Evolutional trends and palaeobiogeography of the Ordovician trilobite *Ovalocephalus* Koroleva 1959

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Ovalocephalus has a long stratigraphic range and wide geographical distribution in Ordovician peri-Gondwana. Based largely on the well-preserved specimens recently collected from China, all known forms are revised and listed. Phylogenetic analysis was conducted on the genus, involving 10 species. As suggested by the strict consensus tree, evolutionary trends of the genus include mainly the isolation of the anterior glabella portion anterior to S1, the forward shifting of eyes and the related lengthening (exsag.) of the posterior fixigena, the reduction of the number of pygidial axial segments and pleural abaxial rounded free tips, the shortening of the pygidial postaxial region, and the development of cranidial genal spines. *Ovalocephalus* may have originated in shallow-water sites of the South China Plate in the Early Floian, but migrated into the deep-water regions from the Darriwilian onwards. All the records of the genus from the Early Floian to Early Katian were confined to eastern peri-Gondwanan plates and terranes in low-latitude zones. It was only restricted to the South China, Tarim and North China plates until the Middle Darriwilian, but the Late Darriwilian eustatic sea-level rise and especially the Sandbian–Early Katian immense transgression may have brought about its dispersal to Alborz, Sibumasu and central Asian terranes. Following the closure of the Tornquist Sea, the genus was even able to spread to Baltica during the latest Katian, and the pre-Hirnantian warming (the Boda event) may have promoted a wider distribution of *Ovalocephalus* to western peri-Gondwana (the Taurides and Armorica terranes) in the then-high latitudes.

Keywords: Trilobita; *Ovalocephalus*; Ordovician; evolutionary trends; palaeobiogeography

1. INTRODUCTION

The Ordovician trilobite genus *Ovalocephalus* Koroleva 1959 has been considered a senior synonym of *Hammatoctenem* Kielan 1960 (Dean & Zhou 1988), *Tzuchiatoctenem* Sheng 1974b (Zhou & Dean 1989) and *Paratzuchiatoctenem* Wu & Xia 1990 (Zhou & Zhou 2008a), and has been recently referred to the subfamily Hammatocteneminae in the family Pliomeridae by Yuan *et al.* (2003). It has a long stratigraphic range and its evolutionary trends have been preliminarily depicted by Lu & Zhou (1979). The genus was capable of migration or dispersion involving distances of thousands of kilometres during periods when eustatic changes of sea level took place, being considered to be of important palaeobiogeographic significance (Lu & Zhou 1979; Zhou & Dean 1989). According to the global Ordovician geographical reconstructions proposed by Cocks & Torsvik (2002) and Fortey & Cocks (2003), the distribution of the genus covered a wide area from tropic to high-latitude zones, but was largely restricted to peri-Gondwana.

In this paper, the known species of *Ovalocephalus* are briefly revised, and on this basis the phylogenetic relationships between the species and palaeobiogeographic pattern of the genus are further reviewed. A series of Ordovician global maps provided by Cocks & Torsvik

(2002) and Fortey & Cocks (2003) are consulted in the following discussion, and the palaeogeographic or tectonic units employed in the ensuing pages are those of Fortey & Cocks (2003) and Zhou & Zhen (2008).

2. CHRONOSTRATIGRAPHIC, GEOGRAPHICAL AND ENVIRONMENTAL SETTING: A LIST OF SPECIES

Ovalocephalus was widely spread in the South China, North China and Tarim plates (China), Sibumasu Terrane (westernmost Yunnan and Xainza, central Tibet, China, southern Thailand and northern Burma), Middle Asian terranes (Kazakhstan, Uzbekistan, Kirghizia and Beishan of China), Alborz Terrane (North and Central Iran), Taurides Terrane (southeastern Turkey), Armorica Terrane (northeastern Spain and southern Sardinia, Italy) and Baltica (Poland) during the Ordovician. It was in full flourish especially in the South China Plate, where an almost complete and consistent sequence of various species has been recorded from the Floian to the early Late Katian (Arenig–Early Ashgill), with each species persisting for a quite short time interval. Largely based on the well-preserved specimens (figure 1) recently collected from the measure sections along bathymetric gradients in the Yangtze area, species of the genus are further revised, in particular those recorded in middle Asia and westernmost Yunnan of China, which were described with no precise stratigraphic age determined. Below are listed all known species of *Ovalocephalus*, but a few species that were established on the basis of ill-preserved material and their

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Figure 1. (Caption opposite.)

morphological characters are difficult to interpret, and some fragmentary specimens that show no diagnostic characters are excluded.

(a) *Ovalocephalus eoprimitivus* Zhou & Zhou 2008b (figure 1 v, y, z)

This species was recorded from the conodont *Oepikodus evae* Biozone–*Paroistodus originalis* Biozone of western Hubei (outer inner shelf; Lu 1975, pl. 45, fig. 6 only, as *Hammatocnemis primitivus* Lu; Turvey & Zhou 2002, pl. 1, fig. 10 only, as *Ovalocephalus primitivus*; Zhou & Zhou 2008b) and southern Anhui (shallow outer shelf build-ups)

(Yuan *et al.* 2003, as *O. primitivus*), South China. It is distributed from the Floian to the Dapingian (Early–Middle Arenig) and characterized by the glabella that gently expands forwards, shows fairly long (tr.) lateral furrows (S2–S4) and lacks the basal transglabellar furrow, by the rearward-situated palpebral lobe with its posterior margin opposite to the abaxial end of S1 or L1, and by the pygidium that displays five axial rings, five pairs of pleurae and a long postaxial region (an incorporated rectangular area of the axial terminal piece and undefined sixth pair of pleurae), which occupies approximately 35 per cent of the pygidial length.

Figure 1. (*Opposite.*) Representative specimens of some *Ovalocephalus* species recorded in China. Figured specimens are deposited at: Nanjing Institute of Geology and Palaeontology; Chinese Academy of Sciences (NIGP); Yichang Institute of Geology and Mineral Resources, Chinese Academy of Geological Sciences (YIGM); and Xi'an Institute of Geology and Mineral Resources, Chinese Academy of Geological Sciences (XIGM). (*a–h, l*) *Ovalocephalus tetrasulcatus* (Kielland 1960). (*a*) NIGP 27579, cranium, $\times 8$, and (*e*) NIGP 27580, pygidium, $\times 6.8$, the upper Pagoda Formation, Liangshan, Nanzheng, southern Shaanxi (respectively, after Zhou, Z. Q. et al. 2000, pl. 2, figs 16 and 15, as *Ovalocephalus ovatus*); (*b*) YIGM OT0098, cranium, $\times 8$, and (*f*) YIGM OT0101, pygidium, $\times 9$, the upper Pagoda Formation, Puxiheqiao, Yichang, southwestern Hubei (respectively, after Zhou et al. 2005, pl. 6, figs 3 and 9, as *O. yangtzeensis*); (*c*) NIGP 27581, cranium, $\times 3.6$, and (*d*) XIGM G174, cranium (after Li et al. 1975, pl. 22, fig. 3, as *Hammatocnemis decoratus*), $\times 3$, the Chientsaokou Formation, Yuanba, Nanzheng, southern Shaanxi; (*g*) XIGM Tr191, cranium (after Zhou et al. 1982, pl. 70, fig. 20), the Xilinkebo Formation, Beishan, northwestern Gansu; (*h*) NIGP 27582, pygidium, $\times 4$, the Chientsaokou Formation, Zhuyegou, Huijiaba, Ningqiang, southern Shaanxi; (*l*) NIGP 27583, cranium, $\times 3$, the Chientsaokou Formation, Qishuba, Mianxian, southern Shaanxi. (*i,n,o*) *Ovalocephalus yichongqiaoensis* (Wu & Xia 1990). (*i*) YIGM OT0104, cephalon, $\times 8$, and (*n*) YIGM OT0106, pygidium, $\times 6.7$, the lowest Pagoda Formation, Puxiheqiao, Yichang, southwestern Hubei (respectively, after Zhou et al. 2005, pl. 6, figs 7 and 17); (*o*) NIGP 27584, cranium, $\times 7.2$, the lowest Pagoda Formation, Yichongqiao, Cili, northwestern Hunan. (*j*) *Ovalocephalus longicervix* (Zhou in Lu et al. 1976), NIGP 27585, cranium, $\times 7.5$, the lower Pagoda Formation, Damugou, Huijiaba, Ningqiang, southern Shaanxi. (*k,m,p,q*) *Ovalocephalus kanlingensis* (Zhang 1981). (*k*) NIGP 150170, cranium, $\times 10$, the lower Pagoda Formation, Yuandun, Mianxian, southern Shaanxi; (*m*) YIGM OT0094, cranium (after Zhou et al. 2005, pl. 6, fig. 14), $\times 12.4$, the lower Pagoda Formation, Huanghuachang, Yichang; (*p*) YIGM OT0096, pygidium (after Zhou et al. 2005, pl. 6, fig. 18), $\times 12$, the lower Pagoda Formation, Puxiheqiao, Yichang, southwestern Hubei; (*q*) NIGP 150171, cranium, $\times 8.8$, the lower part of the Tumuxiuke Formation, Bachu, Xinjiang. (*r,s*) *Ovalocephalus globosus* Abdullaev 1972. (*r*) NIGP 80680, pygidium (after Zhou & Dean 1986, pl. 64, fig. 11, as *Hammatocnemis obsoletus*), $\times 10$, lower part of Chedao Formation, Chedao, Huanxian, eastern Gansu; (*s*) NIGP 150172, cranium, $\times 9$, the Datianba Formation, Maocaopu, Rheshi, Taoyuan, northwestern Hunan. (*t,w*) *Ovalocephalus extraneus* (Lu & Zhou 1979). (*t*) NIGP 56544, pygidium, $\times 8$, and (*w*) NIGP 56542, cranium, $\times 8.2$, the top of the Zuoizhan Formation, Laoshidan, Wuhai, southwestern Inner Mongolia (after Lu & Zhou 1979, pl. 1, figs 12 and 1, respectively, as *Hammatocnemis primitivus extraneus*). (*u,x*) *Ovalocephalus primitivus* (Lu in Lu & Chang 1974). (*u*) NIGP 133782, pygidium (after Turvey & Zhou 2002, pl. 1, fig. 11), $\times 15$, the uppermost Dawan Formation, Daping, Yichang, southwestern Hubei; (*x*) NIGP 127552, cranium (after Chen & Zhou 2002, pl. 1, fig. 7, as *Ovalocephalus* cf. *intermedius* (Lu & Zhou)), $\times 5.5$, the lower part of the Guniutan Formation, Liangshan, Nanzheng, southern Shaanxi. (*v,y,z*) *Ovalocephalus eoprimitivus* Zhou & Zhou 2008b. (*v*) YIGM OT0113, pygidium, $\times 10.8$, and (*y*) YIGM OT0115, cranium, $\times 16.8$, the lowest Dawan Formation, Huanghuachang, Yichang; (*z*) NIGP 133781, cranium, $\times 8$, the upper Dawan Formation, Daping, Yichang, southwestern Hubei, respectively, after text-fig. 1*d,a,c* of Zhou & Zhou (2008b).

(b) *Ovalocephalus primitivus* (Lu in Lu & Chang 1974) (figure 1*u,x*)

This form occurs in South China within the *Undulograptus austrodentatus* graptolite Biozone, and is mainly associated with strata of shallow-outer-shelf facies in northeastern Guizhou (Yin & Lee 1978, as *H. primitivus*), central Hubei (Sun 1984, as *H. primitivus*) and western Hubei (Lu & Chang 1974; Lu 1975, exclusive of pl. 45, fig. 6; Zhou et al. 1977; Sun 1984; all as *H. primitivus*; Turvey & Zhou 2002, pl. 1, fig. 11 only), except for northwestern Hunan, where it has a deep outer shelf setting (Turvey & Zhou 2004). Recently, it was further found from the *Yangtzeplacognatus crassus* conodont Biozone in northwestern Hunan in association with an inner deep outer shelf biofacies (Zhou et al. 2001, as *O. intermedius* Lu & Zhou), and from the lower Guniutan Formation (Middle Darriwilian or Early Llanvirn; shallow outer shelf; Chen & Zhou 2002, as *O. cf. intermedius*) of southern Shaanxi. Outside South China, it was reported from the basal part of the *Lenodus variabilis* conodont Biozone in the Kalpin area (upper slope) of Tarim, Xinjiang (Zhang 1981, as *H. primitivus*; Zhou et al. 1998, as *O. primitivus extraneus*), and from the *Pseudamplexograptus confertus* graptolite Biozone (Lu & Zhou 1979, as *Hammatocnemis intermedius*) in southwestern Inner Mongolia (upper slope of the North China Platform; see Zhou et al. 1989). The species is of Early–Middle Darriwilian (Late Arenig–Early Llanvirn) age, and differs from *O. eoprimitivus* Zhou & Zhou in the development of a basal transglabellar furrow (although becoming much shallower adaxially), the more forwardly expanded glabellar portion anterior to S1 with shorter (tr.) lateral glabellar furrows, the slightly forward-placed palpebral lobe with its posterior margin in line with L2 or the abaxial end of S2 instead of S1, the correspondingly longer posterior

fixigenal area, and the pygidium showing four rather than five pairs of pleurae with the undefined fifth pair merging the axial terminal piece into a trapezoid instead of rectangular pygidial postaxial region that occupies approximately one-quarter rather than 35 per cent of the pygidial length.

(c) *Ovalocephalus extraneus* (Lu & Zhou 1979) (figure 1*t,w*)

This species was established as *H. primitivus extraneus* by Lu & Zhou (1979) from the *Lenodus antivariabilis* conodont Biozone (Early Darriwilian or Late Arenig) of the western marginal area (upper slope of the North China Platform; see Zhou et al. 1989) in southwestern Inner Mongolia. It agrees well with *O. eoprimitivus* in the rearward-placed palpebral lobe and the comparatively long (tr.) lateral glabellar furrows, but otherwise it is indistinguishable from *O. primitivus*.

(d) *Ovalocephalus globosus* Abdullaev 1972 (figure 1*r,s*)

This species was first described from the Ordovician of the Bukantau Mountains, Uzbekistan (Abdullaev 1972). After a critical comparison, several Chinese species are considered as its junior subjective synonyms, including *Tzuchiatoecnemis tzuchiaensis* Sheng 1974b from westernmost Yunnan, *Hammatocnemis obsoletus* Zhou & Dean 1986 from the *Nemagraptus gracilis* graptolite Biozone of eastern Gansu (upper slope of the North China Platform; see Zhou et al. 1989), and *Paratzuchiatoecnemis dialox* Wu & Xia 1990 from the conodont *Yangtzeplacognatus protoramosus* Biozone and *Yangtzeplacognatus jianyeensis*–*Pygodus anserinus* Biozone of northwestern Hunan (shallow outer shelf; see Zhou et al. 2001, as *Ovalocephalus obsoletus*). This form probably

ranges from the Late Darriwilian to Early Sandbian (Late Llanvirn–earliest Caradoc), and is closely allied to *O. extraneus* in many respects. The distinct features are the development of a more strongly forwardly expanded anterior glabellar portion in front of the abaxial end of S2 with S3 and S4 more faintly defined, the slightly forward-placed palpebral lobe with its posterior margin in line with L2, the presence of the genal spine, and the four- rather than five-segmented pygidial axis.

(e) *Ovalocephalus kelleri* Koroleva 1959 and allies (figure 1i,n,o)

There are three closely related species recorded from the Late Sandbian (Early Caradoc). One is the type species *O. kelleri* Koroleva 1959 (holotype cranidium refigured by Fortey 1997, pl. 9, fig. 7; see also Apollonov 1974) from northern Kazakhstan. It was also reported by Abdullaev in Abdullaev & Khaletskaya (1970, as *Hammatocnemis tetrasulcata* Kielan), from Chatkal'skiy Range, Uzbekistan; by Abdullaev (1972, as *H. globosus*), from Bukantau, Uzbekistan; by Repina et al. (1975), from Madygena, Kyrgyzstan; and by Zhou & Dean (1986), from the lower part of the *Sinoceras chinense* cephalopod Biozone of eastern Gansu (upper slope of the North China Platform, see Zhou et al. 1989). The second is *Ovalocephalus yichongqiaoensis* (Wu & Xia), described from the lower part of the *Hamarodus europaeus* conodont Biozone (roughly equivalent to the *Climacograptus wilsoni* graptolite Biozone) by Wu & Xia (1990, as *Paratzuchiatocnemis yichongqiaoensis*) and Ji (1987, as *Hammatocnemis ovatus* Sheng) in northwestern Hunan (inner deep outer shelf), and documented by Zhou et al. (2005) from the same horizon in northwestern Hubei (shallow outer shelf; see Zhou et al. 1999; Zhou, Z. Y. et al. 2000), South China. The third is *Ovalocephalus plewesae* Fortey 1997, erected from the lower part of the Pa Kae Formation, southern Thailand. All of them are closely compared with *O. globosus*, but the cranidium differs in having an elongate, oval to subrhombic anterior glabellar portion with S3 detached from the axial furrow, a basal transglabellar furrow that is deeply incised throughout and a more forwardly situated palpebral lobe with its posterior margin in line with L3. Differences between these forms are tiny. *Ovalocephalus plewesae* agrees well with *O. yichongqiaoensis* (figure 1i,n,o), except for the more forwardly pointed glabella. According to Fortey (1997, p. 436), *O. kelleri* differs from the Thailand form in the less pointed frontal glabellar lobe, the granulose rather than smooth cranidium surface and the more inflated L1.

(f) *Ovalocephalus kanlingensis* (Zhang 1981) (figure 1k,m,p,q)

The species was named as *Hammatocnemis kanlingensis* by Zhang (1981) from the *Corynoides americanus* graptolite Biozone (equivalent roughly to the lower part of the *Dicranograptus clingani* graptolite Biozone) in the Kalpin area and reported from the *Lituites* cephalopod Biozone or the conodont *Pygodus serra* Zone–*Baltoniodus variabilis* Biozone in the Bachu area (upper slope; figure 1q; see Zhou et al. 1992) of Tarim, Xinjiang. It has recently been discovered from South China (figure 1k,m,p) in the middle part of the *H. europaeus* conodont Biozone (roughly equivalent to the graptolite *D. clingani* Biozone) of northwestern Hubei (shallow outer shelf; Zhou et al. 2005)

and northwestern Hunan (inner deep outer shelf; see Zhou et al. 1999; Zhou, Z. Y. et al. 2000), from southern Shaanxi (outer deep outer shelf; see Zhou, Z. Q. et al. 2000), and from Central Iran in the latest Darriwilian (Ghobadi Pour & Popov 2009, fig. 2f–h, as *O. aff. obsoletus* Zhou & Dean). In eastern Gansu (then upper slope of the North China Platform; see Zhou et al. 1989), it was recorded from the *N. gracilis* graptolite Biozone by Zhou & Dean (1986). As suggested by Zhou & Dean (1986), some specimens described as *Hammatocnemis tetrasulcatus* Kielan from Tarim, southern Xinjiang (Lu & Zhou 1979), Madygena, Kyrgyzstan (Repina et al. 1975, pl. 46, figs 1–3, 6–8, 12, 14, non 9–11, 13) and northern Kazakhstan (Apollonov 1974, pl. 13, figs 1 and 3 only) are indistinguishable from, and may therefore be reassigned to, *O. kanlingensis*. In addition, it may also have a distribution in westernmost Yunnan as suggested by a cranidium reported as *H. tetrasulcatus* by Sheng (1974b, pl. 9, fig. 4a only). This form ranges from the Late Darriwilian to the earliest Katian (Late Llanvirn–early Middle Caradoc). Its anterior glabellar portion is elongate, as long as approximately three-quarters of the glabellar length, as in *O. primitivus*, but is more inflated, oval in form with the widest width across its mid-length, and better defined by a deep thorough basal transglabellar furrow in the rear. Furthermore, other characters distinct from *O. primitivus* include the development of a pair of genal spines, the more forwardly situated palpebral lobe with its posterior margin in line with L3 and the four- rather than five-segmented pygidial axis.

(g) *Ovalocephalus tetrasulcatus* (Kielan 1960) and allies (figure 1a–h,j,l)

Ovalocephalus tetrasulcatus was established as *H. tetrasulcatus* from the latest Katian (Middle Ashgill) of the Holy Cross Mountains, Poland by Kielan (1960). Since then it has successively been described as from the Early Katian (Middle Caradoc) of Chongqing (Sheng & Ji 1986); the early Late Katian (Early Ashgill) of the Zap Valley, southeastern Turkey (Dean & Zhou 1988), Chongqing, northeastern Guizhou and northern Sichuan (Sheng 1964), western Zhejiang (Sheng 1974a; Qiu et al. 1983), Beishan, Gansu (Lu & Zhou 1979 as *H. cf. globosus* Abdullaev; Zhou et al. 1982; see figure 1g), and westernmost Yunnan (Sheng 1974b, pl. 9, fig. 4b only); and the latest Katian (Middle Ashgill) of Aragón, northeastern Spain (Hamman 1992, as *Ovalocephalus cf. tetrasulcatus*) and southern Sardinia, Italy (Leone et al. 1991; Hamman & Leone 2007, as *O. cf. tetrasulcatus*). The species was also recorded from Ulugtau (Repina et al. 1975, pl. 43, figs 17–18, as *Hammatocnemis globosus* Abdullaev) and Madygena (Repina et al. 1975, pl. 46, figs 9–11, 13 only), Kyrgyzstan and northern Kazakhstan (Apollonov 1974, pl. 13, figs 2, 4–8, non 1, 3). Moreover, a few specimens (e.g. figure 1l) recently collected from an early Late Katian (Early Ashgill) horizon at Qishuba, southern Shaanxi are likewise typical of this foreign species.

Ovalocephalus longicervix (Zhou in Lu et al. 1976) has a restricted distribution in the deep sites of the outer shelf of the Yangtze sea in northwestern Jiangxi (Zhou in Lu et al. 1976; Lu & Zhou 1979; Qiu et al. 1983), western Zhejiang (Qiu et al. 1983, including also a cephalon (pl. 82, fig. 3) that was assigned to *H. ovatus* Sheng) and the northern part of southern Shaanxi (figure 1j).

It ranges from the upper part of the *H. europaeus* conodont Biozone to the *Nankinolithus* trilobite Biozone (late Early–early Late Katian or late Middle Caradoc–Early Ashgill), being closely allied to *O. kanlingensis* in many respects, especially in having an elongate-oval anterior glabellar portion, but distinct in the more elongate occipital ring, the anterior glabellar portion more adaxially constricted at its base and the more depressed median part of the preoccipital lobe. The last two features in turn render the species quite similar to *O. tetrasulcatus*.

In addition to *longicervix* and *tetrasulcatus*, there were also several additional species of *Ovalocephalus* being widely documented from the Katian outer shelf facies beds (see Zhou et al. 1999; Zhou, Z. Q. et al. 2000; Zhou, Z. Y. et al. 2000; Zhou et al. 2003) in the Yangtze area. *Ovalocephalus ovatus* was erected as *H. tetrasulcatus* var. *ovatus* by Sheng (1964) from the conodont upper *H. europaeus* Biozone–*Protopanderodus insculptus* Biozone (correlated approximately to the graptolite *Diplacathograptus spiniferus* Biozone–lower *Dicellograptus johnstupti*–*Orthograptus quadrimucronatus* Biozone; late Early Katian or late Middle–Late Caradoc) on the basis of cranidia collected at Nanzheng, southern Shaanxi and Yinjiang, northeastern Guizhou. It was subsequently reported from the upper part of the *H. europaeus* conodont Biozone–*Nankinolithus* trilobite Biozone (late Early–early Late Katian or late Middle Caradoc–Early Ashgill) in Hubei (Lu & Chang 1974; Lu 1975; Xia 1978; Sun 1984), Chongqing (Lee 1978; Ji 1986; Xiang & Ji 1986), central Sichuan (Lu 1975), western Hunan (Xiang & Ji 1988), southern Jiangsu (Tripp et al. 1989), southern Shaanxi (Zhou, Z. Q. et al. 2000) and at other localities of Guizhou (Xiang & Ji 1988; Yin et al. 2000). Outside South China Plate, *O. ovatus* occurs in the Pa Kae Formation of southern Thailand (Fortey 1997).

Other forms successively established and described include *Hammatocnemis decorosus* Lu in Lu & Chang 1974 (Li et al. 1975; Lu 1975; Lee 1978; Xia 1978; Lu & Zhou 1979, 1981; Liu 1982; Qiu et al. 1983; Sun 1984; Tripp et al. 1989; Zhou, Z. Y. et al. 2000); *H. hexianensis* Zhang in Qiu et al. 1983; *H. huayinshanensis* Lu in Lu & Chang 1974 (Lu 1975); *H. liangshanensis* Chen in Li et al. 1975; *H. minor* Chen in Li et al. 1975 (Xiang & Zhou in Wang et al. 1987); *H. nanzhengensis* Zhou in Li et al. 1975; *H. orientalis* Chen in Li et al. 1975; *H. pogodus* Chen in Li et al. 1975; and *H. sinensis* Han 1980; *H. (?) tudilingensis* Chen in Li et al. 1975; and *H. yangtzeensis* Lu in Lu & Chang 1974 (Lu 1975; Xia 1978; Sun 1984; Yin et al. 2000; Zhou, Z. Y. et al. 2000; Zhou et al. 2005).

However, after revised by Lu & Zhou (1979) and Yuan et al. (2003), only two of the listed forms—*O. ovatus* and *O. yangtzeensis*—were considered as valid. Recently, Zhou et al. (2005, p. 342) have further suggested that *O. ovatus* was probably a senior subject synonym of *O. yangtzeensis*. A close comparison between the related specimens we collected from Nanzheng, southern Shaanxi (type locality of *ovatus*) and Yichang, western Hubei (type locality of *yangtzeensis*) indicates with confidence that both forms are almost identical in all the diagnostic characters (compare figure 1a,e with figure 1b,f).

On the basis of the holotype cephalon (Kielan 1960, pl. 26, fig. 2), *O. tetrasulcatus* differs from *O. ovatus* mainly in the proportionally much shorter (wider than long) and more strongly forwardly expanded anterior glabellar

portion, but one well-preserved paratype cranium (Kielan 1960, pl. 27, fig. 6) agrees well with that of the Chinese form. As noted by Tripp et al. (1989), Fortey (1997) and Hamman & Leone (2007), some of the superficial differences between the types are preservational, because most of the Polish specimens are external moulds. In this regard, we prefer herein to consider both the species as synonymous.

The young species of *Ovalocephalus*, *O. longicervix* and *O. tetrasulcatus* are characterized by the glabella with strongly inflated and basically oval-shaped anterior portion in front of S1, well isolated and highly convex L1, long and strongly forward-arched occipital ring, and depressed rather than elevated (as in *kanlingensis*) median part of the preoccipital ring.

3. EVOLUTIONAL TRENDS

Ovalocephalus made its earliest appearance in the Floian and was restricted to the shallow-water sites of the South China Plate during the late Early–early Middle Ordovician, then subsequently migrated from the Darriwilian onwards into the deep-water regions. The nearshore origination and offshore development of the genus seems to support the hypothesis (Jablonski et al. 1983) on the macroevolution of marine benthic faunas.

In order to assess the relationships among the 10 species of *Ovalocephalus*, phylogenetic analysis was conducted using PAUP v. 4.0.b10 (Swofford 2003) on the basis of a dataset of 17 scored characters (see appendix A for details). The result is distilled into figure 2.

Ovalocephalus eoprimitivus, the oldest known species of the genus, is considered a probable ancestral form. Two subclades (figure 2) arose from it since the Darriwilian. One is represented by a single representative *extraneus*, and the other includes *primitivus*, *kanlingensis*, *tetrasulcatus*, *longicervix*, *globosus*, *kelleri*, *yichongqiaoensis* and *plewesae*. In the latter subclade, two groups of species are well resolved as monophyletic. The first consists of closely related Late Sandbian forms *kelleri*, *yichongqiaoensis* and *plewesae*, although their relationships are still ambiguous according to the strict consensus tree (see appendix A), each of which retains some primitive characters as shown in *eoprimitivus* and *globosus* (i.e. the comparatively long (tr.) lateral glabellar furrows, the gently convex L1 and the short occipital ring with anterior margin gently arched forwards). As distinct from the allied earlier form *globosus*, all of them basically have an elongate-oval instead of oval anterior glabellar portion.

The second group involves *kanlingensis*, *tetrasulcatus* and *longicervix*. All of them show fairly convex L1, almost abaxially extended pleurae in outer portion of pygidial pleura and fairly short (tr.) lateral glabellar furrows, the latter of which is suggested as a homoplastic feature (appendix A). The Late Darriwilian–earliest Katian representative *kanlingensis* is characterized by the oval-shaped, inflated anterior glabellar portion, the rear of which is well defined by an elevated preoccipital ring. In the young forms *tetrasulcatus* and *longicervix*, the anterior glabellar portion is further inflated, while the preoccipital ring is turned to be rather depressed for most part but with well isolated and highly convex L1, and the occipital ring is much lengthened with anterior margin more strongly arched forwards.

Figure 2. Strict consensus cladogram of *Ovalocephalus* (figure 4, appendix A) plotted against Ordovician chrono-stratigraphic scheme, showing phylogenetic, stratigraphic and geographical relationships among its species. Thick vertical lines indicate stratigraphic ranges based largely on the data from China. Geographical distribution of each species is listed in square brackets. Tre., Tremadocian; Dap., Dapingian; Hir., Hirnantian; AL, Alborz Terrane; AT, Armorica Terrane; BP, Baltica Plate; MA, Middle Asian terranes; NC, North China Plate; SC, South China Plate; ST, Sibumasu Terrane; TP, Tarim Plate; TT, Taurides Terrane.

It is interesting to note that the sequential speciation suggested from the strict consensus cladogram (appendix A, figure 4) seems synchronous with the stratigraphic succession (figure 2). In general, the evolutionary trends exhibited in the whole clade include the development of the basal transglabellar furrow (since the Early Darriwilian); the deepening of the basal transglabellar furrow and the isolation of the anterior glabellar portion (since the Late Darriwilian in the *kanlingensis* species group, but taking place in the Late Sabadian in the *kelleri* species group); the forward shifting of eyes (with their posterior margin in line with S1 in *O. extraneus*, with L2 or the abaxial end of S2 in *primitivus*, with L2 in *globosus*, and with L3 in all other species) and, correspondingly, the lengthening (exsag.) of the posterior fixigena; the reduction of the number of pygidial axial segments from five (in *primitivus* and *extraneus*) to four (in all younger species); the reduction of the number of abaxial rounded free tips of pygidial pleurae from three (in *primitivus*, *extraneus* and *globosus*) to one (in all younger species); and the progressively shortening of the pygidial postaxial region (since the Early Darriwilian). In addition, pleurae in the outer portion of pygidial pleura are almost backwardly extended in older species (*primitivus* and *extraneus*), but become postero-laterally extended in all the species in the *kelleri* group, or almost abaxially extended in species of the *kanlingensis* group. Moreover, in contrast with the older, all the younger (Late Darriwilian–Katian) species of the genus bear a pair of cranidial genal spines.

As revealed by Yuan *et al.* (2003), ontogenetic changes of the earliest known species *O. eoprimitivus* include the widening of the posterior part of the preoccipital glabella; posterior shift of the palpebral lobe and related shortening of the posterior fixigenal field; progressive reduction and finally degeneration of the fixigenal spine; and reduction in the number of pygidial pleurae and axial rings. The adults of the species from the Floian to Late Katian successively exhibit more immature features, suggesting that paedomorphosis plays an important role in the evolution of the genus.

4. PALAEOBIOGEOGRAPHIC IMPLICATIONS

Judging from the morphological features, *Ovalocephalus* is a typical benthic form, but the ontogenetic series of *O. eoprimitivus* does indicate that the genus has a single non-adult-like planktonic anaprotaspis larval stage (Yuan *et al.* 2003, text-fig. 3a,b), suggesting a life-history strategy II of Chatterton & Speyer (1997). The wide distribution of *Ovalocephalus* may, therefore, be a result of its effective larval dispersal. As suggested by Zhou & Dean (1989) and Cocks & Fortey (1990), there is no evidence for the presence of oceanographic barriers that might have prevented migration and dispersal of trilobites between different geographical units of Ordovician Gondwana and peri-Gondwana.

Except for *O. eoprimitivus*, almost all other species from Darriwilian to Katian are associated with outer shelf/slope environments. Despite being a basically deep-water trilobite genus, *Ovalocephalus* shows a relatively restricted palaeogeographic distribution during the Floian–Early Katian. All the records of the genus from these time intervals were confined to eastern peri-Gondwana plates and terranes in low-latitude zones.

It appears that *Ovalocephalus* may have originated in the South China Plate during the Early Floian following the Tremadocian/Early Arenig (Floian) regressive–transgressive couplet (Fortey 1984), which accompanied the development of endemic trilobite faunas as noted by Zhou & Fortey (1986). The dispersion of the genus to other parts of the eastern peri-Gondwana areas seems largely to have been induced directly by the global transgressive events. *Ovalocephalus* was restricted only to a few localities in the South China Plate until the Dapingian. However, the Early Darriwilian transgression (e.g. Nielsen 1992; Su 2001) may have caused scattering in the Yangtze region and intercontinental dispersal of the genus to the Tarim and North China plates. Following a short-period regressive phase occurring between the Middle and Late Darriwilian, a eustatic sea-level rise (e.g. Su 2001; Nielsen 2004) during the Late Darriwilian may have brought about the further dispersal of *Ovalocephalus* to Sibumasu, Alborz and central Asian terranes. The Caradoc (Sandbian–Early Katian) was a period when the Ordovician climax transgression took place (Fortey 1984; Zhou *et al.* 1989, 1992; Barnes 2004). This event may have led to the development of new ecological associations along a range of new environmental niches and, as a result, the increase in species diversity of *Ovalocephalus* in these low-latitude regions may have been especially early at this stage.

Whittington & Hughes (1972) indicated that the trilobite faunas had progressively decreased in provinciality from the Floian or Arenig onwards during the

Figure 3. Cladogram showing one most parsimonious tree with length 31, CI of 0.9355 and RI of 0.9500.

Ordovician. Recently, Fortey & Cocks (2003) have provided further evidence for the Late Katian or Ashgill breakdown of faunal provincialism. Although the Late Katian may represent a stage of lowstand interval in terms of eustatic sea levels (Nielsen 2004), the proposed brief pre-Hirnantian warming or the Boda event (Fortey & Cocks 2005) may have resulted in a poleward invasion, dispersal or migration of the benthic faunas, and promoted a wider distribution of *Ovalocephalus* to western peri-Gondwana (the Taurides and Amorica terranes) in the then-high latitudes prior to its final demise during or before the first episode of the end Ordovician mass extinction event. The latest Katian or Middle Ashgill saw also the spread of the genus onto the Holy Cross Mountain of Poland, a part of Baltica then situated in the low-latitude zones (Cocks & Torsvik 2002; Fortey & Cocks 2003), following the closure of the Tornquist Sea. However, *Ovalocephalus* almost died out in eastern peri-Gondwanan plates and terranes during most of the Late Katian (late Early–Middle Ashgill) due to either the unsuitable living environments (e.g. the wide distribution of graptolite facies beds in the South China Plate and Sibumasu Terrane, of littoral clastics in the Tarim Plate, and of the graptolite facies deposits, carbonate build-ups and inner shelf clastics in the Middle Asian terranes), or the omission of coeval rocks (North China Plate).

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APPENDIX A

In order to assess the relationships among the 10 species of *Ovalocephalus*, cladistic analysis was conducted.

Figure 4. Cladogram showing strict consensus tree of two most parsimonious cladograms.

(a) Characters and character states

An investigation of adult morphology was carried out for the phylogenetic analysis, in which 17 cranial and pygidial characters were scored across the ingroup and outgroup species. As hypostomes have not been found in most species and librigenae usually have no diagnostic characters, characters of them are therefore not employed in the analysis. Although type material was studied where possible, the characters available for analysis were often defined on the basis of well-preserved specimens for most species. Some characters proved to be preservational, which were excluded from the dataset. *Encrinuella* is selected as outgroup taxon as it is closely allied to *Ovalocephalus*. It was coded using *E. tetrasulcata* Ju in Lu & Zhou 1981 (see also Tripp et al. 1989,

fig. 14b,g,h,m) rather than its type species *E. inshangensis* (Reed), as the Chinese form is more completely preserved and the type specimens are more easy to access.

The characters and their states are listed below, of which 6 are binary and 11 are multistates.

- (i) Basal transglabellar furrow: 0, absent; 1, present but shallow mesially; 2, present but deep throughout.
- (ii) Median part of preoccipital ring: 0, absent; 1, present and gently elevated; 2, present and depressed.
- (iii) Isolation of anterior part of glabella anterior to S1: 0, not isolated from the rear glabellar portion; 1, isolated from the rear glabellar portion.
- (iv) Shape of anterior part of glabella anterior to S1: 0, axe shaped; 1, oval; 2, elongate oval.
- (v) Lateral glabellar furrows: 0, long (tr.); 1, short (tr.).
- (vi) Posterior margin of palpebral lobe: 0, in line with abaxial end of S1 or L1; 1, in line with L2 or abaxial end of S2; 2, in line with abaxial end of L3.
- (vii) Fixigenal spine: 0, absent; 1, present.
- (viii) L1: 0, gently convex; 1, fairly convex; 2, well isolated and highly convex.
- (ix) Convexity of anterior part of glabella anterior to S1: 0, gently convex and not overhanging anterior cranial border; 1, convex and slightly overhanging anterior cranial border; 2, strongly convex and overhanging anterior cranial border.
- (x) Anterior margin of glabella: 0, broadly rounded; 1, narrowly rounded; 2, pointed.
- (xi) Occipital ring: 0, short (less than one-third as long as wide) with anterior margin gently arched forwards; 1, long (less than half as long as wide) with anterior margin prominently arched forwards; 2, very long (more than two-thirds as long as wide) with anterior margin strongly arched forwards.
- (xii) Number of pygidial axial rings: 0, 5; 1, 4.
- (xiii) Sagittal pygidial length posterior to fourth axial ring: 0, around 40 per cent of pygidial length; 1, around 30 per cent of pygidial length; 2, around 25 per cent of pygidial length.
- (xiv) Pygidial postaxial region (an incorporated area of the axial terminal piece and posterior undefined pleurae): 0, absent; 1, present and rectangular in shape; 2, present and trapezoid in shape.
- (xv) Number of pygidial pleurae: 0, 5; 1, 4.
- (xvi) Pleurae in outer portion of pygidial pleura: 0, almost backwardly extended; 1, postero-laterally extended; 2, almost abaxially extended.
- (xvii) Number of abaxial rounded free tips of pygidial pleurae: 0, 5; 1, 3; 2, 1.

(b) Results of the cladistic analysis

The data matrix for all the ingroup and outgroup species is presented in table 1. All characters were treated as unordered and unweighted. Parsimony analysis was conducted on PAUP v. 4.0.b10 (Swofford 2003), employing the exact branch and band algorithm and accelerated transformation optimization (ACCTRAN). Within these parameters, two equally parsimonious cladograms of

Table 1. Data matrix for character state distributions used in phylogenetic analysis of *Ovalocephalus* species.

species	i	ii	iii	iv	v	vi	vii	viii	ix	x	xi	xii	xiii	xiv	xv	xvi	xvii
<i>E. tetrasulcata</i>	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0
<i>O. eoprimitivus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>O. primitivus</i>	1	1	0	0	1	1	0	0	1	0	0	0	1	2	1	0	1
<i>O. extraneus</i>	1	1	0	0	0	0	0	0	1	0	0	0	1	2	1	0	1
<i>O. globosus</i>	1	1	0	1	0	1	1	0	0	0	0	1	1	2	1	1	1
<i>O. kelleri</i>	2	1	1	2	0	2	1	0	1	1	0	1	1	2	1	1	2
<i>O. plewesae</i>	2	1	1	2	0	2	1	0	1	2	0	1	1	2	1	1	2
<i>O. yichongqiaoensis</i>	2	1	1	2	0	2	1	0	1	1	0	1	1	2	1	1	2
<i>O. kanlingensis</i>	2	1	1	1	1	2	1	1	1	0	0	1	1	2	1	2	2
<i>O. longicervix</i>	2	2	1	1	1	2	1	2	2	0	2	1	2	2	1	2	2
<i>O. tetrasulcatus</i>	2	2	1	1	1	2	1	2	2	0	1	1	2	2	1	2	2

length 31, consistency index (CI) 0.9355 and retention index (RI) 0.9500 were found. One of the shortest trees and the strict consensus tree are shown in figures 3 and 4, respectively.

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