THE LOWER CAMBRIAN TRILOBITE *BIGOTINA* AND ALLIED GENERA

by G. L. PILLOLA

ABSTRACT. The Lower Cambrian genus *Bigotina* is reinvestigated on the basis of new material (including larval stages and pygidia) from the type locality of *B. bivallata*, from the upper third of the Saint-Jean-de-la-Rivière Formation (Carteret, Normandy, France). A neotype for *B. bivallata* is proposed. The new material clarifies the generic concept of this very early trilobite which exemplifies the primitive morphology of non-olenellid trilobites. The taxonomic position of *Bigotina* is discussed in comparison with early redlichiids (Pararedlichiinae, Wutingaspinae and Abadiellidae) and some ellipsocephalids; at present Bigotinidae are placed in the superfamily Redlichiacea, and the relationship to ellipsocephalids is discussed. The occurrence of *B. bivallata* and related taxa in Western Europe, Morocco and Siberia is of significance for correlation and palaeogeography during Early to Middle Atdabanian time.

IN 1925, Bigot discovered an Early Cambrian trilobite and archaeocyathan fauna, associated with algae, in the Carteret region (Cotentin Peninsula, Normandy, France). These fossils came from limestone beds cropping out at low tide, in front of the beaches of Saint-Jean-de-la-Rivière and Saint-Georges-de-la-Rivière. Some of them were described and figured by Bigot in 1926. The sole species of trilobite discovered, he assigned to *Ptychoparia*. The archaeocyathans were placed in *Spirocyathus* and *Protopharetra*.

Cobbold (1935) described additional trilobite specimens from Carteret, which were provided by Bigot, and erected the new genus and species *Bigotina bivallata* for their reception. Since then, the algae, stromatolites, ichnofossils and sedimentology have been studied by Bigot (1929), Doré (1963, 1969), Derville (1933), Dangeard (1954), Dangeard and Doré (1957); archaeocyathan faunas have been described by Debrenne (1958, 1964).

However, the trilobite *Bigotina* has not been properly investigated and illustrated: for example, the drawing by Cobbold (1935) reproduced in the *Treatise* (Harrington 1959, p. 51, fig. 36c; Henningsmoen 1959, p. 210, fig. 151/1) is misleading in several respects. More recently, Suvorova (1960), erected two new species and Repina (1960, 1966, 1981, *in* Repina and Luchinina 1981) four others, all from Siberia. The genus was recorded by Sdzuy (1981) from Morocco, and Liñán *et al.* (1981) from the Córdoba area (southern Spain). A species assigned to *Bigotina* from Australia (Öpik 1975) is now placed in *Alanisia* (Jell, *in* Bengtson *et al.* 1990). This paper was prepared with a view to providing a description of the genus, which is an important one in the understanding of trilobite phylogenetics; it is the earliest opisthoparian trilobite in several sections and may prove to be pivotal in our understanding of early trilobite evolution. *Bigotina* exhibits much subtle morphological variation and is of importance in considering Lower Cambrian biogeography.

STRATIGRAPHY AND GEOLOGICAL SETTING

Stratigraphy

Following the recognition of Lower Cambrian deposits in the Carteret region by Bigot (1925; Text-fig. 1), the lithostratigraphy and sedimentology have been commented upon and described by Doré (1963, 1969).

The base of the succession comprises the Carteret Formation (620 m of sandstones and siltstones)
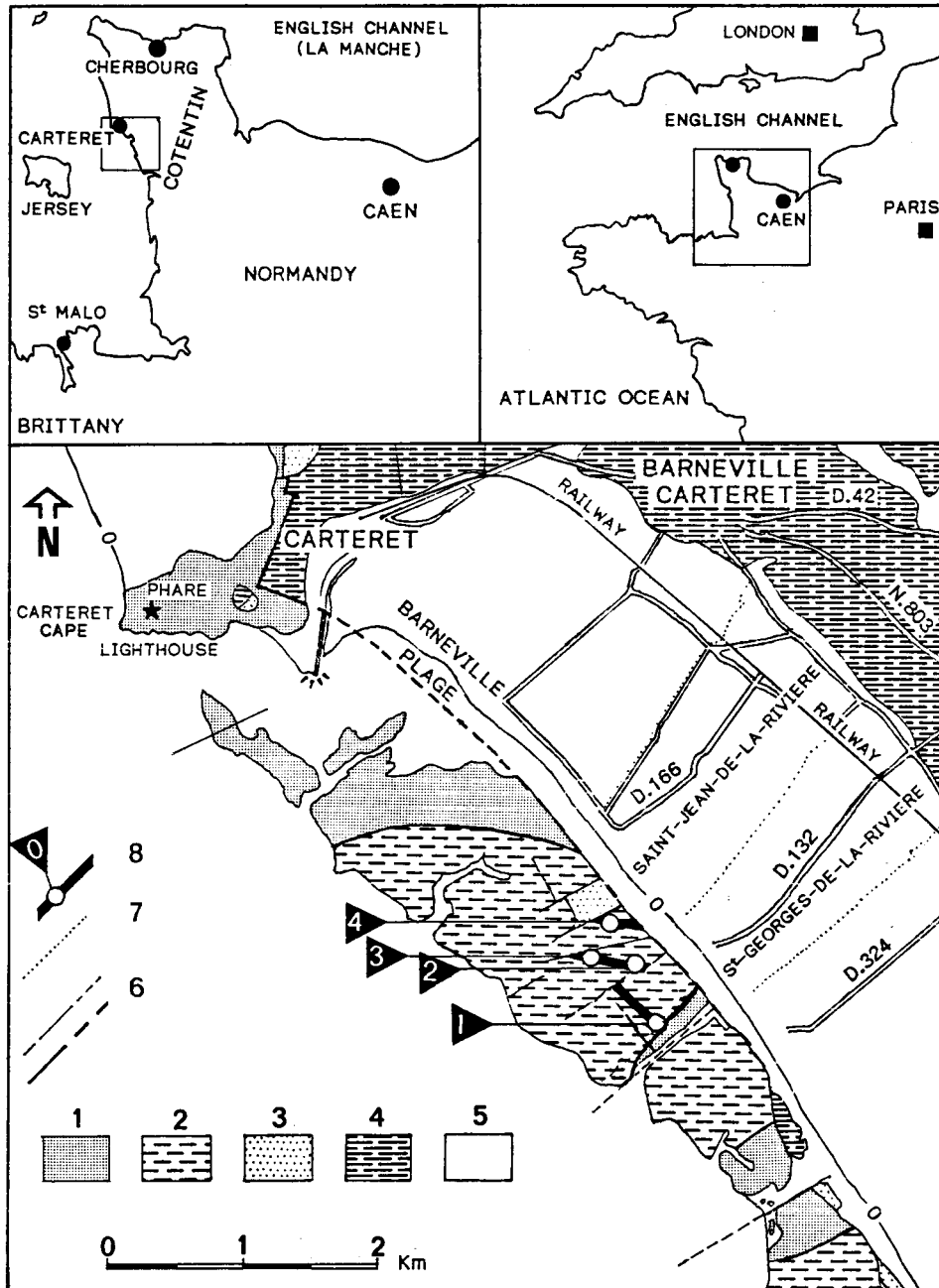
TEXT-FIG. 1. Geographical and schematic geological setting of the study area. 1, Lower Cambrian (Tommotian) Carteret Formation; 2, Lower Cambrian (Atdabanian) Saint-Jean-de-la-Rivière Formation; 3, Upper Ordovician; 4, Devonian; 5, Recent deposits; 6, Faults; 7, municipality territorial divisions; 8, study section (modified after Doré 1969 and Graindor et al. 1976).

overlain by calcareous and terrigenous sediments of the Saint-Jean-de-la-Rivière Formation (170–?200 m); this is overlain by red siltstones and sandstones (about 100 m).

The Carteret Formation is subdivided into: (a) sandstones and siltstones well exposed at the Cape of Carteret, yielding *Allonia*? and trace fossils; (b) silty sandstones with some calcareous nodules containing *Eotheca primitiva* nom. nud. (hyolithid), *Allonia tripodophora* Doré and Reid 1965, and *Chancelloria* sp. (coeloscleritophorans); (c) green to violet slates with some pink sandstones exposed in the Dennemont quarry; and, finally, (d) green silty shales of Barneville, well exposed at the beach of Carteret-Barneville (Doré 1963, 1969, 1984; Doré et al. 1986).

The Saint-Jean-de-la Rivière Formation is composed of dark blue-grey limestones, mostly oolitic and bioclastic, and several levels containing planar stromatolites, relatively small stromatolitic biconstructions with peri-reefal breccias, sometimes associated with rare archaeocyathans especially in the upper part of the formation. The beds are generally thin (10–100 mm), exceptionally reaching 1 m thick. Some of the limestones contain a proportion of detrital material (large quartz grains and black mica are visible to the naked eye). The coarse silt and shale intercalations are about two-thirds of the sequence; trace fossils and rare, poorly preserved trilobites are present in these siliciclastic beds.

Bigotina bivallata occurs from the basal oolitic limestone to the top of the Saint-Jean-de-la-Rivière Formation in the section studied here (Text-fig. 2); archaeocyathans (*Aldanocyathus carteretensis*, *Protopharetra bigoti*, *Sibiricyathus* sp., *Coscinocyathus* sp.) have been found only in the upper part of the formation; trace fossils (*Skolithos*, *Planolites*, *Taphrelminthopsis*, *Phycodes* and *Astropholichnus*), hyolithids and few algae or calcimicrobe taxa (*Epiphyton*, *Renalcis*, *Girvanella*, *Rosnaiella,* *Botomaella*) occur at several levels; rare *Aldanella* (gastropod) and *Indianites* (conchostraca) also occur. All the faunal and sedimentological indications are suggestive of extremely shallow-water deposition.

Geological setting

The study area lies seaward of the Saint-Jean and Saint-Georges-de-la-Rivière beaches, between Carteret–Barneville on the North and Portbail on the South. The rocky plateau, directed NW–SE, is mostly occupied by the Saint-Jean-de-la-Rivière Formation; the Cambrian sequence is tectonically in contact with small outcrops of rocks of Upper Ordovician and Devonian age, as a result of the NW–SE fault. The main structure between the Carteret Cape and Saint-Georges-de-la-Rivière consists of a gentle syncline, with some less important faults and small changes in dip of the strata (10°–30°). The axis of the syncline is directed NE–SW. A wide sandy channel separates the SE limb of the main syncline from an antiform structure. The section is located on the southern limb of the syncline, starting from the wide channel to the axis of the fold. Four main horizons containing trilobites have been found in the section.

1. The lowest one (1b), located about 4 m above the first prominent limestone bed, contains a rich trilobite accumulation layer and very rare hyolithids; trilobite exoskeleton is generally limonitized with some tectonic deformation. Two small cranidia have also been found in the first oolitic bed (1a, at 100 mm from the base of the Saint-Jean-de-la-Rivière Formation).

2. The second important fossiliferous level (2a) occurs at about 90 m from the base; it contains well-preserved specimens of *Bigotina bivallata*, including larval stages.

3. The third level is about 128 m from the base of the formation, but has not yielded abundant material.

4. The most fossiliferous trilobite horizon has been located at about 150 m from the base, midway between the two main archaeocyathan and algal bioconstructions, which are 140–145 m and 160–165 m from the base respectively. Trilobites are found in massive limestone, which is locally oolitic.

The new material is deposited at the Muséum National d'Histoire Naturelle, Paris (MNHN) and at the British Museum (Natural History), London (BMNH).
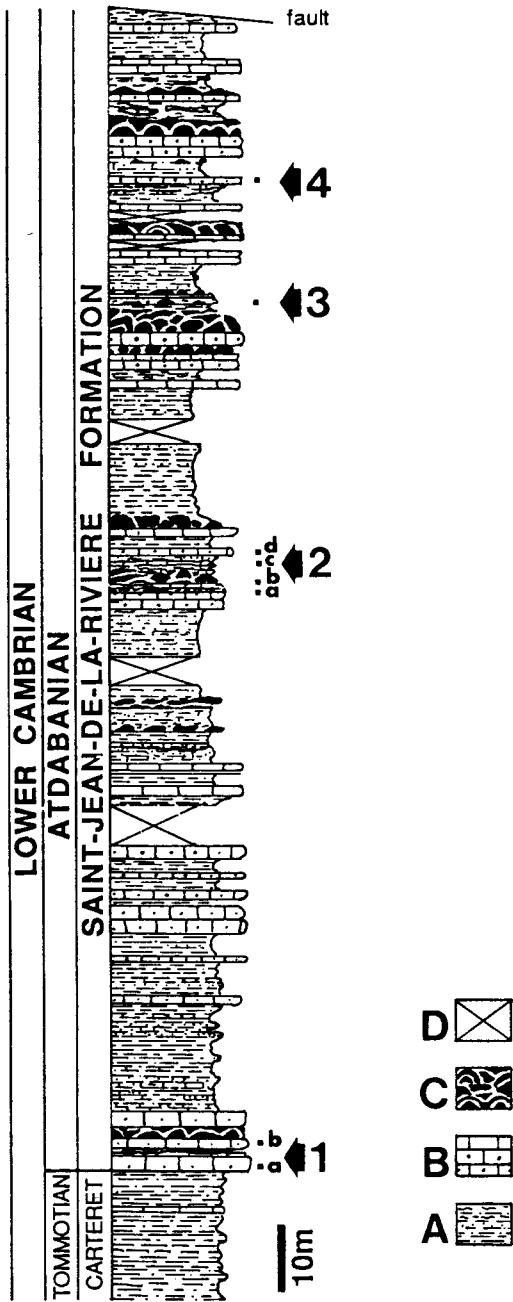
TEXT-FIG. 2. Lithological column and position of the most important trilobite beds. A, siltstones and shales, locally sandy siltstones with calcareous cement; B, limestones, mostly oolitic and/or bioclastic; C, stromatolitic dominated lithofacies and algal-microbial archaeocyathid build-ups; D, not exposed.

TERMINOLOGY

The nomenclature adopted here is mostly that of the Treatise (Moore 1959; Harrington et al. 1959) and Öpik (1958, 1961, 1967); however, some modifications must be emphasized, especially in the description of the cranidial features, because some terms are frequently used for Lower Cambrian trilobites and their definition is sometimes ambiguous.

1. Plectrum (Öpik 1967 (= mesial ridge)). The plectrum is frequent in Lower Cambrian redlichiids, some ellipsocephalids and olenellids. It consists of a more or less wide elevated structure varying to an extremely narrow ridge running between the frontal lobe of the glabella and the anterior border furrow of the cranidium or a rearward projection of the border in front of the glabella. In some cases, the plectrum is confluent with the anterior part of the ocular ridges (= eye ridges, eye lines).

2. Facial lines (Öpik 1958, 1961, p. 435). The facial lines are relatively thin ridges located in the distal portion of the anterior limb, joining the ocular ridge and the anterior border. These ridges are usually divergent anteriorly or, rarely, subparallel to the axis.

3. Parafrontal band (= segment X, of Hupé 1951). Relatively narrow, raised band encircling or flanking the anterior part of the glabella and confluent with the anterior edge of eye ridges.

4. Interocular swelling (Öpik 1967, p. 58; 'bosse fixigenale', Hupé 1953*b*). Usually represented as two more or less prominent humps, located at inner posterior part of interocular fixed cheeks. In some Lower Cambrian trilobites two posterior and one anterior humps may be observed on each interocular cheek. The distal posterior and anterior humps are sometimes coalescent and separated, from the rest of the fixed cheek, by shallow depressions reaching the posterior border furrow. A relationship between the interocular swelling and the traces of the primary pleural segmentation, on the adult fixed cheeks, seems to be possible because these features are more clearly seen during the larval development, and may be assumed a primitive character.

5. Eye ridges and palpebral lobes: ocular furrow, epipalpebral furrow, ocular striga. The ocular furrow (*sensu* Sdzuy 1978, p. 93), is a faint to well-impressed furrow extending from the anterior end of the palpebral lobe up to the posterior end; this furrow separates the palpebral lobe in two parts, sometimes of about equal size (cf. *Lemdadella*) or, more frequently, into a narrow distal part and a more developed internal portion. The internal portion of the palpebral lobe, when it is not interrupted, is in continuity with the posterior 'segment' of the ocular ridge; this latter is separated from the interocular cheek by the palpebral furrow.

The ocular furrow and the eye ridge furrow observed in *Bigotina*, *Lemdadella* and many other redlichiids, is homologous with the 'epipalpebral furrow' (Cowie and McNamara 1978, p. 21) of early olenellids (*Fallotaspis*, *Eofallotaspis*, *Profallotaspis*, *Choubertella*, *Olenellus*). The palpebral furrow of these trilobites extends into S3.

The 'ocular striga' (Öpik 1961, p. 436) was originally designated as the faint furrow that divides the ocular ·ridge into posterior and anterior ridges and extends into the palpebral lobe. In this restricted sense the term 'ocular striga' may be considered as synonym of 'epipalpebral furrow' of olenellids (cf. Öpik 1961, fig. 7). However, the structure of more advanced trilobites (e.g. some metaredlichiids and protolenids, ptychopariids, zacanthoids) seems to be fundamentally different (Pillola 1991, p. 79). Thus, the homology between the different elements constituting the ocular ridges and palpebral lobes of high taxonomic units is not completely elucidated.

## RELATIONS BETWEEN BIGOTINID AND SOME OTHER EARLY CAMBRIAN REDLICHINA

The features seen on adult *Bigotina* are recognizable in larval stages of several redlichiid taxa; these features occur progressively earlier during ontogeny of advanced Wutingaspiinae, Pararedlichiinae, and Redlichiinae respectively. The same features are also present in Dolerolenidae and Metadoxididae during larval development. This suggests that the morphology of *Bigotina* truly represents a primitive one for the non-olenellid Trilobita.

It is relevant, therefore, to consider the similarities and differences between *Bigotina* and the other trilobites from the lowest Cambrian which have been considered as representing primitive morphology.

The ontogeny of *Eoredlichia* Chang, 1950, *Redlichia* (*Pteroredlichia*) Chang, 1966, *Redlichia* (*Redlichia*) Cossmann, 1902 and *Wutingaspis* Kobayashi, 1944 allows an understanding of one of the main trends in evolution of the Redlichiidae (Zhang and Lin, *in* Zhang *et al.* 1980). McNamara (1986*a*) interpreted these genera as an example of a peramorphic evolutionary trend. Further comparisons between the larval stages and/or adults of *Bigotina*, *Bigotinops*, *Chaoaspis* Chang,

1966, *Dolerolenus* Leanza, 1949, *Lemdadella* Sdzuy, 1978, *Metadoxides* and *Parabadiella* Chang, 1966, have been given by Pillola (1991).

These comparisons show that features resembling the adult *Bigotina* are short-lived during the ontogeny of Redlichiinae and generally longer-lasting in Wutingaspiinae (Text-fig. 3).
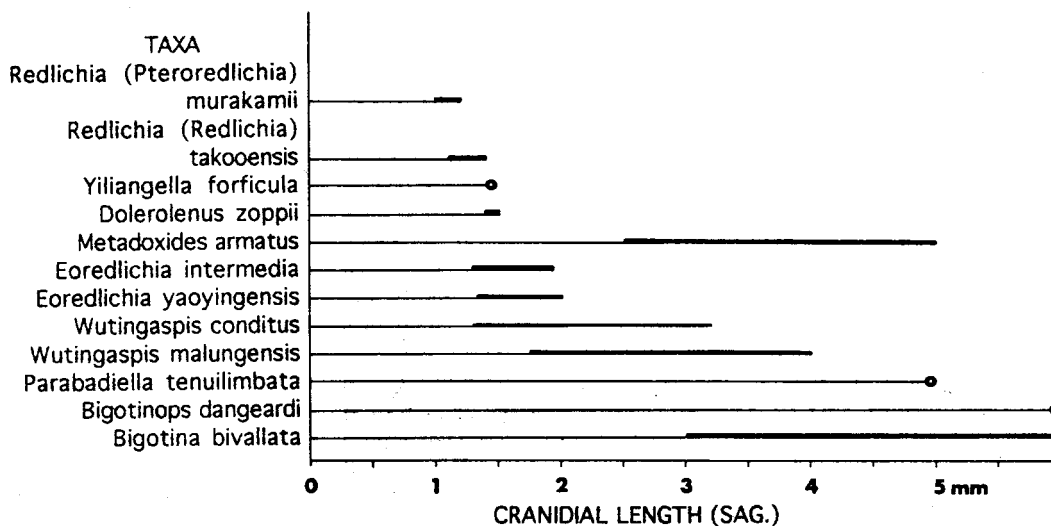
TEXT-FIG. 3. Occurrence of *Bigotina*-like adult cranidial features (indicated by thicker line) during the ontogeny of some redlichiids. Circles indicate the measurement of only one specimen; meraspis to holaspis transition occurs usually at 3–4 mm sagittal cranidial length).

A particular example is represented by *Metadoxides armatus*, in which the features of *Bigotina* occur in large meraspides. Adult specimens of this species may have from 18 to 22 thoracic segments and final length can reach 200 mm. Relatively large cranidia which have some immature features suggest that the entire developmental stage has been 'stretched out'. *Metadoxides* may represent an example of hypermorphosis (*sensu* McNamara 1986a).

The genera included in the Abadiellidae Hupé, 1953, have been claimed to represent an homogeneous group of trilobites; however, the diagnostic characters given by Hupé (1953a, p. 152) are shared with many other redlichiids. The occurrence together of a slender glabella with very shallow, medially and backwardly directed glabellar furrows, strong occipital spine, and advanced genal spine, may represent synapomorphies between the following genera: *Abadiella* Hupé, 1953, *Granolenus* Jago, 1980, and *Lunolenus* Sdzuy, 1961. This could be used to define Abadiellidae in a restricted sense. Inclusion of *Guangyuanaspis* Zhang & Chien, 1974, *Malongocephalus* Zhang and Lin, 1980, *Parabadiella* Chang, 1966, *Shaanxia* Zhang and Lin, 1980, and *Sibiriaspis* Repina, 1960, would serve to blur the distinction between Abadiellidae and Wutingaspiinae and/or Pararedlichiinae. The existence of intermediate morphologies suggests that abadiellids *sensu stricto* are perhaps to be regarded as a subfamily of Redlichiidae.

A few major innovations occur in the most representative ellipsocephalids: lateral glabellar furrows and dorsal furrow are well impressed; more or less interrupted proximal end of ocular ridge, and interrupted palpebro-ocular ridge; L4 well developed, and L5 reduced; plectrum occasionally present. The exoskeleton of ellipsocephalids is smooth or finely punctate, rarely granulose; general convexity of the exoskeleton strong.

The posterior end of the palpebral lobe, commonly close to the posterior furrow of the fixed cheek (except in palaeolenids and *Hamatolenus* (*Myopsolenus*) Hupé, 1953), and the short, nearly straight, posterior branch of the facial suture, the diminutive posterolateral limb and long eye ridges, are

characters usually invoked for a high level distinction between Redlichioidea and Ellipsocephaloidea (Hupé 1953a, 1953b; Henningsmoen 1959; Moore 1959; Poulsen 1959; Öpik 1975; Geyer 1990). The 'distinctive' characters mentioned above occur in some adults of early redlichiids, and in larval development of several taxa belonging to Redlichiacea.

According to Stubblefield (1936) and Whittington (1981), the axial characters (including ventral ones), and especially glabellar features, are of significance in trilobite classification. The axial characters of the cranidia of bigotinids, Abadiellidae, Pararedlichiinae and Wutingaspiinae, are generally similar. The glabellar segmentation pattern and the shape of the glabella is relatively constant; most of the variation can be explained by preservation and/or the stage of growth.

Few changes occur in the central region of the cranidium of more advanced redlichiids: forwardly expanded glabella with more or less impressed S4 (some metaredlichiids); glabellar furrows sub-perpendicular to the axis and sometimes anteriorly directed; shallowing and uniformly impressed glabellar furrows (Dolerolenidae, some Gigantopygidae and some Yinitidae); connection between ocular ridge and anterior part of the glabella, partly interrupted and with some changes in shape, in morphology and relative topographic position from the anterior end of frontal glabellar lobe (late Pararedlichiinae and Wutingaspiinae, Redlichiinae, some abadiellids).

By contrast, modifications of the morphological features are more marked on the peripheral 'characters' (Pillola 1991, p. 75); a relative large spectrum of variability is shown by: relative length (sag.) of preglabellar field and anterior border; presence and shape of plectrum; morphology, position and size of the palpebral lobe; facial suture pattern and relative proportion between fixed and free cheeks and shape of the occipital segment. The combination of these characters, mainly the condition of retraction, stasis or protraction of the glabella, the sutural pattern and position and size of palpebral lobes, comprise a nearly complete view of described Redlichiidae.

Bigotinids lack important derived characters allowing them to be classified either with Ellipsocephalacea or with Redlichiacea. Early representatives of both high taxa share similarities which suggest that bigotinids may represent a morphology close to the common ancestor of the two superfamilies of opisthoparian trilobites at the beginning of Cambrian times.

The provisional assignment of the Bigotinidae to the Redlichioidea seems to be preferable because of their early stratigraphical position and because the ontogeny of redlichiids includes a Bigotina-like phase.

PALAEOBIOGEOGRAPHY

Bigotinids are the earliest opisthoparian trilobites in Lower Atdabanian sequences of northern France, Spain, Morocco and Siberia.

The most ancient trilobite recorded in Morocco is Hupetina antiqua, from level T1 of Tiout (Sdzuy 1978). In the same section Bigotina bivallata occurs in the T2 level, about 10 m above the Hupetina bed. A slightly younger trilobite fauna includes Bigotinops, Lemdadella and Pararedlichia Hupé, 1953 (= Eoredlichia Chang, 1950). The first occurrence of Bigotina in the Córdoba area (southern Spain) is located at the base of Level 9 of the Pedroche Formation and it is replaced higher in the section by Lemdadella (Pararedlichiinae) with which it may coexist (Liñán et al. 1981). Bigotinops is recorded in northern Spain associated with Pararedlichia. In the Carteret region, Bigotina bivallata ranges almost entirely through the Saint-Jean-de-la-Rivière Formation, but only in Level 4 does it coexist with Bigotina sp. 1.

Bigotina is also the oldest opisthoparian trilobite from Siberia, its first occurrence being at the base of the Fallotaspis zone (Zhuravleva 1984); Bigotina is also present in the Atdabanian Tolbachan Formation in Yakutia (Jegorova 1983).

The 'bigotinid bioprovince' (Pillola 1990, 1991) was located on the overlapping area between the 'Olenellid Realm' and the 'Redlichiid Realm' (Cowie 1971); this bioprovince was well defined during Early to Middle Atdabanian time (Text-fig. 4), at which time bigotinids coexisted and gradually were replaced by more advanced redlichiids and ellipsocephalids.

The South Iberian peninsula, northern France, and Tiout-Lemdad areas in Morocco provide a
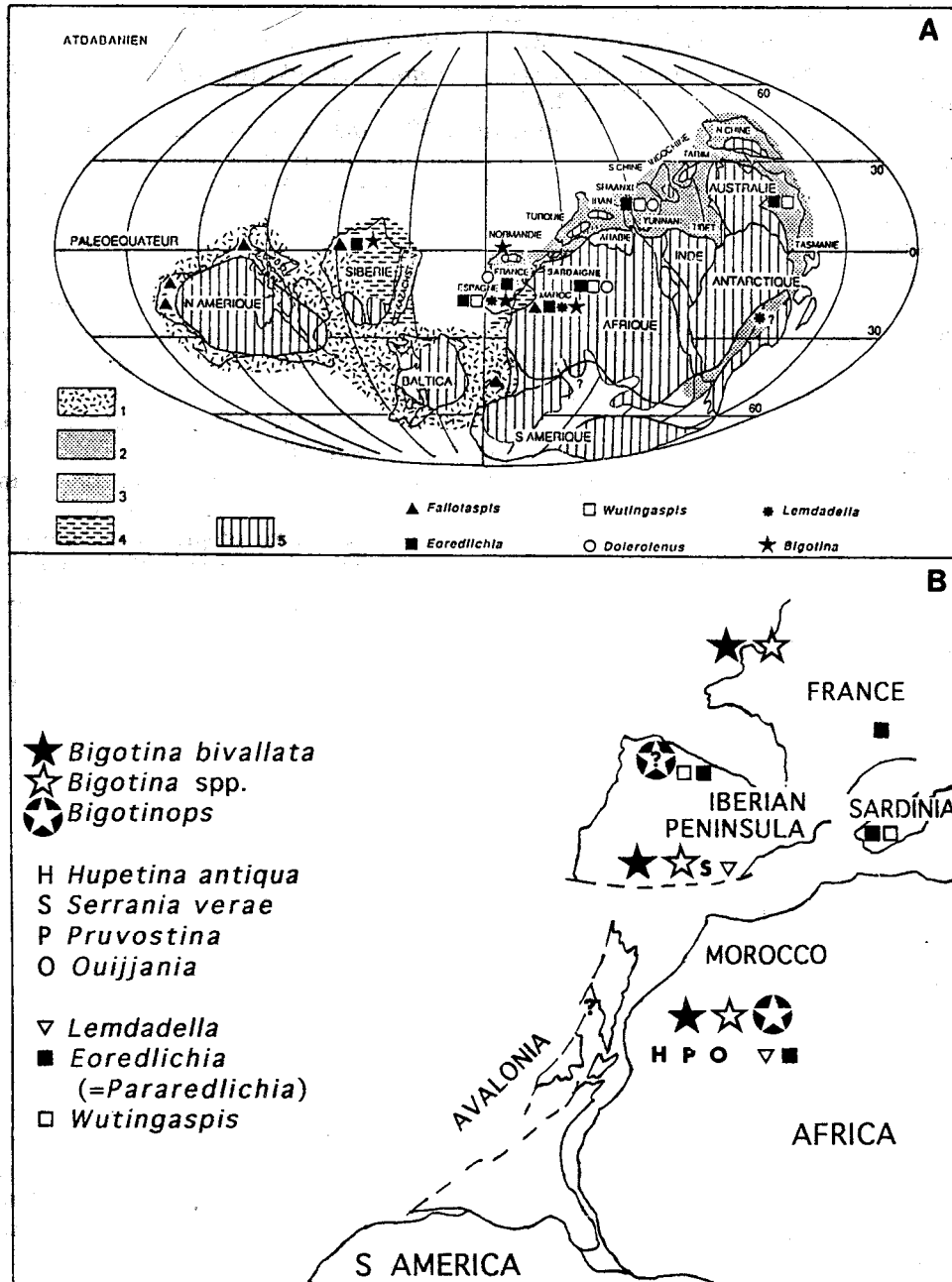
TEXT-FIG. 4. A, land mass distribution during Atdabanian time, and occurrence of selected trilobite genera; 1, 'olenellid Realm'; 2, 'redlichiid Realm'; 3, area with bigotinids, but without olenellids; 4, area with olenellids, redlichiids and bigotinids. After Cowie (1971), Rozanov (1984), McMenamin (1987), Burrett et al. (1990); modified from Pillola 1990, 1991. B, palaeogeographical distribution of selected bigotinids and early Redlichiidae in Western Europe and Morocco.

good example of synchronous similarities of sedimentary environments and fossil composition at the beginning of Atdabanian (Text-fig. 4); a large proportion of archaeocyatha, trilobites and algae are in common in these areas (Doré 1963, 1969; Debrenne and Debrenne 1978; Liñán and Sdzuy 1978; Sdzuy 1978, 1981; Liñán et al. 1981) the lack of early olenellids in Normandy and in the Córdoba area seems unrelated to environmental setting, but no persuasive reasons have been suggested.

Faunal exchange between a circum-Mediterranean area and the Far East (particularly with southwest China) during Atdabanian and Botomian time was well established, as has been recently pointed out on the basis of new data by Pillola (1990, 1991); however, there are remaining problems in understanding paleobiogeographical relationships between peri-Gondwanan terranes.

Early Cambrian palaeomagnetic data indicate that south China and Australia were placed close to one another, and together with Antarctica constituted a large part of Gondwana, located in an intertropical to sub-tropical position. The disposition of facies belts and sedimentary environments (Lin et al. 1985; Burrett et al. 1990) support this. Circum-Mediterranean regions were located in apparently similar climatic conditions in Early Cambrian times.

The close affinities between Chino-Austral-Antarctic faunas and those of Siberia, Mongolia and Kazakhstan, based on small skeletal fossils and trilobites (Bengtson et al. 1990), and the occurrence of strong affinities also with circum-Mediterranean areas allow us to suppose a gradient of faunal exchange all around the Gondwanan and Siberian regions. But lack of fossils from areas between North East Africa (Morocco and Mauritania) and South America–South Africa (only partly filled by Avalonian terranes, and Namibia) is a major limitation to the contribution that palaeontological evidence can make to the model of a Precambrian to Early Cambrian supercontinent, which was dismembered in Cambrian time.

SYSTEMATIC PALAEONTOLOGY

Order REDLICHIIDA Richter, 1933
Suborder REDLICHINA Harrington, 1959
Superfamily REDLICHIOIDEA Poulsen, 1927
Family BIGOTINIDAE Hupé, 1953

[nom. transl. BIGOTININAE Hupé, 1953, emend. Geyer 1990]

Diagnosis. Redlichiacean trilobites typically retaining many primitive features: concave to flat preglabellar field relatively narrow (sag.) or absent; very prominent and wide undifferentiated palpebro-ocular ridge, not interrupted by dorsal furrows, clearly bipartite (especially near the glabella), and parafrontal band; wide plectrum and anterior preocular facial lines present; short (tr.) postocular cheek with wide posterior border furrow. Eyes reaching, or very close to the posterior border furrow, and distant from the glabella. Pygidium small with 4 segments and terminal piece; pleural field narrow and furrowed.

Discussion. The Bigotinidae Hupé, 1953, has been recently revised by Geyer (1990) to accommodate *Bigotina* (the sole genus included by Hupé (1953, p. 212) in his Bigotininae) together with *Bigotinops, Ouijjania* and *Pruvostina* (all Hupé, 1953), *Hupetina* Sdzuy, 1978, from Morocco, *Serrania* Liñán, 1978, from Spain, and the Siberian *Bigotinella* Suvorova, 1960, originally described as a subgenus of *Bigotina.*

Hupé (1953a) assigned the Bigotininae to the Protolenidae (superfamily Ellipsocephaloidea); later, Suvorova (1960, p. 21) placed *Bigotina* in the Neoredlichiidae Hupé, 1953, while Repina (1960) placed it in the Aldonaiidae Hupé, 1953; Henningsmoen (1959, p. 212) and Repina (1966, p. 136, 1969, p. 43), following Hupé, assigned the Bigotininae to the Protolenidae Richter and Richter, 1948. Öpik (1967, p. 151) indicated that *Bigotina* is close to ellipsocephalids and protolenids, and later placed the Bigotininae in the Ellipsocephaloidea (Öpik 1975, p. 38). The affinities between *Bigotina, Bigotinops, Pruvostina* and *Ouijjania* were discussed by Sdzuy (1959,

1961), who assigned them to the Bigotininae, in the Dolerolenidae Kobayashi, 1951. A direct relationship between Bigotinidae, Dolerolenidae and Metadoxididae has been questioned (Rasetti 1972).

Genus BIGOTINA Cobbold, 1935

Type species. *Bigotina bivallata* Cobbold, 1935, by original designation, from the upper part of the Lower Cambrian Saint-Jean-de-la-Rivière Formation; Saint Jean-de-la Rivière rock foreshore, Cotentin peninsula, Normandy, France.

Diagnosis. Relatively wide anterior border, regularly arcuate about mid-line (i.e. neither constricted nor angular in front of the glabella). Glabella occupying 60 to 75 per cent of the total cranidial length. Prominent occipital ring with a small posterior spine. Short stout genal spine. Exoskeleton sculpture granulose.

Geographical distribution and stratigraphical range. Cotentin Peninsula, Normandy, France; Córdoba area, Ossa Morena, southern Spain; northern Spain; Morocco; Siberia. Early Cambrian, Atdabanian.

Discussion. There have been various opinions about the systematic position of *Bigotina*. Suvorova (1960, pp. 37 and 40) erected two subgenera of *Bigotina*, diagnosed as follows:

Bigotina Cobbold, 1935; type species *Bigotina bivallata* Cobbold, 1935, palpebral lobes and ocular ridge narrow, bipartite, short frontal area, preglabellar convexity is well expressed.

Bigotinella Suvorova, 1960; type species *Bigotinella malykanica*, glabella cylindrical or moderately wider. Palpebral lobe and ocular ridge wide, bipleurality not well expressed, frontal area very short, preglabellar field may be absent. Preglabellar convexity weak or absent.

The type material of *Bigotinella* described by Suvorova (Pl. 1, figs 1–4) and her other figured specimens have been studied; additional material is from the right bank of the Lena River (opposite Malykan, 300 km southwest of Yakutsk, Siberia), Pestrotsvet Formation, bed 10 of the local succession (British Geological Survey collections).

The type specimen of *B.* (*Bigotinella*) *malykanica* is a cranidium about 3 mm long (sag.) The glabella is slightly tapered forwards and weakly furrowed; the occipital furrow is subperpendicular to the axis and has a uniform width. The occipital ring is a nearly perfect half-ring shape. The segmentation of the ocular ridge is not well expressed, but this condition is common in many other small specimens, e.g. in *Bigotina bivallata* (Pl. 7, figs 2–3), and in some specimens attributed to

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EXPLANATION OF PLATE 1

Figs 1–4. Bigotinids from Siberia; all figured specimens are plaster replicas obtained from latex casts of the type specimens. 1, '*Bigotina*' (*Bigotinella*) *malykanica* Suvorova, 1960, c. × 6. 2a–c '*Bigotina* (*Bigotina*)' *angulata* Suvorova, 1960, (a) dorsal view, ×4; (b) lateral oblique view, ×4; (c) frontal view, ×7; note the finely punctate sculpture on the whole cranidium and the 'angular' shape of the anterior border due, mostly, to the incomplete preparation of the specimen. 3, '*Bigotinops*' *privus* Suvorova, 1960, × 6. 4, '*Bigotinops*' *patrius* Suvorova, 1960, × 6. Horizon and locality information is in the text.

Figs 5–9. Bigotinids and pararedlichiids from Morocco and Spain. 5, *Pruvostina nicklesi* Hupé, 1953; internal mould of the type G.147 (MNHN R.50887); Lower Cambrian, Zone III; Mektar bou l'Baroud track, near Amouslek, Morocco; c. × 2. 6, *Bigotinops dangeardi* Hupé, 1953; internal mould of the type G.154 (MNHN R.50838); Lower Cambrian, Zone 1; Tazemmourt, Morocco; × 5. 7, Gen. and sp. ind., internal mould, D. Vizcaïno collection; Lower Cambrian, Zone 1; Tazemmourt, Morocco, × 2. 8, *Pararedlichia pulchella* Hupé, 1953 (= *Eoredlichia*); internal mould of the type G.153 (MNHN R.50899); Lower Cambrian, Zone 1; Tazemmourt, Morocco, × 2·6. 9, *Serrania verae* Liñán, 1978; plaster cast of the specimen LPH/O/21, Liñan collection. Lower Cambrian, Tramo III of the Pedroche Formation; Puente de Hierro, Córdoba, Spain, × 5.

PLATE 1
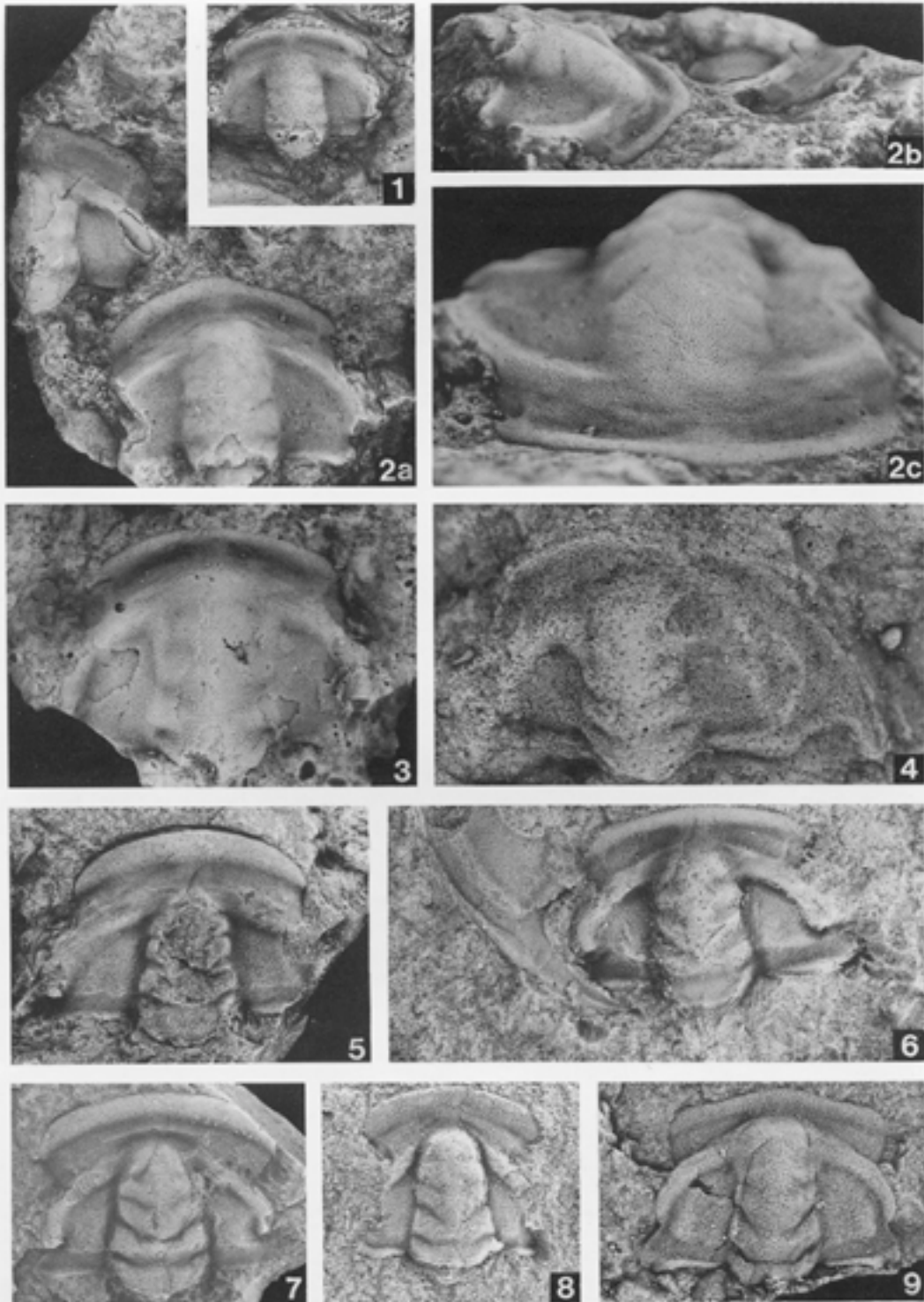
PILLOLA, bigotinids, pararedlichiids

Bigotina angulata. In contrast, the specimens of *malykanica* figured by Repina (1966, pl. 25, figs 1–2) have quite well expressed segmentation and a cranidium 5 mm long has also a well furrowed conical glabella. Other specimens of *B. malykanica* figured by Suvorova (1960, pl. 2, figs 23–25) are small (4·5, 4·0 and 2·6 mm respectively). Repina's (1966, pl. 25, figs 1–2) specimens of *malykanica*, are 2·8 and 5 mm long (sag.). A specimen figured by Sdzuy (1981, fig. 20), attributed to *B.* cf. *angulata*, has faint interocular swellings on the posterior intraocular cheek; the same cranidium shows clearly that the dorsal furrows turn at the level of the anterior corner of the intraocular cheek and reach the palpebral furrow at mid length of L3. This feature has never been observed in *Bigotina*. Specimens of *Bigotinella malykanica* at lengths of 5 to 8 mm do not show any morphological difference from '*Bigotina*' *angulata* Suvorova, 1960. The BGS material (FOR3207–FOR3210), six cranidia with sagittal lengths of 2·5 to 8·0 mm, confirm that *angulata* and *malykanica* are synonyms based on ontogenetic stages.
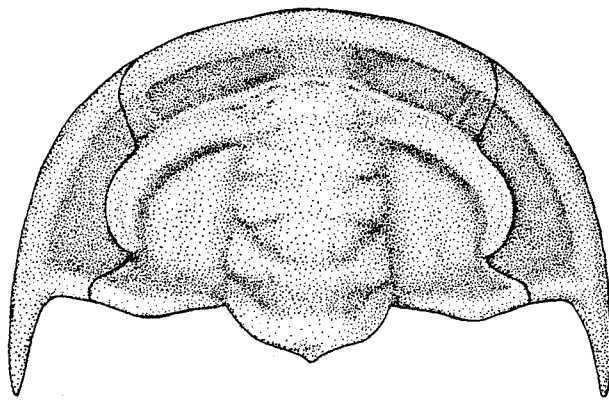

TEXT-FIG. 5. *Bigotina bivallata* Cobbold, 1935; reconstruction of the cephalon, × 8.

I consider that *Bigotinella* Suvorova, 1960 is a valid genus, provisionally a member of the ellipsocephalids, characterized by facial lines, plectrum, with anterior branch of facial sutures very short and subparallel to the axis, and a sculpture of fine punctae of equal size distributed on all parts of the cranidium.

Other species from Siberia have been assigned to *Bigotina*: *B.* (*Bigotina*) *coniferica* (considered a synonym of *egregica*; Repina 1966, p. 138), *B.* (*Bigotina*) *egregica* Repina, 1960, *B.* (*Bigotinella*) *botomica* Repina, 1966 and *B.* (*Bigotinella*) *rara* Repina *in* Repina and Luchinina, 1981. *B. egregica* has a wide cranidium with slender and relatively short glabella, the preglabellar field is about three times wider than the anterior border; this species seems to be related to some members of the Aldonaiidae, for example *Planaspis gelasinica* Repina, 1960. *Bigotinelia botomica* is closely related to *B. malykanica*, has a glabellar segmentation which is faint, except the occipital furrow, and

EXPLANATION OF PLATE 2

Figs 1–6. *Bigotina bivallata* Cobbold, 1935. Saint-Jean-de-la-Rivière Formation, level 4, Lower Cambrian (Atdabanian); Saint-Jean-de-la-Rivière beach, Carteret region, Normandy, France. 1, holotype; reproduced from Bigot 1926, pl. 4, fig. 1, × 6. 2, holotype; reproduced from Cobbold 1935, pl. 17, fig. 1, × 6. 3*a–c* MNHN B.48948a, neotype; 3*a*, incomplete locally exfoliated cranidium; dorsal view, × 6; 3*b*, latex cast of the external mould, showing some parts not preserved in 3*a*, × 6; 3*c*, frontal view of the latex cast, × 6. 4, MNHN B.48968; nearly complete cranidium, × 5. 5, MNHN B.48970; incomplete cranidium, × 6. 6, MNHN B.48947; incomplete sagittally compressed cranidium, × 5.

PLATE 2

PILLOLA, *Bigotina*
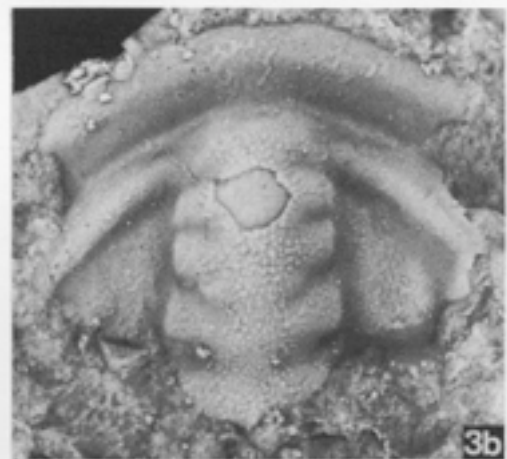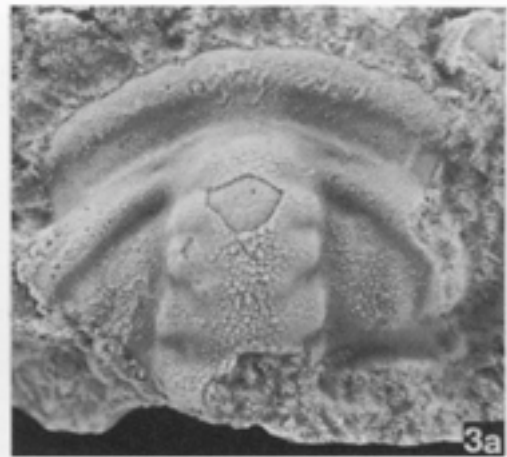
relatively narrow palpebral lobes and ocular ridges. *Bigotinella rara* (compare the specimen figured by Egorova *et al.* 1983, pl. 45, fig. 5), like *Mundocephalina bidjaensis* Repina, 1964 (Ellipsocephaloidea), has a subtriangular occipital ring with a strong occipital spine; all these Siberian taxa are closely similar to Australian and Moroccan ellipsocephalids like *Elicicola* Jell, 1990, *Ornamentaspis* Geyer, 1990, and *Kingaspoides* Hupé, 1953.

Bigotina tina Öpik, 1975 (p. 40, pl. 7, fig. 1) is now placed in *Alanisia guillermoi* (Richter and Richter, 1940; see Jell 1990, and discussion *in* Bengtson *et al.* 1990).

Bigotina differs from *Bigotinops* Hupé, 1953, in having relatively shorter postocular fixed cheek and posterior branch of facial suture; the posterior margin of the occipital ring is not expanded in a cuspid or strong spine. The differences between the two taxa are small for a generic separation. However, the lack of any other specimen assigned to the type species (*Bigotinops dangeardi* Hupé, 1953, from Zone 1, Anti Atlas, Morocco, a cranidium and probably the adjacent librigena, internal mould; Pl. 1, fig. 6), does not allow more accurate comparison. At present, some other specimens originating from Morocco (Sdzuy 1978, fig. 2*b*, horizon T 11, should probably be assigned to *Bigotinops* (Sdzuy 1981, p. 397, fig. 17; Liñán *et al.* 1981, p. 284). This genus is also recorded from Spain, but without illustrations (Liñán and Sdzuy 1978; Sdzuy 1978).

Bigotinops from Siberia is represented by three species: *B. patrius* Suvorova, 1960, *B. privus* Suvorova, 1960 and *B. copiosus* Jegorova, 1983. *Bigotinops privus* (Pl. 1, fig. 3) has the glabella expanded forward, occupying about 80 per cent of total cranidial length, the occipital furrow does not cross the glabella and is interrupted before the dorsal furrow; S1 to S3 weak, not impressed in the distal portions and shallowing toward the middle; narrow (sag.) anterior border and preglabellar field. Posterior border furrow narrow and shallow. The cuticle is finely punctate.

Bigotinops patrius is poorly known. Examination of the latex cast of the type specimen provided by Suvorova (Pl. 1, fig. 4), suggests that this species should be removed from *Bigotinops*. Because no facial sutures have been discerned, this specimen seems to be more probably related to *Fallotaspis* or *Profallotaspis*.

Bigotinops copiosus comes from 15 m above the base of the Tolbachan Formation on the Tolba River section, Yakutia. The figured specimens (Jegorova 1983, pl. 6, figs 4–5) are closely similar to *Bigotina bivallata*; *Bigotinops copiosus* shows both relatively short anterior branches of the facial sutures and short (tr.) postocular cheeks; hence it is suggested that this species more properly belongs in *Bigotina*.

Hupetina Sdzuy, 1978 (type species: *H. antiqua* Sdzuy, 1978, from the Tiout section, horizon TI, Morocco) has a narrow, angular anterior border, widening distally, preglabellar field nearly absent and librigena with a short advanced spine. The diagnosis given by Sdzuy includes also the parallel-sided or slightly tapering glabella and the short, anteriorly directed S3. These characters are present in the type specimen (Sdzuy 1978, pl. 1, fig. 6); however, the other figured specimens (Sdzuy 1978, pl. 1, fig. 7; Sdzuy 1981, fig. 15) show a glabella that tapers forward, and the S3 furrow

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EXPLANATION OF PLATE 3

Figs 1–9. *Bigotina bivallata* Cobbold, 1935. Saint-Jean-de-la-Rivière Formation, Lower Cambrian (Atdabanian); Saint-Jean-de-la-Rivière beach, Carteret region, Normandy, France. 1*a–c*, MNHN B.48857; nearly complete cranidium with well preserved exoskeleton, slightly sagittally compressed (anterior margin incomplete); level 2*a*; 1*a*, dorsal view, ×7; 1*b*, anterior oblique view, showing the clear subdivision of the ocular ridge, ×7; 1*c*, lateral view, ×7. 2, MNHN B.48864; small partly exfoliated cranidium, showing terrace lines on the anterior border, facial lines, wide plectrum, ocular furrows and interocular swellings; level 2*a*; ×7. 3 MNHN B.48862; damaged pygidium; level 2*a*; ×20. 4, MNHN B.48858; incomplete cranidium, internal mould; level 2*a*; ×6. 5, MNHN B.48861; small librigena; level 2*a*; ×12. 6, MNHN B.48867*a*; small cranidium, internal mould; level 2*a*; ×10. 7, MNHN B.48998; small exfoliated and weathered cranidium; level 4; ×5. 8, MNHN B.48895; incomplete pygidium; level 4; ×15. 9, MNHN B.48865; small damaged cranidium; level 2*a*, ×5·5.

PLATE 3
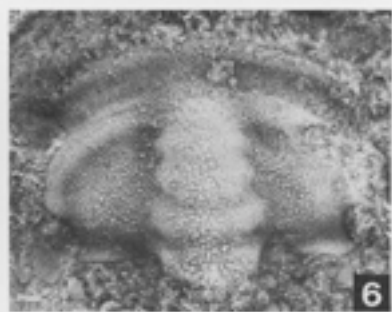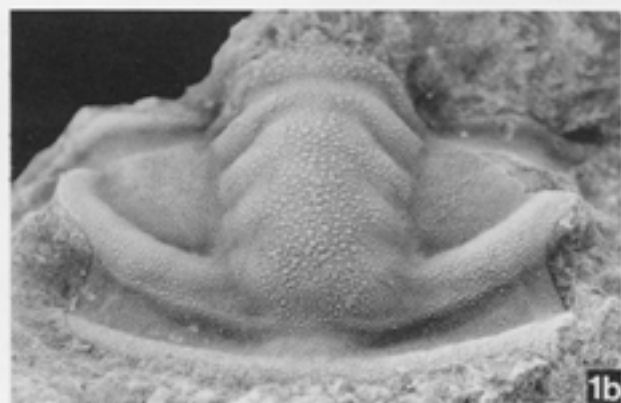
PILLOLA, *Bigotina*

perpendicular to the sagittal line. Finally, an unclassified specimen (Sdzuy 1981, fig. 16), having a cranidial length of 3·5 mm, is similar to some cranidia of *Bigotina* figured here (Pl. 6, fig. 3).

Serrania Liñán, 1978, is also very close to *Bigotina*, but the former has a relatively longer glabella (more than 85 per cent of the cranidial length; cf. Liñán 1978 and Pl. 1, fig. 9), sub-parallel or slightly diverging anterior branches of the facial sutures and a different shape of anterior border. The librigena may be relatively smaller than that of *Bigotina*.

Ouijjania Hupé, 1953a, is monospecific, and represented by only one cranidium, assigned to *O. meridionalis* (Hupé, 1953a, fig. 52); the type specimen has never been figured, and the generic characters are inevitably uncertain.

Pruvostina Hupé, 1953a (type species *P. nicklesi* Hupé, 1953a; cf. Pl. 1, fig. 5) is similar to *Bigotina*; the type specimen, an internal mould of a slightly distorted, incomplete cranidium, shows subparallel anterior branches of facial sutures, relatively wide (tr.) anterior border and occipital ring. The preservation of this specimen (e.g. the partly abraded glabella) does not allow more critical comparison with *Bigotina*.

Tolbinella Jegorova, 1983 (Pararedlichiinae) has been compared with *Bigotina*, from which it differs in the relative length of frontal area and glabella and the long and more divergent anterior branches of the facial sutures.

It is probable that more genera have been created among *Bigotina*-like trilobites than the sparse material really warrants. The present description should allow a more objective assessment of the synonymy in future.

Following the discussion of Siberian bigotinids, only the species described as *Bigotinops copiosus* Jegorova, 1983, belongs in *Bigotina*. All other Siberian '*Bigotina*' should be placed in an intermediate taxonomic unit between redlichiids and ellipsocephalids. Thus the only valid described species are *Bigotina bivallata*, and *Bigotina copiosa* (Jegorova, 1983) which may prove to be a synonym of *bivallata*. In addition, *Bigotina* cf. *bivallata* and *Bigotina* sp. 1 from Carteret are briefly discussed below.

Bigotina bivallata Cobbold, 1935

Plates 2–4; Plate 5, figs 1–3, 5–7, 10; Plates 6–7; Text-fig.5

1926	*Ptychoparia*, Bigot, p. 136, pl. 4, figs 1–4.
1935	*Bigotina bivallata* n. gen. n. sp., Cobbold, p. 384, pl. 17, figs 1–10.
1981	*Bigotina* sp.; Sdzuy, p. 396, fig. 18.
?1981	Gen. and sp. ind., Sdzuy, p. 396, fig. 13.
1981	Gen. and sp. ind., Sdzuy, p. 396, fig. 14.
v.1991	*Bigotina bivallata* Cobbold; Pillola, pl. 31, figs 9–11.

Holotype. Specimen figured by Bigot (1926, pl. 4, fig. 1) and copied by Cobbold (1935, pl. 17, fig. 1) Pl. 2, figs 1–2; missing and presumed destroyed during World War II; originally housed in Caen University (France).

EXPLANATION OF PLATE 4

Figs 1–7. *Bigotina bivallata* Cobbold, 1935. Saint-Jean-de-la-Rivière Formation, Lower Cambrian (Atdabanian); Saint-Jean-de-la-Rivière beach, Carteret region, Normandy, France; all specimens except fig. 1 from level 1*b*. 1*a*–*b*, Caen University collections; slightly damaged cephalon; *a*, dorsal view, × 7; *b*, anterior oblique view, × 7. 2, BMNH It.25629*a*; cranidium, internal mould, × 6. 3, BMNH It.25625; small cranidium, × 10. 4, BMNH It.25621; cranidium, internal mould, × 6. 5, BMNH It.25622; cranidium, internal mould, × 6. 6 BMNH It.25628; cranidium, internal mould, × 6. 7, BMNH It.25699*b*; cranidium, internal mould, × 6.

Fig. 8, *Bigotina* cf. *bivallata* Cobbold, 1935; horizon and locality as for figs 2–7; BMNH It.25630; cranidium, internal mould; with some trace of granulations, on the incompletely removed limonitic layer, × 4.

PLATE 4
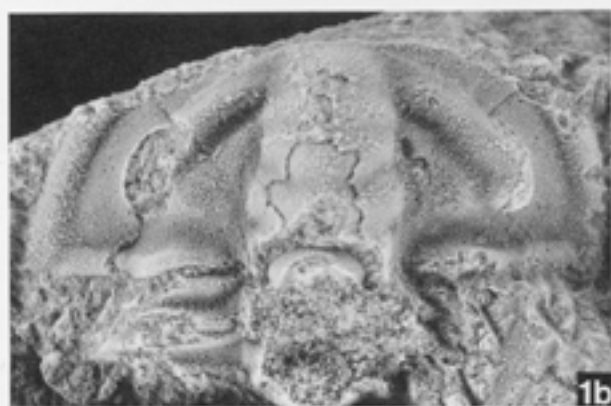
PILLOLA, *Bigotina*

Neotype (proposed herein). Incomplete cranidium MNHN-IP B. 48948, internal and external mould preserved in limestone; Pl. 2, fig. 3*a–c*.

Type locality. Saint-Jean-de-la Rivière rock foreshore, 4·15 km from the Carteret Cape lighthouse (Text-fig. 2); map sheet 1/50000, Bricquebec-Surtainville (B. R. G. M. 1976, feuille XI-XII-11,); cropping out during low tide. Dark grey limestones (bioclastic to oolitic, packstone and grainstone, locally weathered, located in the upper part of the Sain-Jean-de-la-Rivière Formation (about 150 m from the base); Atdabanian, Lower Cambrian.

Material. Level 1*a*: two small cranida, one librigena (BMNH It.25643); level 1*b*, BMNH It.25620–It.25629, It25631–It25639: 22 cranidia and 2 meraspides, one librigena, several fragments including thoracic pleurae. Level 2*a*, MNHN-IP B.48856–B.48932: 96 cranidia (3 mm to 10 mm), 12 meraspides, 8 librigenae, 2 pygidia. BMNH It.25640–It.25642: 4 cranidia and 4 meraspides, 1 librigena. Level 2*b*, MNHN-IP B.48933–B.48942: 5 small cranidia, 7 meraspides, 1 ?protaspis. Level 2*c*, MNHN-IP B.48943–B.48944: 2 cranidia. Level 2*d*, MNHN-IP B.48945–B.48946: 2 cranida. Level 4, MNHN-IP B.48947–B.49005: 48 cranidia and 21 meraspides, 13 librigenae, 2 pygidia. BMNH It.25644–It.25664: 16 cranidia, 13 meraspides, 5 librigenae.

In Caen University collections: one nearly complete cephalon articulated with two poorly preserved thoracic segments, more than 25 cranidia, several librigenae and pleurae, coming, in all likelihood, from level 4. A few specimens of the Feist collection (Montpellier University, France) 9 incomplete or damaged cranida, 1 librigena, 2 meraspides.

All studied material: more than 230 cranidia and 60 larval stages, 40 librigenae and 4 pygidia. Several specimens of *Bigotina bivallata* from Córdoba, Spain, have been studied in Zaragoza University (Liñán collections).

Diagnosis. *Bigotina* with diverging anterior branches of facial sutures; faint ocular furrow, and coarsely granulose sculpture.

Description. Cranidium subrectangular with arcuate anterior border. Glabella convex, elevated, well rounded anteriorly, occupying about 70–75 per cent of the cranidial length (sag.) defined by weak furrows and mostly by a change of slope between the glabella itself and fixed cheeks. Occipital ring longer (sag.) medially, about 3 times as wide (tr.) as long, showing a short posterior median spine. Occipital furrow deepest laterally, shallowing and widening towards the middle, which it crosses transversely. Lateral deep parts of occipital furrow parallel to S1. Three pairs of evenly spaced glabellar furrows, deeply impressed laterally, shallowing progressively toward the middle. S1 particularly bifurcates at about midway between the axial furrow and the sagittal line. Frontal area composed of the concave to flat preglabellar field, almost entirely occupied by a more or less prominent boss, the plectrum, and by anterior border; the last convex and about the same width (sag.) as the preglabellar field, with terrace lines on the anterior edge. Front margin of the cranidium rather gently and uniformly arcuate in outline, anterior border furrow deeply impressed on external side of the plectrum and

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EXPLANATION OF PLATE 5

Figs 1–3, 5–7, 10. *Bigotina bivallata* Cobbold, 1935; Saint-Jean-de-la-Rivière Formation, Lower Cambrian (Atdabanian); Saint-Jean-de-la-Rivière beach, Carteret region, Normandy, France. All specimens come from level 4, except fig. 6 from level 2*a*. 1*a–b*, MNHN B.48996; incomplete weathered cranidium; 1*a*, whitened with ammonium chloride, *c*. × 7; 1*b*, showing caecal network and ocular ridge structure, × 8. 2, MNHN B.48953; damaged cranidium with well-marked ocular furrow and trace of sculpture on the internal mould, × 7. 3, MNHN B.48973; weathered largely exfoliated cranidium, × 6. 5, MNHN B.48955; small incomplete cranidium; the angular shape of the anterior border is due to overlap of matrix, × 10. 6, MNHN B.48870; incomplete cranidium, internal mould, × 3·5. 7, MNHN B.48999; small incomplete weathered cranidium with clear interocular swellings, × 6. 10, MNHN B.48960; librigena, external mould, × 7.

Figs 4, 8–9 *Bigotina* sp. 1; Saint-Jean-de-la-Rivière Formation, Lower Cambrian (Atdabanian); Saint-Jean-de-la-Rivière beach, Carteret region, Normandy, France. All specimens from level 4. 4, BMNH It.25644; small cranidium, internal mould, × 10. 8, MNHN B.48958; incomplete cranidium, × 12. 9, MNHN B.48971; nearly complete cranidium, × 8.

PLATE 5
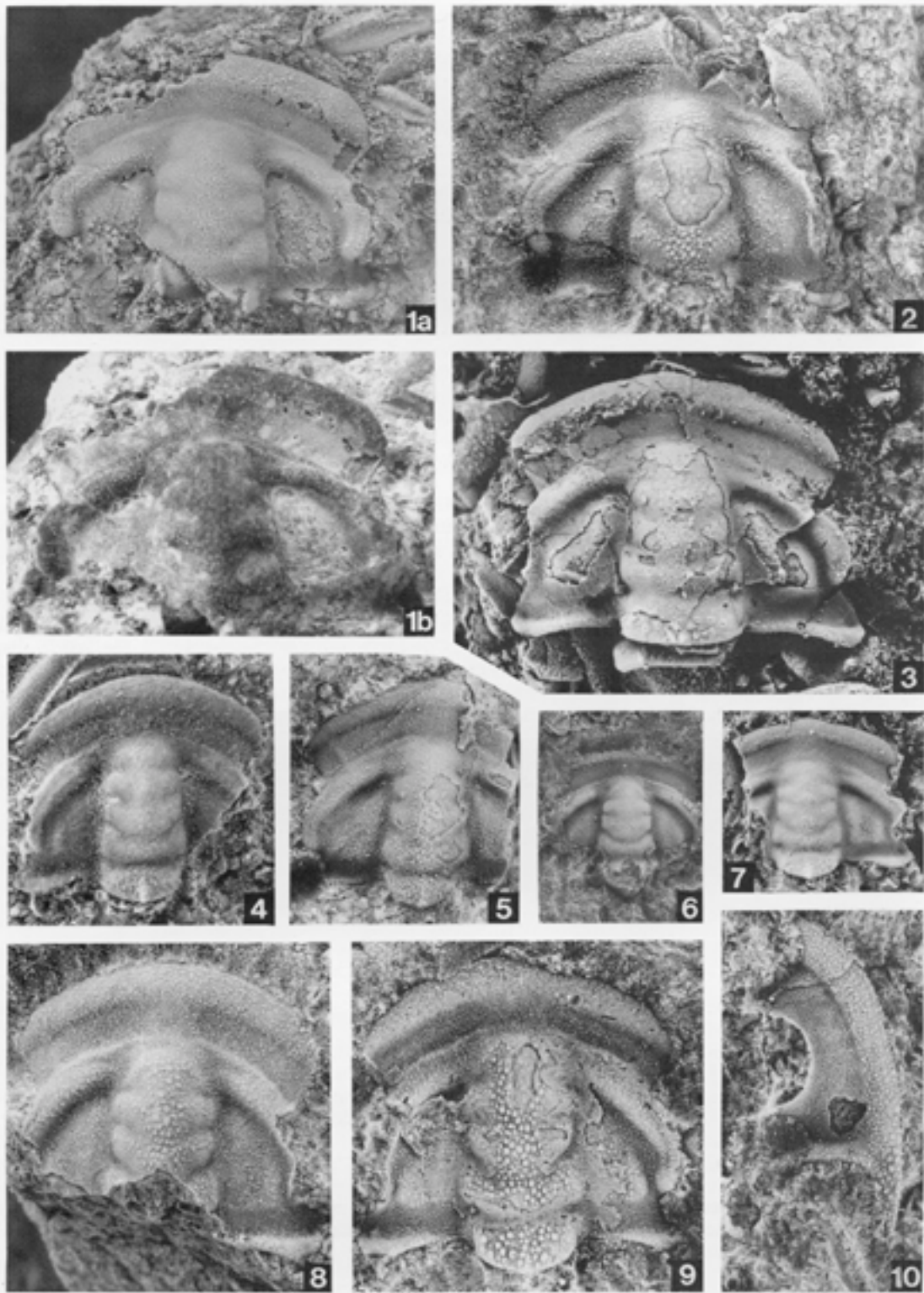
PILLOLA, *Bigotina*

shallow in front of the glabella. Concave to flat downsloping anterolateral limb, widens adaxially slightly, some specimens showing the preocular facial lines (Pl. 2, fig. 3; Pl. 3, fig. 1), which are sometimes faint, forming an angle of 35° with the axial line. Palpebral lobe and ocular ridge continuous, confluent with the anterior part of the glabella, palpebral furrow begins at same level as S3. Crescentic palpebral lobe about one third of the glabellar length, opposite middle third of the glabella. Intraocular cheek with outline of a quarter circle, showing, in some cases, weakly developed interocular swellings posteriorly. Postocular fixed cheek not extended laterally far beyond the palpebral lobe. Exceptionally broad, deep posterior border furrow. Posterior border widens laterally, distally curved downwards.

Anterior branch of facial suture straight and diverging forward at 20–25° to sagittal line, turning inwards across the border. Posterior branch short, sigmoid, well rounded, backwardly directed, cutting the posterior border perpendicularly.

Free cheek when in place, inclined at an angle of about 30° to horizontal. Lateral border wide and gently convex, with abaxial terrace ridges and carrying rows of small granules (Pl. 3, fig. 5); librigenal field flat to slightly concave, relatively narrow, rising towards the upturned circum-ocular region. Short, stout genal spine, turning downwards.

Thorax of unknown number of segments, with a strong relief, each pleural region is slightly wider than the rachis; axial ring relatively wide (sag.), with a small postero-median spine; half ring well developed. Pleurae laterally directed, with distal fulcrum and wide (exsag.) pleural furrow; ending with a short backwardly directed spine. Articulating facet observed in several isolated pleurae (e.g. Pl. 7, fig. 7).

Pygidium small; prominent truncato-conical to oval rachis, with four segments and tiny terminal piece; sub-triangular, furrowed pleural field, not extended beyond the rachis, anterior margin forming an angle of 30° with the axis.

Sculpture consists of fine to coarse granulations distributed on all parts of the relatively thick exoskeleton; the internal mould is usually smooth, but traces of granulation are occasionally observed. Caecal network sometimes revealed by selective weathering in the frontal area (Pl. 4, fig. 1b; Pl. 6, fig. 9).

Discussion. Intraspecific variation in *Bigotina bivallata* shows every intergradation, as illustrated here. I originally considered the specimens on Pl. 4, figs 2–7 as a subspecies of *bivallata*. However, no clear-cut differences can be proved, except the slightly more arcuate anterior margin of the cranidium, and slightly wider posterior furrow of the fixed cheek. The differences in relative sagittal length of preglabellar field and anterior border are due to these specimens being internal moulds. The specimen figured by Sdzuy (1981, fig. 14) is conspecific with *Bigotina bivallata*, and particularly resembles these specimens.

Bigotina copiosa (Jegorova, 1983) is known from only two specimens: one Jegorova (1983, pl. 6, fig. 5) differs from *B. bivallata* in having a relatively more developed L1, but the other, the type specimen has only one feature allowing specific separation from *B. bivallata*: the 'ornament on the cranidium consists of indistinct shallow pits' (Jegorova 1983, p. 60).

Occurrence. Earliest Cambrian (Atdabanian), Saint-Jean-de-la-Rivière Formation; Carteret region (Normandy, France). Pedroche Formation; Córdoba area, Sierra Morena, Spain. Lemdad and Amouslek area, Anti Atlas, Morocco. ?Tolbachan Formation; Tolba River, Southwest Siberian platform.

EXPLANATION OF PLATE 6

Figs 1–8. *Bigotina bivallata* Cobbold, 1935. Saint-Jean-de-la-Rivière Formation, Lower Cambrian (Atdabanian); Saint-Jean-de-la-Rivière beach, Carteret region, Normandy, France. 1, MNHN B.48925; incomplete early meraspis, ×50. 2, MNHN B.48921a; incomplete early meraspis, ×50. 3, MNHN B.48926b; incomplete early meraspis, ×50. 4a–b, MNHN B.48926; meraspis; a, dorsal view, ×40; b, anterior oblique view, ×50. 5, MNHN B.48981; meraspis, ×25. 6a–b, BMNH It.25654; meraspis; a, SEM photograph showing faint interocular swellings on intraocular cheek, ×30; b, with clearly expressed segmentation of proximal end of the ocular ridge, ×25. 7, BMNH It.25655b; meraspis with parallel-sided glabella and transglabellar furrows, ×25. 8a–b, MNHN B.48866; meraspis; a, SEM, ×30; b, with clearly expressed segmentation of proximal end of the ocular ridge, well-outlined frontal lobe, and subangular narrow anterior border, ×20.
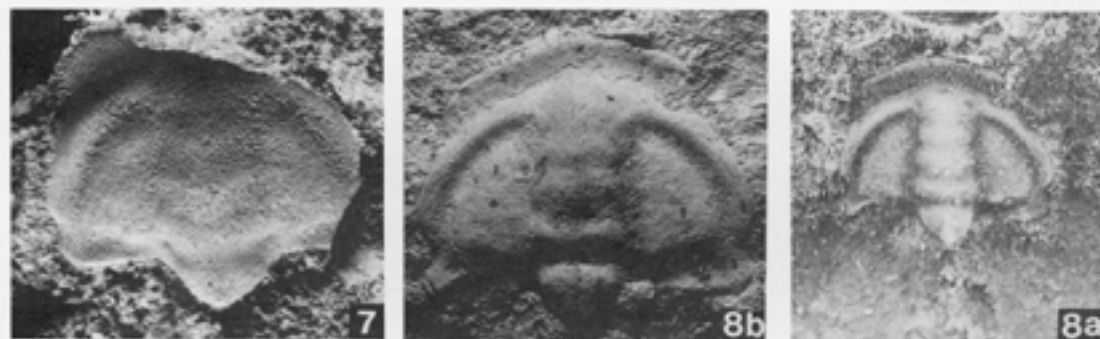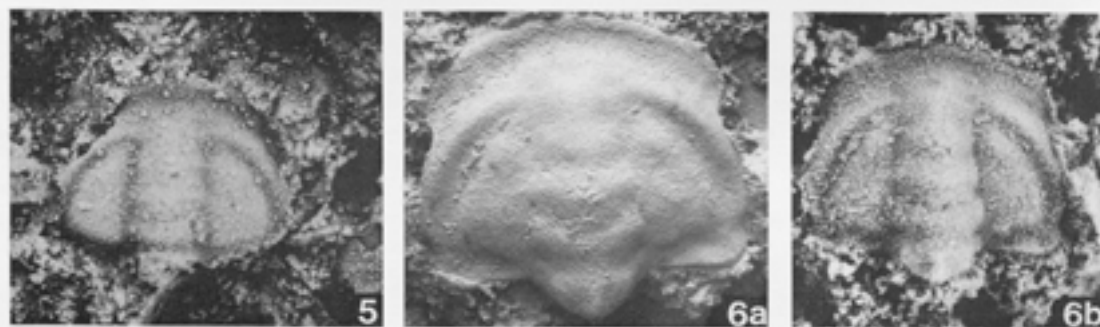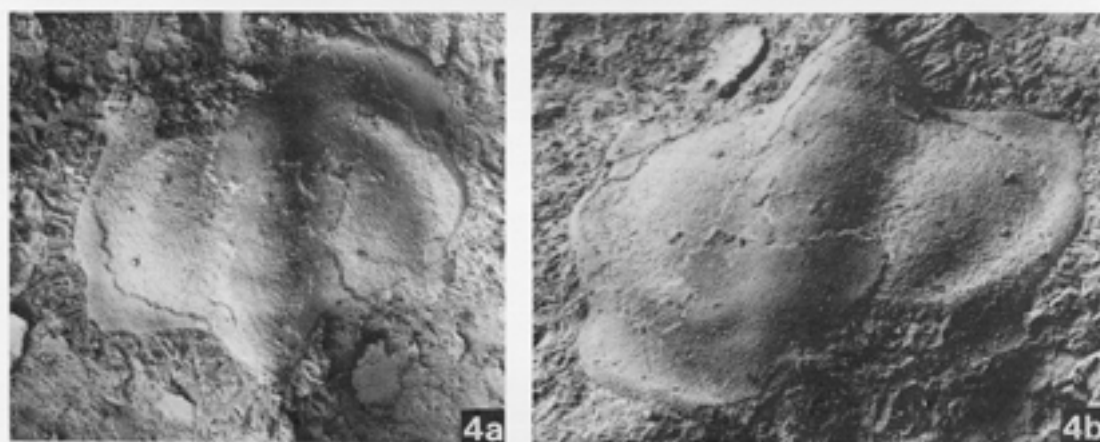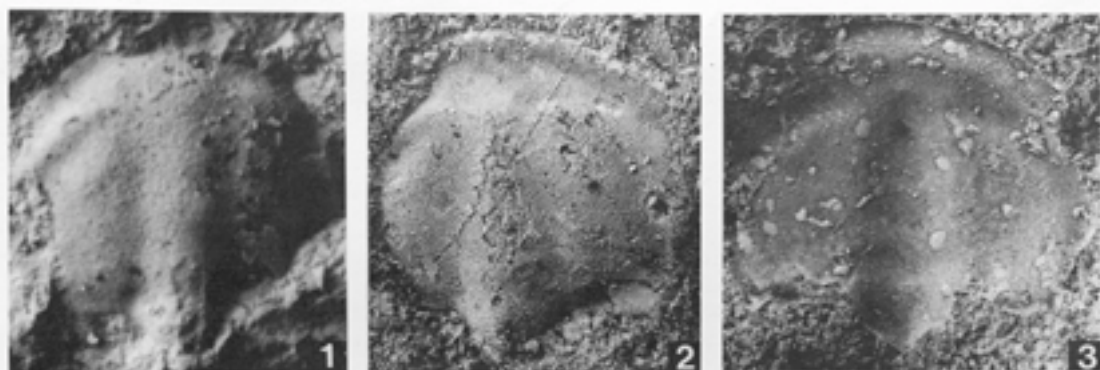
PLATE 6

PILLOLA, *Bigotina*

Bigotina cf. *bivallata* Cobbold, 1935

Plate 4, fig. 8

Material. BMNH It.25630; cranidium.

Discussion. This unique specimen has coarse granulation also on the concave part of the cranidium (i.e. on the posterior border furrow). No other differences from *bivallata* have been discerned, and it may be a variant.

Occurrence. Earliest Cambrian (Atdabanian), Saint-Jean-de-la-Rivière Formation, level 1*b*; Carteret region, Normandy, France.

Bigotina sp. 1.

Plate 5, figs 4, 8–9

Material. Three cranidia: BMNH It.25644; MNHN B.48958, B.48971.

Discussion. Backwardly directed ocular ridge forms, together with palpebral lobe, a nearly perfect half circle; palpebral lobe with well-impressed ocular furrow; the slightly more developed and arched frontal area, and less conical glabella are the only appreciable differences separating these specimens from *bivallata*. A conspecific incomplete cranidium from Carteret, was figured by Sdzuy (1981, fig. 19).

Occurrence. Earliest Cambrian (Atdabanian), Saint-Jean-de-la-Rivière Formation, level 4; Carteret region, Normandy, France.

ONTOGENY

Because heterochrony has been invoked as an important source of evolutionary novelty in early Cambrian trilobites (McNamara 1986*b*), the ontogeny of *Bigotina* is important.

The smallest cranidium of *Bigotina bivallata* (Pl. 6, fig. 1) represents an early meraspid stage. The sagittal length is about 0·9 mm; it is subcircular in shape, overall slightly convex, and has weak segmentation. The glabella is relatively narrow (tr.), reaching, with the anterior part of the ocular ridge, the anterior border furrow; the glabella is defined by wide dorsal furrows shallowing anteriorly. The occipital ring is semicircular, with wide (sag.) occipital furrow. The glabellar furrows (S1–S3) are poorly impressed, transglabellar, and perpendicular to the axis. The frontal lobe is semicircular anteriorly. The preglabellar field is absent, the anterior border furrow weak, and the anterior border narrow. The palpebro-ocular ridge is broad, particularly near the frontal lobe.

EXPLANATION OF PLATE 7

Figs 1–9. *Bigotina bivallata* Cobbold, 1935; Saint-Jean-de-la-Rivière Formation, Lower Cambrian (Atdabanian); Saint-Jean-de-la-Rivière beach, Carteret region, Normandy, France. 1, MNHN B.48924*a*; meraspis, × 30. 2, MNHN B.48923; meraspis, with conical glabella, × 22. 3, MNHN B.48989; meraspis, *c.* × 20. 4, MNHN B.48924*b*; meraspis or holaspis, with faint facial line, ocular furrow and fine granulated sculpture, *c.* × 20. 5, BMNH It.25655*a*; probable early holaspis, with all adult features, × 17. 6, MNHN B.48951; holaspid cranidium with well-impressed ocular furrow, × 10. 7, BMNH It.25662; isolated pleurae, with tiny spines, × 5. 8, MNHN B.48857*b*; small cranidium, × 7. 9, BMNH It.25660; anterior fragment of a cranidium, showing differential weathering of the test; note the two cuticular layers, the caecal network, and probable internal trace of the anterior trunk of the ocular ridge. *a*, anterior border; *b*, boss-plectrum or ocular ridge, × 7.

PLATE 7
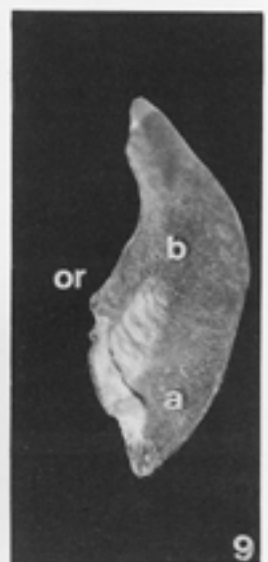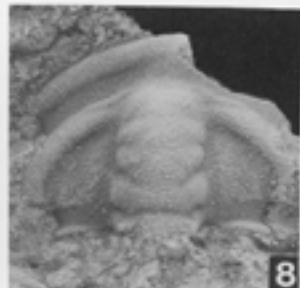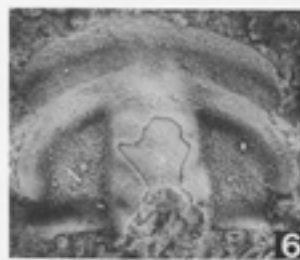
PILLOLA, *Bigotina*

Slightly larger specimens (c. 1·1 mm sagittal length) show anteriorly convergent dorsal furrows up to S3, and an expanded frontal lobe (Pl. 5, figs 2–3); they also have a very broad, poorly defined proximal end of the ocular ridge, and short anterior and posterior branches of the facial suture. A short intergenal spine occurs (Pl. 6, figs 3–4). Cranidial segmentation is better expressed in the larger specimen; the glabella is 80 per cent of the cranidial length, and it is preceded anteriorly by the band. The preglabellar field is absent and the border furrow and anterior rim are better outlined. The occipital and glabellar furrows are broad, and perpendicular to the axis. The occipital ring expands posteriorly, and has a posteromedian spine.

Meraspides of 1·2 mm sagittal cranidial length (Pl. 6, fig. 5) have a well-outlined glabella; S1 is arcuate backward. The posterior end of the palpebral lobe is placed transversely opposite SO. The wide posterior border furrow is partly confluent with the ocular furrow, and the palpebral lobe shows some continuity across the posterior border furrow; with the posterior border, this connection represents a shallow ridge close to the posterior branch of the facial suture. This character persists, with a certain attenuation, in the adult stages.

Some features are well expressed in cranidia of length 1·3 mm or a little more; they are subquadrangular, with a conical to subcylindrical glabella which is well defined by dorsal furrows; the occipital furrow is deep distally; S1 is of same shape as SO, but shallower; S2 and S3 are shallower still and subperpendicular to the axis. The occipital ring is semielliptical, wide medially (tr.), with a well developed spine (or node). The glabellar frontal lobe is rounded anteriorly; the preglabellar field is about twice as wide as the anterior border, and the latter becomes subangular in front of the glabella (Pl. 6, figs 6, 8). The posterior border furrow and ocular furrow are deep and confluent. The ocular ridge is wide, subdivided into three branches in the vicinity of the frontal lobe (Pl. 6, figs 6, 8). The posterior area of the interocular cheek possesses two bosses (interocular swellings), and has another between the ocular furrow and the dorsal furrow close to L3. These faint structures are sometimes observed in adult specimens and may represent the traces of primary furrowed interocular cheeks.

An incomplete cranidium (Pl. 7, fig. 1) c. 1·5 mm long, seems to have a relatively short glabella (75 per cent of cranidial length), due mostly to the small frontal lobe. The latter is, as in previously described specimens, completely surrounded by the ocular ridge system. An incomplete internal mould of a cranidium 2·5 mm long (Pl. 7, fig. 3) clearly shows the same pattern in the frontal lobe-ocular ridge connection, and a wide (tr.) plectrum in the preglabellar field. The anterior border is wide and the anterior furrow deeper.

The external features of specimens sagittally 2·5 to 3·5 mm long (Pl. 7, figs 5–6, 8) are quite similar to those of adult individuals. A faint preocular line connects the anterior border and the ocular ridge; the palpebral lobe is sometimes subdivided by the ocular furrow; a reduction in size of the occipital ring and the occipital spine can be observed. Fine to coarse granulose sculpture and terrace lines are also present.

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