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Revised Wuchiapingian conodont taxonomy and succession of South China

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Abstract.—South China has become the most important area to establish a global stratigraphic framework of the Wuchiapingian Stage because complete Wuchiapingian sequences include the GSSPs for the base and top of the stage. As the markers of the Wuchiapingian GSSP, conodonts are the most important fossil group to establish the Wuchiapingian biostratigraphic framework. However, few documents have investigated in detail the conodont biostratigraphic succession through the entire Wuchiapingian Stage. Furthermore, the conodont taxonomy of several Wuchiapingian *Clarkina* species is still debated. Therefore, we here review all Wuchiapingian *Clarkina* species from South China and figure ontogenetic growth series from juvenile to adult individuals for each valid and important species in order to revise both Wuchiapingian conodont taxonomy and the biostratigraphic succession. Based on the Penglaitan, Dukou, and Nanjiang sections, seven conodont zones (*Clarkina postbitteri postbitteri*, *C. dukouensis*, *C. asymmetrica*, *C. leveni*, *C. guangyuanensis*, *C. transcaucasica*, and *C. orientalis*) are recognized. The Wuchiapingian *Clarkina* species lineage is also reviewed to confirm the conodont biostratigraphic framework. The Guadalupian-Lopingian boundary (GLB) interval represents a sequence boundary. The time framework of the pre-Lopingian extinction interval indicates that the beginning of the end-Guadalupian regression is in the upper part of the *Jinogondolella postserrata* Zone, and the beginning of the early Lopingian transgression is in the lower part of the *Clarkina dukouensis* Zone in South China.

Introduction

Continuous marine depositional sequences of the Wuchiapingian are very limited in distribution because the global end-Guadalupian regression resulted in the emergence of much of the supercontinent Pangea. There are only a few regions along the continental margin and some blocks in the Paleotethys with well-developed marine Wuchiapingian sequences in the world. South China is well known for complete Wuchiapingian sequences and the GSSPs for the base and the top of the Wuchiapingian Stage have been precisely defined by conodonts, respectively in the Penglaitan Section of Guangxi Province and in the Meishan Section of Zhejiang Province (Jin et al., 2006a, b). Thus, South China has become the most important area to establish a global stratigraphic framework of the Wuchiapingian Stage.

Conodonts are one of the most important fossil groups in the Permian because all GSSPs and candidate sections for GSSPs of the Permian either have been or will be defined by conodont species, and the biostratigraphic framework in the Permian was also established based on the evolutionary lineages of conodonts (Henderson, 2017). Wuchiapingian conodonts have been widely documented from many sections in South China, including the Liangshan area in Shaanxi (Wang, 1978), the Meishan sections in Zhejiang (Wang and Wang, 1981; Zhao et al., 1981; Sheng et al., 1987; Mei et al., 2004; Zhang et al., 2009; Yuan et al., 2014a), the Xuanen, Ermen, Wufeng, Tianqiao, and Maoershan sections in Hubei (Clark and Wang, 1988; Duan, 1990; Li, 1991; Wang and Xia, 2004; Zhang et al., 2008), the Shangsi, Dukou, and Nanjiang sections in Sichuan (Li et al., 1989; Mei et al., 1994a, b), the Yangtaoshan and Yangongtang sections in Anhui (Duan, 1990), the Penglaitan, Tieqiao, and Fengshan sections in Guangxi (Mei et al., 1994b, 1998a; Wang et al., 1998; Wang, 2000, 2001, 2002; Henderson et al., 2002; Jin et al., 2006a), the Hushan region in Jiangsu (Duan, 1990), the Suoxiyu, Rencunping, Jiangya, and Matian sections in Hunan (Wang and Dong, 1991; Tian, 1993a, b; Mei and Wardlaw, 1996; Cao et al., 2013), the Qibaoshan Section in Jiangxi (Wang et al., 1997), and the Lengshuixi and Daijiagou sections in Chongqing (Yang et al., 2008; Yuan et al., 2015). However, most of the previous conodont studies focused on the Capitanian-Wuchiapingian (Guadalupian-Lopingian) boundary interval and the Wuchiapingian-Changhsingian boundary interval (e.g., Wang et al., 1997; Wang, 2000, 2001, 2002; Henderson et al., 2002; Mei et al., 2004; Jin et al., 2006a, b), or they simply described a few conodont elements (e.g., Zhao et al., 1981; Clark and Wang, 1988; Duan, 1990; Li, 1991; Wang and Dong, 1991; Wang and Xia, 2004; Yang et al., 2008). Only a few studies have investigated in detail the conodont biostratigraphic succession through the entire Wuchiapingian Stage (e.g., the Dukou and Penglaitan sections in Mei et al., 1994a, b, 1998a). Mei et al. (1994a, b, 1998a) illustrated only a few specimens for most species, which do not display the full range of character morphology and ontogenetic series. The sample-population concept (Wardlaw and Collinson, 1979; Mei et al., 2004; Shen and Mei, 2010; Yuan et al., 2014a) demands the illustration of multiple

specimens that show the range of morphology, including ontogenetic changes in order to avoid potential misunderstanding from a form-species approach.

Meanwhile, the conodont taxonomy of several Wuchiapingian *Clarkina* species, especially *C. postbitteri postbitteri,* which is used to define the base of the Wuchiapingian Stage, is still debated. The First Appearance Datum (FAD) of *C. postbitteri postbitteri* is in Bed 6k at the Penglaitan Section, based on the taxonomy in Mei et al. (1994a) and Henderson et al. (2002). However, Wang et al. (1998), Wang (2000, 2001, 2002), and Wang and Kozur (2007) had a different taxonomic view of some *Clarkina* species, suggesting that the first occurrence of *C. dukouensis*, which is the descendant of *C. postbitteri postbitteri*, occurs in Bed 6k at the Penglaitan Section. In addition, Wang and Dong (1991) described some *C. guangyuanensis* elements in the Maokou Formation, but this species was established and described from the middle part of the Wuchiaping Formation by Li et al. (1989). Thus, these arguments created issues affecting both the basal Wuchiapingian Stage identification and the establishment of a high-resolution conodont succession in the Wuchiapingian Stage.

In this paper, we review all Wuchiapingian *Clarkina* species in South China and figure ontogenetic growth series from juvenile to gerontic individuals for each valid and important species. In doing so, we revise both Wuchiapingian conodont taxonomy and the biostratigraphic succession. The result is a biostratigraphic framework for an interval of stable biodiversity following both a late Guadalupian extinction (Shen and Shi, 2009; Wang et al., 2014) and the latest Guadalupian lowstand that marked the lowest relative sea level of the Phanerozoic.

Stratigraphy

Most regions in South China have Wuchiapingian deposits, except for three lands (the Kangdian, Yunkai, and Cathaysian lands) and the sedimentary deposits have been referred to several formations. Four of them, the Xuanwei, Lungtan, Wuchiaping, and Heshan formations, are representative (Fig. 1.1). The Xuanwei Formation consists of sandstone, shale, and coal seams containing abundant plant fossils and few marine fossils. It represents terrestrial and/or marine-nonmarine transitional sediments, which are distributed mainly east to the Kangdian Land. The Lungtan Formation is dominated by siltstone, shale, and coal, as well as a few limestone beds that contain rare conodonts and abundant brachiopod and plant fossils. It represents a transitional facies between terrestrial and marginal marine. The Wuchiaping Formation is marked at the base by the Wangpo Shale and comprises siltstone, shale, coal, limonite, and ash beds that represent a deposit associated with the sequence boundary between the Wuchiaping limestone and the Kuhfeng and/or Maokou formations and the related Emeishan Large Igneous Province. The main part of the Wuchiaping Formation is composed of limestone with some cherty nodules or bands and contains abundant brachiopods, the fusulinid *Codonofusiella*, corals, and bivalves. The Heshan Formation consists of siliceous limestone, limestone, and many cherty nodules or bands interbedded with coal seams that indicate a shallower-water depositional environment than the Wuchiaping Formation. Therefore, the Wuchiaping and Heshan formations have the optimal successions to establish high-resolution conodont biostratigraphy of the Wuchiapingian Stage.

Conodont succession

The first named Wuchiapingian conodont species, *Neogondolella* (=*Clarkina* in this paper) *liangshanensis*, which was established by Wang (1978) in China, was considered as the only marker of the Wuchiapingian conodont biostratigraphy. Wang and Wang (1981) established two assemblage zones, the *N. liangshanensis-N.* "*bitteri*" Assemblage Zone and the *N. orientalis* Assemblage Zone, in the "Wuchiapingian Stage" based on conodonts from the Wuchiaping and Lungtan formations in South China. However, Mei and Wardlaw (1996) considered that *liangshanensis* and *bitteri* did not coexist in the same stratigraphic interval so that the "*N. liangshanensis-N. bitteri*" Assemblage Zone could not be used. Yang et al. (1987) revised these two assemblage zones as the *Gondolella* (=*Clarkina* in this paper) *liangshanensis* Zone and the *Gondolella* (=*Clarkina* in this paper) *orientalis* Zone, and confirmed *G. liangshanensis* as a marker of the lower part of the Wuchiaping Formation and *G. orientalis* as a marker of the upper part of the Wuchiaping Formation. Clark and Wang (1988) identified a few specimens as *Mesogondolella rosenkrantzi* (their *Neogondolella*) in the upper part of the Wuchiaping Formation. However, Mei and Henderson (2001) considered *M. rosenkrantzi* as a marker of the Wuchiapingian only in the North Cool Water Province. Li et al. (1989) added two marker species, *Neogondolella* (=*Clarkina* in this paper) *leveni* and *N. guangyuanensis*, into the *N. liangshanensis-N. bitteri* Assemblage Zone. They considered that the upper and lower relationships of the two Wuchiapingian assemblage zones were difficult to determine. Wang and Dong (1991) and Tian (1993a, b) recognized the *N. leveni* Assemblage Zone between the *N. liangshanensis-N. bitteri* Assemblage Zone and the *N. orientalis* Assemblage Zone. Mei et al. (1994a) determined seven Wuchiapingian zones, in ascending order: *Clarkina dukouensis*, *C. asymmetrica*, *C. leveni*, *C. guangyuanensis*, *C. transcaucasica*, *C. orientalis*, and *C. inflecta* zones. In addition, Mei et al. (1994b) and Mei and Wardlaw (1996) considered that specimens identified as *N.* "*bitteri*" by Wang and Wang (1981) have a very different mophology from those of North America and established the species *Clarkina postbitteri*. Thus, the *C. postbitteri* Zone, which was considered as the first zone of the Wuchiapingian, was added below the *C. dukouensis* Zone by Mei et al. (1994b). Henderson et al. (2002) named a new subspecies, *C. postbitteri hongshuiensis*, which is considered as the topmost conodont zone of the Capitanian (Guadalupian), making the *C. postbitteri postbitteri* zone as the first zone of the Wuchiapingian. The Wuchiapingian conodont succession now includes the *Clarkina postbitteri postbitteri*, *C. dukouensis*, *C. asymmetrica*, *C. leveni*, *C. guangyuanensis*, *C. transcaucasica*, *C. orientalis*, and *C. longicuspidata* zones (Henderson, 2017) in the latest Permian timescale (Fig. 2).

Clarkina postbitteri postbitteri *Zone*.—This zone is defined by the first occurrence of *Clarkina postbitteri postbitteri* at the base and by the first occurrence of *C. dukouensis* at the top, and is restricted to the upper part of the original *C. postbitteri* Zone established

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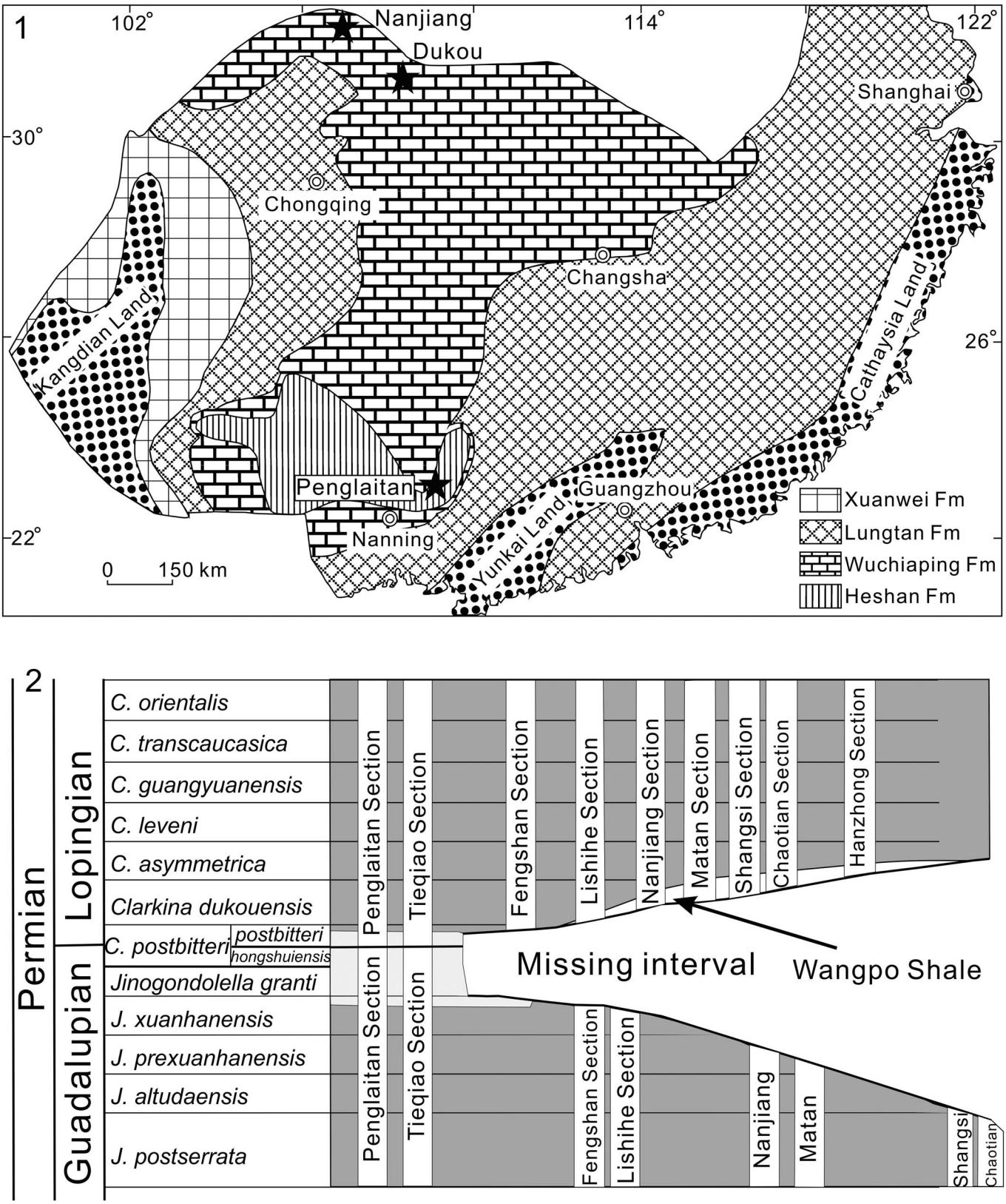

Figure 1. (**1**) Map showing localities (indicated by stars) of sections and the distribution of Wuchiapingian strata in South China (after Feng et al., 1991). (**2**) Schematic cross-section showing relationship of missing strata and conodont zonal distribution associated with a major sequence boundary in the GLB interval of South China (after Mei and Wardlaw, 1996).

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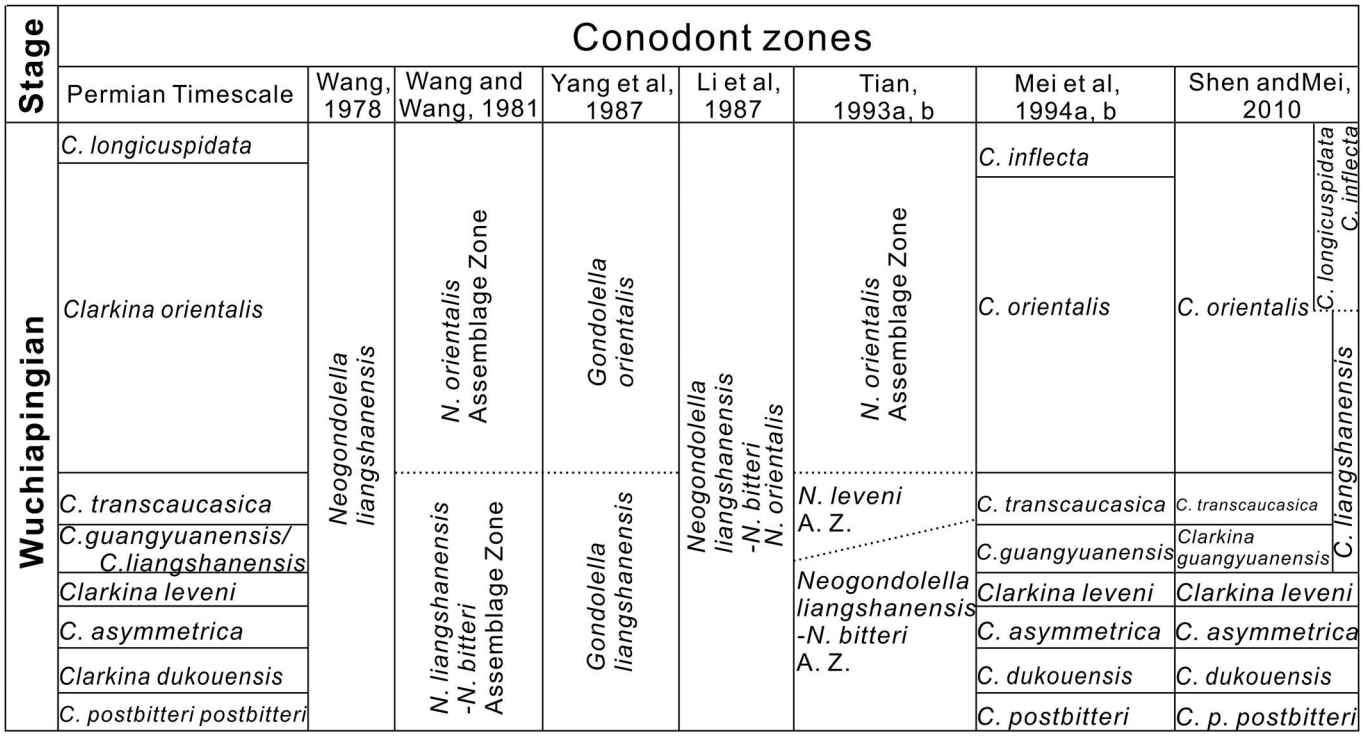

Figure 2. History of different conodont zonal schemes documented by different authors for the Wuchiapingian Stage.

in the Penglaitan and Fengshan sections, Guangxi, and in the Xiaoyuanchong Section, Hunan (Mei et al., 1994b). Zhang et al. (2008) recognized the *Clarkina postbitteri postbitteri* Zone in the Maoershan Section, Hubei. However, some specimens were illustrated that might have serrations (e.g., Zhang et al., 2008, pl. 2, fig. 4), which is a character belonging to *Jinogondolella*. Other specimens may be *Clarkina leveni* (e.g., Zhang et al., 2008, pl. 3, fig. 10) in samples from the *C. transcaucasica* Zone of Zhang et al. (2008). Thus, almost all specimens illustrated in Zhang et al. (2008) cannot be identified as *C. postbitteri postbitteri* and this zone is doubtful in the Maoershan Section. Some *C. postbitteri postbitteri* specimens were identified as *C. dukouensis* by Wang (2000), who did not recognize this zone in the Penglaitan Section (see Systematic paleontology for details). Shen and Zhang (2008) recognized this zone in the uppermost part of Douling Formation in Chenzhou, Hunan. Thus, this zone has only been recognized in a few regions of South China.

Clarkina dukouensis *Zone*.—This zone is defined by the first occurrence of *Clarkina dukouensis* at the base and by the first occurrence of *C. asymmetrica* at the top, and was first established in the Dukou and Nanjiang sections, Sichuan (Mei et al., 1994a). The *Clarkina dukouensis* Zone is the first Wuchiapingian conodont zone in most regions of South China, due to the global transgression following the Guadalupian-Lopingian lowstand interval. However, in some sections, only more advanced specimens of *C. dukouensis* are recognized in the basal part of the Wuchiaping Formation.

Clarkina asymmetrica *Zone*.—This zone is defined by the first occurrence of *Clarkina asymmetrica* at the base and by the first occurrence of *C. leveni* at the top, and was first established in the Dukou and Nanjiang sections, Sichuan (Mei et al., 1994a).

Clarkina leveni *Zone*.—This zone is defined by the first occurrence of *Clarkina leveni* at the base and by the first occurrence of *C. guangyuanensis* at the top, and was first established in Archura, Transcaucasia (Kozur, 1975). It has been recognized in northwest Iran (Henderson et al., 2008; Shen and Mei, 2010). The *Clarkina leveni* Zone cannot be recognized in a few sections, but the reason is not clear. For example, it was not recognized in the Penglaitan Section, but it was in the Tieqiao Section, which is just 10 km west of the Penglaitan Section.

Clarkina guangyuanensis *Zone*.—This zone is defined by the first occurrence of *Clarkina guangyuanensis* at the base and by the first occurrence of *C. transcaucasica* at the top, and was first established in the Dukou and Nanjiang sections, Sichuan (Mei et al., 1994a). The marker species, *C. liangshanensis*, began to occur in this zone. However, the range of *C. liangshanensis* extends to the middle of the *C. orientalis* Zone.

Clarkina transcaucasica *Zone*.—This zone is defined by the first occurrence of *Clarkina transcaucasica* at the base and by the first occurrence of *C. orientalis* at the top, and was first established in the Dukou and Nanjiang sections, Sichuan (Mei et al., 1994a). Abundant *C. liangshanensis* can coexist with *Clarkina transcaucasica* in this zone.

Clarkina orientalis *Zone*.—This zone is defined by the first occurrence of *Clarkina orientalis* at the base and by the first occurrence of *C. wangi* at the top. Mei et al. (1994a) established

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the *C. inflecta* Zone as the topmost Wuchiapingian conodont zone, above the *C. orientalis* Zone in the Dukou and Nanjiang sections. However, only a few *C. inflecta* specimens have been found in these two sections, and a *C. inflecta* population has not been recognized in many other sections. Thus, we don't use the *C. inflecta* Zone in this paper.

Clarkina longicuspidata *Zone*.—This zone occupies the upper part of the *C. orientalis* Zone (Shen and Mei, 2010; Henderson, 2017), and many *C. longicuspidata* specimens are in the uppermost part of Wuchiapingian at some sections in South China. However, some specimens that have a large cusp and no brim behind the cusp and differ from *C. longicuspidata* and *C. transcaucasica* are also found below the *C. orientalis* Zone. In addition, *C. orientalis* is abundant in each sample in the *C. orientalis* Zone and only a few specimens with a large cusp can be found in the lower part of the *C. orientalis* Zone. Thus, the first occurrence (FO) of *C. longicuspidata* and the basal boundary of the *C. longicuspidata* Zone are difficult to recognize, and the full range relationship of *C. longicuspidata* and *C. orientalis* is unclear. Here, *C. orientalis*, which is often found in South China, is chosen as the topmost marker of the Wuchiapingian in South China; the species also ranges into the lowest Changhsingian.

Wuchiapingian *Clarkina* species lineage

Clarkina, the dominant conodont genus of Lopingian strata, was established by Kozur (1989). Its characters and major difference from *Mesogondolella*, *Jinogondolella*, and *Neogondolella*, have been discussed in detail by Kozur (1989), Wardlaw and Mei (1998), Henderson and Mei (2007), and Yuan et al. (2014a). Although its origins are not well understood, most people have hypothesized that it evolved from *Jinogondolella* (Wardlaw and Mei, 1998; Henderson and Mei, 2007; Wardlaw and Nestell, 2010).

The first species/subspecies belonging to the genus *Clarkina* is *Clarkina postbitteri hongshuiensis*, which is considered to have evolved directly from *Jinogondolella*. Based on the specimens from the Penglaitan Section in South China, Henderson et al. (2002) considered that *Clarkina postbitteri hongshuiensis* evolved from *Jinogondolella granti*. However, based on specimens from West Texas, Wardlaw and Mei (1998) and Wardlaw and Nestell (2010) considered that *Clarkina postbitteri hongshuiensis* evolved from *Jinogondolella crofti* or *J. altudaensis*. Wardlaw and Nestell (2010) illustrated only two specimens identified as *Clarkina postbitteri hongshuiensis* from the Apache Mountains, West Texas; they coexist with abundant *Jinogondolella altudaensis* in the same samples. They still have a broad platform, dense denticles, and a very small cusp, which are characters typical within sample populations of *J. altudaensis*. Thus, we do not regard them as *Clarkina postbitteri hongshuiensis*.

Wardlaw and Nestell (2010) also illustrated several specimens of *Jinogondolella granti*. Those specimens have a small cusp, no obvious serrations, a broad platform, and the widest point of platform is in the middle part of platform, which are very different from *J. granti*. Thus, we do not interpret them as *J. granti*. In addition, according to our unpublished Guadalupian conodont data from West Texas and South China, the topmost zone in West Texas is near the *J. prexuanhanensis* Zone, and no transitional population from *J. altudaensis* to *Clarkina postbitteri hongshuiensis* has been found. Therefore, the evolutionary relationship between *Jinogondolella altudaensis* and *Clarkina postbitteri hongshuiensis* cannot be demonstrated based on the West Texas specimens.

Some transitional forms with a relatively narrow platform and nearly parallel lateral margins between *Jinogondolella granti* and *Clarkina postbitteri postbitteri* appear to exist in the *Clarkina postbitteri postbitteri* population at Penglaitan (e.g., Fig. 4.10, 4.11), although we did not recognize a transitional population with abundant individuals from *Jinogondolella granti* to *Clarkina postbitteri hongshuiensis* or *Clarkina postbitteri postbitteri* due to the rapid transition between *Jinogondolella* and *Clarkina*. Thus, based on the strata and conodont sample sequences (Henderson et al., 2002), the most suitable ancestor of *Clarkina postbitteri hongshuiensis* is *Jinogondolella granti* at the Penglaitan Section in South China.

"*Mesogondolella*" *omanensis*, which has weak serrations or no serration and is reported near the Wordian-Capitanian boundary, might be another choice for the ancestor of *Clarkina* in terms of outline of platform and characteristics of denticles. However, a major shortcoming is the lack of transitional forms in a long interval between "*Mesogondolella*" *omanensis* and *Clarkina*, but this may be related to migration.

Mei et al. (1994a, b, 1998a) postulated two possible lineages of the Wuchiapingian *Clarkina* species: (1) *Clarkina postbitteri–C. dukouensis–C. asymmetrica–C. leveni–C. guangyuanensis–C. transcaucasica–C. orientalis* lineage, and (2) *C. dukouensis–C. daxianensis–C. liangshanensis–C. inflecta* lineage. The first lineage is important for stratigraphic correlation because distinctive carinal variation identifies those species. The biggest challenge to the lineage is the evolutionary relationship between *C. transcaucasica* and *C. orientalis*. *Clarkina transcaucasica* originally was established as a subspecies of *C. orientalis* (*C. orientalis transcaucasica*), and later was named as a direct ancestor species of *C. orientalis* (Gullo and Kozur, 1992; Mei et al., 1998a). However, based on some transitional specimens (e.g., Shen, 2007, fig. 5.1, 5.4, 5.7), *C. orientalis* more likely evolved from *C. liangshanesis* based on the posteriorly gradual decrease in carina height in *C. liangshanensis* (Shen, 2007). *Clarkina longicuspidata*, the ancestor of the Changhsingian *Clarkina* species, was considered to first occur in the upper part of the *C. orientalis* Zone by Mei et al. (1994a) and Shen and Mei (2010). However, some specimens with a large cusp and no brim behind the cusp coexist with *C. transcaucasica* or *C. orientalis* in the *C. transcaucasica* and basal part of *C. orientalis* zones. Thus, *C. longicuspidata* could have evolved from early Wuchiapingian *Clarkina* species by transitional forms.

Therefore, the two most reliable *Clarkina* lineages in Wuchiapingian are: (1) *Clarkina postbitteri hongshuiensis–C. postbitteri postbitteri–C. dukouensis–C. asymmetrica–C. leveni–C. guangyuanensis–C. transcaucasica*, and (2) *C. liangshanensis–C. orientalis*.

Remarks on the GLB interval

The global end-Guadalupian regression formed a major lowstand systems tract (LST) and caused widespread erosional truncation around Paleotethys, as well as in most regions of

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Pangea (e.g., Texas), where evaporites or terrestrial deposits occur (Jin et al., 1994; Mei and Henderson, 2001). The lowstand resulted in nearly half of the area of South China being covered by the Lungtan Formation, which represents transitional facies between terrestrial and marine (Fig. 1.2). An obvious sequence boundary, indicated by the Wangpo Shale, is present in the basal part of the Wuchiaping Formation. Only a few structural troughs (e.g., Qin-Fang region) have continuous marine deposition across the Guadalupian-Lopingian boundary (GLB) interval. According to conodont data, the uppermost Guadalupian conodont zone is *Jinogondolella postserrata* in some regions (e.g., Shangsi; Fig. 1.2), which implies that the end-Guadalupian regression might begin in the upper part of the *J. postserrata* Zone in South China. The lowest Lopingian conodont zone is *Clarkina dukouensis* in most regions (Fig. 1.2), which suggests that the beginning of the early Lopingian transgression occurs in the lower part of the *C. dukouensis* Zone in South China. Thus, one or more conodont zones of *Jinogondolella altudaensis*, *J. shannoni*, *J. prexuanhanensis*, *J. xuanhanensis*, *J. granti*, *Clarkina postbitteri hongshuiensis*, or *C. postbitteri postbitteri*, is not recognized around the GLB interval in most regions of South China (Fig. 1.2), and the obvious boundary between the Guadalupian and Lopingian is the same as the distinct transition from *Jinogondolella* to *Clarkina*, which may also indicate the time framework of the pre-Lopingian extinction interval (Shen and Shi, 2009). The *C. postbitteri postbitteri* Zone is missing in almost all regions of South China. However, *Clarkina* juvenile specimens also have an obvious cusp and more discrete denticles, which are similar to *C. postbitteri postbitteri* and are easily misidentified as *C. postbitteri postbitteri*.

Materials and methods

All conodont materials illustrated in this paper are from the Penglaitan, Dukou, and Nanjiang sections (Fig. 1.1). The Penglaitan Section is the GSSP for the base of the Wuchiapingian Stage and is located 20 km east of Laibin, Guangxi Province. The Wuchiapingian Stage in this section consists of the uppermost Maokou Formation and the Heshan Formation (Shen et al., 2007). The Dukou and Nanjiang sections are located in northeastern Sichuan, and are found in Xuanhan and Nanjiang counties, respectively. The Wuchiapingian Stage of both sections consists of the Wuchiaping Formation only. The Penglaitan and Dukou sections were continuously sampled from the top of the Maokou Formation to the top of the Heshan/Wuchiaping Formation. Some SEM illustrated specimens were re-examined from samples previously collected by Mei in Mei et al. (1994a, b, 1998a).

P_1 elements are only used to differentiate *Clarkina* species in this paper, and we herein attempt to illustrate a series of growth stages for each species as completely as possible to show most characteristics of a species and their intraspecific variation. A few elements of the *C. orientalis* apparatus are also illustrated.

Repository and institutional abbreviation.—The new conodont material is stored in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences.

Systematic paleontology

Class Conodonta Eichenberg, 1930
Order Ozarkodinida Dzik, 1976
Family Gondolellidae Lindstroem, 1970
Genus *Jinogondolella* Mei and Wardlaw, 1994

Type species.—*Gondolella nankingensis* Ching (Jin), 1960 from the Kufeng Formation, Jiangsu Province, China.

Jinogondolella granti (Mei and Wardlaw in Mei et al., 1994b)
Figure 3.1–3.18

1994b *Mesogondolella granti* Mei and Wardlaw in Mei et al., p. 229, pl. 1, figs. 8–12.
1998a *Jinogondolella granti*; Mei et al., p. 62, pl. 3, figs. 1–4, 10–14, pl. 7, figs. 8, 9, 12, 15–24.
2000 *Mesogondolella altudaensis*; Wang, pl. 4, figs. 2–10.
2000 *Mesogondolella granti*; Wang, pl. 5, figs. 1–7, 12, pl. 7, figs. 8–12.
2000 *Mesogondolella prexuanhanensis*; Wang, pl. 5, figs. 8, 9, pl. 7, figs. 2–5.
2000 *Mesogondolella shannoni*; Wang, pl. 5, figs.10, 11, 13–18.
2000 *Mesogondolella laibinensis* Wang, pl. 6, figs. 5–12.
2002 *Jinogondolella granti*; Henderson et al., p. 731, pl. 1, figs. 12–16.
2006a *Jinogondolella granti*; Jin et al., figs. 7.11, 7.12.
?2008 *Jinogondolella granti*; Zhang et al., p. 438, pl. 1, fig. 28.
?2008 *Clarkina postbitteri hongshuiensis*; Zhang et al., pl. 1, figs. 19–21, 23, pl. 2, fig. 1.

Holotype.—NIGP123478, from the Maokou Formation, Guangxi Province, China (Mei et al., 1994b, pl. 1, figs. 8, 9).

Original diagnosis.—A species of *Mesogondolella* (=*Jinogondolella* in this paper) characterized by a P_1 element that has a bluntly rounded posterior, slender platform with nearly parallel sides in its posterior part where the platform narrows gradually to the anterior end, high and large terminal cusp, and nearly entirely fused carina in its middle part. The fused carina is nearly flat, with both posterior and anterior ends arching downward when viewed in lateral profile (Mei et al., 1994b, p. 229).

Emended diagnosis.—A species of *Jinogondolella* characterized by a P_1 element with a slender, symmetrical, arched and long platform whose lateral margins are nearly parallel in the middle portion in most individuals, and then narrowing gradually in the

Figure 3. (**1–18**) *Jinogondolella granti* (Mei and Wardlaw in Mei et al., 1994b): (**1, 2**) Holotype, NIGP123478, from sample LPD-117 at Penglaitan Section in Mei et al. (1994b); (**3–18**) from sample PLT 5b at Penglaitan Section, registration nos. NIGP166056-166063. (**19–34**) *Clarkina postbitteri hongshuiensis* Henderson, Mei, and Wardlaw, 2002: (**19, 20**) Holotype, NIGP134579, (**21–34**) Paratypes, NIGP134575–134578, 134580–134584, all from sample Bed 6i at Penglaitan Section in Henderson et al. (2002).

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anterior 1/3 of the element; some specimens have the widest point in the middle portion, narrowing gradually both posteriorly and anteriorly. Posterior end of platform is bluntly rounded, but more upturned. Cusp is erect, terminal, obviously higher and larger than the posterior and middle denticles, and sometimes fused with the posteriormost denticle. It is slightly reclined in juveniles. Tight and numerous denticles are almost equal in height except for those in the anterior in most individuals, or increasing gradually in height anteriorly in juveniles, and the middle denticles on the carina are more fused in gerontic specimens, but less in junior ones. Furrows are moderately wide and smooth. Serrations are in the anterior 1/3 or 1/4 in most specimens, especially in gerontic forms, but not obvious in juveniles and some adults.

Remarks.—*Jinogondolella granti* is the youngest species of *Jinogondolella* in South China. It can be differentiated from *J. xuanhanensis* by its bluntly rounded and upturned posterior end, more fused middle carina, and nearly parallel lateral margins, but *J. xuanhanensis* has a flat, concave and slightly deflected posterior end of platform. *Jinogondolella granti* is similar to *J. shannoni*, however the latter has more discrete denticles than the former in the middle part, and has the widest point in the posterior portion narrowing gradually anteriorly in almost individuals.

Wang (2000) identified one specimen as *Clarkina postbitteri* in Bed 4 at the Penglaitan Section (in the *J. granti* Zone), but it was determined to be sample contamination (Wang, 2000, p. 6). Many specimens were identified by Wang (2000) as *J. altudaensis*, *J. shannoni*, and *J. prexuanhanensis*, which coexisted with *J. granti* at the Penglaitan Section. However, the characteristics of almost all of those individuals coincide with *J. granti* according to the diagnosis, therefore, they are all assigned to *J. granti* herein. Wang (2000) established a new species, *Mesogondolella laibinensis*, in Bed 4, based on the major character of lacking serration. However, despite not having obvious serration, these specimens still have a slender, symmetrical and long platform, bluntly rounded and upturned posterior end, more fused middle carina, and nearly parallel lateral margins, which also coincide with those of *Jinogondolella granti* (see emended diagnosis and Fig. 3.5, 3.6, 3.11, 3.12). Thus, *Mesogondolella laibinensis* is considered to be a synonym of *Jinogondolella granti*. Almost all specimens identified as *J. granti* by Zhang et al. (2008) still have a flat and slightly deflected posterior end of the platform, which characterizes *J. xuanhanensis*; they may be from the samples with transitional *J. xuanhanensis* to *J. granti*.

Genus *Clarkina* Kozur, 1989

Type species.—*Gondolella leveni* Kozur, Mostler, and Pjatakova in Kozur, 1975 from Achura, Azerbaijan.

Remarks.—*Clarkina* has been discussed in detail by Yuan et al. (2014a). In addition to the oral surface, Kozur (1989) also illustrated the aboral surface, which he considered to be different from Triassic Gondolellidae genera, but similar to Permian Gondolellidae genera, with the distinct difference primarily in the oral surface among Gondolellidae genera (e.g., free blade). Thus, the aboral surface difference may be a diagnostic character at genus level, but not for the Permian Gondolellidae genera. The aboral surface is not illustrated because this paper only focuses on the difference among Wuchiapingian *Clarkina* species.

Clarkina postbitteri hongshuiensis Henderson, Mei, and Wardlaw, 2002
Figure 3.19–3.34

?1998a *Clarkina postbitteri*; Mei et al., pl. 5, figs. 1, 7.
2000 *Clarkina postbitteri*; Wang, pl. 1, figs. 10, 11, 14–18.
2002 *Clarkina postbitteri hongshuiensis* Henderson et al., p. 730, pl. 1, figs. 1–11, pl. 2, figs. 9, 10, 12, 13.
2006a *Clarkina postbitteri hongshuiensis*; Jin et al., figs. 7.1, 7.6–7.10, 7.13–7.16.
?2006 *Clarkina postbitteri hongshuiensis*; Sun and Xia, pl. 1, figs. 7–9.
non 2010 *Clarkina hongshuiensis*; Wardlaw and Nestell, pl. 15, figs. 9, 12.

Holotype.—NIGP134579, from the Maokou Formation, Guangxi Province, China (Henderson et al., 2002, pl. 1, fig. 5).

Original diagnosis.—A subspecies of *Clarkina postbitteri* that exhibits a wide range of morphotypes, but always has smooth anterior margins. Almost all mature specimens have a narrow brim and high, fused anterior denticles forming a blade. The diagnostic aspect of this taxon (and other taxa) appears in larger adult forms; small juvenile specimens cannot be used for species discrimination. Some morphotypes show rounded posterior terminations whereas others are more blunt or square with rounded corners. In some specimens, the platform narrows abruptly anteriorly, but in many the platform narrows somewhat more gradually. The number of posterior and middle denticles is rather variable and in some they are mostly discrete, but in others most of the middle denticles become closely spaced to fused. In most specimens, there is a gap between the posterior denticle and the cusp. Some specimens show gaps between the posterior denticles, but in many the posterior denticles are very tightly spaced to fused (Henderson et al., 2002, p. 730).

Emended diagnosis.—A subspecies of *Clarkina postbitteri* characterized by a P_1 element with a slender, symmetrical and slight arched platform whose lateral margins are nearly parallel in the posterior in most individuals, then narrowing gradually in the anterior 1/3 or 1/4 of the element, except for a few specimens in which their platform narrows abruptly anteriorly. Few specimens have the widest point in the posterior end narrowing gradually anteriorly. Posterior end of platform is bluntly rounded, but some larger specimens have a squarely rounded posterior end. Cusp is erect, terminal, and higher and larger than the posterior denticles in most individuals, but is nearly same height as the posterior denticles in gerontic specimens, which usually have a narrow brim in the posterior end. Posterior and middle denticles are closely spaced, but unfused, whereas in juveniles they are more discrete and form gaps. Posterior denticles are about equal in height, then increase gradually and become more fused anteriorly, until they form a free blade in the anterior. The gap between the cusp and the posteriormost denticle is not obvious. Furrows are narrow and smooth in most individuals.

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Remarks.—*Clarkina postbitteri hongshuiensis* is different from species of *Jinogondolella* by having fused anterior denticles forming a free blade and the lack of serration in the anterior part of the platform. It should be differentiated from *J. granti* and *Clarkina postbitteri postbitteri* by comparing separate populations (see Henderson et al., 2002 for detail).

Henderson et al. (2002) divided *Clarkina postbitteri* into two subspecies, *C. p. hongshuiensis* and *C. p. postbitteri*, therefore some specimens of *C. postbitteri* in Mei et al. (1998a) and Wang (2000) with the same characteristics as in *C. p. hongshuiensis* should be identified as *C. p. hongshuiensis*. Sun and Xia (2006) recognized some *C. p. hongshuiensis* in the Dachongling Section, and few specimens are similar to *C. p. hongshuiensis*. However, they are difficult to identify because they are broken and unclear. Zhang et al. (2008) also recognized many *C. p. hongshuiensis* in the Maoershan Section. However, almost all individuals have serrations so that they should be assigned to *Jinogondolella*.

Clarkina postbitteri hongshuiensis was elevated to a species level, *Clarkina hongshuiensis*, by Lambert et al. (2010) and Wardlaw and Nestell (2010). However, it has a very short interval at the Penglaitan Section and cannot be found at any other sections so far. Therefore, it is still considered to be a subspecies in this paper.

Clarkina postbitteri postbitteri Mei and Wardlaw
in Mei et al., 1994b
Figure 4.1–4.17

1994b *Clarkina postbitteri* Mei and Wardlaw in Mei et al., p. 229, pl. 1, figs. 3–6, pl. 2, figs. 7–11.
1995 *Clarkina postbitteri*; Kozur, pl. 5, fig. 26.
1996 *Clarkina postbitteri*; Mei and Wardlaw, pl. 17.1, figs. 16, 18–25.
1998a *Clarkina postbitteri*; Mei et al., p. 61, pl. 4, figs. 1–3, 9–11, pl. 5, figs. 2–4, pl. 8, figs. 1–9.
2000 *Clarkina postbitteri*; Wang, pl. 1, figs.1–8.
2000 *Clarkina dukouensis*; Wang, pl. 2, figs.1–8.
?2000 *Clarkina longicuspidata*; Wang, pl. 6, figs.1, 2.
2002 *Clarkina postbitteri postbitteri*; Henderson et al., p. 730, pl. 2, figs. 1–7.
2006a *Clarkina postbitteri postbitteri*; Jin et al., figs. 7.2–7.5.

Holotype.—NIGP123476, from the Maokou Formation, Guangxi Province, China (Mei et al., 1994b, pl. 1, fig. 6).

Original diagnosis.—A species of *Clarkina* characterized by a P_1 element that has a rounded posterior termination, a small brim, a relatively long and narrow platform that is widest in the anterior half just posterior to the anterior narrowing where the platform is mildly upturned (except for some large forms, which may be widest near the posterior termination), posterior sides of platform are roughly parallel with a slight indentation on the posterior inner side, a moderate cusp of circular to elongate-oval cross section, space between cusp and first posterior denticle is larger than any other on carina, first three or four denticles more widely spaced and less fused than anterior denticles, furrows narrow and well developed, platform margins mildly upturned, anterior narrowing of platform in anterior third to fourth of specimen (Mei et al., 1994b, p. 229).

Emended diagnosis.—A subspecies of *C. postbitteri* characterized by a P_1 element with a symmetrical, relatively long and narrow platform whose widest point is in the middle part, narrowing gradually both anteriorly and posteriorly, or with lateral margins that are nearly parallel. Platform is abrupt, narrowing in the anterior 1/3 to 1/4 of the element. Posterior end of platform is rounded and usually has a narrow brim, except for juveniles. Moderate cusp is erect (adults) to slightly reclined (juveniles), terminal, slightly higher and larger than the posterior denticles. Denticles are more discrete in most individuals whereas in gerontic forms they are more closely spaced. Posterior 3–4 denticles usually nearly equal in height and more widely spaced than anterior denticles. Gap between the cusp and the posteriormost denticle is obvious and larger than any other gap on carina. Furrows are moderate, smooth, and well developed.

Remarks.—*Clarkina postbitteri postbitteri* is usually distinguished from *C. postbitteri hongshuiensis* by much more discrete denticles and abrupt narrowing of the platform in the anterior 1/3.

Some specimens from Bed 6k at the Penglaitan Section were identified as *Clarkina dukouensis* by Wang (2000), but were referred to *C. postbitteri postbitteri* by Henderson (2002), whose viewpoint is accepted in this paper because those specimens gradually narrow in the anterior 1/3 and have more discrete denticles (see Wang, 2000, pl. 2, figs. 4, 5), which are characteristics that belong to the earliest *Clarkina* populations. Some juveniles identified as *C. longicuspidata* by Wang (2000) may be referred to *C. postbitteri postbitteri* based on adult specimens, which coexisted with those juveniles. The three *C. postbitteri postbitteri* specimens that were recognized in the Dacongling Section by Sun and Xia (2006) are difficult to verify. Zhang et al. (2008) recognized a *C. postbitteri postbitteri* range that is from the GLB interval to the *C. guangyuanensis* Zone. However, the morphotypes of those specimens are variable and they should be referred to several other species.

Clarkina dukouensis Mei and Wardlaw in Mei et al., 1994a
Figure 4.18–4.31

1994a *Clarkina dukouensis* Mei and Wardlaw, p. 134, pl. 1, figs. 18, 19.
1994b *Clarkina dukouensis*; Mei et al., pl. 1, figs. 1, 2, pl. 2, figs. 1–6, 12, 13.
1994c *Clarkina liangshanensis*?; Mei et al., pl. 3, fig. 11.
1995 *Clarkina dukouensis*; Kozur, pl. 5, fig. 25.
1998a *Clarkina dukouensis*; Mei et al., pl. 5, figs. 8, 9, pl. 8, figs. 10–19, pl. 10, figs. 1–4.
2000 *Clarkina dukouensis*; Wang, pl. 2, figs. 9–15.
2000 *Clarkina penglaitanensis* Wang, pl. 4, figs. 11–13.
2000 *Clarkina niuzhuangensis*; Wang, pl. 6, figs. 13, 14, 17, 18.
2002 *Clarkina dukouensis*; Henderson et al., p. 729.
2006 *Clarkina dukouensis*; Sun and Xia, pl. 1, figs. 14–16.
2008 *Clarkina dukouensis*; Zhang et al., pl. 2, figs. 7, 8, 16.
?2008 *Clarkina postbitteri hongshuiensis*; Zhang et al., pl. 2, fig. 10.
2010 *Clarkina dukouensis*; Shen and Mei, p. 153, figs. 3.1a–3.7b.

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Holotype.—NIGP121709, from the Wuchiaping Formation, Sichuan Province, China (Mei et al., 1994a, pl. 1, fig. 18).

Original diagnosis.—A species of *Clarkina* characterized by a P_1 element with a blunt, but rounded posterior platform termination; width of platform increasing gradually until the middle; cusp terminally located, erect and larger than the denticles on the posterior half of the element; posteriormost denticle generally small; denticles increasing in size anterior (except the distal two smaller denticles) and discrete posteriorly; furrows moderately developed and smooth; lateral margins slightly upturned at the widest point; platform narrowing sharply on the anterior half and continuing near the anterior end (Mei et al., 1994a, p. 134).

Emended diagnosis.—A species of *Clarkina* characterized by a P_1 element with a bluntly rounded to squarely rounded posterior end of platform. Width of platform slightly increasing from posterior end to middle part where the widest point occurs, then narrows gradually, until it narrows sharply in the anterior 1/4 or 1/3. Inner lateral margin is straight in most individuals, and lateral margins of some specimens are nearly parallel. Cusp is erect (adults) to slightly reclined (juveniles), terminal, and larger than almost all other denticles on the carina, and sometimes fused with the posteriormost denticle. Posteriormost denticle is generally small, then denticles increase in size anteriorly except the distal two or three denticles, and posterior denticles are more discrete than anterior denticles. Denticles on the carina are nearly equal in height in many specimens. Furrows are moderately developed and smooth.

Remarks.—Mei et al. (1994a) established this species at the Dukou Section, and assigned the holotype from sample L-127 (Fig. 4.18, 4.19). However, Mei considered this holotype as an advanced form, and the specimen (Fig. 4.22, 4.23) is a typical form (S.L. Mei, personal communication, 2012). This species can be distinguished from *Clarkina postbitteri postbitteri* by a relatively wide platform, more closely spaced denticles on the carina as well as usual absence of a gap between the cusp and the posteriormost denticle. Gerontic individuals from stratigraphically younger intervals tend to have a more fused middle carina and a relatively wider platform than those of specimens from stratigraphically older intervals, which are more similar to *C. asymmetrica*, and leads to difficulty in recognizing the boundary between the *C. dukouensis* Zone and *C. asymmetrica* Zone.

Wang (2000) established a new species, *Clarkina penglaitanensis*, whose major characteristic is its high, nearly triangular outline platform with a downturned and truncated posterior end. However, this characteristic can be found in *C. dukouensis* populations (e.g., Fig. 4.26), and its paratypes have unfused, but closely spaced denticles on the carina, which is also a characteristic of *C. dukouensis*. Thus, those paratypes are here referred to *C. dukouensis*.

Clarkina asymmetrica Mei and Wardlaw in Mei et al., 1994a
Figure 5.1–5.16

1991 *Neogondolella guangyuanensis*; Wang and Dong, pl. 3, fig. 1.
1991 *Neogondolella bitteri*; Wang and Dong, pl. 1, figs. 14, 16.
1994a *Clarkina asymmetrica* Mei and Wardlaw in Mei et al., p. 132, pl. 1, figs. 12, 15, 16.
1995 *Clarkina niuzhuangensis*; Kozur, pl. 5, fig. 19.
?1998a *Clarkina asymmetrica*; Mei et al., pl. 5, fig. 10.
1998a *Clarkina asymmetrica*; Mei et al., pl. 9, figs. 8–15, pl. 10, fig. 13.
?2000 *Clarkina penglaitanensis* Wang, pl. 4, figs. 14, 15.
?2000 *Clarkina* sp. nov. A Wang, pl. 7, figs. 17, 18.
?2004 *Clarkina postbitteri postbitteri*; Wang and Xia, fig. 3A.
2004 *Clarkina dukouensis*; Wang and Xia, figs. 3I, 3Q.
?2004 *Clarkina asymmetrica*; Wang and Xia, figs. 3K, 3L.
2008 *Clarkina dukouensis*; Zhang et al., pl. 2, figs. 9, 27–29.
2008 *Clarkina asymmetrica*; Zhang et al., p. 439, pl. 2, figs. 17, 30, pl. 3, figs. 1, 12, 13.
2008 *Clarkina guangyuanensis*; Zhang et al., pl. 2, fig. 19.
2010 *Clarkina asymmetrica*; Shen and Mei, p. 153, figs. 3.8a–3.16b.

Holotype.—NIGP121706, from the Wuchiaping Formation, Sichuan Province, China (Mei et al., 1994a, pl. I, fig. 16).

Original diagnosis.—A species of *Clarkina* characterized by a P_1 element with an obliquely squared posterior platform termination; a moderate cusp; posterior three denticles much less fused than the middle portion of the carina, which becomes very fused in larger specimens; denticles increasing in size anteriorly; a small gap between the first posterior denticle and the cusp or the second posterior denticle or both; furrows shallow; platform margins only slightly upturned, with straight to slightly convex inner side and always more convex outer side. Platform extending for 2/3 to 3/4 length of element before narrowing; element bowed; anterior narrowing of the platform beginning on the inner side before the outer side, making it asymmetric in appearance (Mei et al., 1994a, p. 132).

Emended diagnosis.—A species of *Clarkina* characterized by a P_1 element with an obliquely squared to squarely rounded posterior end of platform. Inner side of platform is straight to slightly convex, but outer side is always more convex, and they exhibit obvious narrowing in the anterior 1/4 or 1/3. Anterior narrowing of the platform on inner side is relatively late, but

Figure 4. (**1–17**) *Clarkina postbitteri postbitteri* Mei and Wardlaw in Mei et al., 1994b: (**1**) Holotype, NIGP123476, from sample LPD-115 at Penglaitan Section in Mei et al. (1994b); (**2–17**) from sample Bed 6k at Penglaitan Section, (**2–9, 12–17**) NIGP134595-134601, from Henderson et al. (2002), (**10, 11**) NIGP166064. (**18–31**) *Clarkina dukouensis* Mei and Wardlaw in Mei et al., 1994a: (**18, 19**) Holotype, NIGP121709, from sample L-127 at Dukou Section in Mei et al. (1994a); (**20, 21**) NIGP123496, from sample L-125 at Dukou Section in Mei et al. (1994b); (**22, 23**) NIGP123504, from sample Dg-27 at Nanjiang Section in Mei et al. (1994b); (**24, 25**) from sample Dg-27 at Nanjiang Section, NIGP166065; (**26, 27**) NIGP123472, from sample LPD-111 at Penglaitan Section in Mei et al. (1994b); (**28–31**) from sample LPD-111 at Penglaitan Section, NIGP166066, 166067.

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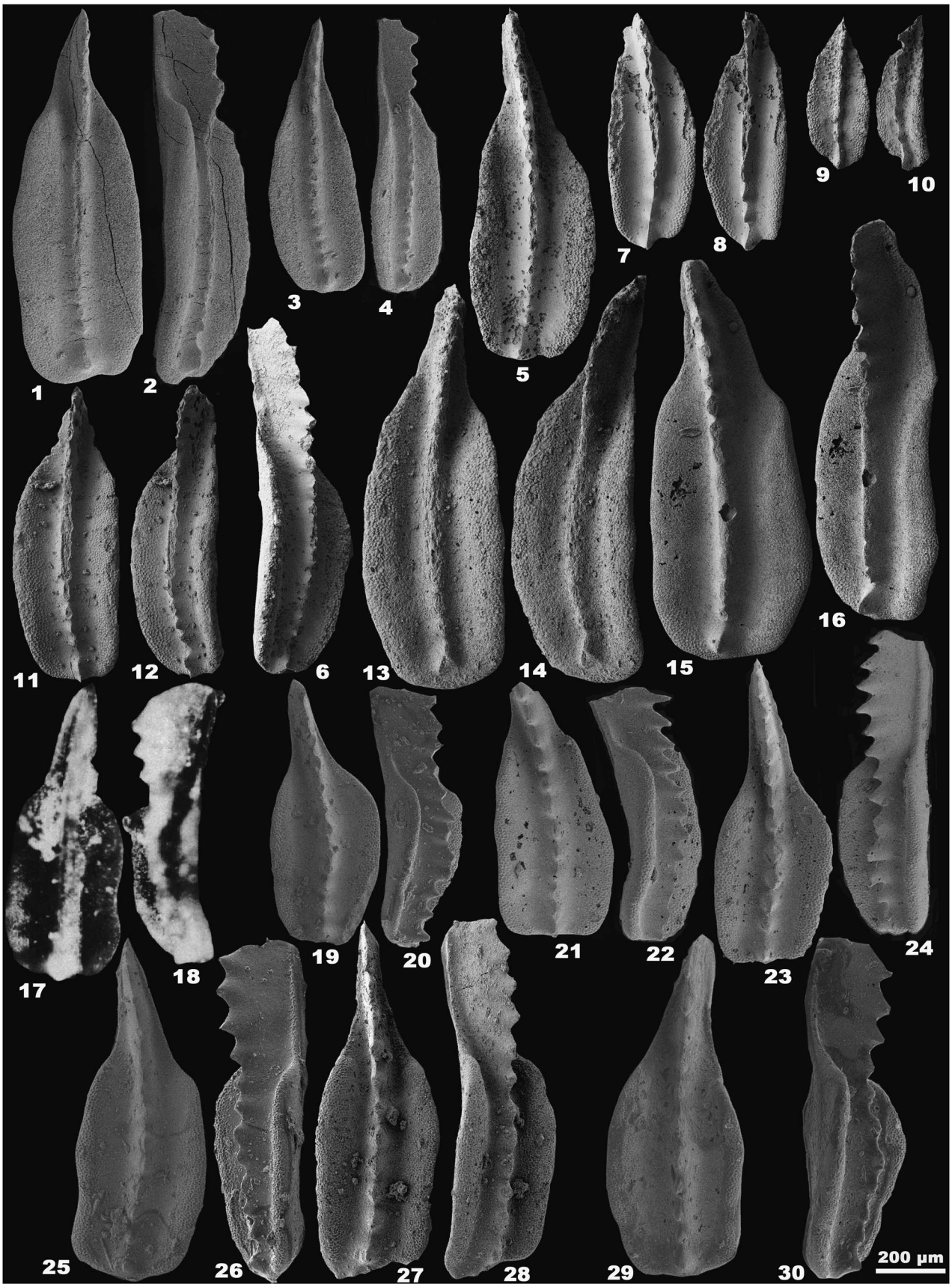

Figure 5. (**1–16**) *Clarkina asymmetrica* Mei and Wardlaw in Mei et al., 1994a: (**1, 2**) Holotype, NIGP121706, (**3, 4**) NIGP121704, all from sample L-145 at Dukou Section in Mei et al. (1994a); (**5–16**) from sample PLTS09 10.36 m at Penglaitan Section, NIGP166068–166073. (**17–30**) *Clarkina leveni* (Kozur et al. in Kozur, 1975): (**17, 18**) holotype, from Achura in Kozur (1975); **(19–30)** from sample L-156 at Dukou Section, NIGP166074–166079.

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sharper than outer side except for juveniles, making the platform asymmetric in the anterior. Cusp is erect (adults) to slightly reclined (juveniles), terminal, slightly larger and higher than the posterior denticles. A small gap is located between the posteriormost denticle and the cusp or the second posterior denticle when the cusp is fused with the posteriormost denticle. Posterior 3–4 denticles are much less fused than other denticles on the carina, which becomes very fused in adult specimens, and denticles gradually increasing in height and size anteriorly. There is a narrow brim behind cusp in some gerontic individuals. Furrows are moderate and smooth.

Remarks.—*Clarkina asymmetrica* can be distinguished from *Clarkina dukouensis* by asymmetric anterior narrowing of the platform, fused denticles on the middle carina, and a small gap between the posteriormost denticle and the cusp. However, a few gerontic *C. dukouensis* that have a more fused carina are similar to *C. asymmetrica*, and some juvenile *C. asymmetrica* that have unfused denticles, as in other *Clarkina* juveniles, are similar to *C. dukouensis*.

The holotype of *Clarkina penglaitanensis* assigned by Wang (2000) has more fused denticles and an obvious gap, and coexisted with *C. asymmetrica*. Thus, it might be *C. asymmetrica*. Some specimens in Wang and Xia (2004) and Zhang et al. (2008) identified as *C. dukouensis* already have a fused carina and an obvious gap, so that they are assigned to *C. asymmetrica* in this paper.

Clarkina leveni (Kozur, Mostler, and Pjatakova in Kozur, 1975)
Figure 5.17–5.30

1975 *Gondolella leveni* Kozur, Mostler, and Pjatakova in Kozur, p. 16, pl. 3, figs. 1–7.
?1988 *Neogondolella leveni*; Clark and Wang, fig. 3.17, 3.18.
1991 *Neogondolella leveni*; Wang and Dong, pl. 1, figs. 4, 5.
?1991 *Neogondolella* sp. A Wang and Dong, pl. 2, fig. 9.
?1993a *Neogondolella leveni*; Tian, pl. 1, fig. 17.
1994a *Clarkina leveni*; Mei et al., p. 135, pl. 1, figs. 13, 17.
1994c *Clarkina leveni*; Mei et al., pl. 3, figs. 12, 13.
1995 *Clarkina leveni*; Kozur, pl. 5, fig. 3.
1998a *Clarkina leveni*; Mei et al., pl. 5, figs. 5, 6.
?2004 *Clarkina bizarrensis*; Wang and Xia, figs. 3D, 3E.
2004 *Clarkina leveni*; Wang and Xia, fig. 3J.
?2008 *Clarkina postbitteri postbitteri*; Zhang et al., pl. 3, fig. 10.
2008 *Clarkina leveni*; Zhang et al., pl. 3, fig. 14.
2008 *Clarkina bizarrensis*; Zhang et al., pl. 3, figs. 16, 17.
2008 *Clarkina longicuspidata*; Zhang et al., pl. 3, fig. 18.
2010 *Clarkina leveni*; Shen and Mei, p. 153, figs. 4.1a–4.10b.

Holotype.—PK1–2, from the basal Dzhulfian, Achura, Azerbaijan (Kozur, 1975, pl. 3, fig. 1).

Original diagnosis.—Platform moderately wide to wide. The clear free blade comprises about a third of the total length of the conodont. At the point where the platform narrows abruptly, a clear tooth occurs on the carina. The 10–13 teeth of the carina are flattened at the front and at the sides, the lower surface and the keel are flat and very broad, distinctly longitudinal (Kozur, 1975, p. 16 [in German]).

Emended diagnosis.—A species of *Clarkina* characterized by a P_1 element with a relatively short platform. It is gradually increasing in width from posterior end to the widest point, which is near the middle of the platform, then narrowing gradually anteriorly, but sharply narrowing in the anterior 1/2 to1/3 of the element. Anterior narrowing of the platform on inner side is relatively sharper than outer side in some individuals. Posterior end of platform is squared to obliquely squared. Cusp is erect, terminal, and nearly equal to the posteriormost denticle in height in most individuals. Denticles are robust and closely spaced, but not fused, generally increasing gradually in height anteriorly; may be fused in a few gerontic specimens. Furrows are wide, deep, smooth, and well developed. Lateral margins are high, upturned, and sharply decline on sharply narrowing platform.

Remarks.—*Clarkina leveni* can be distinguished from *C. asymmetrica* by a relatively short platform, robust but unfused denticles, high upturned lateral margins, and sharp narrowing in the anterior half of the platform.

Clarkina guangyuanensis (Dai and Zhang in Li et al., 1989)
Figure 6.15–6.28

1989 *Neogondolella guangyuanensis* Dai and Zhang in Li et al., p. 228, pl. 42, figs. 8–10.
1989 *Neogondolella liangshanensis*; Li et al., pl. 42, figs. 1, 2, 5–7.
1989 *Neogondolella paraleveni* Dai and Zhang in Li et al., pl. 42, figs. 3, 4, pl. 51, figs. 20–22, pl. 52, figs. 1–3, 9, 10.
?1989 *Neogondolella paraleveni* Dai and Zhang in Li et al., pl. 42, figs. 11–14.
1989 *Neogondolella deflecta*; Li et al., pl. 42, figs. 15–17, pl. 51, figs. 12, 13.
1989 *Neogondolella bitteri*; Li et al., pl. 51, figs. 7–9, 16–19, pl. 52, figs. 4, 5, 22.
1989 *Neogondolella* cf. *leveni*; Li et al., pl. 52, figs. 6–8, 23.
1991 *Neogondolella guangyuanensis*; Wang and Dong, p. 48, pl. II, figs. 4, 10, 11.
1993b *Neogondolella leveni*; Tian, pl. 1, figs. 5, 6.
1994a *Clarkina guangyuanensis*; Mei et al., p. 134, pl. 1, figs. 1, 10.
1998a *Clarkina guangyuanensis*; Mei et al., pl. 9, figs. 1–6; pl. 10, figs. 12.
?2004 *Clarkina transcaucasica*; Wang and Xia, fig. 3F, 3G..
2004 *Clarkina guangyuanensis*; Wang and Xia, fig. 3R, 3S.
?2008 *Clarkina transcaucasica*; Zhang et al., pl. 3, fig. 8.
?2008 *Clarkina postbitteri postbitteri*; Zhang et al., pl. 3, fig. 9.
2008 *Clarkina dukouensis*; Zhang et al., pl. 3, fig. 11.
?2008 *Clarkina longicuspidata*; Zhang et al., pl. 3, fig. 19.
2010 *Clarkina guangyuanensis*; Shen and Mei, p. 155, figs. 5.1a–5.7b.

Holotype.—DY83028, from the Wuchiaping Formation, Sichuan Province, China (Li et al., 1989, pl. 42, figs. 8–10).

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Figure 6. (**1–14**) *Clarkina liangshanensis* (Wang, 1978): (**1, 2**) Holotype, NIGP45448, from sample Acf 2-83 at Liangshan region in Wang (1978); (**3–14**) from sample PLTNC-1 at Penglaitan Section, NIGP166080–166085. (**15–28**) *Clarkina guangyuanensis* (Dai and Zhang in Li et al., 1989): (**15, 16**) holotype, DY83028, from sample GSC-11-1 at Shangsi Section in Li et al. (1989); (**17–28**) from sample QT-120 at Nanjiang Section, NIGP166086–166091.

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Original diagnosis.—Symmetric or near symmetric platform conodont. Platform short and wide, about 2/3 of unit in length. At the middle of the platform margin it is so constrictive that it emerges "Guitarlike" in oral view. Posterior margin narrow and cusp small. Carina with 11–13 denticles. Aboral surface, keel is the 2/3 of platform width (Li et al., 1989, p. 228, 432).

Emended diagnosis.—A species of *Clarkina* characterized by a P_1 element with a wide and nearly symmetric platform whose width is gradually increasing from posterior end to the widest point, which is in the anterior 1/3 of the element in most specimens, then sharply narrowing anteriorly, but the widest point is in the anterior 2/3 of element in some individuals. Posterior end is bluntly rounded to squarely rounded. Cusp is erect (adults) to slightly reclined (juveniles), terminal, and larger and higher than the posterior denticles. Denticles increase gradually in size and height anteriorly and become more fused in some senile specimens. A small gap is between the posteriormost denticle and the cusp or the second posterior denticle when the posteriormost denticle is closed or fused with the cusp. A narrow brim is behind the cusp in some individuals. Furrows are wide, but shallow. Upturned lateral margins are variable.

Remarks.—*Clarkina guangyuanensis* can be distinguished from *C. leveni* by a relatively wide and long platform, short sharply narrowing part in the anterior, and a small gap before cusp, and distinguished from *C. asymmetrica* by a wide and symmetric platform and more robust denticles.

The diagnosis of a new species, *Neogondolella paraleveni*, established by Dai and Zhang in Li et al. (1989) is the same as *N. guangyuanensis* (*Clarkina guangyuanensis*) except for outline of platform, and those two new species were established in one population. Thus, *Neogondolella paraleveni* is considered to be a synonym of *N. guangyuanensis* (=*Clarkina guangyuanensis*).

Clarkina liangshanensis (Wang, 1978)
Figure 6.1–6.14

1978 *Neogondolella liangshanensis* Wang, p. 221, pl. 2, figs. 1–5, 9–13, 16–19, 27–33.
1981 *Neogondolella liangshanensis*; Wang and Wang, pl. 1, figs. 1–3, 11, 12, 14, 15.
?1993b *Neogondolella liangshanensis*; Tian, pl. 1, fig. 2.
?1993b *Dicerogondolella mononica* Tian, pl. 1, fig. 17.
1994a *Clarkina liangshanensis*; Mei et al., p. 135, pl. 2, figs. 10–12.
1995 *Clarkina liangshanensis*; Kozur, pl. 5, fig. 2.
1996 *Clarkina liangshanensis*; Mei and Wardlaw, pl. 17.1, figs. 1–9.
1998a *Clarkina liangshanensis*; Mei et al., pl. 7, fig. 7.
?1998a *Clarkina* aff. *liangshanensis*; Mei et al., pl. 10, fig. 5.
1998a *Clarkina liangshanensis*; Mei et al., pl. 10, figs. 8, 9.
2007 *Clarkina liangshanensis*; Shen, figs. 5.1–5.10.
2010 *Clarkina liangshanensis*; Shen and Mei, p. 155, figs. 5.8a–5.17b.
2014b *Clarkina liangshanensis*; Yuan et al., figs. 3A–3T.
2015 *Clarkina liangshanensis*; Yuan et al., pl. 1, figs. 1–5.

Holotype.—NIGP45448, from the Wuchiaping Formation, Shaanxi Province, China (Wang, 1978, pl. 2, figs. 28, 29).

Original diagnosis.—Platform wide, smooth without sculpture, posterior end rounded or nearly square, lateral margins nearly parallel, and sharply narrowing in the anterior 1/3. Denticles small, low and fused on the posterior and middle carina, cusp is not obvious. Keel wide and flat, loop end nearly square (Wang, 1978, p. 221 [in Chinese]).

Emended diagnosis.—A species of *Clarkina* characterized by a P_1 element with a moderately wide, elongate, and tear-drop platform, which has a little twist in lateral view. The widest point of platform is in the middle, and it sharply narrows in the anterior 1/3 or 1/4 of the element. There is a small concavity in the posterior around 1/3 of inner margin in a few adult individuals. Posterior end is rounded to nearly square in adult specimens. Cusp is very small or even indistinct, and around same size as, or even smaller than, the posteriormost denticle. Denticles are small and slightly increasing in height and more fused anteriorly. Carina is very low in most specimens, and has a downfold in the posterior part. It extends to the posterior end of platform in many individuals. Some specimens have a narrow brim behind the cusp if carina does not extend to posterior end of platform. Furrows are narrow and very shallow.

Remarks.—*Clarkina liangshanensis* is easily found and identified in the middle-upper part of the Wuchiapingian Stage in South China. It can be distinguished from *C. orientalis* by a relatively long platform, extended carina with posteriorly gradually decreasing denticles, and no or very narrow brim.

Dicerogondolella mononica, established by Tian (1993b), has a very small cusp, very low carina, extended carina, and very narrow brim, but a variable outline of the platform. It may be a gerontic specimen of *Clarkina liangshanensis*.

Clarkina transcaucasica Gullo and Kozur, 1992
Figure 7.1–7.13

1975 *Gondolella orientalis*; Kozur, pl. 2, figs. 5–8.
1992 *Clarkina orientalis transcaucasica* Gullo and Kozur, p. 217.
1994a *Clarkina transcaucasica*; Mei et al., p. 137, pl. 1, figs. 5, 14.
1995 *Clarkina transcaucasica*; Kozur, pl. 5, fig. 4.
1998a *Clarkina transcaucasica*; Mei et al., pl. 10, fig.7.
2010 *Clarkina transcaucasica*; Shen and Mei, p.155.
?2017 *Clarkina transcaucasica*; Sun et al., pl. 5, fig. 15.

Holotype.—PK1–13, from the Dzhulfian, Achura, Azerbaijan (Kozur, 1975, pl. 2, fig. 6).

Original diagnosis.—Platform very broad. Posterior platform end broad, blunt, mostly with rounded corners, often somewhat oblique, sometimes broadly rounded. Platform widest at about midlength; in front of its widest part, the platform becomes suddenly narrow, but its height drops gradually. Platform outline asymmetrical; one side is convex to straight, the other side displays mostly a slight to distinct constriction behind the

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Figure 7. (**1–13**) *Clarkina transcaucasica* Gullo and Kozur, 1992: (**1**) holotype, from Achura in Kozur (1975); (**2–13**) from sample L-202 at Dukou Section, NIGP166092–166097. (**14–27**) *Clarkina longicuspidata* Mei and Wardlaw in Mei et al., 1994a: (**14**) holotype, NIGP121717, (**15**) NIGP121718, all from sampleQT-67 at Nanjiang Section; (**16–27**) from sample L-219 at Dukou Section, NIGP166098–166103.

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midlength, or one side is convex, the other one straight or less convex. Free blade very long, only with very narrow platform rudiments. Platform surfaces with microreticulation except the smooth adcarinal furrows.

Carina straight, at its posterior end sometimes a little bent, exceptionally also bifurcated. It ends at, or a little before, the platform end. Therefore, the platform brim behind the carina is either very narrow or missing. The 12–15 denticles on the free blade are long and highly fused. The posterior part of the carina is considerably lower; here the denticles in adult forms are mostly totally fused to a humpy or smooth line.

The "keel" is broad, flat, in adult forms with numerous distinct longitudinal stripes. Basal filling often preserved. Pit elongate, subterminal. Around the pit the "keel" is distinctly elevated (Gullo and Kozur, 1992, p. 217).

Emended diagnosis.—A species of *Clarkina* characterized by a P_1 element with a wide and nearly symmetric platform whose widest point is in the middle part, and narrowing gradually posteriorly and anteriorly, but narrowing sharply in the anterior 1/3. Posterior end is squared or obliquely squared. Cusp is erect, terminal, small, and around same size as the posteriormost denticle. Denticles increase gradually in height anteriorly and become more fused in gerontic individuals. There is a small gap between the cusp and the posteriormost denticle in a few specimens, but not obvious in typical forms. A very narrow brim is behind the cusp in most specimens. Furrows are narrow to moderate, and shallow. Carina deflects towards inner side in the posterior end in a few gerontic individuals.

Remarks.—*Clarkina transcaucasica* is extremely difficult to differentiate from *C. guangyuanensis* based on just a single specimen. It is also very similar to *C. liangshanensis* in view of its characters of the carina, except for the squared posterior end of the platform. Therefore, all three of these species are difficult to distinguish in some samples, and their relationship needs to be re-evaluated based on studies of large populations. Generally, *C. transcaucasica* differs from *C. guangyuanensis* by a small cusp and no gap between cusp and posterior denticle, and from *C. liangshanensis* by its squared (truncated) posterior margin of the platform and more obvious carina in the posterior (Shen and Mei, 2010; Yuan et al., 2014b).

Clarkina longicuspidata Mei and Wardlaw in Mei et al., 1994a
Figs. 7.14–7.27

1987 *Neogondolella orientalis*; Nestell and Wardlaw, pl. 5, figs. 1, 2, 5.
?1993 *Neogondolella subcarinata*; Wang, pl. 51, fig. 19.
1994a *Clarkina longicuspidata* Mei and Wardlaw in Mei et al., p. 136, pl. 2, figs. 7–9.
2003 *Clarkina longicuspidata*; Wang and Henderson, figs. 11–13.
2004 *Clarkina longicuspidata*; Mei et al., p. 117, figs. 3a1–3b2, 4a1–4o2, 5a1–5h2, 6a1–6n.
2006 *Clarkina longicuspidata*; Wang et al., figs. 11–13.
2014a *Clarkina longicuspidata*; Yuan et al., p. 235, pl. 2, figs. 18–29.

Holotype.—NIGP121717, from the Wuchiaping Formation, Sichuan Province, China (Mei et al., 1994a, pl. 2, fig. 7).

Remarks.—The range of this species is unclear, but its diagnosis and distinction were discussed in detail in Mei et al. (2004) and Yuan et al. (2014a).

Clarkina orientalis (Barskov and Koroleva, 1970)
Figure 8.1–8.31

1970 *Gondolella orientalis* Barskov and Koroleva, p. 933, figs. 1a–c.
1973 *Neogondolella orientalis*; Teichert et al., pl. 13, figs. 4–11.
1981 *Neogondolella orientalis*; Wang and Wang, pl. 1, figs. 16, 17.
1981 *Neogondolella orientalis*; Wang and Wang in Zhao et al., pl. 5, figs. 12–14, 17, 18.
1981 *Neogondolella orientalis mediconstricta* Wang and Wang in Zhao et al., pl. 6, figs. 12, 13.
1987 *Gondolella orientalis*; Zhang, pl. 1, fig. 20.
1987 *Neogondolella orientalis*; Duan, pl. 1, figs. 6, 7.
1988 *Neogondolella latimarginata* Clark and Wang, figs. 3.20–3.23.
1989 *Neogondolella orientalis*; Dai and Zhang in Li et al., p. 231, pl. 43, figs. 19, 20.
1990 *Neogondolella orientalis*; Duan, pl. 2, figs. 11, 16.
1993 *Neogondolella latimarginata*; Wang, pl. 51, fig. 18.
1993 *Neogondolella* cf. *latimarginata*; Wang, pl. 52, figs. 13, 14.
1993b *Neogondolella parallela* Tian, pl. 1, figs. 7, 9.
1993b *Neogondolella orientalis*; Tian, pl. 1, figs. 8, 10.
1994a *Clarkina orientalis*; Mei et al., p. 136, pl. 1, figs. 2, 4, 8; pl. 2, figs. 15, 17, 22.
?1994a *Clarkina demicornis* Mei and Wardlaw in Mei et al., pl. 2, figs. 4–6.
1994c *Clarkina orientalis*; Mei et al., pl. 3, fig. 15.
1994 *Neogondolella* ex. gr. *orientalis*; Orchard et al., pl. 1, figs. 1, 2.
1995 *Clarkina orientalis*; Kozur, pl. 5, fig. 5.
1995 *Clarkina mediconstricta*; Kozur, pl. 5, fig. 6.
1998a *Clarkina orientalis*; Mei et al., pl. 10, figs. 10, 16, 17.
?1998a *Clarkina orientalis*; Mei et al., pl. 10, figs. 11, 18.
1998a *Clarkina demicornis*; Mei et al., pl. 10, fig. 15.
1998b *Clarkina orientalis*; Mei et al., pl. 3, fig. F.
2003 *Clarkina orientalis*; Wang and Henderson, fig. 14.
2004 *Clarkina orientalis*; Mei et al., fig. 4p.
2006 *Clarkina orientalis*; Nafi et al., pl. 4, figs. 1, 2, pl. 5, fig. 22.
2006 *Clarkina orientalis*; Wang et al., fig. 4.14.
2007 *Clarkina orientalis*; Shen, figs. 1.1–1.12, 2.1–2.17, 3.1–3.13.
2010 *Clarkina orientalis*; Shen and Mei, p. 155, figs. 6.1a–6.11b.
2012 *Clarkina orientalis*; Fang et al., fig. 3.17.
2014a *Clarkina orientalis*; Yuan et al., pl. 1, figs. 11–20.
2014b *Clarkina orientalis*; Yuan et al., figs. 3U–3X.

Holotype.—From the Dzhulfian, USSR (Barskov and Koroleva, 1970, fig. 1).

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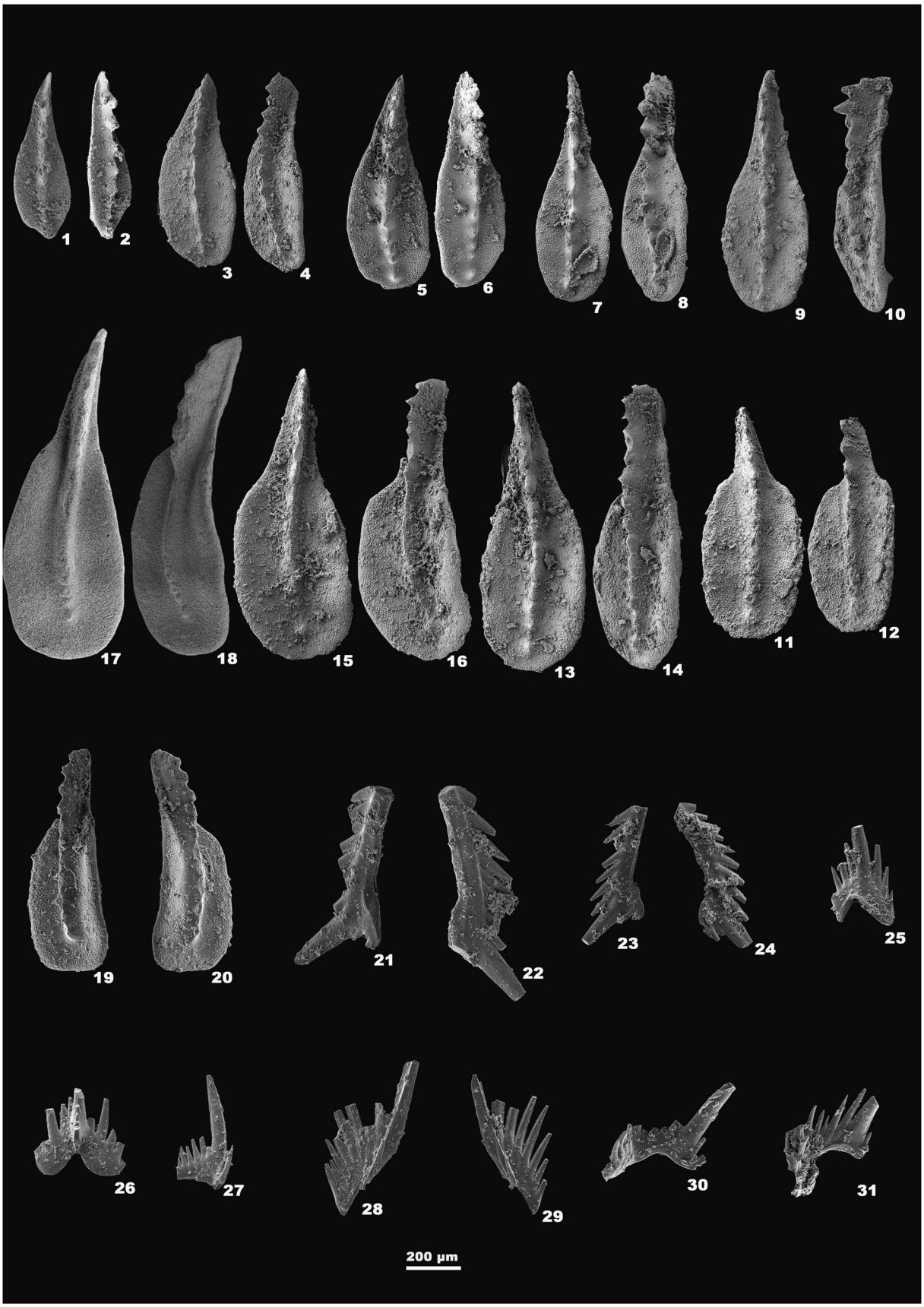

Figure 8. (**1–31**) *Clarkina orientalis* (Barskov and Koroleva, 1970): (**1–16**) from sample PLTNC-15 at Penglaitan Section, registration nos. NIGP166104-166111; (**17, 18**) from sample QT-14 at Nanjiang Section, registration no. NIGP166112; (**19–31**) from sample MRC-12 at Penglaitan Section, registration nos. NIGP166113-166125, (**21–24**) P_2 elements, (**25**) M element, (**26, 27**) S_0 elements, (**28, 29**) S_2 elements, (**30**) S_3 element, (**31**) S_4 element.

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Original diagnosis.—Platform is oval in outline. Inferior surface a broad low carina and small narrow groove. Median crest with flattened denticles that merge anteriorly where they form a laminated, short, practically adenticulate free blade (Barskov and Koroleva, 1970, p. 933 [in Russian]).

Emended diagnosis.—A species of *Clarkina* characterized by a P_1 element with an oval-shaped or tapered platform. Posterior end is bluntly rounded to rounded. Cusp is small, just slightly larger than the posteriormost denticle in most individuals and in some cases fused with the posterior denticles. Posterior denticles are more closed, but not fused; become increasingly fused with age, forming a fused carina in gerontic individuals. They increase gradually in size and height anteriorly. There is an obvious gap between cusp and the posteriormost denticle in most specimens. Posterior brim behind cusp is usually broad. Furrows are very shallow.

Remarks.—*Clarkina orientalis* can be distinguished from *C. transcaucasica* by a broad brim and an obvious gap between cusp and the posteriormost denticle. The *C. orientalis* Zone may occupy nearly 2/3 of the upper part of the Wuchiapingian.

Wang and Wang in Zhao et al. (1981) established a new subspecies, *Neogondolella* (=*Clarkina*) *orientalis mediconstricta*, based on the contraction of the middle platform, which was considered as major difference from *Clarkina orientalis*. We recognize the holotype of that new subspecies as a gerontic *C. orientalis* specimen with variable outline of platform. Clark and Wang (1988, p. 137) established *Neogondolella latimarginata* based on "a distinct wide brim around the posterior platform and a completely fused carina." After Gullo and Kozur (1992) divided *Clarkina transcaucasica*, which has a narrower brim than *C. orientalis*, a broad brim and more fused carina became major characteristics of *C. orientalis*. Thus, *Neogondolella latimarginata* is considered to be a synonym of *Clarkina orientalis*. Tian (1993a, b) established *Neogondolella parallela* in the upper part of the Wuchiapingian, and considered it to have evolved from *N. leveni* by losing the end-node of the carina, and differs from *N. orientalis* by a rectangular platform. However, most characteristics of those specimens belong to *Clarkina orientalis*, so they are referred to *C. orientalis* in this paper. *Clarkina demicornis* established by Mei and Wardlaw in Mei et al. (1994a) may be a synonym of *C. orientalis* based on a tapered platform, a small cusp, an obvious gap, and shallow furrows.

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