopids have exceedingly weak interpleural furrows within their pygidial pleural fields, but some groups of taxa show an interpleural furrow set that is every bit as well developed as that found in outgroup taxa. Here, this also seems to correspond with a high number of congruent segments ([30] mentioned below), which combined to give the pygidium a 'rainbow-like' banding pattern in dorsal view. This character did not display the range of states used by RAMSKÖLD AND WERDELIN (1991), so it has been reduced to a binary character for the present analysis.

States: (0) weak to completely absent; (1) moderately impressed

Characters not included:

Of the 32 characters used in the analysis of RAMSKÖLD AND WERDELIN (1991), only 4 had no apparent bearing on this level of the cladistic analysis. These characters included those that were uninformative at this level of cladistic analysis, including: the relative *length of occipital ring* [2]; the presence or absence of observable *auxiliary muscle impressions* [18]; the presence and prominence of an *occipital median node* [9]; and the presence and prominence of *raised rims along S2 and S3* [10].

Other RAMSKÖLD AND WERDELIN (1991) characters were not used because there were no observable differences between the two character states pertinent to this portion of the phylogeny when photographs were used, or the states depended largely on photograph conditions, like angles or lighting. Problems arose with the difference between character states (2) "distinct" and (3) "very strong, near separate pits", for the lateral *vincular notches* [25]; the difference between varying degrees of furrow continuity

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between lateral apodemal pits in the posterior regions of the pygidial axis (*interring furrows posteriorly* [28]); and the *number of congruent segments* [30] (where the pleural ribs are offset behind their axial ring by less than half their width). Lastly, some characters that appeared to inadvertently add weight to others were avoided, such as the presence and degree of *posterior incisions* [22] along thoracic axial rings (separating medial and lateral lobes), which effectively doubles the weight of the already observed anterior incisions, and is treated by most workers simply as the degree of lateral lobe separation.

HAAS (1998) suggested that the knobs on the distal tips of thoracic segments (for interlocking with the notches in the vincular furrow) were of characteristic shapes in certain lineages and would make excellent characters for cladistic work on Devonian phacopids. Unfortunately, these features are hard to observe, the shape categories created in that study are not distinct, and often multiple character states can be seen within a single individual's thoracic segments (see *Phacops araw* n. sp., Pl. 26.3, and note anterior/posterior variability). This character will not be considered here.

The shape of the hypostomal suture line of the doublure (whether it is straight or concave) has been suggested as a diagnostic character for some phacopids (e.g. ELDREDGE, 1973). Unfortunately, the author's observations agree with those of CAMPBELL (1977), in that this character is not useful, as doublure curvature is both inconsistent and rarely observable.

Finally, characteristics such as subocular distance (between the base of the eye and the cephalic margin), and the position of the lowest point on the genae or highest point on the glabella have been avoided, because they vary hugely based on specimen orientation or distortion, and are based on landmarks that also vary from species to species.

Taxonomic considerations:

Paciphacops logani (HALL, 1861) was coded for only the "large-eyed form" included in the comprehensive study of ELDREDGE (1973). This appears to be the form found in the lectotype of that taxon (NYSM 13885/2; fig. 1H of ELDREDGE, 1973), and is used here because the author is taking a conservative (negative) position with regards to

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dimorphic trilobite taxa. Although this taxon and other taxa covered by ELDREDGE (1973), are widely used as examples of different morphs, the dimorphism has been disputed, and the author does not have enough information available to assess whether the specimens involved are conspecific or not.

Methods/Results:

A cladistic analysis was carried out using PAUP version 4.0b10 (Altivec) (SWOFFORD, 2002) and the results were observed using MacClade 4.06 (D.R. MADDISON AND W.P. MADDISON, 2003). Unlike the analysis of RAMSKÖLD AND WERDELIN (1991), this analysis did not use any ordering of character states. All characters were equally weighted. A heuristic parsimony analysis yielded a single tree with a total length of 235, C.I. of 0.404, R.I. of 0.602, and R.C. of 0.243 (see Fig. 1 for preferred general phylogenetic hypothesis; see Fig. 2 for cladogram indicating character changes). Bremer support values were calculated, and have been indicated next to the relevant clades on the diagram, values greater than 1 occurred on only 4 clades.

Because of the large number of taxa involved, it was not possible to conduct branch-and-bound or exhaustive analyses of the entire data set, so it was broken into two subsets (based on the first analysis), and subjected to exhaustive analyses under the same general conditions. In these analyses, terminal taxa that had consistently placed within a single clade[2] (usually subgenera of the same genus in the old grade-based classification) were merged (effectively treated as genera) to reduce the number of taxa further. In both of these analyses, the clade containing *Paciphacops logani* was treated as the upper or lower limit for inclusion, and any characters that were uninformative at that level of analysis were excluded. Both the 'upper' (*Paciphacops* and its sister group) and 'lower' (the basal clade that includes all *Reedops* species, and a fragment of its sister group, up to *Paciphacops*) analyses resulted in slightly different topologies from those found in the large-scale heuristic analysis.

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[2] Here, consistent placement refers to a sister group relationship that was seldom, if ever, broken by the experimental omission of taxa and characters that was employed to observe their impact.

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The 'upper' group displayed two different topologies in the exhaustive analysis, in which the position of *Eldredgeops rana rana* was the only thing that varied. One topology matched that of the large-scale analysis, while the other placed *E. rana rana* as the sister group to (*Phacops araw* + *Phacops latifrons*). Tree scores for this analysis of the 'upper' group included a tree length of 81, C.I. of 0.654, R.I. of 0.622, and a R.C. of 0.407, with 9 characters excluded because of their uninformative nature.

The 'lower' group displayed a single most parsimonious tree upon exhaustive analysis, but its topology was significantly different from that seen in the large-scale analysis (see Fig. 3). In this instance, the clades themselves were almost identical, but long-branch attraction inverted the nesting order (sister group relationships) because of the sheer number of apomorphies in the *Reedops* group. Other than this general inversion, the only changes to the clades themselves (from those seen in the larger analysis) were the unification of *Boeckops boecki* and *Boeckops stelcki* as sister taxa, and a transfer of *Chotecops auspex* from the sister group of the large (mainly *Phacops* and its derivatives) clade, to the sister group of all of the *Reedops* species. The tree scores for this exhaustive analysis consisted of a tree length of 112, C.I. of 0.580, R.I. of 0.552, and a R.C. of 0.321, with 6 characters excluded because of their uninformative nature at this level of analysis.

Discussion/Conclusion:

Although the large-scale analysis of these taxa resulted in a single most parsimonious tree, it is by no means a strict hypothesis of phylogeny. The consistency indices and Bremer support for most of the large-scale cladogram are fairly weak. This can be viewed as a situation in which slightly different choices in characters or even character codings for a single taxon could cause the topology of the cladogram to change[3]. Analysis on a finer scale also shows the inconsistent placement of some taxa, and suggests that their positioning is questionable at best.

The tentative nature of this study's results suggests that only an extremely conservative cladistic remodeling of Devonian phacopid systematics should be possible

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[3] This has been experimented with, and the problem of clades collapsing into polytomies or the generation of numerous trees with a low-resolution consensus is very real.

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based on this study's phylogenetic hypothesis. Future work is almost guaranteed to alter this hypothesis significantly, so a full classification of the ingroup taxa is completed with some hesitancy, and with the aim of retaining widely accepted and used phacopid taxa, while doing away with obviously polyphyletic or paraphyletic taxa.

The best approximation of stable groupings in this study is taken from clades with Bremer support numbers greater than 1. These groupings are few and dictate that the tuberculate Moroccan species (New Genus B *lebesus*, New Genus B *granulops,* New Genus B *ovatus*, and New Genus B *forteyi*) are more closely related to one another than to members of any other genus, and are probably distinct at the generic level. Here this group of species will simply be referred to informally as New Genus B, because the inclusion of additional taxa in future studies may obscure this clade. A similar, but less supported New Genus A can be seen among the relatively un-sculpted Moroccan species (New Genus A *smoothops,* New Genus A *punctatus,* New Genus A *kermiti*, and New Genus A *salamandar*). Again, this is treated as an informal group here, to avoid creating spurious genera, but it should be noted that they can not be considered species of *Phacops,* if *Phacops* is to remain monophyletic. If these informal groups are accepted as potential (future) genera, there is very little necessary in the way of restructuring to accommodate a sequenced classification for the phacopids used in this study. (A full sequenced classification for the ingroup taxa has been provided below, in Table 2.)

Subfamily Phacopinae HAWLE AND CORDA, 1847
    Genus *Reedops* RICHTER AND RICHTER, 1925
        Reedops bronni (BARRANDE, 1846)
        Reedops pembertoni n. sp.
        Reedops cephalotes hamlagdadianus ALBERTI, 1983
    ? Genus *Chotecops* CHLUPÁC, 1971
        Chotecops auspex CHLUPÁC, 1971
    New Genus A
        New Genus A *smoothops* (CHATTERTON *et al.*, 2006)
        New Genus A *punctatus* n. sp.
        New Genus A *kermiti* n. sp.
        New Genus A *salamandar* n. sp.
    Genus *Boeckops* CHLUPÁC, 1972
        Boeckops boecki (HAWLE AND CORDA, 1847)
        Boeckops stelcki n. sp.
    Genus *Paciphacops* MAKSIMOVA, 1972
        Subgenus *(Viaphacops)* MAKSIMOVA, 1972
            Paciphacops (Viaphacops) cristatus (HALL, 1861)
        Subgenus *(Paciphacops)* MAKSIMOVA, 1972
            Paciphacops (Paciphacops) logani (HALL, 1861)

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New Genus B
    New Genus B *lebesus* (CHATTERTON *et al.*, 2006)
    New Genus B *granulops* (CHATTERTON *et al.*, 2006)
    New Genus B *ovatus* n. sp.
    New Genus B *forteyi* n. sp
?Genus *Eldredgeops* STRUVE, 1990
    Eldredgeops rana rana (GREEN, 1832)
Genus *Phacops* EMMRICH, 1839
    Phacops latifrons (BRONN, 1825)
    Phacops araw n. sp.
Genus *Geesops* STRUVE, 1972
    Geesops schlotheimi (BRONN, 1825)
Genus *Pedinopariops* STRUVE, 1972
    Subgenus *(Pedinopariops)* STRUVE, 1982
        Pedinopariops (Pedinopariops) lentigifer STRUVE, 1970
    Subgenus *(Hypsipariops)* STRUVE, 1982
        Pedinopariops (Hypsipariops) vagabundus STRUVE, 1990
Genus *Drotops* STRUVE, 1990
    Drotops megalomanicus megalomanicus STRUVE, 1990
    Drotops armatus STRUVE, 1995

Table 2: Proposed (sequenced) classification for analyzed members of the family Phacopidae. No tribes are used at this time, as the branching structure of the cladogram does not unequivocally support their existence or monophyly.
? Denotes uncertain generic status.

At the generic level, this study does not support the separation of *Paciphacops* and *Viaphacops* (returning them to subgenera of *Paciphacops* instead), and brings into doubt the validity of *Eldredgeops* as a genus. The position of *Chotecops* relative to the *Reedops* clade and its sister group is somewhat dubious, as is the placement of *Boeckops stelcki* within the genus *Boeckops*. All of the genera recently raised from the rank of subgenera (e.g. *Boeckops*, *Geesops,* etc.) must remain at that rank or else the generic standing of *Drotops* and *Reedops* would be undermined, the subgenera of *Pedinopariops* would have to be abandoned, and *Viaphacops* would cease to exist at even the subgeneric level.

At higher taxonomic levels, the tribes Reedopini and Phacopini are not supported in this study or refuted (but may be real entities if the clade containing *Reedops* were to show significant internal dichotomy when more taxa are added). *Chotecops auspex* may belong to either of these groups, to its own tribe, or the tribe-level of classification may not be of value. On the other hand, the tribe Geesopini is not a monophyletic entity as it was defined by FLICK AND STRUVE (1984). Geesopini is a paraphyletic fragment of

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Phacopini, if the latter taxon should be recognized. Likewise, the tribe Ananaspini, used by HAAS (1998) as an informal taxon, is paraphyletic, and likely polyphyletic too.

Unique "cladistically informative characters" support few of the major clades (PATTERSON, 1988). The bulk of the clade synapomorphies undergo reversals higher within the clade or have homoplastic occurrences outside the clade. In the context of this study, most of the synapomorphies for genera take the form of autapomorphies on the cladogram, and cannot be validated as synapomorphies for the genera themselves until more taxa are included. Any potential synapomorphies for the groups discussed in the Systematic Palaeontology section of this work are further discussed there.

Upon completing this analysis, one question remains: "Why is there no strong phylogenetic signal seen in the data, even though the set incorporates so many characters that were used as diagnostic group features in previous studies?" This is actually something that has been discussed to some extent by CAMPBELL (1975, 1977), and is the main reason he and some other workers argued against the use of cladistics in the classification of phacopid trilobites. He felt that besides obvious offshoots in morphology, the bulk of the phacopids make up "a main 'trunk' of the phylogenetic tree within which one could recognize a number of evolutionary trends, . . . but within which the skein of transformation was so entangled that it was not possible to recognize the separate strands" (1975, p.95). CAMPBELL (1975) also noted that there is great difficulty in recognizing which are truly apomorphic characters and choosing between the relationships that these (often competing) observations support, and that there is no way to assess all potential close relatives to a taxon at one time (even though different taxa may significantly alter the resulting cladogram). Couched in cladistic terms, this basic problem boils down to rampant homoplasy in an enormous, partially represented taxa set, with relatively conservative overall morphology, and poorly understood biogeography.

To cope with this situation, the author suggests that the numerous, competing apomorphies "be allowed to speak for themselves" (MEACHAM, 1984, as quoted in ADRAIN, 1990), and the resulting phylogeny treated in a very conservative manner, as is done above. Future work should likely take the form of more detailed generic analyses, but care should be taken to include the analysis in a larger-scale setting too, so that clades that would otherwise be undermined by homoplasy (poorly supported ones) are not

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allowed to proliferate. The main reason there are so many subdivisions currently within the Phacopidae is that so much work has been permitted to occur in isolation or without rigorous support, and the old grade-based classification did little to stop this. This is something cladistic analyses could end.

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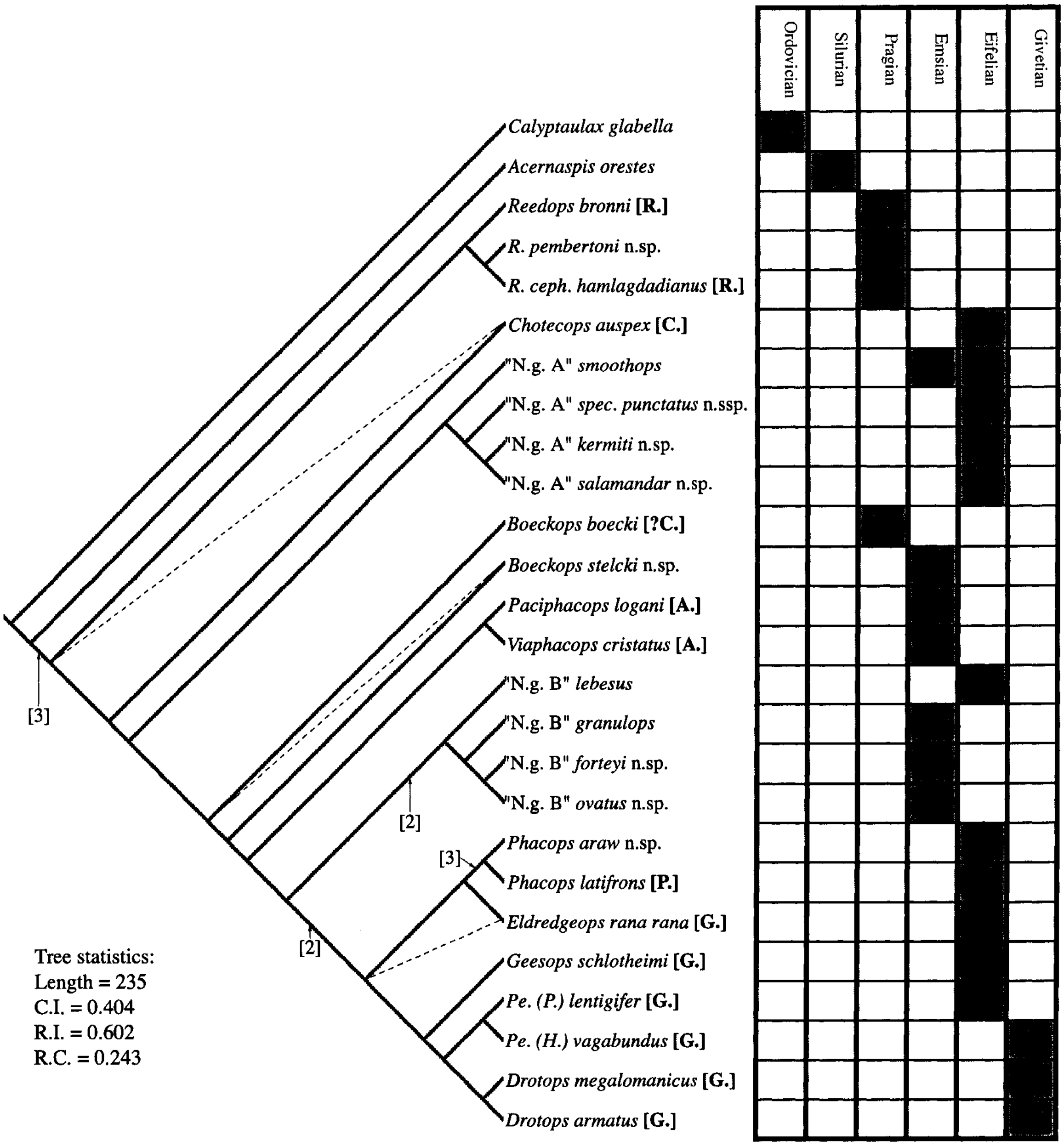

Fig. 1: Large-scale cladogram depicting favoured phylogenetic hypothesis for entire ingroup. Single tree produced by heuristic parsimony analysis of all taxa, using no character weighting or ordering.
[#] Denotes Bremer support number for clade, all unmarked clades have value of [1].
- - - Denotes proposed placement of certain taxa, based on results from smaller-scale exhaustive analyses. Polytomies are suggested in all cases of uncertainty, but *Boeckops stelcki* n. sp. should probably be placed as the sister taxon to *Boeckops boecki*.
Bold bracketed letters following taxa denote tribe membership of established species in current grade-based taxonomy: **[R]**=Reedopini; **[C.]**=Cordapeltini; **[A.]**=Ananaspini; **[P.]**=Phacopini; **[G.]**=Geesopini.

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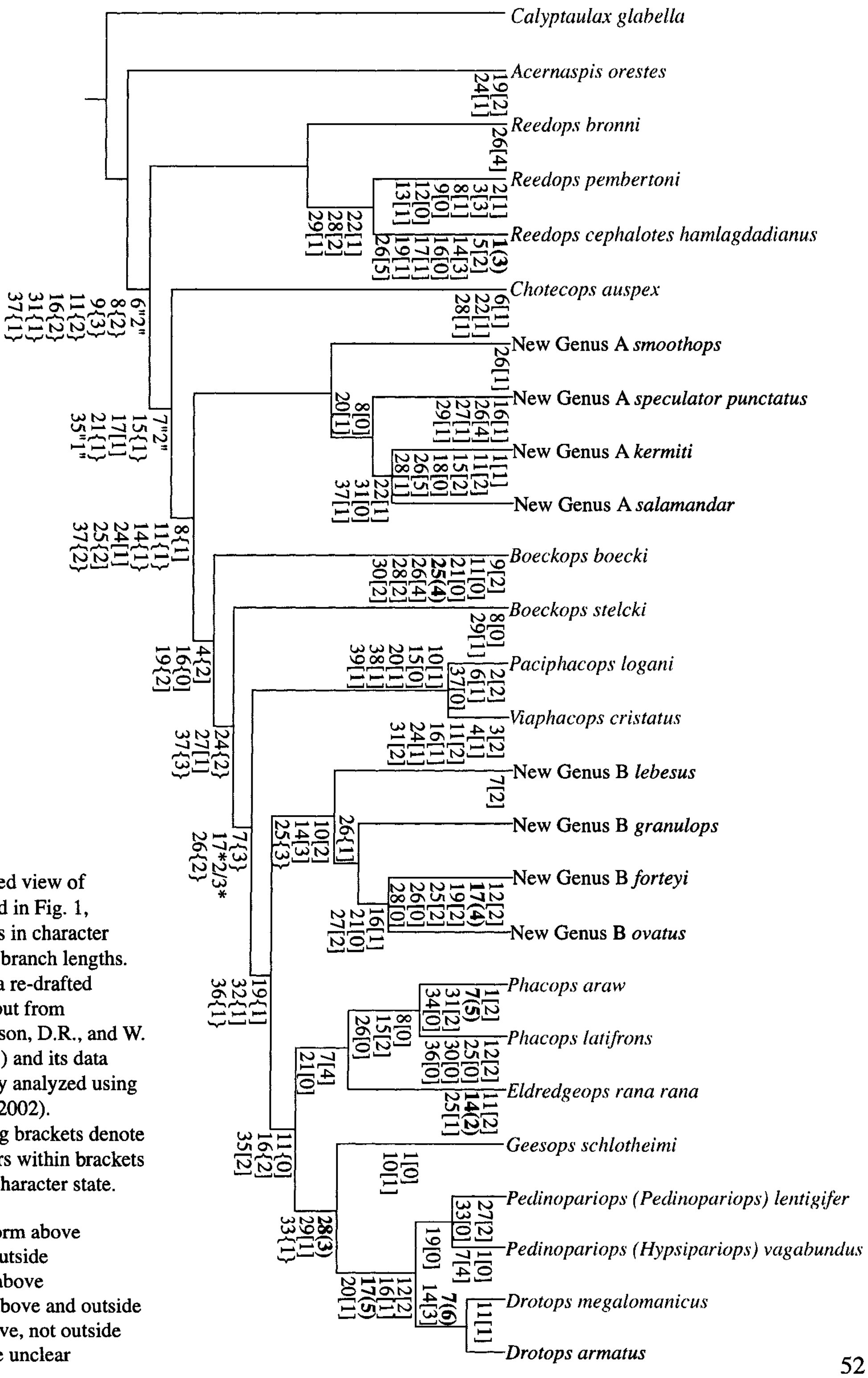

Figure 2: Expanded view of cladogram featured in Fig. 1, displaying changes in character states and relative branch lengths. The cladogram is a re-drafted version of the output from MacClade (Maddison, D.R., and W. P. Maddison, 2001) and its data matrix was initially analyzed using PAUP (Swofford, 2002). Numbers preceding brackets denote characters, numbers within brackets denote change in character state.

(#) = unique, uniform above
[#] = homoplasy outside
{#} = homoplasy above
{#] = homoplasy above and outside
"#" = changed above, not outside
= derived state unclear

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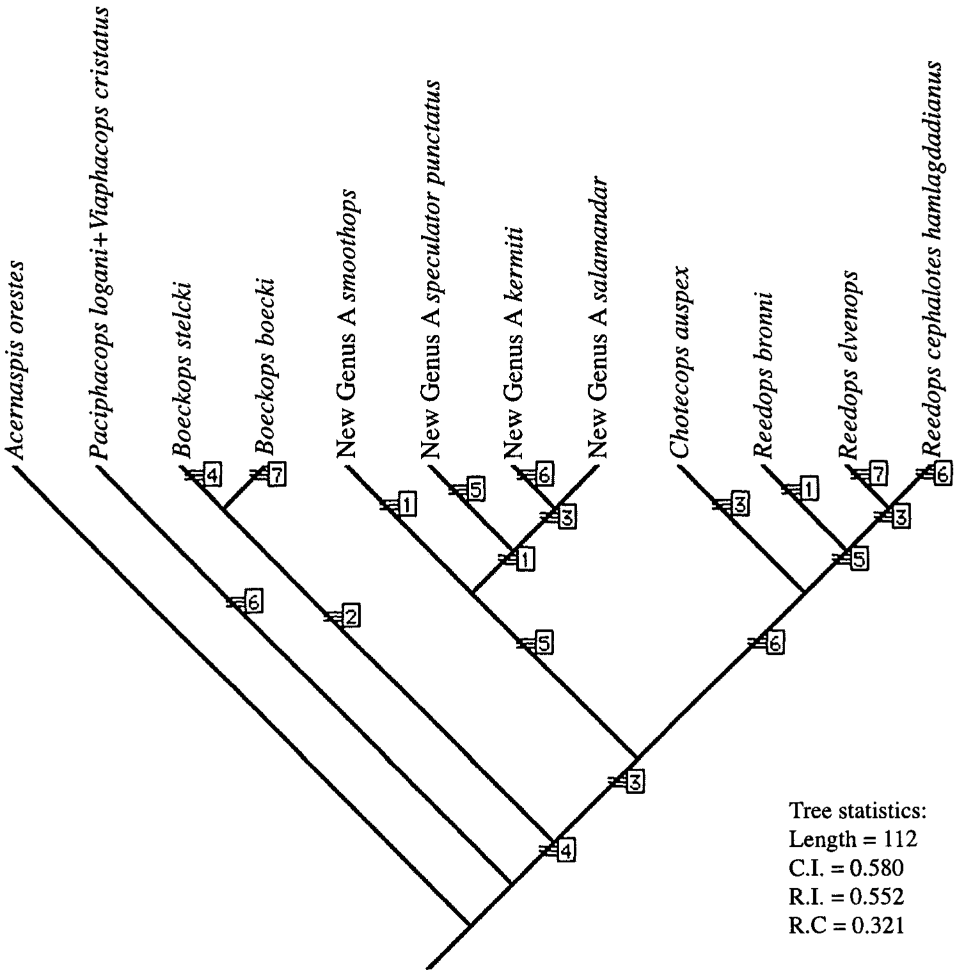

Tree statistics:
Length = 112
C.I. = 0.580
R.I. = 0.552
R.C = 0.321

Fig. 3: Small-scale cladogram of 'lower' half of ingroup taxa (topologically below *Paciphacops logani* + *Viaphacops cristatus*). Cladogram produced as a result of merging congeneric taxa (to reduce number of taxa analyzed), and performing exhaustive parsimony analysis with unweighted, unordered characters.
Boxed numbers denote branch lengths, note length of branches within sister group to '*kermiti* group'.

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CHAPTER 3: SYSTEMATIC PALAEONTOLOGY

'Tribe Reedopini' STRUVE, 1989

Discussion: The Reedopini are a monogeneric tribe as defined by STRUVE (although he hinted at 1-2 more genera within this tribe, he never actually specified which ones he felt belonged here). This taxon is a straightforward elevation of the concept originally backing the genus *Reedops*, but with the stipulation that the vincular furrow need not be completely absent in medial positions.

The cladistic analysis conducted in this study neither supports nor refutes the existence of a monophyletic taxon at this level in the hierarchy, because only three species of *Reedops* were observed. With this said, the taxon will neither be suppressed nor formally recognized here. This is a matter for future work.

Genus *Reedops* RICHTER AND RICHTER, 1925

Type species: *Phacops bronni* BARRANDE, 1846 from the Lower Devonian (Pragian) Dvorce-Prokop Limestones of Bohemia.

Discussion: The genus *Reedops* is problematic at best, from a systematic standpoint. There are very few features that conclusively unite and separate its members from those of similar (but more '*Phacops*-like') genera. The main feature used by WEDEKIND (1911) and R. AND E. RICHTER (1925) to diagnose this genus was the medial discontinuity of the vincular furrow. H. ALBERTI (1965) noted that the type species of this genus did in fact display a complete vincular furrow in a number of specimens, bringing into doubt the ability to diagnose members of this genus, and beginning a scramble to establish new diagnostic features (CHLUPÁČ, 1977).

CHLUPÁČ (1977) stated that he felt the medially weakened vincular furrow, with its lack of prominent inner and outer ridges, was still a reasonably diagnostic feature for the genus. His interpretation seems reasonable, especially when accompanied by other features that are not quite restricted to the genus or uniform within it; things such as the

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elongate glabella that generally overhangs the anterior border, reduced sculpture, effaced pygidium, and elongate body outline.

CAMPBELL (1967) established many other (somewhat) diagnostic features for *Reedops*, but the only ones that he saw repeatedly and consistently were related to a slightly different form of enrollment in this genus. CAMPBELL (1977) stated that *Reedops* species consistently enrolled with their pygidia extended anterior to their vincular furrows, so that the margin of the pygidium or some of the neighbouring thoracic segments crossed the anterior border, thus creating a distinctive (broad, sagittally, and slightly concave in section) pygidial doublure and flattened tips on the thoracic segments involved.

Unfortunately, the enrolled specimens of *Reedops cephalotes hamlagdadianus* and *Reedops pembertoni* in this study do not appear to conform to CAMPBELL's interpretation of enrollment patterns, and some specimens that he assigned to genera such as *Paciphacops*, as well as some clearly '*Phacops*-like' specimens from Morocco, show characteristics he attributes to *Reedops* only. The enrolled *Reedops* specimens from Morocco appear to have the margins of their pygidia tucked into whatever remains of their effaced vincular furrows (and if one traces out the arc prescribed by the deepened lateral ends of the vincular furrow, the pygidium must follow this course). As for the telltale flattened thoracic tips, they really do exist, but this is because the last few thoracic segments have their entire tips jammed into the vincular furrow (confirmed by the very elongate notches seen in the vincular furrow), as opposed to crossing the cephalic margin. This same flattening of thoracic tips can be seen in many phacopids besides *Reedops* species, including CAMPBELL's own figures of *Paciphacops* (1977, Pl. 11) or *Phacops kermiti* (Pl. 13.7). The widened and slightly concave pygidial doublure noted by CAMPBELL is also easily explained by the (variable) lower angle of incidence between the cephalon and pygidium in the enrollment of *Reedops* (the thorax is comparatively longer and narrower), and the lack of a protruding (ventrally) posterior rim to the vincular furrow, as is seen in most genera with a deep vincular furrow and more spherical enrollment. In the end, CAMPBELL's complicated suite of characters is almost identical to stating that the group has an effaced vincular furrow, something that CAMPBELL argues

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against as a diagnostic feature, because it is not seen consistently in *Reedops bronni* itself. This leaves us at a loss for unique diagnostic characters once more.

In the cladistic analysis, *Reedops* was united by a single synapomorphy, the possession of a marginulate cephalon (character 32, state 1), something that is also seen in some of the topologically distal phacopids from Morocco and the Rhenish-Bohemian faunal subprovince. This leaves us with the same basic problem of justifying this taxon at the generic rank. In the past it has been occasionally treated as a subgenus of *Phacops*, but the species included in this taxon are obviously and fundamentally different from the rest of the phacopids – to the extent that untrained observers can pick them out with ease. The problem is that this group is not defined by its own apomorphies, but by the lack of those that are found in the rest of the phacopids. *Reedops* species have such things as a doublure that still retains only equidimensional granules for sculpture, and interlensar sclera that is still recessed and thin relative to the lenses themselves. This is gradational thinking, but it must suffice to define the group for now.

Reedops bronni (BARRANDE, 1846)

Plate 1.1-1.11; Text Figure 1

Synonymy: See CHLUPÁČ (1977) for full synonymy list (it is lengthy but straightforward).

Localities, type and figured material: Lectotype NM IT 356, designated by CHLUPÁČ (in HORNÝ AND BASTL, 1970) – an enrolled individual figured by BARRANDE (1852). Alternative specimens have been recovered in the Barrandian area of Czechoslovakia, the Rhenisches Schiefergebirges and Kellerwald Mountains of Germany, and the Ghtira and Rechoua Limestones of north-western Morocco (CHLUPÁČ, 1977; G. ALBERTI, 1970). The new specimens from southern Morocco (figured here) conform to CHLUPÁČ's species distribution, and occur in the Pragian *Dicranurus* couche and adjacent *Kolihapeltis* couche, as they outcrop in the Ihandar Fm. of the Ma'der basin sections (at Jbel Issoumour and Jbel Oufatene, mainly) (BULTYNCK AND WALLISER, 2000; PLODOWSKI *et al.*, 1999). Plesiotypes UA6843-UA6846.

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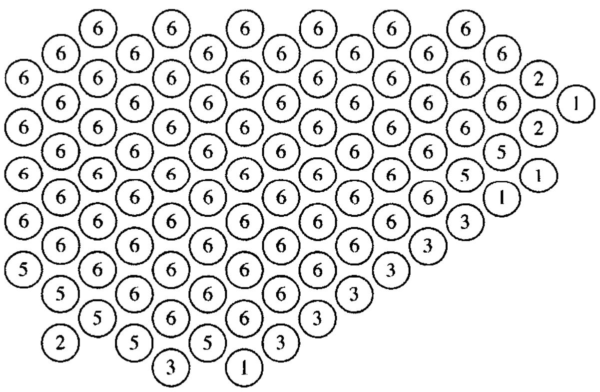
Diagnosis (emended from description of* CHLUPÁČ*, 1977): *Reedops* species with partially reduced eyes borne close to glabella and low on cephalon; eyes bearing 14-16 vertical rows of lenses with maximum of 7-8 lenses per row; postocular area almost equal to eye length (exsag.); intercalating ring broad (tr. and sag.) and vaulted, but merging with back of glabella medially, due to reduced S1 furrow set there; cephalic sculpture of very fine tubercles along anterior face of glabella that become sparse and subdued in posterior (dorsal) positions, and are accompanied by sparse small tubercles across palpebral area, postocular area, intercalating and occipital rings (although there is some variability in degree of sculpture in these areas); vincular furrow faint but distinguishable medially, and broken into set of interconnected facets laterally; only granules found on ventral surfaces, and doublure is long (sag.); glabellar overhang is moderate, preglabellar furrow narrow and deeply impressed; pygidium with 8-10 axial rings plus terminal piece, and 3 clear pleural ribs (followed by 3-4 indistinct ribs); axial skeleton bearing fine tubercles like those on occipital ring.

Description: See CHLUPÁČ (1977), and to a lesser extent G. ALBERTI (1970). CHLUPÁČ had sufficient material for both ontogenetic and basic morphometric observations on this species, fleshing out the cursory description previously given by G. ALBERTI, and making further description here pointless. One addition possible is the completion of a full visual surface diagram (see Text Fig. 1), since CHLUPÁČ described more comprehensive collections than ours, and specimens found here match his description in all regards.



Text Fig. 1: Lens formula diagram for *Reedops bronni* specimens

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Discussion: *Reedops bronni* is comparatively rare within the *Dicranurus* couche and *Kolihapeltis* couche, when compared to the other *Reedops* species, and is represented by approximately 10 individuals in our collections. In the four prepared specimens available at the time of this study, much of the variation seen by CHLUPÁČ (1977) is evident. In many specimens, the limited extent of the visual surface and the relatively large number of lenses has resulted in skewed or mixed vertical rows of lenses (particularly in the upper posterior reaches of the eye), and highly variable numbers of vertical rows and maximum lenses per row (14 to 16 vertical rows, with 7 to 8 maximum lenses per row).

One problem with the work of CHLUPÁČ is his use of the term "granules", especially within this taxon and other *Reedops* species. He described the anterior glabellar sculpture of this species (and many others) as being composed of granules, yet in his plates (1977; pl. 22-23) many of these elements are almost as large as eye lenses (and in some of our specimens larger than lenses). They are clearly different from the granules found within the vincular furrow and upon the doublure of this species, and are very different from the granules that form the sole sculpture on species such as *Acernaspis orestes* (BILLINGS, 1860) (see CHATTERTON AND LUDVIGSEN, 2004; Pl. 33 for detailed examination and a good frame of reference). The sculpture elements found here are best treated as small tubercles, although some might argue that the smallest elements are almost on par with granules seen in other body regions or taxa. If there is any doubt as to their status as tubercles – comparable sculpture found in *Reedops cephalotes hamlagdadianus* specimens from the El'Mdâouer locality in this study (and described in CHLUPÁČ's 1977 monograph coverage of this taxon as granules) show up clearly on the internal moulds of those specimens – something one should not expect of granules. The distinction between tubercles and granules is important because they are often used as cladistic character states for sculpture, and have been used in old phylogenetic studies as a trait defining 'primitive' (granulose) and 'derived' (tuberculate) phacopines.

CHLUPÁČ (1977) suggested that the overall morphology of *Reedops bronni* was most similar to two of G. ALBERTI's northwest Moroccan species, *Reedops maurulus* ALBERTI, 1970 and *R. platilegnotor* ALBERTI, 1970. I agree with this comparison, observing the same lengthened glabellar overhang, more subdued sculpture, and smaller intercalating rings, in the latter two species, and suggest that a slightly larger subocular

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area is found in *R. maurulus* in addition to its longer, lower eyes (1-2 fewer lenses per vertical file). *Reedops platilegnotor* is easily distinguished by its much greater subocular space, broader (tr.) cephalon, and posteroventrally elongate genae. Futhermore, species assigned to other genera/subgenera, like *Prokops,* are quite similar in overall morphology – if one can overlook the complete vincular furrow and a further reduction in the size of their eyes. *Prokops prokopi* CHLUPÁČ, 1971 and *Prokops hoeninghausi* (BARRANDE, 1846), as figured by CHLUPÁČ (1977), appear quite close in overall morphology and sculpture, but appear to differ mainly in terms of their eyes. This is of interest because *Prokops* is considered by most workers to be more closely associated with the *Phacops* lineage that that of *Reedops*, yet cursory observations would suggest that *Reedops bronni* (the type species of *Reedops*) shares more morphological features with some members of *Prokops* than it does with widely accepted *Reedops* species like *Reedops cephalotes.*

In the cladistic analysis, this species was the sister group to all other *Reedops* species. Future analyses may show this taxon to be more closely related to members of the *Reedops* or *Phacops*-based eye reduction series than to the large-eyed forms like *Reedops cephalotes hamlagdadianus* seen here.

Reedops cephalotes hamlagdadianus ALBERTI, 1983

Plate 2.1-2.12; Plate 3.1-3.12; Text Figure 2

Synonymy: See G. ALBERTI (1983) for most recent synonymy.

Localities, type and figured material: Holotype CGMTA, from "Hamar Laghdad III" of G. ALBERTI (1983), near Erfoud, SE Morocco. Topotype material is encountered in this study, and was treated by our research group as part of the Hamar Laghdad Bioherms. Strata are Pragian in age and part of crevasse-fills between the Hamar Laghdad Bioherms, producing quite restricted outcrop exposure, but unmistakable disarticulated concentration deposits in a sparry calcite matrix. At Hamar Laghdad these mounds are part of the Kess-Kess Fm. (BULTYNCK AND WALLISER, 2000). The El'Mdâouer locality, near the town of Foum Zguid, in the Tindouf Basin also bears this subspecies in its Pragian *Ceratonurus* couche, but here it occurs in a marl rich in iron oxides and

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containing a large clastic component. The *Ceratonurus* couche is within the Assa Fm. (BULTYNCK AND WALLISER, 2000). Topotypes UA6847-UA6859, plesiotypes UA6860-UA6861.

Remarks: G. ALBERTI (1983) provided only a differential diagnosis contrasting this subspecies with the very similar *Reedops cephalotes cephalotes* (HAWLE AND CORDA, 1847), and *Reedops cephalotes algericanus* ALBERTI, 1983, because CHLUPÁČ (1977) had so thoroughly described *Reedops cephalotes cephalotes*. Further comparison is not beneficial here, as the taxa involved are nearly identical, but corrections must be made to the work of G. ALBERTI, as the topotype material found here deviates from the description/diagnosis provided, and pygidia differing from those of *R. cephalotes cephalotes* have been recovered, warranting their description.

Differential diagnosis (emended from G. ALBERTI, 1983): *Reedops cephalotes* with: slightly broader, more rounded leading edge and top to glabella; slightly wider (exsag.) postocular pad, approximately 1/2 of eye's length (exsag.); slightly smaller (vertical) subocular distance; more flattened L1 lateral lobes; more pervasive sculpture of fine tubercles on cephalon; eyes bearing 25-27 vertical rows of lenses (usually 25), with 8-9 lenses per row (occasionally 10); pygidium with same 8-9 axial rings and 2-3 pleural ribs, but all features are more effaced, with less obvious interpleural furrows; pygidial sculpture restricted almost exclusively to middle of axis.

Description: Cephalon and hypostome are as described by CHLUPÁČ (1977), and G. ALBERTI (1983). New material only disagrees with their description of cephalic ornament as being granular. Sculpture consists of small, domed tubercles that vary greatly in expression from individual to individual, but are prominent enough to be consistently represented on internal moulds, especially along anterior face of glabella.

Thoracic segments were not recovered in significant quantities or degree of articulation from Hamar Laghdad, but complete specimens are found at El'Mdâouer section. Thoracic segments have broad axial rings (0.37 of total segment width in anteriormost segment, transversely) that are well defined, and have strong dorsal

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convexity and strongly defined lateral lobes. Medial lobe of axial ring is broad (sag.), and nearly flat-topped, with densely arranged fine tubercles across almost entire surface, but concentrated on posterodorsal extremes. Articulating half-ring separated from axial ring by deep ring furrow, but is almost level with ring (dorsally). Lateral axial lobes are bulbously inflated, and set off from medial lobe by deep anterior apodemal pit (that continues beyond exsaggital midpoint of ring), and fairly well incised depression stemming from axial socket depression on posterior edge of segment; sculpture is absent. Axial furrow is deep and round-bottomed, curving around lateral axial lobes (convex laterally), and spans each segment without fading significantly. Pleural furrow is deep and wide, with angular cross-section; fades medially and merges with axial furrow; distally narrowing and fading, but still breaching rim of articulating facet to leave faint trace across posterior half of facet (traces are more pronounced in anterior segments). Anterior and posterior pleural bands are of fairly equal widths (exsag.), with high dorsal convexity. Anterior band is almost cylindrical in section, while posterior is much more like flattened slope; faint patch of fine tubercles is present along anterolateral extreme of anterior band; posterior band has strand of fine tubercles along posterodorsal margin in its proximal regions, which become more prominent and pervasive on surface adjacent and distal to fulcrum, but disappear on vertical face distal to fulcrum. Distal posterior pleural band is almost flat and barren; distal tip has flattened ventral surface with many granules, and anterior segments may bear small knob on anteromedial corner. Articulating facet is slightly concave (laterally), and has raised rim along posterior margin (due to granulation); equidimensional granules are present across entire surface, but more densely packed and prominent near margins.

Pygidia are associated on basis of their size, gross morphology, and relative quantities at Hamar Laghdad (there is only one species of *Reedops* in these beds), and on basis of their occurrence in articulation at El'Mdâouer. Pygidia are proportionately small, and much wider (tr.) than long (sag.), producing almost elliptical outline. Axial region has moderate dorsal convexity, is wide (0.33 of total pygidial width at anterior ring), has strong posterior taper (approximately 30° convergence), and has rather effaced segmentation. 4-5 axial rings are clearly represented (but often require ideal lighting conditions to be seen), and are followed by up to 4 more faint rings shown mostly

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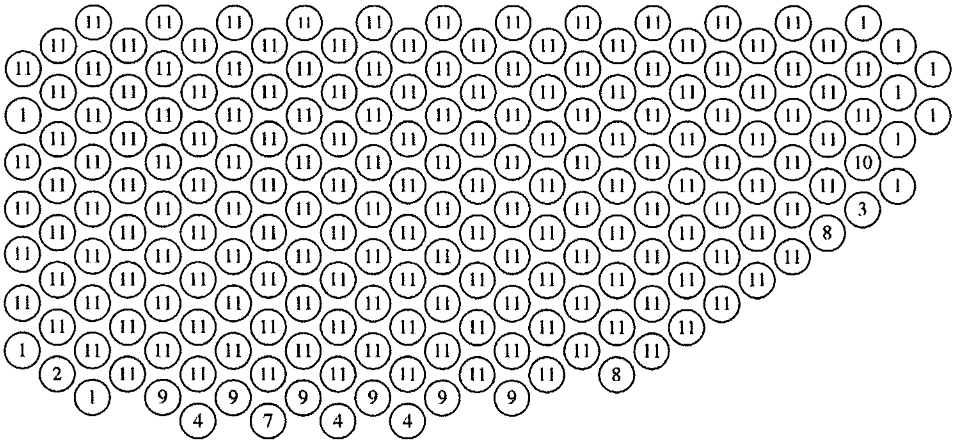
through sculpture patterns, plus terminal piece. Sculpture on rings is of very fine tubercles, and is restricted to medial half of each ring. Interannular rings follow anteriormost 3 axial rings; displaying independent convexity, and (because of effaced axis) are almost level with axial rings, creating "w-shaped" axial rings by notching posterior margins; their sculpture consists of fine tubercles. Axial furrows are broad (tr.), round-bottomed, and shallow; distal continuations of axial ring furrows behind anterior 4 axial rings add depth and slight curvature to axial furrow, which is otherwise straight, and fades posteriorly next to terminal piece; this leaves axis with incomplete closure and mild postaxial ridge. Pleural field has 2 definite ribs, followed posteriorly by 1-2 faint ribs; all ribs are defined by narrow (exsag.), shallow pleural furrows that fade half way to reaching margin, and become progressively more faint posteriorly. Interpleural furrows exist as mere hints upon two anterior ribs. Sculpture consists of exceedingly faint tubercles restricted almost exclusively to dorsal extremes of pleural ribs (medially). Ventral margin forms narrow (in section) lip around edge of pygidium, and bears fine granules.



Text Fig. 2: Lens formula diagram for *Reedops cephalotes hamlagdadianus* specimens

Discussion: The only areas of G. ALBERTI's diagnosis (1983) that did not really apply to the additional material seen in this study were his description of the ornament as being granulose, and his statement that 25 vertical rows of lenses were only seen occasionally (found to be the norm here). His comparisons to the other subspecies of *Reedops cephalotes* appear to be accurate.

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Reedops pembertoni n.sp.

Plate 4.1-4.12; Plate 5.1-5.8; Text Figure 3

Localities, type and figured material: Holotype UA 6862, from the *Dicranurus* couche (horizon), as it appears at Jbel Oufatene (DC), near Alnif, Morocco. Alternative localities include the *Dicranurus* couche, as it appears at nearby Jbel Issoumour, and within the directly overlying *Kolhiapeltis* couche at the same locality. Strata are Pragian in age and part of the Ihandar Formation in the Ma'der basin (BULTYNCK AND WALLISER, 2000). Paratypes UA6863-UA6875.

Etymology: This species is named in honour of DR. S. GEORGE PEMBERTON.

Diagnosis: Elongate (exsag.) genal angles with pointed posterior tip; flared (laterally) anterior portion of genal field projects laterally beyond eye (especially adjacent to axial furrow); moderate-sized eyes have 18 vertical rows of lenses, with 7 (occasionally 8) as maximum number of lenses in one file; cephalic sculpture of very fine, low tubercles concentrated along anterior face of glabella, but almost absent in posterior portions of cephalon; intercalating ring is weakly defined from back of glabella; fairly narrow (exsag.) postocular pad with indistinct distal tip; vincular furrow is incomplete medially and wide (exsag.) doublure bears relatively equi-dimensional granules which coalesce in lateral positions; pygidium is short (sag.) and effaced, with 7 axial rings (4-5 clear), and 2-3 faint pleural ribs.

Description: Cephalon is markedly smooth, forming "D-shaped" outline in dorsal view, with genae protruding posteriorly. In lateral view, most notable features include low-domed glabella that does not extend very far above eyes (dorsally, 0.6 of visual surface's height), bulbous eyes, and broad genal field (exsag.), which extends posteriorly to form pointed trailing edge.

Glabella is nearly flat-topped and bounded laterally by broad (tr.), shallow, straight axial furrows that diverge anteriorly at about 60-65°, retain uniform shape adjacent to visual surface, but fade into anterior genal field, and are redirected

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exsagittally against lateral lobes of L1. Preglabellar furrow does not connect to axial furrows, but originates as shallow depressions just anterior to them; it rapidly narrows and deepens beneath glabella (medially), becoming straight, fine demarcation between mild glabellar overhang, and narrow ventral margin. Sculpture on glabella consists of very fine domed tubercles, bordering upon granule size; distribution is sparse and widespread across dorsal surface, with progressive increase in density, crowding, prominence, and size range in anterior region; in ventral regions (especially laterally), tubercles become slightly elongate, forming weak, broken terrace lines that parallel glabellar contours.

Glabellar furrows are very weakly impressed, especially in anterior regions; on most specimens S3 medial is discernible mainly on basis of colour (due to increased cuticle thickness), and where visible is a faint convex-forward arc trending slightly behind transverse plane (heading laterally); S3 lateral ramus is also faintly impressed, but appears in most specimens as shallow, straight sulcus, which angles into axial furrow adjacent to anterior edge of eye; S2 is slightly more incised, but still faint, forming almost straight line paralleling S1; no glabellar sulci are deep enough to give glabellar lobes L2 or L3 convexity independent from frontal lobe. L1 medial (intercalating ring) is sunken relative to glabella and occipital ring, and unornamented; it has no dorsal convexity (sag.), but matches curvature of occipital ring (tr.), and has relatively uniform width (exsag.) throughout; S1 and S0 form moderately impressed, narrow (exsag.) bounds to anterior and posterior edges, and S1 fades in medial 1/3rd to become shallow, broad (sag.) trench. Lateral L1 lobes have low dorsal convexity and are unornamented; separation from intercalating ring is weak, and achieved through minute sulcus, connecting anterior and posterior apodemal pits in medially-convex arc; anterior and posterior apodemal pits are deep and sharply incised, with straight anterior pit, and arced posterior pit (concave-anteriorly); shallow, broad (tr.), round-bottomed sulcus delineates lateral edge. Occipital ring is similar to axial rings of thoracic segments, but is much broader (sag.), has smaller, less pronounced lateral lobes, and bears a broader (sag.) patch of fine tubercles concentrated in crescent-shape across its posteromedial region. Fixigena, proximal to palpebral furrow, displays little dorsal convexity, and is slightly sunken relative to both palpebral lobe and glabella; posterodistal tip makes smooth transition into

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postocular area, exhibiting some of its strongest dorsal convexity behind back of eye; postocular area is markedly narrow (exsag.) for genus, and is sunken relative to posterior border and posterior edge of eye; posterior border furrow and distinct postocular area fade into genal field near base of eye; sculpture is absent in all portions. No postocular pad is present. Palpebral furrow is weakly impressed, except adjacent to back corner of eye; furrow is broad (tr.) and shallow. Palpebral lobe is almost flat fore to aft, with slight transverse dorsal convexity; laterally, faint sulcus separates it from palpebral rim near middle of eye (exsag.); distal portions bear very fine tubercles in low density patch. Palpebral rim is slightly raised (dorsally), and juts outward (laterally) to overhang upper lenses near middle of eye (exsag.); rim is thick (tr.) and bears fine tubercles, many of which are elongate (exsag.), and which become progressively finer and more tightly packed on rim's lateral face.

Eye is of moderate size relative to rest of cephalon (about 0.41 of total cephalic length, and 0.33 of total cephalic height), and is quite round in most aspects of its appearance. Visual surface bears 18 rows of lenses, with 7 (and very rarely 8) as maximum number of lenses per row, and 94-100 as typical total number of lenses per eye (see Text Fig. 3 for full lens formula). Lenses are closely adpressed, almost touching throughout most of visual surface, and sclera is very minor, being visible only as recessed wedges between lenses, except within areas of reduced lens size (dorsally, near center of eye), where there are small bands between vertically adjacent lenses. Lens distribution does not extend to very margins of eye, leaving broad, rounded margins along anterior, posterior, and particularly ventral edges of visual surface; broad margins, laterally-directed bowing, and low slope of visual surface combine to give very rounded appearance to eye. Small numbers of fine pits and granules are present along ventral margin of eye (pitting within middle 1/3rd of surface, exsagittally). Subocular groove makes smooth, rounded transition into genal field, with no subocular pad, and becomes more deeply incised beneath back corner of eye.

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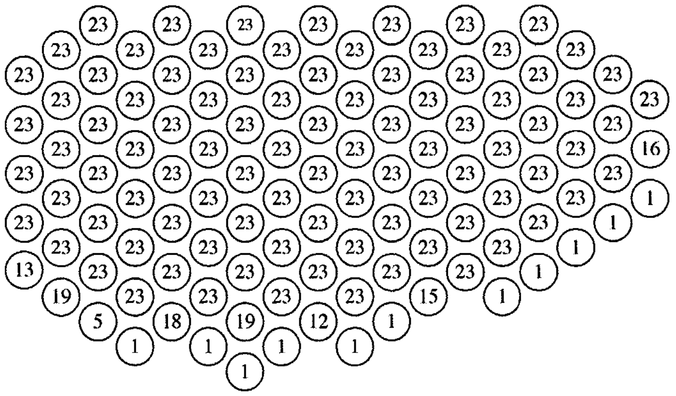

Text Fig. 3: Lens formula diagram for *Reedops pembertoni* n. sp. specimens

Genal angle is long (exsag.) and tall (about 1.3 times eye's height), with fairly vertical orientation to lateral face; tip of genal angle is swept into posteriorly-directed point (although this has been damaged in many specimens); sculpture consists of widely spaced granules, which become progressively more dense and exsagittally elongate in ventral regions; next to ventral margin, short (exsag.) terrace lines are abundant and crowded, with few fine pits interspersed. Anterior portion of genal field has slightly reduced sculpture in dorsal reaches, and flares laterally along ventral margin, creating wide (tr.) lip beneath and anterior to eye, which projects laterally far enough to be visible in dorsal view. Posterior border is wide (exsag.), presents flattened lateral face, and angles sharply into posterior border furrow along its anterior edge; sculpture consists of cluster of minute conical tubercles widely spaced along trailing edge of posterior border, and continuing to small extent onto back of genal angle.

Fused facial suture is visible on small number of specimens, as interruption in sculpture with faint topographic trace; posterior section runs under posterior 1/4 of eye, and traces slightly convex-anterior arc across genal field (delineating large fixigena); anterior section curves anteriorly out of axial furrow to wrap around base of glabella, creating arc above termini of axial and preglabellar furrows.

Ventral margin is semicircular in section, and has raised bead beneath genal field, losing prominence beneath genal angle; margin becomes thinner posteriorly, and much thicker anteriorly, until its leading edge becomes square in section and whole rim is eventually obscured beneath glabella; anastamosing terrace lines cover lateral and ventral

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surfaces of margin, while granulation occurs along surface adjacent to vincular furrow, and is dominant ornament on all surfaces beneath glabella.

Vincular furrow is incomplete medially, but lateral to glabella is round in cross-section and bears fine granules; in medial regions, only faint difference within spacing of granulation shows any indication of path of furrow. Laterally, furrow is broken into series of interconnected pits for accepting tips of thoracic segments; pits are elongate (exsag.) and lateral edge of furrow appears fluted (has twice as many indentations as there are actual pits); all surfaces bear fine granules, but these are most prominent and elongate (exsag.) along ventral extremes.

Doublure is wide (sag.), with posterior margin in line with anterior edge of eyes; overall, surface is fairly flat (tr.) with gentle curvature from anterior to posterior (ventrally convex with low inward slope); surface swings into more vertical orientation (laterally) adjacent to genal field, and extends small flange (medially) to match up with hypostome; central portion of doublure extends below ventral margin, making small mound visible when viewed laterally. Doublure ornament consists of coarse granules anteriorly and medially, which coalesce to form short terrace lines (paralleling nearest margin) in lateral and posterior positions; adjacent to hypostome contact, granules become much finer, and along vertical faces next to vincular pits, ornament is absent entirely.

Hypostome is not available for study.

Thorax contains 11 segments; width (tr.) of axial ring to width of whole segment is about 0.39 in all segments; overall, thorax tapers to about 0.83 of anterior width (tr.), heading posteriorly. Axial rings have poor distinction between medial and lateral lobes, but lateral lobes are slightly more inflated; sculpture is of fine, domed tubercles concentrated upon highest (most dorsal) extent of medial lobe and absent on lateral lobes. Articulating half-ring is almost equal in height (dors.) to axial ring, but is separated by well-incised furrow. Axial furrow is poorly defined, being shallow and broad. Pleural furrow is moderately incised distally, and fairly shallow and broad proximally; it fades before reaching axial furrow, and penetrates rim of articulating facet to leave faint trace in posterior 1/4 of articulating facet. Roughly equal width (exsag.) anterior and posterior pleural bands display low dorsal convexity, with small row of very fine tubercles on

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posterior band adjacent to fulcrum, and very faint, scattered pits distal to this position. Articulating facet bears minute granules evenly distributed across its surface, with concentration of coarser granules along posterior lip. Distal tip of thoracic segment has square posterior corner (more pronounced in posterior segments, and more rounded in anterior segments); ovoid granules are present across entire surface.

Pygidium is small and shaped like American football in outline, (with axis and fulcrum points projecting slightly outside of this outline); little topographic distinction exists between axial and pleural regions. Axis accounts for 0.31 of total pygidial width (tr.) anteriorly, and 0.19 posteriorly; exhibiting gentle, constant taper until terminal piece is reached, and leaving a broad (sag.) postaxial field. 7 rings plus terminal piece make up axis, but only anterior 4-5 rings are clearly delineated by furrows on most specimens (observing sculpture or wetting specimens is often necessary to observe posterior rings). Ring furrows contact axial furrow behind anteriormost 3 rings only; anterior 2-3 ring furrows are deepened, slightly broader (sag.), and more convex-forward in medial portion, corresponding with position of interannular lobes, but no actual lobes are present. Axial sculpture consists of fine, conical tubercles with fine pits concentrated in patches along dorsal extremes of rings 1-5, and fading to fine rows of tubercles in posterior rings. Axial furrow is broad, round-bottomed, and fades posteriorly, adjacent to terminal piece, but still creating terminal closure of axis; small indentations are created within axial furrow where contributions of ring furrows 1-3 increase its depth and breadth. Pygidial pleural region is variably divided into 2-3 faint pleural ribs. Ribs are only delineated by pleural furrows that reach 1/2 way to margin of pygidium, and have exceedingly faint interpleural furrows; both sets of furrows are slightly concave-backwards, and become more faint in posterior sections. Pleural field lacks sculpture. Pygidial margin has minor flat-spot in its curvature opposite axis, to accommodate convex doublure.

Discussion: The most similar material to *Reedops pembertoni* new species is from the slightly younger *Kolihapeltis* couche. Within this horizon exist specimens that are likely assignable to *R. pembertoni*, but are poorly represented in our current collections, and may have a higher total number of lenses per file (8 as opposed to the usual maximum of

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7 for specimens from the *Dicranurus* couche[1]). The proximity of these two taxa to one another suggests that they likely share an ancestor-descendant relationship, and creates the taxonomic problem separating these specimens into two species. Unfortunately, there are large numbers of prepared specimens from the *Dicranurus* couche available, only a few specimens from the *Kolihapeltis* couche available, and too few distinctions between specimens from these two horizons to distinguish two groups clearly. This situation muddies the waters from a taxonomic standpoint, and will be treated conservatively here by assigning one species name for representatives from the two couches, but this may change with additional work.

On a larger scale, *Reedops pembertoni* specimens are problematic in their possession of a *Reedops*-like pygidial character suite, broad postocular area, reduced sculpture, subdued cephalic lobes, and reduced vincular furrow (medially); while still possessing the typical *Phacops*-like eye, and slightly elongate (tr.) doublure granules. In the old classification (graded) scheme, this species could have been placed within either *Boeckops* or *Reedops*, but violated aspects of the diagnoses of both taxa. In the cladistic analysis, this species is the sister group to *Reedops cephalotes hamlagdadianus*, and the two taxa share synapomorphies outlined in the discussion of the latter species. *Reedops pembertoni* possessed 6 autapomorphies, none of which are exclusive to this species.

In terms of general appearance, this species is somewhat similar to *Reedops intermedius* (BARRANDE, 1846), but any sort of close examination shows huge differences. *R. pembertoni* lacks all but the most subtle sculpture; has a very narrow (exsag.) postocular area with no real furrow at its distal tip; has significantly smaller eyes, with fewer lenses; has a smaller, much more effaced pygidium; and has an anterior genal field that projects laterally before joining the glabella.

Phacops (Boeckops) algericus G. ALBERTI, 1983 is much closer in morphology to *R. pembertoni*, but *R. pembertoni* has pointed genal angles, an anterior genal field that flares laterally, slightly smaller eyes (same number of vertical rows, but typically one less

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[1] The one prepared representative available from the *Kolihapeltis* couche has been included here (see Pl. 4.2, 4.5), and has added a single additional lens to the bottoms of rows 4, 6, 7, 8, 10,11,14, 15, and 18 in the eye diagram (Text Fig. 3).

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lens per row), a slightly greater degree of glabellar divergence, a shorter overall glabella with less glabellar overhang, and a slightly narrower (exsag.) postocular area.

'Tribe Phacopini' FLICK AND STRUVE, 1984
(HAWLE AND CORDA, 1847, *nom. transl.*)

Discussion: The Phacopini is a monogeneric tribe as defined by FLICK AND STRUVE (STRUVE later placed two subgenera within *Phacops*, *(Phacops)* and *(Cultrops)*, but never expanded the contents of the tribe, preferring to allocate most phacopid genera to the Geesopini). This taxon is a straightforward elevation of the concept originally supporting the genus *Phacops*, with the conditions that its members must not bear a long, prominent cephalic rim (are non-marginulate); must have a moderate to large postocular area; and may have sculpture elements ranging anywhere from very fine to very large tubercles.

The cladistic analysis conducted in this study neither supports nor refutes the existence of a monophyletic taxon at this level in the hierarchy. The tribe Reedopini could not be justified in a sequenced classification scheme (due to the use of only three *Reedops* species in the analysis), so there is no support for treating the sister group of the '*Reedops* clade' as a tribe either. The taxon Phacopini is neither suppressed nor formally recognized here. This is a matter for future work. It can, however, be stated with certainty that the tribe Geesopini cannot exist as a holophyletic entity, as even the most skeptical viewing of this study's phylogenetic hypothesis suggests that Geesopini is a paraphyletic fragment of Phacopini.

New Genus A

Discussion: New Genus A is an informal grouping of new Moroccan phacopids with subdued sculpture that grade-based taxonomy would include within *Phacops*, but would render the taxon polyphyletic if the cladistic analysis performed in this study is taken as absolutely correct (which is unlikely). In an attempt to avoid excessive taxonomic 'splitting' this group is treated as an informal taxon until more extensive analyses can be

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completed, and its members are referred to as New Genus A species for now. There is the potential for this group to be formally recognized as distinct at the genus level.

New Genus A *smoothops* (CHATTERTON *et al.*, 2006)[2]

Plate 6.1-6.12; 7.1-7.12; 8.1-8.12; 9.1-9.12; Text Figures 4, 5

2006 *Phacops smoothops* CHATTERTON *et al.* – CHATTERTON *et al.*, Middle Devonian Trilobites, Morocco: p.15; Pl. 4-7.

Type material and locality: Holotype is complete enrolled exoskeleton UA 13306, from basal part of section, upper Emsian Timrhanrhart Formation, Jbel Gara el Zguilma, near Foum Zguid, Morocco. Alternative localities include the contemporaneous *Thysanopeltis/Harpes* couche, in the El Otfal Formation, at the bou Dib section, near the town of the same name, in the Ma'der basin of southeast Morocco (BULTYNCK AND WALLISER, 2000). Paratypes UA13307–UA13315.

Diagnosis: *Phacops*-like with distinctive pattern of low tubercles on glabella, with density of tubercles greater on front of glabella, and tubercles on dorsal surface low and sparse, and even absent on all but lateral/posterior margins of cheeks; genal angle is rounded and protrudes posterolaterally only slightly, extending only short distance (1–2 mm) behind occipital ring; eye with moderate number of lenses (about 80, in 18 files with up to 6 lenses per file); files of lenses towards front of eye usually with more lenses per file than those near back of eye; sculpture on thorax and pygidium mainly of small, low tubercles concentrated on posterior pleural bands and most prominent on axis.

Description: Cephalon broadly semicircular in outline, with indentations on either side of occipital ring (L0); glabella is broadly inflated, forming sub-pentagonal lobe that overhangs preglabellar furrow anteriorly, but has low dorsal convexity (sag. and tr.); angle between axial furrows in front of S1 about 60–75°; sculpture of widely spaced,

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[2] This species has been published recently in a monograph in which R.C.M. was a co-author, prior to the completion of this thesis.

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small, low tubercles on dorsal surface of glabella, and of more densely arranged, more prominent and bimodal sized tubercles on front of glabella; tubercles are particularly sparse on glabella near axial furrows; some small, shallow pits present on genal fields; fine granulation may be present both between and on tubercles; S2 and S3 are barely visible as slightly recessed anteriorly convex sub-transverse linear grooves; they do not reach middle of glabella medially or axial furrows laterally; medial portions of S2 and S3 trend 4 and 14 degrees behind transversely, respectively; S3 also occurs as almost straight furrow running anterolaterally from near distal end of more transverse proximal part of furrow, sub-parallel with axial furrow; S1 is deep distally in front of small, slightly inflated and distinct distal L1 lobes, but dies out or becomes very shallow medially, at ends of distinct anteromedian extensions of L1 from in front of median edges of L1; median part of L1 is wider (tr.) than long (exsag.), and only slightly inflated relative to glabella farther forward; median part of L1 usually has few tubercles; lateral L1 lobes have one or two tubercles or no tubercles; L2 and L3 show no independent convexity relative to rest of glabella in front of S0; S0 is firmly impressed and sub-transverse medially, and slightly deeper and concave forward behind distal L1 lobes; L0 is comparatively wide (tr.) and short (sag.); axial furrows are deep opposite anterior part of palpebral lobe, but are shallower farther back; distinct but only moderately impressed preglabellar furrow is placed immediately adjacent to anterior margin of cephalon; palpebral furrow is shallow towards front of eye and deeper near back of eye, and runs sub-parallel with facial suture opposite eye; palpebral lobe is comparatively flat and sub-horizontal near its midlength, but distinctly more curved close to anterior and posterior margins; lateral parts of occipial ring slightly shorter (exsag.) than median part and not distinctly inflated; shape and appearance of occipital ring very similar to those of anterior thoracic axial rings, including presence in some specimens of shallow, transverse sulcus near midlength; posterior border furrow shallow to moderately impressed proximally, and curved forward to disappear distally, behind eye; fixed cheeks opposite eye may have some tubercles on highest region; irregular row of tubercles present on outer half of palpebral lobe.

Eye with about 80 lenses in 18 files of up to 5 or 6 lenses per file, with slightly more lenses in files near front of eye than near back (see Text Figs. 4 and 5 for full lens

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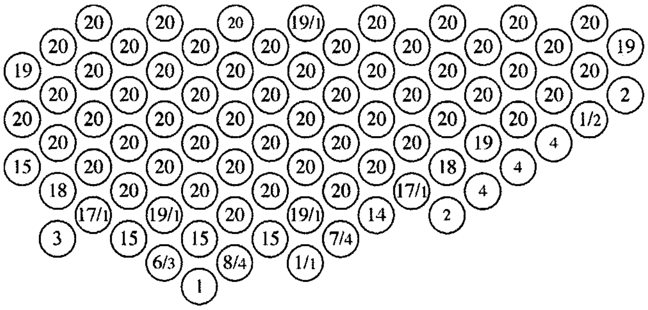
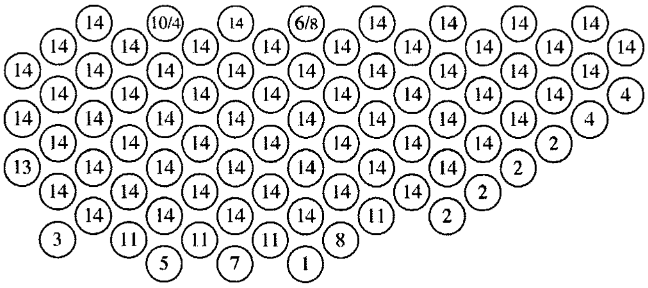
fomula); interlensar sclera is minor in area compared to area taken up by lenses that are strongly convex and protrude well above intralensar sclera; ventral to lenses, cuticle is smooth for short distance before curving inward sharply to overhang adjacent part of cheek; exsagittal length of ocular surface is approximately 0.23 that of cephalon; height of eye is about 0.32 height of cephalon; eye is immediately adjacent to axial furrows anteriorly but distant by more than width of palpebral lobe from axial furrow posteriorly; palpebral lobe and eye are convex laterally, with curve tighter towards back of eye than towards front of eye; back of visual surface is slightly lateral (exsag.) of position of front of visual surface, and almost reaches posterior border furrow; glabella is slightly canted up forward, so that when specimen is viewed in lateral profile, with top of glabella horizontal, eye appears to slope downward 10–20° forward.



Text Fig. 4: Lens formula diagram for New Genus A *smoothops* specimens from the upper couche of Jbel Zquilma (ZGEE3).



Text Fig. 5: Lens formula diagram for New Genus A *smoothops* specimens from the lower couches of Jbel Zquilma (ZGEE 1-2).

Genal field is broad, fairly flat and slopes steeply distally; genal field has sparse tubercles that are often denser toward front and back of genal field than near midlength; in large specimens, tubercles become very low; some specimens show fine pits in genal

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field; doublure has distinct vincular furrow anteromedially and vincular notches posterolaterally; sculpture on doublure consists of many fine, discontinuous terrace ridges (steep slope forward), with grooves in between ridges anastomosing, and ridges that are broken into particularly short segments posteromedially; sculpture at outer margin of vincular furrow consists of fine, transverse, asymmetrical granules that become more extended and ridge-like on margin, where they are periodically interrupted by two irregular rows of distinct pits; facial sutures are fused in all mature specimens, but path of sutures is still apparent (posterior part curves forward under back of eye and then back distally, anterior part runs close to margin of glabella); genal angle is rounded.

Hypostome is unknown.

Thorax contains 11 segments. Ratio of width (tr.) of axial ring to width of thorax is about 0.34 near front of thorax and about 0.32 towards back; more posterior segments are narrower (tr.) than more anterior segments; sculpture of small tubercles usually is present on more dorsal regions of axial ring, often in median, anteriorly convex crescentic field, and on posterior pleural rib; shallow, transverse sulcus is present often near midlength of axial ring; articulating furrow is firmly impressed and steeper along anterior margin; apodemal pits at ends of articulating furrow are elongate-oval in plan; pleural furrows are firmly impressed, trend outward about 16° behind transversely, die out on distal articulating facet, and are deepest near fulcrum; large articulating facet, with curved posterior margin, is present across most of segment distal to fulcrum; tip of segment is sculpted with dense granules that coalesce into longitudinal terrace ridges at margin.

Pygidium is nearly semicircular; pygidial axis has 7 or 8 axial rings and terminal piece; back of axis is rounded; anterior three segments with broad w-shape, more posterior rings are transverse; ring furrows are deeper anteriorly than posteriorly; very short (sag.) interannular lobe is usually discernible behind first axial ring or first and second axial ring; axis tapers backwards, being 0.32 – 0.34 maximum width of pygidium anteriorly; axial furrows are moderately impressed laterally, and become shallow posteromedially; pleural furrows are only moderately impressed, but are distinctly deeper than interpleural furrows; both pleural and interpleural furrows disappear some distance from margins, delineating a smooth border, although no border furrow is present; first

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two pleural furrows are distinct, and up to four may usually be discerned; number of interpleural furrows is usually one fewer than number of pleural furrows; sculpture of small, low, uniform sized tubercles is most visible on axial rings, and is usually discernible on some pleural ribs; up to 5 segments may be picked out by row of tubercles on posterior pleural band; border region is smooth, and weakly concave outward; difference in slope between proximal and distal regions of pleurae is not marked.

Discussion: New Genus A *smoothops* is common in ZGEE1 and ZGEE2, and in several beds about 45–50 meters higher in the same section (around and including ZGEE3). Given the slightly smaller size of most of the specimens from ZGEE3, and the range of variation in each of the collections from these two levels, there were no useful characteristics that could be use to separate these collections into two distinct taxa. Good specimens are illustrated from the two levels on separate figures to allow other researchers to compare the forms.

New Genus B *granulops* can be distinguished from New Genus A *smoothops* occurring in the same beds in that it has a more prominent, coarser and denser sculpture of tubercles; L2 is always, and L3 is generally, much more distinct, despite the much more granular sculpture on the glabella; the back of the visual surface is directly behind (exsag.) the front of the visual surface, so the librigena is not as wide (tr.) opposite the back of the eye; the number of lenses in the eye is lower (typical maximum of 4 lenses per file; total of about 60 lenses versus about 80); there is almost always one more file of lenses (19 versus 18) in the eye; there are always coarse, scattered granules or small tubercles on the lower part of the visual surface, below the lenses; the pleural furrows, behind the first segment of the pygidium, are distinctly deeper; the interannular lobes, behind the first two pygidial axial rings, are even more inconspicuous ; the front of the pygidial axis (first 2 segments) does not flare (increase in width, tr.) as distinctly forwards; the axis is slightly more arched; the axial furrows are deeper; and the back of the pygidial axis is more distinct. Despite these numerous differences, these two species are similar in overall size and shape. However, they are clearly distinct at the species level, and there is no problem with assigning any reasonably preserved specimen from the lower part of the section at Jbel Gara el Zguilma to one or other of these species.

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New Genus A *smoothops* is most directly comparable in morphology to *Phacops* (*Phacops*) *sparsinodosus struvei* SCHRAUT (2000, fig. 8g–q). These species are very similar in most aspects, yet distinct based on a suite of characteristics that largely pertain to their eyes. In New Genus A *smoothops*, the eyes are much closer to the glabellar surface, and have no raised dorsolateral rim on the palpebral lobes. This results in a visual surface with a slope sub-parallel to that of the glabella, as opposed to the more vertical configuration of *P. (P.) sparsinodosus struvei.* The visual surface of New Genus A *smoothops* is more reniform in outline when viewed laterally, and its surface is less convex in transverse section. New Genus A *smoothops* does not develop a different style of sclera as it progresses towards the largest specimens recovered in this study—the lenses in the largest forms remain tightly adpressed to one another, instead of becoming sunken and spaced out within a massive sclera, as has been postulated for *P.* (*P.*) *sparsinodosus struvei* (SCHRAUT, 2000). Noticeable differences are also to be found in the finer and more widely spaced tubercles on the glabella of New Genus A *smoothops*. Additionally, the pygidia of New Genus A *smoothops* are typically less deeply ribbed in the pleural region, and consistently bear one fewer pleural rib and axial ring.

MORZADEC (1969, pl. 3, figs. 2–5, 7) illustrated some specimens that he called "*Phacops* sp. A cf. *fecundus degener* BARRANDE, 1852", from the lower Couvinian (Eifelian) of Brittany, northwestern France. These are also similar New Genus A *smoothops*, sharing the rather suppressed sculpture on top of the glabella, with a greater number of more visible small tubercles on the front of the glabella. The eyes of these two forms appear similar but New Genus A *smoothops* typically has 10 more lenses per eye, and a maximum lens count per file of 5–6, and not just 5. The postocular pads appear slightly smaller in our Moroccan specimens.

G. ALBERTI (1970, 1981, 1983) described a number of phacopid trilobites from Devonian strata of Morocco, but described none that appears especially close to this species.

Cladistic analysis shows places this species as sister group to all other members of the New Genus A, with a single autapomorphic character, the possession of relatively short eyes with a typical maximum of 5 lenses (character 26, state 3, something that is repeated outside this clade). New Genus A *smoothops* has also not developed the

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foreshortened postocular area or reduced degree of pygidial axis closure that serve as synapomorphies for its sister group. From a morphological standpoint, New Genus A *smoothops* is very close to New Genus A *speculator punctatus* n. ssp., but lacks the much taller eyes with an additional 2-3 lenses per file, and many more lenses in posterior files; the pervasive pitting and raised-rim pits found within the glabellar surface of New Genus A *speculator punctatus*; the transversely elongate tubercles found on its anterior glabellar face; the truly effaced interpleural furrows seen in the pygidium, and some of the axial width there; some of the definition between its axial lateral lobes; and the minute subocular pad.

New Genus A *speculator* (ALBERTI, 1970)

New Genus A *speculator speculator* (ALBERTI, 1970)

Plate 12, Figures 1, 2, 5, 6 (G. ALBERTI, 1970)

1951 *Phacops fecundus* BARRANDE – GIGOUT, Etudes géologiques: 331.

1955 *Phacops fecundus* BARRANDE – GIGOUT, Recherches géologiques: Tab. B.

1965 *Phacops fecundus* BARRANDE – GIGOUT in GIGOUT *et al.*, Carte géologique de la Meseta: 9.

1969 *Phacops (Phacops)* cf. *rana milleri* STEWART – G. ALBERTI, Trilobiten I: p. 437.

partim 1970 *Phacops (Phacops) speculator* ALBERTI – G. ALBERTI, Trilobiten II: p. 91; Pl.12, Fig. 1-2, 5-6. (*non* Fig. 3-4).

Localities, type and figured material: Holotype in ICSR (pl. 12. fig. 2 of G. ALBERTI, 1970), from Middle Devonian (likely Eifelian) strata near Sidi Abdallah des Rehamna, in western Morocco.

Diagnosis: Large eyes typically bear 18 vertical rows of lenses, with up to 8 lenses per file; eyes have rounded margins, bulbous visual surfaces, and unusually round posterior corner (typically with 3 lenses in posteriormost file); total number of lenses can range

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from 111-122; glabella is sub-spherical, and bears sparse, low tubercles, as well as complete transition to terrace lines on front of glabella; pitting is present on palpebral lobe, and front of glabella; pygidial axis contains 8 discernible rings plus terminal piece, and pleural field contains 4 distinct ribs followed by two weaker posterior ribs; interannular rings (following anteriormost 4 axial rings in pygidium) and posterior sweep of distal reaches (adjacent to axial furrow) produce axial rings with pronounced "w-shape", when viewed dorsally.

Description: See G. ALBERTI (1970), or for English equivalent, with thorax described, see description of New Genus A *speculator punctatus* n. ssp. below, taking into account mild subspecific differences mentioned in its discussion section.

Discussion: G. ALBERTI created this species based on a few rather fragmentary cephala, so it is with some hesitancy that the new subspecies below is assigned to the species. (This is an effort to avoid unnecessary taxonomic 'splitting'.) There is an overwhelming similarity between the two sets of specimens, warranting their inclusion in the same species, but the new subspecies brings to light some problems with the nominate subspecies.

There is little chance that the specimens in G. ALBERTI's figures 3 or 4 (pl. 12, 1970) could belong to the same species as his type specimen. The specimen in his figure 3 lacks an intercalating ring, appears to have a different glabellar outline, and has much coarser and more densely packed tubercles across its glabellar surface. The specimen in his figure 4 has a genal outline that is not produced by even the largest specimens of *P. speculator punctatus* n. ssp. (below), ruling out an allometric explanation for its shape: even as an internal mould, the gena is too long (exsag.), extending well behind the occipital ring, and its angle appears too acute.

New Genus A *speculator punctatus* n. ssp.

Plate 10.1-10.11; Plate 11.1-11.8; Text Figure 6

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Localities, type and figured material: Holotype UA6876, from the *Treveropyge* couche (horizon), as it appears at Jbel Oufatene (OTC), near Lahfira, Morocco. Additional specimens from *Lobopyge* couche (OLC), as it appears at Jbel Oufatene, 1-1.5 meters below *Treveropyge* couche. Strata are Eifelian in age and part of the El Otfal Formation (MORZADEC, 2001). Paratypes UA6877-UA6883.

Etymology: This subspecies is named in reference to the raised-rim pits interspersed amongst its glabellar sculpture, and pervasive pitting – on a number of scales – elsewhere (*punctatus* is Latin for "punctured").

Diagnosis: Large eyes typically bear 18 vertical rows of lenses, with up to 8 lenses per file; total lens counts per eye range from 103-117; eyes have rounded margins, bulbous visual surfaces, and unusually round posterior corner (typically with 3 lenses in posteriormost file); glabella is markedly bulbous, and bears distinctive pits with raised margins among otherwise reduced tuberculation, as well as complete transition to terrace lines on front of glabella; pygidial axis contains 8 discernible rings plus terminal piece, and pleural field contains 4 distinct ribs followed by two weaker posterior ribs; sculpture of thorax and pygidium is concentrated largely into crescent-shaped patches along posterodorsal extremes of axial rings, and is accompanied by fine pitting.

Description: Cephalon is semicircular in dorsally viewed outline, with eyes extending laterally to slightly overhang cephalic margin; and glabella is very short (sag.), giving very rounded overall appearance. Lateral profile (with palpebral lobes horizontal) is dominated by large eyes (0.48-0.5 of total cephalic length typically), which become proportionately larger in bigger holaspides; glabella is extremely round, protruding well above tops of eyes in smaller holaspides, and nearly flush with palpebral areas of largest holaspides. Glabella bears general resemblance in shape to broad kernel of corn (maize) with flat base. Axial furrows on either side are broad (tr.), relatively shallow, round-bottomed, and diverge from one another at approximately 60°; become much more deeply incised along anterior edge of eyes, forming deep depressions against anteroventral corner of eye with ventral continuations that seem to sweep beneath eyes as

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as much as continuation to preglabellar furrow; posterior portions deviate in course upon contact with lateral L1 and associated anterior apodemal pit (distal end of S1). Preglabellar furrow is narrow, round-bottomed, and barely overhung by glabella in medial portions; becomes broad and flat in lateral positions, and does not meet very smoothly with anteroventral tip of axial furrow.

Sculpture on glabella is comprised of sparsely distributed, low, domed tubercles of consistent size for each region of glabella; posterior regions have large tubercles, which are replaced by tightly-packed, mid-sized tubercles in anterior portions, and eventually by truncated terrace lines on front of glabella; all terrace lines become progressively more interconnected in ventral regions of frontal lobe, and have long axes that trend parallel to nearest edge of glabella. Unique to this species is presence of very short, broad tubercles with hollow cores, producing 'caldera-shaped' tubercles in posterior portions of glabella; distinctive tubercles are replaced by slightly rimmed pits amongst mid-sized anterior glabella tubercles, by simple shallow pits in anterior regions, and are not present amongst terrace lines in anteriormost positions. Largest holaspides display dense fields of pitting between all tubercles, with pits comparable in size to granules or very small tubercles.

Sulci between glabellar lobes are almost non-existent in smaller holaspides, but fairly visible in larger individuals. Medial S3 is very short (tr.), is separated from axial furrow by distance equal to its own length, is convex-forward in shape, and generally trends transversely; lateral section of S3 is straight, more deeply impressed than medial portions, and runs subparallel to axial furrow. L3 differs from frontal lobe of glabella only in its distal extreme, which forms raised bulge where remainder of glabella is sloping ventrally to meet axial furrow. S2 is straight, trends about 18° behind transverse plane, and is usually only visible due to smoothness of surface in this region. L2 is completely nondescript aside from its narrowness (exsag.). Lateral apodemal pits are extremely deep and straight, but S1 fades almost completely by time sagittal line is reached; S1 halves trend about 22° behind transversely, producing pointed intercalating ring with anterior tip that seems to blend into back of glabella. Bulk of intercalating ring matches glabellar profile closely, except for pronounced pad near midline, which commonly bears 2 pitted-dome tubercles with small cluster of diminutive tubercles

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between (medially); pad is short (sag.) and narrow (tr.), and becomes more prominent in larger holaspides. Lateral lobes of L1 are bulbous with moderate dorsal convexity and smooth margins, and nearly smooth with very few small tubercles and pits. S0 is slightly convex-forward in shape, and has lateral extremes that sweep in behind L1 lateral lobes to reach apodemal pits that are teardrop-shaped and deep.

Occipital ring appears quite similar to thoracic axial rings, but has greater length (exsag.), and bears greater ornamentation; sculpture consists of few small tubercles and numerous fine pits constrained to posteromedial portion of ring, and accompanied by slightly raised posterior rim due to high number of tubercles and pits occurring along this margin; all sculpture is faint and stretched out in transverse direction; usually, occipital ring extends laterally well beyond lateral L1 lobes.

Palpebral area forms broad (exsag.) but short (tr.) ridge with large slope leading down to posterior border furrow, and very mild dip connecting to axial furrow; sculpture occurs as small patch of tubercles and pits constrained to dorsal-most lateral extreme. Palpebral furrow is much shallower near its midlength; furrow is deep adjacent to posterior corner of eye, but only present ahead of this position as faint, broad, depression. Palpebral lobe is rounded and dorsally convex in medial positions, then becomes concave adjacent to its raised palpebral rim. Sculpture on lobe consists of strings of mid-sized tubercles and pits running parallel to palpebral rim, with pitting becoming more dominant in depression beside palpebral rim, and fine, exsagittaly elongate tubercles dominating palpebral rim.

Eye is very large and prominent, occupying 0.5 of total cephalic length and having height nearly equal to that of glabella; eye does not project outward (laterally) from remainder of cephalon, overhanging lateral margin only slightly, and not rising above top of glabella. Visual surface is composed of 18 vertical files of lenses, with typical maximum of 8 lenses per file, and 103-117 as typical total number of lenses (see Text Fig. 6 for full lens formula); posteriormost file typically contains 3 lenses, giving posterior corner of eye rounded appearance (as opposed to more common angular 'corner' seen in most phacopids). Interlensar sclera is reduced, with neighbouring lenses nearly making contact, and projecting well above sclera. Lens distribution continues to very edges of visual surface along dorsal and ventral margins (creating fairly sharp

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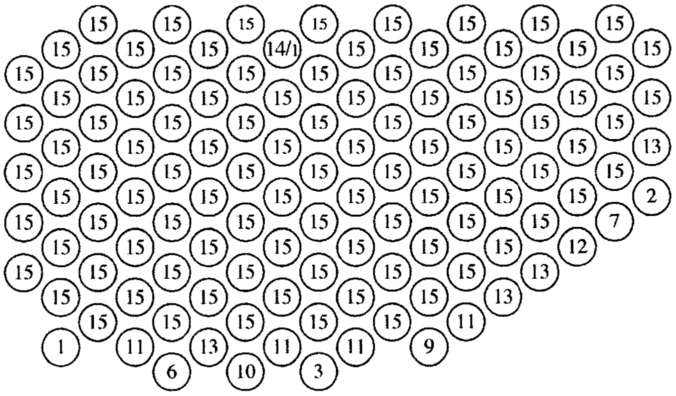
margins), while not continuing to anterior and posterior extremes (leaving rounded border and corner, respectively). Beneath eye is steeply sloping subocular area, which is completely smooth and completely overshadowed by visual surface. Posterior to eye is very deep posterior border furrow, which shallows distally, and makes smooth contact with subocular groove – both regions have exceedingly subtle pads without ornament. Posterior border is rounded in medial sections, and develops raised lateral rim on trailing edge in lateral positions, sculpture consists of fine tubercles and pits along this rim.



Text Fig. 6: Lens formula diagram for New Genus A *speculator punctatus* n. ssp. specimens

Genal angle is inflated compared to surrounding regions, terminates in well-rounded corner, and bears sculpture of fine tubercles and pits; nearer to ventral margin and in anterior portions of genal field, sculpture becomes progressively extended parallel to margin, forming truncated terrace lines and elongate tubercles. Remnant facial sutures are only visible as slight depression where posterior border furrow meets subocular grove. Ventral margin consists of raised lip that becomes more pronounced and slightly narrower (on leading edge) in anterior regions; ventral edge is rounded laterally, but becomes almost flat beneath glabella; sculpture is composed of anastamosing and straight terrace lines, but these are interrupted in medial sections of ventral face by fields of deep pits.

Vincular furrow is typical for genus, with smooth, rounded, continuous furrow beneath glabella, and series of longitudinally directed, interconnected pits beneath cheeks; granulation is pervasive in furrow. Doublure is fairly short (exsag.), and

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relatively flat, with very little change in convexity leading into flange that is extended ventrally to match edge of hypostome; lateral to hypostomal contact, doublure sweeps inwards (dorsally), rapidly becoming vertical in its lateral reaches; anastamosing terrace lines run parallel to nearest margin, except for in vicinity of hypostome, where they become truncated into elongate granules oriented transversely; anterior margin of doublure extends far enough ventrally to be seen as prominent ventral ‘lip’ in lateral view.

Hypostome has been discovered but was not prepared at time of publication.

Thorax contains 11 segments and tapers to about 0.75 of its total anterior width (tr.) in posterior segments. Axial rings comprise 0.4 of total thoracic width in anterior segments and posterior segments; only larger holaspides have readily defined lateral axial lobes, which are delineated by faint sulci arising from anterior apodemal pits. Axial rings are generally smooth, and appear wide (tr.) and low (dorsally), compared to other species in genus, with very small fields of fine tubercles and pits constrained to anterior sagittal regions, and one small row of similar ornament along dorsal extreme of trailing edge; all sculpture appears to be accompanied by very fine, short terrace lines running transversely. Axial furrow is shallow, broad, and can only be traced with confidence across posterior pleural band. Anterior pleural band is low and smooth, with flattened top; and it extends medially to reach almost to anterior apodemal pit. Posterior pleural band is considerably more raised and rounded, but becomes flattened in lateral positions, and even slightly concave behind articulating facet. Pleural bands are separated by deep pleural furrow with angular cross-section and slightly rounded bottom; furrow fades out medially inside axial region, and distally continues onto face of articulating facet – creating fine concave-anterior, hook shape on facet that intrudes 1/4 way across facet (exsag.); both bands also bear no sculpture aside from faint pitting along highest surfaces. Articulating facet is mildly concave; it bears granules along its posterior half, and along its ventral portions to a similar breadth; posterior and ventral margins of facet form raised granulated rim above surface of posterior pleural band, and rim becomes more pronounced in ventral extremes. Distal tip of segment is flattened (ventrally facing), and has notched, granular appearance, due to overhang of articulating facet.

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Pygidium is relatively long (length is 0.62 of overall width), creating roughly semicircular dorsal outline. Axial region is pronounced against comparatively effaced pleural field, and tapers sharply (from 0.33 of total pygidial width to 0.18 in posterior region). Axis is composed of 8 easily discerned rings plus terminal piece in all cases; first 3 axial rings are followed by strong interannular rings, creating large (and occasionally bilobed) depressions in their posterior margins; depressions differ from many other species in that posterior indentation is exceedingly vertical in contact. Anteriormost axial rings are strongly "w-shaped", due to remnants of lateral axial lobes being positioned slightly ahead of each medial lobe. Sculpture on axis consists of clusters of large and mid-sized tubercles and pits concentrated solely near posterior portion of sagittal area. Ring furrows are strong and trend transversely in median portions, but weakly impressed laterally (only making it to axial furrow in first three segments), and trend anterolaterally, as convex-forward arcs, in lateral sections. Axial furrows are deeply incised, round-bottomed, and run almost straight courses until terminal piece of axis is reached; at terminal piece furrows die out and turn medially, but still leave an indistinct raised area in pleural field that may be homologous with postaxial ridge found in other groups. Pleural field has 4 distinct ribs and exceedingly faint fifth and sixth ribs; first 3 ribs show faint interpleural furrows, and all ribs are separated by deep, round-bottomed pleural furrows that extend 2/3 of distance to margin in anterior section, and 1/2 way in posterior sections; furrows become less distinct posteriorly. Sculpture consists of mid-sized pits densely populating all areas except for within furrows. Ventral margin is slightly raised, rounded lip of consistent thickness around entire outer edge of pygidium, and bears short terrace lines along its entire surface.

***Discussion*:** Tubercles similar to those found in this species have been associated with trilobites such as the calymenids and *Trimerocephalus* by STØRMER (1980), and appear infrequently (at least in this shape) within Moroccan phacopids studied here. Many phacopids encountered in this study bear hollow pitted conical or rounded tubercles, but no other species have such a broad central cavity.

In general, New Genus A *speculator punctatus* n. ssp. is most directly comparable to New Genus A *smoothops* (CHATTERTON *et al.*, 2006) (see comparison under discussion

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of latter species), and *Phacops (Phacops) speculator* ALBERTI, 1970 (modified and restricted to a subspecies above).

New Genus A *speculator punctatus* is almost identical to New Genus A *speculator speculator* (Alberti, 1970), but differs fundamentally in its sculpture and visual surface. New Genus A *speculator punctatus* has raised rim pits across its glabellar surface, and pervasive pitting across its genal field and throughout its axial region (which the other taxon apparently lacks, although this may be influenced by preservation, photography, or degree of magnification). Although the type specimen of New Genus A *speculator punctatus* falls within the range of total lens counts established by G. ALBERTI for New Genus A *speculator speculator* (111-122), *punctatus* specimens of comparable size bear as few as 103 lenses, and specimens that are up to 30% larger than his type still do not reach the maximum he stated (122 lenses). Furthermore, the lens distributions are different, with G. ALBERTI's specimens bearing 1-2 additional lenses per vertical row in the anterior third of the eye, when compared to even the largest specimens of *punctatus*. These are likely regional differences, as these two subspecies are found within two different basins, on opposite sides of the Atlas Mountains. G. ALBERTI (1970) compared his *P. (Phacops) speculator* to *Eldredgeops rana milleri* (STEWART, 1927), but for this similarity to be true, his specimens would likely have to differ from New Genus A *speculator punctatus* new species even more than his description and figures indicate (see BURTON AND ELDREDGE, 1974 for good illustrations of *E. rana milleri*).

The cladistic analysis places New Genus A *speculator punctatus* as the sister group to (New Genus A *kermiti* n. sp. + New Genus A *salamandar* n. sp.). New Genus A *speculator punctatus* has autapomorphic codings for its moderately defined lateral axial lobes, high maximum number of lenses per vertical row, weak subocular pad, and fairly low thoracic taper – none of these were unique outside of the New Genus A clade itself. New Genus A *speculator punctatus* is not part of its sister group because these two species have three synapomorphies: they possess few axial rings in their pygidia, they have low glabellar divergence angles, and their pygidial tubercles are restricted to their axes only. The huge disparity in morphology that accompanies these differences will be discussed in the following species descriptions.

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New Genus A *kermiti* n. sp.

Plate 12.1-12.10; Plate 13.1-13.11; Text Figure 7

Localities, type and figured material: Holotype UA6884, from the *Diademaproetus* couche (horizon), as it appears at Jbel Oufatene (MOD1, ODC), near Lahfira, Morocco. Also occurring in the South Oufatene proetid couche (SOP), approximately 10 meters lower in the Oufatene section. Strata are Eifelina in age and part of the El Otfal Formation (BULTYNCK AND WALLISER, 2000; GIBB, 2005). Paratypes UA6885-UA6891.

Etymology: This species is named for the uncanny resemblance of its cephalon to that of Kermit the Frog, a character from JIM HENSON's "The Muppet Show".

Diagnosis: Pronounced eyes typically bear 18 vertical rows of lenses, with up to 9 lenses per file (occasionally 10), and lens totals ranging from approximately 127-138 lenses per eye; eye is large enough to crowd out genal field, creating impression of small genae; glabella is markedly low and effaced, slopes distinctly in anterior direction, and bears faint tubercles almost exclusively on anterior 1/3rd, (which are replaced by terrace lines on ventral-facing surface); degree of glabellar divergence is markedly low (50-55 degrees); pygidium is also effaced, with axis bearing 4-5 visible rings followed by 3 faint rings plus terminal piece, and pleural region showing 3 faint ribs.

Description: In dorsal view, cephalon is subtriangular in outline, and becomes slightly more equidimensional as growth occurs within holaspides. In profile, (eye horizontal), glabella's dorsal surface is nearly flush with palpebral area, has very little dorsal convexity (sag. and tr.), and slopes rapidly anterior to eye, forming rounded apex; distance of apex from anterior edge of eye is typically 0.6-0.7 of eye's exsagittal length, and distance becomes reduced in larger holaspides. Glabella is subpentagonal in dorsal view, with anterior edges reduced and rounded relative to others; axial furrows bordering frontal lobe of glabella are weakly impressed, are almost straight until reaching apodemes in front of lateral L1, and generally diverge from one another at 50-55°; posterior end of axial furrow all but disappears between lateral L1 and palpebral area, but when traceable,

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appears to run parallel to axial furrow in thoracic segments; anterior end of axial furrow is sharply incised running along anterior margin of eye, and shallows significantly while swinging anteriorly to meet preglabellar furrow, junction is higher than base of eye. Preglabellar furrow is distinct and deeply incised in all except medial portions, where glabella overhangs moderately; in anterior view, preglabellar furrow and anterior border form mild 'm-shape' due to downward curvature along contact with genae, and again to accommodate ventral protrusion of glabella in medial position. Aside from very fine tubercles, sculpture on glabella is nearly absent posterior to lateral part of S3 (consisting of very few and widely spaced minute tubercles); anterior to lateral part of S3, low, sparse tubercles are replaced by slightly more pronounced and tightly packed tubercles; along anterior apex of glabella occurs complete transition to anastamosing terrace lines (horizontal in orientation, and similar to those found on doublure) for whole anteroventral surface of glabella.

S1, S2, S3 and correspondingly, L1, L2, and L3 vary slightly from specimen to specimen, but in general, anterior sulci and lobes are weak and hard to detect. Occipital ring is nearly identical to thoracic counterparts, except for its greater length (exsag.) due to gentle anterior slope lasting up to 1/3rd of distance through lateral L1 lobes' length. S0 separates occipital and intercalating (L1 medial) rings with moderate-to-well incised straight sulcus; sulcus (distally) abuts middle of each lateral L1. Intercalating ring weakly convex, tapering to anterior point that fades into frontal lobe of glabella, and connecting without significant impression of S1; similarly, L1 medial lobe grades smoothly into L1 lateral lobes; L1 lateral lobes are smooth, almost flat-topped, borne posterior to bulk of intercalating ring, delineated anteriorly and posteriorly by sharply incised, straight apodemes, and have distal tips barely distinct from adjacent palpebral areas. S2 and S3 are weakly impressed or indiscernible; where present S2 is straight, short (tr.) and parallel to lateral reaches of S2 (approximately 5° behind transverse plane); S3 is short (tr.), convex-anterior, and trends roughly 10° ahead of transverse plane; lateral segments of S3 unconnected to medial portions, straight, and trending subparallel to axial furrow. Palpebral areas have little topography; narrow (tr.) palpebral lobe and palpebral area (for one side of cephalon combine to form about 0.2 of total cephalic width) are separated by

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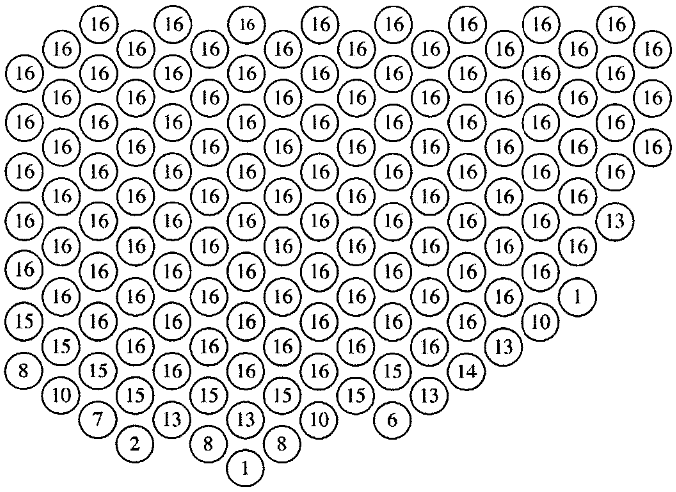
weak palpebral furrow, both bearing only faint tuberculation. Palpebral rim is similarly effaced.

Visual surface is composed of 18 vertical rows with a maximum of 9 or 10 lenses per row; total lens counts typically range from 127-138, (see Text Fig. 7 for full formula). Sclera is fairly prominent, maintaining relatively uniform spacing of lenses even within regions of diminutive lenses (noticeable in uppermost middle portion of visual surface); lenses abut absolute margins on all edges of visual surface, which extend to make contact with edge of glabella, subocular area, and postocular area; lenses are strongly convex and protrude well above sclera. Visual surface is unique in its 'droopy' appearance, with ventral border extending significantly into region usually occupied by subocular region of librigena with a defined lower lip, and visual surface bowed slightly convex-outward (in anterior and lateral views), as well as canted (inward dorsally) by approximately 15° off vertical plane.



Text Fig. 7: Lens formula diagram for New Genus A *kermiti* n. sp. specimens

Genal field is significantly reduced, especially below eye, and to some extent within genal angle, due to massive visual surface. Posterior border proceeds almost vertically into genal angle; genal angle terminates in variably subcircular or subsquare corner (squareness due to posterodorsally projecting nub found in some specimens but not others); anterior portions (subocular) of genal field are short (dorsoventrally), composing only 0.17 of total cephalic height. Sculpture on genal field consist of tubercles

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coarser than most others on cephalon upon all raised surfaces; tubercles become elongate (anteroposteriorly) in all positions near ventral margin, eventually transforming into full terrace lines on or slightly above margin. Remnant facial sutures are visible along posterior border of librigena (as faint distortions within sculpture patterns), tracing convex-forward arc beneath back 1/4 of eye; anterior arm of fused suture and portions adjacent to visual surface are not visible.

Ventral margin subcircular in cross section within posterior regions, and broadens (becomes rectangular in cross section) along its contact with glabella; near midline of glabella, anterior border fades to become almost nonexistent; along entire surface of ventral margin are terrace lines, which are more widely spaced and more pronounced in anteromedial positions.

Vincular furrow is very shallow in medial region, but easily detectable, and deepens significantly lateral to glabellar contact; posterolateral section of furrow contains notches for accepting thoracic segment tips; facets are elongate (exsag.). Sculpture within vincular furrow consists of slightly elongate (parallel to furrow) granules in portions adjacent to glabella, and simple granulation in more lateral segments.

Doublure appears typical for genus, with gentle slope towards dorsal direction in medial portion, which becomes significantly steeper, and eventually vertical, proceeding laterally from edge of glabella; contour of medial portion follows that of glabella, with slight ventral-directed flange to match straight anterior border of hypostome. Entire doublure is ornamented with anastamosing terrace lines that run parallel to ventral margin, except for region anterior to hypostomal contact; here more posterior-facing trend occurs (more closely paralleling hypostomal border) in lateral positions; medially, terrace lines are abbreviated to form ovoid granules.

Hypostome has not been recovered.

Thorax contains 11 segments; width (tr.) of axial ring to with of whole segment is about 0.36 in all segments; overall, thorax tapers to 0.87 of anterior width (tr.), heading posteriorly. Axial rings are generally smooth with few tubercles restricted to posteromedial, crescentic patch which dies out before reaching lateral lobes; lateral lobes slightly more convex than, but otherwise indistinguishable from, medial ring. Contact with articulating half-ring is sharply defined, but is brought about with little change in

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height. Axial furrow is shallow, broad, and ill-defined; it leads to anterior and posterior pleural bands with low dorsal convexity and nearly equal widths (exsag.); bands separated by sharp and deep pleural furrow, which begins shallowly (medial end), terminates distally in sharp contact with articulating facet surface, and trends behind transversly. Tubercles are faint and restricted to narrow strand along highest points of posterior pleural band (from region of fulcrum to distal terminus), and on anterior pleural band occur as minute patch bordering articulating facet. Articulating facet is typical shape for genus and bears minute, ovate granules on posterior half of surface. Posterior pleural band ends distally in raised ridge, giving posterior rim of pleural lobes 'square' appearance, and entire tip is ornamented with ovoid granules.

Pygidium is roughly semicircular in outline, with slight posterior indentation adjacent to axial region (when viewed dorsally); generally small, with little topography, and quite similar to pygidia found in *Reedops*. Axial region comprises about 0.28 of total pygidial width in anterior section, and tapers mildly heading posteriorly (18-20° convergence); axis is composed of 4-5 easily discernible rings (although ring furrows do not appear to reach axial furrow consistently behind second ring), followed by additional 3 rings discernible only due to sculpture or specimens showing muscle-scar colouration, and ending in smooth, undifferentiated terminal piece. First 2-3 axial rings are followed by fairly distinct, lenticular interannular lobes, producing indentations on posterior edges of rings. Axial furrow is broad, rounded, and fades posteriorly into mere slope change between tip of axis and posterior border, leaving mild postaxial ridge. Where present, axis bears sculpture as single strands of fine tubercles along trailing edges of anteriormost axial rings. Pygidial pleural region is devoid of large-scale sculpture and displays only 3 pleural ribs/furrows; interpleural furrows are exceedingly faint where present; pleural furrows only continue distally 1/2 way to margin of pygidium and proceed along straight courses.

Discussion: The poorly impressed nature of the vincular furrow and general appearance of the pygidium would suggest that this species may belong within the genus *Reedops*, but there is a whole suite of characters that suggest a much stronger affinity to *Phacops*. These characters include: the small proportion of the cephalon taken up by the postocular

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area and posterior border (due to the size and position of the eye); the relative size and shape of the glabella; and the nature of the doublure and its sculpture.

Within the genus *Phacops* this species is similar to very few established species, and closest in morphology to the new species placed within New Genus A (it is contrasted with New Genus A *salamandar* under that taxon's discussion, and the other members of the group here). In lateral view, New Genus A *kermiti* bears a moderate resemblance to *Eldredgeops rana milleri* (STEWART, 1927) or *Phacops proniceps* STRUVE, 1970, but the resemblance is superficial. The low glabellar vaulting and relatively large eyes shared by all three species are no match for the incredibly narrow glabella, effaced cephalic furrows, sub-triangular cephalic outline, terrace-lined anterior glabellar face, and nearly absent tubercles seen in New Genus A *kermiti* alone. Muscle scars are seen as dark patches below the translucent cuticle of a pair of New Genus A *kermiti* specimens and this species appears to match most closely the observations of ELDREDGE for the cephalic musculature of *Eldredgeops rana* (1971). New Genus A *kermiti* is moderately similar to New Genus A *smoothops* and New Genus A *speculator punctatus*, but is easily distinguished from them on the basis of the aforementioned characteristics.

Cladistic analysis places this species as the sister group to New Genus A *salamandar*, which is no surprise based on their very similar morphology, but there are many autapomorphies for New Genus A *kermiti*. New Genus A *kermiti* has unique character codings (within this clade) for characters 1, 11, 15, 18, 26, and 28 – differences that are effectively summed up above. New Genus A *kermiti* and New Genus A *salamandar* are united by their (local) synapomorphic possession of few axial rings in the pygidium (22=0), low degree of glabellar divergence (31=0), and the fact that they have pygidial tubercles almost exclusively upon the axial region (37=1).

New Genus A *salamandar* n. sp.

Plate 14.1-14.10; Text Figure 8

Localities, type and figured material: Holotype UA6892, from the *Diademaproetus* couche (horizon), as it appears at Jbel Oufatene (MOD1, ODC), near Lahfira, Morocco.

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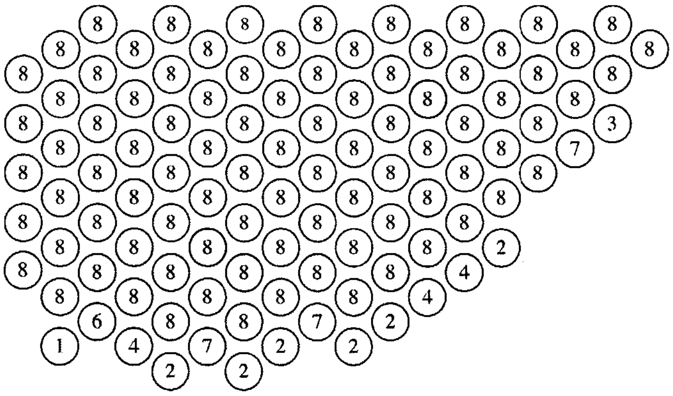
Strata are Eifelian in age and part of the El Otfal Formation (BULTYNCK AND WALLISER, 2000). Paratypes UA6893-UA6896.

Etymology: The specific epithet *salamandar* is Arabic for "salamander", and is referring to the general resemblance seen in its cephalic shape.

Diagnosis: Pronounced eyes typically bear 18 vertical rows of lenses, with up to 7 lenses per file; glabella is relatively low and bulbous, and bears faint tubercles almost exclusively in positions anterior to eyes, (which are replaced by minute terrace-like tubercles next to ventral margin); intercalating ring is slightly raised pad with triangular dorsal outline; pygidial axis has very low dorsal convexity and blends seamlessly into postaxial area with no distinct terminal closure.

Description: This species is quite similar to New Genus A *kermiti* new species, so a differential diagnosis (in the discussion section below) forms an adequate description with full lens formula presented in Text Fig. 8 (below).



Text Fig. 8: Lens formula diagram for New Genus A *salamandar* n. sp. specimens

Discussion: New Genus A *salamandar* n. sp. most closely resembles New Genus A *kermiti* n. sp., (which is found in the *Diademaproetus* couche and the South Oufatene proetid couche), but differences are present mainly in terms of its proportions and sculpture. New Genus A *salamandar* has a significantly smaller eye, shorter visual surface, more bulbous and foreshortened glabella, and lacks the dominant terrace lines

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found on the anteroventral face of the glabella in New Genus A *kermiti.* Additionally, New Genus A *salamandar* has an intercalating ring that is a distinct raised pad with a triangular dorsal outline (as opposed to almost flat), lateral L1 lobes that are domed as opposed to flat-topped, a more deeply incised S1/S2/S3 furrow set, deeper incision of the vincular furrow in medial positions, and a less pronounced lip along the lower margin of its visual surface. The eye of New Genus A *salamandar* also bears fewer lenses, with the same 18 vertical rows, but with only 7 as opposed to 9 for the maximum number of lenses in any row. This means that the eye occupies a smaller portion of the total cephalic height (0.51 as opposed to 0.59), and does not intrude into anterior genal field or overhang the genae to as great an extent as in New Genus A *kermiti.*

Thoracic segments are all but identical between the two taxa, but the pygidium of New Genus A *salamandar* exhibits lower convexity throughout its axis, with a less distinct closure at the axial terminus, and increased taper heading backwards (approximately 25° convergence angle, as opposed to 18-20°). Axial ring furrows also appear to have less of a posteriorly-directed curvature to their distal portions in New Genus A *salamandar.* Comparisons of pygidia between these two taxa are made with some reservations, as only 2 specimens of New Genus A *salamandar* have been collected with complete pygidia, and one of these has been moderately abraded.

The distinction between these species is mildly problematic from a taxonomic standpoint, because they co-occur in the *Diademaproetus* couche, which makes it necessary to justify not 'lumping' them together. These species are close enough in morphology that they likely would have occupied the same niche, and cases of direct competition between close relatives are relatively rare. Furthermore, they are present in very low ratios in the *Diademaproetus* couche, and New Genus A *kermiti* appears in another horizon (SOP section) without New Genus A *salamandar*, so they are unlikely to be morphs of the same species. There are numerous distinctions to support the separation into two species-level taxa (outlined above), and the author believes that their co-occurrence may actually be an artifact of collecting through different horizons that are close to one another. (The ODC section is an approximately 1 meter thick sample interval through a series of muddy limestones that probably represent multiple depositional events, and the mined trench is overhung by outcrop, so stratigraphic control over the

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collection may not be as tight as in other sections.) This interpretation stems from the fact that there are approximately 5 times as many representatives of New Genus A *kermiti* than New Genus A *salamandar* in our collection, and that collections were built over the course of many trips, by numerous workers, to the same 30-40 meters of laterally exposed outcrop.

The position of New Genus A *salamandar* in the cladistic study has been commented on above. As for autapomorphies for this species, none are generated using the characters in this study.

Genus *Boeckops* CHLUPÁČ, 1972

Diagnosis: See CHLUPÁČ (1977) for full diagnosis and his remarks.

Discussion: This taxon began as a subgenus of *Phacops*, but was essentially elevated to the generic level by STRUVE (1982), as a byproduct of his work on *Geesops*, and was first treated as a full genus in print in the work of FLICK AND STRUVE (1984). Few other authors have treated it as a full genus since then.

Boeckops was portrayed by CHLUPÁČ (1972; 1977) and CAMPBELL (1977) as a group characterized by morphology intermediate between that of *Phacops s.s.* and *Reedops s.s.*, and this is truly the case with the specimens encountered in this study. Specimens added in this study (such as *Reedops pembertoni* n. sp.) further blur the lines between *Phacops, Reedops,* and *Boeckops*, because the pygidial characters and vincular furrow seen here are much more akin to *Reedops*, yet members of this species meet most of the diagnostic criteria set out by CHLUPÁČ for *Boeckops*. This is one area where extensive cladistic work is necessary to clean up the rather arbitrary assignment to one of these three genera, as there appear to be few consistent diagnostic differences between them.

The initial (tentative) placement of this genus within the cladistic analysis of this study suggests that it is much closer to species traditionally viewed as members of *Phacops* than to those traditionally viewed as members of *Reedops*. The specimens that would surely have fallen within this taxon if grade-based taxonomy were to be used, were

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found to be just outside the branch containing the type species of this genus in the cladogram. If more taxa were to be included in future analyses close to this section of the tree, it is felt that this distinction would likely be lost, so the new Moroccan material is assigned to this genus without hesitation.

Boeckops stelcki n. sp.

Plate 15.1-15.10; Plate 16.1-16.6; Text Figure 9

Localities, type and figured material: Holotype UA6897, from the *Moroccanites* couche (horizon), at Taharajat d'Oufatene (TT-02), near Alnif, Morocco. Strata are Emsian in age and part of the Bou Tiskaouine Formation (MORZADEC, 2001). Paratypes UA6898-UA6903.

Etymology: This species is named in honour of DR. CHARLES R. STELCK.

Diagnosis: *Boeckops* with large glabellar length (sag.), width (tr.), and moderate overhang; dorsal surface of glabella with low dorsal convexity, but glabella otherwise bulbous; eyes bear 18 vertical files of lenses, with maximum of 8 lenses per file, and are borne low on cephalon; small subocular slope between visual surface and genal field; sculpture is of fine tubercles, that are lower across more dorsal surfaces of glabella and thorax; pygidial axis contains 8 rings plus terminal piece, and pleural region contains 6 discernible ribs; pygidium is short (sag.).

Description: Cephalon is elongate compared to species of *Phacops*, producing semi-ellipse in dorsal outline, with genal angles extending well behind occipital ring; small holaspides have even more elongate cephalon due to more pronounced glabellar contribution. Viewed laterally, glabella is long (sag.) and has low dorsal convexity, protrudes about 0.7 of visual surface's height above eye, and extends 0.8-0.9 of visual surface's length ahead of eye; eye is born low on cephalon, providing unobstructed lateral view of intercalating ring and L1 lateral lobe. Angle of glabellar divergence is approximately 70-75°, an formed by broad, shallow axial furrows. Axial furrows are

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uninfluenced by glabellar furrows ahead of S1, but deviate medially and become sharp and deep near contact with anterior part of palpebral lobe, as eye encroaches upon glabella; furrow retains narrowness along anterior edge of eye, but shallows farther forward. Preglabellar furrow is well impressed, round-bottomed, and consistent throughout its anterior portions, but becomes shallow and angular adjacent to axial furrow; glabellar overhang of furrow is moderate; medial 2/3 of furrow deviates slightly ventrally, medially, producing weak 'm-shape' in anterior view. Glabellar sculpture composed of small, low-profile, conical tubercles of fairly uniform size; tubercles widely distributed on dorsal surface, but are more densely packed on front of glabella; very small tubercles occur sparsely between large ones, and become slightly more common in anterior portions of glabella and genal field.

Glabellar furrows are shallow in all specimens and may be difficult to see in larger holaspides. Medial portion of S3 is exceedingly shallow, trends about 12° behind transverse plane, and has minor posterior-facing concavity; lateral branch of S3 is slightly recurved, trends subparallel to axial furrow, and is separate from medial branch. S2 is almost straight, but develops slight anterior-facing concavity in distal portions; it trends about 25° behind transverse plane, is best defined of sulci in frontal lobe, yet does not delineate L3 from remainder of glabella's dorsal surface. L2 is narrow (exsag.) and rectangular in medial portions, and bears subtriangular distal tip; distal termination against apodeme is sharp because there is little slope in distal portions of L2. Intercalating ring (L1 medial) is shaped like short isosceles triangle; defined by S1 fading to mild depression in medial 1/3rd, trending parallel to S2, and deepening laterally en route to distal apodeme; S0 forms base of triangle with narrow (exsag.), shallow furrow which is deflected sharply backward by L1 distally. Fine tubercles (comparable to glabella's) occur as single cluster on faint pad medially. Lateral part of L1 is distinctly dorsally inflated (domed), and bears few fine, slightly ovoid tubercles. Occipital ring is broader (exsag.) than adjacent thoracic axial rings, and does not have bulbous lateral lobe, while still displaying posterior 'wing' seen in lateral lobe of thoracic segments (see below for detailed description).

Eye is borne low on cephalon, with palpebral area (proximal to palpebral furrow) sloping ventrally to reach palpebral lobe, and displaying strong dorsal convexity with tiny

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tubercles and pits on dorsal surface; back of fixigena extends laterally into mid-sized postocular pad, and is separated from palpebral lobe by sharp and relatively deep palpebral furrow, which shallows anteriorly. Palpebral lobe is flat and slightly downturned distal to palpebral furrow; bears mid- to small-sized tubercles; has narrow (tr.) barren space adjacent to palpebral rim with 2-3 large depressions widely spaced within; palpebral rim is raised lip (with little lateral extension) bearing densely packed tubercles, many of which are elongated (exsag.). Eye is large (0.40 of total cephalic height, 0.46 of total cephalic length); is tightly adpressed behind glabella, with anterior margin forming slight indentation in side of glabella, and minor lateral protrusion of visual surface; visual surface overhangs ventral margin of cephalon due to cephalic narrowness (tr.) and vertical orientation of genal surfaces. Visual surface bears 18 vertical rows of lenses, with maximum 8 lenses per row, and 90-110 as typical lens totals per eye (see Text Fig. 9 for complete lens formula); interlensar sclera makes minor contribution to visual surface, but is more prominent in regions of small lenses (upper, middle portion of surface), and contributes to band at base of eye. Lens surface typically convex, extending well above sclera, nearly contacting vertical neighbours, (but slightly more distant from horizontal neighbours); crowding creates adpressed or conjoined lenses in posterior portions of many eyes. Lens-free edges of visual surface are narrow due to intrusion of lenses into area; eye margins still maintain smooth transition into surroundings, are inflated along anterior margin, are rather abrupt ventrally, and are inflated along posterior margin (with occasional lens intruding). Ventral margin of eye extends laterally as much as anterior genal field, producing deep, round-bottomed subocular groove with small patch of very fine, anteroposteriorly elongate tubercles in its posterior half. Postocular pad is consistently narrow (exsag.) throughout, with slight flare before distal termination; is delineated by shallow, round furrows; and bears numerous very fine tubercles with no fixed arrangement in its distal reaches.

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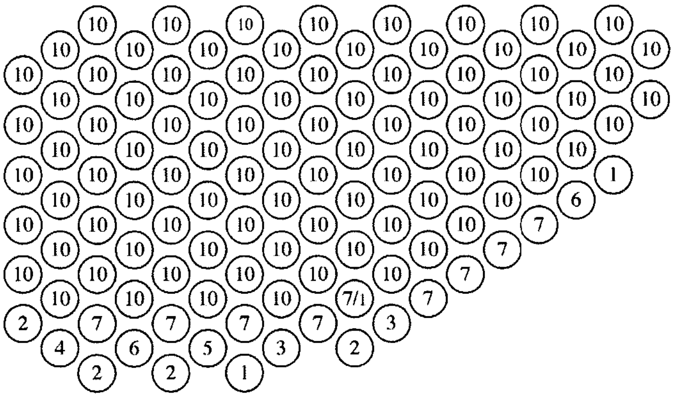

Text Fig. 9: Lens formula diagram for *Boeckops stelcki* n. sp. specimens

Genal angle has short (exsag.), rounded corner with small subangular apical tip; near equality in posterior border and lateral border forms 'boomerang-like' shape; vertical orientation of outer portion of genae contributes to narrow (tr.) cephalon. Genal sculpture is densely packed; ranges from small to large domed tubercles, with granules filling spaces between; tuberculate sculpture fades and becomes elongate (exsag.) in ventral positions, to eventually form abbreviated terrace lines along margin, ahead of posterior facial suture, and nearly barren field behind facial suture; tubercles become more prominent and conical along trailing edge of posterior border, and coarser and more bulbous beneath eye.

Facial suture remnants are more prominent than in most species of *Phacops*; posterior arm traces are clear, convex-forward, and forming semi-circular arc through genal field, but lose topographic distinction adjacent to postocular pad; anterior arm may contribute to sharp contact between glabella and genal field, but loses all definition outside of contact.

Ventral margin is rectangular in section in medial positions, and becomes more circular laterally; anterior/lateral prominence of margin diminishes posteriorly, becoming negligible behind posterior arm of facial suture; ornament consists of fine terrace lines along lateral and anterior surfaces, ventral surface is similar in lateral portions but terrace lines become foreshortened approaching mid-line. Vincular furrow is firmly impressed around whole ventral surface, with broad, round-bottomed furrow narrowing slightly adjacent to its lateral notches; granules are present on all surfaces. Lateral notches are more deeply incised than remainder of furrow; become more sunken in posterior

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portions; and appear to have more steeply inclined medial faces than lateral faces. Medial rim does not protrude as far ventrally as in most species of *Phacops*.

Doublure surface is almost flat from anterior to posterior, with mild ventral bulge in posteromedial section to match hypostome contact; transversely, surface extends ventrally to approximate contours of glabella in medial positions, and sweeps to near vertical orientation near vincular facets. Doublure ornament consists of broken terrace lines that trend parallel to nearest margin in anterior and lateral extremes of surface and rapidly become fragmented and foreshortened in posteromedial positions, leaving only elongate (tr.) granules near contact with hypostome. Doublure projects ventrally below margin of cephalon, producing minor 'lip' in lateral view.

Hypostome is unknown for this species.

Thorax composed of 11 segments; width (tr.) of axial ring to width of whole segment is approximately 0.42 in anterior segments and 0.40 in posterior segments; posteriormost segment is about 0.8 width (tr.) of anteriormost segment, showing weak taper in thorax. Axial rings of thorax are well rounded dorsally, and have very distinct lateral lobes. Medial lobe is flat-topped, with rounded trailing edge and long, gentle slope leading down to articulating half-ring. Sculpture occurs along most of dorsal surface; consists of numerous small to medium conical tubercles with spacing roughly equal to tubercle size; becomes more pronounced and densely packed along trailing edge, and sparse along leading edge. Lateral lobe is separated from median part by pronounced, broad furrow originating near thoracic apodeme (anterior), fading and turning posterolaterally near middle of ring, and terminating along trailing edge of axial ring. Lateral lobe has two components; anterior component is largest, bulbous, and sculpted with small to medium tubercles and few elongate granules concentrated around dorsal extreme; posterior component is smaller, only slightly inflated, separated from anterior component to varying extents (more so in large holaspides), forms small 'wing' trailing posteriorly off axial ring, and bears small to medium sized tubercles concentrated along its posterior edge; posterior component is reduced in posterior thoracic segments, and is less pronounced in small holaspides. Articulating half-ring separated from axial ring by round-bottomed furrow that is steeply sloping against half-ring and shallow against axial ring; furrow appears to intrude into axial ring near midline; half-ring has very fine

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granules along its posterior half. Axial furrow is round in profile; strongly impressed behind anterior pleural band, but fades across band; has posterior 'wing' from lateral axial ring lobe overhanging in anterior segments. Anterior band of pleura is rounded (dorsally) in proximal positions; only sculpture is patch of small tubercles adjacent to distal tip, concentrated along leading edge. Posterior band sits higher than anterior band; is strongly rounded (dorsally) and becomes less so in distal and proximal positions; sculpture consists of small to large domed tubercles that begin as faint band across dorsal surface, and become quite prominent and densely packed near and distal to fulcrum; sculpture coarsest near middle (exsag.) of segment, and forms ridge of dense, small tubercles adjacent to articulating facet. Pleural furrow begins at axial furrow; consists of a narrow (especially in proximal positions), angular trench, that breaches rim of articulating facet to terminate distally in fine, concave-forward arc extending across posterior half of facet and 1/3rd of distance down it. Articulating facet is flat and bears granules across its surface; granules are concentrated along trailing edge and become faint in anterior half of facet. Thoracic segment tip has rounded square appearance due to significant posterolateral flange at posterior corner; flange and doublure both bear fine granulation.

Pygidium markedly short (sag.) compared to width (tr.), with total width 1.75 times that of length; elliptical in dorsal outline, and strongly convex dorsally. Axis of pygidium is prominent; shaped like blunt-tipped cone with slight flare to front; composed of 8 rings plus terminal piece; last 2 rings poorly defined but discernible due to rows of tubercles; axial width (tr.) is approximately 0.36 of total pygidial width in anterior section; taper is fairly strong, with approximately 25° convergence angle, heading posteriorly; terminal closure begins adjacent to second last ring, but is not strong, terminal piece slopes into pleural field. Ring furrows reach axial furrows in first 5 rings; creating posteriorly directed depressions in axial furrow behind first 3 rings. Ring furrows are partially filled by small, narrow (sag.) interannular rings behind first 3-4 axial rings. Interannular rings bear granules and produce slight indentations in posterior edges of preceding axial rings. Axial ring sculpture consists of densely packed, medium to small, conical tubercles across dorsal surface; sculpture restricted to single row of tubercles in segments 6-8, and diminutive in anterior and lateral portions of axial rings.

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Axial furrow is broad and round-bottomed; fades next to last axial ring; has faint or no true closure, dissipating behind terminal piece at low postaxial ridge in pleural field. Pleural region of pygidium has 6 discernible ribs, with fifth and sixth faint and defined by shallow furrows and sculpture rows. Three pleural furrows are deep and plainly visible, and 3 more become progressively fainter posterior to these; all run relatively straight courses; furrows extend about 2/3rd of way through pleural field. Interpleural furrows are barely visible on first 3 ribs, being very shallow and visible largely due to rows of tubercles running parallel courses. Pleural field has scattering of small tubercles, which are accompanied by faint pits in ventral reaches of larger holaspides. Ventral margin forms slight, laterally extending rim, with granules along ventral surface.

Discussion: *Boeckops stelcki* n. sp. differs greatly from all other Moroccan phacopids encountered in this study. It also differs significantly from other species attributed to *Boeckops* by other authors. *Boeckops boecki* (HAWLE AND CORDA, 1847) is very similar in most regards, but lacks the pervasive, much denser and more evenly distributed fine tubercles seen in *B. stelcki*; has a much broader (exsag.) postocular pad; typically has 3 additional vertical rows of lenses within its eyes; and possesses a much longer (vertical) slope between the bottom of the visual surface and the contact with the genal field. *Boeckops propontius* (HAAS, 1968) is also fairly similar in overall morphology, but close examination shows that this species lacks most of the sculpture seen in *B. stelcki*; as well as having a wider (exsag.) postocular pad; a shorter visual surface with the same number of vertical rows, but 2-3 less lenses per row; an eye that is borne much higher on the cephalon; a more expansive genal angle and anterior genal field; and a slightly more elongate glabella, relative to the length (exsag.) of the visual surface.

The large-scale cladistic analysis places *Boeckops stelcki* n. sp. at the base of the sister group to *Boeckops boecki*, but this is likely an inaccurate depiction of its true relationship. The exhaustive analysis of just the lower half of the large-scale group placed these two taxa on the same clade, united by the (locally) synapomorphic possession of a wide pygidial axis (19=2), well-defined lateral axial lobes within the thorax (16=2), and prominent L1 lateral lobes (4=2). The addition of more taxa pertinent to this region of the tree might eliminate the separation between these two taxa seen in

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the larger cladogram. Autapomorphies for *B. stelcki* (in the large-scale analysis) include the locally unique possession of a narrow postocular area (8=0), and weak thoracic taper (29=1).

Aside from a single incidence of clear teratology within one eye (and lens fusion within another), there were remarkably few asymmetries within this species. Coupled with the bizarre occurrence of lens fusion, this regularity may make *B. stelcki* a worthwhile subject for future growth studies on lens development.

New Genus B

Discussion: New Genus B is an informal grouping of tuberculate Moroccan phacopids that grade-based taxonomy would include within *Phacops* or *Paciphacops*, but would render either taxon polyphyletic if the cladistic analysis performed in this study is taken as absolutely correct (which is unlikely). In an attempt to avoid excessive taxonomic 'splitting' this group is treated as an informal taxon until more detailed analyses can be completed, and its members are referred to as New Genus B species for now.

The cladistic analysis is slightly at odds with the fine-scale stratigraphic data for the occurrence of these species within the Ma'der basin of southern Morocco. In order of occurrence the sequence from earliest to latest is: New Genus B *ovatus,* New Genus B *forteyi,* New Genus B *granulops,* New Genus B *lebesus* – which is basically inverted in the large-scale cladogram (in Chapter 2). This is most likely a consequence of the large number of autapomorphies seen in New Genus B *forteyi* (there are 6, one of which is unique for the whole ingroup), while most other taxa in this clade have 1 or 0 autapomorphies, and at most 3 synapomorphies uniting sister groups.

New Genus B is united by the (locally) synapomorphic possession of a palpebral lobe that sits lower than the palpebral area (10=2), a palpebral lobe and area with no pitting between tubercles (14=3), and an eye with 19 vertical rows of lenses in its visual surface (25=3, with a reversal in New Genus B *forteyi*). With a Bremer support number of 2, this clade is fairly robust in this analysis.

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New Genus B *granulops* (CHATTERTON *et al.*, 2006)[3]

Plate 17.1-17.10; Plate 18.1-18.12; Text Figure 10

2006 *Phacops granulops* CHATTERTON *et al.* – CHATTERTON *et al.*, Middle Devonian Trilobites, Morocco: p.12; Pl. 1-2.

***Type material and locality*:** Holotype enrolled exoskeleton UA13295, from the upper Emsian Timrhanrhart Formation, basal part of section at Jbel Gara el Zguilma (ZGEE1), near Foum Zguid, Morocco. Paratypes UA13296–UA13300, UA13302.

***Diagnosis*:** *Phacops*-like with large conical (hemispherical when worn) tubercles (up to 0.8 mm diameter); long, low eyes that have 19 files of up to 6 lenses (but typically 4–5) per file (Text Fig. 10); short (sag.) glabellar profile that appears tilted upward and forward relative to eyes in lateral profile; postocular pad is present, with tubercles concentrated distally; distinct row of small tubercles skirts eye lobe below lenses.

***Description*:** Cephalon is broad and rounded in dorsal view, progressing from subtriangular outline in small holaspides to semicircular outline in large holaspides. In profile, when eye is horizontal, top of glabella is both convex dorsally and slopes upward forward, with apex near front of glabella, in front of eyes; and anterior part is sub-vertical. Anterior divergence of axial furrows on either side of frontal lobe of glabella ranges from 70–80° (n = 6); firmly impressed axial furrows are not quite as divergent forward opposite L1, and diverge backward slightly or are sub-parallel opposite occipital ring; axial furrows are deepest opposite front of eyes, and are distinct but not deep, curving inward to merge with preglabellar furrow in front of eyes. In dorsal view, glabella is rounded sub-pentagonal in outline. In lateral profile, it has weakly convex dorsal surface that becomes more convex forward until it curves down sub-vertically at front, and overhangs short (sag.), comparatively smooth anterior border. Preglabellar furrow is distinct, and firmly incised. Sculpture consists of closely packed, tall, conical tubercles, with a subset of smaller tubercles interspersed between large tubercles, and

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[3] This species has been published recently in a monograph in which R.C.M. was a co-author, prior to the completion of this thesis.

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relative proportion of smaller tubercles and density of all tubercles increases on steep front of glabella; tubercles are absent on slopes into axial furrows, but dense up to edge of preglabellar furrow; tubercles are slightly smaller and more widely spaced on genal fields, palpebral lobes, L1 and occipital ring (L0); broad region of lateral border near genal angle and slightly farther forward is devoid of large tubercles. Small pits are present around lateral and anterior margins, between ridges that run parallel with and along margin. Lateral L1 is small, distinct, inflated, circular to slightly ovoid, and sculpted with small number of small tubercles; median part of L1 is lenticular, tuberculate, delineated anteriorly by moderately to firmly impressed, convex forward S1, and posteriorly by firmly impressed, sub-transverse S0. Distal parts of S1 and S0 are deeply impressed over apodemes; S2 is posterolaterally directed (about 20° from transverse line), distinct, dies out close to axial furrows, and is absent in median 1/3 of glabella; S3 is usually slightly shallower than S2, with median portion sub-transverse to slightly posterolaterally directed, usually slightly convex forward; lateral part of S3 may or may not merge with median portion, runs sub-parallel with axial furrows to region just in front of eyes.

Occipital ring is long (0.15 of length of cephalon) and wide (0.35 of width, tr., of cephalon), longer (sag.) medially than laterally behind L1 lateral lobes; occipital ring is very similar in form to anteriormost thoracic axial ring, and may have shallow transverse depression at midlength. Palpebral lobes are large and kidney-shaped in dorsal view, delineated medially by posteriorly deep and anteriorly shallow palpebral furrow that runs sub-parallel to facial suture; anterior margins of eye are adjacent to axial furrows, and posterior margins almost reach posterior border furrow. Posterior end of eye is distant slightly more than width of palpebral lobe from axial furrow, exsagittally behind anterior end of eye.

Eye has 19 files of lenses, with maximum of 6 (typically 4 or 5) lenses per file (53–72 large lenses per eye, usually plus 3 or 4 very small lenses near top of eye; Text Fig. 10); lenses are tightly packed towards base of eye, but with slightly more interlensar sclera towards top. Typical number of lenses per eye is about 70 (66, 72 and 74 counted for 3 specimens). Base of visual surface has distinct row or rows (1 or 2) of small tubercles running just below and parallel with base of lenses, for about half of length of

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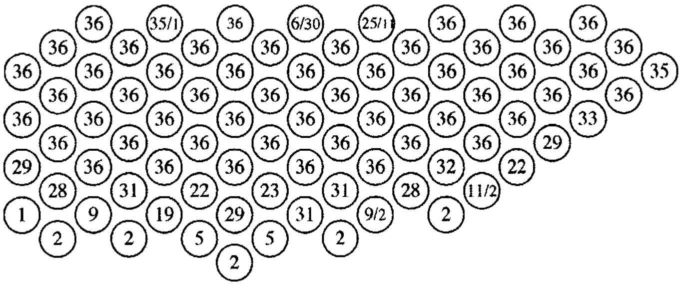
eye (extending from near anterior edge to slightly behind midlength of eye). Some specimens have eyes with typically one fewer lens per file than other holaspides of comparable size (up to 4 lenses per file). Sculpture on palpebral lobe is of moderate sized tubercles medially and fine tubercles along margin distal to narrow, shallow but discernible furrow that runs near and parallel to margin.



Text Fig. 10: Lens formula diagram for New Genus B *granulops* specimens

Sculpture on fixigena is of tubercles only slightly smaller than those on top of glabella. Narrow, low, almost recessed, socle-like ridge lacking in tubercles runs around and under anterior two-thirds of eye. Postocular pad occurs below and behind posterior third of eye, with distal part sculpted by number of tubercles, but short (exsag.) proximal part behind eye is smooth or has few sparse, fine tubercles. Shallow pits may take place of tubercles in ventral half of genal field; distal part of region between genal angle and eye has few or very small tubercles. Facial suture is fused in adults, but can be traced, showing usual path for genus. Posterior border is longer (exsag.) distally than proximally, and has sparse, low tubercles proximal to fulcrum, and more numerous and more prominent tubercles distally, particularly close to posterior margin. Tubercles are abundant on anterior part of genal field, distal and more posterior parts of posterior border, and upper part of genal field outside socle-like ridge. Posterior border furrow is deep, concave, and runs outward slightly behind transversely proximally, and then curves forward and inward around postocular pad distally to disappear against posterior end of subocular socle-like ridge. Sculpture on median part of cephalic doublure consists of numerous short terrace ridges that run sub-parallel to margins; ridges on doublure are shorter and more granulose, with more posteromedian long axes, posteromedially.

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Continuous vincular furrow is present medially, and vincular groove continues laterally but is serrated by vincular notches for tips of thoracic segments. Back of median portion of doublure is slightly turned ventrally, and convex backward to fit anteromedian part of hypostome (Pl. 18.3).

Hypostome is shield-shaped. Width (tr.) is almost twice length (sag.) due to broadly splayed anterior wings. Hypostomal suture bows forward smoothly in an arc. Anterior lobe of middle border is large, slightly inflated and subcircular in outline. Posterior lobe is much smaller and crescent-shaped, delineated from anterior lobe by shallow, posteriorly convex middle furrow. Maculae are not distinct. Sculpture consists of fine, discontinuous asymmetrical (steep side forward) terrace ridges that run subparallel with middle furrow. Lateral and posterior border furrows are shallow. Anterior border furrows are shallow, and converge with anterior margin to disappear at anterior margin medially. Sides of hypostome converge backward. Posterior margin is not well preserved on specimens available to us, but it seems to be convex backward (possibly angular).

Thorax has 11 segments. Ratio of width (tr.) of axial ring to width of whole segment is fairly consistent from front to back of thorax (about 0.35–0.42, n = 3). Thorax tapers backward so posteriormost segments are about 0.75 of width (tr.) of anteriormost segments. Sculpture of scattered fine tubercles is most prominent on more dorsal parts of axial rings and more distal and posterior parts of pleural ribs. Articulating facets are minutely granulose. Distal tips of segments are granulose. Axial rings are moderately arched dorsally, slightly convex forward medially, and concave forward distally. Change in direction of articulating furrow corresponds with short furrow that extends backward part way across ring, delineating distal from medial parts of ring. Even shorter indentation occurs in back side of ring slightly farther from sagittal line. Dorsomedian part of axial ring may be indented by very shallow transverse furrow near midlength of each ring. Pleural furrows are firmly impressed and they extend outward about 15° behind transversely, and shallow abruptly adjacent to large articulating facets, disappearing in upper regions of facets.

Pygidium is 0.68 of length (sag.) of cephalon, and is fusiform in plan view. Maximum width (tr.), near midlength, is about 0.73 width of cephalon. Axial furrows are

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firmly impressed. Axis tapers backward, most strongly posteriorly, but also slightly more strongly near front of axis than near midlength. 8–9 axial rings plus very short (sag.) terminal piece are present. Anterior rings are longer and more distinct than posterior rings. Pleural ribs are almost straight and directed posterolaterally. About 6 pleural furrows are moderately impressed, and 5–6 interpleural furrows are much shallower. Both sets of furrows die out before reaching margin, leaving comparatively smooth border, not delineated by furrow. Sculpture of fine tubercles is present on axial rings and both anterior and posterior pleural ribs, but absent or particularly sparse on border.

***Discussion*:** New Genus B *granulops* is most similar to *Phacops* (*Phacops*) *tafilaltanus* ALBERTI, 1983 (1983, fig. 12), New Genus B *lebesus* (CHATTERTON *et al.*, 2006), and New Genus B *ovatus* n. sp. (see below under latter two species for their comparison). New Genus B *granulops* differs from *P. tafilaltanus* in that its visual surface appears generally more rounded in lateral view—the ventral margins bow ventrally near the midpoint, and the anterodorsal corner of the visual surface is significantly more rounded. Other qualitative differences include more pronounced and dense tuberculation on the glabella of New Genus B *granulops*, as well as more incised lateral branches of the S3 set. Quantitative differences include an additional dorsoventral file of lenses within the eyes of New Genus B *granulops* (19 compared to 18 typical for *P. tafilaltanus*), and an additional lens per file in most of the rows near the middle of the eye in New Genus B *granulops*. The eye is closer to the posterior border furrow in New Genus B *granulops*, resulting in a postocular pad that is smaller in area, but much more distinct.

New Genus B *granulops* shares gross-morphological features with *Phacops* (*Phacops*) *turco praecedens* HAAS, 1968 (pl. 30, fig. 6, *non* fig.7). These two species can be distinguished by the lack of a socle in New Genus B *granulops*, as well as coarser glabellar tuberculation, less inflated anterolateral glabellar 'corners', a longer (exsag.) posterior border, a less pronounced postocular pad (that is more rounded distally, and more closely parallel with the base of the eye), and by a conspicuous patch of non-sculpted gena (ventral to the postocular pad, along the fused facial suture). Furthermore, there is a suite of characters associated with the eyes that separate these species. In New Genus B *granulops* there are a similar number of lenses in each vertical file, but there is

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one more vertical file present. There is also a significantly more rounded anteroventral corner to the visual surface, and an inflated, tuberculate ventral margin to the visual surface. These features, coupled with the more ventral position of the eye and its more prominent sclera, give New Genus B *granulops* a more 'drop-shaped' eye in lateral view, something that becomes more pronounced in larger holaspides.

New Genus B *granulops* also bears a resemblance to *Phacops degener* BARRANDE, 1852 (see CHLUPÁČ, 1977, pl. 9), and *Phacops major* BARRANDE, 1852 (see CHLUPÁČ, 1977, pl. 10), but the similarity is largely superficial, and much weaker than to the taxa discussed above.

Cladistic analysis places New Genus B *granulops* as the sister group to New Genus B *ovatus* and New Genus B *forteyi*, but (as was discussed under the generic discussion) this placement may be misleading. In the topology advocated by the large and fine-scale analyses, New Genus B *granulops* is united with its sister group by the (local) synapomorphy of having 5 lenses as the maximum typical number in a single file (26=3, with a reversal in New Genus B *forteyi*), and New Genus B *granulops* has no autapomorphies.

New Genus B *lebesus* (CHATTERTON *et al.*, 2006)[4]

Plate 19.1-19.9; Text Figure 11

2006 *Phacops lebesus* CHATTERTON *et al.* – CHATTERTON *et al.*, Middle Devonian Trilobites, Morocco: p.14; Pl. 3.

***Type material and locality*:** Holotype enrolled exoskeleton UA13304, from bed ZGEE3 (Eifelian), Timrhanrhart Formation, Jbel Gara el Zguilma, in the Tindouf basin south of Foum Zguid, southern Morocco. Alternative localities include the contemporaneous *Thysanopeltis/Harpes* couche, in the El Otfal Formation, at the bou Dib section, near the town of the same name, in the Ma'der basin of southeast Morocco (BULTYNCK AND WALLISER, 2000). Paratypes UA13303, UA13305.

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[4] This species has been published recently in a monograph in which R.C.M. was a co-author, prior to the completion of this thesis.

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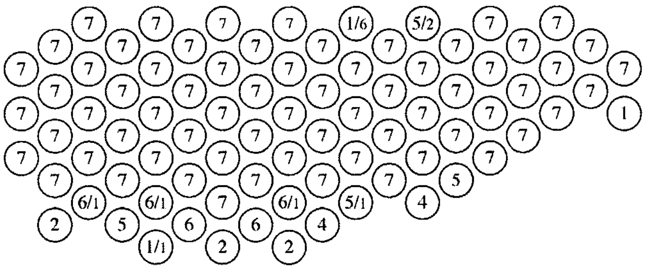
Diagnosis: *Phacops*-like with short row of large, tall tubercles on base of visual surface; sculpture on glabella of coarse tubercles; sculpture on occipital ring is of numerous small tubercles on raised rim at back of occipital ring and fewer tubercles on lenticular portion of ring farther forward; large gap between tuberculose sculpture of free cheek and base of eye; eye with 19 files of up to 6 lenses per file; frontal lobe of glabella only moderately divergent forward 60–70°; S1 is shallow medially in front of lenticular median portion of L1; postocular pad is comparatively large, low, and with very few tubercles.

Description: This species is so similar to New Genus B *granulops* new species (described in detail above) that the differential diagnosis provided below under the discussion suffices for a description of New Genus B *lebesus* new species.



Text Fig. 11: Lens formula diagram for New Genus B *lebesus* specimens

***Discussion*:** New Genus B *lebesus* occurs almost 50 meters stratigraphically above New Genus B *granulops*, in the same section. It differs from that species in having slightly fewer, coarser tubercles on the glabella; the tubercles on the occipital ring are concentrated on a posterior marginal ridge or more sparsely scattered in the lenticular anteromedian portion; a low, lunate lobe without tubercles occurs under the anterior two-thirds of the eye in each of these species, but the lobe is much wider (tr.) in New Genus B *lebesus* than in New Genus B *granulops*; the anterior lobe of the glabella is less divergent forward (60–70° in New Genus B *lebesus* and about 70–80° in New Genus B *granulops*); and the postocular pad is larger but lower, and has fewer, smaller tubercles on New Genus B *lebesus*. These differences certainly warrant separation of these two forms at the species level. However, given the great similarity in other characteristics of these species

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and their relative stratigraphic positions in the same section, in rather similar lithofacies, it is likely that New Genus B *granulops* was ancestral to New Genus B *lebesus.*

Comparisons to taxa such as *Phacops turco praecedens* HAAS, 1968 show New Genus B *lebesus* to be even more disparate in morphology than was New Genus B *granulops.* New Genus B *lebesus* may have slightly more similar eyes to the other taxon, but has a much narrower glabella with a lower degree of anterior divergence to its axial furrows; lacks its strong postocular and subocular pads with pronounced sculpture; and has coarser, more widely spaced glabellar tubercles.

The pillar-like eye and strand of coarse tubercles upon the base of its visual surface in New Genus B *lebesus* invites comparison to *Eldredgeops rana africanus* (BURTON AND ELDREDGE, 1974), as well as *Geesops sparsinodosus sparsinodosus* (STRUVE, 1970). These latter taxa are hugely different in that they have a much wider glabella, pustulose sculpture elements, and thick interlensar sclera, as well as a host of smaller differences.

The cladistic analysis placed New Genus B *lebesus* n. sp. as the sister group to all other members of New Genus B (but again, this may not be the most realistic hypothesis of relationship). New Genus B *lebesus* showed a single (local) autapomorphy, the possession of coarse tubercles in a moderately dense arrangement (7=2).

New Genus B *ovatus* n. sp.

Plate 20.1-20.11; 21.1-21.10; 22.1-22.4; Text Figure 12

Localities, type and figured material: Holotype UA6908, from the *Moroccanites* couche (horizon), as it appears at Taharajat d'Oufatene (TT-02), near Alnif, Morocco. Alternative specimens come from the *Metacanthina* couche[5] at Taharajat, which is stratigraphically separated from the *Moroccanites* couche by three meters. Strata are upper Emsian to lower Eifelian in age and part of the Tazouläit Formation (BULTYNCK AND WALLISER, 2000). Paratypes UA6909-UA6919.

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[5] '*Metacanthina* couche' is the locally used name for a trilobite horizon that is actually rich in *Hollardops* specimens; it is a bit of a misnomer, but is retained here because of its widespread use.

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Etymology: This species is named for the distinctive ovoid tubercles borne along the dorsal surface of its occipital ring and all thoracic axial rings; hence the Latin adjective *ovatus* is used.

Diagnosis: *Phacops* with abnormally elongate (tr.) large tubercles across axial surfaces of thorax and covering occipital ring; eyes bearing 19 vertical files of lenses with maximum of 6 lenses per file (more commonly 5); strong postocular and weak subocular pads are present, with varying tubercular sculpture; inflated glabella bears low conical tubercles (up to 1.0 mm in diameter) and extends dorsally above top of eye to height equal to that of visual surface; visual surface bears row of fine tubercles along anterior half of its ventral edge.

Description: Cephalic outline is nearly semicircular in dorsal view, but with genal angles and occipital ring protruding significantly towards posterior; smaller holaspides have more prominent glabella, and narrower (tr.) cephalic outline. In lateral profile (with palpebral lobes horizontal), glabella extends dorsally above top of eye for distance equaling visual surface's height, but bulbous shape of glabella results in sharp posterior downturn aligning S1 furrow with posterodorsal corner of eye, and anteriormost projection of glabella to occur within approximately one eye's length (exsag.) of eye's anterior edge (0.88-1.07, with ratio lower in larger holaspides). Glabella is bounded by deep axial furrows that diverge at 69-75°, straight course of furrows is uninterrupted by glabellar furrows ahead of S1, but veers more posteriorly around lateral L1 lobes; axial furrows are narrowest adjacent to anterior edge of eye, but rapidly shallow next to ventral corner of eye in order to join preglabellar furrow. Preglabellar furrow is round in section, and becomes narrower as glabellar overhang increases nearer to midline (glabellar overhang is small, presenting nearly vertical anterior face); medial half of furrow deviates slightly ventrally around tip of glabella (medially), producing low 'm-shape'.

Sculpture on glabella consists mainly of large hemispherical to wide conical tubercles, which occasionally display change in slope near tip (producing mammalon-shapes); large tubercles are separated from neighbours by gaps equivalent to their own

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width, and sparse, much smaller tubercles in varying sizes occasionally fill gaps; tubercles become progressively smaller and more densely packed near anteroventral portion of glabella.

L3 matches profile of frontal lobe and is defined by weak medial S3, with much deeper lateral branch, and moderately impressed S2; S3 medial portion trends transversely and is slightly convex-forward, while lateral/anterior ramus is separate, straight, and subparallel to axial furrow; S2 is straight, trends 20° behind transverse plane, and dies out before intersecting axial furrow. L2 is narrow (exsag.) and angular in appearance; adjacent S1 forms steep slope to meet intercalating ring (which is considerably lower), creating square-cornered sulcus. Intercalating ring is triangular in dorsal view with S1 that runs subparallel to S2, fades medially, and occasionally has small tubercles in medial portions; lobe bears raised pad with 4-5 tubercles, and intrudes into posterior edge of glabella. S0 is straight, round-bottomed, and fairly deep medially with slight shallowing before butting out against middle of lateral L1's. Lateral L1 is strongly inflated (hemispherical or slightly elliptical) and sharply defined by furrow pit above straight anterior apodeme, concave-forward posterior apodeme, and axial furrow (which is narrowed in this vicinity); variable numbers of small tubercles adorn highest points of lobe.

Occipital ring is very similar to thoracic axial rings in ovate tubercle sculpture and general shape, but is slightly longer (sag.), and has less defined lateral lobes. Fixigena, proximal to palpebral furrow, is well defined, strongly convex (dorsally), and raised above remainder of fixigena, yet appears sunken due to prominence of eye (especially compared to posterodorsal corner of eye); region bears mid-sized conical tubercles along its highest surface; posterior distal tip of region flows seamlessly into narrow (exsag.) postocular pad, which bears two strands of fine tubercles containing varying numbers of loosely organized tubercles, generally paralleling long axis of pad; distal tip of pad fades gradually into posterior border furrow, but sulci on anterior and posterior margins remain distinct until very tip. Palpebral furrow is distinct along its entire length, and becomes progressively deeper toward posterior corner of eye. Palpebral lobe has strong dorsal convexity, and deviates from contours of fixigena in posterior reaches; sculpture consists of three rows of conical tubercles paralleling palpebral rim

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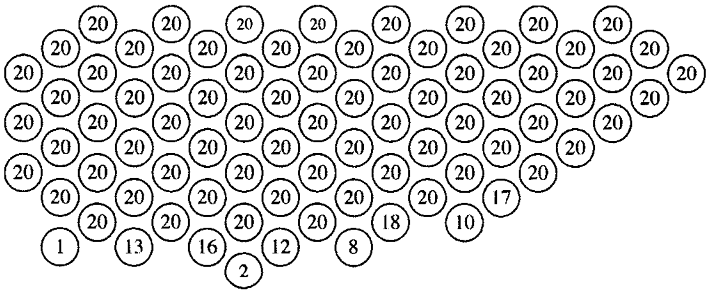
and composed of progressively larger tubercles in more distal rows; space between palpebral lobe and palpebral rim is occupied by mild sulcus with 2-3 invaginations (typically near middle of eye) which are as large in area as biggest tubercles, but shallow, and have small tubercles situated between them. Palpebral rim is prominent and projects laterally farther than lenses project out of visual surface (providing narrow lens shade); small tubercles cover most of rim's surface.

Eye is fairly small overall (0.25-0.31 of total cephalic height, and approximately 0.43 of total cephalic length); is closely appressed to side of glabella anteriorly, and matches contours of gena exceptionally well. Visual surface bears 19 rows of lenses, with 5 (and occasionally 6) as maximum number of lenses per row, and 72-79 as typical total number of lenses per eye (see Text Fig. 12 for full lens formula). Sclera maintains fairly even spacing of lenses, even in areas of reduced lens size (upper, middle portion of eye); lenses are always fully separated by sclera, but nearly contact in crowded regions; sclera is prominent, projecting almost as far outward as lenses do in upper portions of eye, but crowding of lenses reduces this prominence near margins of eye. Lens distribution does not extend to very margin of eye, leaving space for rounded smooth anterior and posterior margins, and ventral margin covered by a field of low profile, variably positioned, shaped, and sized tubercles in anterior but not anteriormost half of eye. Shallow, broad subocular groove is occupied by weakly defined subocular pad with small number of conical tubercles in varying sizes.



Text Fig. 12: Lens formula diagram for New Genus B *ovatus* n. sp. specimens

Genal angle is long (exsag.) and much taller than eye in larger specimens; tip of genal angle is smooth and gently rounded; sculpture consists of low, broad, hemispherical

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tubercles ranging in size from very small to as large as glabellar tubercles, and becoming more conical in shape heading anterior in genal field; sculpture fades near ventral margin of cephalon, and is interspersed with small tubercles near posterior terminus of facial suture. Inflation and dorsal projection of genal field is great and continues forward under most of eye, intruding into subocular groove ahead of posterior branch of facial suture. Posterior border is fairly wide, presenting flat lateral face and rounded dorsal surface, both with sculpture concentrated along trailing edge; sculpture composed of low, rounded tubercles that become more transversely elongate in posterior positions, and diminish in numbers in more medial positions. Posterior border furrow is deeply impressed medially, but shallows adjacent to postocular pad, and fades while wrapping around distal tip of postocular pad.

Most ventral anterior and posterior sections of fused facial suture are traceable on some specimens (as concave-forward arc originating from axial furrow, and convex-forward arc across cheek, respectively), but are accompanied by only slight topography shifts and very mild interference in sculpture patterns.

Ventral margin consists of semicircular (in section) bead that is consistent in thickness throughout its extent, but loses lateral prominence near genal angle; anastamosing terrace lines cover exterior and ventral surfaces of margin, while granulation occurs along surface adjacent to vincular furrow.

Vincular furrow is deeply incised in all sections, with round-bottomed trough flowing smoothly beneath glabella, and broken into interconnected pits for thoracic segment tips, beneath genal field; granules are most prominent along anterior side of furrow, but are present along all faces. Doublure is fairly flat beneath glabella (extending only minor flange to match contact with hypostome), but rapidly swings into vertical orientation beneath cheeks; somewhat broken, wavy terrace lines cover vast majority of doublure, and run sub-parallel to nearest margin; terrace lines show minor deviations along their lengths – hinting at component ornament structures; terrace lines break down into elongate (trans.) granules in posteromedial portion of doublure. Doublure, along inner edge of vincular furrow, is distinctly lower than that outside furrow, forming protruding ‘lip’ visible in lateral view.

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Hypostome has been recovered, but was poorly preserved and needed further preparation at time of writing.

Thorax contains 11 segments; width (tr.) of axial ring to width of whole segment is about 0.46 in anterior segments and 0.37 in posterior segments; overall, thorax tapers to 0.83 of anterior width (tr.), heading posteriorly. Thoracic axial rings are notably wider (tr.) and lower (dors.) than is typical for many other New Genus B members; axial rings have distinct medial and lateral lobes. Medial lobe is flat-topped, broad (tr.), and bears distinctive sculpture with crescent-shaped patch of tubercles concentrated along posteromedial position; tubercles are large, elongate (tr.), with mild striations between some tubercles (striae, and degree of elongation varying from specimen to specimen and are accentuated in larger holaspides). Lateral axial lobes make smooth contact with medial lobe posteriorly, but contact point is impinged by thoracic apodeme (anterior), and much milder (posterior) continuation of axial socket depression (distal to apodemal depression); lateral lobe of axial ring is bulbous, compared to adjacent medial lobe, and sub-triangular in outline, due to depressions mentioned above. Articulating half-ring is connected to axial ring by deep, sharp-sided, and round-bottomed furrow; small granules are present across posterior half of half-ring. Axial furrow is strongly impressed, round-bottomed, and only fades against anterior pleural band. Anterior band of pleural lobe is lower (dorsally) than posterior band; is round in section within proximal region, and is flatter distally; width (tr.) is great, reaching up to 0.44 of total thoracic width on each side; surface is smooth except for variably expressed small tubercles along leading edge of distal tip. Posterior band is much more pronounced, with rounder section view, which continues past fulcrum in slightly diminished form; sculpture differs within segments of single specimens, but generally consists of 1-3 rows of tubercles running along most dorsal or lateral portions of band – in all cases tubercles are coarsest near posterior edge of band, leave a barren patch adjacent to axial furrow, and fade just before distal tip is reached. Pleural furrow is narrow (exsag.) and angular in section, becoming deepest near middle (tr.) of anterior pleural band; furrow extends to make contact with axial furrow, and breeches rim of articulating facet to leave shallow, fine, concave-forward trace extending 1/4 of way down articulating facet. Articulating facet is nearly flat, and bears circular granules along its posterior half, and as strip of equivalent breadth along its distal

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tip. Distal tip of thoracic segment is blunt and segment narrows to blade shape along front of articulating facet; flat surface faces slightly anterior and creates corner along its contact with posterior pleural band; along corner is small posterolaterally directed flange, creating slightly 'winged' tip; whole distal tip bears granules.

Pygidium is short (sag.) and broad (tr.), forming dorsal outline more elliptical than semicircular in shape. Pygidial axis is composed of 7 well-defined axial rings, single (eighth) ring that is poorly defined in most cases, followed by terminal piece; axial width is 0.33 of overall pygidial width in anterior region, slowly tapers to 0.6 of its anterior width in posterior region, then undergoes rapid closure behind sixth axial ring; ring furrows only reach axial furrow behind first 3 rings, and create posterolaterally-directed oblong pits inside axial furrow wherever contact occurs; small interannular rings are present behind first 3 rings, producing slight indentations along their posterior edges; sculpture along axial rings is mostly large, conical tubercles (unlike thoracic segments), 2-3 deep across anterior rings, and 1-2 deep across posterior rings. Axial furrow is quite similar to that found in thoracic segments (near first three segments), becomes much straighter and deeply incised beside axial rings 4 to 7, then fades somewhat adjacent to terminal piece; shallow closure occurs behind terminal piece. Weak 'postaxial ridge' extends halfway to posterior margin of pygidium, but only forms mild and poorly delineated bulge.

Pygidial pleural region is divided into 5 pleural ribs, with fifth rib poorly defined, and remnants of potential sixth rib visible in small holaspides (due almost entirely to aligned tubercles in cases of low definition). Pleural furrows 1-4 are deep and plainly visible, and generally straight in course; become progressively shallower, heading backward, and also shorter (tr.), with first furrow extending 3/4 of distance to margin, and fourth furrow only making it slightly over half way to margin. Interpleural furrows are present in anterior four pleural ribs, but are exceptionally shallow and show up due to sculpture aligning along highest points on adjacent posterior and anterior pleural bands of neighbouring fused segments. Pleural field bears moderate density of mid- to small-sized tubercles, which die out before reaching margin. Ventral margin makes raised lip that extends slightly outward around tail and is granulose.

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Discussion: This species is close to New Genus B *granulops* of Zquilma, and although some workers might argue to place it as a subspecies of New Genus B *granulops* the author thinks that the cumulative differences between the two taxa warrant separation at the species level. The main differences between New Genus B *ovatus* and New Genus B *granulops* are details of sculpture. Within New Genus B *ovatus*: tubercles on occipital and axial rings are much more transversely elongate (ovate), more densely packed, and cover more of anterior reaches of rings; tubercles on glabella are more sparsely distributed, lower, broader, less conical, and more bimodal in size distribution; a weak subocular pad is always present between the base of the visual surface and the top of the genal field, is sculpted with fine tubercles (larger tubercles in larger holaspides), and creates a slight indentation in the top of the anterior genal field; the front of the intercalating ring is less distinct from the back of the glabella (shallower, broader S1 with more medial fade), and often has isolated tubercles in its medial portions; sculpture on the pygidial axis and pleural regions is much coarser, more bimodal in tubercle size, more densely distributed, and extends much farther toward the pygidial margin. Additionally, New Genus B *ovatus* lacks the diminutive lenses seen along the lower edge of the visual surface of many New Genus B *granulops*, (admittedly, this may be a function of having more small exemplars for New Genus B *granulops*). Even within smaller holaspides, New Genus B *ovatus* typically bears one more lens in each vertical file behind the second file, giving the visual surface a taller appearance in holaspides of comparable size.

Aside from these differences in sculpture and minor details of the cephalon, these two forms are nearly identical in morphology. For comparison with other species, see section on New Genus B *granulops*, as similarity is overwhelming between these two species, and comparisons made to most other phacopids in that section are valid for both taxa.

New Genus B *ovatus* appears to share a lot more features with *Phacops major* BARRANDE, 1852 (see CHLUPÁČ, 1977, Pl. 10) than does New Genus B *granulops*, but New Genus B *ovatus* has a cephalon with a greater length (sag.) compared to its width (tr.); a much lower degree of glabellar divergence; coarser glabellar tubercles, with denser packing; a narrower (exsag.) postocular pad; and a pygidium with finer sculpture,

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narrower and shallower pleural furrows, less sunken axial furrows, and less obvious interannular rings.

In the cladistic analysis, New Genus B *ovatus* is placed in a sister group relationship with New Genus B *forteyi* by three synapomorphies. Shared derived features included moderately defined lateral axial lobes within the thorax and occipital ring (16=1), interannular rings represented by narrow gaps in the pygidial axis (21=1), and the presence of fairly strongly inflated subocular pads (27=2). There were no autapomorphies for this taxon.

New Genus B *forteyi* n. sp.

Plate 23.1-23.12; 24.1-24.12; 25.1-25.12; Text Figures 13, 14

non 1968 *Phacops (Phacops) turco praecedens* – HAAS, Trilobiten: pp. 108-110. pl. 30.

partim 1977 *Phacops turco* aff. *praecedens* HAAS 1968 – FORTEY AND MORRIS, Variation in lens packing: pp. 25-32, pl. 1-2 (*non* Pl.1, Fig. 7; Pl. 2, Fig. 3)

Localities, type and figured material: Holotype UA6920, from the *Psychopyge* couche (horizon), as it appears at bou Dib (MBD1) in the Ma'der basin, near the town of bou Dib, southeastern Morocco. Alternative localities include the *Psychopyge* couche at Jbel Issoumour in the Ma'der basin, and surface specimens recovered from the base of the Merzouga section, in the Tafilalt basin, near the town of Merzouga. Strata at bou Dib and Jbel Issimour are part of the Tazoulait Formation, and late Emsian in age. Merzouga specimens are taken from the age equivalent Amerboh Group (GIBB, 2005; BULTYNCK AND WALLISER, 2000). Paratypes UA6921-UA6934 (bou Dib and Issoumour), UA6940-UA6948 (Merzouga).

Etymology: This species is named in honour of DR. RICHARD FORTEY, who originally discovered the species with MORRIS (1977), but was forced to attribute it to an existing species (*Phacops turco* aff. *praecedens* HAAS, 1968), due to the limited material available.

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Diagnosis: Similar to *Phacops,* with extremely pronounced sclera, often bearing single or paired tubercles on raised surfaces directly above and below lenses, and producing unique cruciform arrangement of lenses within visual surface; eye has 18 vertical rows of lenses with maximum of 4 (more often 3) lenses per vertical row, which is markedly low for visual surface size; palpebral furrow is deep; sculpture is of coarse conical tubercles with fairly dense distribution; doublure bears slightly elongate (tr.) granules with weak interconnection; pygidial axis is relatively short and wide, with fairly complete terminal closure, and is composed of 7-8 clear rings plus terminal piece; pygidial pleural field typically bears 4-5 ribs.

Description: In true dorsal view, outline of cephalon is close to half-circle, with genal angles protruding slightly behind midline, and broad (tr.) glabella shaped like kernel of corn (maize), forming bulk of cephalon; smaller holaspides have slightly more ovate outline due to narrower cephalon (tr.) and longer glabella (sag.). In true lateral view, glabella appears bulbous with slightly flattened dorsal surface that protrudes dorsally above top of eye to height approximately 1.2-1.5 times that of visual surface itself; with sharp posterior downturn placing S1 furrow well anterior to posterodorsal corner of eye; and with gentle anterior curvature placing anterior extreme within distance equal to length (exsag.) of visual surface.

Glabella is defined by deep axial furrows. Axial furrows with round bottoms that shallow and are redirected (exsagittally) adjacent to L1 lateral lobes; diverge anteriorly at approximately 75-80°; become progressively narrower and more deeply incised anteriorly, adjacent to front of eye; and fade dramatically ahead of eye, before connecting with preglabellar furrow. Preglabellar furrow is circular in section and runs fairly straight course beneath glabella, with slight narrowing medially, and minor glabellar overhang (almost no overhang in large holaspides, but minor overhang in small holaspides). Glabella is dissected by moderately incised glabellar furrows (that are variably disturbed by sculpture elements, more so in larger holaspides), and these define glabellar lobes with no independent convexity. L3 is defined anteriorly by medial S3 with fairly strong curvature (convex-forward), that trends about 12° behind transverse plane, and almost

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connects with its lateral ramus, because S3 lateral ramus is long (exsag.) and does not parallel axial furrows as closely as in many other phacopids. S2 trends about 23° behind transverse plane, has slightly convex-forward curvature, is long (tr.), and almost connects with axial furrow/anterior apodemal pit, outlining nearly rectangular L2 with slightly rounded and expanded distal corners. S1 is narrow and deeply incised laterally, but shallows and fades medially, to become negligible ahead of median third of intercalating ring, and intruding into back of glabella.

Glabellar sculpture is of coarse, conical tubercles with broad bases, and smaller subset of fine tubercles between; all often wear down to domes; and increased crowding seen in larger holaspides distorts circular outlines due to interference between adjacent tubercles. Tubercles are coarser and more widely spaced on posterodorsal region of glabella, and finer and more crowded along anterior face, but fairly circular shapes are maintained throughout. Intercalating ring is sub-triangular, has high dorsal curvature (tr.) (bringing it up to level of glabella surface), and bears its own central pad of coarse, crowded, conical tubercles, which become more numerous with increased holaspide size and partially fill medial region of S1 in largest individuals. Lateral L1 lobes are distinct, globular, and bear numerous intermediate size tubercles on dorsal surface; anterior and posterior apodemal pits are deep, short (tr.), and relatively straight, producing slight transverse elongation to shape of L1 laterals. Occipital ring is very similar to thoracic axial rings, except for its less defined lateral lobes (shown through posterior offset relative to medial lobe, and slight depression arising from posterior apodemal pit), its greater length (sag.), and more numerous tubercles (which are mid-sized cones and domes concentrated along posterodorsal extremes and transversely elongated at posterior margin).

Palpebral area is strongly convex (dorsally), and sits slightly above level of palpebral lobe in lateral view, with mild downward slope to its surface (heading distally); all edges are well defined, with strong axial furrow, very steep-sided, deep posterior broader furrow, and distinct palpberal furrow. Palpebral area flows smoothly into relatively broad (exsag.) postocular pad with same great definition, and postocular pad terminates distally in scimitar-shaped tip against wide, distinct furrow heading into facial suture; sculpture is of small to mid-sized tubercles densely distributed across entire dorsal

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surface for both palpebral area and postocular pad. Palpebral furrow is round-bottomed and distinct across its entire course, but is noticeably deeper adjacent to anterior and posterior corners of eye, producing raised rear corner to eye. Palpebral lobe has slight dorsal convexity (transversely, in section view), but is largely flattened and down-turned (sloping distally), especially near middle of eye; sculpture consists of numerous mid-sized tubercles concentrated on dorsolateral surfaces, accompanied by fine pits, and series of 4-5 large, exsagittally elongate depressions adjacent to palpebral rim (perhaps muscle scars). Palpebral rim forms raised bead, extending lateral to and above palpebral lobe (particularly near mid-point of eye); fine, domed tubercles are extremely crowded across its surface, and often display exsagittal elongation; lateral extension is equal to or greater than features of visual surface below.

Eye is fairly small overall (about 0.25 of total cephalic height, and approximately 0.36-0.42 of total cephalic length); is short and borne relatively low on cephalon: is closely abutted to side of glabella anteriorly, and matches contours of gena exceptionally well. Visual surface bears 18 rows of lenses, with 4 (but more often 3) as maximum number of lenses per row, and 41-55 as typical total number of lenses per eye (see Text Fig. 13 for full lens formula of bou Dib and Issoumour specimens, and Text Fig. 14 for representation of Merzouga specimens). Interlensar sclera is markedly thickened directly above and below each lens, altering packing pattern of eyes to produce cruciform arrangement of neighbours, as opposed to normal hexagonal packing (FORTEY AND MORRIS, 1977); sclera projects laterally well beyond height of lenses, and often bears tubercle(s) on its surface. Sculpture on sclera depends on position in visual surface – ventrally, lenses are more closely spaced, resulting in rectangular sclera typically bearing two fine tubercles; dorsally, lenses are farther apart, resulting in square to orthorhombic sclera with greater prominence, but only one tubercle evident; posteriorly, sclera is often reduced in corner of eye. Lenses are typical size and shape for genus, and do not appear sunken in sclera, because they almost touch their diagonal neighbours, unlike species with pervasively thickened sclera. Visual surface is fairly short, is drawn upwards in its posterior reaches, bears lenses right up to its anterior and posterior margins, and has raised tuberculate margins on both its dorsal and ventral margins, producing fairly rounded appearance with hard upper and lower limits. Slope to subocular furrow is

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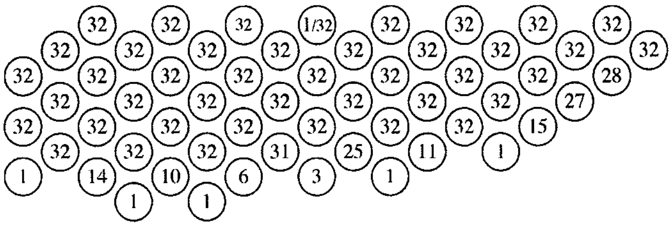
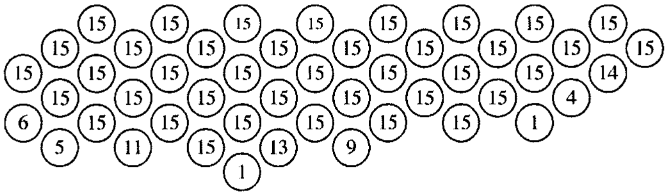
gradual and rounded, and occasionally has small stray tubercles in it. Subocular pad has little inflation, but always bears strand of small to mid-sized tubercles, and is set apart from genal field by relatively broad, shallow, barren depression, ventrally.



Text Fig. 13: Lens diagram for bou Dib New Genus B *forteyi* n. sp. specimens



Text Fig. 14: Lens diagram for Merzouga New Genus B *forteyi* n. sp. specimens

Posterior border is roughly twice width (exsag.) of postocular area throughout its course; border is round (in section) proximally, narrows significantly adjacent to fulcrum, then expands into flattened wing, heading into genal angle; slope into posterior border furrow is steep and barren; sculpture consists of few fine tubercles along dorsal surface, and many mid-sized to coarse conical tubercles along lateral face with greater spacing than that seen in glabella (and usually leaving fulcral region relatively naked). Genal angle shows similar sculpture to posterior border, but this becomes finer ventrally, and is subdued next to posterior section of facial suture; angle itself is rounded and often has posterolaterally-directed node; surface of angle and anterior genal field are inflated to match lateral projection of visual surface. Anterior genal field has moderate to coarse tubercles broadly distributed across its surface.

Relicts of facial suture are traceable as faint topographic shifts and interruptions in sculpture along its anterior and posterior extremes; its course is typical for genus. Ventral margin is raised (laterally) lip which begins adjacent to posterior section of facial suture, and gains prominence anteriorly; sculpture consists of short, broken terrace lines

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running parallel to ventral margin, and often accompanied by faint pitting, that is replaced anteriorly by granules and broader, more square profile to lip (in section view).

Vincular furrow is complete, distinct, and circular in section, and is broken into interconnected pits for thoracic segment tips beneath genal field; furrow is covered in granules that become more dense along its anterior edge. Doublure is fairly narrow (sag,, exsag.) and flat, with minor flange along posteromedial rim, to match contours of hypostome. Doublure surface is slightly recessed (dorsal to) ventral margin, and is oriented subparallel to it, with strong sweep into vertical orientation beneath genae; edge adjacent to vincular furrow protrudes ventrally and is visible in lateral view; sculpture consists of slightly elongate granules (stretched parallel to nearest margin), which coalesce to form discontinuous terrace lines laterally, and become more circular in medial positions.

Hypostome is shield-shaped. Relative length (sag.) appears to be nearly equal to maximum width (tr.), but this is hard to determine because anterior wings have not been fully uncovered. Hypostomal suture bows forward smoothly in an arc. Anterior lobe of middle body is large and nearly hemi-cylindrical in section. Posterior lobe is much smaller and crescent-shaped, faintly delineated from anterior lobe by very shallow, posteriorly convex middle furrow. Maculae are not distinct. Sculpture consists of fine, discontinuous asymmetrical (steep side forward) terrace ridges that run sub-parallel with middle furrow. Lateral and posterior border furrows are shallow. Sides of hypostome converge backward and have very narrow (tr.) lateral borders. Posterior border is relatively broad (exsag.) and presents slightly concave ventral surface with raised posterior and lateral rim. Posterior rim bears three spinous processes; medial process is long and triangular, while two lateral processes are minute nubs (may have been damaged in preparation here).

Thorax contains 11 segments; width (tr.) of axial ring to width of whole segment is about 0.40 in anterior segments and 0.39 in posterior segments; overall, thorax tapers to about 0.76 of anterior width (tr.), heading posteriorly. Thoracic axial rings have moderately defined lateral lobes; and are fairly wide (tr.) and low (dors.), with flattened dorsal surface. Medial lobe is separated from lateral lobe anteriorly by mild depression stemming from anterior apodemal pit that fades before reaching midpoint (exsag.) of

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ring, and posteriorly by exceedingly faint depression stemming from axial socket depression; resulting lateral lobe is boxy in appearance, and becomes less distinct in posterior segments. Axial sculpture is of small to mid-sized conical and domed tubercles covering all dorsal surfaces, but fading in anterior and lateral extremes. Articulating half-ring sits well below axial ring height, and is separated by deep, round-bottomed ring furrow; faint granules are present across half-ring surface, and become more pronounced in anterior 1/3rd of surface. Axial furrow is distinct throughout its course, with slight overhang by lateral axial lobes, and circular cross-section. Anterior and posterior pleural bands are roughly equal in width (exsag.); anterior band displays typical 'boomerang-shape' with more rounded contours in proximal half, and flatter surface in distal half; distal half also bears patch of fine tubercles (sometimes extending partially into proximal region). Posterior pleural band is very circular in cross-section proximal to fulcrum, and presents flattened lateral surface distally; sculpture consists of 2-3 loosely arranged rows of tubercles that are reduced on dorsal surface, but gain prominence on lateral surface, with coarsest tubercles along posterior margin, and numerous fine tubercles crowded against rim of articulating facet. Pleural furrow is deeply incised, and v-shaped in section view; it is deepest near fulcrum, fading proximally on its way to contact axial furrow, and fining distally on its way to breach articulating facet rim and leave faint trace across posterior half of facet (in mild concave-forward arc). Articulating facet presents faintly concave surface (laterally); bearing fine ovoid granules that are dense posteriorly, and sparse anteriorly. Distal tip of thoracic segment is flattened, producing square posteroventral corner, and bears medial knob (exsagittally elongate to form keel) that interlocks with notch in vincular furrow; all surfaces are highly granulose.

Pygidium is short (sag.) and broad (tr.), forming elliptical shape with protruding articulating facets and anterior half-rib. Pygidial axis is composed of 7-8 well-defined axial rings, plus 1 additional ring defined solely on basis of tubercle alignment, plus terminal piece; axial width is near 0.40 of total pygidial width (tr.), and axis tapers at about 25° to form almost complete closure of axis, occupying about 0.82 of total pygidial length (sag.), and is followed by mild postaxial ridge. Axial rings are sub-rectangular in cross section, and closely abut one another; leaving faint gaps behind anteriormost 3 rings (for minute interannular rings), through slight indentations in posterior margins of rings;

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sculpture is of small to mid-sized conical tubercles across entire dorsal surface, and occurring in 2-3 loosely arranged rows on anterior rings and only one row in posterior rings. Axial furrow is deeply impressed relative to both axis and pleural field and is moderately wide; small longitudinal depressions and squiggles in its path are created by lateral continuations of ring furrows behind anterior 3 axial rings, and path straightens and slowly fades behind this. Four clear pleural ribs trail away from axis in almost straight courses, and are followed by 1-2 ribs observable on basis of sculpture alone. Anterior 4 pleural furrows are narrow and deep, extending 3/4 of way to margin before abruptly fading; posterior furrows are shallow, and appear broad because of lack of ornament. Interpleural furrows are weak or absent in most specimens, usually showing up as result of sculpture alignment and disruption (tubercles are often segregated into loose bands 1-2 tubercles wide). Entire pleural field bears small to medium size tubercles that become finer and more sparsely distributed in distal positions. Ventral margin is very fine raised (laterally) lip bearing fine granules.

Discussion: There is a small degree of uncertainty in assigning specimens from Merzouga to the same species as those specimens recovered from bou Dib and other Ma'der basin localities where the *Psychopyge* couche outcrops. This problem exists because there is little overlap in the size ranges of specimens found at the different sites, and the Merzouga specimens are surface collected with reduced stratigraphic control. Merzouga specimens are on average half the size of those New Genus B *forteyi* collected from the Ma'der basin, where there is a collection bias towards larger specimens. At Merzouga, specimens are surface collected from a recessive shale unit below the main Merzouga section, and this interval has been severely picked over by collectors (to the extent that it is now difficult to find any specimens at all, even the small ones previously collected). The size discrepancy may be tied to collecting bias, a difference in depositional setting (the smaller size may be due to ecological factors), or attributable to the specimens coming from slightly different time intervals (representing different portions of a single lineage).

Besides overall size, the largest discrepancies to arise between the Merzouga and Ma'der sets of New Genus B *forteyi* specimens pertain to their intercalating rings and eye

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lens formulas. Merzouga specimens have proportionately more prominent and unimodal tubercles on their cephala, resulting in smaller looking intercalating rings and more pronounced glabellar furrow sets; and typically bear 1 less lens per vertical file on their visual surface (while still falling within the basic lens formula for larger representatives), giving the eye a slightly more sunken appearance. Furthermore, less pronounced axial sculpture is seen within the thorax, and pygidium, These differences are easily attributable to size discrepancies, so specimens are treated as members of the same species here: additional specimens may show these differences to be distinctive on the subspecies or species level, but it is unlikely.

FORTEY AND MORRIS (1977) found their specimens to be closest to *Phacops (Phacops) turco praecedens* HAAS, 1968, and this was a reasonable observation. Aside from one questionable coarsely tuberculate specimen figured by HAAS (1968; pl.30, fig. 7), this Eifelian taxon is quite close to New Genus B *forteyi* new species. Differences emerge in terms of how the eye is shaped – it is shorter in New Genus B *forteyi* and in a lower position on the cephalon, giving the eye a more rounded outline, causing the palpebral area to project above the palpebral lobe, giving the palpebral lobe a sloped appearance, and creating an overhang of both the cheek and ventral margin by the eye – features not seen in the other taxon. It may be a result of lighting, but *P. (P.) turco praecedens* also appears to have a more prominent subocular pad, and has finer, less dense tubercles on its genal area that fade well before reaching the axial furrow anteriorly. It is difficult to comment on sculpture, but based on plates and text figures, it appears as though *P. (P.) turco praecedens* has finer, sparser tubercles on almost all cephalic surfaces. The eyes of the two species are completely different, largely due to the interlensar sclera 'spacers' in New Genus B *forteyi*. The tuberculate sclera change the lens arrangement from the typical hexagonal packing to a cubic or cruciform arrangement (FORTEY AND MORRIS, 1977). Although the two species have the same number of vertical rows in their eyes, specimens of New Genus B *forteyi* 1.5 times the size of the *P. (P.) turco praecedens* specimens figured by HAAS typically bear 2-3 less lenses in most of their vertical rows, and specimens of comparable size are even more disparate. The fact that broader studies have shown that New Genus B *forteyi* is often the only representative of the Phacopidae found in the *Psychopyge* couche, or is present in overwhelming

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quantities with a stable morphology, casts doubt on whether specimen It 14073 (the *P. (P.) turco* aff. *praecedens* specimen of FORTEY AND MORRIS with hexagonal lens packing and slightly coarser sculpture) belongs in this taxon, so it has been excluded here.

In terms of other Moroccan specimens, New Genus B *forteyi* resembles New Genus B *granulops* (CHATTERTON *et al.* 2006), but is clearly distinct – in addition to the differences between *P. (P.) turco praecedens* and New Genus B *granulops* (see discussion section of latter taxon), New Genus B *granulops* mainly lacks the characteristics created by scleral dividers in New Genus B *forteyi*. Besides having many more lenses per vertical file, New Genus B *granulops* has an additional file. Unlike New Genus B *granulops*, New Genus B *forteyi* has a strong subocular pad, coarser cephalic tubercles, a raised intercalating ring with less incised S1 furrow set ahead of its median 1/3rd, a more defined palpebral furrow, more downturned palpebral lobes, a pygidial axis with almost complete terminal closure, no pronounced interannular rings between pygidial axial rings, and more numerous and coarse tubercles upon all its axial rings. New Genus B *granulops* is much closer in morphology to New Genus B *ovatus* than either species is to New Genus B *forteyi*, so most of the distinctions outlined above are true for New Genus B *ovatus* as well.

Cladistic analysis places New Genus B *forteyi* as the sister group to New Genus B *ovatus* n. sp. (and again, this should be viewed with some skepticism). These two taxa are united by synapomorphies outlined in the discussion of the latter species, and New Genus B *forteyi* bears 6 autapomorphies, which are included in the species diagnosis above.

Genus *Phacops* EMMRICH, 1839

Type species: *Calymene latifrons* BRONN, 1825 from the Middle Devonian (Eifelian Junkerberg Formation), Gerolstein, Germany, by subsequent designation of BARRANDE, 1852.

Discussion: The definition of this genus and its numerous closely related genera (or subgenera, depending on opinion) has been variable and a serious problem for the last 40 plus years of phacopid systematics. This study starts off by using the most recent

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systematics of the phacopids. It recognizes all of the potential divisions within the old concept of "*Phacops*" as independent genera, in order to assess whether they actually perform as independent entities. To achieve this end, the strictest definition of *Phacops* must be used here (that provided in CAMPBELL, 1967 – but ignoring his need for the hypostomal suture to be concave and the pygidium to have 9-11 axial rings). The group of species that CAMPBELL (1967; 1977) originally assigned to this genus has subsequently been pared down by their inclusion in the numerous new genera that were created largely by STRUVE (*Geesops*, *Eldredgeops*, etc.), and most of these new groupings are based on very few characteristics. The use of cladistics will show whether these new groupings are just paraphyletic fragments of *Phacops*, or realistic holophyletic divisions.

Surprisingly, the cladistic analyses performed so far support the retention of most of the genera formed from the species that were once part of *Phacops* (under its most restrictive diagnosis). There is disagreement between the large- and small-scale analyses as to the placement of *Eldredgeops rana rana* as the sister group to just *P. latifrons* and *P. araw* (making *Eldredgeops* more likely to be a *Phacops* species and an invalid generic division), or as the sister group to these species and the members of *Geesops*, *Pedinopariops*, and *Drotops* included here (making it more likely to be a valid genus). To accommodate this disagreement, the genus is retained for the present, and represented as originating from a polytomy (see Chapter 2, Fig. 1). If the large-scale cladogram is an accurate depiction of relationship, only two of the ingroup taxa actually belong within *Phacops*, and it is a genus defined by the (local) synapomorphies of a very narrow (exsag.) postocular area (8=0), terrace lines upon the anterior face of the glabella[6] (15=3), and a low maximum number of lenses in any vertical row of the visual surface (26=4).

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[6] The terrace lines seen in the *Phacops* clade are really keeled tubercles, as opposed to the true terrace lines seen in *"Phacops" kermiti*; an additional character state in future studies would make this a true synapomorphy across the entire ingroup.

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Phacops araw n. sp.

Plate 26.1-26.15; Text Figure 15

Localities, type and figured material: Holotype UA 6904, from the South Oufatene *Proetus* couche (SOP horizon), as it appears at an isolated locality on the southern end of Jbel Oufatene, near Lahfira, southeastern Morocco. Alternative localities include the *Greenops*[7] couche at Mrakib (slightly farther south). Strata are Eifelian in age and part of the El Otfal Formation in the Ma'der basin (BULTYNCK AND HOLLARD, 1980). Paratypes UA6905-UA6907.

Etymology: This species is named *araw* (berber term for ogre), due to the calloused appearance created by the large, pustular tubercles it bears, as well as its remarkably thick cuticle.

Diagnosis: *Phacops* with large, pustular (broad and domed) tubercles across axial surfaces of glabella; lack of ornament on thoracic axial rings (pitting only); cuticle thickness of exoskeleton is twice that of most tuberculose phacopids of comparable size; eyes bear 18 (and in a rare case 19) vertical files of lenses, with maximum of 4 lenses per file; visual surface is dominated by sclera, which protrudes almost as much as lenses and separates lenses to create square lens packing patterns; intercalating ring sunken relative to glabella, or absorbed completely into back of glabella, and almost indiscernible; pygidium has 8 axial rings plus terminal piece, and 6 well defined pleural ribs followed by weak 7th rib in most cases; pygidial axis is wide and has low taper, producing boxy outline; pleural ribs are very circular in section and separated by deep, wide pleural furrows.

Description: Cephalic outline forms broad crescent in dorsal view, dominated by inflated glabella and long (exsag.), backwards swept genae; lateral view depicts bulbous nature of glabella, great size and angularity of cheek, and relatively small eye borne fairly high on

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[7] This horizon is also known as the '*Mrakibina* couche', due to its contents.

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cephalon; larger holaspides have comparatively wider (tr.) cephala, and more bulbous and foreshortened (sag.) glabella.

Glabella extends dorsally beyond top of eye about 0.6 of visual surface's height; reaches highest point just ahead of eye; slopes downward behind eye rapidly, causing back of eye to conceal its posterior termination. Axial furrows diverge around frontal lobe of glabella at approximately 70° and are not redirected by L1 lateral lobes; are straight, broad, deep, and round-bottomed against palpebral area, but become narrow and deeper adjacent to front of palpebral lobe – maintaining sharply incised furrow (comparable in depth to width (tr.) of palpebral lobe) along anterior edge of eye, and dissipating in contact with deep subocular groove. Preglabellar furrow is broad and shallow in lateral positions, but becomes rounded in section, narrower, and consistent in width under medial 2/3 of glabella; slight ventral deflection beneath glabella produces low 'm-shape'; glabellar overhang is slight (comparable to thickness of ventral margin) in large holaspides, and slightly greater in small holaspides.

Glabellar sculpture consists of robust, pustular tubercles with widths reaching 1.5mm in larger holaspides; dorsal surface tubercles are distributed evenly, with some contact/interference, but most are 1/2 of tubercle's width from neighbours; spacing becomes more crowded and tubercles are smaller along anterior edge of glabella; transition to elongate (tr.), keeled tubercles occurs along anteroventral face of glabella; and keeled tubercles coalesce to form short, coarse terrace lines in ventral and medial positions.

Frontal lobe has undifferentiated L3 and L2 faintly delineated by S3 and S2 which are obscured by sculpture in large holaspides. In small holaspides: S3 medial is short (tr.), straight, and trends slightly behind transverse plane; S3 lateral portion is slightly less faint, trends subparallel to axial furrow, and is separated from medial branch of S3 by sizeable gap; S2 is also short (tr.), trends substantially behind transverse plane, and fails to reach axial furrow. Intercalating ring (L1 medial) is melded with base of frontal lobe ('basisolution of the glabella' of R. AND E. RICHTER, 1939); intercalating ring is sunken into frontal lobe, with slight independent convexity and faint sculpture of small tubercles. S1 creates most of intrusion into frontal lobe, but is broad, faint, fades medially, and becomes deep near apodeme in lateral position. S0 is expansive (exsag.), deep, and

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round-bottomed; proceeding straight between L1 laterals. L1 lateral lobes are diminutive, low domes, with no obvious ornamentation; contact with adjacent apodemes is abrupt. Anterior apodemes are straight, narrow (exsag.) and deep in dorsal view. Posterior apodemal pits are set well behind S0 and infringe upon occipital ring; curve around posterior edges of L1 laterals, and are slightly broader (exsag.) than anterior apodemal pits. Occipital ring is relatively smooth and inflated, lacks tubercles and has only large pits for ornamentation; anterior edge is much higher (less sloped forward) than in many other phacopids; little differentiation between lateral lobes and medial lobe, except for slight posterior indentation opposite apodeme.

Palpebral area is narrow (exsag.), with pronounced dorsal convexity; it is adorned with large domed tubercles concentrated along distal tip of dorsal surface; and it is bounded posteriorly by deep, round-bottomed posterior border furrow, which shallows significantly distal to eye. Palpebral furrow fades into axial furrow in anterior extreme, becomes deep and narrow (tr.) behind posterodorsal corner of eye, and wraps around posterior of eye as very sharp and well-incised postocular groove. Palpebral lobe is broad (tr.) and reniform, with low dorsal convexity; sculpture consists of large, domed tubercles clustered around dorsal extreme and interspersed with large pits; adjacent to palpebral rim is largely barren, with series of approximately 12 large pits spread out along medial edge of palpebral rim. Palpebral rim is dorsally inflated but lacks ornament or significant lateral overhang of visual surface.

Eye is comparatively small (about 0.34 of total cephalic height, and 0.42 of total cephalic length); high position on cephalon, deep surrounding furrows, and pronounced rims all contribute to 'pedestal-like' appearance of eye. Visual surface bears 18-19 rows of lenses, with 18 as standard number of vertical rows, 4 as maximum number of lenses per row, and 58-59 as typical total number of lenses per eye (see Text Fig. 15 for full lens formula). Interlensar sclera is extremely prominent; spaces between lenses are 1/2-2/3 of lens' width from nearest neighbour, and this creates somewhat "cubic" lens packing (where each lens has 4 nearest neighbours, as opposed to more common 6-neighbour arrangement); (see FORTEY AND MORRIS, 1977); projects laterally well above lens' surface; forms expansive and bulbous margins to visual surface. Margins of eye are comparatively broad; lenses do not extend to very edge of eye; margins are raised relative

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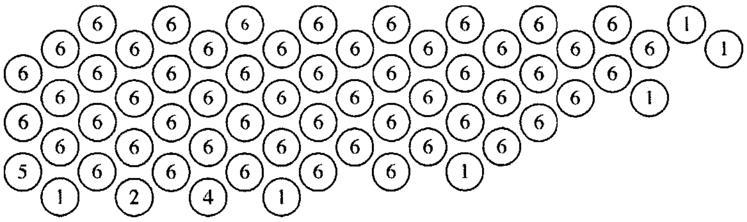
to surroundings; anterior, posterior, and dorsal margins are smooth and inflated; ventral margin is flatter, broader (dorsoventrally), and ornamented with numerous, variable pits concentrated near middle of eye. Subocular groove is broad and deep; it slopes gently down from base of eye to finish in round-bottomed sulcus at top of genal field; and it contains faint subocular pad on slope, near middle of eye. Mid-sized pits are widely distributed along slope dorsal to subocular pad, and along its ventral edge. Postocular pad is questionable (faint, with clear distal tip only in large holaspides); it clearly flows from posterior of palpebral area, with consistent width (exsag.) until slight flare near distal tip; and it bears no ornament.



Text Fig. 15: Lens formula diagram for *Phacops araw* n. sp. specimens

Genal angle is well-rounded and extends far beyond eyes (laterally) and occipital ring (posteriorly); sculpture composed of dense, low, domed tubercles mixed with large pits; sculpture becomes lower in profile and more pit-dominated in posterior reaches of gena, with trend exaggerated in larger holaspides; very small transition zone occurs in posteroventral (especially) and ventral margins of gena, where tubercles are replaced by elongate (exsag.) tubercles and then short terrace lines. Anterior genal field has raised tubercles with more numerous pits between; pits become prevalent in strip near ventral margin, and tubercles become reduced in size along upper margin of field. Posterior border is fairly narrow (exsag.); smooth along dorsal surface, and showing continuation of genal ornament in distal tip. Remnant facial sutures inconspicuous. Ventral margin presents raised, tubular lip (laterally as well as ventrally) towards front of cephalon, which becomes more rectangular in section beneath middle 1/3 of glabella; coarse, continuous terrace lines make up ornament beneath cheek, and degrade into shorter, anastamosing terrace lines beneath glabella.

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Vincular furrow is broad, flat-bottomed, and deeply impressed; channel narrows beneath medial 1/4 of glabella, widens slightly in more lateral positions, then narrows slightly as it breaks up into cojoined pits for accommodating thoracic segment tips; lateral portions of furrow appear shallower and broader than in many other *Phacops* species; behind second or third pit (from anterior) successive pits become shortened (exsag.), taking on nearly circular outlines; ornament consists of uniform granules throughout furrow.

Doublure is short (sag.), basically flat (anterior to posterior), with slight ventral convexity paralleling that of glabella (side to side); medial posterior margin has raised lip for articulation with hypostome, lip displays greater ventral deflection than most phacopid. Lateral portions of doublure create wide (tr.) rim to medial side of vincular furrow pits. Sculpture on doublure is composed of complete terrace lines in lateral segments, replaced by shortened (tr.) and less pronounced, anastamosing terrace lines in anteromedial positions, and elongate (tr.) granules in posteromedial positions. Anterior edge of doublure projects clearly below outer margin, producing visible 'lip' in lateral view; rim adjacent to vincular furrow facets protrudes to lesser extent.

Hypostome unknown for species.

Thorax contains 11 segments; width (tr.) of axial ring to width of whole segment is about 0.35 for all segments; overall, thorax tapers to approximately 0.72 of anterior width (tr.), heading posteriorly. Thoracic axial rings have 'puffy' appearance, with rounded anterior and posterior margins, and high dorsal convexity; lateral lobes differ little from medial lobe with negligible change in slope, and anterior and posterior furrows that make mild indentations in leading/trailing edge, but do not proceed across dorsal surface; slope and lack of distinct lateral lobes gives axis broad, low appearance; pits are only form of ornament, large pits are widely dispersed along posterior and middle portions of ring, while anterior edge has small band of mid-sized tubercles; slope on anterior edge, heading into articulating half-ring, is very steep. Articulating half-ring is on par (dorsally) with base of axial ring; is separated from axial ring by shallow, round-bottomed transverse furrow; and has fine granulation along posterior half of surface. Axial furrow is firmly impressed, round-bottomed, and steeper on axial side; deeper in posterior end and slightly effaced while crossing anterior pleural band. Pleural section of

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segment is dominated by posterior band and has reduced 'corner' in vicinity of fulcrum – producing rounded appearance. Anterior pleural band is lower (dorsally) than posterior band; has rounded dorsal surface with few small pits concentrated near dorsolateral extreme; and is markedly short (tr.). Pleural furrow is deep and round-bottomed with deepest point mid-way along anterior pleural band (tr.); fades into axial furrow proximally; narrows and fades distally, but manages to carry on to articulating facet surface, forming minor concave-forward arc before terminating. Posterior pleural band is generally rounded; has slight dorsal arch in proximal position (as opposed to common horizontal orientation); is semi-circular in section; has poorly defined anterior edge to separate it from articulating facet; and lacks distinct 'corner' near fulcrum; sculpture composed of low, domed tubercles widely distributed along middle (exsag.) of distal part of posterior band from below fulcrum to distal tip, large pits are interspersed among tubercles, with concentrations along anterior edge of band and near distal tip. Articulating facet has reduced surface concavity and bears faint granules that retain circular outlines and wide spacing over entire surface; distal end of pleural furrow breaches margin of articulating facet but does not continue across facet surface very far. Thoracic segment tips of species are somewhat distinctive, with usual flattened edge accompanied by large anterodistally protruding 'knob' for insertion in vincular furrow; 'knob' becomes more elongate and blade-like in posterior segments; rim of flattened thoracic tip bears slight, laterally projecting ridge; ridge, ventral surface, and 'knob' all have coarse granules.

Pygidium is semicircular in dorsal outline; maximum length (sag.) is about 0.53 of maximum width (tr.). Pygidial axis is well defined, and comparatively flat-topped in medial region (transversely); it contains 8 axial rings plus terminal piece; axis tapers from 0.32 of total pygidial width (tr.) in anterior ring, with approximately 21° convergence angle, and taper increases behind sixth ring; no connection of axial furrows occurs behind terminal piece, leaving subtle postaxial ridge in pleural field; ornament consists of large pits and very low, broad tubercles widely distributed and mainly upon dorsal surfaces of rings 2-5. Ring furrows reach axial furrow behind anterior 6 rings, and create posteriorly-directed depressions within axial furrow (distally) behind anterior 3 rings; anterior 4 rings are followed by smooth interannular lobes, creating indents in trailing edge of first ring and in leading edge of subsequent rings, altering curvatures slightly. Axial furrow is

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broad (tr.), deep, and fairly round-bottomed; recessed relative to axis and proximal tips of pleural ribs; runs slightly curved course around bulk of anterior axial rings, and curving medially behind 6th axial ring; fades posteriorly adjacent to terminal piece, with slight impression in pleural field, and no closure behind axis. Pygidial pleural region has 6 prominent ribs and weakly defined 7th rib (posterior); ribs have strong dorsal curvature (laterally) and are rounded in section view; anterior ribs extend 5/6 of way to pygidial marigin, while posterior ribs only extend slightly over 1/2 way; ornament along ribs consists of very low, domed tubercles and mid-sized pits widely distributed along posterior bands, and posterior bands bearing small clusters of small, pronounced tubercles. Interpleural furrows are fine and shallow, making it hard to detect small (exsag. and tr.) anterior bands fused to backs of first 4 ribs, without using sculpture patterns. Pleural furrows are comparatively deep and narrow (exsag.); travel relatively straight courses, and fade gradually into pleural field at distal ends. Pleural field is comparable in slope and ornament to distal tips of thoracic segments; slope is high; sculpture has high density of mid-sized pits, and additionally numerous mid-sized, domed tubercles. Ventral margin of pygidium has significant lateral extension to its raised lip, fading medially; ventral surface of margin is flattened; ornament consists of elongate (parallel to margin) granules that are longer in lateral portions of pygidium and become shortened in medial and ventral portions.

Discussion: Of the two phacopid species recovered from the South Oufatene proetid couche, *Phacops araw* n. sp. is by far the least common (bordering on rare). This species is slightly more common within the *Greenops* (*=Mrakibina*) couche at Mrakib. *Phacops araw* stands out from other phacopids encountered in this study because of its remarkably thick cuticle, and near lack of post-cephalic sculpture. These two features are likely related to one another, as the remnants of tubercles are still visible in most regions, but seem overwhelmed by a general inflation of the exoskeleton. Furthermore, pitting is very coarse in most regions – likely because of the depth to which the pits must penetrate. This species would be a prime candidate for future work on the nature and purpose of cuticular pits, because they are so pronounced that their distribution (even on the anterior face of

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the glabella) can be easily mapped, and internal structure is likely to be represented by infilling of voids.

Phacops araw n. sp. is most similar in morphology to *Phacops latifrons* (BRONN, 1825), but some significant differences exist between the two taxa. *P. araw* has eyes with at least 3 additional vertical rows of lenses (18 vs. 15), and typically one more lens per row in the posterior regions of the eye; a visual surface with much thinner interlensar sclera, and a more vertical orientation of the surface; a more bulbous glabella that actually overhangs the anterior border; the same pitting and keeled tubercles along the anterior face of the glabella, but without the effacement of the tubercles ventrally; an intercalating ring that is completely blended with the back of the glabella, or severely sunken; a less prominent and narrower (exsag.) postocular pad that does not extend into the genal field as far ventrally; and less inflated (laterally) genae, without short terrace lines extending from the ventral margin to reach half-way to the base of the eye. There is very little chance that these two taxa could be subspecies of the same species.

Some might argue a superficial similarity between *P. araw* and *Eldredgeops rana africanus* (BURTON AND ELDREDGE, 1974), but aside from similar ornament, their morphology differs greatly. *P. araw* has eyes that are borne much lower on the cephalon, with the same number of vertical rows of lenses, but typically 1-2 less lenses per file; a visual surface with pitting along its ventral edge, and less of a 'visor' produced by lateral prominence at the dorsal edge; a ventral margin that is not marginulate; a glabella that is not nearly as wide, and bears slightly finer, more widely spaced pustules; an intercalating ring that is almost completely assimilated by the back of the glabella; and a pygidium with many fewer pleural ribs and axial rings.

The cladistic analysis placed *Phacops araw* as the sister taxon to *Phacops latifrons*, making it the only unquestionable *Phacops* species of all of the Moroccan material covered here. These two taxa were united by three local synapomorphies (detailed in the generic discussion), and *P. araw* was shown to have 4 autapomorphies: a fairly wide glabella (1=3), strong glabellar divergence (31=2), poor S1 definition medially (34=1), and widespread glabellar pustules (7=5, which are unique for the whole ingroup).

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Genus *Pedinopariops* STRUVE, 1972

Subgenus *Pedinopariops (Hypsipariops)* STRUVE, 1982

Discussion: This genus and subgenus (created by STRUVE to contain some of his marginulate phacopid species) were considered to be of dubious systematic value when this study was first begun. The skepticism was due to the overwhelming similarity of *Pedinopariops* representatives from Morocco to the slightly younger *Drotops* specimens (with most distinctions between the higher-level taxa derived from small differences in sculpture or eye positioning), and the low numbers of species on each side of these divisions. The cladistic analysis performed as part of this study found that these divisions really do seem to exist – at least with this preliminary analysis. The addition of more taxa to this region of the tree may undermine these divisions, but the support numbers suggest that this is unlikely. In recognition of these fairly robust divisions, the taxa they denote are recognized in this work.

Pedinopariops is placed as the sister group to *Drotops*, and these genera are shown to share 3 local synapomorphies, a distinct palpebral furrow (12=2), weakly defined lateral axial lobes (16=1), minor closure of the pygidial axis with a fairly strong postaxial ridge (20=1), and one truly unique synapomorphy, the possession of hexagonal lens packing through thick interlensar sclera with tubercles (17=5).

Pedinopariops (Hypsipariops) vagabundus STRUVE, 1990

Plate 27.1-27.11; 28.1-28.14; Text Figure 16

Localities, type and figured material: Holotype SMF 49402, an enrolled complete individual preserved as an internal mould with fragmentary cuticle from the 'Black *Phacops* couche' of Jbel Issoumour, near Alnif, Morocco (numerous paratypes give full representation). Alternative specimens (figured here) come from same couche outcropping at Aferdou de Mrakib. Strata are Givetian in age (STRUVE placed this taxon's occurrence just beneath the Eifelian-Givetian boundary in his 1990 work, but BULTYNCK AND WALLISER, 2000, and KAUFMANN, 1998, both place these strata within the Givetian,

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based on much more detailed studies), and are part of the Bou Dib Formation. Plesiotypes UA6935-UA6939.

Diagnosis (emended from* S*TRUVE*, *1995): Close in overall morphology to *Pedinopariops (Hypsipariops) eurycaulus* (STRUVE, 1970), but with dorsal glabellar sculpture of moderately impressed, rounded pustules with flattened tops and mild interference with neighbours; pustules can be in excess of 2mm wide in large holaspides. Postocular distance relatively large (0.10-0.15, with 0.17 as absolute maximum) length (exsag.) of visual surface, and subocular area large (0.85-1.0 times height of visual surface). Eye bears 18 (occasionally 19) vertical rows of lenses, with 7 (occasionally 8) lenses per row; lenses in hexagonal pattern and separated by wide interlensar sclera with faint tubercles at all six corners of each lens. Palpebral lobe is broad (exsag.) near posterior border furrow, forming broad triangular outline, and sloping strongly into posterior border furrow contact. Genal field ahead of eye is only moderately sloping, and posterior margin of genal angle bears single row of robust, short spines.

Description: Works by STRUVE (1990; 1995) have so far only provided diagnosis and figures for this species, so more complete specimens are figured here and description provided.

General appearance of exoskeleton comparable to many species of *Drotops* (in body size, proportions, position/size/shape of eye, and in position of ornament), but differs significantly in having pustular glabellar sculpture, reduced sculpture on interlensar sclera, and is nearly lacking spines except on trailing edge of posterior genal border.

Cephalon has semi-circular dorsal outline (which becomes much more triangular in compressed specimens); and is dominated by broad (tr.), short (sag.) glabella, and tall, long (exsag.) eyes spanning almost entire distance from glabella to posterior border. Glabella is sub-pentagonal in dorsal outline; broadly domed (sag. and tr.), with no significant overhang of anterior border, and dorsal projection above top of eye equal to 0.30 of visual surface's height. Glabellar sculpture is of broad, low pustules on dorsal surface, whose crowding causes much interference in their outlines and many polygonal

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outlines; anterior portions of glabella bear progressively smaller, less crowded tubercles, with hemispherical to conical shapes and sparse pits between; anteroventral portion of glabella bears faint transversely directed keels on tubercles with numerous fine pits interspersed between. Axial furrows are moderately impressed, broad (tr.) and straight; diverge around anterior glabellar lobe at about 62°; shallow and become more exsaggitally directed adjacent to lateral L1; deepen and become narrower adjacent to front of eye, and deep section terminates in broad pit abutting anteroventral corner of eye (next to anterior ramus of facial suture), before flowing in shallow arc to connect with preglabellar furrow. Preglabellar furrow is uniformly shallow and round in section, and bows ventrally (around medial half of glabella) to very slightly. L2 and L3 show no independent convexity compared to frontal lobe of glabella, and S2 and S3 are indiscernible based on anything besides mild interruptions in sculpture and become less visible in larger holaspides. Intercalating ring is markedly subdued except for very narrow (tr. and sag.), ovate, raised pad it bears at its center; pillar-like pad extends dorsally and bears 3-5 pustules similar to those of glabella, resulting in height similar to occipital ring; flattened remainder of intercalating ring intrudes into back of glabella, but is clearly demarcated by broad, shallow S1, S0, and lateral furrows. L1 lateral lobes are low domes with fairly polygonal outlines and no sculpture except for small number of pits; apodemal pits anterior and posterior to lobes are straight, narrow (exsag.), deep, and long (tr.), running almost entire width (tr.) of lobes, and producing their straight edges.

Occipital ring is very similar to thoracic axial rings in subdued pustular sculpture, but is significantly longer (exsag.) throughout its medial lobe (about 1.18 times length of anterior thoracic segment's axial ring), as it intrudes anteriorly 1/3rd of distance (exsag.) across lateral L1; lateral lobes of occipital ring are also less distinct because of its extended medial portion.

Fixigena proximal to palpebral furrow exhibits low dorsal convexity, and is situated below height of palpebral lobe and glabella (disappearing behind eye in lateral view); sculpture here consists of mid-sized, low, broad pustules, close to one another, but with little distortion, across highest (dors.) areas; posterior distal tip of region flows into narrow (exsag.), effaced postocular pad, which bears few faint tubercles and pits in distal extremes, but transition is almost severed by posterior corner of eye; postocular pad

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extends ventrally well beyond base of eye, fading distally into genal field, and demarcated anteriorly from subocular pad only by mild trace from posterior ramus of facial suture. Palpebral lobe has moderate dorsal convexity, and sits well above remainder of fixigena in posterior reaches; sculpture consists of two rows of large, low, slightly conical pustules paralleling palpebral rim (with distal row pustules double size of others); numerous pits are interspersed among pustules, and space between palpebral rim and palpebral lobe is occupied by broad (tr.), barren sulcus with single row of concentrated pits along its lateral margin. Palpebral rim is prominent ledge matching lateral extension of scleral surface (described below); rim bears single row of fine tubercles which become less bulbous and more pointed above posterior portion of eye; many fine pits are interspersed among rim tubercles, and occur in slightly more concentrated strip just above visual surface. Palpebral furrow is shallow and broad near midlength (exsag.) of eye; becomes broader and slightly deeper anteriorly, before joining axial furrow; becomes much narrower and deeper adjacent to posterior corner of eye; and flows into sharp postocular sulcus beneath visual surface.

Eye is long, occupying about 0.45 of total cephalic length (exsag.) and tall (approximately 0.40 of total cephalic height); it is closely adpressed to glabella anteriorly, and reaches posteriorly almost to posterior border; height and vertical orientation of visual surface, accompanied by broad flare of genal angles, cause eye to protrude compared to contours of genal field. Visual surface bears 18 rows of lenses, with 7 as typical maximum number of lenses per row, and 101-110 as typical total number of lenses per eye (see Text Fig. 16 for full lens formula). Sclera is prominent and maintains very even spacing of lenses, even in regions of reduced lens size; sclera projects well above height of lenses, and forms strong hexagonal shape around each lens; consistently, at each corner of hexagon there is single faint tubercle, which becomes more inflated and less pointed in larger holaspides. Lens distribution extends to very margin of eye, leaving narrow, inflated margins anterior and ventral to visual surface, and slightly broader margin behind posterior corner; ventral margin (beneath anterior 2/3rd of eye) and its downslope into subocular groove contain many small pits, while remainder of margin is smooth. Subocular groove exhibits extreme breadth (vertically); it has its dorsal half partially filled by weak subocular pad adorned with sparse faint tubercles and few fine

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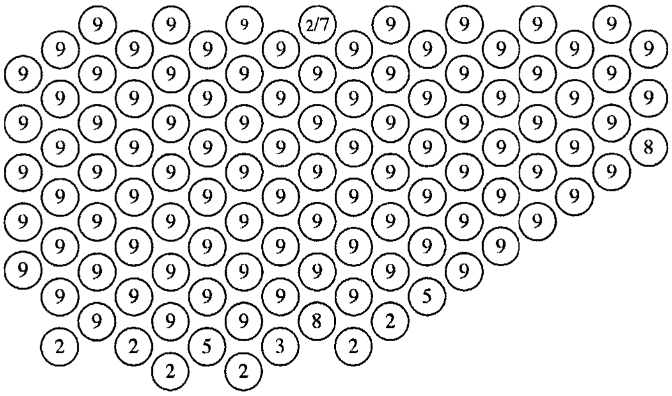
pits; oddly, deepest part of otherwise shallow groove is directly abutting anterior portion of genal field (beneath anteriormost half of eye), giving eye appearance of having inset base.



Text Fig. 16: Lens formula diagram for *Pedinopariops (Hypsipariops) vagabundus* specimens

Genal angle is very tall (roughly 1.5 times visual surface's height); angle does not extend very far posteriorly behind occipital ring, but is laterally expansive; surface of angle is strongly inflated, giving subocular area inset appearance; sculpture consists of sparse, low, slightly conical pustules, and numerous widely distributed fine pits beneath posterior half of eye; pits become more densely packed and much larger just behind posterior ramus of facial suture; pustules become more prominent in posterior reaches; trailing edge of gena and posterior border bears single row of tall, posterolaterally directed, conical tubercles, which are reduced proximally, but are large enough to be considered spines in distal region. Posterior border furrow is straight proximally, round-bottomed and moderately impressed, fades slightly and curves forward distally at distal tip of postocular pad, and merges proximally with apodemal pit behind L1 lateral. Posterior border slopes gradually into posterior border furrow, increasing prominence of its trailing edge, and is significantly lower than posterior corner of eye due to low dorsal curvature found between occipital ring and genal angle. Anterior genal field extends laterally well beyond visual surface, and surface is much less vertically oriented than in *Phacops*, creating sharper junction with glabella at anterior edge; sculpture consists of very subdued pustules with sparse pits between which become more concentrated

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adjacent to ventral margin. Ventral margin forms raised rim with nearly circular cross-section in lateral regions; rim continues posteriorly to very corner of genal angle, with gradual posterior reduction; beneath glabella, margin becomes rectangular in section, and has numerous pits along its anteroventral surface; fine, anastamosing terrace lines form bulk of sculpture on margin, and trend parallel to margin's edge.

Vincular furrow is deep, round-bottomed, and of uniform dimension throughout its course; beneath genae, it is divided into interconnected ovate pits to accept tips of thoracic segments; granules appear on all surfaces of furrow. Doublure surface has moderate ventrally-directed convexity beneath glabella, and strong dorsally-inclined slope, producing posterior margin situated well ahead of first (ant.) vincular pit, and overall short (sag.) surface. Hypostomal contact surface seems relatively wide (tr.), but no hypostome has been recovered. Sculpture consists of low anastamosing terrace lines, which parallel closest margin of surface; are most pronounced along ventral extremes; and fade posteromedially to be replaced by elongate granules. Doublure, along inner edge of vincular furrow, is distinctly lower than that outside furrow, forming protruding 'lip' visible in lateral view, and anterior-facing medial portion of vincular furrow.

Hypostome not recovered for species.

Thorax contains 11 segments; width (tr.) of axial ring to width of whole segment is about 0.34 in anterior segments and 0.33 in posterior segments; overall, thorax tapers to about 0.87 of anterior width (tr.), heading posteriorly. Thoracic axial rings have relatively low dorsal curvature, and indistinct lateral lobes. Medial lobe is flat-topped and bears crescentic patch of low pustules (typically two deep, exsaggitally) along posteromedial portion; fairly coarse pitting is scattered throughout field of pustules, but becomes concentrated in posterior section, with densely-packed pits occurring on posterior face of each axial ring. Lateral axial lobes are separated from medial lobe along anterior half (exsag.) by moderately impressed, exsagittally directed sulcus continuing backward from thoracic apodemal pit; posterior margin shows faint indentation or surface flattening due to anterodorsal continuation of axial socket depression; lateral lobes follow curvature of medial lobe, with little independent convexity, dorsal outline that is roughly rectangular, and very few fine pits for ornament. Articulating half-ring is separated from axial ring by deep, round-bottomed furrow; half-ring surface has strong dorsal convexity

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(tr. and sag.), and bears granules in posterior 2/3rd, with transition to exceptionally fine finger print-like pattern of terrace lines across anterior 1/3rd of surface (too fine for figures to display). Axial furrow is strongly impressed, round-bottomed, and fades against anterior pleural band (ant.) and interpleural furrow (post.). Anterior pleural band is round in section proximally and distally, with flattened surface adjacent to fulcrum; ornament consists of very faint and sparse strand of fine pits and tubercles along distal half of highest surface. Posterior pleural band rises slightly higher (dors.) than anterior band, and displays more circular section, which continues past fulcrum in slightly diminished form; sculpture begins medially as sparse fine pits, but (just medial to fulcrum) makes distal transition to denser, low, conical tubercles and much coarser pits; tubercles are variable between specimens, but are typically arranged in 1-2 rows along most lateral portions of band, with most prominent tubercles along middle (exsag.) of surface. Pleural furrow is narrow (exsag.), steep-sided, and deeply impressed; it fades medially against axial furrow, and shallows distally near fulcrum, but breaches rim of articulating facet to create fine trace across posterior portion of facet. Articulating facet is almost flat, and bears granules over its entire surface; granules fade along anterodorsal portion of facet, but become more dense and coarse along posteroventral portions, forming coarse granular posterior rim to facet. Distal tip of thoracic segment is granulose, flat-tipped (anteroventrally), and meets posterior pleural band in rounded corner.

Pygidium is long (sag.) for its width (tr.), very near semi-circular in dorsal outline, and dominated by long (sag.), narrow (tr.) axis; axial width is about 0.27 of overall pygidial width in anterior region, slowly tapers at about 18° convergence, then undergoes more significant closure next to terminal piece. Pygidial axis is made up of 12 rings plus terminal piece; posteriormost 3 rings are faint due to their narrowness (sag.), and delimited in many specimens by tubercle rows; clear interannular rings are present behind anterior 5 axial rings, and diminish posteriorly, leaving questionable gaps behind sixth and seventh axial rings in some specimens; ring furrows make contact with axial furrow behind first 6 axial rings, creating concave-posterior arcs and small fossae in axial furrow, and leaving small indentations within proximal tip of neighbouring pleural rib. Interannular rings create strong indentations in posterior margin of adjacent axial ring. Behind 2-3 anteriormost axial rings, interannular ring often has small medial protrusion

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(from axial ring ahead of it) overhanging it (see Pl. 27.9). Interannular rings and backward-swept distal tips of axial rings combine to give broad (tr.) “w-shape” to anterior 5 axial rings. Axial sculpture consists of mid-height, rounded pustules crowded atop dorsal extremes of rings in 1-2 transverse rows and fading anterolaterally; fine pits occur along posterior half of each ring; pitting becomes more crowded in posteromedial portions of each ring. Axial furrow is impinged upon by ring furrows, but is otherwise well impressed, wide (tr.), sub-angular in section, and relatively straight in course; interruptions from axial rings cease behind sixth axial ring and are accompanied by slight increase in medially directed curvature, which becomes much greater next to terminal piece; closure is not complete behind terminal piece, due to shallowing of furrow, leaving weak ‘postaxial ridge’, which extends almost to margin of pygidium. Pygidial pleural region bears 7 clear pleural ribs, followed posteriorly by 2 faint ribs defined largely by their sculpture; anterior ribs are defined 3/4 of distance across pleural field, and more posterior ribs only extend 2/3 of distance. Pleural furrows are deep, narrow (exsag.), and round-bottomed; each trends posteriorly with slight posterior concavity (most pronounced distally); proximal termination occurs within fossa created by lateral extension of axial ring furrows, creating indentation in anterior pleural band, and forward-swept appearance to proximal rib tips. Broad (tr.) fossae occur adjacent to distal tips of ribs; pleural furrows are redirected (turned laterally) upon connecting with fossae, and shallow to die out upon leaving distal ends of fossae. Interpleural furrows are weakly defined, and visible on anteriormost 5 pleural ribs largely due to lack of sculpture. Sculpture upon highest points of ribs is of mid-sized, low, slightly conical pustules, occurring in single file rows across each band of anterior 5 pleural ribs, and jumbled into double or single rows with dense packing in posterior ribs; fine pits are scattered amongst pustules; pitting becomes more dense, and pustules become coarser in distal portions of ribs. Pleural field, distal to ribs, displays mild continuation of pleural furrows through lack of ornament, but otherwise bears small to mid-sized pustules with slight conical shapes, and fine pits, both of which become progressively smaller and more densely packed near ventral margin; pits fully replace pustules adjacent to ventral margin. Ventral margin forms thin (in section) raised lip that extends ventrolaterally around tail; margin bows dorsally beneath medial half of pygidium, and flares laterally adjacent to anterior

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articulating facet, producing slight corner distal to anteriormost pleural rib; faint terrace lines are present on surface of margin.

Discussion: There is some argument over the validity of *Pedinopariops* as a genus – CHLUPÁČ (1977) refused to recognize this taxon, even when it occupied a subgeneric position. Although some of the other subgenera put forward by STRUVE (and later elevated to genera) are questionable, this particular genus seems well supported by a large number of characters (more so than some other widely used phacopid genera).

Cephalic differences between gigantic members of the 'Geesopini' are largely a matter of sculpture. Basically, members of *Pedinopariops* have a crowded pustular glabellar sculpture, which STRUVE (1995) described as looking like a worn cobble-stone road, while members of *Drotops* have tall conical or spinose tubercles that are much more extensive, widely distributed, and pronounced across the cephalon. STRUVE (1995) noted differences in pygidial curvature and sculpture that distinguish *P. (H.) vagabundus* from similar size (and morphologically similar) specimens of *Drotops armatus* and *D. megalomanicus*. These include a less vaulted pygidium, with more faintly incised axial rings and pleural ribs, a narrower axis, and subtler sculpture in *Pedinopariops*. Also, members of *Drotops* have a subocular distance equal to or greater than the height of the visual surface, while *Pedinopariops* species all have a distance less than the height of the visual surface (STRUVE, 1995). *Pedinopariops (Hypsipariops) vagabundus* has so many distinctive features tied to its gigantism, that it is less likely to be mistaken for other members of its own subgenus or genus than for members of *Drotops*. There is no point in contrasting it against closer (congeneric) relatives here.

Cladistic analysis suggests that *Pedinopariops (Pedinopariops)* and *Pedinopariops (Hypsipariops)* are united by the local synapomorphy of a remarkably narrow pygidial axis (19=0). Each subgenus has 2 local autapomorphies.

Genus *Drotops* STRUVE, 1990

Discussion: Unfortunately, members of this genus are poorly represented in our collections. High commercial demand has driven the prices of even unprepared material

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to great heights, and has created a large market for composite specimens. These circumstances have left us with very little in the way of complete specimens of the same quality as those already represented by STRUVE (1995). Most of the material purchased or collected by our research group is either an obvious composite (with pieces of uncertain origin), or of such fragmentary nature that it cannot be identified with certainty. Instead of repeating work already completed by STRUVE, this work will provide basic eye diagrams for those taxa that can be indentified.

The cladistic analysis completed here provides mild support for the genus *Drotops*, with one local synapomorphy, a palpebral area with no pits between its tubercles (14=3), and one truly unique synapomorphy, glabellar sculpture of tall conical to spinose tubercles (7=6). The individual species within *Drotops* are weakly supported, by a single local autapomorphy. Combine this with the fact that many of the 'forms' of *Drotops armatus* that STRUVE (1995) depicted are fairly disparate in morphology, and there is a good chance that there may be some systematic restructuring when more detailed analyses are completed on this portion of the large-scale cladogram.

Drotops megalomanicus megalomanicus STRUVE, 1990

Text Figure 17

Localities, type and figured material: Holotype SMF 49340, an enrolled complete individual most likely from the Taboumakloûf section on the dip slope of Jbel Issoumour, near Alnif, Morocco (numerous paratypes give full representation). Alternative specimens (figured here) were commercially mined and likely from the equivalent *Drotops megalomanicus* couche outcropping at Jbel Mrakib (farther southeast), or potentially Jbel Oufatene (farther south), in the Ma'der basin. Strata are Givetian in age, and part of the Bou Dib Formation (CAMPBELL *et al.*, 2002; BULTYNCK AND WALLISER, 2000).

Diagnosis: See STRUVE (1995) for diagnosis.

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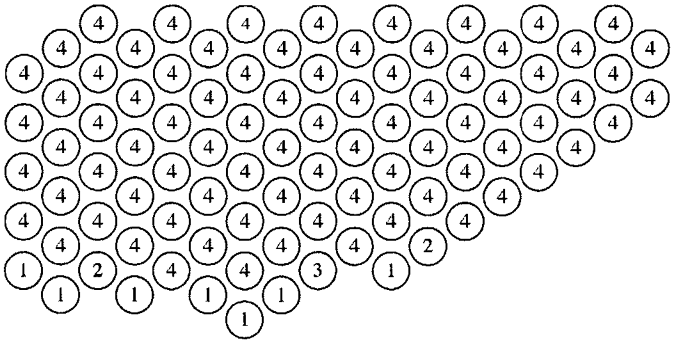
Description: Only 2 outstretched composite specimens and 1 weathered enrolled individual are available for comment in this study. Their origins and veracity are questionable (especially those specimens built from fragments), so no further description is possible here. Eye formula diagrams have been completed (see Text Fig. 17), but are of limited value until these specimens have better representation and it is certain that no further subdivisions exist in their taxonomy. Further subdivisions are very likely, as this species can be found in the *Drotops megalomanicus* couche, in the overlying *Drotops armatus* couche (to a lesser extent), and sporadically throughout approximately15 meters of outcrop in between. It, or very similar forms, also occur beneath the *Drotops megalomanicus* couche.



Text Fig. 17: Lens formula diagram for *Drotops megalomanicus megalomanicus* specimens

Discussion: Although it is not possible to add to the work of STRUVE here, besides expanding the list of localities in which this species occurs, it should be noted that the subspecies *Drotops megalomanicus megalomanicus* and *D. megalomanicus subornatus* occur within a fairly restricted portion of each section. Just as STUVE (1995) predicted, this species is a fairly reliable biostratigraphic marker within the Ma'der basin. Cladistically, this taxon bears a single localized autapomorphy, having distinct globular L1 lateral lobes (11=1).

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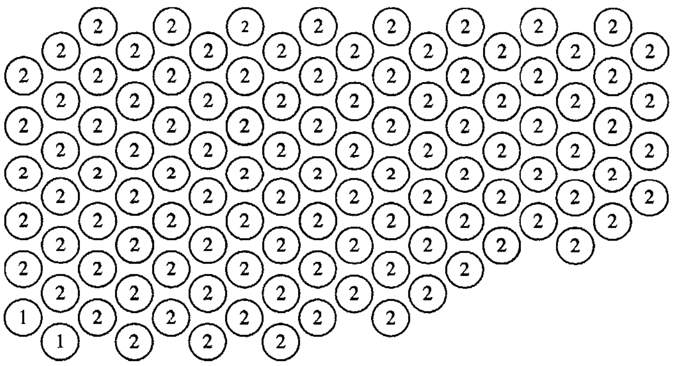
Drotops armatus STRUVE, 1995

Text Figure 18

Localities, type and figured material: Holotype SMF 49480, an outstretched complete individual most likely from the Taboumakhloûf section on the dip slope of Jbel Issoumour, near Alnif, Morocco (numerous paratypes give full representation). Alternative specimens (figured here) were commercially mined and likely come from the equvalent *Drotops armatus* couche outcropping at Zireg (farther southeast). Strata are Givetian in age, and part of the Bou Dib Formation (CAMPBELL *et al.*, 2002; BULTYNCK AND WALLISER, 2000).

Diagnosis: See STRUVE (1995) for diagnosis.

Description: Only 1 outstretched composite specimen and 1 enrolled specimen are available for comment here. Their origins and veracity are questionable (especially the specimen built from fragments), so full description is not possible at this time. Both specimens have many of their spines fractured and replaced with automotive body filler that has been dyed black, and one appears to have had spines' length exaggerated in this process. Neither specimen is assignable to 'forms' named by STRUVE (1995), because of uncertainty in size of sculpture elements, and doubts as to whether all points where spines originate actually bore spines prior to preparation. Regardless of these taxonomic problems, diagrammatic representation of eye formula has been provided in Text Fig. 18. This tentative representation applies at species level, not to one individual form.



Text Fig. 18: Lens formula diagram for *Drotops armatus* specimens

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Discussion: The only addition to the work of STRUVE (1995) that is possible here is to increase the number of localities in the Ma'der basin that are known sources for this species. If all 4 forms of this species espoused by STRUVE are distinct groups and of very limited stratigraphic occurrence (*Drotops armatus* does not appear to have the same breadth of distribution found in *Drotops megalomanicus*), then this species is likely a good candidate for studies on polymorphism in trilobites or morphological changes on a very fine timescale. More extensive and detailed work is necessary to give *Drotops armatus* a stable systematic position and internal structure, and many more specimens (set in a detailed stratigraphic framework) are needed to validate the multiple forms proposed by STRUVE.

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PLATE 1

Figs. 1–11. *Reedops bronni* (BARRANDE, 1846) from iron-rich marls near base of Oufatene and Issoumour sections, within Ma'der basin ('*Dicranurus* couche' and '*Kolihapeltis* couche' slightly above), strata are Pragian in age, and part of Ihandar Fm.

Plesiotype UA6846 (partially enrolled, complete individual, from '*Kolihapeltis* couche'):
1. Lateral detailed view of left eye, X8.67.
3. Lateral view of exoskeleton, X2.0.

Plesiotype UA 6844 (outstretched, mostly Moroccan prepared specimen, from '*Dicranurus* couche'):
2. Anterior view of cephalon, X2.6.
4. Dorsal view of cephalon, X2.7.
5. Ventral view of cephalon (doublure), X2.6.
8. Dorsal view of pygidium (specimen preparation-damaged on left side), X3.6.
10. Dorsal overview of arched exoskeleton, X2.7.
11. Lateral view of complete exoskeleton, X2.7.

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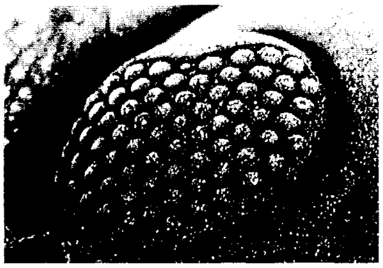

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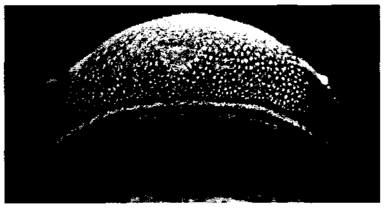

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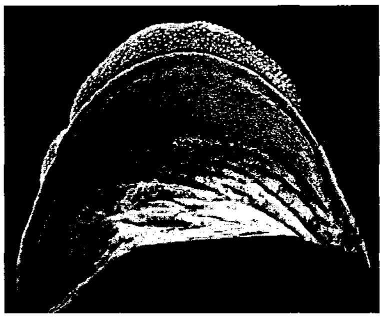

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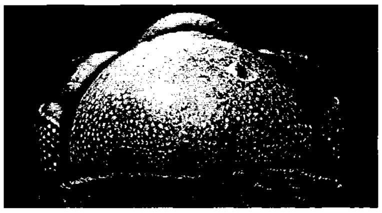

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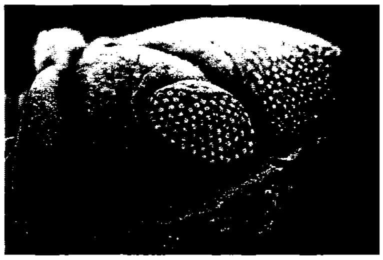

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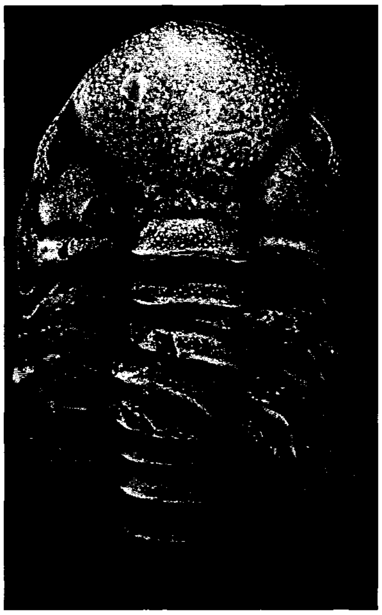

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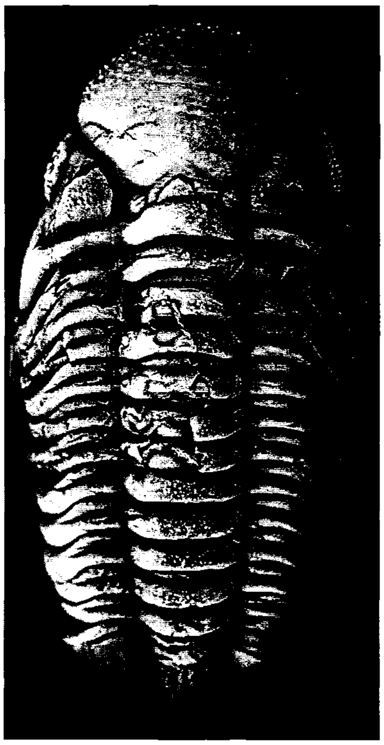

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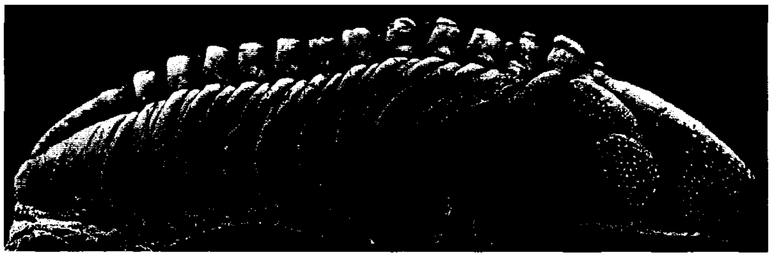

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Plate 1

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PLATE 2

Figs. 1–5. *Reedops cephalotes hamlagdadianus* ALBERTI, 1983 from loosely cemented, sparry calcite masses within crevasse-fills, between algal mud-mounds at Hamar Laghdad, in Tafilalt basin. Strata are Pragian in age, and part of Kess-Kess Fm.

Plesiotype UA6848 (isolated cephalon):
1. Dorsal view (palpebral lobes flat), X1.5.
2. Anterior view (palpebral lobes horizontal), X1.5.
3. Anterodorsal view, X1.5.
4. Posterodorsal view (top of glabella flat), X1.5.
5. Left eye and postocular pad, detailed view, X4.1.

Figs. 6-12. *Reedops cephalotes hamlagdadianus* ALBERTI, 1983 from iron-rich calcareous mudstones at base of El'Mdâouer section, in Tindouf basin. Strata are Pragian in age, and part of Assa Fm.

Plesiotype UA6861 (outstretched individual with minor damage to anterior glabella)
6. Lateral view of cephalon, X2.1.
7. Left eye and postocular pad, detailed view, X3.9.
8. Dorsal view of cephalon (top of glabella flat), X1.5.
9. Dorsal view of cephalon (palpebral lobes flat), X1.5.
10. Dorsal view of pygidium, X1.8.
11. Dorsal overview of exoskeleton, X1.5.
12. Lateral overview of exoskeleton, X1.4.

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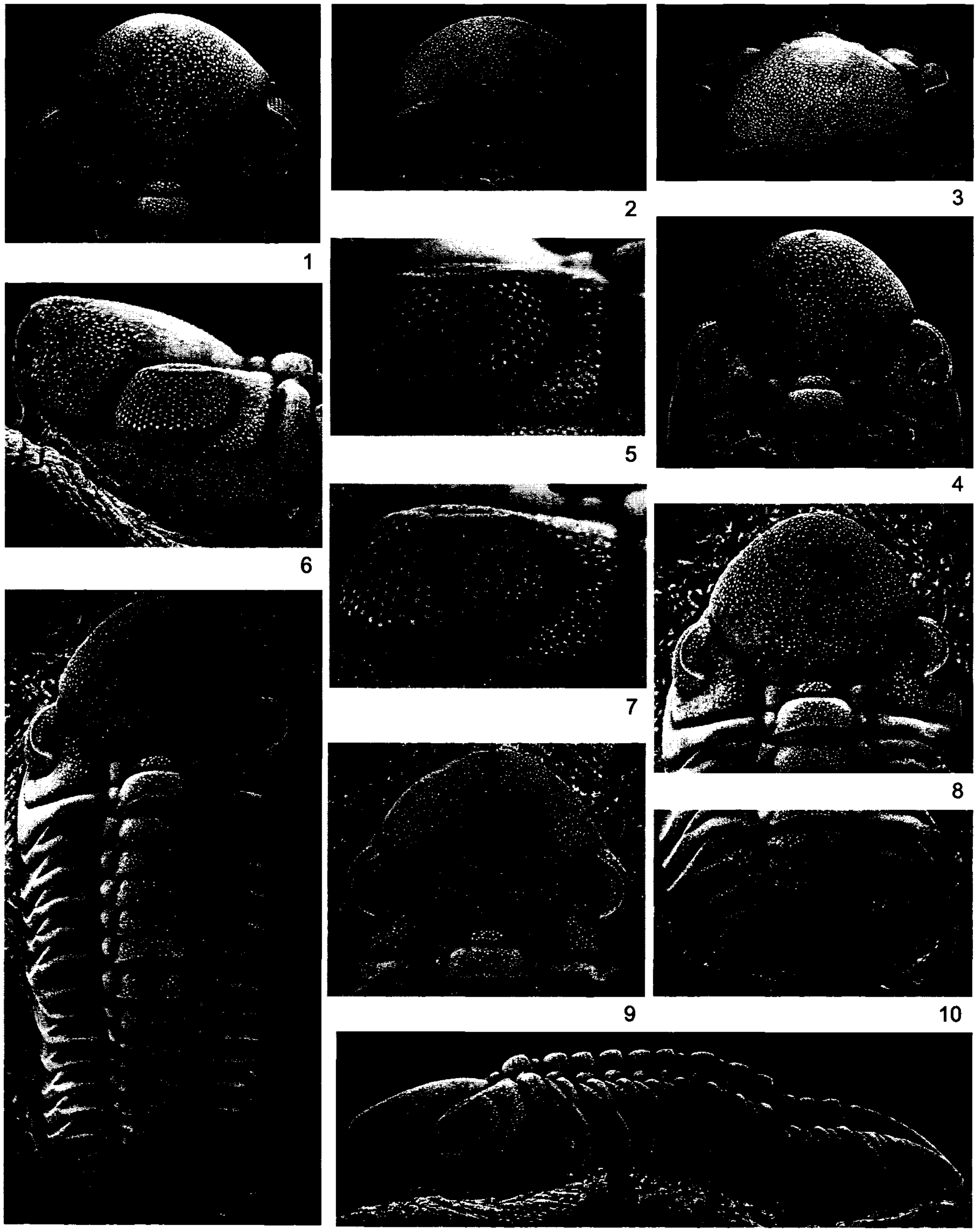

Plate 2

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PLATE 3

Figs. 1–5. *Reedops cephalotes hamlagdadianus* ALBERTI, 1983 from loosely cemented, sparry calcite masses within crevasse-fills, between algal mud-mounds at Hamar Laghdad, in Tafilalt basin. Strata are Pragian in age, and part of Kess-Kess Fm.

Plesiotype UA6856 (isolated cephalon, missing left side, fragmented posterior):
1. Lateral view, X2.2.
7. Ventral view (of doublure), X1.5.

Plesiotype UA6854 (isolated cephalon, missing left side, fragmented posterior):
2. Lateral view, X2.0.
3. Anteroventral view, (note shallow vincular furrow medially), X1.7.
5. Right eye and postocular pad, detailed view, X3.9.

Plesiotype UA6848 (isolated cephalon):
4. Lateral view, X2.0.

Plesiotype UA6851 (isolated cephalon, decorticated in some spots):
6. Anterodorsal view, X2.0.
9. Lateral view, X2.9.
11. Dorsal view, (palpebral lobes flat), X2.0.

Plesiotype UA6853 (isolated pygidium):
8. Dorsal view, X2.4.
10. Posterior view, X2.2.

Plesiotype UA6849 (isolated cephalon, missing patch of glabella cuticle):
12. Lateral view, X2.1.

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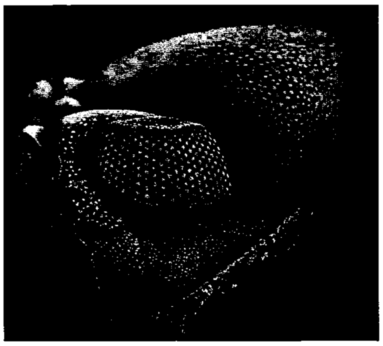
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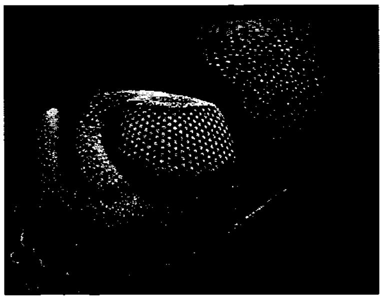
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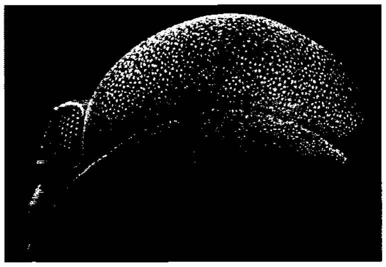
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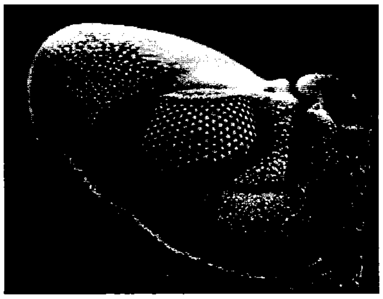
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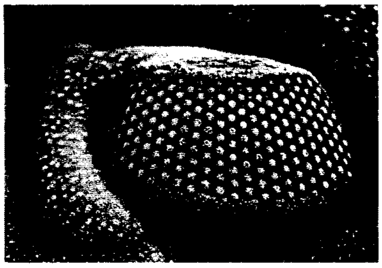
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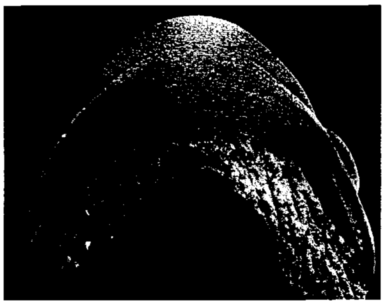
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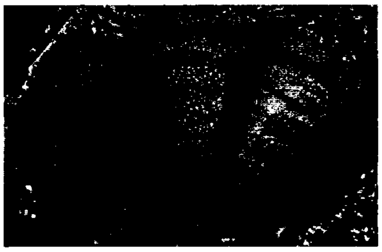
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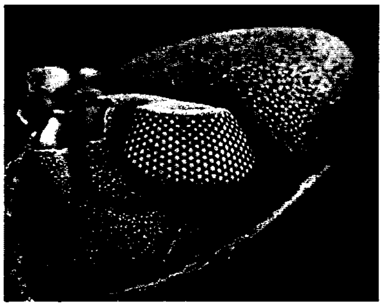
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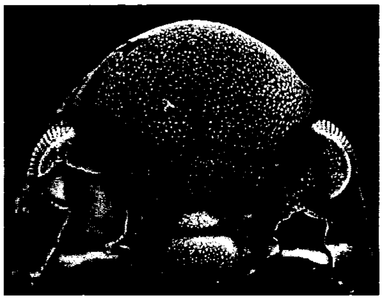
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Plate 3

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PLATE 4

Figs. 1–12. *Reedops pembertoni* n. sp. from iron-rich marls near base of Oufatene and Issoumour sections, within Ma'der basin ('*Dicranurus* couche' and '*Kolihapeltis* couche' slightly above). Strata are Pragian in age, and part of Ihandar Fm.

Holotype UA6862 (enrolled individual, missing pygidium, from '*Dicranurus* couche'):
1. Anterior view, (palpebral lobes almost horizontal), X2.4.
4. Anterodorsal view, (note low intercalating ring), X2.4.
7. Anteroventral view, (note very shallow vincular furrow), X2.5.
10. Dorsal view, (palpebral lobes flat), X2.4.
11. Lateral view, X2.6.
12. Ventral view, (note shallow vincular furrow and doublure sculpture), X2.5.

Paratype UA6864 (complete outstretched individual, cephalon prepared, from '*Kolihapeltis* couche'):
2. Lateral view, X2.9.
5. Right eye and postocular pad, detailed view, X7.0.

Paratype UA6875 (complete, partially enrolled individual, Moroccan prepared, from '*Dicranurus* couche'):
3. Pygidium in posterior view, X2.9.
4. Pygidium, dorsal view, X2.9.

Paratype UA6871 (complete, partially enrolled individual, Moroccan prepared, from '*Dicranurus* couche'):
8. Lateral view of cephalon, X3.4.
9. Dorsal view of pygidium, (markings on left side and right anterior are preparation scratches), X3.2.

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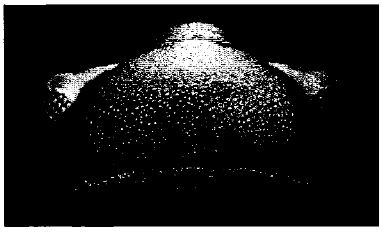
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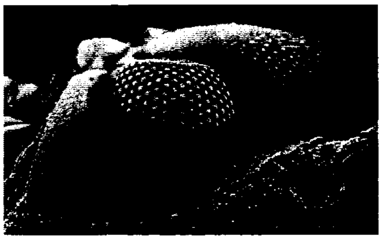
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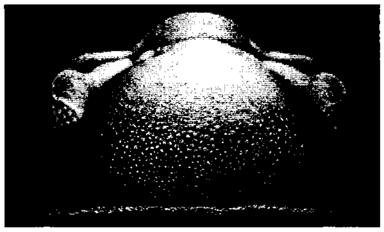
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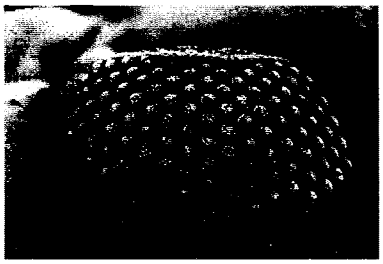
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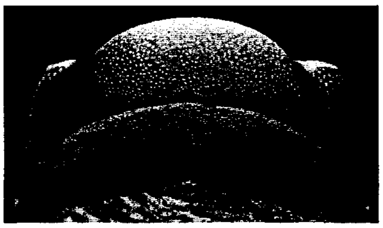
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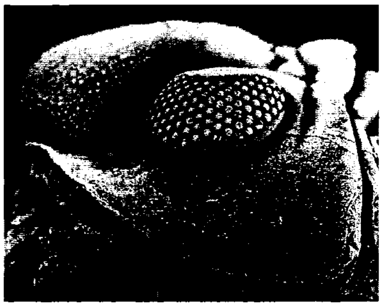
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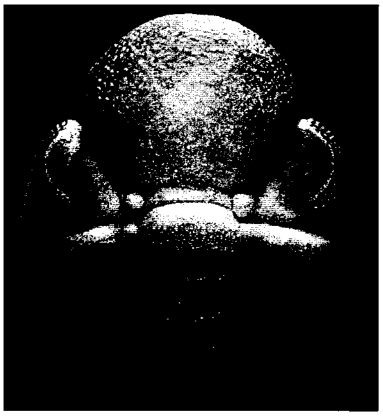
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Plate 4

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PLATE 5

Figs. 1–8. *Reedops pembertoni* n. sp. from iron-rich marls near base of Oufatene and Issoumour sections, within Ma'der basin ('*Dicranurus* couche'). Strata are Pragian in age, and part of Ihandar Fm.

> Paratype UA6863 (nearly complete, outstretched individual from '*Dicranurus* couche' – note some loss of detail due to air-abrasive preparation):
> 1-4. Cephalon in anterior, right lateral, left lateral, and dorsal (with palpebral lobes flat) views, X2.4, X3.1, X3.4, X2.4, respectively.
> 5. Dorsal view of pygidium, X3.0.
> 6-8. Whole specimen in left lateral, right lateral, and dorsal views, X 2.5, X2.4, X2.3, respectively.

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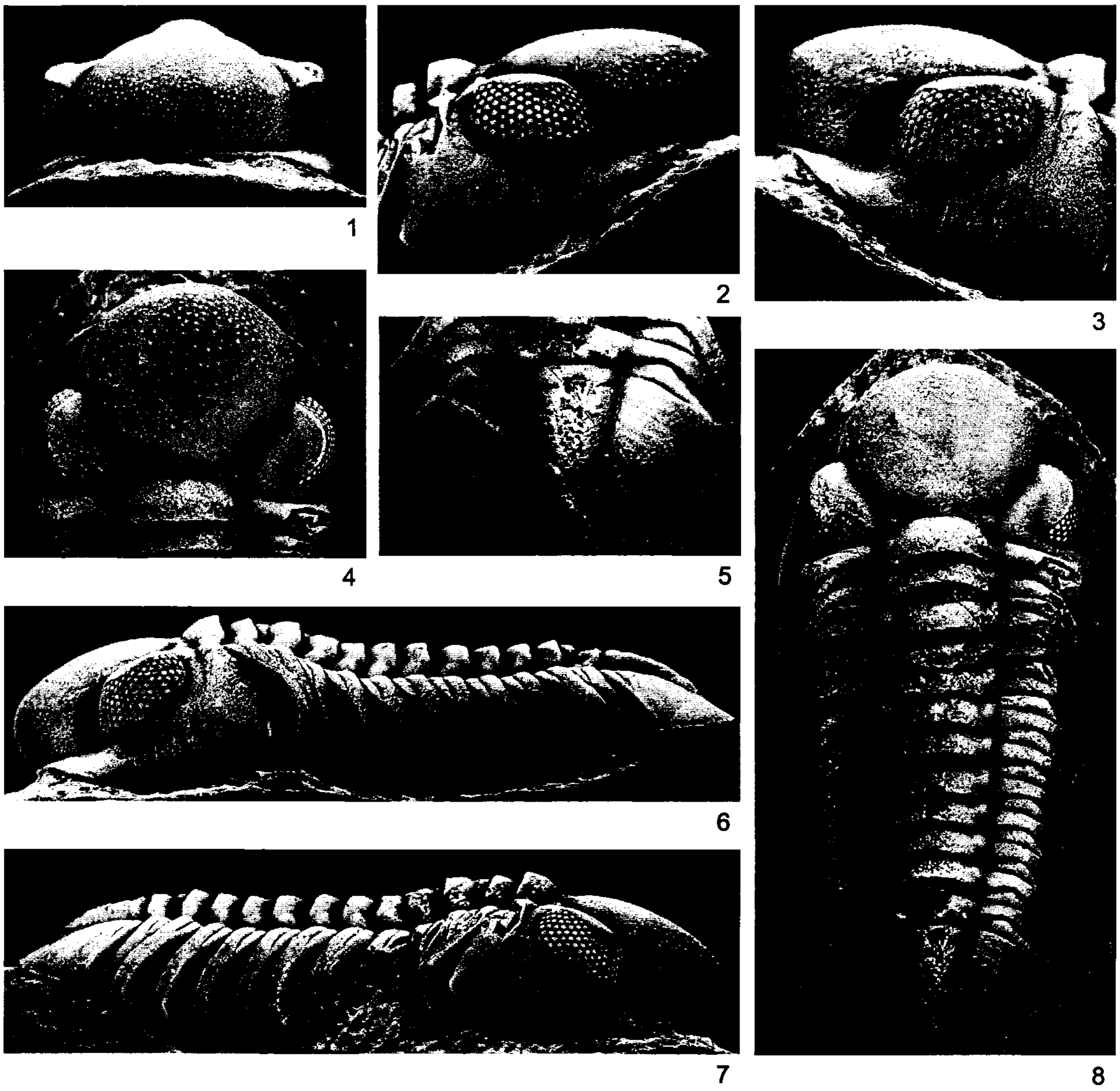

Plate 5

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PLATE 6

Figs. 1–12. New Genus A *smoothops* (CHATTERTON *et al*., 2006), from basal 4 meters of section through Timrhanrhart Formation (localities ZGEE1 and ZGEE2), northeast of Jbel Gara el Zguilma.

Holotype UA13306:
1–3, 9. Exterior views of enrolled exoskeleton, X3.5.

Paratype UA13307:
4–5. Exterior views of enrolled exoskeleton, X4.1, X3.6, respectively.

Paratype UA13308:
6. Exterior view of enrolled exoskeleton, X3.8.

Paratype UA13309:
7. Exterior view of enrolled exoskeleton, X2.2.

Paratype UA13310:
8, 12. Right lateral view, and detail of left eye of enrolled exoskeleton, X4.3, X10.2, respectively.

Paratype UA13311:
10. Lateral view of right eye of enrolled exoskeleton, X10.6.

Paratype UA13312:
11. Exterior view focusing on doublure of enrolled exoskeleton, X5.4.

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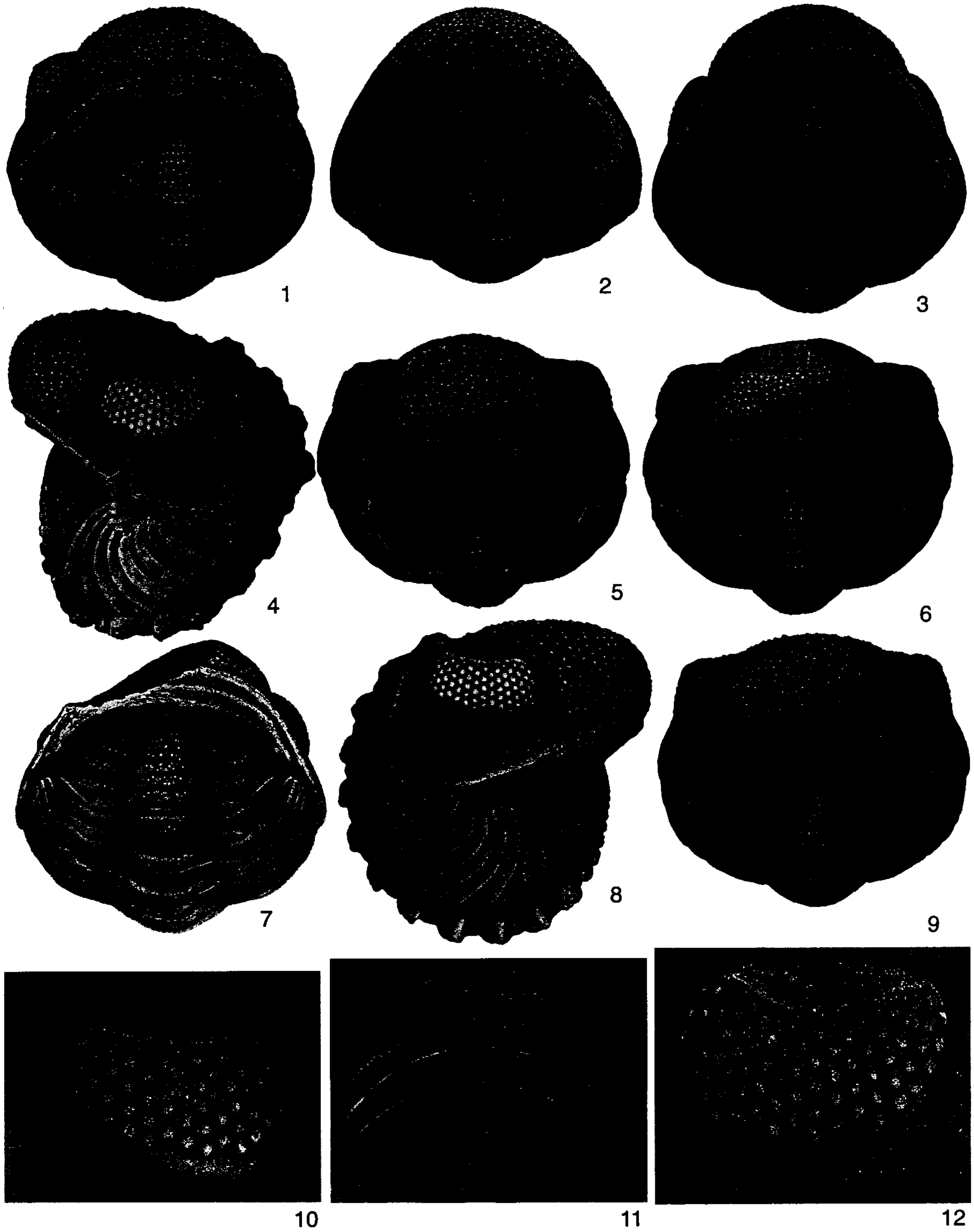

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PLATE 7

Figs. 1–12. New Genus A *smoothops* (CHATTERTON *et al.*, 2006), from basal 4 meters of section through Timrhanrhart Formation (localities ZGEE1–ZGEE2), northeast of Jbel Gara el Zguilma.

Paratype UA13311:
1, 11. Dorsal and lateral views of enrolled exoskeleton, X3.7, X4.5, respectively.

Paratype UA13313:
2, 12. Dorsal and lateral views of partly enrolled partial exoskeleton, X3.2, X4.1, respectively.

Paratype UA13307:
3, 5. Exterior views of enrolled exoskeleton X3.6.

Paratype UA13357:
4. Exterior view of enrolled exoskeleton, X2.5.

Paratype UA13312:
6, 9. Exterior views of enrolled exoskeleton, X4.25.

Paratype UA13308:
7. Exterior view of enrolled exoskeleton, X3.8.

Paratype UA13314:
8. Exterior view of enrolled exoskeleton, X3.2.

Paratype UA13315:
10. Lateral view of enrolled exoskeleton, X3.1.

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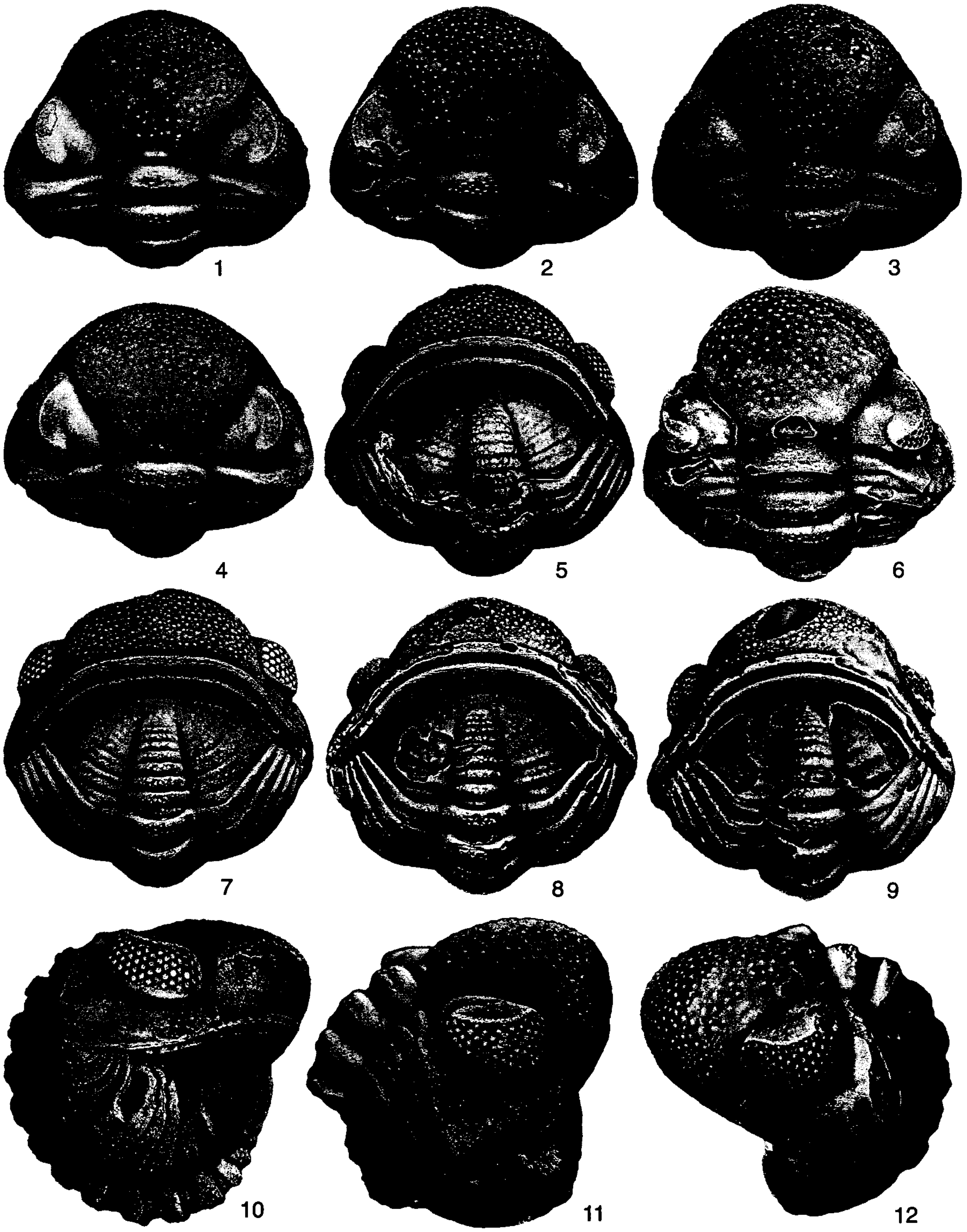

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PLATE 8

Figs. 1–12. New Genus A *smoothops* (CHATTERTON *et al.*, 2006), from about 50 meters above base of section through Timrhanrhart Formation (locality ZGEE3), northeast of Jbel Gara el Zguilma.

1–2, 4. UA13316, dorsal, anterior and lateral views of small cephalon, X9.9, X9.9, X14.0, respectively.

3. UA13317, anterior view of cephalon, X5.2.

5, 7. UA13318, lateral and exterior views of slightly disarticulated exoskeleton, X6.2, X4.8, respectively.

6. UA13319, lateral view of cephalon, X4.3.

8. UA13320, lateral view of partly enrolled exoskeleton, X4.4.

9. UA13321, lateral view of partial exoskeleton, X3.8.

10. UA13322, exterior view of enrolled exoskeleton, X3.6.

11. UA13323, exterior view of enrolled exoskeleton, X3.8.

12. UA13324, lateral view of enrolled exoskeleton, X4.8.

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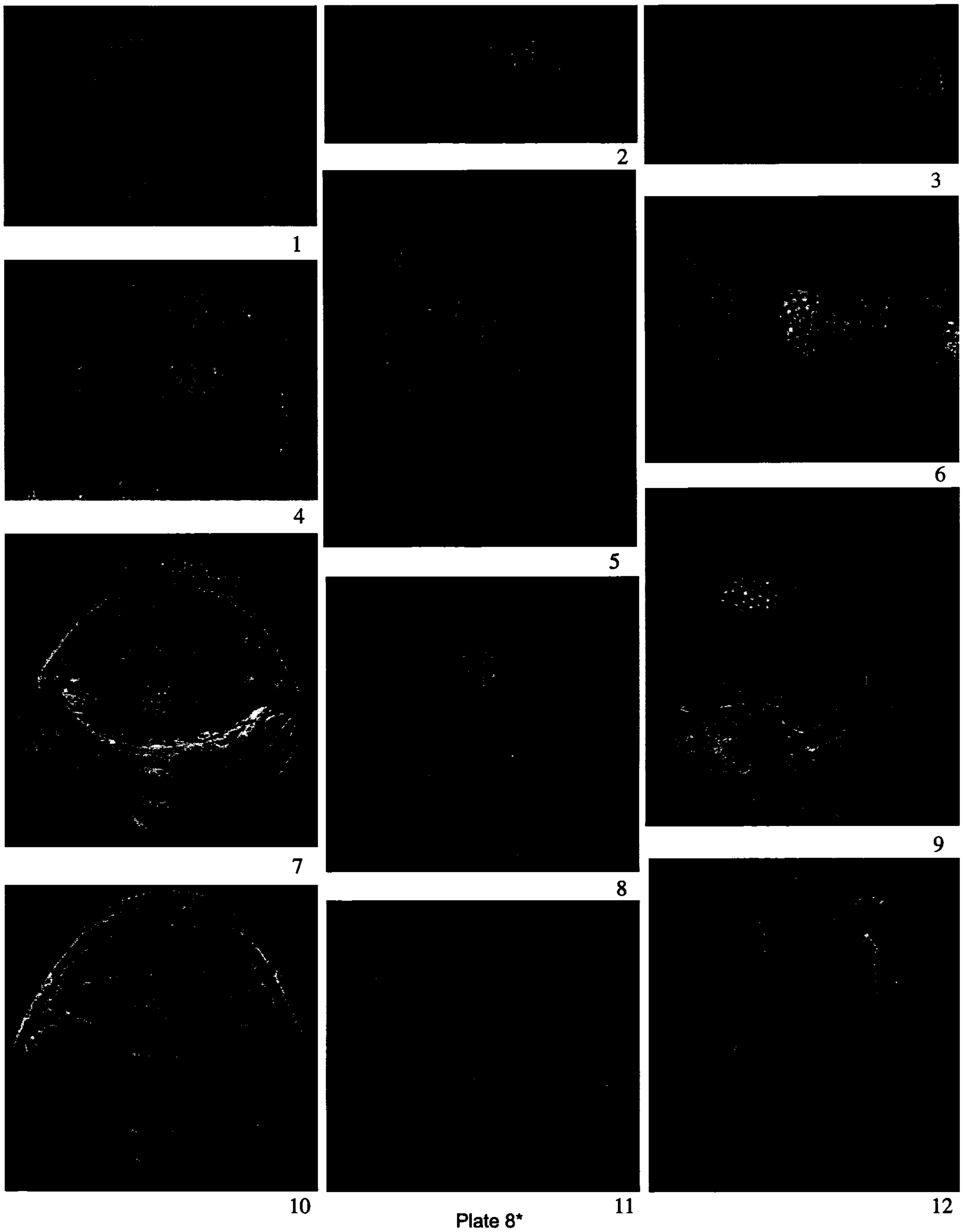

Plate 8*

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PLATE 9

Figs. 1–12. New Genus A *smoothops* (CHATTERTON *et al*., 2006), from about 50 meters above base of section through Timrhanrhart Formation (Locality ZGEE3), northeast of Jbel Gara el Zguilma.

1–2. UA13322, exterior views of enrolled exoskeleton, X3.8, X3.6, respectively.

3. UA13317, dorsal view of cephalon, X5.2.

4, 9. UA13319, anterior and dorsal views of cephalon, X3.1.

5. UA13325, exterior view of enrolled exoskeleton, X4.8.

6. UA13326, exterior view of partly enrolled exoskeleton, X3.0.

7, 12. UA13327, lateral and exterior views of enrolled exoskeleton, X3.6, X3.1, respectively.

8. UA13324, exterior view of enrolled exoskeleton, X4.0.

10. UA13328, dorsal view of pygidium, X3.8.

11. UA13323, exterior view of exoskeleton, X3.8.

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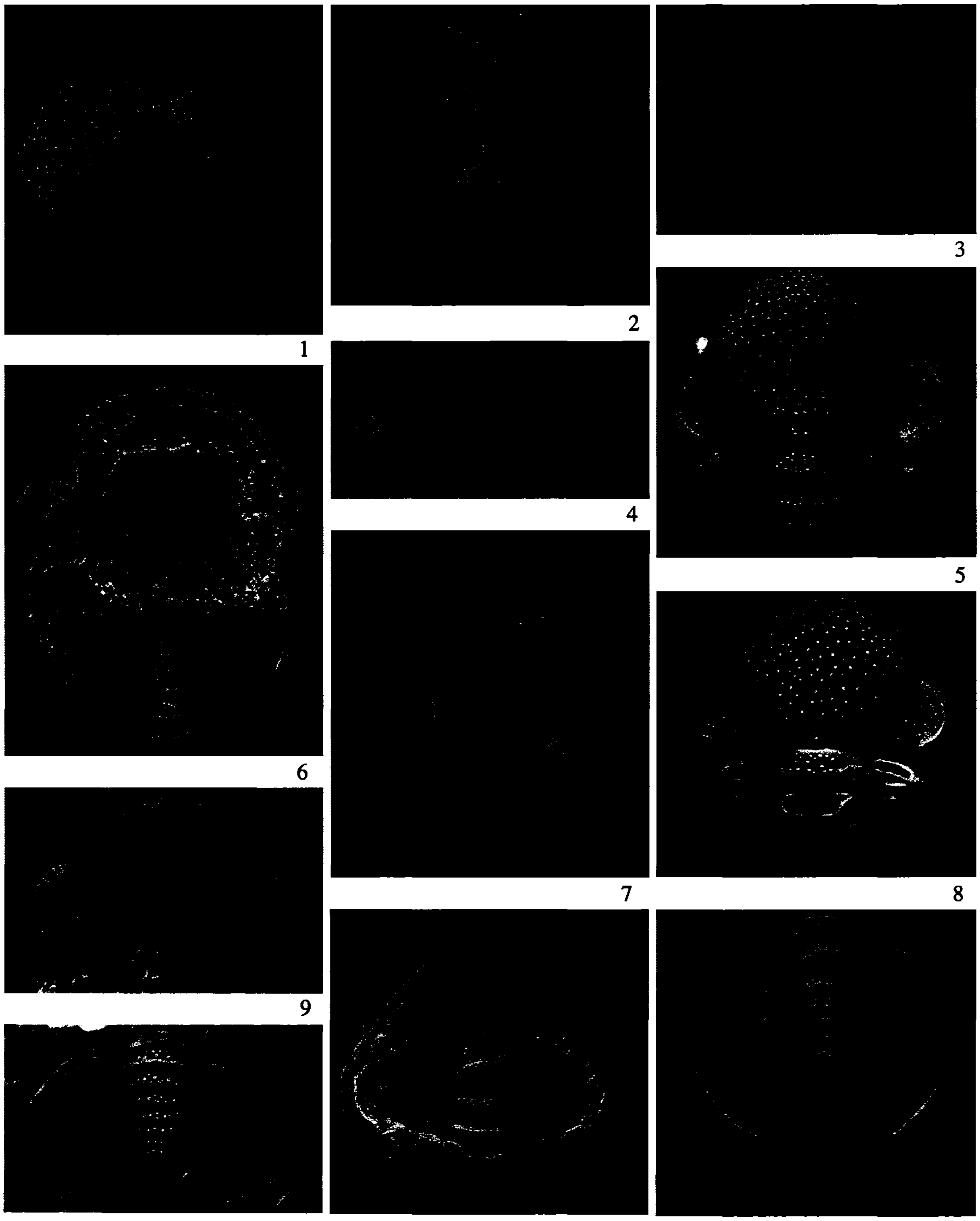

Plate 9*

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PLATE 10

Figs. 1–11. New Genus A *speculator punctatus* n. ssp. from El Otfal Formation, Oufatene section, in Ma'der basin ('*Lobopyge* couche' and '*Treveropyge* couche' slightly above, both are medium-gray, dense, muddy limestones, and Eifelian in age).

Paratype UA6878 (outstretched, almost complete individual, with distorted thorax, from '*Lobopyge* couche'):
1. Dorsal view of cephalon, (palpebral lobes flat), X2.3.
7. Anterodorsal view of cephalon, X2.4.

Paratype UA 6879 (partly enrolled, almost complete individual, with distorted thorax, from '*Treveropyge* couche'):
2. Anterior view of cephalon, X2.3.
6. Lateral view of cephalon, (depression in gena is preparation chip), X3.2.

Paratype UA6882 (isolated cephalon from '*Treveropyge* couche'):
3. Dorsal view of cephalon (palpebral lobes flat), X2.3.
4. Lateral view of cephalon, X3.1.
8. Ventral view of doublure, X2.3.
10. Anterodorsal view, X2.3.
11. Lateral view, (lenses damaged in middle of eye), X3.1.

Paratype UA6881 (enrolled, nearly complete individual from '*Lobopyge* couche'):
5. Ventral view of doublure, and external view of pygidium, X2.4.

Paratype UA6877 (oustretched, nearly complete individual from '*Treveropyge* couche'):
9. Detailed view of sculpture on right side of cephalon (from bottom to top, frame contains part of occipital ring, half of L1 medial and all of L1 lateral lobes, and most of L2 and L3 lobes.) Note pervasive pitting, especially raised-rim pits as largest sculpture, X12.1.

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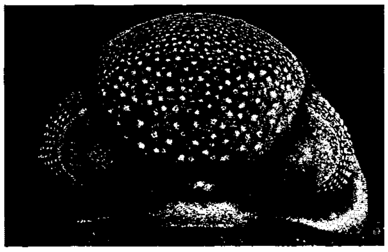
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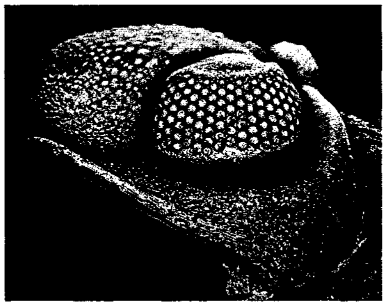
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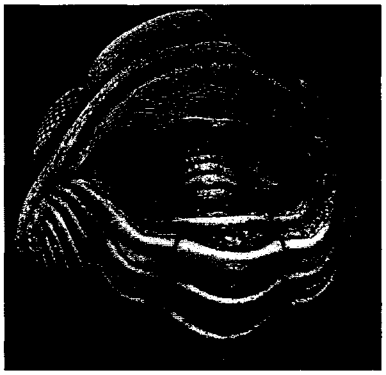
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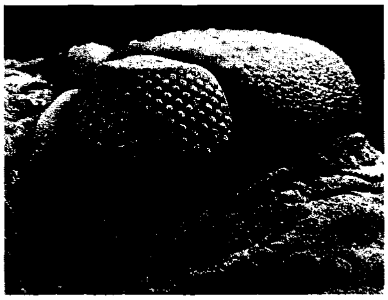
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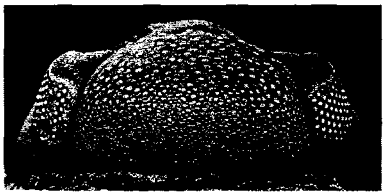
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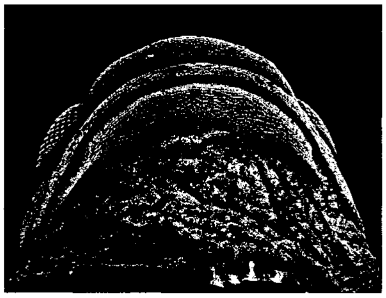
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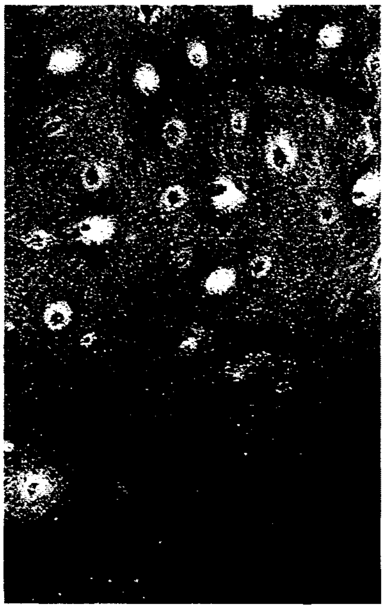
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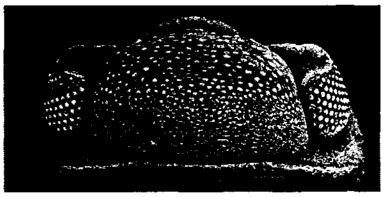
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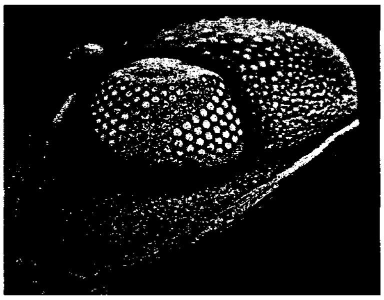
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Plate 10

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PLATE 11

Figs. 1–11. New Genus A *speculator punctatus* n. ssp. from El Otfal Formation, Oufatene section, in Ma'der basin ('*Lobopyge* couche' and '*Treveropyge* couche' slightly above, both are medium-gray, dense, muddy limestones, and Eifelian in age).

Paratype UA6878 (outstretched, almost complete individual, with distorted thorax, from '*Lobopyge* couche'):
1. Dorsolateral view of cephalon, X3.3.

Paratype UA6881 (enrolled, nearly complete individual from '*Lobopyge* couche'):
2. Detailed view of right eye, X7.2.
4. Lateral view of exoskeleton, X2.6.

Holotype UA6876 (bowed, almost complete individual from '*Treveropyge* couche):
3. Dorsal view of pygidium, X3.5.
5. Posterodorsal view of cephalon and overview of thorax, X1.9.
7. Lateral overview of exoskeleton, X2.6.

Paratype UA6880 (partially enrolled, almost complete individual from '*Lobopyge* couche'):
8. Lateral overview of entire exoskeleton, X3.7.

Paratype UA6877 (oustretched, nearly complete individual from '*Treveropyge* couche'):
6. Dorsal view of pygidium, X2.8.

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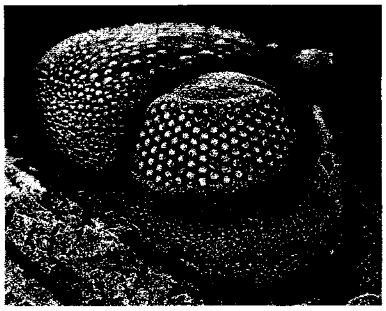

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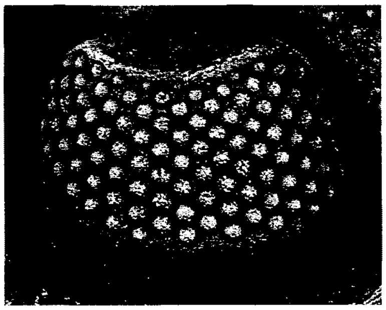

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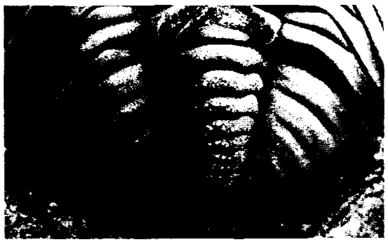

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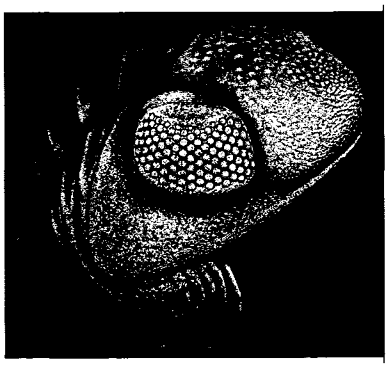

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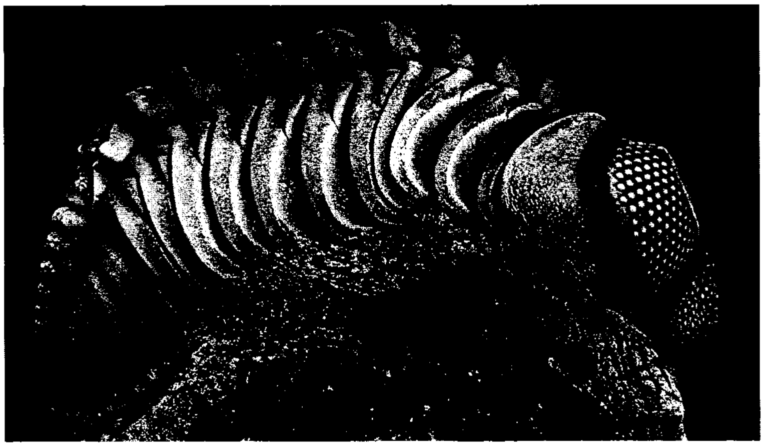

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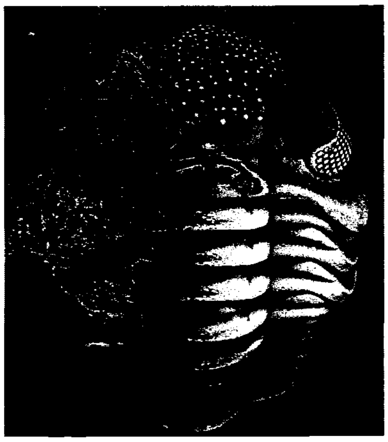

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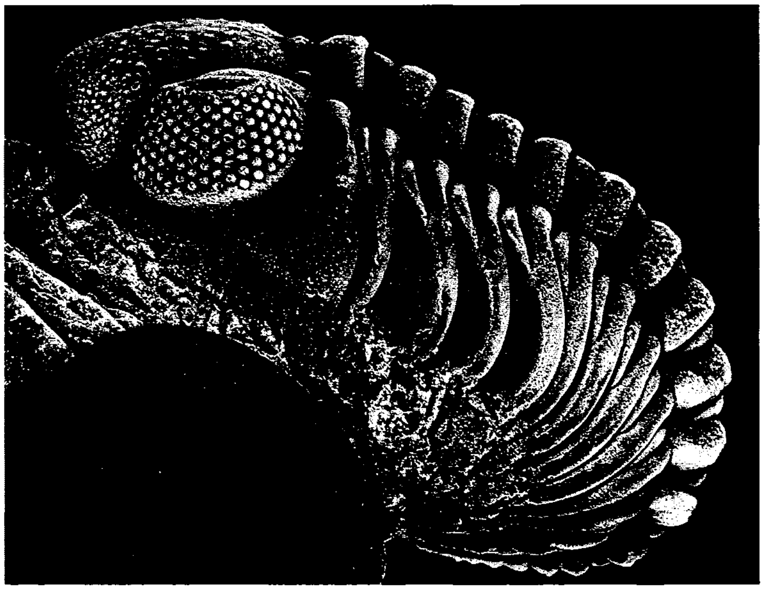

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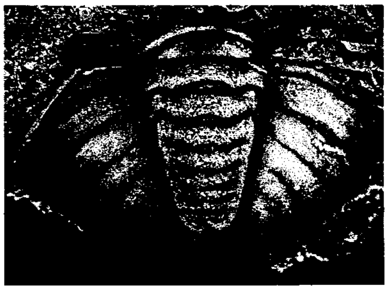

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PLATE 12

Figs. 1–10. New Genus A *kermiti* n. sp. from 'South Oufatene proetid couche' (SOP), and 'Oufatene *Diademaproetus* couche' (ODC), at Oufatene section, within Ma'der basin. Strata are part of part of El Otfal Fm., Eifelian in age, and typically medium-gray muddy limestones.

Holotype UA6884 (enrolled, complete individual, with pygidium forced into body cavity, from SOP horizon):
1. Anterior view of cephalon, external view of all else, X2.4.
4. Lateral view of cephalon, X3.5.
9. Dorsal view of cephalon (main focus), X2.6.
10. Ventral view of doublure, dorsal view of pygidium (note shallow, broad vincular furrow), X2.6.

Paratype UA6888 (arched, complete specimen with slight torsion in thorax, from ODC horizon):
2. Anterior view of cephalon, X3.2.
3. Dorsal view of pygidium (there may be slight lateral compression), X4.2.
7. Dorsal overview of anterior section, with cephalic focus, X3.1.
8. Lateral overview of entire exoskeleton, X4.5.

Paratype UA6889 (arched, nearly complete specimen, with some weathering, from ODC horizon):
5. Lateral view of cephalon, X3.2.
6. Dorsal view of cephalon, (palpebral lobes flat, missing much of occipital ring), X2.7.

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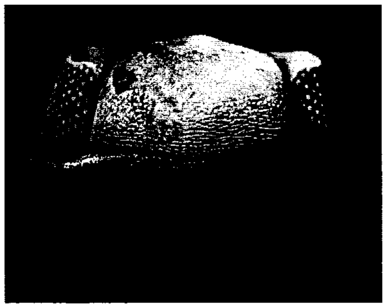
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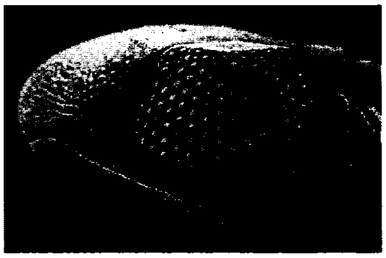
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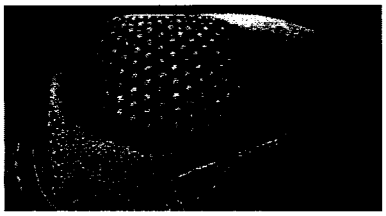
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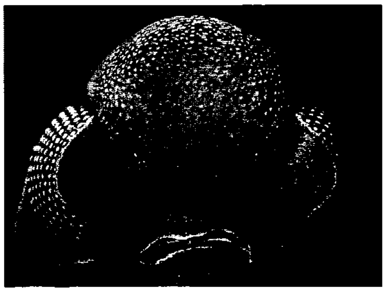
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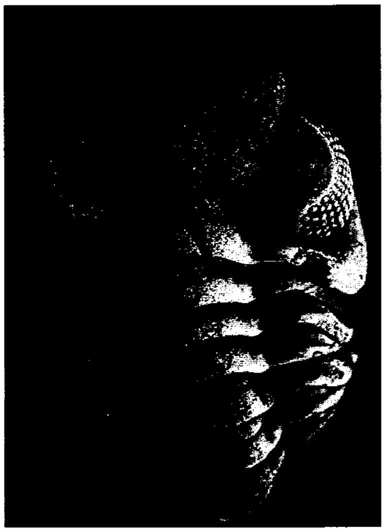
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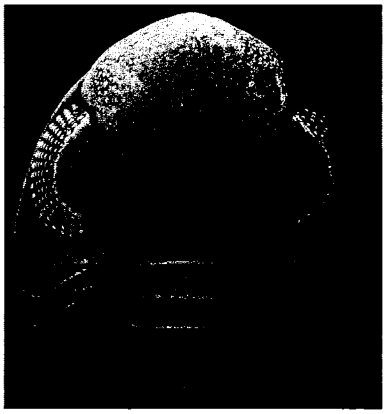
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PLATE 13

Figs. 1–11. New Genus A *kermiti* n. sp. from 'South Oufatene proetid couche' (SOP), and 'Oufatene *Diademaproetus* couche' (ODC), at Oufatene section, within Ma'der basin. Strata are part of part of El Otfal Fm., Eifelian in age, and typically medium-gray muddy limestones.

Paratype UA6885 (enrolled, complete individual with pygidium forced into body cavity, from SOP horizon):
1. Anterior view of cephalon, and dorsal view of pygidium, X3.0.
2. Dorsal view of cephalon (mainly, with palpebral lobes flat), X 3.0.
3. Lateral overview of exoskeleton, X3.3.
4. External view emphasizing dorsal surface of pygidium, X3.1.
6. External view emphasizing ventral surface of doublure, X3.1.

Paratype UA6887 (arched, almost complete individual from SOP horizon, slight compression in cephalon):
5. Lateral view of cephalon, X4.0.
7. Lateral overview of exoskeleton, X3.7.
8. Anterior view of cephalon, X3.0.
9. Dorsal view of cephalon (note compression distortion, and fracturing), X3.0.
10. Dorsal overview (of thorax, mainly), X3.0.
11. Dorsal view of fractured pygidium, X3.2.

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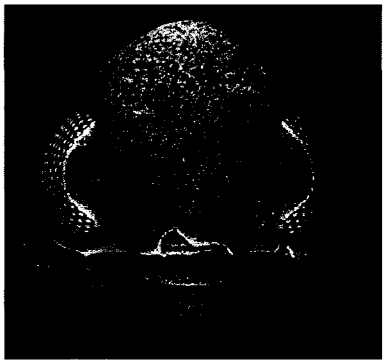

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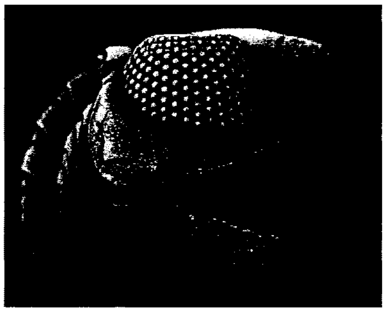

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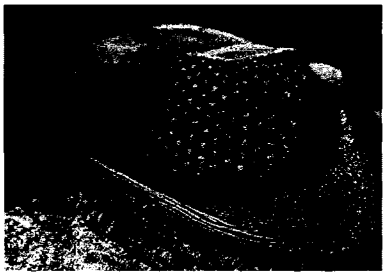

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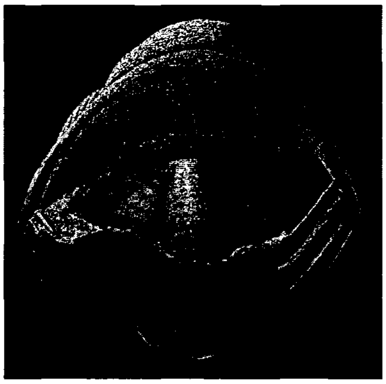

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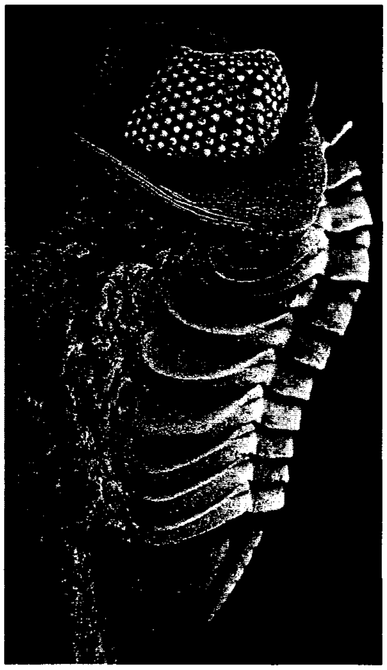

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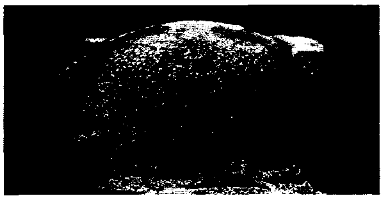

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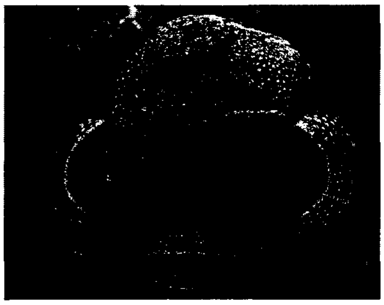

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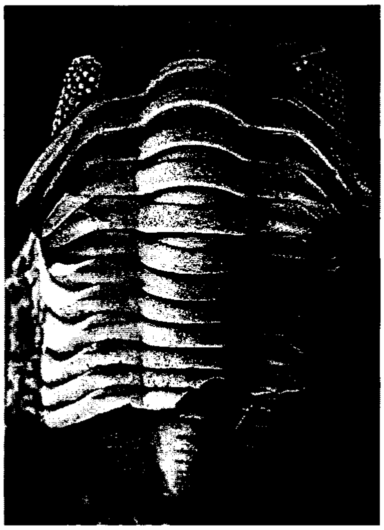

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PLATE 14

Figs. 1–10. New Genus A *salamandar* n. sp. from 'Oufatene *Diademaproetus* couche' (ODC), at Oufatene section, within Ma'der basin. Strata are part of part of El Otfal Fm., Eifelian in age, and typically medium-gray muddy limestones.

Holotype UA6892 (partially enrolled, complete individual):
1. Dorsal view of cephalon (palpebral lobes flat), and external view of other regions, X3.5.
3. External view focusing on anteroventral aspect of cephalon, X3.6.
5. External view focusing on dorsal surface of pygidium and ventral surface of doublure, X3.5.
6. Lateral view of cephalon, X5.0.
9. External view focusing on anterior/anterodorsal aspect of cephalon, X3.5.

Paratype UA6894 (partially enrolled individual, complete except for portions of pygidium and thorax):
2. Anterior view of cephalon, X3.1.
7. Dorsal view of cephalon (mainly, with palpebral lobes flat), X3.1.
10. Lateral view of cephalon, X4.2.

Paratype UA6893 (partially enrolled individual, missing pygidium only):
4. Anterior view of cephalon, X2.9.
8. Dorsal view of cephalon (palpebral lobes flat), X2.9.

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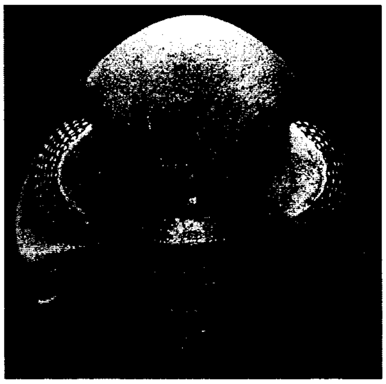

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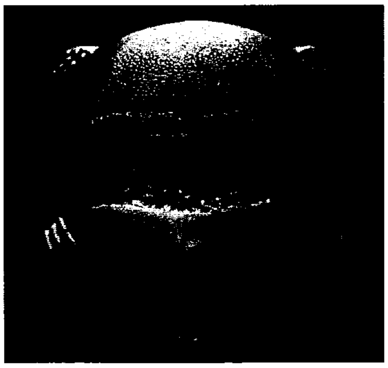

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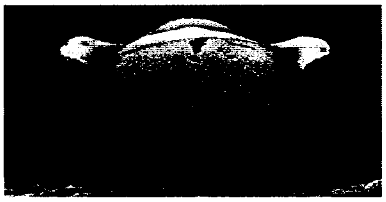

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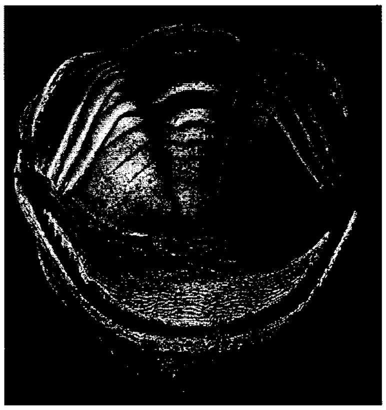

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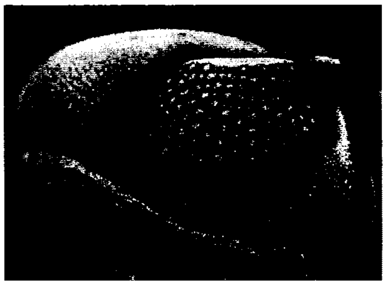

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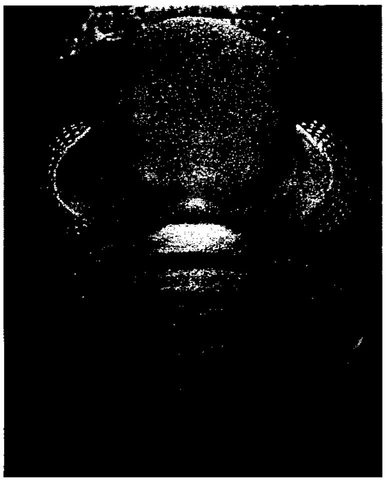

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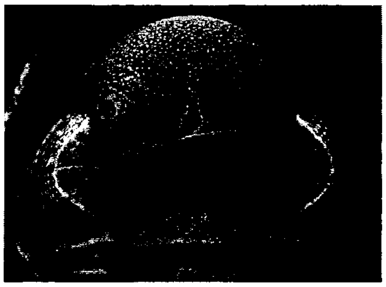

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Plate 14

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PLATE 15

Figs. 1–10. *Boeckops stelcki* n. sp. from Taharajat d'Oufatene, an outlying section representing a middle position within the main Oufatene section. Specimens from '*Moroccanites* couche', which is part of Bou Tiskaouine Fm., a very dense buff-gray limestone of Emsian age in Ma'der basin.

Holotype UA6897 (partially enrolled, complete individual):
3. External view of exoskeleton (focusing on anterior of cephalon mainly), X2.0.
4. Dorsal view of cephalon (palpebral lobes flat), X2.1.
6. Lateral view of cephalon, X2.5.
7. Ventral view of doublure, X2.2.
9. Dorsal view of pygidium, X2.8.

Paratype UA6898 (arched, complete specimen with minor glabellar weathering):
1. Lateral view of cephalon, X3.7.
2. Anterior view of cephalon, X3.5.
5. Dorsal overview of specimen (focusing on thorax and posterodorsal view of cephalon, left side of which is weathered), X3.4.
8. Dorsal view of cephalon (palpebral lobes flat, left side of glabella weathered), X3.5.
10. Lateral overview of exoskeleton, X4.2.

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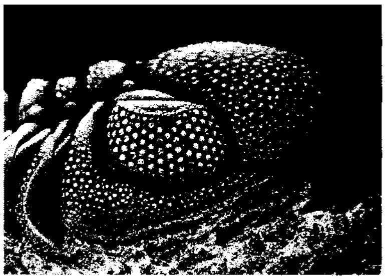
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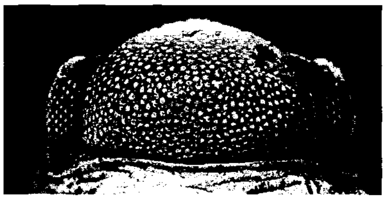
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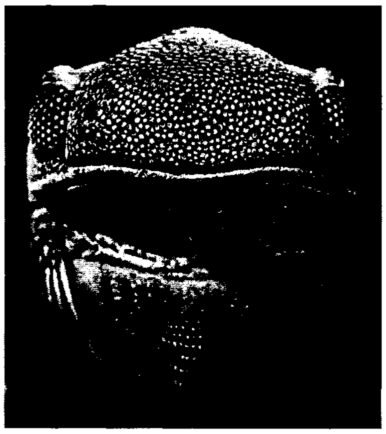
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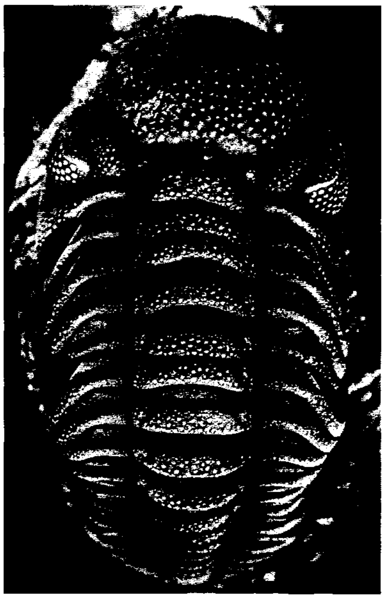
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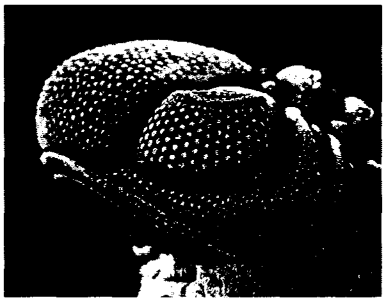
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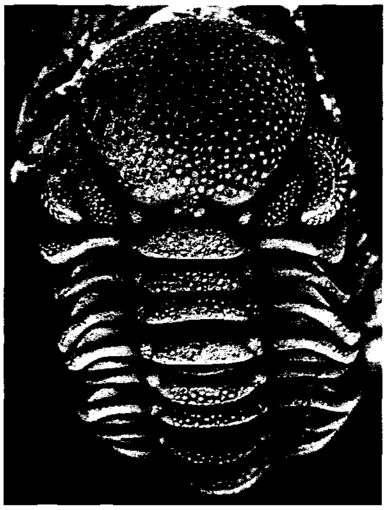
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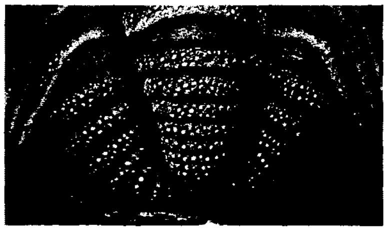
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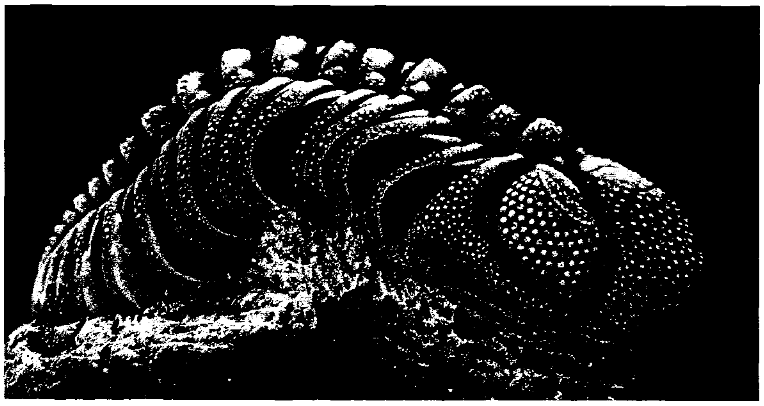
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PLATE 16

Figs. 1–6. *Boeckops stelcki* n. sp. from Taharajat d'Oufatene, an outlying section representing a middle position within the main Oufatene section. Specimens from '*Moroccanites* couche', which is part of Bou Tiskaouine Fm., a very dense buff-gray limestone of Emsian age in Ma'der basin.

Paratype UA6899 (enrolled, nearly complete small holaspid):
1-5. External views of exoskeleton focusing on pygidium, anterior aspect of cephalon, lateral aspect, dorsal surface of cephalon (with palpebral lobes nearly flat), and lateral details of cephalon, X3.7, X3.7, X3.6, X3.9, X4.3, respectively.

Paratype UA6898 (arched, complete specimen with minor glabellar weathering):
6. Dorsal view of pygidium, X4.5.

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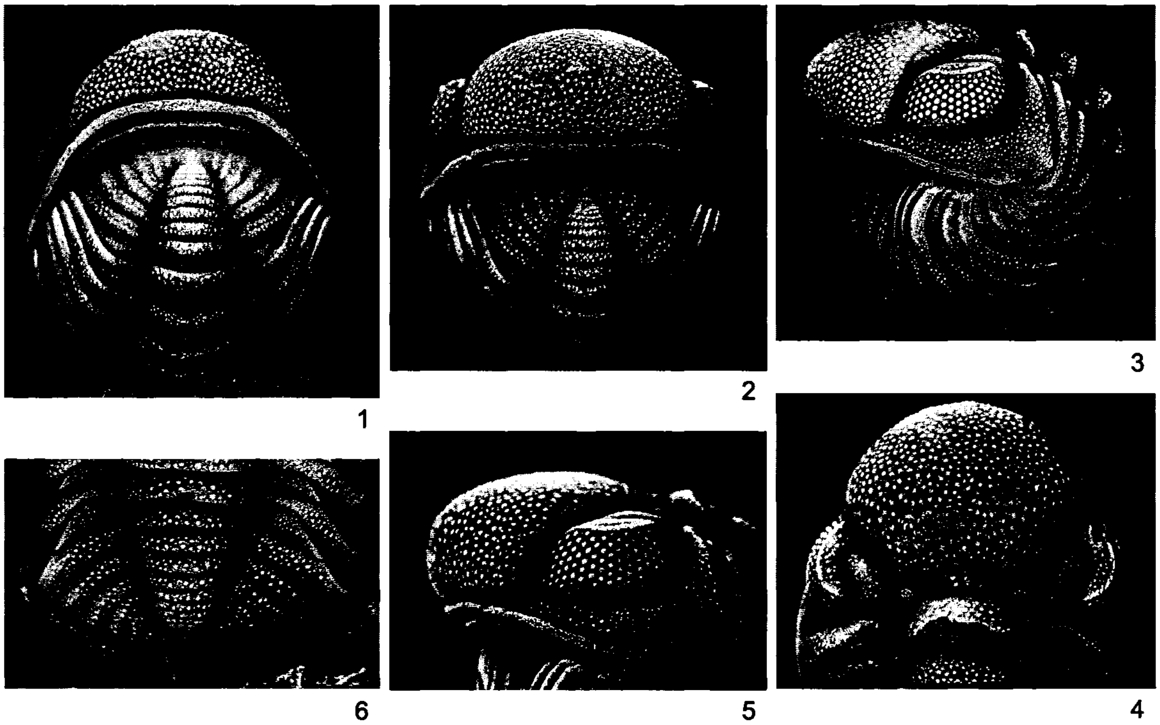

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PLATE 17

Figs 1–10. *Phacops granulops* (CHATTERTON *et al.*, 2006). Unless stated otherwise, all specimens are from basal 4 meters of section through Timrhanrhart Formation (localities ZGEE1–ZGEE2), northeast of Jbel Gara el Zguilma.

Holotype UA13295:
2, 5, 9. External, external and lateral views of enrolled exoskeleton, X3.5, X4.3, X3.5.

UA13294:
1, 3, 8. Lateral, anterodorsal and dorsal views of almost complete exoskeleton, X3.1, X3.7, X3.2, from locality NZ1 (lowest meter of exposed strata of Timrhanrhart Formation in "Near Zguilma" Section).

Paratype UA13296:
4. External view of enrolled exoskeleton, X1.9.

Paratype UA13297:
6–7. Lateral and dorsal views of enrolled exoskeleton, X4.3, X4.0.

Paratype UA13298:
10. External view of enrolled exoskeleton, X3.1.

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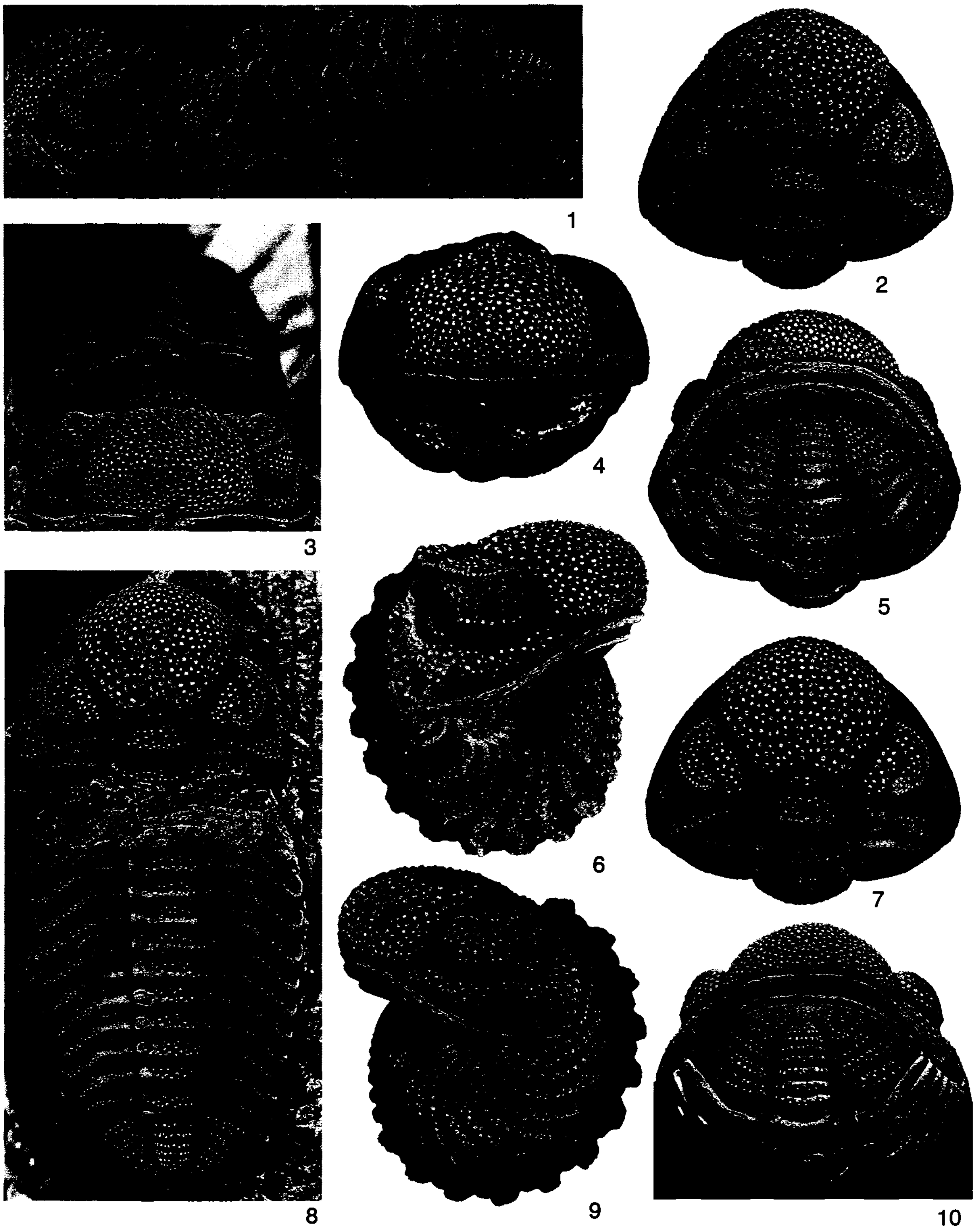

Plate 17*
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PLATE 18

Figs. 1–12. *Phacops granulops* (CHATTERTON *et al.*, 2006). Unless stated otherwise, all specimens are from basal 4 meters of section through Timrhanrhart Formation (localities ZGEE1–ZGEE2), northeast of Jbel Gara el Zguilma.

Paratype UA13299:
1–2, 4–5. Lateral, ventral view of hypostome, anteroventral view of hypostome, and dorsal views of partly enrolled exoskeleton, X2.4, X5.6, X5.0, X2.6, respectively.

Paratype UA13300:
3. Ventral view of part of cranidium and hypostome, X5.6.

UA13301:
6, 9. Lateral and dorsal views of exoskeleton X1.7, X2.3, respectively (specimen purchased near locality, from uncertain location).

Paratype UA13302:
7–8, 10–12. Dorsolateral, dorsal, dorsal, dorsolateral, and posterodorsal views of exoskeleton, X0.9, X1.6, X1.5, X1.9, X2.1, respectively.

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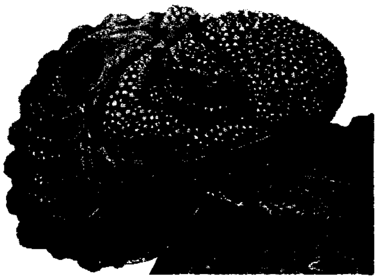

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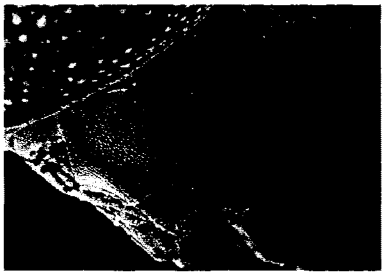

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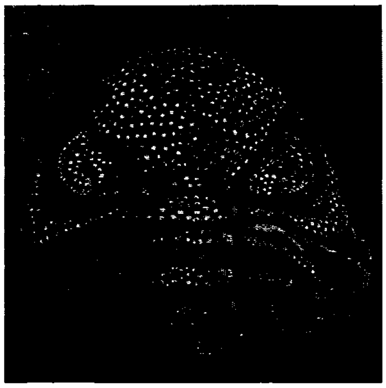

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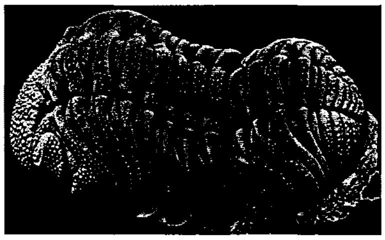

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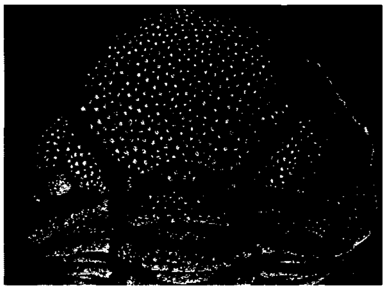

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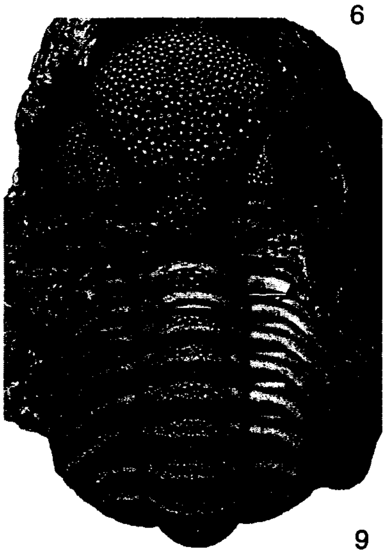

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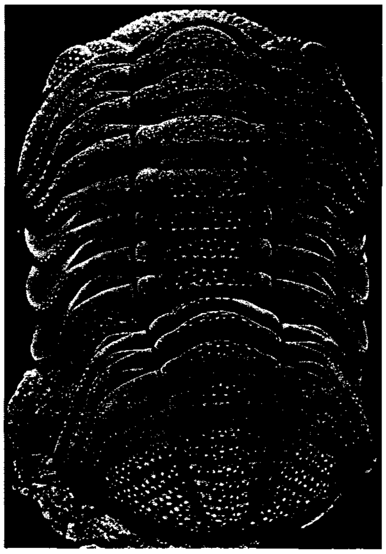

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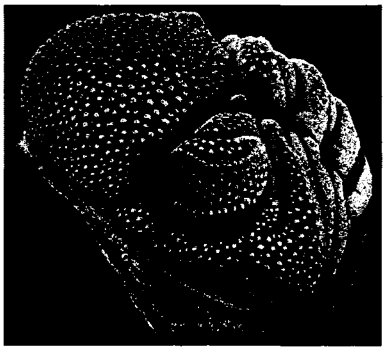

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Plate 18*
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PLATE 19

Figs. 1–9, *Phacops lebesus* (CHATTERTON *et al.*, 2006), from about 50 meters above base of section through Timrhanrhart Formation (Locality ZGEE3), northeast of Jbel Gara el Zguilma.

Paratype UA13303:
1–3. Dorsal, lateral and dorsolateral views of partial exoskeleton, X2.2, X3.1, X1.6, respectively.

Holotype UA13304:
4–7. Exterior views of enrolled exoskeleton, X4.6, X4.6, X4.6, X4.9, respectively.

Paratype UA13305:
8–9. Exterior views of enrolled exoskeleton, X2.8.

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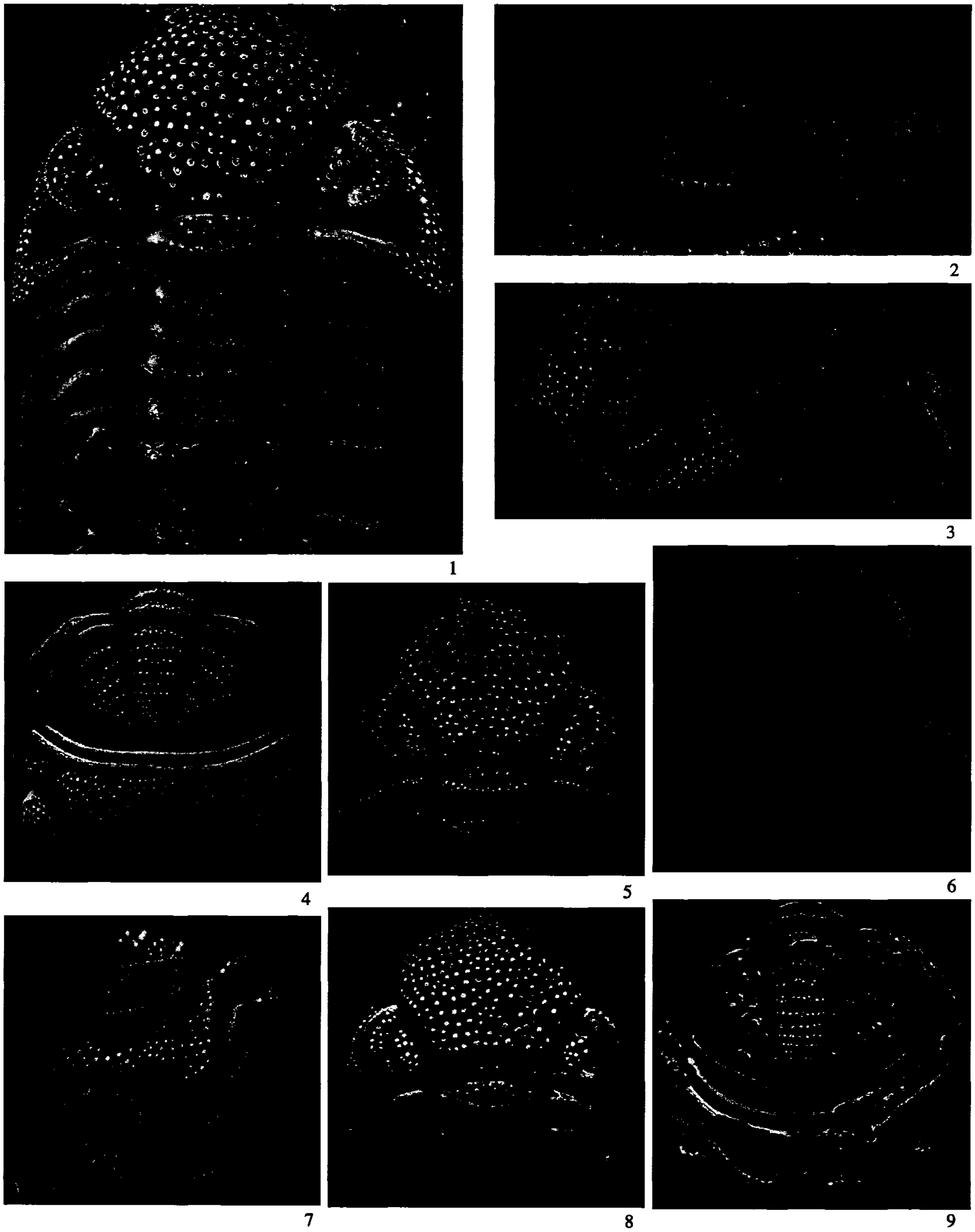

Plate 19*

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PLATE 20

Figs. 1–11. New Genus B *ovatus* n. sp. from Taharajat d'Oufatene, an outlying section representing a middle position within the main Oufatene section. Specimens from '*Moroccanites* couche' and '*Metacanthina* couche' (3m higher), which are part of Tazouläit Fm., and composed of dense buff-grey limestone of Emsian age in Ma'der basin.

Paratype UA 6909 (outstretched, complete individual, large holaspid from '*Metacanthina* couche'):
1. Dorsal view of cephalon (palpebral lobes flat), X1.1.
3. Dorsal overview of exoskeleton, X1.1.
7. Anterior view of cephalon, X1.1.
11. Lateral overview of exoskeleton, X1.2.

Paratype UA6913 (partially enrolled, complete, small holaspid from '*Morrocanites* couche'):
2. Lateral view of exoskeleton, X2.7.
4. External view of exoskeleton (focusing on anterior of cephalon), X2.7.
6. External view of exoskeleton (focusing on dorsal surface of pygidium), X2.8.
8. Dorsal view of cephalon (top of glabella flat), X2.7.

Paratype UA6910 (enrolled, partial, small holaspid from '*Moroccanites* couche'):
5. Dorsal view of cephalon (palpebral lobes almost flat), X2.9.
9. Lateral view of cephalon, X4.0.

Holotype UA6908 (partially enrolled, complete individual from '*Moroccanites* couche'):
10. Detailed view of thoracic segment axial ring, X5.3. Note ovoid tubercles and short ridges between posterior (bottom of fig.) tubercles.

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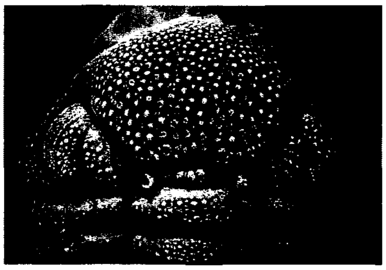
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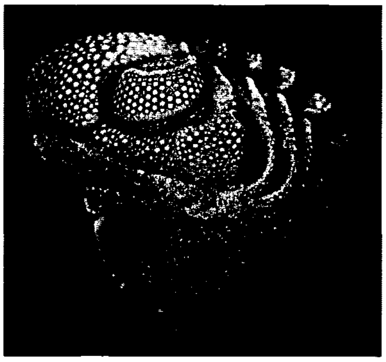
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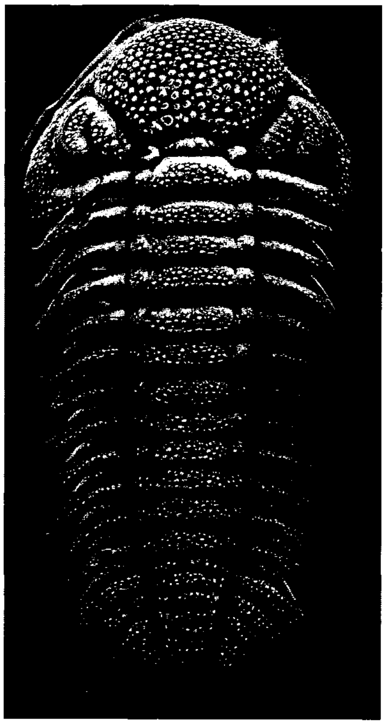
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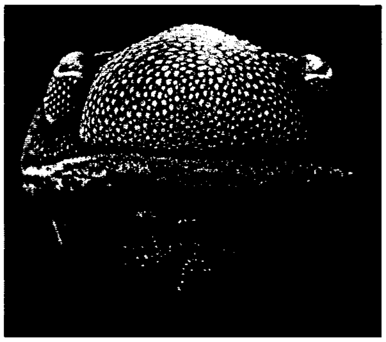
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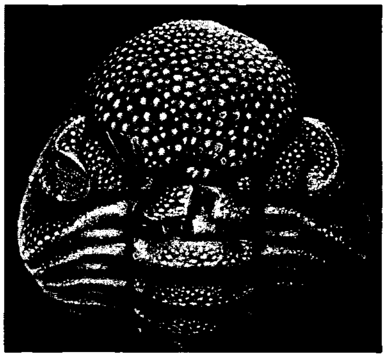
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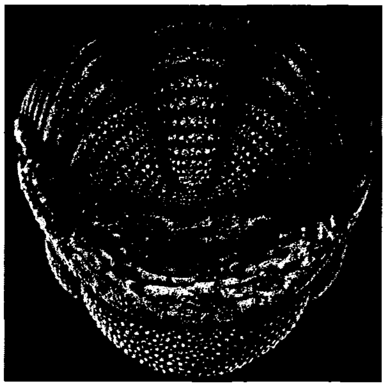
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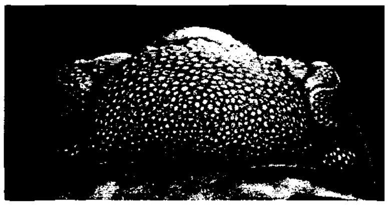
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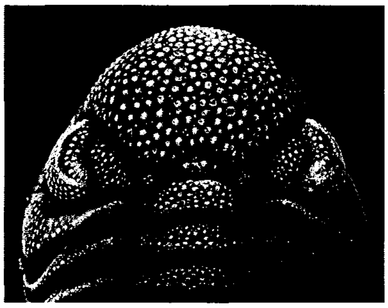
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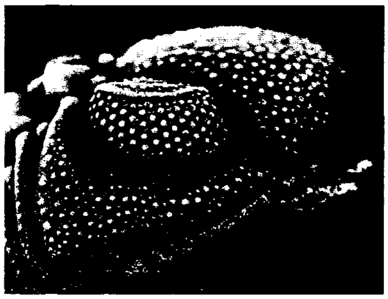
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Plate 20

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PLATE 21

Figs. 1–10. New Genus B *ovatus* n. sp. from Taharajat d'Oufatene, an outlying section representing a middle position within the main Oufatene section. Specimens from '*Moroccanites* couche' and '*Metacanthina* couche' (3m higher), which are part of Tazouläit Fm., and composed of dense buff-gray limestone of Emsian age in Ma'der basin.

Paratype UA6914 (isolated cephalon from '*Moroccanites*' couche):
1. Lateral view of cephalon, X3.5.
2. Anterodorsal view of cephalon, X2.2.
3. Anterior view of cephalon (palpebral lobes nearly horizontal), X2.2.

Paratype UA6912 (outstretched, nearly complete individual, Moroccan prepared, anterior two thoracic segments have left side distal tips replaced with coloured filler):
4. Lateral view of cephalon, X2.5.
5. Dorsal view of cephalon (palpebral lobes flat), X1.6.
6. Dorsal overview of exoskeleton, X1.6.
7. Anterior view of cephalon, X1.6.
8. Lateral overview of exoskeleton, X1.6.
9. Dorsal view of pygidium, X2.2.
10. Lateral overview of exoskeleton, X1.6.

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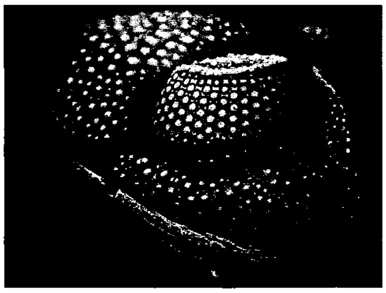

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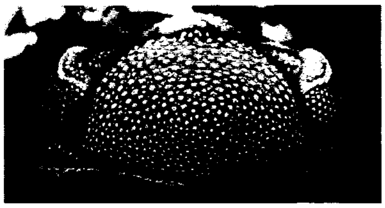

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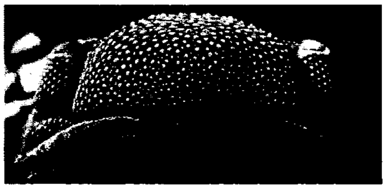

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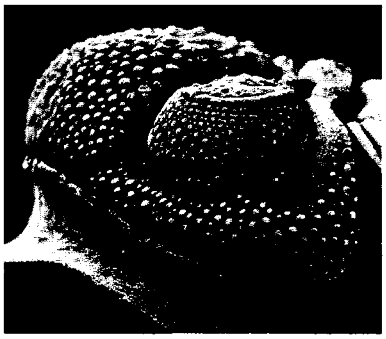

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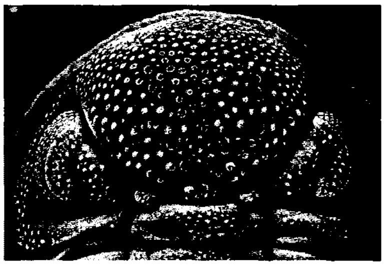

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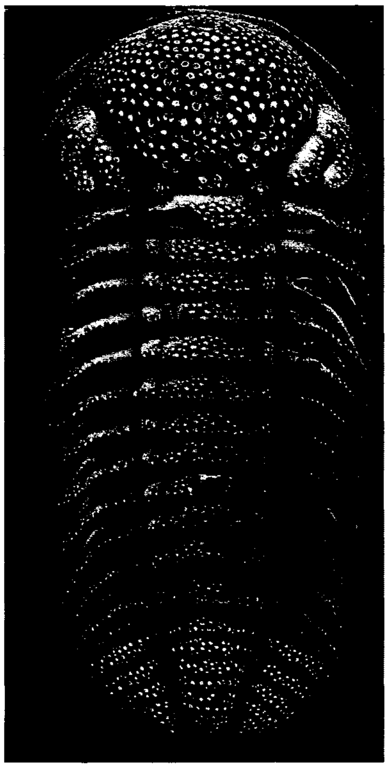

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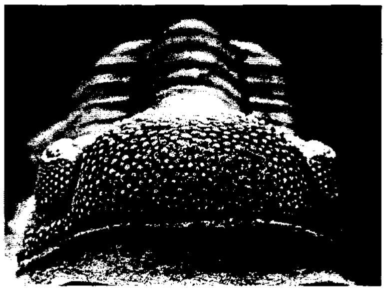

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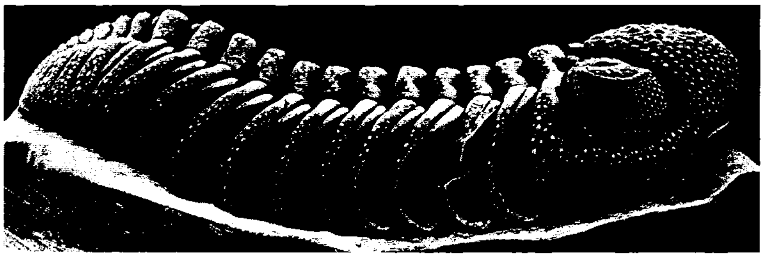

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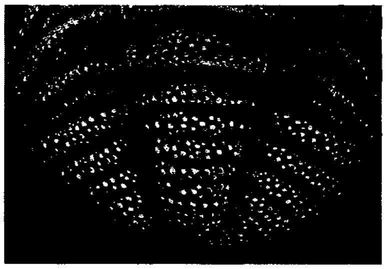

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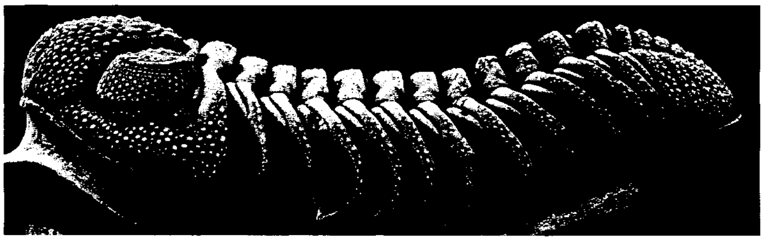

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PLATE 22

Figs. 1–4. New Genus B *ovatus* n. sp. from Taharajat d'Oufatene, an outlying section representing a middle position within the main Oufatene section. Specimens from '*Moroccanites* couche' and '*Metacanthina* couche' (3m higher), which are part of Tazouläit Fm., and composed of dense buff-grey limestone of Emsian age in Ma'der basin.

Holotype UA6908 (partially enrolled, complete individual from '*Moroccanites* couche'):
1. Dorsal overview of exoskeleton, with cephalon oriented so that palpebral lobes are flat, X1.5.
2. Lateral overview of exoskeleton, X2.0.
3. Anterior view focusing on cephalon, X1.7.

Paratype UA6911 (partially enrolled, nearly complete individual, with minor thoracic weathering, form 'Moroccanites couche'):
4. Ventral view of doublure, X1.9.

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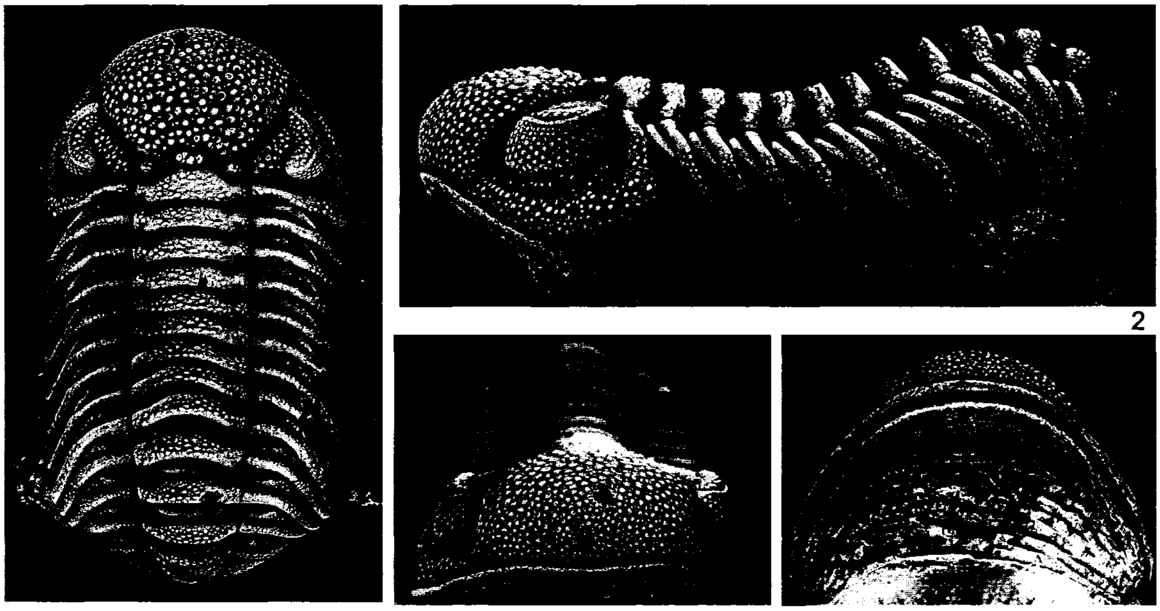

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PLATE 23

Figs. 1–12. New Genus B *forteyi* n. sp. from '*Psychopyge* couche' of Ma'der basin. Specimens are from Issoumour (IS) and bou Dib (BD) sections, both of which are dark grey, muddy limestones, of the Tazouläit Fm., and late Emsian age.

Paratype UA6926 (enrolled, nearly complete individual, from BD):
1.Dorsal view of cephalon, (mainly), X1.9.

Holotype UA6920 (enrolled, nearly complete individual *in situ* from BD):
2. Detailed view of right eye and post/subocular pads, X6.2.
3. Lateral overview of exoskeleton, X1.7.

Paratype UA6932 (enrolled, complete except for missing pygidium, *in situ* from IS):
4. Dorsal view of cephalon (mainly), X1.8.

Paratype UA6927 (enrolled, complete individual with minor compression distortion, from BD):
5. Lateral overview of exoskeleton, X2.0.

Paratype UA6921 (enrolled, complete individual, with minor weathering, from BD):
6. External view focusing on pygidium, X1.7.

Paratype UA6922 (enrolled individual cut and prepared to display hypostome, from BD):
7. Posteroventral view (focusing on hypostome), X1.9.
10. Ventral view (focusing on doublure, but showing topography of hypostome), X1.7.
11. Ventral view (focusing on doublure and its sculpture), X2.0.

Paratype UA6924 (enrolled individual missing pygidium from BD):
8. Anterior view of cephalon (mainly), X1.8.
9. Anterodorsal view of cephalon (mainly), X1.9.
12. Ventral view of doublure (mainly, focusing on doublure sculpture), X2.2.

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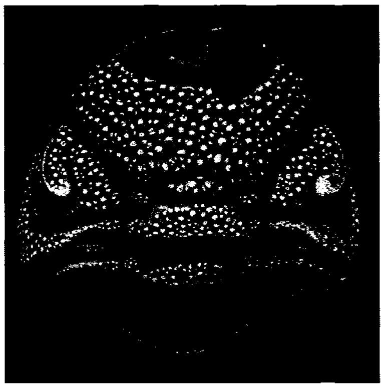

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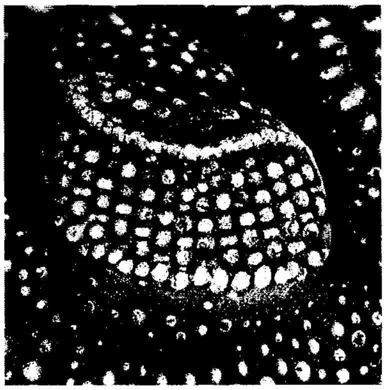

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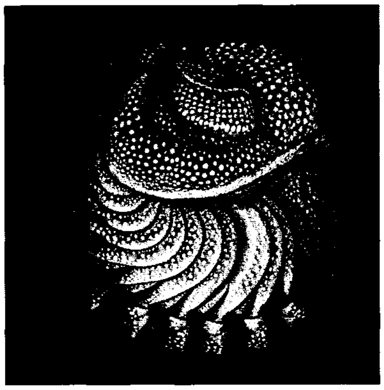

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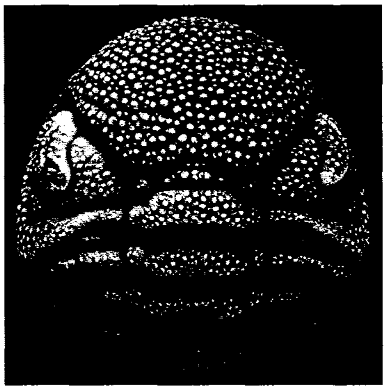

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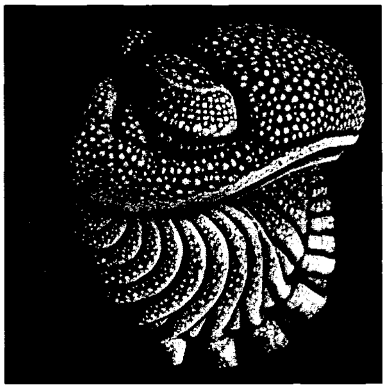

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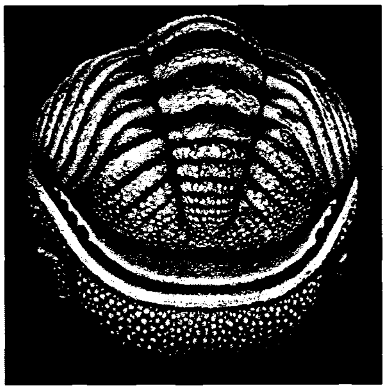

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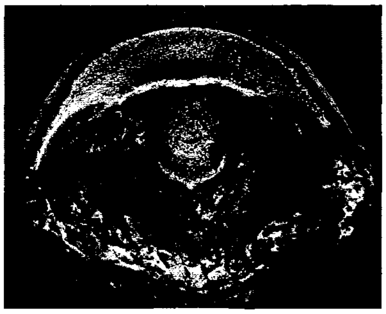

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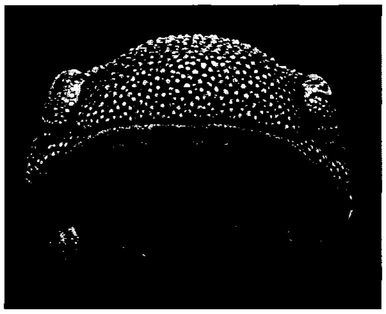

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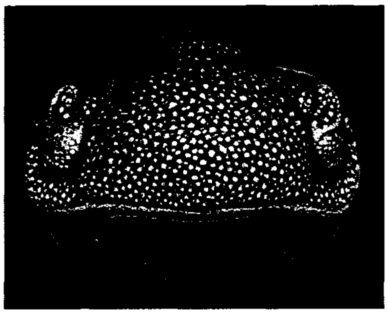

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Plate 23

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PLATE 24

Figs. 1–12. New Genus B *forteyi* n. sp. from basal portion of Merzouga section. Specimens are found in recessive shale (surface collected), which belongs to the Amerboh Group, and is late Emsian in age. Plate provided by B.D.E. Chatterton.

Paratype UA6943 (enrolled, complete individual, with pygidium pushed into body cavity, and significant compression distortion and cracking):
1. External view of exoskeleton (focusing on dorsal surface of cephalon, with palpebral lobes flat), X3.7.

Paratype UA6940 (enrolled specimen, complete except for missing pygidium):
2-4, 9. External views of exoskeleton, focusing on dorsal surface of cephalon, anterior aspect of cephalon, posterodorsal aspect of cephalon (and dorsal surface of thorax), and anterodorsal aspect of cephalon, X3.2, X3.3, X3.3, X3.3, respectively.

Paratype UA6942 (enrolled, complete individual):
5-8, 10. External views of exoskeleton, focusing on pygidium and vincular furrow, dorsal surface of thorax, lateral view of entire specimen, anteroventral view of cephalon and dorsal view of pygidium, and detailed view of eye and subocular pad, X3.2, X3.2, X3.6, X3.2, X6.1, respectively.

Paratype UA6944 (enrolled, complete specimen, missing large portions of cuticle):
11. Detailed view of doublure and its sculpture, X4.9.

Paratype UA6941 (enrolled, complete individual with mild compression distortion):
12. Lateral overview of exoskeleton, X3.5.

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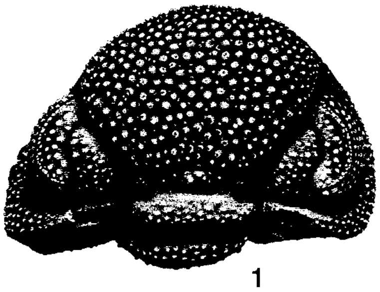

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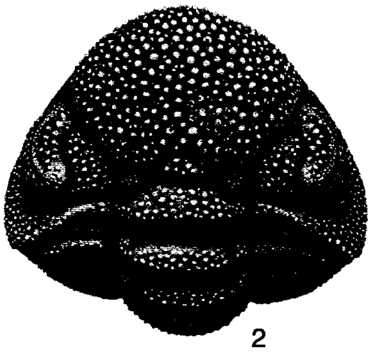

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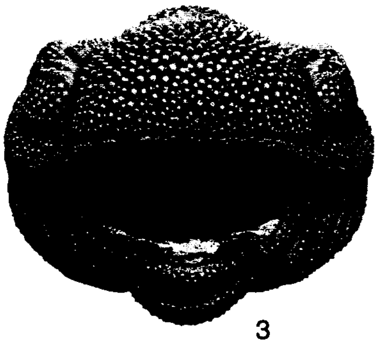

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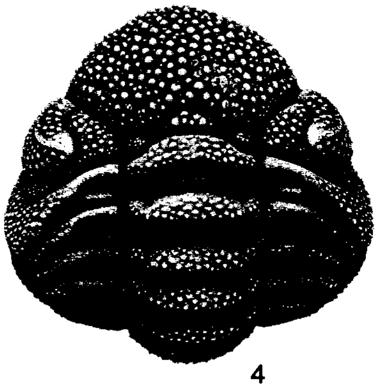

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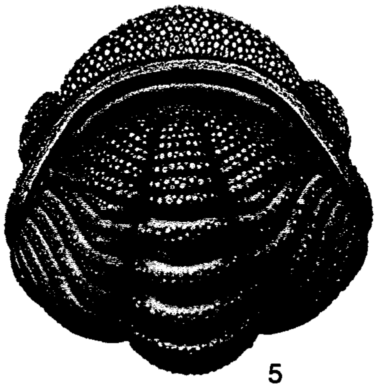

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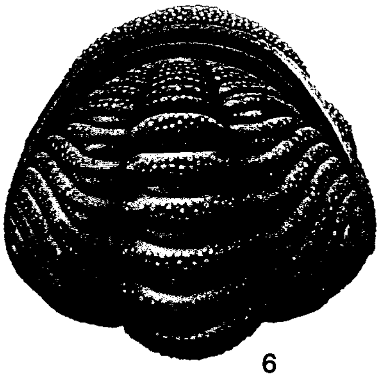

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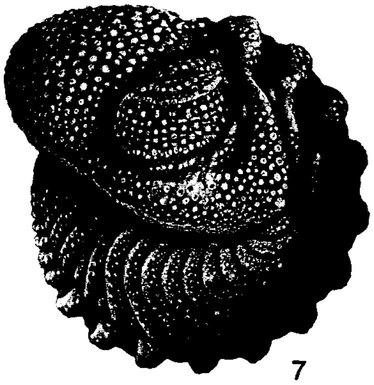

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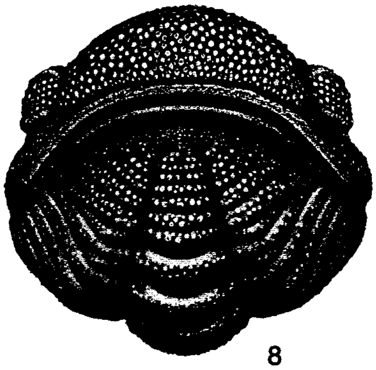

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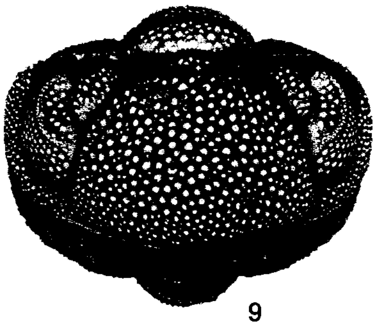

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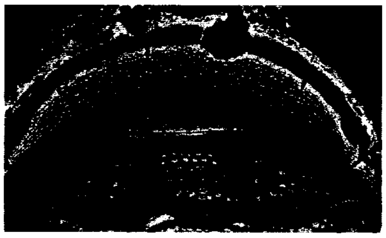

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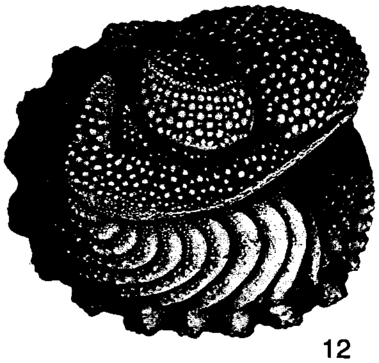

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Plate 24

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PLATE 25

Figs. 1–12. New Genus B *forteyi* n. sp. from basal portion of Merzouga section. Specimens are found in recessive shale (surface collected), which belongs to the Amerboh Group, and is late Emsian in age. Plate provided by B.D.E. Chatterton.

Paratype UA6941 (enrolled, complete individual with mild compression distortion):
1, 2, 8, 9. External views of exoskeleton, focusing on cephalon and pygidium in oblique view, cephalon in anterior view and pygidium in dorsal view, pygidium and cephalon in oblique view, and detailed view of eye and postocular pad, X3.2, X2.8, X 3.3, X6.5, respectively.

Paratype UA6943 (enrolled, complete individual, with pygidium pushed into body cavity, and significant compression distortion and cracking):
3, 5, 11. External views of exoskeleton, focusing on cephalon in oblique anterior view, cephalon in oblique lateral view, and detailed view of eye and postocular pad, X3.7, X5.3, X8.8, respectively.

Paratype UA6944 (enrolled, complete specimen, missing large portions of cuticle):
4, 10. External views of exoskeleton, focusing on doublure in ventral view, and distal tips of thoracic segments and notches in lateral portion of vincular furrow in detailed view, X3.4, X8.5, respectively.

Paratype UA6940 (enrolled specimen, complete except for missing pygidium):
6, 7, 12. External views of exoskeleton, focusing on doublure in ventral view, cephalon in lateral oblique view, and doublure in detailed view, X3.2, X3.9, X11, respectively.

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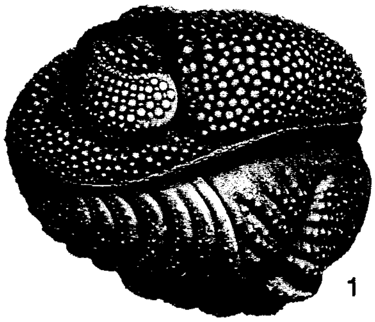

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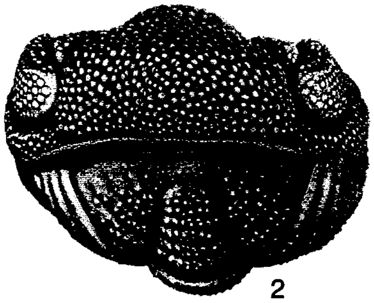

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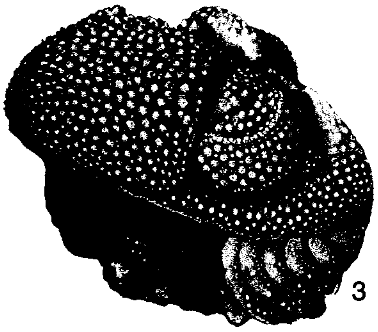

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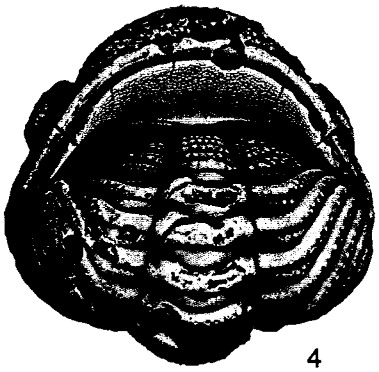

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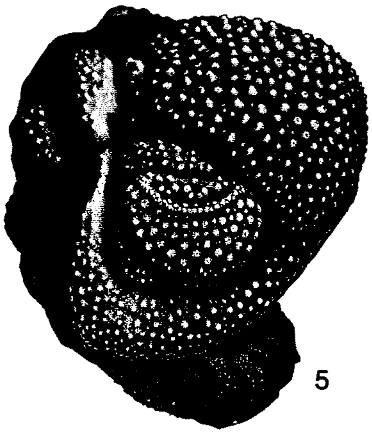

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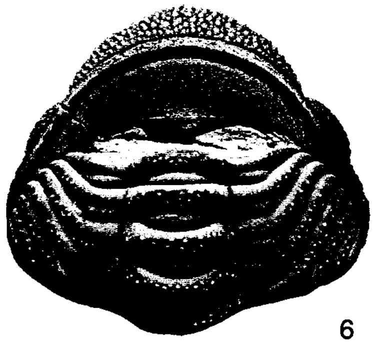

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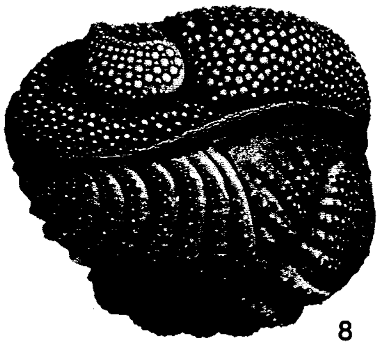

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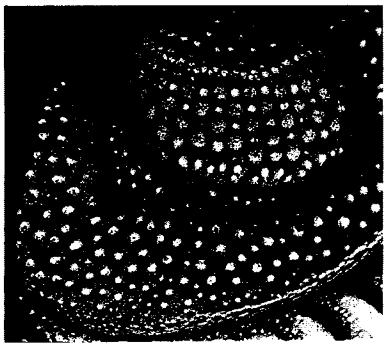

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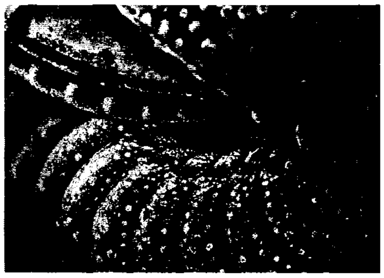

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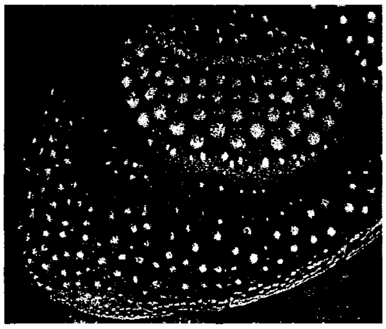

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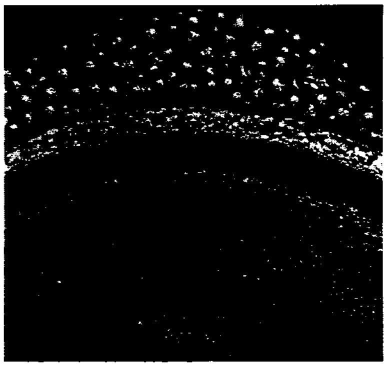

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Plate 25

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PLATE 26

Figs. 1–13. *Phacops araw* n. sp. from 'South Oufatene proetid couche' (SOP) at Oufatene section, within Ma'der basin. Strata are part of part of El Otfal Fm., Eifelian in age, and typically medium-gray muddy limestones.

Holotype UA6904 (arched specimen, nearly complete, missing much of left side anterior cuticle):
1. Anterior view of cephalon, X1.9.
2. Dorsal view of cephalon (palpebral lobe flat), X1.8.
3. Lateral overview of entire specimen, X2.0.
5. Lateral view of cephalon, X2.6.
6. Detailed view of right eye and postocular pad, X6.0.
7. Dorsal overview of thorax and pygidium, X4.1.
8. Detailed view of thoracic axial rings, X4.8.
9. Detailed view of anterior glabellar surface, X2.7.
10. Dorsal view of pygidium, X2.6.

Paratype UA6905 (arched specimen, nearly complete small holaspid, missing part of left side of cephalon due to cutting, and prepared for cephalon only, because much of pygidium is missing):
4. Dorsal view of cephalon (palpebral lobes flat), X2.3.
11. Lateral view of cephalon, X3.4.
12. Anteroventral view of cephalon, X2.5.
13. Ventral view of cephalon, focusing on doublure and vincular furrow, X2.5.

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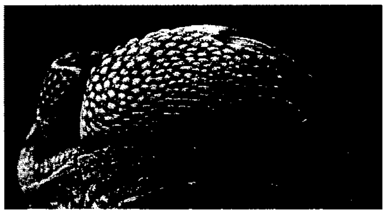
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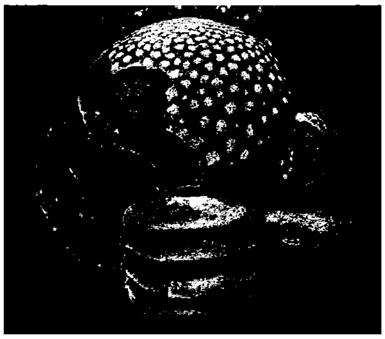
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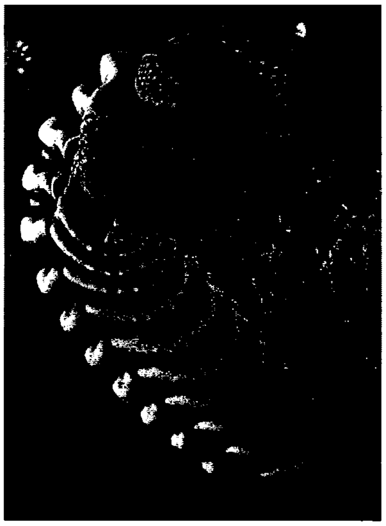
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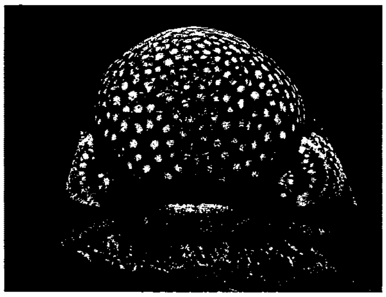
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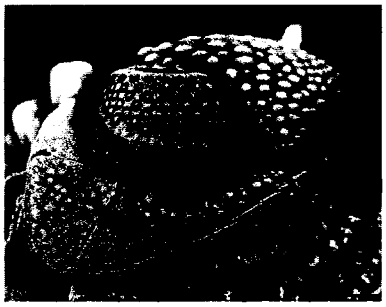
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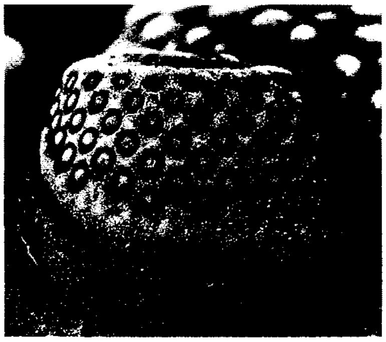
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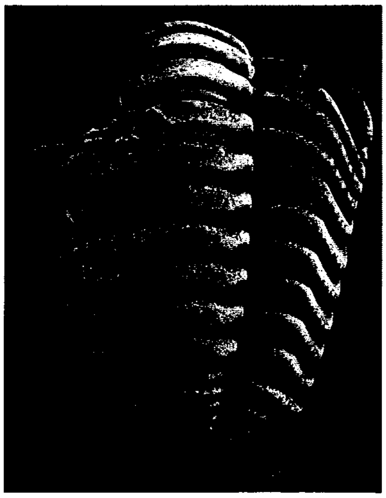
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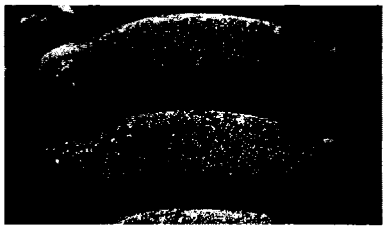
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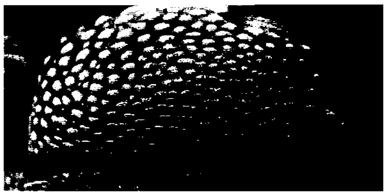
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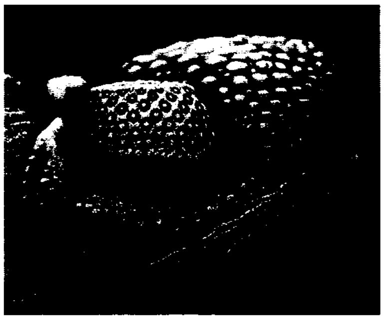
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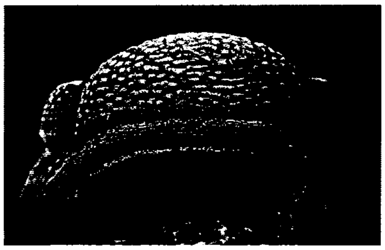
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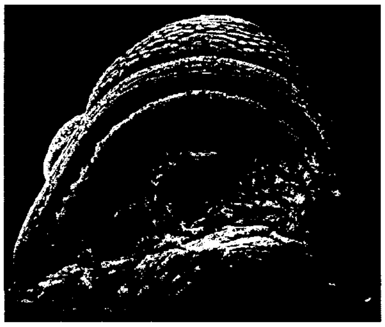
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Plate 26

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PLATE 27

Figs. 1–12. *Pedinopariops (Hypsipariops) vagabundus* STRUVE, 1990, purchased specimens largely from Aferdou de Mrakib, in Ma'der basin. Horizon is known locally as '*Phacops* noire couche', and is part of Givetian Bou Dib Formation.

Plesiotype UA6935 (outstretched, complete individual, with portions of thorax dislocated, partially Moroccan prepared, partially prepared by author):
1-4, 6, 7. Cephalon in anterior, anteroventral, dorsal (with palpebral lobes flat), lateral, lateral, and lateral oblique views, X0.9, X0.9, X0.9, X1.5, X1.6, X1.6, respectively.
5. Detailed view of left eye, X3.5.
8. Detailed view of anterior face of glabella, X4.6.
9. Dorsal view of pygidium, X1.1.
10-12. Overviews of exoskeleton in dorsal, lateral, and lateral views, X0.8, X1.1, X1.1, respectively.

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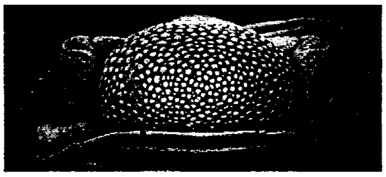
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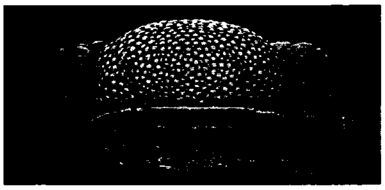
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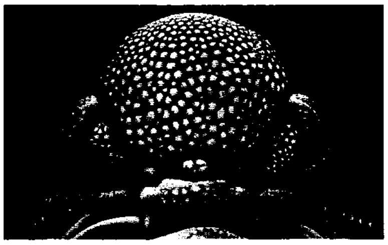
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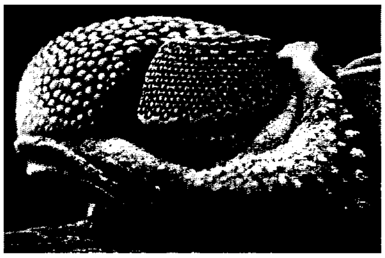
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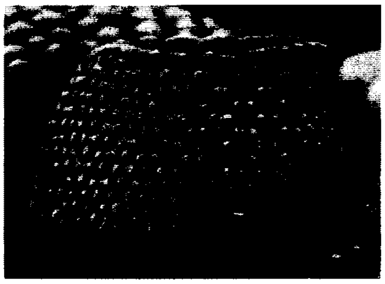
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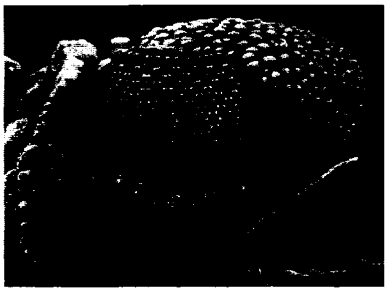
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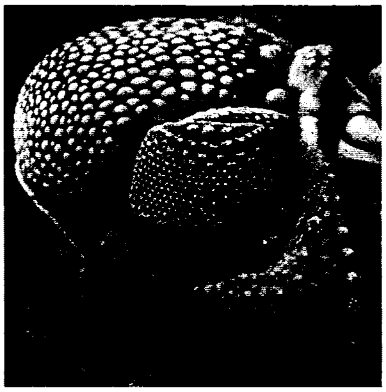
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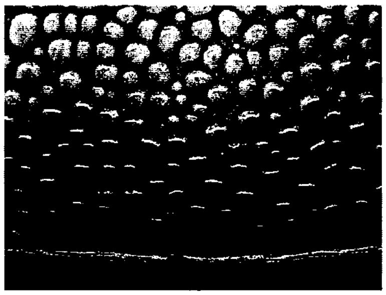
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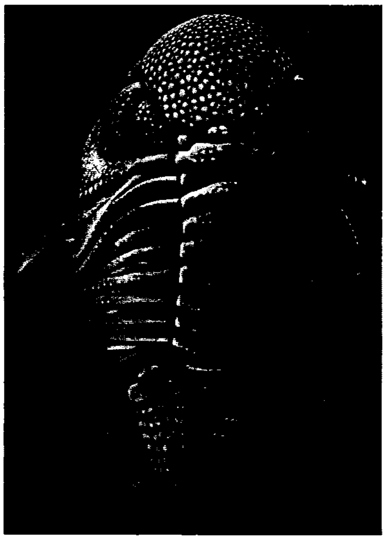
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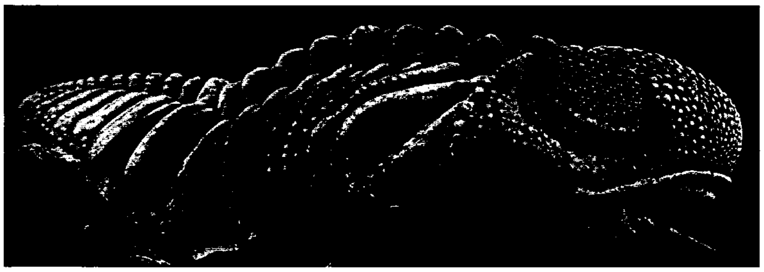
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PLATE 28

Figs. 1–14. *Pedinopariops (Hypsipariops) vagabundus* STRUVE, 1990, purchased specimens largely from Aferdou de Mrakib, in Ma'der basin. Horizon is known locally as '*Phacops* noire couche', and is part of Givetian Bou Dib Formation.

Plesiotype UA6936 (outstretched, complete individual, with significant dorsoventral compression, partially Moroccan prepared, partially prepared by author):

1-6, 8, 12. Cephalon in anteroventral, anterodorsal, anterior, anteroventral (with different lighting), dorsal (with palpebral lobes flat), ventral, lateral, and lateral views, X1.2, X1.2, X1.2, X1.2, X1.2, X1.2, X1.9, X1.9, respectively.
7. Detailed view of left eye, X4.3.
9. Detailed view of doublure sculpture, X1.8.
11. Dorsal view of pygidium, X1.4.
10, 13, 14. Overview of exoskeleton in dorsal, lateral and lateral views, X1.1, X1.4, X1.4.

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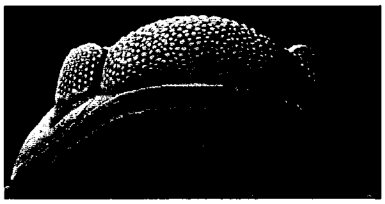
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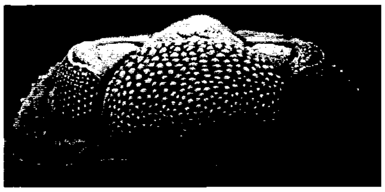
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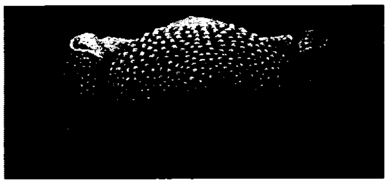
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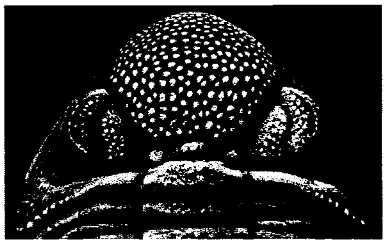
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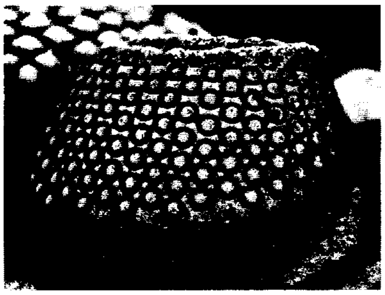
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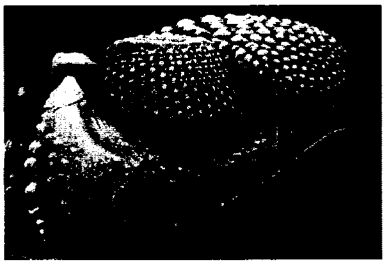
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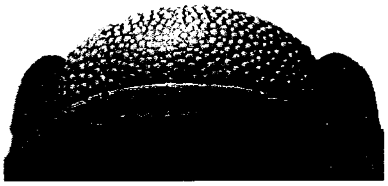
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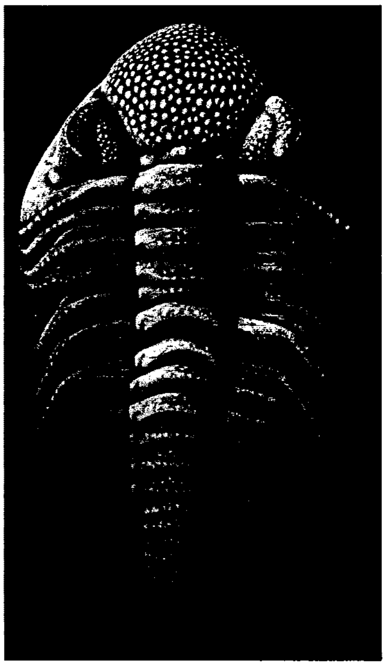
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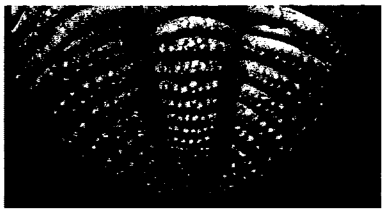
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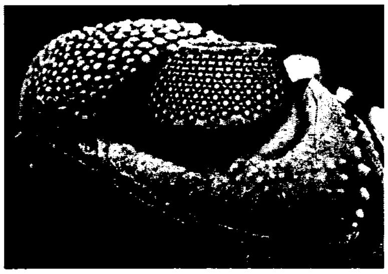
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Plate 28

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CHAPTER 4: CONCLUSION

Implications for phacopid systematics:

This study has implications for the tribes currently established within the Phacopidae, especially if a sequenced classification scheme is the desired end product. The informal taxon 'Ananaspini' of HAAS (1998), and the formal taxa 'Geesopini' of FLICK AND STRUVE (1984) and 'Cordapeltini' of STRUVE (1989) appear to be either paraphyletic or polyphyletic, and their use can not be advocated here. 'Ananaspini' is brought into question by the position of *Paciphacops* and *Viaphacops* relative to *Acernaspis*, and the expected (basal) position of the un-included genus *Ananaspis* that most existing works advocate (which would render the tribe polyphyletic). 'Geesopini' could potentially be salvaged in this analysis by excluding *Eldredgeops*, but this is likely an indicator of a much more widespread problem in resolving the tribe's members. 'Cordapeltini', as depicted here, is paraphyletic, and the members of New Genus A in its midst would be better assigned to the Phacopini in a grade-based classification, making its recognition difficult. Branching structure within this study's preferred cladogram also makes the recognition of tribes difficult or impossible. Primary branching appears to coincide with generic taxa, and any attempt to force the use of tribes would alter the generic standing of many groups, or require many new tribes to be recognized. There is neither support for nor evidence against the existence of a holophyletic Reedopini or Phacopini, due to the lack taxa within of so their use is optional.

At the generic level, some currently used genera are suggested to be unstable at best, and perhaps even paraphyletic. This includes *Eldredgeops*, which may actually be a paraphyletic fragment of the *Phacops* lineage (but this is not shown with enough certainty to dismiss the taxon's validity). The same problem exists with the multiple placements suggested for the genus *Chotecops* (in one analysis it is a holophyletic genus forming the sister group to all ingroup taxa excluding the *Reedops* spp., in another analysis it is a paraphyletic taxon forming the sister group to all of the *Reedops* spp. studied, creating the same uncertainty). The validity of *Viaphacops* is brought into question once again, due to its position within the clade containing *Paciphacops*. This previously contested genus should be treated as at most a subgenus of *Paciphacops* in

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future studies. Additionally, it should be noted that the genus *Burtonops* is suppressed as a junior objective synonym of *(Viaphacops)*.

No new genera are created as a result of this study, but the informal New Genus A and New Genus B are proposed to contain the (respectively) tuberculate and reduced-ornament phacopid species from Morocco. New Genus B displays morphologies intermediate between those commonly seen in members of *Phacops* and *Paciphacops*, and New Genus A displays many hallmark *Phacops* features, while presenting *Boeckops*- and *Chotecops*-like sculpture and eye characteristics, hence their positions within the cladogram. Any attempt to force these species into one of the pre-existing genera would ruin a holophyletic taxon. Furthermore, the groupings do not show strong support, in terms of either cladogram-based statistics, or prominent, reliable morphological characteristics. For these reasons, the groupings are left as informal, instead of suggesting new genera or stretching existing genera. Future work will show if they are robust, holophyletic taxa.

In order for the phylogeny proposed in this study to work as the basis for a sequenced classification of the phacopids, the debate over treating most divisions within the family as genera or subgenera must settle on using generic taxa (for the time being). The distinctions between genera are weak enough that it is hard to warrant treatment as genera within a grade-based classification scheme, but the large-scale branching pattern seen in this study suggests that the divisions must be treated as genera. Opting for the extensive use of subgenera would result in the loss of *Reedops* and *Drotops* as distinct genera (something contrary to even most conservative taxonomies), and would sink the subgenera of *Pedinopariops*.

At the specific level, the placement of *Boeckops stelcki* n. sp. within the genus *Boeckops* is somewhat questionable, but it is placed there intentionally. The grade-based taxonomy of the phacopids places this species clearly within *Boeckops*, but here it is poorly supported as an independent clade. This is a case where leaving the species outside of the genus would only lead to unnecessary higher-level taxa.

Other species, such as *Phacops latifrons* and *Phacops araw*, are shown to be so closely related (so strongly supported as sister taxa, in an otherwise weakly supported phylogeny) that there is some temptation to relegate the latter taxon to a subspecies of *P.*

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latifrons. This has been avoided here, since the differences in morphology are too significant.

Biostratigraphic conclusions:

The usefulness of phacopid trilobites as index fossils within Devonian strata has not yet been fully realized. The phacopids are some of the most abundant and widespread fossils within the Devonian of Morocco, and are relatively common elsewhere. Furthermore, the idea that "they all look alike" is incorrect; most phacopid species can be quickly identified on the basis of a few distinctive characteristics (it is really a lack of comprehensive and coherent literature coverage that diminishes their usefulness). Within southern Morocco, the phacopids can be used for high-resolution biostratigraphy, acting as indicators for a number of horizons, and helping to correlate these horizons within and between basins. The family Phacopidae also has a wide distribution, and is not as ecologically restricted as many other trilobite groups, meaning that its members can be useful in correlating on a broader scale, and that their detailed dispersal routes might be useful for palaeobiogeographic studies. Below is a summary of the biostratigraphic and biogeographic conclusions that can be drawn from the Moroccan specimens encompassed within this study.

In the Ma'der basin, *Reedops pembertoni* n. sp. can be used to correlate the '*Dicranurus* couche' and '*Kolihapeltis* couche' throughout their occurrences within the lowermost portions of the Oufatene and Issoumour sections (across the Ma'der basin). It is also the most abundant trilobite species within these horizons, making it a better indicator than the currently used (rarer) *Dicranurus*. The presence of *Reedops bronni* within these same beds is useful because it connects the region to the faunal contents of Bohemia, where *R. bronni* is used as a Pragian index fossil (CHLUPÁČ, 1977). The basins are further correlated through the occurrence of *Reedops cephalotes hamlagdadianus* at both El'Mdouar (Tindouf basin), and Hamar Laghdad (Tafilalt basin), 300 kilometers apart. (There is also a *Reedops* species that may be conspecific with *R. cephalotes hamlagdadianus* within the Ma'der basin's '*Dicranurus* couche', but this requires more detailed preparation and study to be certain).

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The Eifelian strata in the uppermost portions of most Ma'der basin sections are also easily correlated due to the *Drotops* and *Pedinopariops* species they bear. Although the stratigraphic origin of most of the complete *Drotops* specimens in this study is not known with certainty, field collections of fragmentary material have shown that there is a definite order of occurrence and that this is predictable throughout the Ma'der. From oldest to youngest, the sequence *Drotops megalomanicus*, *Drotops armatus*, *Pedinopariops (Hypsipariops) vagabundus* is repeated at the tops of Mrakib (Aferdou) and Issoumour (Taboumakhlouf), and in part at Oufatene. This has been used by STRUVE as an indicator for uppermost Eifelian strata (although BULTYNCK AND WALLISER, 2000, KAUFMANN, 1998, and CAMPBELL *et al.*, 2002 all appear to have given the strata an early Givetian age).

The occurrence of New Genus A *smoothops* and New Genus B *lebesus* in the upper ('ZGEE3/T*hysanopeltis* couche') of the Zquilma section, as well as in the '*Harpes/Thysanopeltis* couche' of the bou Dib section helps to correlate these beds between the Tindouf and Ma'der basins, respectively. The bou Dib section can also be tied in with the remainder of the Ma'der basin sections to the south (particularly Issoumour), and the basal portion of the Merzouga section (within the Tafilalt basin, to the East), on the basis of its '*Psychopyge* couche' and the distinctive and abundant New Genus B *forteyi* found therein.

From a more palaeobiogeographic perspective, the occurrence of New Genus A *speculator punctatus* n ssp. in the Ma'der basin shows that there are definite and very close associations between the south Moroccan trilobite fauna studied here and the northern and western faunas studied by G. ALBERTI (1970). This indicates that the faunal contents of even the most widespread Moroccan basins were relatively uniform in the Middle Devonian, suggesting that other, closely related taxa may exist, or have close counterparts in these basins as well, and that the biostratigraphic patterns seen here may be repeated elsewhere.

Phacops araw is very similar to *Phacops latifrons* (the type species of the genus), a constituent of the Rhenish-Bohemian faunal subprovince (mainly Germany), and shows slightly less affinity to *Eldredgeops rana rana*, a constituent of the Appalachian Realm (*E. rana* has been suggested by workers like CAMPBELL and ELDREDGE (1977; 1972) to

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be an interloper in this realm from lineages started in the Old World Realm). These close relationships suggest that the Moroccan Meseta and Rhenish-Bohemian region were in fairly open communication in the Middle (and likely Early) Devonian, but that there was enough isolation to produce regional species with significant cumulative differences in morphology. It also adds support to the suggestion that *Eldredgeops* is so different from its North American contemporaries on account of its closest relatives having originated in a different realm. The overwhelming similarity of many tuberculate-sculpted Moroccan phacopids (e.g. New Genus B *granulops*) to taxa such as *Phacops degener* BARRANDE, 1852, and its affiliates also contributes to the notion of Morocco bearing a Rhenish-Bohemian fauna with slight regional differences.

Palaeoecological conclusions:

A phacopid-like morphology is often seen as an indicator of inhabiting a muddy substrate at an intermediate water depth, and acting as a generalist feeder or pursuing shallow infaunal organisms (FORTEY AND OWENS, in KAESLER, 1997). Although there is no definitive connection between specific phacopid morphologies and particular depositional environments (habitats), there are a few reasonably good associations. The main morphological features that have been linked to palaeoecology include eye size, glabellar volume, cuticle thickness, and sculpture elements.

In his work on Bohemian phacopids, CHLUPÁČ (1977) noted that shallower water carbonate facies often harbored a lower diversity of phacopids, but possessed greater abundances, especially of large-eyed forms. He also observed that muddy substrates in deeper waters (similar to the bulk of the trilobite horizons studied here) possessed the highest phacopid diversities, but that there was no obvious dominance of small- or large-eyed forms in this setting (1977). Similar observations were made of the Moroccan phacopids. Most of the Moroccan trilobite horizons probably represented deeper water settings in the euphotic or dysphotic zone, perhaps on the continental shelf near the top of the slope. Here there is a mixture of large and small-eyed phacopids, and their relative abundance appears to be determined by substrate, and their preference/ability to burrow in it for food, as opposed to general deep water (low light) eye reduction. Trilobite horizons interpreted as shallower depositional settings (such as the *Drotops* couches, and

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perhaps the Hamar Laghdad bioherms) also followed the trends discussed by CHLUPÁČ, with a phacopid assemblage dominated by large-eyed forms. Interestingly, substrate type did not appear to have a strong affect on species such as *Reedops cephalotes hamlagdadianus*, which can be found in the iron-rich calcareous mudstone of El'Mdâouer, as well as within the pure carbonate, sparry calcite deposits of Hamar Laghdad (among algal mud mounds).

The internal volume of the glabella has been suggested as an indicator of semi-infaunal or epibenthic detritivorous life modes within phacopids, in works such as that of ELDREDGE (1971). Conversely, FORTEY AND OWENS (1999) have suggested a carnivorous/scavenging lifestyle for phacopids, based largely on *Phacops* itself, by placing emphasis on the developed eyes of *Phacops* (for predatory purposes instead of defense) and its hypostome style, and by dismissing its sheer numbers (low trophic tier), and the unnecessary possession of a large crop if energy-rich food (tissue) is consumed. Here a large glabella volume is interpreted as representing a semi-infaunal or infaunal lifestyle, in which huge amounts of sediment are churned through for food particles, and an expanded glabella is needed to accommodate the bigger stomach and anterior digestive tract necessary for food processing. This seems to be a reasonably good indicator of epibenthic or semi-infaunal life modes within the Moroccan specimens, since it parallels trends seen within the sculpture and eyes of most taxa, but it is occasionally at odds with observations made of other features. Most notably, *Reedops cephalotes hamlagdadianus* possesses a very large glabella, but also has eyes that are large, and prominent enough to interfere with active burrowing. The same contradiction is seen in the somewhat reduced sculpture of *Boeckops stelcki*, which still looks as though it would complicate the burrowing that its expanded glabella would suggest. It may be more reasonable to equate a large glabella with the ability to process sediments (a generalist feeder capable of detritivory, compared to a reliance on carnivory or scavenging), instead of evidence for burrowing behaviour. Ultimately, the interpretation of feeding behaviour is speculative until more is known about the soft tissue anatomy of phacopids.

Cuticle thickness has been used by FORTEY AND WILMONT (1991) as a general indicator of habitat depth for trilobites. In the most general sense, their study found that cuticles consistently were thicker in trilobites inhabiting shallower settings. As a group,

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the phacopids have relatively thick cuticles to begin with, but this thickness was exaggerated in some species or groups, and significantly reduced in others. Within the Moroccan specimens, there was an additional trend of cuticle thinning in putative infaunal or semi-infaunal species, such as *Reedops bronni* and *R. cephalotes hamlagdadianus*. In some of the shallower water forms like *Drotops* spp., even in specimens that had not achieved 'giant' holaspid sizes, the cuticle was moderately thickened. *Phacops araw* also bore remarkably thick cuticle for its size, which could be attributable to a shallower water habitat, or an epibenthic life mode requiring more defense or in a higher energy setting.

The last major source of information on the life modes of phacopids stems from studies of their sculpture element functions. Terrace lines have suggested functions such as to aid in burrowing, to grip substrate, or to aid in the perception of current flows (WHITTINGTON AND WILMONT, in KAESLER, 1997; MILLER, 1975). Those terrace lines found on the ventral doublures of phacopids are of particular interest, because they show great variability. These regions can be covered with sculpture elements ranging from granules (largely in *Reedops* and its allies, and 'primitive' phacopids); to "scaly ridges" of discontinuous terrace lines (seen in genera such as *Chotecops*, and also in New Genus B); to continuous prominent terrace lines (seen in *Drotops* spp., and New Genus A) (CHLUPÁČ, 1977). The spectrum of forms seen here begs the question of their use. The answer best supported by the Moroccan phacopids is that provided by CHATTERTON AND CAMPBELL (1993), of creating a firmer "friction lock" when the trilobite is fully enrolled, something that is most necessary in epifaunal, shallower water dwellers. Additionally, strong terrace lines may have contributed to the hydrodynamic properties of outstretched individuals in a current – influencing or disrupting flow across the ventral and anterior surfaces in order to reduce the lift experienced, and keep the trilobite firmly planted on the substrate.

Other forms of sculpture, such as tubercles, pustules, spines, and pits have typically been studied through the use of thin-sections, and little is known with certainty about their function. It has been speculated that large-diameter canals (erupting surficially as pores) likely housed sensory setae, were filled by integumental glands, or allowed oxygen/water transfer through the cuticle (WHITTINGTON AND WILMONT, in KAESLER,

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1997). The Moroccan phacopids showed positioning of the largest canals in marginal positions, along the anterior face of the glabella, and across the cheek beneath the eye, which definitely supports the sensory interpretation of their function: the most pitted specimens were also those that are typically viewed to be epibenthic. Tubercles and pustules are seen in a variety of forms in this study, and are typically associated with sensory functions or defense. Researchers have suggested that these elements house mechanical or chemical sensory structures (STØRMER, 1980), and provide thickened cuticle that is better camouflaged, harder to grip with a suction device (CHATTERTON, 1980), and may influence current flows across the exoskeleton. Little is definitively known about the function of tubercles or pustules, largely due to a lack of solid modern analogues, but the Moroccan material shows a reduction in all but anterior sculpture in the supposed semi-infaunal taxa, and that taxa with thickened cuticles (probable shallower water dwellers) typically bear pustules instead of conical or domed tubercles. Spines were also observed in the study group, and most likely served as defensive devices, with no prominent axial canals denoting secondary functions.

Taphonomic observations:

From a taphonomic standpoint, the phacopid contents of some horizons go a long way towards deciphering the genesis and taphonomic conditions for certain units. Phacopids are among the most numerous fossils found within many of the Lower and Middle Devonian strata of southern Morocco, and have relatively thick exoskeletons capable of surviving transport: this, coupled with their behaviour, provides some insight into depositional conditions.

The most commonly seen behaviour in phacopids is enrollment. In horizons such as the bou Dib '*Psychopyge* couche', enrolled, complete individuals can account for 80-90% of the specimens recovered, or more. Some of these individuals are not fully enrolled – their pygidia are tucked in to meet the back of the doublure surface instead of catching within the vincular furrow, forming a position termed the "*phillipsinellid* type" of enrollment (CHLUPÁČ, 1977; quoting MOORE, 1959). In either case, enrollment is typically viewed as a defense technique, and provides strong evidence for rapid live burial, or changes in local water conditions that were dramatic enough to elicit a

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defense/coping response. At the bou Dib section, the pervasive enrollment is probably representative of rapid burial by an obrution deposit; the deposit either solidified (dewatered) rapidly, trapping the enrolled New Genus B *forteyi* in large numbers, or contained inhospitable conditions within its pore-fluids, which overwhelmed them. The fact that many of these trilobites have their pygidia pushed back along their doublures, or stuffed into their body cavities, suggests that there was inward-pressure from the compacting sediments around them, but the presence of individuals with the pygidia ejected outwards into the surrounding sediment suggests that decay played a greater role in their taphonomic history (see discussion of disarticulation below for more detail).

The incidence of enrollment is much lower in members of the *Reedops* lineage studied here. Of the 34 plus articulated *Reedops* specimens dealt with in this study, only 4 show enrollment, and 2 of these have their pygidia adpressed to the doublure instead of within the vincular furrow. This relative lack of enrollment may have to do with the prevalent life mode within this group, which is most likely semi-infaunal or shallow-infaunal in nature. If sediments mobilize, or there is a sudden influx of sediments, those trilobites living within the substrate are least likely to get a chance to enroll without the sediment around them constraining their motions.

Taphonomically speaking, the presence of many complete, enrolled individuals, within massive limestone units, and among a high diversity of other trilobite taxa, is a reasonable indicator that the fossil assemblages within most horizons have probably had little time averaging. Since there are large numbers and a high diversity of organisms buried at random orientations, there appears to be no subsequent winnowing or reworking, and there is little or no sign of escape traces or subsequent bioturbation, it is fairly safe to conclude that the beds represent a snapshot of the benthic community. This appears to be the general pattern seen within most of the studied horizons. Noteable exceptions to this rule include the Hamar Laghdad deposit (described in detail below), and the recessive shales (between the mined horizons and other prominent limestone beds), which tend to produce more disarticulated phacopids than enrolled or otherwise complete individuals (as occurs at the base of the Merzouga section). The favoured explanation for the genesis of horizons containing a high diversity of articulated trilobites at the Zquilma locality is provided in detail in CHATTERTON *et al.* (2006), and this

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mechanism is evident to varying degrees within the other trilobite horizons studied. Restated simply, the beds seen here are the result of episodic slumped obrution deposits (mud-rains followed by small-scale underwater mudslides) caused by storm events farther upslope. The organisms trapped within these fine-grained slurries are not transported far before the sediments dewater and the flow solidifies. This traps a broad spectrum of benthic organisms (and slightly reworked remains or exuviae) in a matrix that can be rapidly cemented or undergo more compaction before diagenesis. Because the event is episodic in nature, it can repeatedly sample the benthic community, but its representation is that of an event, not continuous deposition. In most horizons, the fauna is dominated by phacopids, in terms of abundance, and sometimes diversity as well. This is likely an accurate representation of their presence as generalists within the benthic community.

The preservation of articulated, complete exoskeletons, composed of many loosely bound sclerites serves as an excellent indicator of depositional and taphonomic conditions. In some deposits studied, such as Hamar Laghdad's crevasse-fills between algal mud-mounds, the complete absence of articulated individuals (in a sample set as large as that of this study) speaks volumes. Preservation such as this suggests that the bulk of the fossil material within these fills was either subjected to relatively high water energies (in a shallow water setting), or that sediment input was exceptionally low (prolonging exposure and decay/scavenging). Combined with the sparry calcite matrix that cements the trilobite and brachiopod fragments together in this horizon, the latter set of taphonomic conditions is most supported.

Partial disarticulation is also common within the phacopids studied here. The first, and most common, form that partial disarticulation can take is the dislocation of the pygidium and posterior thoracic segments in enrolled individuals. Often, the pygidium is found lodged within the body cavity of the enrolled trilobite, or dislocated into the adjacent external matrix. This form of disarticulation has more to do with post-burial taphonomy than with depositional conditions. SPEYER (1987) indicated that the bulk of the enrolled specimens that he had studied in which the pygidia had 'imploded' into the body cavity were almost assuredly cases where decay (and its subsequent degassing) had dislocated part of the body, and allowed sediments to be injected into the body cavity.

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The fact that some individuals seen here also appear to have had their pygidia 'explode' into the surrounding sediments, adds support to SPEYER'S ideas about forcible degassing.

The second, and less common, form of partial disarticulation seen within the phacopids (and many other groups of trilobites within these strata) is that of twisted or slightly offset thoracic sections within outstretched individuals. This 'wrenching' of specimens has been related to burial in a moving flow of sediments, and the flow's subsequent dewatering or compaction, by workers such as CHATTERTON *et al.* (2006) and SPEYER (1987).

The presence of phacopid exoskeletons found in moult positions is both an indicator of behaviour (and conditions favourable for the behaviour to take place), and environmental conditions that would have affected the cast exuvium after moulting. Cast exuviae were found sporadically within many of the studied horizons, but not in any sort of concentration deposit. The fact that these sclerites were still articulated to the extent of being recognizable in moult positions, with the separated cephalon still adjacent to the connected thorax and pygidium, shows just how low the water energy levels would have been (HENNINGSMOEN, 1975). Additionally, the presence of cast exuviae, and the preservation of some "paper-shell stage" (post-ecdysial) specimens, suggests that many of the localities may represent ecological regions that were relatively safe for soft-shelled, post-ecdysial phacopids (perhaps deeper water), or that this behaviour was performed partly within the uppermost substrate layers. Some localities, such as Merzouga (above the interval containing New Genus B *forteyi*), and portions of the Zquilma locality, also contained phacopids inside the internal mould material of orthoconic nautiloids, but none of the material observed showed moulting positions or multiple individuals within a single shell-void. This would suggest that the trilobites may have been driven into these voids due to sediment compaction, or may have sought shelter within the shells, but this is by no means cryptic behaviour on the scale of, or with the same degree of certainty, as that seen within the Silurian phacopids of CHATTERTON *et al.* (2003).

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Future work:

The most pressing issue for future studies on the family Phacopidae is addressing its phylogeny and taxonomy in some sort of uniform, concerted effort. For a such a large group of trilobites that has been worked upon for so long, and by so many workers, there is remarkably little in terms of robust taxonomy or systematics within the literature.

The simplest solution to the current taxonomic problem is to try to ensure that existing material is properly figured and described; redescribing type material, as was done by CHLUPÁČ (1977) and KOWALSKI (1989); and that new material is treated the same way and receives thourough comparisons to existing taxa. Many of the problems that have arisen in phacopid taxonomy were due to unclear concepts or figuring of types. This is something easily remedied by providing more comprehensive descriptions (instead of just diagnoses), and figuring all major sclerites recovered (instead of just providing cephalic diagrams, and stating that post-cephalic remains are the same as another species). The use of a cladistic framework for future studies demands that these conditions be met by future works, or the taxa generated will not be possible to code and analyze.

The systematic problem in phacopids is largely the result of many workers focusing on restricted field areas, or small taxonomic and systematic problems, without much in the way of large-scale studies. RAMSKÖLD AND WERDELIN (1991) provided a starting point for solving this problem, when they produced a cladistic analysis that could act as a relatively objective connector for future work. As this study shows, the cladistic characters and codings they used do not apply to all phacopids, but can easily be modified or supplemented to analyze specific groups. With this in mind, it is now possible to have a relatively uniform approach to phacopid systematics. This uniformity of approach is key, if there is to be any sort of stable systematic scheme for the Phacopidae. Additionally, the uniformity of approach, and the demand for rigorous collection and description that the use of cladistics demands leaves behind more than just hypotheses of relationship in the literature – its demands produce solid taxonomic foundations for future work.

Future work for the author (in particular) involves using the basic phylogeny created within this thesis to explore smaller-scale groups of phacopids more extensively.

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In specific, preparations have begun for a detailed analysis of the genus *Reedops*, and some of the reduced-eye phacopids with which it may share affinities. The completion of this thesis has also brought to attention additional new species in need of description (particularly those found in the Zireg section), and has generated an interest in resolving the taxonomy within the genera *Drotops* and *Pedinopariops*. In a more general sense, the biotstratigraphic and biogeographic work begun here will develop greater resolution as a result of any additional taxonomic work performed within the Phacopidae. The sheer diversity of Devonian Moroccan trilobites and their host lithologies also provides intriguing opportunities to connect specialized phacopids to particular palaeoenvironments, and to observe general evolutionary trends within the family, as contrasted to the trends within other groups of trilobites. The work on Moroccan phacopids is far from complete, and extends well beyond the scope of this thesis, but my interest in this group of trilobites is far from satiated.

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APPENDIX 1: Characters used in the phylogenetic analysis of select phacopids.

1. **Glabellar width** [1 modified] – transverse width of frontal lobe adjacent to anteroventral corner of eye, as a percentage of total cephalic width (tr.): (0) 51-55.9%; (1) 56.0-60.9%; (2) 61.0-65.9%; (3) 66.0-70.9%; (4) 71.0-75.9%
2. **Occipital ring width** [3 modified] – transverse width of occipital ring, measured from axial furrow to axial furrow, and expressed as a percentage of total cephalic width (tr.): (0) ≥38%; (1) 36.0-37.9%; (2) 34.0-35.9%; (3) 32.0-33.9%; (4) 0-31.9%
3. **Intercalating ring** [4 modified] – shape and position of intercalating ring (L1), relative to the surrounding glabella and L1 lateral lobes: (0) small, subtriangular, displaying independent inflation, and typically barren of sculpture; (1) mid-sized to large, raised pad with sculpture; (2) small, circumscribed by furrows, set anterior to L1 lateral lobes; (3) faint or absent with no sculpture
4. **L1 lateral lobe size** [5] – relative size of lobe and its distinction from the intercalating ring by an obvious furrow: (0) L1 lateral very small; (1) L1 lateral medium-sized; (2) L1 lateral large, with distinct adaxial edge; (3) L1 lateral large, with indistinct adaxial edge
5. **Length of L2 versus length of L3** [6 modified] – exsaggital length of L2 across its long axis, expressed as a percentage of the same measure for L3: (0) 40-49%; (1) 50-59%; (2) 60-69%; (3) ≥70%
6. **Granules on glabella** [7 modified] – presence and concentration of granules on various surfaces and sculpture of the glabellar surface: (0) granules present on all convex surfaces; (1) granules reduced between tubercles; (2) granules absent between tubercles
7. **Tubercles on glabella** [8 modified] – generalized class of large sculpture elements and their distribution upon the glabella: (0) tubercles absent or bordering on granule-size; (1) tubercles weak, sparse; (2) tubercles distinct, medium density; (3) tubercles distinct to coarse, high density; (4) tubercles pustular, dense; (5) tubercles pustular, relatively sparse; (6) tubercles tall, conical or spinose
8. **Postocular area length** [11] – exsaggital length of area between back of eye and posterior border furrow, measured at posterior-most extreme of eye when specimen is viewed dorsally, and expressed as fraction of posterior border length (exsag.), directly behind first measurement: (0) less than half the length of posterior border; (1) half to equal length of posterior border; (2) longer than posterior border
9. **Lateral border furrow** [12 modified] – definition and shape of lateral border furrow behind posterior branch of facial suture (i.e. posterior border furrow where it swings anteriorly below tip of postocular pad), and the resulting effect this has upon definition of the postocular pad: (0) absence or hint of furrow, pad fades distally; (1) narrow, weak furrow, pad has poorly defined tip; (2) narrow, deep furrow, pad has sharply defined tip; (3) wide, distinct furrow, pad has rounded tip; (4) wide, shallow furrow, pad has sloping tip
10. **Palpebral area height** [13 modified] – in true frontal view, the height of the palpebral lobe relative to the dorsal surface of the palpebral area, and the glabella:

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(0) regions are about level; (1) palpebral area lower than palpebral lobe;(2) palpebral area markedly higher than lobe

11. **Lateral L1 definition and shape** [14 modified] – the distinction of the L1 lateral lobe from the adjacent (abaxial) palpebral area, and its general shape and sculpture: (0) distinct, globular, unornamented; (1) distinct, globular, unornamented; (2) indistinct, nearly flat, unornamented
12. **Palpebral furrow definition** [15] – depth of the palpebral furrow in the median 1/3rd of its course: (0) faint to absent; (1) weak; (2) distinct; (3) deep
13. **Genal angle** [16] – shape of genal angle and any prominences it may bear: (0) drawn out, with acute tip or large spine; (1) drawn out, with small spine; (2) rounded angular, with distinct node at corner; (3) rounded, with or without hint of node
14. **Palpebral sculpture** [19 modified] – presence of pitting on the palpebral lobe (which shows some correspondence to pitting in the genal field), and other sculpture elements present: (0) even surface; (1) pitted surface; (2) perforated appearance, with deep, wide pits; (3) smooth between tubercles
15. **Terrace lines** – presence of terrace lines (fragmentary or continuous) on various regions of the dorsal surfaces of the cephalon: (0) absent or nearly so; (1) on ventral margin only; (2) on glabella, cheek, and ventral margin
16. **Definition of lateral axial lobes** [21 modified] – the definition of the lateral axial lobes of the occipital ring (as delimited by the furrow arising from the apodemal pit directly ahead of it), and the definition of the lateral axial lobes in the thoracic segments, (which are controlled by the same factor): (0) lobes are strongly defined, furrow runs halfway across occipital ring; (1) lobes are weak to distinctly inflated, moderately defined; (2) distinct lobes are absent or effaced, poorly defined
17. **Sclera in eyes** [23 modified] – nature of interlensar sclera within the visual surface of the eye: (0) thin sclera throughout; (1) sclera slightly thickened, dorsally only; (2) sclera considerably thickened dorsally, only weakly ventrally; (3) entire sclera surface thickened; (4) tubercles on thickened sclera, lenses in cruciform arrangement; (5) tubercles on thickened sclera, lenses in hexagonal arrangement
18. **Vincular furrow** [24 modified] – the course and depth of the medial part of the vincular furrow: (0) wide shallow furrow; (1) deep distinct furrow; (2) completely absent medially, or only shown through ornament
19. **Width of pygidial axis** [26 modified] – width (tr.) of pygidial axis across first axial ring, expressed as a percentage of total pygidial width (tr.) excluding articulating facets: (0) 25-29.9%; (1) 30-34.9%; (2) 35-39.9%; (3) 40-44.9%
20. **Closure of pygidial axis** – degree of closure of the axial furrows behind the terminus of the pygidial axis: (0) nearly complete closure, leaving mild postaxial ridge; (1) minor closure, often leaving strong postaxial ridge
21. **Interannular rings** [27 modified] – presence of interannular rings behind anteriormost axial rings of pygidium, and their appearance: (0) widened furrow or hint of ring; (1) distinct ring present; (2) strong ring, near level with axial ring in front, and ornamented

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22. **Number of axial rings** – generalized number of axial rings in pygidium, roughly corresponding to use of 'richly' or 'poorly' segmented as axis descriptors: (0) 7-11 well defined rings, relatively numerous; (1) 4-6 well defined rings, relatively few
23. **Number of clear pleural ribs** – generalized number of clear pleural ribs in pygidium, based on independent inflation, and roughly corresponding to use of 'richly' or 'poorly' segmented pleural field descriptions: (0) 2-5 clear pleural ribs, few; (1) 6-10 clear pleural ribs, many
24. **Depth of pleural furrows** [31] – depth and profile shape of pleural furrows in pygidium: (0) weak, thin pleural furrows; (1) deep, thin pleural furrows; (2) deep, steep-sided to medium-wide pleural furrows; (3) deep, wide pleural furrows, usually with circular profiles
25. **Number of vertical rows in eye** – the typical number of vertical rows of lenses within the visual surface of a relatively large holaspid, excluding specimens showing teratological or atypical features: (0) 14-16; (1) 17; (2) 18; (3) 19; (4) 21; (5) 25
26. **Maximum number of lenses per vertical row** – the typical maximum number of lenses found within a single vertical row of the visual surface of a fairly large holaspid free from teratological or otherwise atypical features: (0) 4; (1) 5; (2) 6; (3) 7; (4) 8: (5) 9
27. **Subocular pad** – presence and relative inflation of a raised pad beneath the eye and dorsal to the genal field: (0) pad absent; (1) pad weak; (2) pad strong
28. **Pygidial axis length** – length (sag.) of pygidial axis from base of first axial ring to tip of terminal piece, expressed as a percent of total pygidial length (sag.), from base of first axial ring to pygidial margin: (0) short, <84%; (1) long, >84%; (2) exceptionally short, <78%; (3) exceptionally long, >89%
29. **Thorax shape** – backwards taper of thorax, measured by observing total width (tr.) of first and last thoracic segments, and expressed as the percentage of the first that the last segment comprises: (0) strong taper, last segment <80% of first segment's total width; (1) weak taper, last segment >80% of first segment's total width
30. **Degree of glabellar overhang** – qualitative judgment of how much glabella overhangs anterior border furrow and anterior border, usually taking into account the position of the vincular furrow as well: (0) no overhang; (1) frontal face of glabella vertical or with mild overhang; (2) high degree of overhang
31. **Degree of glabellar divergence** – angle of divergence found between axial furrows, as they spread anteriorly around sides of glabella: (0) low, <60°; (1) moderate, 60-70°; (2) high, >70°
32. **'Marginulation'** – the presence of a raised (laterally) bead along the ventral margin of the cephalon, to a position behind that of the eye and usually all the way to the genal angle, without disappearing into the gena: (0) rim incomplete or absent; (1) rim complete, reaching almost or fully to genal angle
33. **Posterior border spines or tubercle row** – the presence of a locally prominent concentration of coarse tubercles or spines along the posterolateral margin of the posterior border: (0) absent; (1) present

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34. **S1 medial continuity** – whether or not the medial portion of the S1 furrow is continuous and easily traceable between the intercalating ring and the back of the glabella: (0) discontinuous or effaced furrow; (1) continuous furrow
35. **Doublure sculpture** – the nature of the sculpture elements upon the doublure, especially its medial portion beneath the glabella: (0) relatively equidimensional granules dominant; (1) short, broken terrace lines, or granules severely elongated transversely; (2) fully developed, largely continuous terrace lines dominant
36. **Base of visual surface with tubercles** – the presence or absence of a row of coarse tubercles along the ventral margin of the visual surface, often these have become broad and rounded in nature: (0) absence of strong tubercles; (1) presence of strong tubercles
37. **Sculpture on pygidium** – the nature and extent of tuberculation upon the various regions of the pygidium: (0) tubercles absent; (1) tubercles restricted to axis only; (2) tubercles faintly present on pleural ribs; (3) tubercles moderately to strongly present on pleural ribs, and also upon marginal field
38. **Accessory lens row** – the presence of an additional horizontal row of lenses, beginning near the middle of the visual surface and continuing posteriorly, usually composed of diminutive lenses, as opposed to a consistently level top row proceeding from the anterior corner of the eye: (0) accessory lens row absent; (1) accessory lens row present
39. **Interpleural furrow strength** – depth of impression for the interpleural furrows of the pygidium: (0) weak to completely absent; (1) moderately impressed

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APPENDIX 2: Data matrix for cladistic analysis.

	1								10										20										30									39
Calyptaulax glabella	1	0	3	2	?	0	0	0	0	0	0	0	2	0	0	0	?	?	0	1	2	0	0	0	5	0	0	0	?	0	0	?	0	0	?	?	0	?	1
Acernaspis orestes	0	2	0	0	3	0	0	0	0	0	0	1	3	0	0	0	0	1	2	0	0	0	0	1	0	3	0	0	0	0	0	0	0	0	0	0	0	1	0
"N. g. B" granulops	2	3	1	2	?	2	3	1	2	2	1	1	3	3	1	0	2	1	1	0	1	0	0	2	3	1	1	1	0	1	2	1	0	1	1	1	3	0	0
"N. g. A" smoothops	2	3	1	3	1	2	1	1	0	0	1	0	3	1	1	2	1	1	0	0	1	0	0	1	2	1	0	0	0	1	1	0	0	0	2	0	2	0	0
"N. g. B" ovatus	2	2	1	2	2	2	3	1	3	2	1	1	3	3	1	1	2	1	1	0	0	0	0	2	3	1	2	1	0	1	1	1	0	1	1	1	3	0	0
P. araw	2	1	2	1	?	2	5	0	1	0	0	1	3	1	2	2	3	1	1	1	0	0	1	3	2	0	1	2	0	1	2	?	0	0	2	1	3	0	0
"N. g. A" speculator pun	2	1	1	3	1	2	1	0	0	0	1	0	3	1	1	1	1	1	1	1	0	0	1	2	4	1	0	1	1	1	0	0	0	2	0	2	0	0	0
"N. g. A" kermiti	1	3	3	3	1	2	1	0	0	0	2	0	3	1	2	2	1	0	0	1	1	1	0	1	2	5	0	1	?	1	0	0	0	0	2	0	1	0	0
"N. g. A" salamandar	2	3	0	3	1	2	1	0	0	0	1	0	3	1	1	2	1	1	1	1	1	1	0	1	2	3	0	0	0	1	0	0	0	0	2	0	1	0	0
Boeckops stelcki	4	0	1	2	1	2	2	0	3	0	1	1	2	1	1	0	1	1	2	0	1	0	0	2	2	3	1	0	1	1	1	0	0	0	1	0	3	0	0
"N. g. B" lebesus	2	3	1	2	2	2	2	1	3	2	1	1	3	3	1	0	2	1	1	0	1	0	0	2	3	2	1	1	0	1	1	1	0	1	1	1	3	0	0
"N. g. B" forteyi	2	1	1	2	2	2	3	1	2	2	1	2	3	3	1	1	4	1	2	0	0	0	0	2	2	0	2	0	0	1	2	1	0	1	1	1	3	0	0
R. pembertoni	2	1	3	3	1	2	0	1	0	0	2	0	1	0	0	2	0	2	0	0	0	1	0	0	2	3	0	2	1	1	1	1	0	0	0	0	1	0	0
R. cephalotes hamlagdadi	3	2	1	3	2	2	0	2	3	2	2	1	2	3	0	0	1	2	1	0	0	1	0	0	5	5	0	2	1	2	1	1	0	0	0	0	1	0	0
Reedops bronni	2	2	1	3	1	2	0	2	3	2	2	1	2	0	0	2	0	0	0	0	0	0	0	0	4	0	0	0	2	1	1	0	0	0	0	1	0	0	
Pe. (P.) lentigifer	1	2	1	2	?	2	3	1	3	0	0	2	2	?	1	1	5	1	0	1	?	0	1	3	2	4	2	?	?	1	1	1	0	1	2	1	3	0	0
Pe. (H.) vagabundus	0	4	1	2	2	2	4	1	3	0	0	2	2	1	1	1	5	1	0	1	1	0	1	3	2	3	1	3	1	1	1	1	1	1	2	1	3	0	0
D. megalomanicus	1	2	2	3	?	2	6	1	4	0	1	2	2	3	1	1	5	1	1	1	1	0	1	3	2	2	1	3	1	1	1	1	1	1	2	1	3	0	0
D. armatus	1	3	2	3	?	2	6	1	4	0	0	2	2	3	1	1	5	1	1	1	1	0	1	3	2	3	1	3	1	1	1	1	1	1	2	1	3	0	0
E. rana rana	1	3	1	3	?	2	4	1	4	0	2	1	3	2	1	2	3	1	1	0	0	0	1	3	1	2	1	1	?	1	1	1	0	1	?	?	3	0	0
Chotecops auspex	2	1	1	3	?	1	2	2	3	2	2	1	3	0	1	2	1	0	0	0	1	1	0	0	0	3	0	1	0	1	1	0	0	0	1	0	1	0	0
Boeckops boecki	2	0	1	2	?	2	2	1	2	0	0	1	2	?	1	0	1	0	2	0	0	0	0	1	4	4	0	2	?	2	1	0	0	0	1	0	2	0	0
Paciphacops logani	1	2	1	2	3	1	3	1	3	1	1	1	1	?	0	0	2	1	2	1	1	0	1	2	1	2	1	1	?	1	1	0	0	1	1	0	0	1	1
Viaphacops cristatus	1	3	2	1	0	2	3	1	3	1	2	1	0	?	0	1	3	1	2	1	1	0	1	1	0	2	1	0	?	1	2	0	0	0	1	0	3	1	1
Geesops schlothelmi	0	3	2	1	?	2	3	1	4	1	0	1	2	?	1	2	3	1	1	0	1	0	1	2	2	2	1	3	1	1	1	1	1	1	?	1	3	0	0
Phacops latifrons	1	2	2	1	?	2	4	0	3	0	0	2	3	1	2	2	3	1	?	?	0	0	1	3	0	0	1	?	0	0	1	0	0	1	2	0	3	0	0

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APPENDIX 3: Collections data

ID Num	Type Stat	Scientific Name	Species Name	Formation	Collected by	Date	Country	Province/S	District/Area
6843	Plesiotype	Reedops bronni	(Barrande, 1846)	Ihandar Fm.	R. McKellar	2003	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene)
6844	Plesiotype	Reedops bronni	(Barrande, 1846)	Ihandar Fm.	Berber miner	2003	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene)
6845	Plesiotype	Reedops bronni	(Barrande, 1846)	Ihandar Fm.	K. Brett	2000	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene)
6846	Plesiotype	Reedops bronni	(Barrande, 1846)	Ihandar Fm.	K. Brett	2000	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene)
6847	Topotype	Reedops cephalotes hamlagdadian	Alberti, 1983	Kess-Kess Fm.	B. Chatterton and S.Gibb	2005	Morocco	(southeast)	Tafilalt Basin (Hamar Laghdad Bioherms)
6848	Topotype	Reedops cephalotes hamlagdadian	Alberti, 1983	Kess-Kess Fm.	B. Chatterton and S.Gibb	2005	Morocco	(southeast)	Tafilalt Basin (Hamar Laghdad Bioherms)
6849	Topotype	Reedops cephalotes hamlagdadian	Alberti, 1983	Kess-Kess Fm.	B. Chatterton and S.Gibb	2005	Morocco	(southeast)	Tafilalt Basin (Hamar Laghdad Bioherms)
6850	Topotype	Reedops cephalotes hamlagdadian	Alberti, 1983	Kess-Kess Fm.	B. Chatterton and S.Gibb	2005	Morocco	(southeast)	Tafilalt Basin (Hamar Laghdad Bioherms)
6851	Topotype	Reedops cephalotes hamlagdadian	Alberti, 1983	Kess-Kess Fm.	B. Chatterton and S.Gibb	2005	Morocco	(southeast)	Tafilalt Basin (Hamar Laghdad Bioherms)
6852	Topotype	Reedops cephalotes hamlagdadian	Alberti, 1983	Kess-Kess Fm.	B. Chatterton and S.Gibb	2005	Morocco	(southeast)	Tafilalt Basin (Hamar Laghdad Bioherms)
6853	Topotype	Reedops cephalotes hamlagdadian	Alberti, 1983	Kess-Kess Fm.	B. Chatterton and S.Gibb	2005	Morocco	(southeast)	Tafilalt Basin (Hamar Laghdad Bioherms)
6854	Topotype	Reedops cephalotes hamlagdadian	Alberti, 1983	Kess-Kess Fm.	B. Chatterton and S.Gibb	2005	Morocco	(southeast)	Tafilalt Basin (Hamar Laghdad Bioherms)
6855	Topotype	Reedops cephalotes hamlagdadian	Alberti, 1983	Kess-Kess Fm.	B. Chatterton and S.Gibb	2005	Morocco	(southeast)	Tafilalt Basin (Hamar Laghdad Bioherms)
6856	Topotype	Reedops cephalotes hamlagdadian	Alberti, 1983	Kess-Kess Fm.	B. Chatterton and S.Gibb	2005	Morocco	(southeast)	Tafilalt Basin (Hamar Laghdad Bioherms)
6857	Topotype	Reedops cephalotes hamlagdadian	Alberti, 1983	Kess-Kess Fm.	B. Chatterton and S.Gibb	2005	Morocco	(southeast)	Tafilalt Basin (Hamar Laghdad Bioherms)
6858	Topotype	Reedops cephalotes hamlagdadian	Alberti, 1983	Kess-Kess Fm.	B. Chatterton and S.Gibb	2005	Morocco	(southeast)	Tafilalt Basin (Hamar Laghdad Bioherms)
6859	Topotype	Reedops cephalotes hamlagdadian	Alberti, 1983	Kess-Kess Fm.	B. Chatterton and S.Gibb	2005	Morocco	(southeast)	Tafilalt Basin (Hamar Laghdad Bioherms)
6860	Plesiotype	Reedops cephalotes hamlagdadian	Alberti, 1983	Assa Fm.	B. Chatterton	2000	Morocco	(southern)	Tindouf Basin (El'Mdouar section)
6861	Plesiotype	Reedops cephalotes hamlagdadian	Alberti, 1983	Assa Fm.	Berber miner	2005	Morocco	(southern)	Tindouf Basin (El'Mdouar section)
6862	Holotype	Reedops pembertoni n.sp.	McKellar and Chatte	Ihandar Fm.	R. McKellar	2003	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene and surroundings)
6863	Paratype	Reedops pembertoni n.sp.	McKellar and Chatte	Ihandar Fm.	K. Brett	2000	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene and surroundings)
6864	Paratype	Reedops pembertoni n.sp.	McKellar and Chatte	Ihandar Fm.	K. Brett	2000	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene and surroundings)
6865	Paratype	Reedops pembertoni n.sp.	McKellar and Chatte	Ihandar Fm.	B. Chatterton and S.Gibb	2002	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene and surroundings)
6866	Paratype	Reedops pembertoni n.sp.	McKellar and Chatte	Ihandar Fm.	Berber miner	2003	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene and surroundings)
6867	Paratype	Reedops pembertoni n.sp.	McKellar and Chatte	Ihandar Fm.	Berber miner	2003	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene and surroundings)
6868	Paratype	Reedops pembertoni n.sp.	McKellar and Chatte	Ihandar Fm.	Berber miner	2003	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene and surroundings)
6869	Paratype	Reedops pembertoni n.sp.	McKellar and Chatte	Ihandar Fm.	Berber miner	2003	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene and surroundings)
6870	Paratype	Reedops pembertoni n.sp.	McKellar and Chatte	Ihandar Fm.	Berber miner	2003	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene and surroundings)
6871	Paratype	Reedops pembertoni n.sp.	McKellar and Chatte	Ihandar Fm.	Berber miner	2003	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene and surroundings)
6872	Paratype	Reedops pembertoni n.sp.	McKellar and Chatte	Ihandar Fm.	Berber miner	2003	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene and surroundings)
6873	Paratype	Reedops pembertoni n.sp.	McKellar and Chatte	Ihandar Fm.	Berber miner	2003	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene and surroundings)
6874	Paratype	Reedops pembertoni n.sp.	McKellar and Chatte	Ihandar Fm.	Berber miner	2003	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene and surroundings)
6875	Paratype	Reedops pembertoni n.sp.	McKellar and Chatte	Ihandar Fm.	Berber miner	2003	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene and surroundings)
6876	Holotype	Phacops speculator punctatus n. ss	McKellar and Chatte	El Otfal Fm.	2004 Morocco field crew	2004	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene)
6877	Paratype	Phacops speculator punctatus n. ss	McKellar and Chatte	El Otfal Fm.	2004 Morocco field crew	2004	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene)
6878	Paratype	Phacops speculator punctatus n. ss	McKellar and Chatte	El Otfal Fm.	2004 Morocco field crew	2004	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene)
6879	Paratype	Phacops speculator punctatus n. ss	McKellar and Chatte	El Otfal Fm.	2004 Morocco field crew	2004	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene)
6880	Paratype	Phacops speculator punctatus n. ss	McKellar and Chatte	El Otfal Fm.	2004 Morocco field crew	2004	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene)
6881	Paratype	Phacops speculator punctatus n. ss	McKellar and Chatte	El Otfal Fm.	2004 Morocco field crew	2004	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene)
6882	Paratype	Phacops speculator punctatus n. ss	McKellar and Chatte	El Otfal Fm.	2004 Morocco field crew	2004	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene)
6883	Paratype	Phacops speculator punctatus n. ss	McKellar and Chatte	El Otfal Fm.	2004 Morocco field crew	2004	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene)

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APPENDIX 3: Collections data

Lithology	Geologic Age	Measurement	Notes
iron-rich marl	Pragian	3.1cm long	outstretched, missing pygidium
iron-rich marl	Pragian	3.6cm long	outstretched, pygidium chipped
iron-rich marl	Pragian	1.1cm long	just cephalon
iron-rich marl	Pragian	2.3cm diameter (sag.)	enrolled, partially prepared
bioclastic limestone with sparry calcite cement	Pragian	10cm block (longest dimension)	2 cephala and 1 pygidium
bioclastic limestone with sparry calcite cement	Pragian	3.02cm wide (tr.)	complete cephalon
bioclastic limestone with sparry calcite cement	Pragian	2.09cm long (sag.)	half-prepared cephalon
bioclastic limestone with sparry calcite cement	Pragian	2.00cm wide (tr.)	small fragmentary cephalon
bioclastic limestone with sparry calcite cement	Pragian	2.29cm wide (tr.)	complete cephalon, some chips
bioclastic limestone with sparry calcite cement	Pragian	3.2cm wide (tr., eye to eye)	large cephalon, glabella weathered
bioclastic limestone with sparry calcite cement	Pragian	2.01cm wide (tr.)	isolated pygidium
bioclastic limestone with sparry calcite cement	Pragian	3.3cm (longest dimension)	half of cephalon, diagonally broken
bioclastic limestone with sparry calcite cement	Pragian	2.3cm wide (tr., eye to eye)	half-prepared cephalon, with doublure details
bioclastic limestone with sparry calcite cement	Pragian	3.10cm (longest dimension)	half of cephalon, diagonally broken
bioclastic limestone with sparry calcite cement	Pragian	4.9cm (longest dimension)	partially exposed cephalon
bioclastic limestone with sparry calcite cement	Pragian	2.9cm wide (tr., midline to genal a	weathered, half of cephalon, very large individual
bioclastic limestone with sparry calcite cement	Pragian	11.3cm block (longest dimension)	pygidium (and associated hypostome?)
iron-rich marl	Pragian	2.94cm wide (tr.)	enrolled, complete specimen, partially prepared
iron-rich marl	Pragian	6.59cm long (sag.)	outstretched, complete, Moroccan and Lindoe pre
iron-rich marl	Pragian	1.90cm wide (tr.)	enrolled, missing pygidium
iron-rich marl	Pragian	4.01cm long (sag.)	outstretched, complete, slightly burned by Airbrasi
iron-rich marl	Pragian	1.91cm wide (tr.)	partially enrolled, complete, partially prepared, in b
iron-rich marl	Pragian	1.81cm wide (tr., eye to eye)	partially enrolled, almost complete, partially prepar
iron-rich marl	Pragian	3.13cm long (sag., bent)	bowed concave ventrally, complete, Moroccan pre
iron-rich marl	Pragian	3.35cm long (sag.)	outstretched, missing pygidium
iron-rich marl	Pragian	2.65cm long (sag., bent)	partially enrolled, complete, Moroccan prepared, g
iron-rich marl	Pragian	2.52cm long (sag., bent)	partially enrolled, complete, Moroccan prepared, s
iron-rich marl	Pragian	3.03cm long (sag., bent)	pygidium tucked ventrally, complete, calcite rind
iron-rich marl	Pragian	2.49cm long (sag., bent)	partially enrolled, complete, Moroccan prepared, p
iron-rich marl	Pragian	2.64cm long (sag., bent)	partially enrolled, complete, Moroccan prepared, m
iron-rich marl	Pragian	2.76cm long (sag., bent)	pygidium tucked ventrally, complete, Moroccan pre
iron-rich marl	Pragian	2.61cm long (sag., bent)	partially enrolled, complete, Moroccan prepared,oc
iron-rich marl	Pragian	2.61cm long (sag., bent)	partially enrolled, complete, Moroccan prepared, a
medium gray, dense, muddy limestone	Eifelian	3.30cm long (sag., bent)	bowed concave ventrally, complete except for mis
medium gray, dense, muddy limestone	Eifelian	2.44cm wide (tr.)	bowed concave dorsally, complete except for tip o
medium gray, dense, muddy limestone	Eifelian	2.06cm wide (tr.)	cephalon only prepared, thorax fragmented and dr
medium gray, dense, muddy limestone	Eifelian	2.04cm wide (tr.)	cephalon only prepared, thorax partially enrolled,
medium gray, dense, muddy limestone	Eifelian	2.77cm long (sag., bent)	pygidium tucked ventrally, complete except for son
medium gray, dense, muddy limestone	Eifelian	1.95cm wide (tr.)	enrolled, complete specimen, pygidium displaced i
medium gray, dense, muddy limestone	Eifelian	1.97cm wide (tr.)	isolated cephalon
medium gray, dense, muddy limestone	Eifelian	2.32cm long (sag., bent)	partially enrolled, complete, thorax dislocated, som

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APPENDIX 3: Collections data

6884	Holotype	Phacops kermiti n. sp.	McKellar and Chatte	El Otfal Fm.	2004 Morocco field crew	2004	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene)
6885	Paratype	Phacops kermiti n. sp.	McKellar and Chatte	El Otfal Fm.	2004 Morocco field crew	2004	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene)
6886	Paratype	Phacops kermiti n. sp.	McKellar and Chatte	El Otfal Fm.	2004 Morocco field crew	2004	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene)
6887	Paratype	Phacops kermiti n. sp.	McKellar and Chatte	El Otfal Fm.	2004 Morocco field crew	2004	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene)
6888	Paratype	Phacops kermiti n. sp.	McKellar and Chatte	El Otfal Fm.	B. Chatterton and S.Gibb	2002	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene)
6889	Paratype	Phacops kermiti n. sp.	McKellar and Chatte	El Otfal Fm.	R. McKellar	2004	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene)
6890	Paratype	Phacops kermiti n. sp.	McKellar and Chatte	El Otfal Fm.	K. Brett	2000	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene)
6891	Paratype	Phacops kermiti n. sp.	McKellar and Chatte	El Otfal Fm.	B. Chatterton and S.Gibb	2002	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene)
6892	Holotype	Phacops salamandar n. sp.	McKellar and Chatte	El Otfal Fm.	2004 Morocco field crew	2004	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene)
6893	Paratype	Phacops salamandar n. sp.	McKellar and Chatte	El Otfal Fm.	K. Brett	2000	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene)
6894	Paratype	Phacops salamandar n. sp.	McKellar and Chatte	El Otfal Fm.	2003 Morocco field crew	2003	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene)
6895	Paratype	Phacops salamandar n. sp.	McKellar and Chatte	El Otfal Fm.	K. Brett	2000	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene)
6896	Paratype	Phacops salamandar n. sp.	McKellar and Chatte	El Otfal Fm.	K. Brett	2000	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene)
6897	Holotype	Boeckops stelcki n. sp.	McKellar and Chatte	Bou Tiskaouine	2003 Morocco field crew	2003	Morocco	(southeast)	Ma'der Basin (Teharajat d'Oufatene)
6898	Paratype	Boeckops stelcki n. sp.	McKellar and Chatte	Bou Tiskaouine	Berber miner	2003	Morocco	(southeast)	Ma'der Basin (Teharajat d'Oufatene)
6899	Paratype	Boeckops stelcki n. sp.	McKellar and Chatte	Bou Tiskaouine	2003 Morocco field crew	2003	Morocco	(southeast)	Ma'der Basin (Teharajat d'Oufatene)
6900	Paratype	Boeckops stelcki n. sp.	McKellar and Chatte	Bou Tiskaouine	Berber miner	2003	Morocco	(southeast)	Ma'der Basin (Teharajat d'Oufatene)
6901	Paratype	Boeckops stelcki n. sp.	McKellar and Chatte	Bou Tiskaouine	2003 Morocco field crew	2003	Morocco	(southeast)	Ma'der Basin (Teharajat d'Oufatene)
6902	Paratype	Boeckops stelcki n. sp.	McKellar and Chatte	Bou Tiskaouine	Berber miner	2005	Morocco	(southeast)	Ma'der Basin (Teharajat d'Oufatene)
6903	Paratype	Boeckops stelcki n. sp.	McKellar and Chatte	Bou Tiskaouine	Berber miner	2005	Morocco	(southeast)	Ma'der Basin (Teharajat d'Oufatene)
6904	Holotype	Phacops araw n. sp.	McKellar and Chatte	El Otfal Fm.	R. McKellar and S. Gibb	2004	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene, South Oufatene Pr
6905	Paratype	Phacops araw n. sp.	McKellar and Chatte	El Otfal Fm.	R. McKellar and S. Gibb	2004	Morocco	(southeast)	Ma'der Basin (Jbel Oufatene, South Oufatene Pr
6906	Paratype	Phacops araw n. sp.	McKellar and Chatte	El Otfal Fm.	Berber miner	2005	Morocco	(southeast)	Ma'der Basin (Jbel Mrakib, Greenops Couche)
6907	Paratype	Phacops araw n. sp.	McKellar and Chatte	El Otfal Fm.	Berber miner	2005	Morocco	(southeast)	Ma'der Basin (Jbel Mrakib, Greenops Couche)
6908	Holotype	Phacops ovatus n. sp.	McKellar and Chatte	Tazouläit Fm.	B. Chatterton and S.Gibb	2002	Morocco	(southeast)	Ma'der Basin (Teharajat d'Oufatene)
6909	Paratype	Phacops ovatus n. sp.	McKellar and Chatte	Tazouläit Fm.	Berber miner	2005	Morocco	(southeast)	Ma'der Basin (Teharajat d'Oufatene)
6910	Paratype	Phacops ovatus n. sp.	McKellar and Chatte	Tazouläit Fm.	B. Chatterton and S.Gibb	2002	Morocco	(southeast)	Ma'der Basin (Teharajat d'Oufatene)
6911	Paratype	Phacops ovatus n. sp.	McKellar and Chatte	Tazouläit Fm.	B. Chatterton and S.Gibb	2002	Morocco	(southeast)	Ma'der Basin (Teharajat d'Oufatene)
6912	Paratype	Phacops ovatus n. sp.	McKellar and Chatte	Tazouläit Fm.	Berber miner	2005	Morocco	(southeast)	Ma'der Basin (Teharajat d'Oufatene)
6913	Paratype	Phacops ovatus n. sp.	McKellar and Chatte	Tazouläit Fm.	2003 Morocco field crew	2003	Morocco	(southeast)	Ma'der Basin (Teharajat d'Oufatene)
6914	Paratype	Phacops ovatus n. sp.	McKellar and Chatte	Tazouläit Fm.	B. Chatterton and S.Gibb	2002	Morocco	(southeast)	Ma'der Basin (Teharajat d'Oufatene)
6915	Paratype	Phacops ovatus n. sp.	McKellar and Chatte	Tazouläit Fm.	Berber miner	2005	Morocco	(southeast)	Ma'der Basin (Teharajat d'Oufatene)
6916	Paratype	Phacops ovatus n. sp.	McKellar and Chatte	Tazouläit Fm.	Berber miner	2005	Morocco	(southeast)	Ma'der Basin (Teharajat d'Oufatene)
6917	Paratype	Phacops ovatus n. sp.	McKellar and Chatte	Tazouläit Fm.	Berber miner	2005	Morocco	(southeast)	Ma'der Basin (Teharajat d'Oufatene)
6918	Paratype	Phacops ovatus n. sp.	McKellar and Chatte	Tazouläit Fm.	B. Chatterton and S.Gibb	2002	Morocco	(southeast)	Ma'der Basin (Teharajat d'Oufatene)
6919	Paratype	Phacops ovatus n. sp.	McKellar and Chatte	Tazouläit Fm.	Berber miner	2005	Morocco	(southeast)	Ma'der Basin (Teharajat d'Oufatene)
6920	Holotype	Phacops forteyi n. sp.	McKellar and Chatte	Tazouläit Fm.	R. McKellar	2004	Morocco	(southeast)	Ma'der Basin (bou Dib section)
6921	Paratype	Phacops forteyi n. sp.	McKellar and Chatte	Tazouläit Fm.	Berber miner	2003	Morocco	(southeast)	Ma'der Basin (bou Dib section)
6922	Paratype	Phacops forteyi n. sp.	McKellar and Chatte	Tazouläit Fm.	Berber miner	2004	Morocco	(southeast)	Ma'der Basin (bou Dib section)
6923	Paratype	Phacops forteyi n. sp.	McKellar and Chatte	Tazouläit Fm.	Berber miner	2004	Morocco	(southeast)	Ma'der Basin (bou Dib section)
6924	Paratype	Phacops forteyi n. sp.	McKellar and Chatte	Tazouläit Fm.	Berber miner	2004	Morocco	(southeast)	Ma'der Basin (bou Dib section)
6925	Paratype	Phacops forteyi n. sp.	McKellar and Chatte	Tazouläit Fm.	2004 Morocco field crew	2004	Morocco	(southeast)	Ma'der Basin (bou Dib section)
6926	Paratype	Phacops forteyi n. sp.	McKellar and Chatte	Tazouläit Fm.	Berber miner	2004	Morocco	(southeast)	Ma'der Basin (bou Dib section)

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APPENDIX 3: Collections data

medium gray, dense, muddy limestone	Eifelian	1.79cm wide (tr.)	enrolled, complete specimen, pygidium displaced
medium gray, dense, muddy limestone	Eifelian	1.52cm wide (tr.)	enrolled, complete specimen, pygidium displaced
medium gray, dense, muddy limestone	Eifelian	1.50cm wide (tr.)	enrolled, complete specimen, pygidium jutting out
medium gray, dense, muddy limestone	Eifelian	2.20cm long (sag., bent)	outstretched, complete, cephalon downturned, mis
medium gray, dense, muddy limestone	Eifelian	1.39cm wide (tr.)	partially enrolled, complete, thorax and pygidium d
medium gray, dense, muddy limestone	Eifelian	1.71cm wide (tr.)	partially enrolled, complete, dissolution hole in left
medium gray, dense, muddy limestone	Eifelian	2.00cm wide (tr.)	partially enrolled, complete, Airbrasive burned, tho
medium gray, dense, muddy limestone	Eifelian	2.71cm long (sag., bent)	partially enrolled, complete, highly weathered and
medium gray, dense, muddy limestone	Eifelian	1.33cm wide (tr.)	enrolled, complete, immaculate, slight gap betwee
medium gray, dense, muddy limestone	Eifelian	1.72cm wide (tr.)	partially enrolled, missing pygidium, Airbrasive bur
medium gray, dense, muddy limestone	Eifelian	1.51cm wide (tr.)	partially enrolled, missing posterior 2 thoracic seg
medium gray, dense, muddy limestone	Eifelian	0.95cm wide (tr.)	partially enrolled, small holaspid, Airbrasive burne
medium gray, dense, muddy limestone	Eifelian	1.75cm wide (tr., compressed)	partially enrolled, compressed specimen, pygidiu
gray-buff, dense limestone	Emsian	2.08cm wide (tr.)	partially enrolled, complete, pygidium almost reac
gray-buff, dense limestone	Emsian	2.18cm long (sag., bent)	mostly outstretched, complete, small patch on left
gray-buff, dense limestone	Emsian	1.14cm wide (tr.)	enrolled, complete, immaculate except for chips o
gray-buff, dense limestone	Emsian	1.07cm wide (tr.)	enrolled, complete, highly weathered with large po
gray-buff, dense limestone	Emsian	1.96cm wide (tr.)	partially enrolled, complete, not fully prepared due
gray-buff, dense limestone	Emsian	4.73cm long (sag., bent)	outstretched with concave dorsal, complete, Moro
gray-buff, dense limestone	Emsian	3.85cm long (sag., bent)	outstretched with pygidium tucked underneath, co
medium gray, dense, muddy limestone	Eifelian	3.16cm long (sag., bent)	partially enrolled, almost complete, missing large
medium gray, dense, muddy limestone	Eifelian	1.24cm long (sag., just cephalon)	partially enrolled, complete?, partially prepared for
medium gray, dense, muddy limestone, some ir	Eifelian	5.01cm long (sag.)	outstretched, complete, Moroccan prepared using
medium gray, dense, muddy limestone, some ir	Eifelian	1.85cm wide (tr.)	partially enrolled, complete?, partially prepared for
gray-buff, dense limestone	L. Emsian to E. Eif	2.67cm wide (tr.)	outstretched with pygidium tucked underneath, co
gray-buff, dense limestone	L. Emsian to E. Eif	7.27cm long (sag.)	outstretched, complete, slight dorsal concavity, M
gray-buff, dense limestone	L. Emsian to E. Eif	1.61cm wide (tr.)	enrolled, missing pygidium, small holaspid
gray-buff, dense limestone	L. Emsian to E. Eif	2.50cm wide (tr.)	partially enrolled, complete, missing sections of th
gray-buff, dense limestone	L. Emsian to E. Eif	5.86cm long (sag.)	outstretched, complete, slight dorsal concavity, M
gray-buff, dense limestone	L. Emsian to E. Eif	2.68cm wide (tr.)	enrolled (mostly), complete, doublure not prepare
gray-buff, dense limestone	L. Emsian to E. Eif	2.04cm wide (tr.)	isolated cephalon
gray-buff, dense limestone	L. Emsian to E. Eif	2.80cm wide (tr.)	partially enrolled, pygidium tucked under, complet
gray-buff, dense limestone	L. Emsian to E. Eif	2.59cm wide (tr.)	partially enrolled, pygidium tucked under, complet
gray-buff, dense limestone	L. Emsian to E. Eif	2.89cm wide (tr.)	outstretched with concave dorsal, complete, Moro
gray-buff, dense limestone	L. Emsian to E. Eif	2.65cm wide (tr.)	outstretched with pygidium slightly dislocated and
gray-buff, dense limestone	L. Emsian to E. Eif	2.69cm wide (tr.)	outstretched with concave dorsal, complete excep
med.-dark gray limestone, with high iron content	Late Emsian	2.40cm wide (tr.)	enrolled, complete, missing small patch on anterio
med.-dark gray limestone, with high iron content	Late Emsian	2.49cm wide (tr.)	enrolled, complete, pygidium positioned back on d
med.-dark gray limestone, with high iron content	Late Emsian	2.44cm wide (tr.)	enrolled, prepared to show hypostome (just cepha
med.-dark gray limestone, with high iron content	Late Emsian	2.34cm wide (tr.)	enrolled, complete specimen, weathered on left si
med.-dark gray limestone, with high iron content	Late Emsian	2.28cm wide (tr.)	enrolled, missing pygidium, cephalon almost perfe
med.-dark gray limestone, with high iron content	Late Emsian	2.40cm wide (tr.)	enrolled, complete specimen, pygidium displaced
med.-dark gray limestone, with high iron content	Late Emsian	2.40cm wide (tr.)	enrolled, complete, pygidium positioned back on d

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APPENDIX 3: Collections data

6927	Paratype	Phacops forteyi n. sp.	McKellar and Chatte	Tazouläit Fm.	Berber miner	2003	Morocco	(southeast)	Ma'der Basin (bou Dib section)
6928	Paratype	Phacops forteyi n. sp.	McKellar and Chatte	Tazouläit Fm.	Berber miner	2004	Morocco	(southeast)	Ma'der Basin (bou Dib section)
6929	Paratype	Phacops forteyi n. sp.	McKellar and Chatte	Tazouläit Fm.	Berber miner	2004	Morocco	(southeast)	Ma'der Basin (bou Dib section)
6930	Paratype	Phacops forteyi n. sp.	McKellar and Chatte	Tazouläit Fm.	Berber miner	2003	Morocco	(southeast)	Ma'der Basin (bou Dib section)
6931	Paratype	Phacops forteyi n. sp.	McKellar and Chatte	Tazouläit Fm.	Berber miner	2004	Morocco	(southeast)	Ma'der Basin (bou Dib section)
6932	Paratype	Phacops forteyi n. sp.	McKellar and Chatte	Tazouläit Fm.	Berber miner	2004	Morocco	(southeast)	Ma'der Basin (Jbel Issoumour section)
6933	Paratype	Phacops forteyi n. sp.	McKellar and Chatte	Tazouläit Fm.	Berber miner	2004	Morocco	(southeast)	Ma'der Basin (Jbel Issoumour section)
6934	Paratype	Phacops forteyi n. sp.	McKellar and Chatte	Tazouläit Fm.	Berber miner	2004	Morocco	(southeast)	Ma'der Basin (Jbel Issoumour section)
6935	Plesiotype	Pedinopariops (Hypsipariops) vagal	Struve, 1990	Taboumakloûf	Berber miner	2004	Morocco	(southeast)	Ma'der Basin (Aferdout de Jbel Mrakib)
6936	Plesiotype	Pedinopariops (Hypsipariops) vagal	Struve, 1990	Taboumakloûf	Berber miner	2005	Morocco	(southeast)	Ma'der Basin (Aferdout de Jbel Mrakib)
6937	Plesiotype	Pedinopariops (Hypsipariops) vagal	Struve, 1990	Taboumakloûf	Berber miner	2000	Morocco	(southeast)	Ma'der Basin (?Aferdout de Jbel Mrakib)
6938	Plesiotype	Pedinopariops (Hypsipariops) vagal	Struve, 1990	Taboumakloûf	Berber miner	2000	Morocco	(southeast)	Ma'der Basin (?Aferdout de Jbel Mrakib)
6939	Plesiotype	Pedinopariops (Hypsipariops) vagal	Struve, 1990	Taboumakloûf	Berber miner	2000	Morocco	(southeast)	Ma'der Basin (Aferdout de Jbel Mrakib)
6940	Paratype	Phacops forteyi n. sp.	McKellar and Chatte	Amerboh Group	Kevin Brett/B.D.E. Chatter	1995	Morocco	(southeast)	Tafilalt Basin (Merzouga surface collection)
6941	Paratype	Phacops forteyi n. sp.	McKellar and Chatte	Amerboh Group	Kevin Brett/B.D.E. Chatter	1995	Morocco	(southeast)	Tafilalt Basin (Merzouga surface collection)
6942	Paratype	Phacops forteyi n. sp.	McKellar and Chatte	Amerboh Group	Kevin Brett/B.D.E. Chatter	1995	Morocco	(southeast)	Tafilalt Basin (Merzouga surface collection)
6943	Paratype	Phacops forteyi n. sp.	McKellar and Chatte	Amerboh Group	Kevin Brett/B.D.E. Chatter	1995	Morocco	(southeast)	Tafilalt Basin (Merzouga surface collection)
6944	Paratype	Phacops forteyi n. sp.	McKellar and Chatte	Amerboh Group	Kevin Brett/B.D.E. Chatter	1995	Morocco	(southeast)	Tafilalt Basin (Merzouga surface collection)
6945	Paratype	Phacops forteyi n. sp.	McKellar and Chatte	Amerboh Group	Kevin Brett/B.D.E. Chatter	1995	Morocco	(southeast)	Tafilalt Basin (Merzouga surface collection)
6946	Paratype	Phacops forteyi n. sp.	McKellar and Chatte	Amerboh Group	Kevin Brett/B.D.E. Chatter	1995	Morocco	(southeast)	Tafilalt Basin (Merzouga surface collection)
6947	Paratype	Phacops forteyi n. sp.	McKellar and Chatte	Amerboh Group	Kevin Brett/B.D.E. Chatter	1995	Morocco	(southeast)	Tafilalt Basin (Merzouga surface collection)
6948	Paratype	Phacops forteyi n. sp.	McKellar and Chatte	Amerboh Group	Kevin Brett/B.D.E. Chatter	1995	Morocco	(southeast)	Tafilalt Basin (Merzouga surface collection)
6949									
6950									
6951									
6952									
6953									
6954									

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APPENDIX 3: Collections data

med.-dark gray limestone, with high iron content	Late Emsian	2.65cm wide (tr.)	enrolled, complete, pygidium positioned back on d
med.-dark gray limestone, with high iron content	Late Emsian	3.35cm wide (tr.)	enrolled, prepared to show hypostome (just cepha
med.-dark gray limestone, with high iron content	Late Emsian	2.28cm wide (tr.)	enrolled, complete, pygidium positioned just outsid
med.-dark gray limestone, with high iron content	Late Emsian	1.74cm wide (tr.)	partially enrolled, complete, small holaspid with lig
med.-dark gray limestone, with high iron content	Late Emsian	2.97cm wide (tr.)	enrolled with slight gap between cephalon and pyg
med.-dark gray limestone, with high iron content	Late Emsian	2.55cm wide (tr.)	enrolled, missing pygidium, highly oxidized cuticle
med.-dark gray limestone, with high iron content	Late Emsian	2.51cm wide (tr.)	enrolled, complete, pygidium positioned just outsid
med.-dark gray limestone, with high iron content	Late Emsian	2.75cm wide (tr.)	partially enrolled, complete, pygidium tucked unde
med.-dark gray limestone, clay-rich	Late Eifelian	4.96cm wide (tr., cephalon)	partially disarticulated, complete individual, Moroc
med.-dark gray limestone, clay-rich	Late Eifelian	7.09cm long (sag.)	outstretched, complete, slightly compressed, with
med.-dark gray limestone, clay-rich	Late Eifelian	6.08cm wide (tr., cephalon)	composite specimen (outstretched, but composed
med.-dark gray limestone, clay-rich	Late Eifelian	7.65cm wide (tr., cephalon)	composite specimen (outstretched, composed of 4
med.-dark gray limestone, clay-rich	Late Eifelian	7.54cm long (sag.)	outstretched, complete, large diagonal crack throu
med. gray shale	Late Emsian	1.45cm wide (tr.)	enrolled, missing pygidium, doublure prepared
med. gray shale	Late Emsian	1.67cm wide (tr.)	enrolled, complete, compressed with pygidium shi
med. gray shale	Late Emsian	1.49cm wide (tr.)	enrolled, complete, pygidium positioned slightly ba
med. gray shale	Late Emsian	1.30cm wide (tr.)	enrolled, pygidium forced into body cavity, whole s
med. gray shale	Late Emsian	1.42cm wide (tr.)	enrolled, complete, pygidium tucked in behind dou
med. gray shale	Late Emsian	1.53cm wide (tr.)	enrolled, complete, pygidium pushed back on dou
med. gray shale	Late Emsian	1.55cm wide (tr.)	enrolled, complete, pygidium just behind vincular f
med. gray shale	Late Emsian	1.34cm wide (tr.)	enrolled, complete, pygidium pushed back on dou
med. gray shale	Late Emsian	1.63cm wide (tr.)	enrolled, complete, pygidium pushed back on dou