

Biostratigraphy and avian origins in northeastern China

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ABSTRACT

The Late Jurassic age frequently attributed to fossils from the Yixian Formation (Liaoning and Hebei provinces, People's Republic of China), including theropod dinosaurs with feathers or integumentary structures (for example, *Beipiaosaurus*, *Caudipteryx*, *Protarchaeopteryx*, *Sinornithosaurus* and *Sinosauropteryx*) and the primitive bird *Confuciusornis*, is based heavily on biostratigraphic arguments. However, most Yixian taxa are endemic, known only from singular localities and few specimens. Accurate biostratigraphic correlation requires geographically widespread taxa represented by many specimens and restricted stratigraphic ranges. Other support for a Late Jurassic age based on fauna-level differences from well-constrained Early Cretaceous faunas and assumed "stage of evolution" comparisons are dubious when taphonomic and paleoecological factors are taken into account. Precise dating of the beds is important because, if these are truly Late Jurassic, then the hypotheses advocating a maniraptoriform theropod ancestry of birds are complicated. Radiometric dates obtained from interbedded volcanics in the Yixian Formation yield Early Cretaceous ages, which contrast sharply with many of the biostratigraphic data, implying that the primitive Yixian taxa may be relicts. Given the problems with Yixian biostratigraphy, the radiometric data, which indicate Cretaceous ages between 120 and 25 my, must be viewed as the best evidence for the age of the Yixian Formation.

KEYWORDS

Sihetun, geochronology, Liaoning, birds, feathered dinosaurs, Yixian.

Introduction

The recent discoveries of a biota consisting of a diverse avifauna (for example, *Confuciusornis* and *Liaoningornis*; Hou 1997a; Hou, Zhou, Gu and Zhang 1995), theropod dinosaurs with in-

tegumentary coverings (*Sinosauropteryx*, *Beipiaosaurus*, *Sinornithosaurus*, *Caudipteryx* and *Protarchaeopteryx*; Chen et al. 1998; Q. Ji and S. Ji 1996, 1997; Ji et al. 1998; Xu, Tang et al. 1999; Xu, Wang et al. 1999) and probable angiosperm remains (see Cao et al. 1998; Ren 1998a; Sun et al. 1998) from the Yixian Formation of Liaoning Province, China, have focused worldwide attention on this region, especially near the village of Sihetun (Figure 1). Feathered theropods provide strong support for a dinosaurian origin for birds and the presence of primitive ornithurans alongside nonornithurans indicates modern-style birds came about early in avian evolution (Hou et al. 1996). Exactly how early, however, has become a matter of some debate.

While consensus seems to have been reached that the overlying Jiufotang Formation is Lower Cretaceous (e.g., Fan 1996), arguments have ensued as to whether the Yixian Formation dates to the Tithonian (Late Jurassic) or the Early Cretaceous (Li and Liu 1994; Hou, Zhou, Gu and Zhang 1995; Smith et al. 1995; Q. Ji and S. Ji 1996; Chen et al. 1998; Smith et al. 1998; Ji et al. 1999; Swisher et al. 1999). As the Yixian birds *Eoenantiornis* and *Liaoningornis* are heralded as the oldest members of their clades (Hou, Zhou, Gu and Zhang 1995; Zhou and Hou 1998), and given apomorphies beyond *Archaeopteryx* possessed by *Confuciusornis* (for example, an edentulous beak and a pygostyle), the age of the Yixian Formation is critical to our understanding of early bird evolution. If this primitive avifauna is Tithonian (about 145 Ma), it is coeval with *Archaeopteryx* (currently the oldest, most basal bird). *Archaeopteryx* is then unsuitable as a progenitor of the Chinese birds (see Q. Ji and S. Ji 1996; Martin et al. 1998), and significantly earlier ancestral taxa are necessary for both *Archaeopteryx* and the Chinese taxa. A Tithonian Yixian also complicates the theropodan bird origins hypothesis as maniraptoriforms (sensu Sereno 1999) have yet to be found in sediments older than the Late Jurassic. The age of the Yixian Formation thus demands careful attention. However, most work concerning the age of the Yixian has been based on biostratigraphy that has been largely ambiguous or problematic. The age of the Yixian Formation is a problem better suited to radiometric geochronology than biostratigraphy, and most current Yixian radiometric dates are around 120 to 125 Ma—significantly younger than *Archaeopteryx*.

Geological Context

Lying unconformably on the Middle Jurassic Tuchengzi Formation in the Sihetun region, the Yixian Formation forms the base of the Jehol Group, which consists of the fluvial, lacustrine, volcanoclastic and volcanic fill of several Mesozoic extensional basins in western Liaoning (see Figure 2). The Yixian consists of some 2000 to 4700 m of intercalated volcanic and sedimentary rocks (Chen et al. 1982b; Wang and Sun 1983; Mao et al. 1990; Wang, Hu et al. 1995). The sediments are predominantly laminated siltstones and shales with tuffaceous sandstones. It is generally agreed (and our field observations confirm) that the sediments occur as distinct, fairly continuous horizons intercalated with the igneous rocks (Deng 1994; Wang, Hu et al. 1995). The most basal of the four major intercalations is the unit of interest. In the Sihetun area, the Yixian is a package of sedimentary and igneous rocks that strike generally northeast, are conformably overlain by the Jiufotang Formation to the west, and are bounded on the southeastern side by a northeastward trending normal fault system, into which they dip about 10° to the southeast (see Figure 2 map).

The lithostratigraphic nomenclature of the Yixian Formation has a complex history, having been variably divided (or not) based on lithologic differences, geographic differences (between provinces or depositional basins) and, apparently, paleontological differences. Wang et al. (1990), Wang (1991), and Ren, Guo et al. (1995) reviewed numerous other names previously given to subdivisions of alternating sedimentary and volcanic beds (including Dabeigou, Dadingzi, Dalinghei, Daobazi (Zhuanchenzi), Daxinjinzi, Huajiying, Huanghuashan, Jingangshan, Jianchang, Sunjialiang, Yushugou, and Zhangjiakou). Q. Ji, S. Ji et al. (1999) recently separated the lowermost portion of the Yixian Formation out into the Chaomidiazi Formation, which appears to consist of the lower 25 m of the Yixian Formation and includes the fossil horizons in the Sihetun area. However, the separation of these lower sedimentary intercalations into a new

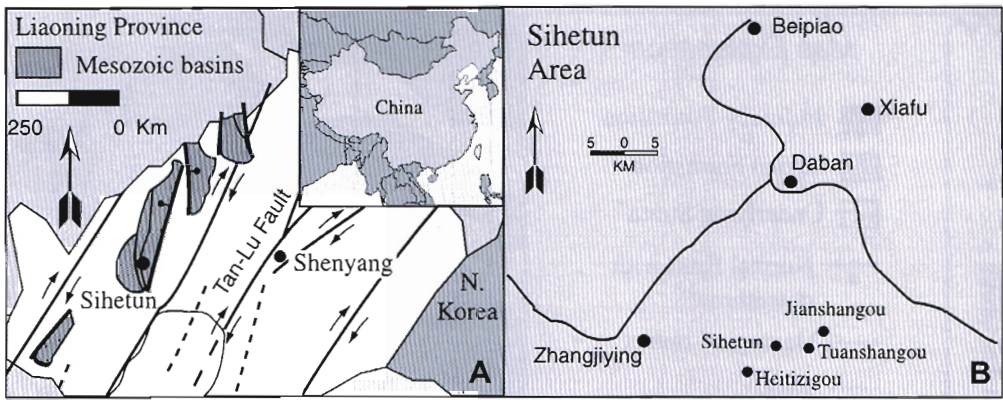


FIGURE 1. A, location of the Sihetun area within the Mesozoic extensional basins of western Liaoning Province, northeast China (note that these basins are very simplified here). B, locus map of the Sihetun area south of Beipiao (after X. Wang et al. 1998).

unit has been resisted (see Swisher et al. 1999). This is not surprising as there is no real change in lithology in the lower part of the Yixian Formation, as is required by international stratigraphic guidelines, to justify a new formation. As such, we follow Ren, Gu et al. (1995) and recognize here only an undivided Yixian Formation.

The “Feathered Dinosaur Age Problem”

Although the age of the Liaoning dinosaurs and birds has received recent attention, the age of the Yixian Formation has been controversial for more than 100 years. However, it seems unlikely that the younger Jehol Group units are older than the Barremian (Lower Cretaceous; see Li and Liu 1994). The Yixian has been assigned Triassic, Early Middle and Late Jurassic, Late Cretaceous (Woodward 1901; Grabau 1923; T’an 1923; Endo 1940; Zhou 1995), and even Tertiary (Sauvage 1880) ages. Grabau (1928) instead proposed an Early Cretaceous age for the Yixian characterized by an *Eosesthesia* (conchostracan), *Ephemeroptera* (mayfly) and *Lycoptera* (teleost) assemblage. Gu (1962) proposed a Tithonian age for the formation. Subsequent studies of Yixian taxa have generally supported Tithonian or various Cretaceous ages, or have suggested that the J–K boundary is within the basal Yixian Formation (Chen et al. 1982b; Liu et al. 1986; Li, Yu et al. 1986; Wang 1991; Chen and Chang 1994; Li et al. 1994; Wu and Tong 1994; Chen 1996a, 1996b; Fan 1996; Luo and Li 1997; Chen et al. 1998).

Biostratigraphy

Historically, Yixian Formation age assignments and placement of the terrestrial J–K boundary in northeast China have largely been questions of biostratigraphy. An absence of Mesozoic marine index fossils in Liaoning has forced a reliance on correlations between terrestrial taxa and the marine Qihulin Formation in Heilongjiang, which is interbedded with terrestrial rocks that produce Jehol forms (Wang and Sun 1983; see below). Part of the problem of assessing the position of the Yixian Formation with respect to the J–K boundary is that there is no marked extinction event (Remane 1991). There is general agreement on the J–K boundary’s absolute age (Obradovich 1993; Gradstein et al. 1995), and there is a global magnetostratigraphic definition that adheres to the biostratigraphic definition (Galbrun et al. 1986; Ogg et al. 1991; Ogg et al. 1994). However, magnetostratigraphy has yet to be applied to the Yixian Formation.

Terrestrial biostratigraphic interpretation is often complicated because of taxonomic and spatial distribution problems associated with small sample sizes. In the Yixian, various taxa have been interpreted as supporting either Jurassic or Cretaceous ages. Moreover, these taxa are often unsuitable for biostratigraphy (e.g., rare terrestrial tetrapods with small geographic ranges).

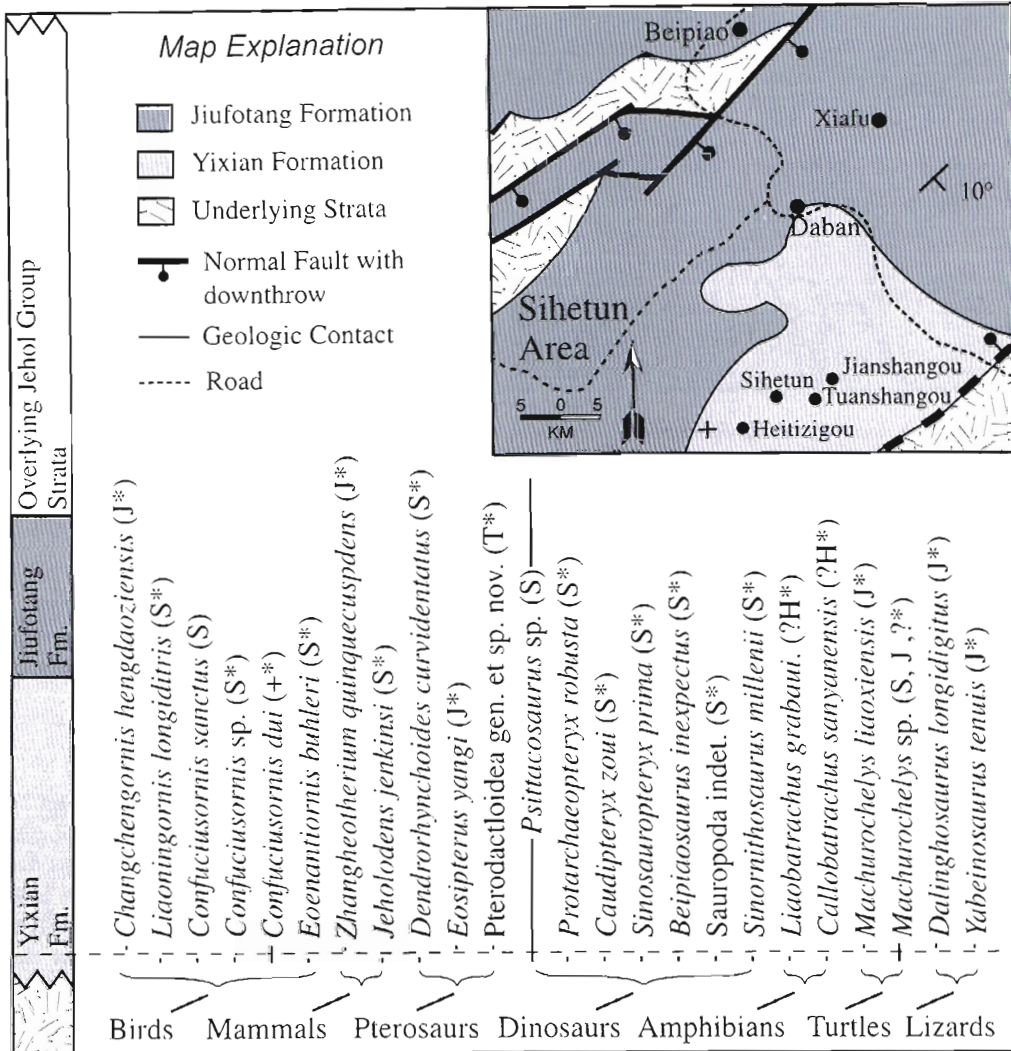


FIGURE 2. Stratigraphic, geologic and geographic relationships of Sihetun area fossil tetrapods. Dashed line at base of Yixian Formation schematically indicates approximate stratigraphic position of the fossil horizons. Stratigraphic ranges of taxa are shown by vertical lines (these lines are effectively dots for taxa known from only one locality). Taxa occurring only in the "lower" horizon at Sihetun (S) and Heitizigou (H) are below the dashed line. Jianshangou (J) and Tuanshangou (T) taxa are located in the "upper" horizon and are above the line. Letters after the taxa names correlate with their localities. An asterisk (*) indicates taxa known from less than 10 specimens. A plus sign (+) indicates the approximate location of *Confuciusornis dui* near Zhangjiying (see inset map). Note that virtually all these taxa are known from less than 10 specimens from a single stratigraphic horizon in a single basin. (This illustration should not be interpreted as a measured, scaled section.)

The remaining forms have largely been freshwater species known either only from within the units in question or from units that themselves have questionable ages (Chen et al. 1982a, 1982b; Wang 1991; Li et al. 1994), a problem exacerbated by a lack of stratigraphic precision across northeastern China.

With respect to the J-K boundary, correlation is difficult because the stratotype Berriasian section is marine (defined by ammonites and various calpionellids in the Tethyan realm [Le Hégarat 1980; Galbrun et al. 1986]) and correlations between the Tethyan and Boreal realms (including England's Purbeck and Wealden groups) have problems of their own (e.g., Hoedemaeker

1987). Regrettably, as the Yixian is wholly terrestrial, correlations have been made indirectly, relying on mixed terrestrial and marine assemblages or on terrestrial biotas bracketed between marine index fossils. Depending on which taxonomic group is used for correlation (for example, palynomorphs or ostracodes), ages can differ depending on the zonation of the taxa accepted by subspecialists of that group, a problem common to terrestrial units (see Kowallis et al. [1998] for an example of this problem concerning the age of North America's Morrison Formation).

A frequent comparer to, and likely correlate of, the Yixian Formation are the lacustrine rocks of Transbaikalian Russia and Mongolia, which share many palynomorphs, plants, invertebrates and vertebrates with the Jehol Group (Gu 1992; Krassilov et al. 1992; Neustrueva et al. 1977) and are usually considered Lower Cretaceous. The Chinese, Mongolian and Russian lakes may have all been deposited simultaneously as part of a common system (Grabau 1928; Kurochkin 1999) similar to the Green River Formation of North America (Grande 1984). However, the precise age of these deposits is uncertain for many of the same reasons as is that of the Yixian, and does not provide either resolution or a solid basis for correlation with the latter. As such, and because examination of the Russian and Mongolian deposits is beyond the scope of this work, we tacitly include them as a very provisional "extension" of the "Jehol biotic system" with respect to biostratigraphic correlation. Many researchers have used the terms "*Eosestheria*–*Ephemeropsis*–*Lycoptera* fauna" or "*Lycoptera* beds" as if these forms diagnose a single, isochronological horizon. However, since these taxa occur in multiple Jehol units, their occurrences elsewhere are impossible to correlate specifically with any one Jehol formation without more detailed stratigraphic work. (Interestingly, it is thus possible that the Mongolian ornithuran bird *Ambiortus* may be coeval with the purportedly oldest, but still more primitive, *Liaoningornis*.)

Biostratigraphic correlations are best supported when based on identical taxa (preferably species). These taxa must have narrow stratigraphic but wide geographic ranges. Much of the existing Yixian Formation biostratigraphy has used taxa that fail to meet these criteria. The Appendix illustrates the correlative utility, available in the literature, of taxonomic groups represented in the Yixian biota. Because the lithostratigraphic definition of the Yixian Formation has fluctuated somewhat, older references of some taxa are not corroborated by later studies; that is, either (1) taxa are not listed in later references, or (2) taxa are reported from formations considered by others to be either identical or entirely unrelated to the Yixian Formation. We discuss here only forms reported specifically from the Yixian Formation and assume that their Yixian occurrence is verified. We must also assume here the accuracy of the ages of taxonomic occurrences outside the Yixian Formation.

Palynological correlations are very desirable schemes for dating the Yixian Formation because, as a result of their very small size, palynomorphs are easily transported by air across great distances and can be deposited in both marine and terrestrial environments. Most of the 30 Yixian palynomorphs have either long chronological or restrictive geographic ranges. *Cicatricosisporites sibiricus*, from the Berriasian–Aptian of Europe, is an exception (Antonescu 1973; Dörrhöfer 1977). *C. spiralis* is even more limited, known only from the Hauterivian and Barremian of Spain, North America, the Ukraine and China (Mas 1981; Fensome 1983; Voronova 1984; Li 1992), and the Albian–?Cenomanian of North America and Tanzania (Playford 1971; Srivastava 1975, 1979, 1994; Sweet 1992); but even this, the most restricted Yixian palynomorph, offers no better age resolution than late Early Cretaceous.

Nonpalynomorph paleobotany of the Yixian Formation has focused primarily on the occurrences of primitive angiosperms, which have been used for at least regional correlation (e.g., Li et al. 1986). Although it is rarely possible to directly associate palynomorphs with specific megafossil species, the latter are generally useful because, as a result of palynomorph transportability, they can be widespread, although actual growth is dependent on the depositional climate. Yixian Formation plant fossils produce a mixed age signal (see below).

Neither the Bivalvia nor the Gastropoda have been predominant taxa in J–K boundary biostratigraphy, except when used with other taxa (e.g., ostracodes [Morter 1984]). The 40 species of bivalves represented in the Yixian Formation, while largely restricted to eastern Asia, gener-

ally have extensive ranges. The Yixian gastropod fauna is somewhat depauperate compared to those of the overlying Jehol Group, and most of the taxa also occur in the younger Jehol Group units as well as the Yixian (Yu et al. 1987; W. Wang et al. 1990).

Most regional Yixian Formation biostratigraphy has involved conchostracans. The Jehol fauna is, in large part, based on *Eosestheria*, which occurs widely in China and has been used to support a Tithonian age for the Yixian (e.g., Chen et al. 1982a, 1982b; Chen 1988). The Yixian conchostracans are very speciose, with only 12 genera but 91 species. However, Chinese conchostracan taxa may be grossly oversplit (for example, Chen [1985] considered *Diformograptia*, *Dongbeiestheria* and *Liaoningestheria* to be junior synonyms of *Eosestheria*, though he did not specify whether or not the species of those genera should be considered new species). W. Wang (1987) continued to use the separate genera, and we will provisionally retain them here. Lucas and Kirkland (1998) noted that there is a great deal of morphological overlap among conchostracan "genera" and that many other probable synonymies exist (for example, Lucas and Kirkland [1998] suspected that *Lioestheria* from the Morrison Formation is cogenetic with *Eosestheria*). Thus, correlations using Yixian conchostracans may be suspect, as they apparently require much more alpha-level taxonomy.

Before the Late Jurassic, nonmarine ostracode diversity was relatively low, involving only the Cytheracea and the Darwinulacea, compared to the subsequent dispersal and rapid diversification of the Cypridacea. This success was the result of two factors: the evolution of an improved reproductive strategy, including parthenogenesis and small, desiccation-resistant eggs that can be transported by air, and the ability to swim freely (Helmdach 1979; Whatley 1992). Both these factors are virtually nonexistent in cytheraceans and *Darwinula* (Whatley 1992). With the terrestrial invasion of the Cypridacea, ostracodes have been frequently used in biostratigraphy (with some caveats), particularly where marine taxa are absent (Colin and Lethiers 1988). Members of all three ostracode clades are present in the Yixian Formation (with some 40 species), but the Cypridacea, and *Cypridea* in particular, dominates. *Cypridea* spp., although virtually pandemic at the generic level, show a great deal of regional endemism (Neale 1977; Sohn 1969; Whatley 1992), and the other Yixian ostracods have very long temporal ranges. Moreover, *Cypridea* spp. dominance of ostracode faunas is considered a post-Kimmeridgian event (Whatley 1992).

The Yixian Formation's famous insect fauna (89 genera) forms a substantial component of the biota. The Jehol fauna is, in part, defined by the presence of the mayfly *Ephemeroptera*. Of particular recent interest have been brachyceran flies, which possess feeding apparatuses typical of forms that feed in deep flowers, suggesting the existence of true angiosperms (see Ren 1998a). This putatively advanced adaptation, when few angiosperms were supposedly present, implies a much earlier origin of angiosperms (in the Jurassic per Ren 1998a). Aside from problematic "stage of evolution" arguments, Yixian Formation insects do not seem to be well suited to biostratigraphic correlation, and the Jurassic "flavor" of the Yixian insect fauna is, at least in part, due to the greater number of well-studied Jurassic insect-bearing Lagerstätten (e.g., Karatau, Solnhofen) than Cretaceous or Triassic ones.

Yixian Formation biostratigraphy becomes even more problematic where the vertebrates are concerned, based largely on unreliable techniques or unusable taxa. Twenty-eight vertebrate genera (including 22 tetrapods) have been described from the Yixian Formation. The only Yixian vertebrates known from outside the formation are the osteichthyans *Lycoptera* and *Sinamia* and the ceratopsian dinosaur *Psittacosaurus*. *Lycoptera* and *Peipiaosteus* are poor choices for biostratigraphy as they appear below the beds in question and extend well upward into rocks of the upper Jehol Group. The tetrapods in particular are disastrous biostratigraphic choices. Most Yixian tetrapods come from the same 45-meter thick section of a single depositional basin in the Sihetun region and have a geographic range of less than 100 km² (Figure 2). Most are known from only a few specimens from a single locality. *Psittacosaurus*, long considered a marker of an exclusively Early Cretaceous east Asian biochron (e.g., Dong 1993; Lucas and Estep 1998), may be an exception. However, while *Psittacosaurus* supports an Early Cretaceous Yixian Formation, it suffers problems at the specific level and provides no further degree of resolution.

Problems with previous correlations

Excepting the Mongolian and Transbaikalian deposits, only a few formations outside the Jehol Group have been frequently cited as probable correlates of the Yixian Formation. These include the Tithonian Solnhofen Limestone of Germany, the Middle or Upper Jurassic Karabastau Formation of Kazakhstan, and the Tithonian–Hauterivian Purbeck and Wealden groups of southern England. Most of these correlations have been made by comparing taxa that are identical neither at the generic nor species level. Instead, they have been based on either the ranges of higher-level taxa (assumed range limitation arguments), fauna-level comparisons, or on assumptions about evolutionary rates and changes (“stage of evolution” arguments).

Assumed range limitation arguments have been applied to Yixian occurrences of the compsognathid theropod *Sinosauropteryx*, the rhamphorhynchoid pterosaur *Dendrorhynchoides* and the ardeosaurid lizard *Yabeinosaurus*, which have been correlated with Solnhofen’s *Compsognathus*, *Rhamphorhynchus* and *Ardeosaurus*, respectively (Cocude-Michel 1963; Q. Ji and S. Ji 1996; Chiappe et al. 1999; S. Ji et al. 1999). That ardeosaurids, compsognathids and rhamphorhynchoids are known only from the Jurassic has been offered as evidence that the Chinese forms must also be Jurassic. Although the case for *Dendrorhynchoides* is a moot point, as it is, at least in part, an apparent forgery (Friend 2000), comparisons with *Compsognathus* and *Ardeosaurus* are suprageneric level correlations—an inherently imprecise practice because higher-level taxa generally have fluctuating membership and are often longer-lived than lower-level taxa. Moreover, new discoveries can always override previously established occurrence data; if *Yabeinosaurus* and *Sinosauropteryx* had been recovered from firmly dated Cretaceous rocks elsewhere, they would have been reported as the first Cretaceous representatives of their clades. Occurrences of isolated tetrapod specimens from a given formation cannot be used to infer the age of that formation. If this were true, then *Sinosauropteryx* either suggests a Cretaceous occurrence of compsognathids or the Yixian *Psittacosaurus* specimens suggest that these ceratopsians occurred in the Tithonian. Which range should be considered the more valid?

S. Ji et al. (1999) contrasted the Yixian fauna with the well-constrained Early Cretaceous fauna from the United Kingdom’s Purbeck and Wealden groups to show that the Yixian cannot be Early Cretaceous. The fluvial Wealden sediments produce partial skeletons of large dinosaurs, including ornithomorphs, thyreophorans, sauropods and theropods. Smaller Wealden (and contemporary deposits in North Africa) plants, invertebrates and small vertebrate taxa are becoming better known, including lizards, small theropods and mammals (Anderson 1973; Hunt 1985; Howse and Milner 1993; Allen et al. 1998; Milner and Evans 1998; Sigogneau-Russell et al. 1998; Sigogneau-Russell and Ensom 1998; Naish 1999). However, these differ markedly in preservational mode and taxonomic composition from the Yixian fauna, which preserves articulated specimens of small taxa but only fragments of larger forms. A better comparison can be made to the Early Cretaceous Lagerstätten at Cuenca and Montsec in Spain, which, like the Yixian Formation, produce ostracods, arthropods, plants, birds and theropods with preserved integument, and other small vertebrates (Brenner et al. 1974; Whalley and Jarzembowski 1985; Sanz, Bonaparte et al. 1988; Sanz, Wenz et al. 1988; Lacasa-Ruiz 1989; Pérez-Moreno et al. 1994; McGowan and Evans 1995; Sanz et al. 1995; Evans and Barbadillo 1997; Briggs et al. 1997). These also contrast with the Purbeck and Wealden faunas, but the age of the Spanish deposits has not been disputed using faunal differences. That the Yixian preserves small taxa in exquisite detail whereas the Purbeck and Wealden do not is due more to sedimentology than faunal differences. Comparing lacustrine and fluvial systems is complicated because each biases its respective fossil records in different ways. As such, comparisons based on the faunal contents of the Yixian and the Wealden are very weak and of little biostratigraphic value.

The biostratigraphic technique most frequently used to support a Tithonian age for the Yixian involves generalized “stage of evolution” comparisons between genera from the Yixian and from other formations. This technique assumes that morphologically and phylogeneti-

cally similar taxa are of similar age because they are of similar phylogenetic "distance" from a common ancestor. It has been applied to several Yixian taxa, including the ostracode *Cypridea*, the brachyceran flies *Florinmestrius* and *Palaeopangonius*, the osteichthyans *Peipiaosteus* and *Yanosteus*, the sphenodontian *Monjurosuchus*, the pterodactyloid pterosaur *Eosipterus*, and the bird *Confuciusornis*. These taxa have been considered to be of a similar "stage of evolution" as Purbeck and Wealden ostracodes (Li et al. 1988; Pang and Whatley 1990), Karabastau Formation flies (Ren 1998a), the Karatau/Transbaikalian osteichthyans *Stichopterus* and *Spherosteus* (Fan 1995), and the Solnhofen sphenodontians *Homoeosaurus* and *Leptosaurus*, pterodactyloid *Pterodactylus* spp., and avian *Archaeopteryx* (Hou, Zhou, Gu and Zhang 1995; S. Ji 1995; Hou 1996; Ji 1998; S. Ji et al. 1999), respectively. The "stage of evolution" argument is fallacious because morphological similarity, while probably indicative of close *phylogenetic* relationship, is a poor measure of *temporal* distance, and does not by itself provide unequivocal evidence of age.

As above, the most reliable hypothesis for biostratigraphic correlation can be established only when *identical* taxa (ideally, species) occur in widely disparate localities and narrow stratigraphic intervals, a condition met by precious few Yixian taxa. Hypotheses using progressively more distantly related taxa (that is, those in successively more inclusive, suprageneric clades) are avoided by biostratigraphers for two reasons: suprageneric clades typically have such long chronological spans that they are useful only for the grossest levels of resolution, and because phylogenetic distance does not translate into temporal distance, especially when a common ancestor is either unknown or occurs substantially earlier in time (creating ghost lineages per Norell [1996] and Norell and Novacek [1992]). Although *some* time is accepted to have elapsed, the *absolute* length of time between the branching of sister taxa from a common ancestor and the occurrence of presumed coeval terminal taxa themselves *cannot* be inferred from their phylogeny unless all evolutionary rate variables are understood and accounted for. When *identical* taxa are present in disparate locations, however, no such time-phylogeny disparity is involved—the most parsimonious interpretation is that the individuals of the taxon in question evolved at the same time and place and spread from that locus. Because a taxon (particularly a terrestrial taxon) may enjoy different longevities in different places, thus adversely affecting the resolution of the biostratigraphic hypothesis, biostratigraphic correlations based on multiple organisms are always preferred, as in the tetrapod-based faunachronology of the global Late Triassic (Lucas 1999). Here again, Yixian Formation forms prove to be poor choices for biostratigraphy.

Morphology evolves to adapt an organism to a set of ecological conditions which, when stable, provide no impetus for evolutionary change (beyond random walk); conversely, when ecological conditions change, selective pressure is applied, and organisms in the ecosystem will either evolve or become extinct. The "similarity," but not generic or species-level congruity, of the Chinese taxa to other taxa implies *only* that the ecological conditions in the habitats of the taxa in question were similar, and that taxa were evolving to fill similar niches—it says little about the timing of the events. "Stage of evolution" arguments assume that, for a given taxon, evolutionary rates and the pressures that drive them are fully understood and apply universally. In general, it is true that primitive taxa occur in older sediments than more derived forms. However, primitive taxa can and do persist, and myriad examples are known, including Holocene occurrences of *Latimeria* and *Sphenodon*, which are both very similar to Jurassic and Cretaceous forms despite more than 80 my separating them (Thomson 1991; Reynoso 1996; Erdmann et al. 1998). A particularly relevant example is the primitive bird *Rahonavis*, which occurs in the Upper Cretaceous of Madagascar but is phylogenetically closest (again, roughly 80 my) to the older *Archaeopteryx* (Forster et al. 1998). Though these are somewhat extreme examples, they show that the existence of taxa in the Yixian with a similar degree of plesiomorphy as undisputed Jurassic forms does not necessarily indicate coeval age (see also Barrett 2000). While this does not *prevent* the age of the Yixian taxa from being Jurassic, it cannot be offered as *proof* of a Tithonian age because the Yixian paleoecosystem may have remained stable longer than in

other places and its taxa may have not been subject to the same pressures as their relatives outside the restricted Chinese basins. Alternatively, it may have been a similar ecosystem at a different time and acted as a refugium for primitive taxa.

Without resorting to assumed range limitation or "stage of evolution" arguments used on many taxa, and restricting correlations to shared taxa, there are two contradictory biostratigraphic signals (that is, taxa with the narrowest determined ranges and presently known range limits) in the Yixian biota. One is composed of insect genera also known from the Jurassic in Eurasia, such as *Aeschnidium densum*, *Blattula*, *Geotrupoides*, *Karataviella*, *Protempis*, *Karatavoblatta*, *Liadoxylea*, *Mesoraphidia*, *Nipponoblatta*, *Paroryssus*, *Protonemestrius* and *Sinohagla*, plants such as *Czekanowskia rigida*, *Phoenicopsis* cf. *augustiofolia* and *Podozamites lanceolatus*, the bivalve *Tutuella*, and the gastropod *Sibericoncha*. It seems to indicate a Jurassic age for the lower Yixian. However, as described above, the taphonomy of insect preservation reduces these correlations to essentially point comparisons, which render their correlations dubious. Some shared taxa (e.g., *Kalligramma*) also occur in undoubtedly Barremian rocks in Spain, indicating that the ranges of many insect taxa may be too long for refined correlation. The second signal is indicated by the palynomorphs *Cicatricosisporites sibiricus* and *C. spiralis*, the plants *Tyrmia*, *Elatocladus manchurica* and *Onychiopsis psilotoides*, the bivalves *Margaritifera* and *Mesocorbicula*, the gastropods *Viviparus onogoensis* and *Zaptychius*, the ostracodes *Lycoptero-cypris* and *Mongolianella*, and the dinosaur *Psittacosaurus*. It indicates a late Early Cretaceous age. Because these taxa are known from many more specimens, and do not suffer from the taphonomic biases of the insects, we consider this signal more representative of the true age of the biota.

There remain some problems with previously used biostratigraphic correlations using Yixian Formation fossils to determine the age of the formation. Most taxa are endemic or have chronological spans that render them useless for correlation. Other clades (such as conchostracans) have internal taxonomic problems that confound straightforward biostratigraphic use. For many taxa, the basis for comparison does not support any particular age; many could be used equivocally to support Late Jurassic or Early Cretaceous ages. Given that the taxa thus far recovered from the Yixian Formation are *individually* unsuitable for correlation, does the Jehol fauna, or at least a significant (and unique) portion of it, occur anywhere else in Asia where it is either bracketed by, or mixed with, marine index fossils? Many other formations across China contain elements (usually genera, particularly conchostracans and insects) of the Jehol biota (see the summary in Gu 1996), but two sedimentary packages in particular, the Longzhaogou and Jixi groups in Heilongjiang Province, have been tied to the Jehol Group. Gu (1992) reviewed the correlations between the Jehol, Longzhaogou and Jixi groups; shared taxa, including palynomorphs, plants and bivalves, all occur throughout the Jehol Group, not the Yixian Formation in particular. Thus, in a broad sense, the Jehol, Longzhaogou and Jixi groups are probably coeval.

As with the Yixian Formation, divisory schemes of the Longzhaogou Group have varied. Most authors accept the group as containing, in ascending order, the Peide, Qihulin, Yunshan and Zhushan formations (Wang and Sun 1983; Sha et al. 1994; Futakami et al. 1995; contra Ju et al. 1982); the Yixian Formation was correlated specifically or in part with the Qihulin Formation by Gu (1982) and Wang and Sun (1983). The Qihulin Formation is an ideal correlate because it consists of terrestrial and marine intercalations (W. Li et al. 1986) and because many of the Jehol biota taxa, including many plants and bivalves, occur in the terrestrial beds (Gu 1982; Wang and Sun 1983). Age assessments of the Longzhaogou Group sediments, like those of the Jehol Group, have fluctuated markedly, ranging from Middle Jurassic to late Early Cretaceous (see Futakami et al. [1995] for a summary). The Jurassic age was based largely on ammonite and bivalve correlations. Recently, the reidentification in the Qihulin Formation of ammonites previously considered Bathonian (such as *Arctocéphalites*) as the Barremian taxa *Pseudohaploceras* and *Phyllo-pachyceras* (Kelly et al. 1994; Futakami et al. 1995) strongly constrains the age of fossils on the overlying formations and corroborates a Barremian age for both formations.

Like the Longzhaogou Group, the Jixi Group contains intercalating terrestrial sediments containing elements of the Jehol fauna and marine sediments containing index fossils. Using marine fossils (particularly bivalves), parts of the Jixi Group have been correlated with the Longzhaogou Group. The Jixi Group consists of the Didao, Chengzihe and Muling Formations (some authors [e.g., W. Li et al. 1986; Liu et al. 1986] recognize a Shihebei Formation between the Didao and Chengzihe formations), which have also been correlated with the Yixian Formation (and the Jehol Group as a whole), but precise interformational correlations have fluctuated. Wang and Sun (1983) considered the Yixian to be correlative of the Didao and Chengzihe formations (in their system, no Shihebei Formation was recognized). Liu et al. (1986) considered the Yixian (and, largely, the Jiufotang) formations to be correlates of the Didao and Shihebei formations. Gu (1992) considered only the uppermost portion of the Yixian coeval with the Didao. Jixi Group units that correlate with the Yixian are of particular interest because the Chengzihe Formation has produced plant fossils (e.g., *Asiatofolium elegans*, *Chengxihella obovata*, *Xingxueina heilongjiangensis*, *Jixia pinnatipartita* and *Shenkuoa caloneura* [Sun et al. 1993; Sun and Dilcher 1997]) previously described as the oldest angiosperms before the description of new Yixian taxa (Sun et al. 1998).

Sha (1991), Sha and Fürsich (1993), and Sha et al. (1994) showed that Chengzihe and Yunshan formation bivalves previously identified as species of the Jurassic indicator *Buchia* actually belong to the Cretaceous genus *Aucellina* and indicate a Barremian–Aptian age for both; Zheng and Liang (1995) note that Chengzihe Formation dinoflagellates are Early Cretaceous index taxa. If these sediments correlate to the Yixian, then they place a powerful constraint on the age of the latter. Based on the new studies of the Longzhaogou and Jixi group ammonites and bivalves, Gu, who founded the most recent Late Jurassic age assertion for the lower Jehol Group, has recently recanted his original age assessment and embraced a Lower Cretaceous age for the Yixian (Gu 1996). In toto, the biostratigraphic and correlative evidence for the age of the Jehol Group, including the Yixian Formation, certify a late Early Cretaceous (probably Hauterivian or Barremian), not Late Jurassic or early Early Cretaceous, age.

Radiometric geochronology

Ultimately, it is unlikely that biostratigraphy in any series of restricted tensional basins would provide a reliable solution to this sort of age dispute without independent geologic data for calibration. As such, it is especially fortunate that the lower Yixian is characterized by volcanic rocks directly proximal to the sediments that can provide absolute radiometric ages. Virtually all the isotopic dates that have been produced from the lower Yixian Formation in the Sihetun area (see Wang and Diao 1984; Mao et al. 1990; Smith et al. 1995; Hou 1997a; Ostrom et al. 1997; Swisher et al. 1999; Wang, Wang, Fan et al. 1999) indicate ages significantly younger than the Tithonian. An age of 137 ± 7 Ma obtained by ^{40}K – ^{40}Ar dating of stratigraphically low volcanics intercalated with the lacustrine Lagerstätten was considered Tithonian by Wang and Diao (1984), but is Early Cretaceous according to more recent work (Gradstein et al. 1995; Gradstein et al. 1997). Moreover, these dates are considered unreliable because they were obtained from glauconite, which is subject to loss by recoil (Faure 1986). Subsequent ^{40}Ar – ^{39}Ar dates, using more reliable methods dealing with sanidine crystals, consistently yield Early Cretaceous ages (121.1 ± 0.2 Ma [Smith et al. 1995]; 124.6 ± 0.3 Ma [Swisher et al. 1999]).

It has been asserted (e.g., Martin et al. 1998), though not shown in print, that the volcanics intercalated with the fossil-bearing sediments are deep intrusives and that the isotopic dates retrieved from them are indicative only of the date of their emplacement; the age of the fossils must therefore be older by superposition principles. However, Swisher et al. (1999) have produced radioisotope dates from tuffs (which are, by definition, extrusive) that bracket the sediments containing the fossils. These dates, which were painstakingly produced and are considered quite reliable, are Barremian (124.6 ± 0.3 Ma). They are in close agreement to the dates of Smith et al. (1995) and Ostrom et al. (1997) from Yixian basalts and tuffs. As tuffs are

extrusive volcanics, that their ages tend to conform to the Yixian basalt ages suggests that the Yixian volcanic rocks were emplaced during basin formation, rather than after. This is further reinforced by the petrography of the Yixian basalts, which is incongruous with volcanism occurring long after basin formation (see Smith et al. 1998).

Concluding Thoughts

Biostratigraphy is a poor means by which to determine the age of the Yixian Formation. While some data are indicative of the Early Cretaceous, many Yixian forms, while differing at the generic level, are broadly similar to well-constrained Late Jurassic taxa. "Similarity" alone, however, is not a reliable means of correlating taxa; primitive forms can persist when ecological conditions are favorable. Endemicity of the bulk of the biota implies that the organisms were largely insulated from evolutionary pressures applied to extrabasinal forms, creating a refugium in which primitive taxa persisted. Ultimately, either a few taxa (for example, *Psittacosaurus*) must have their ranges extended from the Lower Cretaceous into the Upper Jurassic based on singular occurrences, thereby rendering them unsuitable for biostratigraphic correlation, or some primitive taxa (such as *Sinosauropteryx*) must be perceived as relicts, persisting beyond a time when similar taxa were replaced elsewhere by more derived forms. The latter is quite feasible given the tectonically and structurally induced isolation of the Liaoning depositional basins and is here considered the more parsimonious conclusion.

The most reliable radiometric dates consistently give late Early Cretaceous ages, and thus provide more reliable evidence than biostratigraphic correlation for the Yixian Formation and its biota. Indeed, Swisher and co-workers (1999) have provided the strongest data thus far towards solving this dilemma: data that unambiguously point to a Barremian age. Even if Yixian biostratigraphy were not fraught with problems, a well-constrained radiometric age always outweighs the phylogenetic signal of a fossil assemblage. Isotopic signatures are independent from the evolution of the contemporaneous biota and are indeed *the* means by which assemblages are rooted in time. The general "primitiveness" of the Yixian Formation biota must be interpreted with respect to these isotopic ages, not in isolation from them. As such, the biota is thus reasonably interpreted as having existed within an Early Cretaceous refugial ecosystem and the Yixian avifauna, although important to early avian evolution and diversity, does not alter our current understanding of avian origins and early evolution.

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Appendix

The appendix accompanying this paper is also available online at the Yale Peabody Museum website at <http://www.peabody.yale.edu/collections/vp/>.

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Addendum

While this publication was in press, several new, and many previously unreported, taxa from the Yixian Formation were published. In the interest of maintaining a complete biotic checklist, we list those taxa here, but do not assess their biostratigraphic utility. Citations below with page numbers refer to abstracts published in Shi and Zhang (2000).

PALYNOMORPHS. *Abietinaepollenites pectinellus*, *Acanthtriletes varispinosus*, *Baculatisporites comamensis*, *Bicestopollis wulanensis*, *Cedripites microsaccoides*, *C. pusillus*, *Densoisporites stenotomus*, *Ephedripites* sp., *Ginkgocycadophytus nitidus*, *Granulatisporites* sp., *Jiaohepollis flesuosus*, *Jugella claribaculata*, *Leiotriletes* sp., *Pinuspollenites divulgatus*, *Podocarpidites multesimus*, *P. ornatus*, *Protoconiferus funarius*, *Protopinus* sp., *Psophosphaera* sp., *Punctatisporites* sp., *Quadraeculina anellaeformis*, *Schizosporis* sp. (Li and Liu 2000:16–17).

CHAROPHYTES. *Mesochara producta*, *M. voluta*, *M. xuanziensis*, *Minhechara?* sp., *Peckisphaera multispira* (Lu and Wang 2000:17).

PTERIDOPHYTA. *Coniopteris spectabilis*, *C. tatungensis*, *Eboracia lobifolia* (Wu 2000:34–35)

GINKGOPHYTA. *Solenites muerayana* (Wu 2000:34–35).

CONIFEROPHYTA?. *Liaoningocladus boii* (Sun et al. 2000), *Nageiopsis* sp., *Piceoxylon zaocishanense* (Ding 2000), *Pityospermum* sp. (Z. Cao 2000:5), *Protophyllocladoxylon franconium*, *Protopodocarpoxyylon jingangshanense*, *Xenoxylon hopeiense*, *X. latiporusum* (Ding 2000).

ANGIOSPERMAE. *Lilites* sp., *Orchidites* sp., *Typhaera* sp. (Wang, Wang, Zhou et al. 2000:41–63).

BIVALVA. *Arguniella* sp. (J. Chen 2000:6).

GASTROPODA. *Amplovalvata* sp., *Gyraulus* sp., *Ptychostylus harpaeformis* (Pan and Zhu 2000:23–24).

INSECTA. *Angaridyela endemica*, *A. exculpta*, *A. robusta*, *A. suspecta*, *Ceratoxyela decorosa*, *Heteroxyela ignota*, *Isoxyela rudis*, *Lethoxyela excurva*, *L. vulgata*, *Liaoxyela antiqua*, *Sinoxyela viriosa*, *Xylites lingyuanensis* (Zhang and Zhang 2000).

CAUDATA. *Jeholotriton paradoxus* (Wang 2000).

THEROPODA. *Caudipteryx dongi* (Zhou and Wang 2000).

AVES. *Protopteryx fengningensis* (Zhang and Zhou 2000).

MAMMALIA. *Repenomamus robustus* (Li et al. 2001).

We also note that *Liaoxia chenii* was referred to the Gnetales by Wu (2000:34–35) and *Monjurosuchus splendens* belongs in the Choristodera, not the Sphenodontia as reported in the Appendix. The specimen of *Dendrorhynchoides*, except the tail, has been confirmed as an anurognathid “rhamphorhynchoid” pterosaur by Unwin et al. (2000). The hymenopteran *Manlaya* has now been reported from the Barremian limestones at Montsec in Spain (Rasnitsyn and Ansoerge 2000), and *Angaridyela* and *Xylites* were previously known only from Cretaceous deposits in Kazakhstan (Rasnitsyn 1966).

Concurrent with these new taxa, new analyses continue to reveal the problems in dating the Yixian Formation. Other biostratigraphic analyses were published by X. Wang, Y. Wang, Z. Zhou et al. (2000:41–63) and X. Wang, Y. Wang, F. Zhang, J. Zhang, Z. Zhou et al. (2000). Pan (2000:23) considered regional portions of the Yixian Formation to range from possibly Middle Jurassic through Lower Cretaceous. P. Chen (2000:6–7) continues to maintain a Late Jurassic age, which has been supported by J. Chen (2000:6) using bivalves, Zhang (2000:38) using insects, and Wu (2000:34–35) using plant megafossils. Based on ostracodes, M. Cao (2000:4–5)

assessed the Yixian to straddle the Jurassic–Cretaceous boundary. Palynomorphs (Li and Liu 2000:16–17), plant megafossils, charophytes and bivalves have also been used to support an early Early Cretaceous age of the Yixian Formation. Radiometric ages supporting a late Early Cretaceous age were cited by X. Wang, Y. Wang, F. Zhang, J. Zhang, and G. Gu. (2000:31–32) and Xu and Wu (2000:35). Occurrences of *Lycoptera* spp. were considered in relation to east Asian Jurassic and Cretaceous ichthyofaunas by Sytchevskaya (2000:29–30), while occurrences of *Ephemeropsis*, *Coptoclava* and *Lycoptera*, in addition to paleofloral components, from western Mongolia were considered either early or late Early Cretaceous by Jähnichen and Kahlert (2000). Wang et al. (2001) reported an age of 125.2 ± 0.9 Ma determined using U–Pb dating of zircons from tuffs at Sihetun, closely matching the previously reported Ar–Ar dates. Lastly, Luo (1999) also interpreted the Early Cretaceous biota of western China to possibly represent a refugium, although this was, in part, challenged by Manabe et al. (2000).

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Appendix: Biota of the Yixian Formation and the endemism of its taxa

Abbreviations and symbols used in the table are as follows: **N**, endemic; **G**, both genus and species endemic to Yixian Formation; **S**, species (only) endemic to Yixian Formation; **J**, liufotang Formation; **H**, Shaihai Formation; **F**, Fuxin Formation; **O**, older; **C**, coeval; **Y**, younger; **E**, Early; **M**, Middle; **L**, Late; **Ord**, Ordovician; **Carb**, Carboniferous; **P**, Permian; **Tr**, Triassic; **Jr**, Jurassic; **K**, Cretaceous; **Pal**, Paleocene; **Eoc**, Eocene; **Olig**, Oligocene; **Mio**, Miocene; **Plio**, Pliocene; **Plei**, Pleiocene; **Holo**, Holocene; **Plg**, Paleogene; **Neog**, Neogene; **X**, reference in the last column mentions species without reference or notes further references that either were not cited or could not be obtained for this analysis. A question mark (?) indicates unknown or uncertain; an asterisk (*) indicates the species is identical between Yixian and other formation (absence of an asterisk indicates only the genus is shared); minus (-) indicates “no,” plus (+) indicates “yes,” but more specific information is unavailable. Citation numbers refer to numbered references in the Literature Cited. Footnotes are listed at the end of the table.

| | Principal citations for Yixian Fm | Taxon occurs | | | Chronological Range | | | Citations (for earliest occurrences of |
|--|-----------------------------------|----------------------|-------------------|------------|---------------------|-------------|------------|--|
| | | Higher within Jethol | Elsewhere in East | Elsewhere | | | | |
| Palynomorph | | | | | | | | |
| <i>Abietinaepollenites</i> sp. | 168 | ? | ? | O, C, Y | O, C, Y | L Tr?-Quat | ? | 259, 301/186, 115 |
| <i>Aequitriradites spinulosus</i> | 148, 221 | — | J*, H*, F* | C?, Y* | O*, C*, Y* | I. Jr-Mio | L Jr-Mio | 331 [†] , 323/132 |
| <i>A. verrucosus</i> | 221 | — | J*, H*, F* | C?, Y* | O*, C*, Y* | L Jr-Mio | L Jr-Eoc | 331 [†] /93 [†] |
| <i>Bayanhuaspora setacea</i> | 221 | — | J*, F* | C?* | — | E K? | E K? | 348 [†] |
| <i>Cicatricosisporites australiensis</i> | 148, 221 | — | J*, H*, F* | C?, Y* | O*, C*, Y* | L Tr?-Neog | L Tr-Neog | 64 [†] , 129, 16/113 |
| <i>C. curvatus</i> | 148, 221 | — | H* | — | — | L Tr?-Neog | E. K | 221 [†] |
| <i>C. dovogensis</i> | 221 | — | — | C?, Y* | O*, C*, Y* | L Tr?-Neog | F. Jr-Neog | 332 [†] /57 [†] |
| <i>C. liaoningensis</i> | 221 | S | — | — | — | L Tr?-Neog | S | 221 [†] |
| <i>C. ludbrookii</i> | 148, 221 | — | J*, H*, F* | O*, C?, Y* | O*, C*, Y* | L Tr?-Neog | L Jr-Pal | 167 [†] /91 [†] |
| <i>C. minor</i> | 148, 221 | — | J*, H*, F* | C?, Y* | O*, C*, Y* | I. Tr?-Neog | L Jr-Pal | 244 [†] /281 [†] |
| <i>C. minutaestriatus</i> | 148, 221 | — | J*, H*, F* | C?, Y* | O*, C*, Y* | L Tr?-Neog | F. Jr-Olig | 300 [†] /133 [†] |
| <i>C. sibiricus</i> | 148, 221 | — | — | Y* | O*, C*, Y* | L Tr?-Neog | E K | 6 [†] , 53 [†] |
| <i>C. spiralis</i> | 148, 221 | — | J* | C?, Y* | C*, Y* | L Tr?-Neog | F K-I K | 176 [†] , 70 [†] , 299 [†] /216 [†] , 270 [†] , 271 [†] , 272 [†] |
| <i>C. subinensis</i> | 221, 274 | S | — | — | — | L Tr?-Neog | S | 221 [†] , 274 [†] |
| <i>Classopollis annulatus</i> | 221 | — | J*, H*, F* | O*, C?, Y* | — | I. Tr-Pal | I. Tr-Pal | 28 [†] /222 [†] |
| <i>Concavissimisporites minor</i> | 147, 221 | — | J*, H*, F* | O*, C?, Y* | O*, C*, Y* | M Jr-L K | M Jr-E K | 245, 223 [†] , 19 [†] /202, 216 [†] , 334 |
| <i>C. punctatus</i> | 221 | — | J*, H*, F* | C?, Y* | O*, C*, Y* | M Jr-L K | M Jr-L K | 223 [†] , 19 [†] |
| <i>C. variverrucatus</i> | 221 | — | J*, H*, F* | C?, Y* | O*, C*, Y* | M Jr-L K | M Jr-L K | 223 [†] , 19 [†] |
| <i>Coptospora granulata</i> | 221 | — | F* | C?* | — | E K | E K | 335 [†] |
| <i>Couperisporites complexus</i> | 148, 221 | — | J* | C?, Y* | O*, C*, Y* | L Jr-E K | I. Jr-E K | 1 [†] /216 [†] |
| <i>Cyathulites australis</i> | 221 | — | J*, H*, F* | O*, C?, Y* | O*, C*, Y* | M Tr-Neog | L Tr-Mio | 71 [†] , 254 [†] , 129/132 [†] , 250 |
| <i>C. minor</i> | 221 | — | J*, H*, F* | O*, C?, Y* | O*, C*, Y* | M Tr-Neog | L Tr-Mio | 71 [†] , 254 [†] /132 [†] |
| <i>Cycadopolites nitidus</i> | 221 | — | J*, H*, F* | O*, C?, Y* | O*, C*, Y* | L P-Olig | L P-Olig | 49 [†] , 205 [†] /4 [†] |
| <i>Densosporites microrugulatus</i> | 221 | — | J*, H* | O*, C?, Y* | O*, C*, Y* | L Tr-I. K | L Tr-L K? | 254 [†] , 89, 94 [†] /141, 10 [†] , 134 |
| <i>D. perinatus</i> | 168, 221 | — | J*, H*, F* | O*, C?, Y* | O*, C*, Y* | L Tr-L K | L Tr-L K | 254 [†] , 94 [†] /135 [†] , 134 [†] |
| <i>D. velatus</i> | 221 | — | J*, H*, F* | C?, Y* | O*, C*, Y* | L Tr-L K | L Tr-L K | 254 [†] , 94 [†] /135 [†] , 134 [†] |
| <i>Fixisporites tortus</i> | 148, 221 | — | J*, H*, F* | O*, C?, Y* | — | E K | E K | 348 [†] |

Continued.

Appendix, continued.

| Type | Taxon | Taxon occurs | | | | | Chronological Range | | Citations (for earliest occurrences of genus/species) ^{a, g} |
|---------------------|--|--|----------------|--|---|------------------------------------|---------------------|----------------------|--|
| | | Principal citations for Yixian Fm occurrence ^a | N ^b | Higher within Jethol Group ^c | Elsewhere in East Asia ^d | Elsewhere globally ^e | Genus ^f | Species ^f | |
| | <i>Foraminisporites</i> sp. ^h | 168 | ? | ? | ? | ? | ? | ? | ? |
| | <i>Heliosporites</i> sp. | 221 | ? | J | ? | ? | ? | ? | ? |
| | <i>Hsuisporites jinfortangensis</i> | 221 | — | J*, H* | ? | — | E K-Eoc | E K | 310/146, 221 [†] |
| | <i>H. multiradiatus</i> | 221 | — | J*, H*, F* | O*, C*? | — | E K-Eoc | E K-L K | 334 [†] /347 [†] |
| | <i>H. rugatus</i> | 221 | — | H*, F* | O*?, C*? | — | E K-Eoc | E K-Pal | 333 [†] /305 |
| | <i>Impardecispora apiverrucata</i> | 148, 221 | — | J*, H*, F* | C*?, Y* | O*, C*, Y* | M Jr-L K | M Jr-L K | 47 [†] , 43 [†] /303 [†] , 169 [†] |
| | <i>Imperturopollenites</i> spp. | 221 | ? | J, H, F | O, C?, Y | O, C, Y | L Carb-Plei | ? | 198/211, 18 |
| | <i>Khukisporites pseudoreticulatus</i> | 221 | — | J*, H*, F* | O*, C*?, Y* | O*, C*, Y* | L Tr-Plg | L Tr-Mio | 301 [†] /132 [†] |
| | <i>K. variegatus</i> | 221 | — | J*, H*, F* | O*, C*?, Y* | O*, C*, Y* | L Tr-Plg | E Jr-M Eoc | 130 [†] /181 [†] |
| | <i>Leptolepidites verrucatus</i> | 221 | — | J*, H*, F* | C*?, Y* | O*, C*, Y* | L Tr-Plio? | L Tr-Plio? | 265 [†] /187 [†] , 166 [†] |
| | <i>Lycopodiacidites cerniidites</i> | 221 | — | J* | C*?, Y* | O*, C*, Y* | F Jr-L K | E Jr-L K | 43 [†] /12 [†] |
| | <i>Lycopodiumsporites austroclavatidites</i> | 221 | — | J*, H*, F* | O*, C*? | O*, C*, Y* | L Tr-Mio | L Tr-Mio | 228 [†] /13 [†] |
| | <i>L. reticulatumsporites</i> | 221 | — | J* | O*, C*? | O*, C*, Y* | L Tr-Mio | M Tr-L K | 50 [†] /158 [†] |
| | <i>Lygodiumsporites subsimplex</i> | 221 | — | J*, H*, F* | C*?, Y* | O*, C*, Y* | M Jr-L K | M Jr-L K | 2 [†] /182 [†] |
| | <i>Osmundacidites speciosus</i> | 221 | — | J*, H*, F* | C*?, Y* | — | L Tr-Mio | E K | 349 [†] |
| | <i>O. wellmanii</i> | 221 | — | J*, H*, F* | ? | O*, C*, Y* | L Tr-Mio | L Tr-Mio | 48 [†] /287 [†] |
| | <i>Piceapollenites</i> spp. | 221 | ? | J, H, F | O, C?, Y | O, C, Y | L Carb-Plei | ? | 296, 88/269, 177 |
| | <i>Pinuspollenites</i> spp. | 221 | ? | J, H, F | O, C?, Y | O, C, Y | L P-Plei | ? | 351/252 |
| | <i>Podocarpidites</i> spp. | 221 | ? | J, H, F | O, C?, Y | O, C, Y | E P-Plei | ? | 220/115 |
| | <i>Rusatisporites kazouensis</i> | 221 | S | — | ? | — | E K | E K | 221 [†] |
| | <i>Schizaeosporites certus</i> | 221 | — | J*, H*, F* | C*?, Y* | — | L Jr-Plg | L Jr-Plg | 249 [†] /133 [†] |
| | <i>Torisporites yixianensis</i> | 221 | S | F | O, C?, Y | O, C, Y | L P-L Mio | S | 214, 215/204, 62 |
| | <i>Triporoletes reticulatus</i> | 148, 221 | — | J*, H*, F* | C*?, Y*? | O*, C*, Y* | L Jr?-L K? | L Jr?-L K? | 245 [†] /23 [†] , 137 [†] |
| Sphenophyta | | | | | | | | | |
| | <i>Equisitites</i> sp. | 24, 352 | ? | J, H, F | O, C? | O, C, Y | Carb?-Holo? | ? | 291, 292 |
| Pteridophyta | | | | | | | | | |
| | <i>Cladophlebis</i> spp. | 54 | ? | J, H, F | O, Y | O, C?, Y | L Tr-L K | ? | 8/297 |
| | <i>Coniopteris</i> sp. | 24 | ? | H, F | O | C?, Y | M Jr-L K | ? | 291/297 |
| | <i>Onydiopsis psilotoides</i> (= <i>O. elongata</i>) | 152, 297 | — | J*, H*, F* | Y*? | O | L Jr-L K | E K | 297 [†] , 278 [†] |
| | ? <i>Ruffordia</i> sp. | 24 | ? | F | Y | O, C?, Y | E K-L K | ? | 291/297 |
| Ginkgophyta | | | | | | | | | |
| | <i>Baiera</i> cf. <i>gracilis</i> | 152 | — | J*, F* | O* | O, C, Y | E Jr-L K | L Jr-L K | 188 [†] , 291, 297 [†] |
| | <i>B. orientalis</i> | 152 | S | J, F | O | O, C, Y | E Jr-L K | S | X |
| | <i>Czekanowskia rigida</i> | 152 | — | J*, H* | O*, C? | O, C | E Jr-L K | E Jr-E K | 297 [†] , 278, 352 [†] |
| | <i>Ginkgoites sibiricus</i> | 152 | — | J*, F* | O?, C*? | O, C, Y? | L Tr-Holo? | M Jr-E K | 8, 320, 352/291, 297 |
| | <i>Leptostrobus</i> sp. | 24 | ? | — | O, C?, | O, | E Jr-E K | ? | 291, 297 |
| | <i>Nageiopsis?</i> sp. | 34 | ? | ? | ? | Y | ?-L K | ? | 297 |
| | <i>Phoenicopsis</i> cf. <i>angustifolia</i> | 24, 352 | — | J*, H, F | O*? | O, C?, Y | L Tr-L K | E Jr-E K | 8, 352 [†] /297 [†] |
| | <i>Solenites</i> sp. | 24, 352 | ? | J, H | O | — | L Jr-E K | ? | 352/278 |
| | <i>Sphenobaiera longifolia</i> | 54 | — | F* | O*, C?, Y | O | L Tr-L K | M Jr-E K | 188 [†] , 8/297 [†] |

Continued.

Appendix, continued.

| Type | Taxon | Taxon occurs | | | | | Chronological Range | | Citations (for earliest occurrences of genus/species) ^{a, g} |
|-----------------------------|--|--|----------------|--|---|------------------------------------|---------------------|----------------------|--|
| | | Principal citations for Yixian Fm occurrence ^a | N ^b | Higher within Jethol Group ^c | Elsewhere in East Asia ^d | Elsewhere globally ^e | Genus ^f | Species ^f | |
| Cycadophyta | | | | | | | | | |
| | <i>Tyrnina</i> sp. | 24 | ? | J, H | O | — | E Jr-F K | ? | 320/297 |
| Coniferophyta | | | | | | | | | |
| | <i>Elatocladus manchurica</i> | 54 | — | J, H*, F* | O*, C?, Y | O, C?, Y | L Tr-L K | ? | 9/297 [†] |
| | <i>Pityolepis</i> sp. | 24 | ? | J | O, C? | C? | E Jr-E K | ? | 352/297 |
| | <i>Pityophyllum</i> cf. <i>lindstroemi</i> | 152 | S | H, F | O* | O, C, Y | E Jr-L K | S | 297 |
| | <i>Podocarpites lanceolatus</i> | 152 | — | J, H, F* | O*, C, Y | O, C, Y | M Tr-L K | E Jr-E K | 116/297 |
| | <i>Schizolepis jeholensis</i> | 152 | — | J*, H | C?, | O, C? | L Tr-E K | S | 8/139, 152 [†] |
| | <i>Sequoia? jeholensis</i> | 152 | — | J* | ? | Y | L Jr-Holo | E K | 294/297 |
| | <i>Yanhuoia sinensis</i> | 54 | — | ? | O*, C*? | — | M Jr?-E K? | M Jr?-E K? | X, 320 [†] , 346 [†] |
| Gnetalesⁱ | | | | | | | | | |
| | <i>Chaoyangicarpus liangi^j</i> | 55 | G | G | G | G | G | G | G |
| | <i>Eragrostes changii</i> | 24 | G | G | G | G | G | G | G |
| Angiospermae | | | | | | | | | |
| | <i>Archaeofructus liaoningensis</i> | 279 | G | G | G | G | G | G | G |
| | <i>Davallia? niehhtzuensis</i> | 152 | G | G | G | G | G | G | G |
| | <i>Liaoxia chenii</i> | 24 | G | G | G | G | G | G | G |
| | <i>Potamogeton?</i> (= <i>Ranunculus</i>) <i>jeholensis</i> | 24, 152 | — | ? | C*? | Y | E K-Mio | ? | 320 [†] , 139/291 |
| Bivalvia | | | | | | | | | |
| | <i>Ferganoconcha</i> cf. <i>burejensis</i> | 340 | — | J, H*, F* | O*, C*?, Y*? | — | M Jr-E K | E K? | 44/188, 340 [†] , 261 [†] , 313 [†] , 336 |
| | <i>F. curta</i> | 340 | — | J, H*, F* | O*, C*, Y*? | — | M Jr-E K | E K? | 340 [†] , 261 [†] , 313 [†] |
| | <i>F. estheriaeformis</i> | 338 | — | J, H, F | O*, C, Y | — | M Jr-F K | E K? | 340 [†] , 261 [†] , 313 [†] |
| | <i>F. hebeiensis</i> | 338 | S | J, H, F | O, C, Y | — | M Jr-E K | S | S |
| | <i>F. jorekensis</i> | 340 | — | J*, H*, F* | O*, C?, Y? | — | M Jr-E K | E K? | 340 [†] , 261 [†] , 313 [†] |
| | <i>F. junssica</i> | 338 | S | J, H, F | O, C*?, Y | — | M Jr-E K | S | S |
| | <i>F. lingyuanensis</i> | 338, 340 | — | J, H*, F* | O, C*?, Y* | — | M Jr-E K | E K? | 340 [†] , 261 [†] , 313 [†] , 356 [†] |
| | <i>F. pingquanensis</i> | 338 | S | J, H, F | O, C, Y | — | M Jr-E K | S | S |
| | <i>F. quadrata</i> | 338, 340 | — | J, F* | O, C*?, Y* | — | M Jr-E K | E K? | 340 [†] , 261 [†] , 313 [†] , 356 [†] |
| | <i>F. sibirica</i> | 308 | — | J*, H*, F* | O*, C*?, Y* | — | M Jr-E K | M Jr-E K? | 340 [†] , 261 [†] , 313 [†] , 356 [†] |
| | <i>F. subcentradis</i> | 338, 340 | — | J*, H*, F* | O*, C*?, Y* | — | M Jr-E K | M Jr-E K? | 340 [†] , 261 [†] , 313 [†] , 356 [†] |
| | <i>F. toniensis</i> | 338 | — | J, H, F | O, C*, Y* | — | M Jr-E K | E K? | 338 [†] , 356 [†] |
| | <i>F. cf. yanshanensis</i> | 338 | — | J, H, F | O, C*?, Y | — | M Jr-E K | E K? | 338 [†] , 356 [†] |
| | <i>Margaritifera</i> (?= <i>Mengyinaia</i>) sp. | 35 | ? | J, H, F | O, C? | Y | L K-Holo | ? | 44 |
| | <i>Myrene</i> (=? <i>Corbicula</i>) (= <i>Mesocorbicula</i>) <i>tetoriensis</i> | 35 | — | — | O, C*? | C? | M Jr-E K | M Jr-E K | 178 [†] , 179 [†] , 44 |
| | <i>Neomiodon hebeiensis</i> | 338 | S | J | C? | O, C? | M Jr-E K | S | 44/338, 355 [†] |
| | <i>Sibreconcha? dageensis</i> | 338 | S | — | O | — | L Tr-M Jr | S | 45/188, 261, 338 [†] |

Continued.

Appendix, continued.

| Type | Taxon | Taxon occurs | | | | | Chronological Range | | Citations (for earliest occurrences of genus/species) ^{a, g} |
|------|--|--|----------------|--|---|------------------------------------|---------------------|----------------------|--|
| | | Principal citations for Yixian Fm occurrence ^a | N ^b | Higher within Jethol Group ^c | Elsewhere in East Asia ^d | Elsewhere globally ^e | Genus ^f | Species ^f | |
| | <i>S. fengningensis</i> | 338 | S | — | O | — | L Tr-M Jr | S | 338 [†] |
| | <i>S. sichuanensis</i> | 338 | — | — | O | — | L Tr-M Jr | ? | X |
| | <i>Sphaerium</i> cf. <i>anderssoni</i> | 313 | — | J*, H*, F* | C?, Y? | C?, Y | L Jr-Holo | ? | 44, 261 [†] , 313 [†] , 336 [†] , 338 [†] , 354 [†] , 356 [†] |
| | <i>S. jeholense</i> | 35 | — | J*, H*, F* | C?, Y*? | C?, Y | L Jr-Holo | ? | 188 [†] , 261 [†] , 336 [†] , 338 [†] , 354 [†] , 356 [†] |
| | <i>S. cf. orientalis</i> | 338 | S | J, H, F | C?, Y? | C?, Y | L Jr-Holo | S | 338 [†] |
| | <i>S. pingquanense</i> | 338 | S | J, H, F | C?, Y? | C?, Y | L Jr-Holo | S | 338 [†] |
| | <i>S. pijiangense</i> | 338 | — | J*, H*, F* | C?, Y*? | C?, Y | L Jr-Holo | ? | X, 188 [†] |
| | <i>S. aff. rectiglobosum</i> | 338 | — | J, H, F | C?, Y? | C?, Y | L Jr-Holo | ? | X |
| | <i>S. rotundum</i> | 338 | — | J*, H, F | C?, Y? | C?, Y | L Jr-Holo | ? | 313 [†] ; 356 [†] |
| | <i>S. simplex</i> | 338 | S | J, H, F | C?, Y? | C?, Y | L Jr-Holo | S | 338 [†] |
| | <i>S. subplanum</i> | 340 | — | J*, H*, F* | C?, Y*? | C?, Y | L Jr-Holo | ? | 188 [†] , 354 [†] , 356 [†] |
| | <i>S. selenginense</i> | 340 | — | J*, H*, F | C?, Y? | C?, Y | L Jr-Holo | ? | X, 188 [†] , 354 [†] , 356 [†] |
| | <i>S. aff. yanbianense</i> | 338 | — | J, H, F | C?, Y*? | C?, Y | L Jr-Holo | ? | X |
| | <i>S. elliptiformis</i> | 338 | S | J | — | — | E K? | S | 338 [†] |
| | <i>S. huanpingensis</i> | 338 | S | J | — | — | E K? | S | 338 [†] |
| | <i>S. sinensis</i> | 338 | S | J | — | — | E K? | S | 338 [†] |
| | <i>S. subcentralis</i> | 338 | — | J* | — | — | E K? | E K? | 338 |
| | <i>S. triangulates</i> | 338 | S | J | — | — | E K? | S | 338 [†] |
| | <i>Tetoria?</i> sp. | 338 | ? | J | C? | — | M Jr-E K | ? | 178 |
| | ? <i>Tituella rotunda</i> | 338 | — | — | O*, C*? | — | E Jr-E K? | ? | 44, 188 [†] , 261 [†] , 338 |
| | <i>Weichangella angularia</i> | 338 | — | — | C? | — | E K | E K | 337 |
| | <i>W. antiqua</i> | 338 | — | — | C*? | — | E K | E K | 337 [†] |
| | <i>W. caelata</i> | 338 | — | — | C*? | — | E K | E K | 337 [†] |
| | <i>W. oblonga</i> | 338 | — | — | C? | — | E K | E K | X |
| | <i>W. qingquanensis</i> | 338 | — | — | C? | — | E K | E K | X |
| | <i>W. shalingouensis</i> | 338 | — | — | C*? | — | E K | E K | 337 [†] |
| | <i>W. trapezoidalis</i> | 338 | S | — | C? | — | E K | S | S |
| | <i>Xishanococoncha</i> sp. | 338 | ? | ? | Y? | — | E K? | ? | 338 [†] |

Gastropoda

| | | | | | | | | | |
|--|-----------------------------------|----------|---|------------|------------|----|------------|----------|-------------------------------------|
| | <i>Ammicola chaoyangensis</i> | 339 | — | J*, H*, F | O, Y? | Y | M Jr?-Holo | E K? | 206, 339 [†] /46, 342 |
| | <i>Bithynia haizhouensis</i> | 308, 339 | — | J*, H*, F* | O, C? | Y | M Jr?-Holo | E K? | 206, 339 [†] /46, 342 |
| | <i>Campeloma clavilithiformis</i> | 79 | S | J, H, F | Y? | Y | ?-Plio | S | 79/46 |
| | <i>C. fengtienensis</i> | 79 | S | J, H, F | Y? | Y | ?-Plio | S | S |
| | <i>C. tani</i> | 79 | — | J*, H*, F* | Y? | Y | ?-Plio | E K? | 79, 339 [†] /46 |
| | <i>C. yihsiensis</i> | 79 | S | J, H, F | Y? | Y | ?-Plio | S | S |
| | <i>Galba minuta</i> | 339 | S | H, F | O, Y? | Y | M Jr?-Holo | S | 206/339, 342 |
| | <i>G. cf. obrutschevi</i> | 339 | — | H*, F* | O, C*?, Y* | Y | M Jr?-Holo | E K-L K? | 206, 339 [†] , 342 |
| | <i>G. pseudopalustris</i> | 339 | — | H*, F | O C*? | Y | M Jr?-Holo | E K? | X, 339 [†] |
| | <i>Probaicalia gerassimovi</i> | 339 | — | J*, H*, F* | C*?, Y* | — | E K? | E K-L K? | 313 [†] , 356 [†] |
| | <i>P. vitimensis</i> | 308, 339 | — | J*, H*, F* | C*?, Y* | — | E K? | E K-L K? | 356 [†] |
| | <i>Reesidella robusta</i> | 304 | — | H | C*? | C? | ? | ? | 313 |
| | <i>Viviparis? matumotoi</i> | 313 | — | J*, H*, F* | C?, Y | Y | ?-Holo | ? | 46, 339 [†] , 342 |
| | <i>V. onogoensis</i> | 33 | — | H*?, F*? | C?, Y*? | Y | ? | ? | 339 [†] , 356 [†] |

Continued.

Appendix, continued.

| Type | Taxon | Taxon occurs | | | | | Chronological Range | | Citations (for earliest occurrences of genus/species) ^{a, b} |
|---------------------|--|--|----------------|--|---|------------------------------------|---------------------|----------------------|--|
| | | Principal citations for Yixian Fm occurrence ^a | N ^b | Higher within Jethol Group ^c | Elsewhere in East Asia ^d | Elsewhere globally ^e | Genus ^f | Species ^f | |
| | <i>Zaptychius</i> (<i>Omozaptychius</i>) <i>angulatus</i> | 339 | — | H*, F* | Y | ? | E, K-L, K | E, K? | 339 [†] , 355 |
| Conchostraca | | | | | | | | | |
| | <i>Chaoyangestheria diformis</i> | 301 | G | G | G | G | G | G | G |
| | <i>C. xiasanjiaziensis</i> | 301 | G | G | G | G | G | G | G |
| | <i>C. yanjiagouensis</i> | 301 | G | G | G | G | G | G | G |
| | <i>Clithroglypta guialingensis</i> | 301 | G | G | G | G | G | G | G |
| | <i>C. lingyuanensis</i> | 301, 313 | G | G | G | G | G | G | G |
| | <i>C. ovata</i> | 301 | G | G | G | G | G | G | G |
| | <i>C.? polyreticulata</i> | 301 | G | G | G | G | G | G | G |
| | <i>C. xiaodonggouensis</i> | 301 | G | G | G | G | G | G | G |
| | <i>Diestheria abnormis</i> | 301 | S | H | C? | — | E, K | S | 27, 29, 37, 188, 260, 309 |
| | <i>D. dadianziensis</i> | 309 | S | H | C? | — | E, K | S | S |
| | <i>D. daluochangensis</i> | 309 | S | H | C? | — | E, K | S | S |
| | <i>D. gigantea</i> | 309 | S | H | C? | — | E, K | S | S |
| | <i>D.? heichengziensis</i> | 27 | S | H | C? | — | E, K | S | S |
| | <i>D. hejiazimensis</i> | 301 | S | H | C? | — | E, K | S | S |
| | <i>D. jeholensis</i> | 27, 301 | S | H | C? | — | E, K | S | S |
| | <i>D. lijiagouensis</i> | 301 | S | H | C? | — | E, K | S | S |
| | <i>D. longinqua</i> | 27, 309 | S | H | C? | — | E, K | S | S |
| | <i>D. ovata</i> | 309 | S | H | C? | — | E, K | S | S |
| | <i>D. shangyuanensis</i> | 27, 301 | S | H | C? | — | E, K | S | S |
| | <i>D. suboblunga</i> | 27, 301 | — | H | C? | — | E, K | E, K | 37 [†] , 188 [†] |
| | <i>D. yixianensis</i> | 27, 301 | S | H | C? | — | E, K | S | S |
| | <i>Difformoglypta gongyingziensis</i> | 301 | — | J* | C? | — | E, K | E, K | 311, 312 [†] |
| | <i>D. cf. middendorffi</i> | 301 | — | J* | C? | — | E, K | E, K | 301 [†] |
| | <i>D. opipera</i> | 301 | — | J* | C? | — | E, K | E, K | 301 [†] |
| | <i>D. persculpta</i> | 301 | ? | J | C? | — | E, K | E, K | X |
| | <i>D. cf. pullica</i> | 301 | S | J | C? | — | F, K | S | S |
| | <i>D. triformis</i> | 301 | ? | J | C? | — | E, K | E, K | X |
| | <i>D. vera</i> | 301 | — | J* | C? | — | E, K | E, K | 301 [†] |
| | <i>Dongbeiestheria fixingimensis</i> | 301 | S | J | C? | — | E, K | S | S |
| | <i>D. tereovata</i> | 301 | S | J | C? | — | E, K | S | S |
| | <i>D. yushugouensis</i> | 301 | S | J | C? | — | E, K | S | S |
| | <i>Eosetheria bella</i> | 309 | S | J, H | C? | — | E, K | S | 27, 29, 37, 188, 260, 309 |
| | <i>E. brevis</i> | 56 | S | J, H | C? | — | E, K | S | S |
| | <i>E. changshanziensis</i> | 301 | — | J*, H | C? | — | E, K | E, K | 27, 29, 37, 188, 260, 309, 301 [†] |
| | <i>E. cf. chui</i> | 195, 309 | ? | J, H | C? | — | E, K | E, K | X |
| | <i>E. donggouensis</i> | 309 | S | J, H | C? | — | E, K | S | S |
| | <i>E.? elliptica</i> | 27, 301 | S | J, H | C? | — | E, K | S | S |
| | <i>E. cf. elongata</i> | 309 | ? | J, H | C? | — | F, K | F, K | X |
| | <i>F. erisopsiformis</i> | 309 | S | J, H | C? | — | E, K | S | S |
| | <i>E. fengningensis</i> | 309 | S | J, H | C? | — | E, K | S | S |

Continued.

Appendix, continued.

| Type | Taxon | Taxon occurs | | | | Chronological Range | | |
|---------------------------------------|----------|---|----------------|---|-------------------------------------|---------------------------------|--------------------|---|
| | | Principal citations for Yixian Fm occurrence ^a | N ^b | Higher within Jethol Group ^c | Elsewhere in East Asia ^d | Elsewhere globally ^e | Genus ^f | Species ^f |
| <i>E. fengshanensis</i> | 309 | S | J, II | C? | — | EK | S | S |
| <i>E. gibba</i> | 309 | S | J, H | C? | — | EK | S | S |
| <i>E. heshanggouensis</i> | 195, 309 | S | J, H | C? | — | EK | S | S |
| <i>E. fangangshanensis</i> | 27, 301 | S | J, H | C? | — | EK | S | S |
| <i>E. lahaigouensis</i> | 309 | S | J, H | C? | — | EK | S | S |
| <i>E. lingyuanensis</i> | 27, 309 | S | J, H | C? | — | EK | S | S |
| <i>E. linjiangensis</i> | 309 | S | J, H | C? | — | EK | S | S |
| <i>E. longiquadrata</i> | 309 | S | J, H | C? | — | EK | S | S |
| <i>E. middendorfi</i> | 27, 31 | — | J, H | C? | — | EK | EK | 29 [†] , 37 [†] , 188 [†] , 260 [†] |
| <i>E. minor</i> | 195, 309 | S | J, H | C? | — | EK | EK | S |
| <i>E. ovaliformis</i> | 27, 301 | S | J, H | C? | — | EK | EK | S |
| <i>E. persculpta</i> | 27, 309 | S | J, H | C? | — | EK | EK | S |
| <i>E. quinquanensis</i> | 309 | S | J, H | C? | — | EK | S | S |
| <i>E. radiata</i> | 309 | S | J, H | C? | — | EK | S | S |
| <i>E. ramulosa</i> | 309 | S | J, H | C? | — | EK | S | S |
| <i>E. reticulata</i> | 309 | S | J, H | C? | — | EK | S | S |
| <i>E. shangshixiaensis</i> | 309 | S | J, H | C? | — | EK | S | S |
| <i>E. songyingensis</i> | 309 | S | J, H | C? | — | EK | S | S |
| <i>E. takechenensis</i> | 195, 309 | ? | J, H | C? | — | EK | EK | X |
| <i>E. triiformis</i> | 27, 31 | S | J, H | C? | — | EK | S | S |
| <i>E. weichangensis</i> | 309 | S | J, H | C? | — | EK | S | S |
| <i>E. (Isoestheria) qingquanensis</i> | 309 | S(G) | G | G | G | S(G) | S(G) | S(G) |
| <i>E. (I.) yanbizigouensis</i> | 309 | S(G) | G | G | G | S(G) | S(G) | S(G) |
| <i>Fengninggrapta huajiyiensis</i> | 309 | — | — | — | — | EK? | EK? | X |
| <i>Filigrapta corpulepta</i> | 301 | ? | J | — | — | EK? | EK? | X |
| <i>F. equilateralis</i> | 313 | ? | J | — | — | EK? | EK? | X |
| <i>F. jianshangouensis</i> | 301 | — | J* | — | — | EK? | EK? | 313 [†] |
| <i>F. phalosana</i> | 301 | S | J | — | — | EK? | S | S |
| <i>F. producta</i> | 301 | ? | J | — | — | EK? | EK? | X |
| <i>F. taipinggouensis</i> | 301 | S | J | — | — | EK? | S | S |
| <i>F. zhuanchenziensis</i> | 301 | ? | J | — | — | EK? | EK? | X |
| <i>Liaoningestheria ovata</i> | 27, 34 | S | J, H | — | — | EK? | S | 27, 34 |
| <i>L. cf. shangyuanensis</i> | 34 | S | J, H | — | — | EK? | S | S |
| <i>Oncabrestheria elliptica</i> | 195 | G | G | G | G | G | G | G |
| <i>O. inflata</i> | 195 | G | G | G | G | G | G | G |
| <i>O. latiovata</i> | 195 | G | G | G | G | G | G | G |
| <i>O. orbiculata</i> | 195 | G | G | G | G | G | G | G |
| <i>O. ovata</i> | 195 | G | G | G | G | G | G | G |
| <i>O. subquadrata</i> | 195 | G | G | G | G | G | G | G |
| <i>O. subtriangularis</i> | 195 | G | G | G | G | G | G | G |
| <i>O. tuberculata</i> | 195 | G | G | G | G | G | G | G |
| <i>Taemiestheria ovata</i> | 194 | G | G | G | G | G | G | G |
| <i>T. qingquanensis</i> | 194 | G | G | G | G | G | G | G |
| <i>T. reticulata</i> | 194 | G | G | G | G | G | G | G |
| <i>T. suboblonga</i> | 194 | G | G | G | G | G | G | G |
| <i>T. subquadrata</i> | 194 | G | G | G | G | G | G | G |

Continued.

Appendix, continued.

| Type | Taxon | Taxon occurs | | | | | Chronological Range | | |
|------------------|--|---|----------------|---|-------------------------------------|---------------------------------|---------------------|----------------------|--|
| | | Principal citations for Yixian Fm occurrence ^a | N ^b | Higher within Jethol Group ^c | Elsewhere in East Asia ^d | Elsewhere globally ^e | Genus ^f | Species ^f | Citations (for earliest occurrences of genus/species) ^{a,g} |
| | <i>Yanjiestheria</i> (= <i>Yanshanina</i>) <i>dabeigouensis</i> | 27, 308 | S | H | C? | — | E K? | S | 27, 260, 306, 309 |
| | <i>Y.</i> (= <i>Y.</i>) <i>fengningensis</i> | 309 | S | H | C? | — | E K? | S | S |
| | <i>Y.</i> (= <i>Y.</i>) <i>subquadrata</i> | 27, 308 | S | H | C? | — | E K? | S | S |
| Ostracoda | | | | | | | | | |
| | <i>cf. Cymocypris scolio</i> | 345 | — | J* | C?, Y*? | O, C | E J?–E K | ? | 17, 208 [†] , 344 [†] |
| | <i>Cypridea</i> aff. <i>sainschandaensis</i> | 313, 345 | ? | J, H, F | Y? | O, C, Y | L Jr–F Eoc | ? | 253, 282, 322/87, X |
| | <i>C. altidorsangulate</i> | 210 | ? | J, H, F | Y? | O, C, Y | L Jr–E Eoc | ? | X |
| | <i>C. sulcata</i> | 151 | ? | | | | L Jr–E Eoc | ? | X |
| | <i>C. xitaiyanpoensis</i> | 210 | ? | J, H, F | Y? | O, C, Y | L Jr–E Eoc | ? | X |
| | <i>C. (C.) deflexa</i> | 313, 345 | S | J, H, F | Y | O, C, Y | L Jr–E Eoc | S | S |
| | <i>C. (C.) dorsobispina</i> | 313, 345 | — | J*, H, F | Y | O, C, Y | L Jr–E Eoc | E K | 345 [†] |
| | <i>C. (C.) ganzhaensis</i> | 313, 345 | S | J, H, F | Y | O, C, Y | L Jr–F Eoc | S | S |
| | <i>C. (C.) fangangshuensis</i> | 313, 345 | S | J, H, F | Y | O, C, Y | L Jr–E Eoc | S | S |
| | <i>C. (C.) liaoningensis</i> | 313, 345 | S | J, H, F | Y | O, C, Y | L Jr–E Eoc | S | S |
| | <i>C. (C.) placida</i> | 313, 345 | S | J, H, F | Y | O, C, Y | L Jr–E Eoc | S | S |
| | <i>C. (C.) prognata</i> | 313, 345 | ? | J, H, F | Y | O, C, Y*? | L Jr–E Eoc | ? | 344 [†] |
| | <i>C. (C.) ex. gr. sinensis</i> | 345 | ? | J, H, F | Y | O, C, Y | L Jr–E Eoc | ? | X |
| | <i>C. (C.) spatiosa</i> | 313, 345 | S | J, H, F | Y | O, C, Y | L Jr–E Eoc | S | S |
| | <i>C. (C.) suborthocera</i> | 313, 345 | S | J, H, F | Y | O, C, Y | L Jr–F Eoc | S | S |
| | <i>C. (C.) tubercularis</i> | 313, 345 | ? | J, H, F | Y | O, C, Y | L Jr–E Eoc | ? | X |
| | <i>C. (C.) vemistata</i> | 313, 345 | S | J, H, F | Y | O, C, Y | L Jr–E Eoc | S | S |
| | <i>C. (C.) veridica</i> | 313, 345 | — | J*, H, F | Y | O, C, Y | L Jr–E Eoc | E K | 345 [†] |
| | <i>C. (C.) zaocishanensis</i> | 313, 345 | S | J, H, F | Y | O, C, Y | L Jr–E Eoc | S | S |
| | <i>C. (Uhvellia) muciculata</i> | 313, 345 | S | J, H | Y? | O, C, Y | L Jr–F Eoc | S | S |
| | <i>C. (U.) semovata</i> | 345 | S | J, H | Y? | O, C, Y | L Jr–E Eoc | S | S |
| | <i>C. (Yumenia) sp.</i> | 345 | ? | J | Y? | O, C, Y | L Jr–F Eoc | ? | 345 |
| | <i>Damonella circulata</i> | 345 | — | J*, H*, F* | O?, C? | O, C? | L Jr–E K? | ? | 209, 345 [†] |
| | <i>D. extensa</i> | 313, 345 | ? | J, H, F | O?, C? | O, C? | L Jr–E K? | ? | X |
| | <i>D. subsymmetrica</i> | 313, 345 | S | J, H, F | O?, C? | O, C? | L Jr–E K? | S | S |
| | <i>Darwinula contincta</i> | 345 | — | J*, H*, F* | O, C*?, Y* | O, C, Y | Ord?–Holo | ? | 17, 208 [†] , 344 [†] |
| | <i>D. oblonga</i> | 345 | — | F | C*?, | O, C, Y | Ord?–Holo | ? | 17 |
| | <i>Djungarica caminata</i> | 313, 345 | — | J* | C?, Y | — | L Jr–E K | ? | 209, 345 |
| | <i>D. procurva</i> | 313, 345 | S | J | C?, Y | — | L Jr–E K | S | S |
| | <i>Lycocypris debilis</i> | 345 | — | J*, H*, F* | C*?, Y* | O, C*?, Y | E K–Pal | F K | 189, 190, 344 [†] /285 |
| | <i>L. infantilis</i> | 345 | — | J*, H*, F* | C*?, Y* | O, C, Y | F K–Pal | E K | 344 [†] 345 [†] |
| | <i>Mongolianella subtrapezoides</i> | 345 | ? | J | C?, Y | C, Y | E K–L K | ? | 286, X |
| | <i>Rhinocypris dadingsiensis</i> | 210 | ? | J, H | C?, Y? | ? | L Jr–E K | E K? | 17 |
| | <i>R. echinata</i> | 210, 345 | — | J*, H | C*?, Y*? | C? | L Jr–E K | E K? | 208 [†] , 344 [†] 345 [†] |
| | <i>R. foveata</i> | 210 | — | J, H | C*?, Y*? | C? | L Jr–E K | E K? | 208 [†] |
| | <i>R. subechinata</i> | 210 | ? | J, H | C?, Y? | C? | L Jr–E K | E K? | X |
| | <i>Timirisevia jianshangouensis</i> | 313, 345 | S | J, H | C?, Y | O, C | M Jr–Pal | S | 17/285 |
| | <i>T. opinabilis</i> | 210 | ? | J, H, F | C?, Y | O, C | M Jr–Pal | ? | X |
| | <i>T. pusilla</i> | 345 | — | J*, H*, F* | C*?, Y*? | O, C | M Jr–Pal | ? | 344 [†] 345 [†] |
| | <i>Yanshanina dabeigouensis</i> | 210 | ? | — | C?, Y | — | E K | F K | X, 210 [†] , 209 [†] |
| | <i>Y. elongata</i> | 210 | ? | — | C?, Y | — | E K | E K | X |

Continued.

Appendix, continued.

| Type | Taxon | Taxon occurs | | | | Chronological Range | | | |
|----------------|--|---|----------------|---|-------------------------------------|---------------------------------|--------------------|----------------------|---|
| | | Principal citations for Yixian Fm occurrence ^a | N ^b | Higher within Jethol Group ^c | Elsewhere in East Asia ^d | Elsewhere globally ^e | Genus ^f | Species ^f | Citations (for earliest occurrences of genus/species) ^{a, g} |
| | <i>Y. postitricata</i> | 210 | ? | — | C?, Y | — | E K | E K | X |
| | <i>Y. subovata</i> | 210 | — | — | C?, Y* | — | E K | E K | 209 [†] |
| | <i>Ziziphocypsis linchengensis</i> | 345 | — | J, H, F | C?, Y*? | C, Y | E K-L K | L K | 179/286, 344 [†] , X |
| Insecta | | | | | | | | | |
| | <i>Aeschnidium densum</i> | 343 | — | J* | +* | O*, C, Y | L Jr-E K | L Jr-E K | 15, 90, 155/343 [†] |
| | <i>A. heishankowense</i> (= <i>Sinuoeschnidia</i>) <i>heishankowensis</i> , <i>Pseudosamarura largina</i> , <i>Archaeogomphus labius</i> , <i>Yixiangomphus labius</i>) | 343 | — | J*? | ?C* | O, C, Y | L Jr-E K | F K | 343 [†] |
| | <i>Aeschnidiella kabanovi</i> | 34, 313 | S | — | C? | — | E K | S | 341 |
| | <i>Aethephasma megista</i> | 234 | G | G | G | G | G | G | G |
| | <i>Alleromononmus liaoningensis</i> | 237 | G | G | G | G | G | G | G |
| | <i>A. xingyi</i> | 237 | G | G | G | G | G | G | G |
| | <i>Allogaster ovata</i> | 240 | G | G | G | G | G | G | G |
| | <i>Allomyia ruderalis</i> | 236 | G | G | G | G | G | G | G |
| | <i>Alloraphidia anomala</i> | 232 | S | — | — | C? | E K | S | 25 |
| | <i>A. longistigmata</i> | 230 | S | — | — | C? | E K | S | S |
| | <i>A. obliquivenatica</i> | 230 | S | — | — | C? | E K | S | S |
| | <i>Alloxylehula lingyuanensis</i> | 240 | G | G | G | G | G | G | G |
| | <i>Atalosciophila yanensis</i> | 240 | G | G | G | G | G | G | G |
| | <i>Baissodes gribaudi</i> | 240 | S | — | C? | C? | E K | S | 225, 227 |
| | <i>Baissoptera eumeura</i> | 232 | S | — | — | O? | L Jr-F K | S | 175 |
| | <i>B. grandis</i> | 240 | S | — | — | O? | L Jr-E K | S | S |
| | <i>Basilorhagio venustus</i> | 240 | G | G | G | G | G | G | G |
| | <i>Bibitica hebeiensis</i> | 98 | G | G | G | G | G | G | G |
| | <i>Blattula delicatula</i> | 240 | S | — | + | O | F Jr-E K | S | 90, 298 |
| | <i>B. exaristata</i> | 240 | S | — | + | O | F Jr-E K | S | S |
| | <i>B. platypa</i> | 240 | S | — | + | O | F Jr-F K | S | S |
| | <i>Caloraphidia glossophylla</i> | 232 | G | G | G | G | G | G | G |
| | <i>Cephenopsis mirabilis</i> | 98 | G | G | G | G | G | G | G |
| | <i>Chengdesorphus petiolatus</i> | 240 | G | G | G | G | G | G | G |
| | <i>Chironomaptera</i> (= <i>Mesotendipes</i>) <i>gregaria</i> | 154, 213 | — | J* | C*? | — | E K | E K | 155 [†] , 98 [†] |
| | <i>Chironomopsis gracilis</i> | 213 | — | ? | C*? | O | L Jr-E K | E K | 90/100 [†] , 188 [†] |
| | <i>Choromyrmeleon othneius</i> | 238 | G | G | G | G | G | G | G |
| | <i>Chrysogomphus beipiaoensis</i> | 231 | G | G | G | G | G | G | G |
| | <i>Clypostemma xyphidie</i> | 98, 308 | — | ? | C*? | C? | E K-L K | E K | 155 [†] /156 |
| | <i>Coptoclava longipoda</i> | 154, 213 | — | J* | C*? | — | E K | F K | 155 [†] , 98 [†] , 188 [†] |
| | <i>Eopangonius pletus</i> | 236 | G | G | G | G | G | G | G |
| | <i>Ephemeroptera trisetalis</i> | 154, 213 | — | J* | C*? | — | E K? | E K? | 155 [†] , 98 [†] , 188 [†] |
| | <i>Euryxylea longhuaensis</i> | 98 | G | G | G | G | G | G | G |
| | <i>Florimnestrius pulcherrimus</i> | 235, 236 | G | G | G | G | G | G | G |
| | <i>Geotrupoides songyingziense</i> | 98 | S | — | C? | O | L Jr-E K | S | 90/98 [†] , 99 |
| | " <i>Glypta</i> " <i>qingshilaensis</i> ^k | 240 | — | — | Y*? | — | E K | E K | 98 |
| | <i>Habrohaqia curtivenata</i> | 240 | G | G | G | G | G | G | G |

Continued.

Appendix, continued.

| Type | Taxon | Taxon occurs | | | | | Chronological Range | | Citations (for earliest occurrences of genus/species) ^{a, g} |
|------|--|--|----------------|--|---|------------------------------------|---------------------|----------------------|--|
| | | Principal citations for Yixian Fm occurrence ^a | N ^b | Higher within Jethol Group ^c | Elsewhere in East Asia ^d | Elsewhere globally ^e | Genus ^f | Species ^f | |
| | <i>Hagiphasma paradoxa</i> | 234 | G | G | G | G | G | G | G |
| | <i>Hebeiaeschnidia fengningensis</i> | 98 | ? | ? | ? | — | E K? | E K? | X |
| | <i>Hebeihagla songyingziensis</i> | 98 | — | ? | C? | — | E K? | E K? | 97 |
| | <i>Helempis eualla</i> | 236 | G | G | G | G | G | G | G |
| | <i>H. yixianensis</i> | 236 | G | G | G | G | G | G | G |
| | <i>Jeholoropronia pingi</i> | 240 | G | G | G | G | G | G | G |
| | <i>Jibeicossus qingshilaense</i> | 98 | G | G | G | G | G | G | G |
| | <i>Kalligramma liaoningensis</i> | 238 | S | — | — | O | M Jr-E K | S | 207/171 |
| | <i>Karataviella pontiforma</i> | 154 | S | — | O, C? | O | M Jr-E K | S | 155 |
| | <i>Karatavoblatta formosa</i> | 240 | S | — | — | O | M Jr?-E K | S | 298 |
| | <i>Lasionylus newi</i> | 238 | G | G | G | G | G | G | G |
| | <i>Lembochrysa miniscula</i> | 238 | G | G | G | G | G | G | G |
| | <i>L. polyneura</i> | 238 | G | G | G | G | G | G | G |
| | <i>Leptermochaetus lithoecius</i> | 236 | G | G | G | G | G | G | G |
| | <i>Leptoplectia zhangshanyingensis</i> | 98 | S | ? | ? | — | E K? | S | X |
| | <i>Liadoxyela chengdeensis</i> | 240 | S | — | — | O | E Jr?-E K | S | 26 |
| | <i>Liaotoma linearis</i> | 240 | G | G | G | G | G | G | G |
| | <i>Lichnoplectia kovalevi</i> | 240 | G | G | G | G | G | G | G |
| | <i>Liogomphus yixianensis</i> | 239 | G | G | G | G | G | G | G |
| | <i>Longhuaia rara</i> | 98 | G | G | G | G | G | G | G |
| | <i>Longipadia pingquanensis</i> | 98 | G | G | G | G | G | G | G |
| | <i>Luapingia senjituensis</i> | 98 | S | ? | C? | V | E K? | S | X, 224 |
| | <i>Manlaya flexosus</i> | 240 | S | — | C? | — | E K | S | 226 |
| | <i>Megabittacus beipiaoensis</i> | 233 | G | G | G | G | G | G | G |
| | <i>M. colossetus</i> | 233 | G | G | G | G | G | G | G |
| | <i>Mesascalaphus yangi</i> | 240 | G | G | G | G | G | G | G |
| | <i>Mesaulacinus rasnitsyni</i> | 240 | S | ? | — | C? | M Jr?-E K | S | 174 |
| | <i>Mesoblattina sinica</i> | 213 | S | ? | C? | O, C? | L Jr?-E K | S | 20, 96 |
| | <i>Mesocordulia boreala</i> | 239 | G | G | G | G | G | G | G |
| | <i>Mesohemerobius jeholensis</i> | 213 | G | G | G | G | G | G | G |
| | <i>Mesoleuctra peipiaoensis</i> | 213 | S | — | C? | — | L Jr?-E K? | S | 20 |
| | <i>Mesoraphidia amoena</i> | 232 | S | — | + | C? | M Jr?-E K | S | 172, 173 |
| | <i>M. heteroneura</i> | 232 | S | — | + | C? | M Jr?-E K | S | S |
| | <i>M. sinica</i> | 232 | S | — | + | C? | M Jr?-E K | S | S |
| | <i>Mesosirex volantis</i> | 98 | G | G | G | G | G | G | G |
| | <i>Mioraphidia</i> (<i>Mesoraphidia</i>) <i>furcivenata</i> | 232 | G | G | G | G | G | G | G |
| | <i>Multimodus dissitus</i> | 240 | S | — | C? | — | E K | S | 275 |
| | <i>M.? elongatus</i> | 240 | S | — | C? | — | E K | S | S |
| | <i>M. stigmaeus</i> | 240 | S | — | C? | — | E K | S | S |
| | <i>Necrotaulus qingshilaense</i> | 98 | S | — | C? | O | E Jr-E K | S | 90/98 |
| | <i>Nipponoblatta acerba</i> | 240 | S | — | O | — | E Jr-E K | S | 74 |
| | <i>Oiobrachyceron limnogenus</i> | 236 | G | G | G | G | G | G | G |
| | <i>Oloberotha sinica</i> | 238 | G | G | G | G | G | G | G |
| | <i>Opiparifungivora aliena</i> | 240 | G | G | G | G | G | G | G |
| | <i>Orephasma eumorpha</i> | 234 | G | G | G | G | G | G | G |
| | <i>Orsobrachyceron chinensis</i> | 236 | G | G | G | G | G | G | G |

Continued.

Appendix, continued.

| Type | Taxon | Taxon occurs | | | | Chronological Range | | | Citations (for earliest occurrences of genus/species) ^{a, g} |
|------|---|--|----------------|--|---|------------------------------------|--------------------|----------------------|--|
| | | Principal citations for Yixian Fm occurrence ^a | N ^b | Higher within Jethol Group ^c | Elsewhere in East Asia ^d | Elsewhere globally ^e | Genus ^f | Species ^f | |
| | <i>Orthophlebia liaoningensis</i> | 233 | S | — | C? | O | F, Jr-E K | S | 90 |
| | <i>Palaeopangonius eupterus</i> | 235, 236 | G | G | G | G | G | G | G |
| | <i>Parachorista miris</i> | 154 | G | G | G | G | G | G | G |
| | <i>Paroryssus suspectus</i> | 154 | S | — | — | O | M Jr-E K | S | 174, 224 |
| | <i>Patrolacus sinicus</i> | 213 | G | G | G | G | G | G | G |
| | <i>Pauromyia oresbia</i> | 236 | G | G | G | G | G | G | G |
| | <i>Perlariopsis peipiaoensis</i> | 213 | G | G | G | G | G | G | G |
| | <i>Phiradia myrioneuva</i> | 232 | S | — | — | O | L Jr-E K | S | 324 |
| | <i>Probelus sinicus</i> | 98 | S | — | — | O | M Jr-E K | S | 7 |
| | <i>Protapiocera ischyra</i> | 236 | G | G | G | G | G | G | G |
| | <i>P. megista</i> | 236 | G | G | G | G | G | G | G |
| | <i>Protenipis minuta</i> | 236 | S | — | — | O | M Jr-E K | S | 295 |
| | <i>Protonemestrinus beipiaoensis</i> | 236 | S | — | — | O | M Jr-E K? | S | 243 |
| | <i>P. junassicus</i> | 235 | S | — | — | O | M Jr-E K? | S | 243 |
| | <i>Pseudohalga pospelovi</i> | 313 | — | ? | O* | — | M Jr?-E K? | ? | X |
| | <i>Rudialeschna limnobia</i> | 239 | G | G | G | G | G | G | G |
| | <i>Rudiraphidia</i> (Baissoptera) <i>liaoningensis</i> | 232 | G | G | G | G | G | G | G |
| | <i>Sibirobituacus atalus</i> | 233 | S | — | C? | — | E K | S | 276 |
| | <i>Siboptera</i> (Liaoraphidia) <i>fornicata</i> | 232 | S | — | C? | — | E K | S | 219 |
| | <i>Sinoelaterium melancolor</i> | 213 | G | G | G | G | G | G | G |
| | <i>Sinogomphus taushanensis</i> | 98 | ? | ? | ? | — | E K? | E K? | X |
| | <i>Sinohagla pleioneura</i> | 240 | S | — | O, C? | — | E Jr-E K? | S | 97, 153 |
| | <i>Simonemoura grabaui</i> | 213 | G | G | G | G | G | G | G |
| | <i>Sinoperla abdominalis</i> | 213 | G | G | G | G | G | G | G |
| | <i>Sinosepilca gigathoracalis</i> | 240 | G | G | G | G | G | G | G |
| | <i>Sinoviparosiphum lini</i> | 240 | G | G | G | G | G | G | G |
| | <i>Solichneumon</i> (Yanichneumon) <i>rectivenius</i> | 240 | G | G | G | G | G | G | G |
| | <i>Sophogramma eucalla</i> | 238 | G | G | G | G | G | G | G |
| | <i>S. papilionacea</i> | 238 | G | G | G | G | G | G | G |
| | <i>S. plecophlebia</i> | 238 | G | G | G | G | G | G | G |
| | <i>Tetraphalerus laetus</i> | 154 | S | — | — | Y | M Jr-Holo | S | 217, 218/26 |
| | <i>T. lentus</i> | 240 | S | — | — | Y | M Jr-Holo | S | 217, 218/26 |
| | <i>Xynoraphidia polyphlebia</i> | 232 | G | G | G | G | G | G | G |
| | <i>X. (Archeraphidia)</i> <i>shangyuanensis</i> | 232 | G | G | G | G | G | G | G |
| | <i>Yanocleistogaster canaliculata</i> | 240 | G | G | G | G | G | G | G |
| | <i>Yanocossus guoi</i> | 240 | G | G | G | G | G | G | G |
| | <i>Yanoraphidia gaoi</i> | 240 | G | G | G | G | G | G | G |
| | <i>Yanorthophlebia hebeiensis</i> | 240 | G | G | G | G | G | G | G |
| | <i>Yanosmylus rarivenatus</i> | 240 | G | G | G | G | G | G | G |
| | <i>Yenshamia hopeiensis</i> | 98 | ? | ? | ? | — | E K? | E K? | X |

Decapoda

| | | | | | | | | |
|---------------------------------|-----|---|---|---|---|---|---|---|
| <i>Cricoidosecelosus aethus</i> | 290 | G | G | G | G | G | G | G |
| <i>Palaeocambarus licenti</i> | 290 | G | G | G | G | G | G | G |

Continued.

Appendix, continued.

| Type | Taxon | Taxon occurs | | | | Chronological Range | | | |
|--------------------------------|--|---|----------------|---|-------------------------------------|---------------------------------|--------------------|----------------------|---|
| | | Principal citations for Yixian Fm occurrence ^a | N ^b | Higher within Jethol Group ^c | Elsewhere in East Asia ^d | Elsewhere globally ^e | Genus ^f | Species ^f | Citations (for earliest occurrences of genus/species) ^{a,g} |
| Osteichthyes | | | | | | | | | |
| | <i>Jinanichthys longicephalus</i> (= <i>Changichthys dalinghensis</i> and <i>Liaoxiichthys longicephalus</i>) | 68 | — | J, H | C? | — | E, K | E, K | 165 [†] , 68 [†] |
| | <i>Lycoptera davidi</i> (= <i>L. middendorffi</i> and <i>L. tokunagai</i>) | 68, 164 | — | J | C? | — | E, K | E, K | 11 [†] , 58 [†] , 288 [†] , 192 [†] |
| | <i>L. muroii</i> | 68 | — | J, H | — | — | E, K | E, K | 11 [†] |
| | <i>L. (Asiatolepis) sinensis</i> | 68 | S | J, H | C? | — | E, K | S | 288 [†] , 188 |
| | <i>Peipiaosteus fengningensis</i> | 159 | S | — | — | — | E, K | S | 159 |
| | <i>P. pani</i> | 68 | — | J | — | — | E, K | E, K | 11 [†] , 68 [†] |
| | <i>Protosephurus liui</i> | 68, 159 | — | J | — | — | E, K | E, K | 68 [†] |
| | <i>Sinamia</i> sp. | 314 | ? | Y | C? | — | E, K | E, K | 188, 273, 330 |
| | <i>Yanosteus longidorsalis</i> | 67, 68 | G | G | G | G | G | G | G |
| Anura | | | | | | | | | |
| | <i>Callobatrachus sanyanensis</i> | 316 | G | G | G | G | G | G | G |
| | <i>Liaobatrachus gubanii</i> | 314 | G | G | G | G | G | G | G |
| Chelonia | | | | | | | | | |
| | <i>Manchurochelys liaoxiensis</i> | 123 | G | G | G | G | G | G | G |
| | <i>M. manchoukuoensis</i> | 60 | G | G | G | G | G | G | G |
| Diapsida incertae sedis | | | | | | | | | |
| | <i>Hypalosaurius</i> (= <i>Sinohydrosaurus</i>) <i>lingyuanensis</i> ¹ | 77, 145 | G | G | G | G | G | G | G |
| Sphenodontia | | | | | | | | | |
| | <i>Mojurosuchus splendidus</i> (= "Rhynchosaurus" orientalis) | 314 | G | G | G | G | G | G | G |
| Lacertilia | | | | | | | | | |
| | <i>Dalinghosaurus longidigitus</i> | 314 | G | G | G | G | G | G | G |
| | <i>Yabeinosaurus tenuis</i> | 314 | G | G | G | G | G | G | G |
| Pterosauria | | | | | | | | | |
| | <i>Dendrorhynchoides curvidentatus</i> ^m | 126, 128 | G | G | G | G | G | G | G |
| | <i>Eosipterus yangi</i> | 125, 128 | G | G | G | G | G | G | G |
| Ceratopsia | | | | | | | | | |
| | <i>Psittacosaurus</i> sp. (= <i>P. meileyingensis</i> or <i>P. mongoliensis</i>) ⁿ | 127, 327 | ? | J, H | C?, Y? | — | F, K | F, K | 52, 161 |

Continued.

Appendix, continued.

| Type | Taxon | Taxon occurs | | | | Chronological Range | | | |
|-----------|--|---|----------------|--|-------------------------------------|---------------------------------|--------------------|----------------------|---|
| | | Principal citations for Yixian Fm occurrence ^d | N ^b | Higher within Jehol Group ^c | Elsewhere in East Asia ^d | Elsewhere globally ^e | Genus ^f | Species ^f | Citations (for earliest occurrences of genus/species) ^{g, h} |
| Theropoda | | | | | | | | | |
| | <i>Beipiaosaurus inexpectus</i> | 328 | G | G | G | G | G | G | G |
| | <i>Caudipteryx zoni</i> | 121 | G | G | G | G | G | G | G |
| | <i>Protarchaeopteryx robusta</i> | 118, 121 | G | G | G | G | G | G | G |
| | <i>Sinornithosaurus millenii</i> | 329 | G | G | G | G | G | G | G |
| | <i>Sinosauropteryx prima</i> | 39, 117 | G | G | G | G | G | G | G |
| Aves | | | | | | | | | |
| | <i>Changchengornis hengdaoziensis</i> | 119 | G | G | G | G | G | G | G |
| | <i>Confuciusornis dui</i> ^o | 110 | G | G | G | G | G | G | G |
| | <i>C. sanctus</i> (= <i>C. chuozhous</i> , <i>C. sumae</i>) ^o | 103, 105, 106, 110 | G | G | G | G | G | G | G |
| | <i>Eoenantiornis buhleri</i> | 109, 314 | G | G | G | G | G | G | G |
| | " <i>Fibeinia luanthera</i> " ^p | 103 | G | G | G | G | G | G | G |
| | <i>Liaoningornis longuligutris</i> | 102, 108, 314 | G | G | G | G | G | G | G |
| | <i>Liaoxiornis delicatus</i> | 104 | G | G | G | G | G | G | G |
| Mammalia | | | | | | | | | |
| | <i>Jeholodens jenkinsi</i> | 120 | G | G | G | G | G | G | G |
| | <i>Zhangotherium quinquecuspiden</i> | 112, 314 | G | G | G | G | G | G | G |

^a Numbers in these columns refer to numbered references in the bibliography.

^b "Endemic" refers to the Yixian Formation specifically, where only the species is endemic; information in following columns refers to other occurrences of the genus. A question mark (?) indicates that, since no species has been specified, endemicity cannot be assessed.

^c "Higher within the Jehol Group" includes the Jiufotang, Shahai and Fuxin Formations, but does not include the Mongolian and Transbaikalian deposits.

^d "Elsewhere within East Asia" includes other formations in China, Mongolia, eastern Russia, Japan, Thailand and Korea. Because many of the formations in which the taxa co-occur suffer from the same types of dating problems as the Yixian Formation (e.g., the Mongolian and Transbaikalian taxa; see text), whether or not the occurrences outside the Jehol Group are coeval is not assessed here.

^e Age comparisons use the Barremian–Aptian age of the Yixian Formation supported in this paper.

^f Where a genus or species is limited to the Yixian and possibly coeval formations within China or East Asia that have been considered Late Jurassic, we denote them here as Early Cretaceous based on our conclusions of the age of the Yixian Formation; any other formations are not necessarily Early Cretaceous and may represent earlier occurrences of the genus or species. Occurrences in other formations include cf. and aff. attributions.

^g A dagger (†) indicates that the reference pertains to the species (absence of a dagger indicates that the reference is only for the genus). References for genus are given only with first occurrence of the genus on the list.

^h No further reference could be found for the genus *Foraminisporites*; it may be a misspelling of *Foraminisporis*, or it may be a wholly endemic taxon.

ⁱ *Chaoyangiacarpus* and *Eragrostis* were initially described as angiosperms, but are considered gnetalean by Sun et al. (1998).

^j The generic name *Chaoyangia* Duan 1998 is not to be confused with the ornithurine bird *Chaoyangia* Hou 1993 from the Jiufotang Formation, though both names are valid because they belong to different Linnean kingdoms.

^k The generic name "*Glypta*" was given to a coleopteran by Hong (1984), but the name appears to be preoccupied by *Glypta* Gravenhorst 1829, a hymenopteran, per Carpenter (1992). If the coleopteran discussed by Hong (1984) is a valid taxon, it requires a new name.

^l Gao et al. (1999) and Li et al. (1999) separately named and described part and counterpart of the same specimen; *Hypulosauros* is considered here to have priority over *Sinohyulosauros*.

^m *Dendrorhynchoides* has been identified as a composite of a pterodactyloid pterosaur onto which a dromaeosaurid theropod tail has been grafted, and does not constitute a rhamphorhynchoid pterosaur occurrence in the Yixian Formation. See the text for further discussion.

ⁿ The Yixian Formation specimen of *Psittacosaurus* was not placed into a known species by Xu and Wang (1998) but was differentiated from others and described as "more primitive" than known species. Numerous specimens and species of *Psittacosaurus* are known from many formations in Asia; see Lucas and Estep (1998) for details.

^o *C. chuozhous* and *C. sumae* were shown to be synonyms of *C. sanctus* by Chiappe et al. (1999); they also suspected *C. dui* to be a synonym, although we provisionally retain its species distinction here.

^p Hou (1997b) used the name "*Fibeinia luanthera*" in the figure caption of a photograph of a fossil bird from the Yixian Formation in Hebei Province, but did not provide a formal description of the bird, so the name is presently a nomen nudum.

