

Article

Taxonomic Revision of the Cambrian Trilobite *Abadiella* and its Stratigraphic Significance in Gondwana

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Simple Summary: The first appearance of trilobite has long been considered an important bioevent to mark the Cambrian Series 2 and Stage 3. Although *Abadiella*/*Parabadiella* is not the oldest trilobite taxon on a global scale, its first appearance is still a key level for the subdivision and correlation of the Cambrian Stage 3, especially in Australia (East Gondwana) and South China. The taxonomic revision of *Abadiella* and its species makes it possible to establish species-based correlation in Gondwana region, which boosts the correlation potential and resolution of the earliest trilobite succession.

Abstract: The taxonomy of trilobites *Abadiella* Hupé, 1953 and *Parabadiella* Zhang, 1966 from the lower Cambrian of Gondwana has long been a controversy. Based on newly-collected and formerly-reported materials, 94 trilobite cranidia within 21 species are selected for morphometric analyses: principal components analysis (PCA) and canonical variates analysis (CVA). The integrated morphological characters are successfully accounted for by two principal components in PCA. The further validations for the presupposed qualitative groupings are indispensable to detect and calibrate the ultimate taxonomic results in CVA. By this way, all specimens distributed in a consistent morphospace in PCA and the short distances between them demonstrate their close morphological affinity, supporting their congeneric status within *Abadiella*. Additionally, three morphotypes were recognized from all selected specimens and they were eventually revised and incorporated into *A. bourgini* Hupé, 1953, *A. huoi* Zhang, 1966, and *A. yunnanensis* Luo, 1981, through stepwise test-calibration to get a high correct rate as far as possible in CVA. From this, it is certain that *A. huoi* is conspecific in South Australia and South China. Its occurrence allows to correlate the Australian *A. huoi* Range Zone to the identical zone in South China (in platform), having an approximately consistent stratigraphic range in the two regions. In comparison with *A. huoi*, *A. bourgini* was reported from fewer localities in South China. Nevertheless, its presence in the *Daguinaspis* Zone of Issendalenian Stage in Morocco permits a correlation with Chinese and Australian *A. huoi* Zone. As an auxiliary marker for *A. huoi*, the occurrence of *A. bourgini* in Morocco, South Australia and South China reinforce the correlation potential and resolution in species-level for the Cambrian Stage 3 in Gondwana region.

Keywords: *Abadiella*; South China; Gondwana; stratigraphic correlation; Cambrian Stage 3

1. Introduction

Abadiella huoi (Zhang), 1966 (= *Parabadiella huoi*) was recognized as the oldest polymerid trilobite in Australian East Gondwana (e.g. [1-4,15,17,26,]) and South China (e.g. [22-25,30,37, 40,43]). *Abadiella* Hupé, 1953 [12] was first introduced with two species, *A. bourgini* Hupé, 1953 [12] and *A. meteora* Hupé, 1953 [12] from the lower Cambrian Amouslek Formation (respectively at Oujjane and Amouslek) in the southeast of Tiznit, Morocco [10,12]. The type species *A. bourgini* was described based on the holotype of an incomplete cranidium. However, after re-examination of latex casts and original

specimens, Jell [1] clarified that the features used to distinguish the two species were taphonomic artefacts. That is, *A. meteora* was considered as a junior synonym of *A. bourgini*. *Parabadiella* Zhang, 1966 [38] and its type species *P. huoi* Zhang, 1966 [38] were erected based on a holotype and a paratype of two well-preserved cranidial specimens collected from the lower Cambrian Guojiaba Formation in the Dannangou section in Hanzhong, Shaanxi Province, China, and was assigned to the family Abadiellidae Hupé, 1953 [12]. Subsequently, more specimens resembling *Parabadiella* were reported from a number of localities along the west margin of South China, e.g. northern Sichuan [18,21,39], southern Shaanxi [5,39], and eastern Yunnan [22,39], and some were described as separate taxa, e.g., the subgenus *P. (Danangouia)* Chen, 1985 [5], and the genus *Guangyuanaspis* Zhang and Qian, 1974 [21]. Similar specimens from the Cambrian of Australia were described as *Abadiella huoi* [1,15] or *A. officerensis* [14]. Up to date, a total of 22 available species of *Parabadiella* and *Abadiella* were documented globally (details see below). Their taxonomic assignment has long been a controversial issue (e.g. [1,8,14,30,41, 42]), which hinders the stratigraphical correlation across regions. Lin [19] proposed a taxonomic revision for Chinese species of the taxon by using a single cluster analysis, a single specimen to each species. Finally, 18 species were incorporated into 9 species. However, the result of the cluster analysis commonly has multiple interpretations because the method is an unsupervised learning. Hence, the taxonomic result needs further tests and validations by other methods and more specimens.

Here we describe new specimens of *Abadiella* (= *Parabadiella*) recently collected from the type locality of *A. huoi* (Figure 1) and carry out morphometric quantitative analyses to re-tackle the problem of over-splitting species within the genus. The result makes conspecific correlation possible in the contemporary strata of Gondwana regions.

2. Geological setting

The study area, Hanzhong, is located in the northwest margin of Yangtze platform (Figure 1A). Neoproterozoic–Early Paleozoic strata are well developed. The Cambrian strata mainly crop out in the south part of the Liangshan syncline. The Danangou section, the type locality of *A. huoi*, is situated in the southeast wing of the Liangshan syncline, approximately 10 km west to Hanzhong city (Figure 1B). In the Danangou section, the Ediacaran–Cambrian succession is subdivided into, in ascending order, the late Ediacaran Dengying Formation, and the lower Cambrian Guojiaba and Xiannüdong Formations (Figure 1C). The Guojiaba Formation, 450m thick, is chiefly composed of argillaceous siltstone, silty mudstone and calcareous mudstone. More than 300 trilobite specimens were collected from the middle part of the Guojiaba Formation from 188m to 283m above its base at the Danangou section (Figure 1C). Most specimens are disarticulated exoskeletons, including 310 cranidia, 21 librigenae, 1 specimens of thoracic segments and 1 pygidium. All materials are housed in the collection of Shaanxi Key Laboratory of Early Life and Environments (LELE), Department of Geology, Northwest University, Xi'an, China.

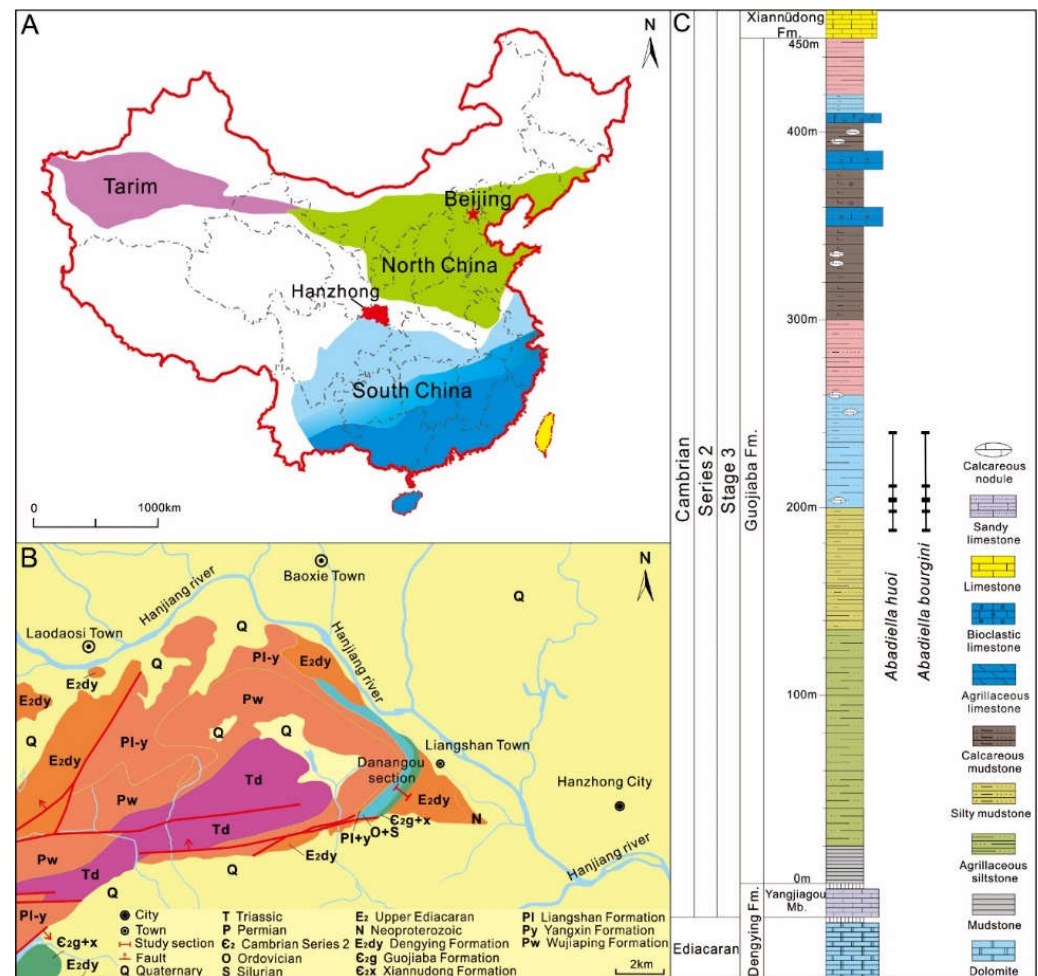


Figure 1. (A) Map showing the location of the study area (Hanzhong) in the northwest margin of Yangtze platform. (B) Geological map of the study area, showing the distribution of Cambrian outcrops and the location of the Danangou section. (C) Stratigraphic column of the Danangou section and stratigraphic ranges of collected trilobites.

3. Material and Methods

Fifty-four newly collected cranidia, as complete as possible and with less deformation, are selected for morphometric analyses on account of their morphological characteristics can be correctly transmitted during digitizing them. Together with 40 previously described specimens within 21 species (embracing two species cf.), a total of 94 specimens were finally determined for PCA and CVA: 2 from Morocco, 3 from South Australia and 89 from South China. For convenience and brevity in expression, we in most cases use abbreviations of species name or morphotypes of specimens in figures and text (details see Table 1).

Table 1. Abbreviations of related trilobite species and morphotypes, with their full name, specimen sources and references: *P*=*Prabadiella*, *PD*=*Parabadiella* (*Danangouia*), *A*=*Abadiella*, *G*=*Guangyuanaspis*.

Abbr.	Full (species) name	Reference (Specimens sources)	Abbr.	Full (species) name	Reference (Specimens sources)
T1-3	Morphotypes 1-3		Pz	<i>P. zhongliangsiensis</i> Chen, 1985	[5] (pl. 1, fig. 11)
Phuo	<i>P. huoi</i> Zhang, 1966	[38] (pl. 1, fig. 1,2)	Gm	<i>G. modaoyaensis</i> Zhang and Qian, 1974	[20] (pl. 33, fig. 7)
Pc	<i>P. conica</i> Luo,1981	[22] (pl. 27, fig. 8,9)	Gs	<i>G. shaanxiensis</i> Zhang et Lin, 1980	[39] (pl. 47, fig. 9, 11)
Pt	<i>P. tenuilimbata</i> Zhang and Lin, 1980	[39] (pl. 46, fig. 8,9)	Gf	<i>G. fandianensis</i> Zhang and Lin, 1980	
Ps	<i>P. shaanxiensis</i> Zhang and Lin, 1980	[39] (pl. 47, fig. 1-3)	Gw	<i>G. wudingensis</i> Zhang and Lin, 1980	
Po	<i>P. obscurata</i> Zhang and Lin, 1980	[39] (pl. 46, fig. 10,11)	Ah	<i>A. huoi</i> Zhang, 1966	[15] (p. 410, fig. 3D)
Pl	<i>P. longmenshanensis</i> Li, 1978	[18] (pl. 94, fig. 8,9)	Ab	<i>A. bourgini</i> Hupé, 1953	[42] (p. 302, fig. 4.2)
Pe	<i>P. elevate</i> Li, 1978		Am	<i>A. meteora</i> Hupé, 1953	[12] (pl. 19, fig. 10)
PDq	<i>P. (D.) quadrata</i> Chen, 1985	[5] (pl. 1, fig. 5-7)	Ao	<i>A. officerensis</i> Jago, 2002	[14] (p. 431, fig. 3.5)
PDt	<i>P. (D.) transversa</i> Chen, 1985	[5] (pl. 1, fig. 1-4)	Ah cf	<i>A. cf. huoi</i>	[1] (p. 278, fig. 183H)
Phan	<i>P. hanzhongensis</i> Chen, 1985	[5] (pl. 1, fig. 8)	Ph cf	<i>P. cf. huoi</i>	[44] (p. 150, fig. 2A)
Pn	<i>P. nanzhengensis</i> Chen, 1985	[5] (pl. 1, fig. 10)	Py	<i>P. yunnanensis</i> Luo, 1981	[22] (pl. 27, fig. 2-17)
Ge	<i>G. elegans</i> Li, 1974	[18] (pl. 95, fig. 11)			[24] (pl. 15, fig. 3)

Selected specimens were photographed under a SLR (single lens reflex) camera (Canon EOS 5DS) using digital heads (EF 100mm and MP-E 65mm) and 2 lights (Godox SL60W) respectively in the upper left and upper right around the lens for illumination. Uniform lighting and horizontal fixation of specimens are helpful to get better images from which accurate digitalized data were deprived for further analyses. Software CorelDraw (ver. 2018) and Photoshop (ver. 2022) were used for producing the scale bars, line art reconstructions and image processing.

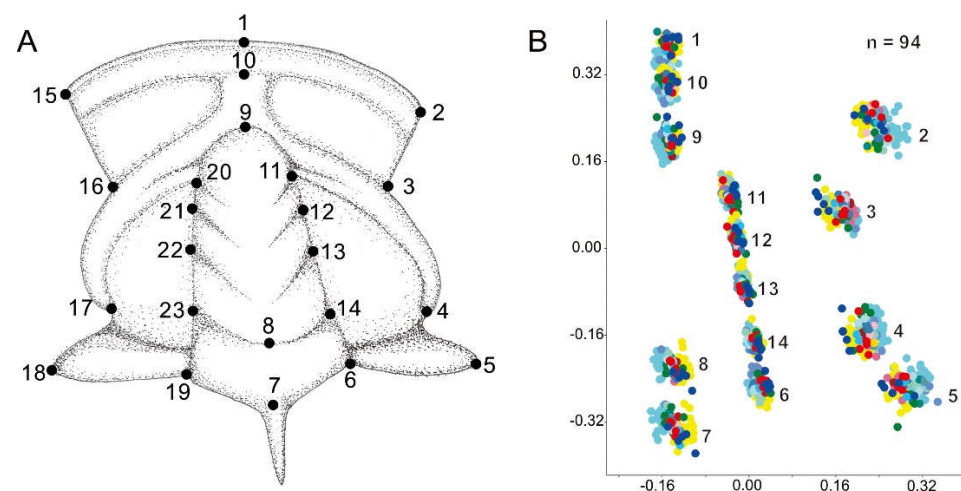


Figure 2. Landmarks on cranium chosen to represent the overall morphology of the crania. (A) A total of 23 landmarks on cranium. (B) Superimposition plot of all landmarks on selected cranial specimens (total number of cranial: 94).

After all photographs were taken, landmarks on them were digitalized using the software TpsDig (ver. 2.31) [27] by which we could also flip the image (usually left to right) when necessary. A total of 23 landmarks were chosen (Figure 2A) to represent the overall morphology of the crania, five along with the sagittal axis and nine pairs averagely on both side of it. A detail needs to be explained that in practice, the nine landmarks on one side of the sagittal axis were omitted and the rest of 14 landmarks (Figure 2B) were ultimately used to represent synthetical morphology symmetrically. This to some extent promotes the effectiveness of data collecting. Then, a set of morphological data of a specimen could be obtained and such data of all could then be arranged in one TSP file or other formats.

The data set, a set of landmark coordinates, was directly input to the software PAST (ver. 3.08) [11] to execute analyses. Before analyzing, it is necessary to standardize the data to Procrustes coordinates, using a Procrustes-fitting transformation by removing position, size and rotation. This is a process of aligning each landmark with which Procrustes superposition is produced (Figure 2B). Principal components analysis (PCA) was performed accounting for the variations between specimens or groups. And, it is used to reduce the multivariate data set to only two variables (the two first components) visualized by PC1 (horizontal axis) and PC2 (vertical axis) in scatter plots (Figure 3A-C; Figure 4A,C). Commonly, if the first one or two components could account for the most of the variance, the PCA has in a sense been successful. In other words, these two can be regarded as the most important components correlated with underlying variables of the data set for certain morphological characteristics.

To test the difference of two or more groups, we carried out the discriminant analysis (LDA). The latter is sometimes called canonical variates analysis (CVA). A scatter plot of specimens along the first two canonical axes was given, producing maximal and second to maximal separation between all groups. The axes are as the components in PCA. In CVA routine, a classifier provides a function to assign each individual to the given groups, according to the distance between the point and group mean. In this way, the predicted classification could be tested and corrected visually. Besides, the correct rate of the previous grouping could be shown by Jackknife validation (see Figure 3, Figure 4). Incidentally, some specimens with uncertain group could be classified in this module practically.

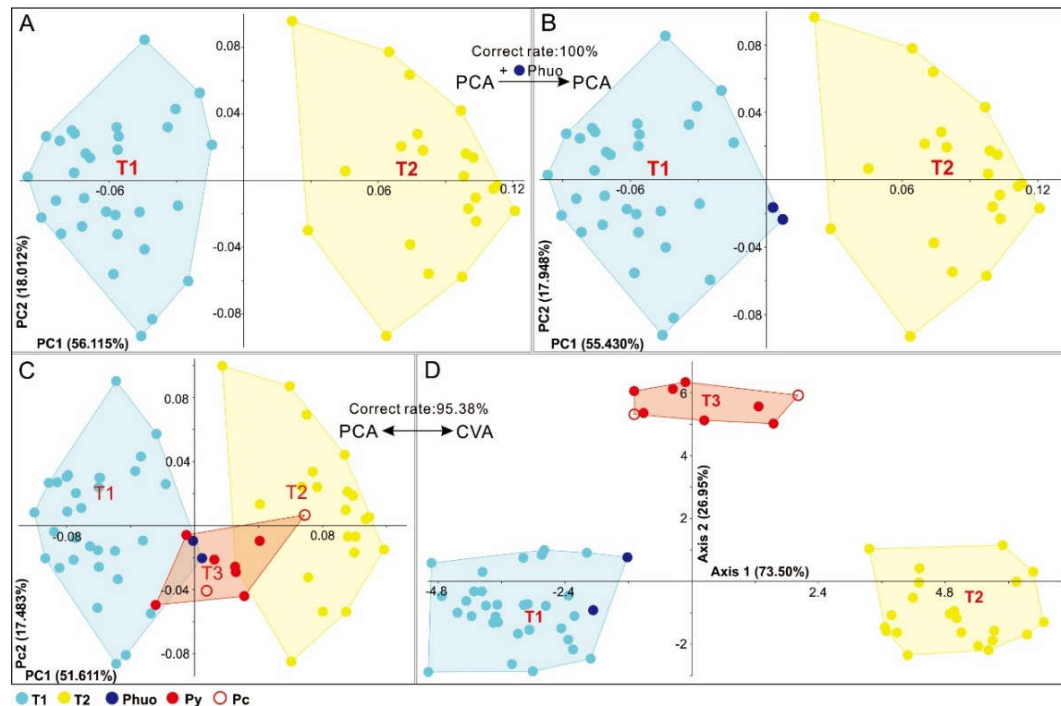


Figure 3. Scatter plots of principle principal components analysis (PCA) and canonical variates analysis (CVA), with the correct rate of Jackknife validation in CVA. (A) PCA of newly collected specimens, showing two recognized morphotypes (T1 and T2). (B) PCA of T1 and T2, added with two type specimens of original *P. huoi* (Phuo). (C) PCA of T1, T2, Phuo, Py and Pc, indicating the 3rd morphotype distinguished. (D) Corresponding CVA of T1, T2, Phuo, Py and Pc, to test the result of PCA: three morphotypes are clearly distinguished with a high correct rate of 95.38%.

4. Morphometric results

After the Procrustes-fitting transformation was carried out, a superposition plot of 94 samples was derived out directly (Figure 2B). In this graph, the superpositions of landmark 11-14 occupy closer areas relative to looser ones occupied by landmark 2-5, 7 and 8, which manifests a morphologically stable glabellar furrow and by comparison, a variant facial suture (including anterior branch, palpebral lobe and posterolateral limb) among all individuals or species.

In PCA of the specimens collected from the Danangou section, PC1 and PC2 accounts for 51.611% and 17.483% of the total variation (Figure 3A), and when two of Phuo were added in, they kept in 55.430% and 17.948% (Figure 3B). In this situation, two morphotypes are distinguished respectively within two separate regions (blue region of T1 and yellow region of T2). In addition, grouping assignment is tested by a Jackknife validation procedure in CVA and the correct rate reaches 100% (Figure 3A,B). In short, T1 (=Phuo) and T2 are two morphotypes recognized in specimens from the Danangou section.

In accordance with the above method, specimens of other species were progressively added into PCA and CVA. First, when adding Py and Pc (both from eastern Yunnan, South China), PC1 and PC2 respectively reaches 51.611% and 17.483% in PCA (Figure 3C). Py and Pc occupy a space discriminated from T1 and T2, which is in between and marked as a red region (T3). In corresponding CVA (Figure 3D), T1, T2 and T3 show an obvious distance from each other with a jackknifed correct rate of 95.38%. It is known directly from above that T1, T2 and T3 are reliable morphological grouping.

Second, when Phan, Pn, Pz, PDq, PDt, Pt, Po, Pl, Ps, Gm, Ge, Gs and Ph cf (all from South China) were included, equally three morphotypes are recognized with an area of gathering points in scatter plot (Figure 4A), with PC1 and PC2 of 45.56% and 15.745%. Here, Ph cf. is given an original assignment and when executing PCA and CVA, Ph cf. falls into a space near T2 (Figure 4A,B). Meanwhile, Gm, Ge, Gs, Phan, Pn, PDq, PDt, Pt,

Pl and Ps are grouped in T1, Pz is grouped in T2 and Po is grouped in T3, giving a jackknifed correct rate of 89.89% (Figure 4B).

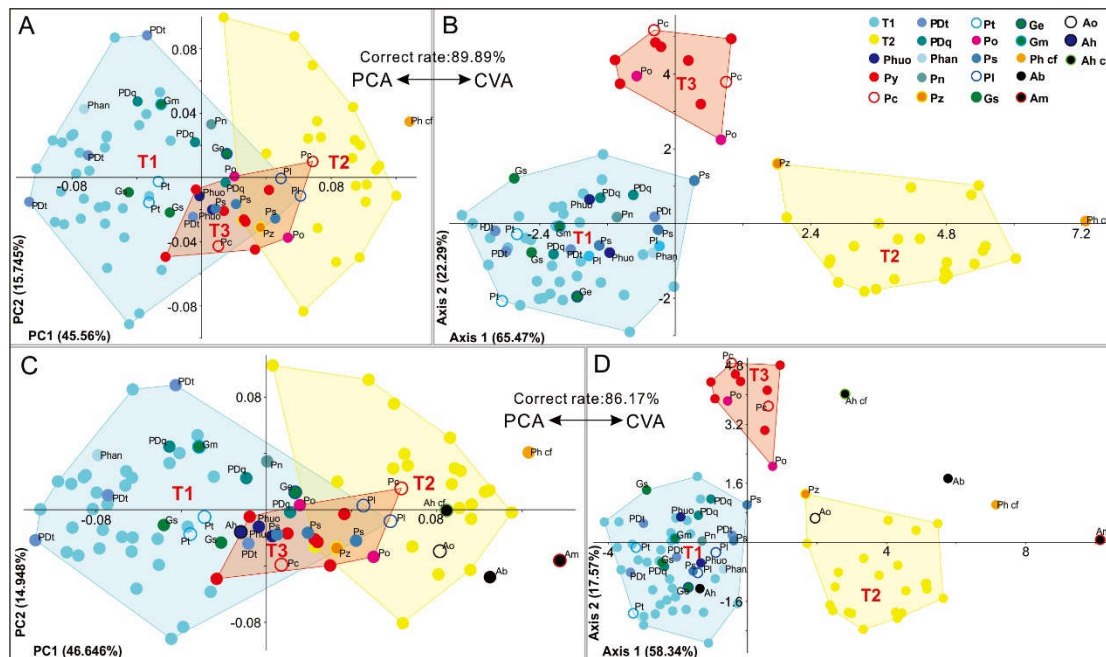


Figure 4. Scatter plots of PCA and CVA, with the correct rate of Jackknife validated in CVA. (A) PCA of Chinese *Abadiella* (involving 16 species), showing three recognizable morphotypes. (B) CVA of Chinese *Abadiella* (corresponding to A). (C) PCA of all selected specimens (involving 21 species). (D) CVA of all selected specimens (corresponding to C), showing a low correct rate Jackknife validation when giving the original taxonomic assignment of Ph cf, Ab, Am, Ao and Ah cf, which means here the assignment needs emendation.

Eventually, Ab and Am from Morocco, Ao, Ah and Ah cf from South Australia were involved. Given their original assignment of Ab, Am, Ao and Ah cf, the notable thing is that in PCA (Figure 4C), Ah falls in the vicinity of Phuo (original *Parabadiella huoi*), while Ao and Ah cf are in the area of T2, with PC1 and PC2 reaching 46.646% and 14.948%. Additionally, Ab and Am are near the area of T2 both in PCA and CVA (Figure 4C,D), and Ph cf is between Ab and Am (Figure 4D). In this step, the jackknifed correct rate declines slightly lower to 86.17% compared to the results in the steps above. This means that the original group needs revision, verifying the fact that *A. bourgini* (Ab) and *A. meteora* (Am) is conspecific as mentioned above.

5. Discussion

5.1. Valid status of *Abadiella* Hupé, 1953

As shown in PCA (Figure 4C), Ab, Am (=Ab), Ao, and Ah cf occupy a morphospace close to or partly overlaps that of T2. And, in CVA, the jackknife validation result shows a lower correct rate. This reveals that their close affinity to T2 determined at least by PC1 (46.646%) and PC2 (14.948%). Accordingly Ab, Am (=Ab), Ao and Ah cf can be grouped to T2. In other aspect, the morphospace of Ah in the vicinity of Phuo (original *Parabadiella huoi* from South China) in PCA (Figure 4C) confirms its conspecific fact to Phuo (original *Parabadiella huoi*).

To sum up, 40 specimens of 21 previously described species that were respectively assigned to *Abadiella*, *Parabadiella* and *Guangyuanaspis*, manifest a consistent morphospace in PCA (Figure 3A-C, 4A,C). Furthermore, by the law of priority in ICZN (International Code of Zoological Nomenclature)[13], *Parabadiella* Zhang, 1966, *Guyuanaspis* Zhang and Qian, 1974 [21] and *Parabadiella* (*Danangouia*) Chen, 1985 [5] are junior synonyms of *Abadiella* Hupé, 1953 [12] (see below).

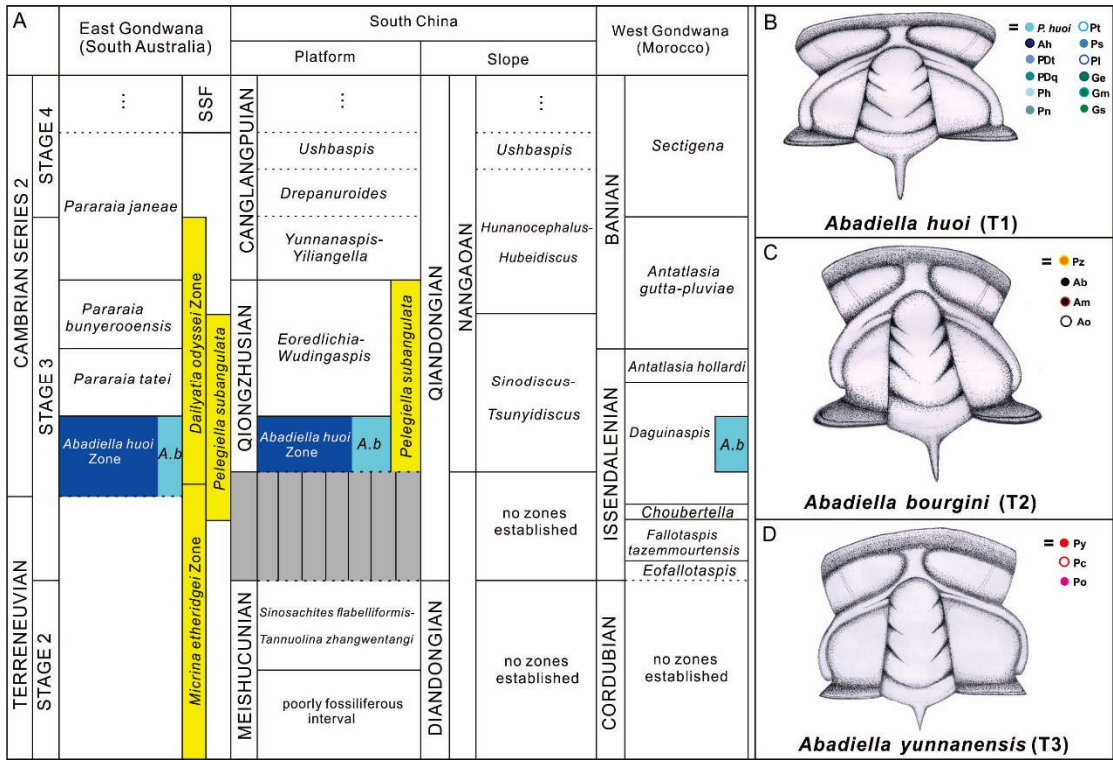


Figure 5. Tentative correlation chart of Cambrian Stage 3 between South China and Gondwana (modified from Zhang et al., 2017; Betts et al., 2018; Steiner et al., 2007; Peng, 2020) and reconstructions of three morphospecies of *Abadiella*. (A) Correlation chart of trilobite zonation of South China, East Gondwana and West Gondwana, showing revised zone of *Abadiella huoi* (in lake blue) with a potential correlation marker of *A. bourgini* (in light blue). (B–D), Reconstructed cranidia of *Abadiella* species: *A. huoi* (T1), *A. bourgini* (T2) and *A. yunnanensis* (T3).

5.2. Revision of species within *Abadiella*

The present results of PCAs and CVAs (Figure 3, 4) demonstrate that three main morphospecies can be recognized within *Abadiella* and are ultimately revised as three species: *Abadiella huoi* (Zhang, 1966 [38] = T1 (Phuo, Ah, Phan, Pn, PDq, PDt, Pt, Pl, Ps, Gm, Ge, Gs); *Abadiella bourgini* Hupé, 1953 [12] = T2 (Ab, Am, Ao, Ah cf, Ph cf, Pz); *Abadiella yunnanensis* (Luo), 1981 [22] = T3 (Py, Pc, Po) (more details see Figure 5B–D).

Three species Pe, Gf and Gw are not involved in morphometric analyses as a result of extremely obscure images. Here, we have no more discussion on their taxonomy, but merely provisionally assign them to *Abadiella* in accordance with the original figures and descriptions.

5.3. Paleogeographic distribution and stratigraphical range of *Abadiella*.

Abadiella bourgini was introduced from the Amouslek Formation (definition see [6,9]) at Oujjiane section in the western Anti-Atlas of Morocco (West Gondwana), with the original *A. meteora* (= *A. bourgini*) at Amouslek section from the identical lithostratigraphic unit and region [12]. In relation to the revised *A. bourgini*, it occurred in the *Daguinaspis* Zone, the uppermost zone of Issendalenian Stage in Morocco [7–10]. Its range in Atlas region approximately corresponds to the upper part of the Amouslek Formation accompanied with dominated fallotaspide trilobites [7,8].

In South Australian (East Gondwana), *A. huoi* has been known from the Arrowie and Satansbury Basins with a short range in the middle of the Ajax Limestone and the top of the Wilkawillina Limestone and Wirrapowie Limestone [1–4,15,32,33]. The *A. huoi* (= *Parabadiella huoi*) Zone equates to the upper part of the *M. etheridgei* Zone and corresponds to the lower part of the range of *Pelagiella subangulata* (2–4). In addition, the first appearance of *A. huoi* occurs below the peak of the Cambrian Arthropod Radiation isotope Excursion

[4] (CARE see [45]) and higher than those of the first appearances of *Liangshanella circum-bollina* in Ajax Formation at AJAX-M section [4,32]. *A. bourgini* was known only from the Ouldburra Formation in eastern Officer Basin [14] (= *A. officerensis*) and the Wilkawillina Limestone in Arrowie Basin [1] (= *A. huoi* cf., p. 278, fig. 183H). And its occurrence at Old Wirrealpa Mine should equate to that of *A. huoi* inferred by related fossil range [1] (p. 13, fig. 7).

A. huoi has a widespread distribution in South China (in platform), especially in eastern Yunnan, northern Sichuan and southern Shaanxi (see above). In eastern Yunnan, *A. huoi* was recognized with *A. yunnanensis* from the base of Yu'an-shan Member of Heilipu Formation [22,23,25]. In southern Shaanxi, *A. huoi* and *A. bourgini* co-occurs in the middle part of the Guojiaba Formation (Figure 1). As the first trilobite zone of the Cambrian System, *Abadiella* (= *Parabadiella*) *huoi* Zone overlaps the lowermost of the stratigraphic range of *Pelagiella subangulata* [31].

5.4. Stratigraphic significance of revised *Abadiella huoi* and *A. bourgini*

Abadiella (= *Parabadiella*) *huoi* Zone is the first trilobite zone of the lower Cambrian in South Australia (e.g. [1-4,15]) and has long been correlated with the *Parabadiella* Zone in South China (e.g. [1,22,30,40,43]). Jago et al. [15] reviewed the Cambrian biostratigraphy of South Australia and published a figure of *A. huoi* (p. 410, fig. 3D) and regarded it identical to *P. huoi* from South China. This specimen was subsequently examined by Betts et al. [3] and also emphasize the conspecific relation with Chinese *P. huoi*. This viewpoint is again supported by the morphometric results herein. Therefore, it is certain that *A. huoi* (= *P. huoi*) is a species that exists both in South Australia (East Gondwana) and South China (in platform) [Figure 6]. Additionally, previous *Parabadiella* Zone or *P. huoi* Zone should be emended by *A. huoi* Range Zone in South China.

In South Australia, the earliest trilobite sequence was well identified in the lower Cambrian, having close affinities with those of South China (e.g. [1,22,24]). *A. huoi* Zone is well constrained by associated trilobites and other faunas, e.g. bradoriids and small shelly fossils [2-4,26,32,33] and this make its correlation with South China more precise and convenient. The presence of *Eoredlichia shensiensis* in the overlying *Pararaia tatei* Zone permits the correlation with the lower part of the *Eoredlichia-Wudingaspis* Zone of South China (Jell in [1]) and its presence helps to constrain the upper boundary of *A. huoi* Zone, most likely asynchronous in the two continents. The first appearance of *Abadiella huoi* in South Australia is evident as discussed above. In South China, it commonly appears in an interval overlying unconformities or a poorly fossiliferous strata (e.g. [31,43,44,46]). In addition, *A. huoi* first appeared alongside abundant bradoriids, e.g. *Liangshanella liangshanensis*, *Hanchiangella alta* and *Shensiella crassa* [16], in the Guojiaba Formation at the studied section (herein, Danangou section). In views of the above, the first appearance of *A. huoi* in platform of South China is slightly higher than it first appearance in South Australia. Overall, *A. huoi* has a consistent stratigraphic range in the two regions (Figure 5A).

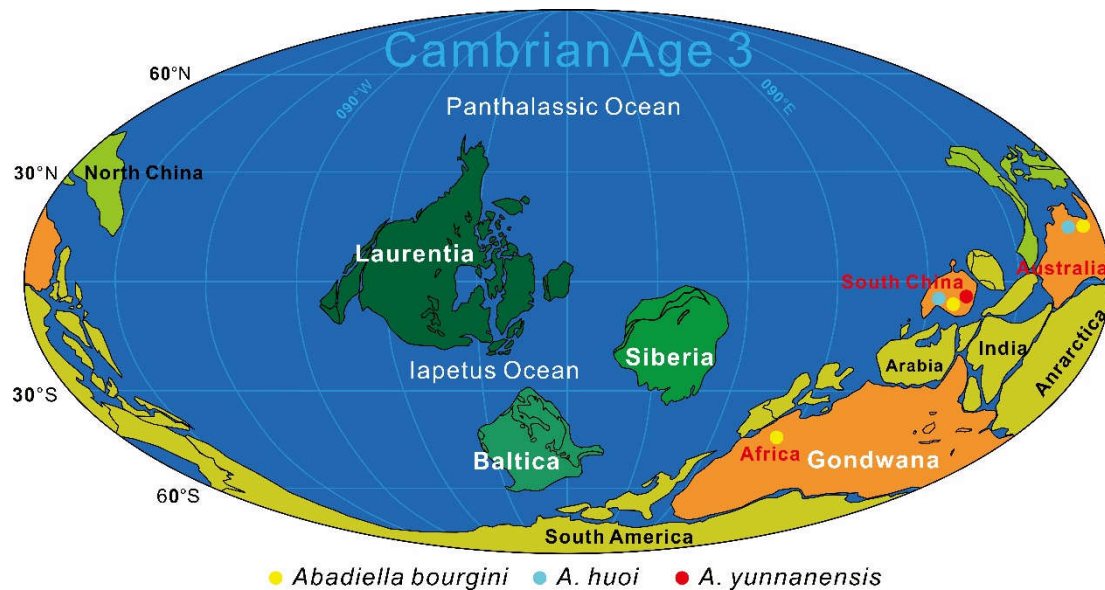


Figure 6. Reconstruction of paleogeographic map with distribution of emended *A. bourgini*, Hupé, 1953, *A. huoi* Zhang, 1966, and *A. yunnanensis* Luo, 1981 in the Cambrian Age 3 (modified from Scotese C.R., 2001), showing the correlation potential of *A. bourgini* and *A. huoi* in South China, South Australia (East Gondwana) and Morocco (West Gondwana).

In comparison with *A. huoi*, *A. bourgini* was reported from less localities, and with very few specimens excepting in the Dannangou section. Nevertheless, its presence in the *Daguinaspis* Zone of Issendalenian Stage in Morocco permits a correlation with Chinese and Australian *Abadiella huoi* Zone (Figure 5A). Its occurrences help to reinforce the correlation resolution in Gondwana regions: Morocco, South Australia and South China, as an auxiliary indicator for *A. huoi* (Figure 5A, 6)

6. Conclusion

Selected cranidium specimens constrain the morphospace of *Abadiella* shown in the scatter plots. PC1 and PC2 stoutly represent the morphological character with high weightings in PCA. Further validation for the presupposed taxonomy was performed by CVA to calibrate the ultimate classification. In this way, short distances between specimens confined in a consistent morphospace demonstrate their close morphological affinity, supporting the congeneric concept. That is, *Parabadiella* Zhang, 1966 [38], *Guangyuanaspis* Zhang and Qian, 1974 [21], and *Parabadiella* (*Danangouia*) Chen, 1985 [5] are junior synonyms of *Abadiella* Hupé, 1953 [12]. And that, three morphospecies were chiefly recognized from 94 cranidial specimens within 21 species of *Abadiella*, respectively representing *A. bourgini* Hupé, 1953 [12], *A. huoi* Zhang, 1966 [38] and *A. yunnanensis* Luo, 1981 [22] (revised taxonomy see below).

According to the morphometric results, *A. huoi* cooccurs in South Australia and South China, which allows to correlate the Australian *A. huoi* Range Zone to the identical zone in platform facies of South China, as the first trilobite zone in two regions. By comparison with previous genus-based correlations, as an auxiliary marker for *A. huoi*, the occurrence of *A. bourgini* in Morocco, South Australia and South China reinforce the correlation potential and resolution in species-level for the Cambrian Stage 3 in Gondwana regions.

7. Systematic palaeontology

Morphological terms used herein follow those of Whittington and Kelly [36]. In the following descriptions, “long” and “short” are used with reference to longitudinal (sagittal, sag., and exsagittal, exs.), and “broad” (or “wide”) and “narrow” are used with reference to transverse (tr.) dimensions [35] (p. 2).

Class Trilobita Walch, 1771

Order Redlichiida Richter, 1933
 Suborder Redlichiina Richter, 1932
 Superfamily Redlichioidea Poulsen, 1927
 Family Abadiellidae Hupé, 1953
 Genus *Abadiella* Hupé, 1953

- 1953 *Abadiella* Hupé; p. 204 [12].
 1963 *Abadiella* Hupé; Lu et al., p. 56 [20].
 1966 *Parabadiella* Zhang; p. 163 [38].
 1974 *Parabadiella* Zhang; Lu et al., p. 87, pl. 33, fig 1 [21].
 1974 *Guangyuanspis* Zhang and Qian in Lu et al.; p. 88 [21].
 1978 *Parabadiella* Zhang; Li, p. 202 [18].
 1978 *Guangyuanspis* Zhang and Qian, Li, p. 212 [18].
 1980 *Parabadiella* Zhang; Zhang et al., p. 173 [39].
 1980 *Guangyuanspis* Zhang and Qian; Zhang et al., p. 177 [39].
 1981 *Parabadiella* Zhang; Luo, p. 336 [22].
 1982 *Parabadiella* Zhang; Luo et al., p. 210 [23].
 1984 *Parabadiella* Zhang; Xing et al., p. 226 [37].
 1984 *Parabadiella* Zhang; Luo et al., p. 59 [24].
 1985 *Parabadiella* Zhang; Chen, p. 332 [5].
 1985 *Parabadiella* (*Danangouia*) Chen; p. 333 [5].
 1987 *Parabadiella* Zhang; Zhang; p. 4 [40].
 1990 *Abadiella* Hupé (part); Jell in Bengtson et al., p. 276 [1].
 1994 *Parabadiella* Zhang; Luo et al., p. 126 [25].
 1997 *Abadiella* Hupé; Zhang in Kaesler, p. 461 [41].
 1997 *Guangyuanspis* Zhang and Qian; Zhang in Kaesler, p. 461 [41].
 1997 *Parabadiella* Zhang; Zhang in Kaesler, p. 462 [41].
 2001 *Parabadiella* Zhang; Zhang et al., p. 303 [42].
 2001 *Abadiella* Hupé; Zhang et al., p. 305 [42].
 2002 *Abadiella* Hupé; Jago et al., p. 429 [14].
 2006 *Abadiella* Hupé; Jago et al., p. 410 [15].
 2020 *Parabadiella* Zhang; Zhang et al., p. 155 [44].
 2020 *Abadiella* Hupé; Peng, p. 168 [28].

Type species. *Abadiella bourgini* Hupé, 1953 [12] (p. 204, fig. 45, 2), *Daguinaspis* Zone, Issendalenian, Tiznit, Morocco.

Other species. *Abadiella huoi* Zhang, 1966 [38], Chiungchussu Formation, South China, early Age 3, South Australia; *Abadiella yunnanensis* Luo, 1981 [22], Chiungchussu Formation, South China.

Emended diagnosis. Glabella subtruncato- or truncato-conical, with three pairs of lateral furrows. Occipital ring with a median spine. Eye ridge oblique, undifferentiated from palpebral lobe, dividing at axial end into a parafrontal band and a posterior trunk entering the frontal lobe of the glabella. Mesial ridge conspicuous on the preglabellar field, its posterior portion connects with the parafrontal band. Anterior border convex and slightly arcuate. Posterior lateral limb short and narrow. Librigena moderately convex; narrow posterior border meets genal spine at an angle of approximately 90°.

Remarks. In accordance with the morphometric results, *Parabadiella*, *Guangyuanspis* and *Parabadiella* (*Danangouia*) are here considered as junior synonymies of *Abadiella*. The differences, such as shape of cranidium or glabella, course of the facial suture, shape of occipital ring and form of posterior lateral limb, originally used for discriminating genera or subgenera, are interspecific variations.

Distribution and age. Morocco, late Issendalenian; South China; early Nangaoan (=“Chiungchussuan”). South Australia, *Pelagiella subangulata* Zone (provisional Cambrian Age 3).

Abadiella huoi (Zhang), 1966 (Figure 5a, Figure 7)

1966 *Parabadiella huoi* Zhang, 1966; p. 164, pl. 1, figs. 1-2, text-fig. 17 [38].

- 1974 *Parabadiella huoi* Zhang; Lu et al., p. 87, pl. 33, fig1 [21].
- 1974 *Guangyuanaspis modaoyaensis* Chang and Qian in Lu et al.; p. 88, pl. 33, fig. 7 [21].
- 1978 *Parabadiella longmenshanensis* Li; p. 202, pl. 94, figs. 8-9 [18].
- 1978 *Guangyuanaspis modaoyaensis* Zhang and Qian in Li; p. 212, pl. 95, fig. 10 [18].
- 1978 *Guangyuanaspis elegans* Li; p. 213, pl. 95, fig. 11 [18].
- 1980 *Parabadiella huoi* Zhang; Zhang et al., p. 174, pl. 46, figs. 1-6 [39].
- 1980 *Parabadiella shaanxiensis* Zhang and Lin in Zhang et al.; p. 174, pl. 47, figs. 1-3 [39].
- 1980 *Parabadiella tenuilimbata* Zhang and Lin in Zhang et al.; p. 175, pl. 46, figs. 7-9 [39].
- 1980 *Guangyuanaspis modaoyaensis* Chang and Qian; Zhang et al.; p. 178, pl. 47, fig. 8 [39].
- 1980 *Guangyuanaspis shaanxiensis* Zhang et Lin in Zhang et al.; p. 178, pl. 47, figs. 9-11 [39].
- 1985 *Parabadiella hanzhongensis* Chen; p. 332, pl. 1, figs. 8-9 [5].
- 1985 *Parabadiella nanzhengensis* Chen; p. 332, pl. 1, fig. 10 [5].
- 1985 *Parabadiella (Danangouia) transversa* Chen; p. 334, pl. 334, figs. 1-4 [5].
- 1985 *Parabadiella (Danangouia) quadrata* Chen; p. 334, pl. 1, figs. 5-7 [5].
- 1987 *Parabadiella huoi* Zhang; Zhang, p. 4, pl. 1, figs. 3-11 [40].
- 1990 *Abadiella huoi* Zhang (part); Jell in Bengtson et al., p. 277, fig. 183A-G, J, K [1].
- 1997 *Guangyuanaspis modaoyaensis* Zhang and Qian; Zhang in Kaesler, p. 461, fig. 297,2 [41].
- 1997 *Parabadiella huoi* Zhang; Zhang in Kaesler, p. 462, figs. 298.1a, 298.1b [41].
- 2001 *Parabadiella huoi* Zhang; Zhang et al., p. 304, fig. 3.1-3.3, non fig. 3.4 [42].
- 2006 *Abadiella huoi* Zhang; Jago et al., p.410, fig.3B [15].
- 2020 *Abadiella huoi*; Peng, p. 168, pl. 58, figs. 4-8 [28].
- Holotype*. Cranidium [38] (fig. 1.1, NIGP 18139) from Guojiaba Formation, Liangshan, Hanzhong, southern Shaanxi, China.
- Paratype*. Cranidium [38] (fig. 1.2, NIGP 18140) from the same locality and horizon of Holotype.
- Material*. 195 cranidia.

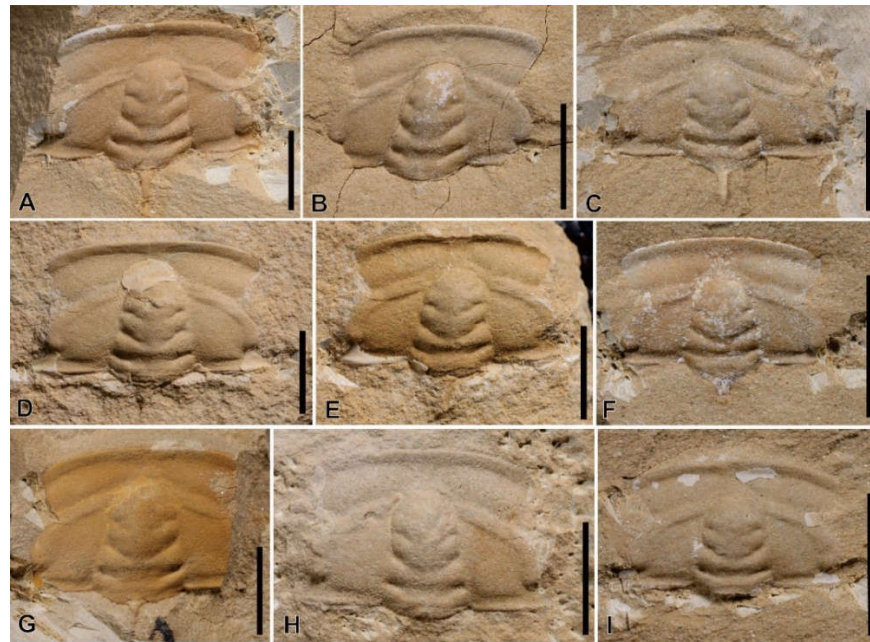


Figure 7. *Abadiella huoi* (Zhang), 1966 from the middle part of the Guojiaba Formation in the Dan-nangou section (Liangshan, Shaanxi Province, China), scale bars = 5mm. (A-I) Carnidia: HLD190-43, HLD168-88, HLD168-38, HLD168-30, HLD168-77, HLD168-51, HLD184-65, HLD190-8, HLD168-60.

Diagnosis. Cranidium rectangular and slightly wider than long. Glabella tapers gently forward, with long and deeply incised S1 and S2 furrows. Eye ridge thick, oblique moderately. Palpebral lobe arcuate gently, half as long as glabella, lying immediately behind cranidial mid-length. Anterior border with a weak or stout plectrum running almost onto preglabellar furrow.

Description. Cranidium rectangular and transversely broad, gently convex and with anterior margin arched gently forward. Glabella truncatoconical, tapering forward with a rounded anterior end; three pairs of lateral furrows, with length and horizontal angle decreasing forward; S1 and S2 well impressed, deepest near axial furrow and shallowing gradually towards axis; S3 at level of middle of eye ridge, with deep pit laterally. Axial furrow shallow. Occipital furrow deepest abaxially and shallowing in axial section. Occipital ring gently convex, tapering slightly laterally, and with a median occipital spine. Eye ridge oblique, undifferentiated from palpebral lobe, dividing at axial end into a parafrontal band and a posterior trunk entering the frontal lobe of the glabella. Palpebral lobe short somewhat and arcuate prominently outwards. Palpebral region as wide as middle section of glabella. Preocular limb elongate, subtriangular, sloping down to border furrow, with a pair of prominent, oblique and slight arcuate preocular facial lines. Preglabellar limb long with a conspicuous mesial ridge of which posterior portion connects with the parafrontal band. Anterior border prominently convex with an even length. Border furrow with moderate depth and breadth. Anterior branch of facial suture slightly diverges up to border furrow before converging slightly to anterior margin. Posterior branch of facial suture diverges markedly. Posterior lateral limb short and narrow. Posterior border furrow long, running from axial furrow, becoming longer and shallower on lateral descending posterior part of fixigena. Posterior border short and convex, slightly longer laterally, with relatively long posterior slope to margin becoming flatter and longer as a facet on lateral slope.

Remarks. With the revision of the concept of *Abadiella*, we transfer *Parabadiella huoi* to *Abadiella huoi* as a valid species name. As discussed in Zhang et al. [43], *Abadiella huoi* was recognized and regarded as a morphotype with a larger glabella and shorter occipital spine differing from the other morphotype assigned to *A. bourgini* in this paper (see below) and it was verified here that these characteristics reflects interspecific variations.

Horizon and locality. The middle of the Guojiaba Formation, lowest Yuanshan Member of Heilinpu Formation, lower Qiongzhusian, eastern Yunan, northern Sichuan and southern Shaanxi, South China; the middle of the Ajax Limestone, the upper of the Wilkawillina Limestone and Wirrapowie Limestone, provisional Cambrian Stage 3, Arrowie and Satansbury Basins, South Australia.

***Abadiella bourgini* Hupé, 1953 (Figure 5C, Figure 8)**

1953 *Abadiella bourgini* Hupé, 1953; p. 205, fig. 45.2 [12].

1953 *Abadiella meteora* Hupé, 1953; p. 205, fig. 45.3, fig. 36.16, pl. 19. fig. 10 [12].

1963 *Abadiella bourgini*; Lu et al., p. 56, pl. 5, fig. 10 [20].

1985 *Parabadiella zhongliangsiensis* Chen; p. 333, pl. 1, fig. 11 [5].

1990 *Abadiella* sp. cf. *A. huoi* Zhang; Jell in Bengtson et al., p. 281. fig. 183H [1].

1997 *Abadiella bourgini*, Zhang in Kaesler, p. 461, fig. 297.1 [41].

2002 *Abadiella officerensis*, Jago et al., p. 430, fig. 3.9-3.9 [14].

2020 *Abadiella* cf. *huoi* Zhang, 1966; Zhang et al., p. 155. fig. 2 [44].



Figure 8. *Abadiella bourgini* Hupé, 1953 from the middle part of the Guojiaba Formation in the Dan-nangou section (Liangshan, Shaanxi Province, China), scale bars = 5mm. (A-I) Cranidia: HLD168-69, HLD190-51, HLD168-16, HLD168-12, HLD168-34, HLD168-35, HLD168-44, HLD168-50, HLD168-58.

Holotype. Cranidium [12] (fig. 45.2) from the Amouslek Formation, Oujjiane section, western Anti-Atlas, Morocco.

Material. 115 cranidia.

Diagnosis. Cranidium sunquadrangle and longer than wide. Glabella long and narrow. Eye ridge oblique notably. Palpebral lobe long and arched slightly.

Description. Cranidium rectangular and longitudinally long, gently convex and with anterior margin arched gently forward. Glabella truncatoconical, long and narrow, tapering forward strongly with a rounded anterior end; three pairs of lateral furrows, with length and horizontal angle decreasing forward; S1 and S2 well impressed, deepest near axial furrow and shallowing gradually towards axis; S3 at level of middle of eye ridge,

with deep pit laterally. Axial furrow shallow. Occipital furrow deepest abaxially and shallowing in axial section. Occipital ring gently convex, tapering slightly laterally, and with a median occipital spine. Eye ridge oblique strongly, undifferentiated from palpebral lobe, dividing at axial end into a parafrontal band and a posterior trunk entering the frontal lobe of the glabella. Palpebral lobe long somewhat and arched slightly. Palpebral region as wide as middle section of glabella. Preocular limb elongate, subtriangular, sloping down to border furrow, with a pair of prominent, oblique and slight arcuate preocular facial lines. Preglabellar limb long with a conspicuous mesial ridge of which posterior portion connects with the parafrontal band. Anterior border prominently convex with an even length. Border furrow with moderate depth and breadth. Anterior branch of facial suture slightly diverges up to border furrow before converging slightly to anterior margin. Posterior branch of facial suture diverges markedly. Posterior lateral limb short and narrow. Posterior border furrow long, running from axial furrow, becoming longer and shallower on lateral descending posterior part of fixigena. Posterior border short and convex, slightly longer laterally, with relatively long posterior slope to margin becoming flatter and longer as a facet on lateral slope.

Remarks. This species has a relatively longer cranidium, longer and narrower glabella, more oblique eye ridge and longer palpebral eye lobe distinguished from *A. huoi*. Zhang et al. [43] observed that the morphological characteristics of the new materials of T2 resemble those of original *A. officerensis* [14] (p. 430, figs. 3.1-3.9) from South Australian and *A. bourgini* [12] (p. 204, Figures 45 and 2) from Morocco. The morphometric results support their conspecific status.

Horizon and locality. The middle part of Guojiaba Formation, Xihaoping Member of the Dengying Formation, early Qiongzhusian, southern Shaanxi, South China; Ouldburra Formation, eastern Officer Basin, South Australian; Amouslek Formation, the uppermost zone of Issendalenian Stage, Oujjane and Amouslek, western Anti-Atlas in Morocco.

Author Contributions: Conceptualization, X.L.Z. and M.K.W.; methodology, X.L.Z. and M.K.W.; investigation, X.L.Z. and M.K.W.; sampling, M.K.W.; visualization, M.K.W.; software, M.K.W.; writing original draft preparation, M.K.W.; writing-review and editing, X.L.Z. and S.C.P.; supervision, X.L.Z.; funding acquisition, X.L.Z. All authors have read and agreed to the published version of the manuscript.

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