

Early Cretaceous terrestrial ecosystems in East Asia based on food-web and energy-flow models

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Abstract

In recent years, there has been global interest in the environments and ecosystems around the world. It is helpful to reconstruct past environments and ecosystems to help understand them in the present and the future. The present environments and ecosystems are an evolving continuum with those of the past and the future. This paper demonstrates the contribution of geology and paleontology to such continua.

Using fossils, we can make an estimation of past population density as an ecosystem index based on food-web and energy-flow models. Late Mesozoic nonmarine deposits are distributed widely on the eastern Asian continent and contain various kinds of fossils such as fishes, amphibians, reptiles, dinosaurs, mammals, bivalves, gastropods, insects, ostracodes, conchostracans, terrestrial plants, and others. These fossil organisms are useful for late Mesozoic terrestrial ecosystem reconstruction using food-web and energy-flow models. We chose Early Cretaceous fluvio-lacustrine basins in the Choyr area, southeastern Mongolia, and the Tetori area, Japan, for these analyses and as a potential model for reconstruction of other similar basins in East Asia. The food-web models are restored based on taxa that occurred in these basins. They form four or five trophic levels in an energy pyramid consisting of rich primary producers at its base and smaller biotas higher in the food web. This is the general energy pyramid of a typical ecosystem. Concerning the population densities of vertebrate taxa in 1 km² in these basins, some differences are recognized between Early Cretaceous and the present. For example, Cretaceous estimates suggest 2.3 to 4.8 times as many herbivores and 26.0 to 105.5 times the carnivore population. These differences are useful for the evaluation of past population densities of vertebrate taxa. Such differences may also be caused by the different metabolism of different taxa. Preservation may also be a factor, and we recognize that various problems occur in past ecosystem reconstructions.

Counts of small numbers of confirmed species and estimates of maximum numbers of species present in the basin are used for the analysis and estimation of energy flow. This approach applies the methods of modern ecosystem analysis.

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Keywords: Cretaceous; East Asia; Terrestrial ecosystems; Food web; Energy flow; Population density

1. Introduction

In recent years, various modern environments and ecosystems have been studied around the world. Reconstructing past environments and ecosystems helps understand the

evolving continuum from past to present and future. Using fossils, we can estimate past population densities as an ecosystem index based on food-web and energy-flow models. This is one of the best examples showing the contribution of geology and paleontology to modern society.

Because ecosystems are significantly influenced by environmental phenomena, we can use them to study environmental variation. The term “ecosystem” is used here to denote the

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biological community together with the abiotic environment in which it is set. Both are strongly linked to each other by fluxes of energy and matter (Begon et al., 1996). Thus, it is important to understand energy flow in order to understand ecosystems.

In the Early Cretaceous Epoch, the evolution of terrestrial ecosystem is thought to have been largely controlled by continental rifting and accompanying environmental change (Obata, 1993; Barrera and Johnson, 1999). At that time, continental rifting formed the framework of the present continental distribution and the angiosperms appeared, established their niche, and expanded their distribution, influencing the whole animal kingdom. Thus, terrestrial biotas and their ecosystems and environments can be understood using energy-flow models. On the basis of analyses and reconstructions of Cretaceous and other past-terrestrial ecosystems, we can perhaps better understand present and future terrestrial ecosystems. In this respect, the Cretaceous terrestrial ecosystem analyses contribute to an understanding of history of the Earth as a dynamic, ongoing process.

There have been some previous attempts to reconstruct paleoecosystems. For example, Jacobs and Murry (1980) dealt with vertebrate communities of the Upper Triassic Chinle Formation of the southwestern United States, Anderson et al. (1997) examined Upper Triassic paleoecosystems of southern Africa, Lucas et al. (1998) discussed Cretaceous terrestrial ecosystems, and Wilde and Frankenhauser (1998) touched on the Paleogene terrestrial ecosystem in Europe. These authors only considered fauna and flora interrelationships based on fossils they sampled. Bakker (1972) tried to reconstruct Late Cretaceous dinosaur communities by inferring energy flow, to prove endothermy among dinosaurs. Farlow (1976) estimated dinosaur metabolism from present endothermic and ectothermic animals and tried to reconstruct large dinosaur communities aiming at understanding the trophic dynamics of the Upper Cretaceous Oldman Formation. Foster (2003a,b) also conducted a paleoecological study of the Morrison Formation. Although there are some problems such as biases of fossil preservation, many assumptions in reconstruction processes, and lack of detailed examination of food-web models, the methods used by these authors nevertheless suggest ways of approaching the trophic dynamics of ancient vertebrate communities. Paul (1988) estimated predatory dinosaur populations based on energy flow and used it to infer evidence of endothermic dinosaurs. These methods have various problems of procedure and influence that are probably difficult to overcome entirely (Bakker, 1972; Farlow, 1976).

Early Cretaceous nonmarine deposits are distributed widely on the eastern Asian continent and contain various kinds of fossils such as fishes, amphibians, reptiles, dinosaurs, mammals, bivalves, gastropods, insects, ostracodes, conchostracans, terrestrial plants, and trace fossils. In this area, we can fill in data for the Early Cretaceous terrestrial biota that has been lacking in other regions. In this paper, we analyze the Early Cretaceous fluvio-lacustrine systems in the Choyr basin, southeastern Mongolia, and the Tetori basin, Japan. These analyses may help reconstructions in similar basins in East Asia.

2. Characteristics of Cretaceous terrestrial basins in East Asia

Cretaceous strata are distributed across East Asia in several belts from the Asian continent to the Japanese Islands with a northeast-southwest trend (Fig. 1). From west to east, the strata are characterized principally by nonmarine, alternating nonmarine and marine, and marine deposits, which are interpreted to have accumulated in fluvio-lacustrine through shallow marine shelf to trench environments. Additionally, these Lower Cretaceous strata show an asymmetric array of sedimentary facies and represent deposition in continental, back-arc, fore-arc, and trench settings. This setting can be compared with present sedimentary basins in similar tectonic settings (Haggart et al., 2006). Cretaceous terrestrial deposits are distributed in continental, back-arc and fore-arc basins. These settings correspond to the Cretaceous stratigraphic units in the Choyr Basin succession (southeastern Mongolia), the Yanji and Jixi Groups (eastern China), the Tetori Group (Japan), and the Gyeongsang Group (Korea) and the Sanchu Cretaceous (Japan), respectively (Matsukawa, 1983; Matsukawa et al., 1993, 1997a,b, 1998, 2003b).

2.1. Choyr Basin (southeastern Mongolia)

The Choyr Basin consists of fluvial-lacustrine delta-lake systems that are middle to late Albian in age (Nichols et al., 2006). Rich dinosaur, crocodylian, turtle, small lizard, pterosaurs, fish, bivalve, insect, terrestrial plant and pollen biotas are reported from these deposits (Novodvorskaya, 1974; Shuvalov, 1974; Barsbold and Perle, 1984; Matsukawa et al., 1997b; Hicks et al., 1999; Nichols et al., 2002, 2006; Ichinnorov, 2003; Kobayashi and Barsbold, 2003; Ito and Matsukawa, 2003; Ito et al., 2006). Based on studies of the stratigraphy and paleoenvironments of the basin, these rich zoo- and phyto-assemblages occur from deposits of topsets of lacustrine deltas, fluvial channels and river-mouth bars (Matsukawa et al., 1997b; Ito et al., 2006). Vegetation at the waterside and in the hinterland plateau is reconstructed based on taphonomic analysis of megafossil plant remains and scattered pollen and spores (Okubo, 1998; Saiki and Okubo, 2006). Various well-preserved vertebrate fossils occur in topset deposits of lacustrine deltas. Thus, food-web and energy-flow models can be made from analysis of faunal species composition, diversity censuses and inferred feeding habits.

2.2. Tetori Basin (inner zone of southwest Japan)

The basin of the Tetori Group consists of fluvial-lacustrine delta-lake system deposits (Matsukawa et al., 2003a,b; Ito et al., 2006). Various kinds of fossils such as fishes, amphibians, reptiles, dinosaurs, mammal-like reptiles, mammals, bivalves, gastropods, insects, and terrestrial plants occur in the Tetori Group (Kimura et al., 1978; Manabe et al., 1989;

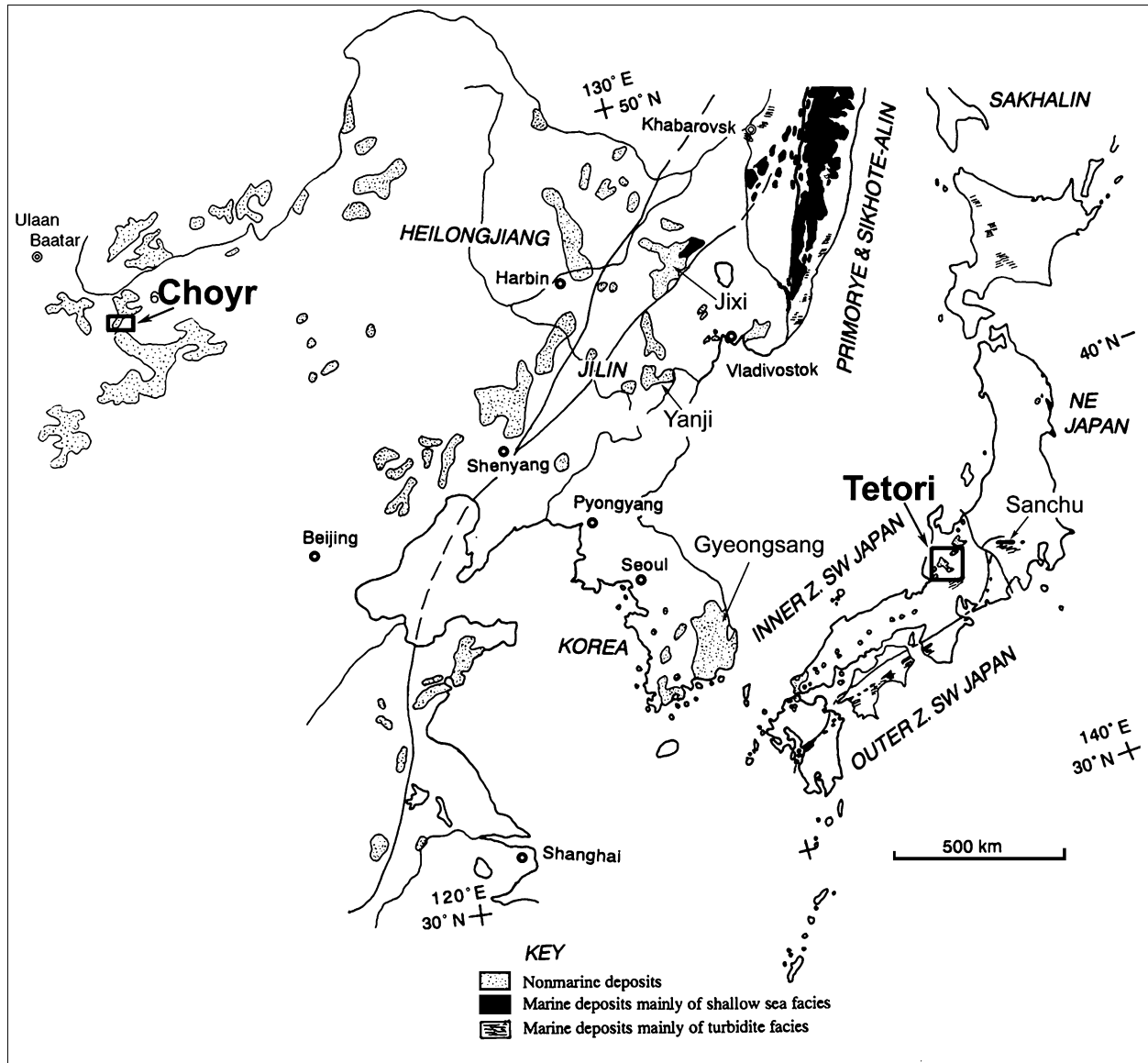


Fig. 1. Map showing the localities of two sites used the Early Cretaceous ecosystem analyses and Lower Cretaceous exposures in East Asia with three different types of facies ranging from terrestrial to deep marine through shallow marine environments.

Azuma, 1991; Matsukawa and Ido, 1993; Matsukawa and Obata, 1994; Matsukawa et al., 1997a; Hirayama, 2000; Azuma and Currie, 2000; Kobayashi and Azuma, 2003; see also papers and references in Matsuoka et al., 2000). These rich zoo- and phyto-assemblages mainly come from the Izuki Formation that correlate to the Tithonian to Berriasian, and the Kuwajima and Okurodani formations to the Valanginian to Barremian (Matsukawa et al., 2003a,b, 2006).

The phyto-assemblages of megafossil plants reflect water-side vegetation. Five assemblages of nonmarine bivalves show that these assemblages reflect certain grades of environment from brackish to freshwater, and the species composition of any assemblage varies with salinity (Matsukawa and Ido, 1993; Matsukawa and Nakada, 1999). Dinosaur ichnofossil assemblages share common ichnotaxa with the Lower

Cretaceous Yanji Group, China, and include a fluvio-lacustrine member (Matsukawa et al., 1995).

3. Process of reconstruction model of a paleoecosystem

It is necessary to know the food-web structure of a paleoecosystem in order to reconstruct it. Trophic dynamics of ecosystems consist of the flow of matter and energy. Although matter keeps recycling semi-permanently in the ecosystem, energy flow is one-way. Solar energy represents the primary input that is eventually released in the air as heat, as it leaves the trophic dynamic cycles. Therefore, energy flow can be considered a key factor of ecosystems, including the food-web structure, because of its one-way property. The food-web structure can be generally modeled using energy flow

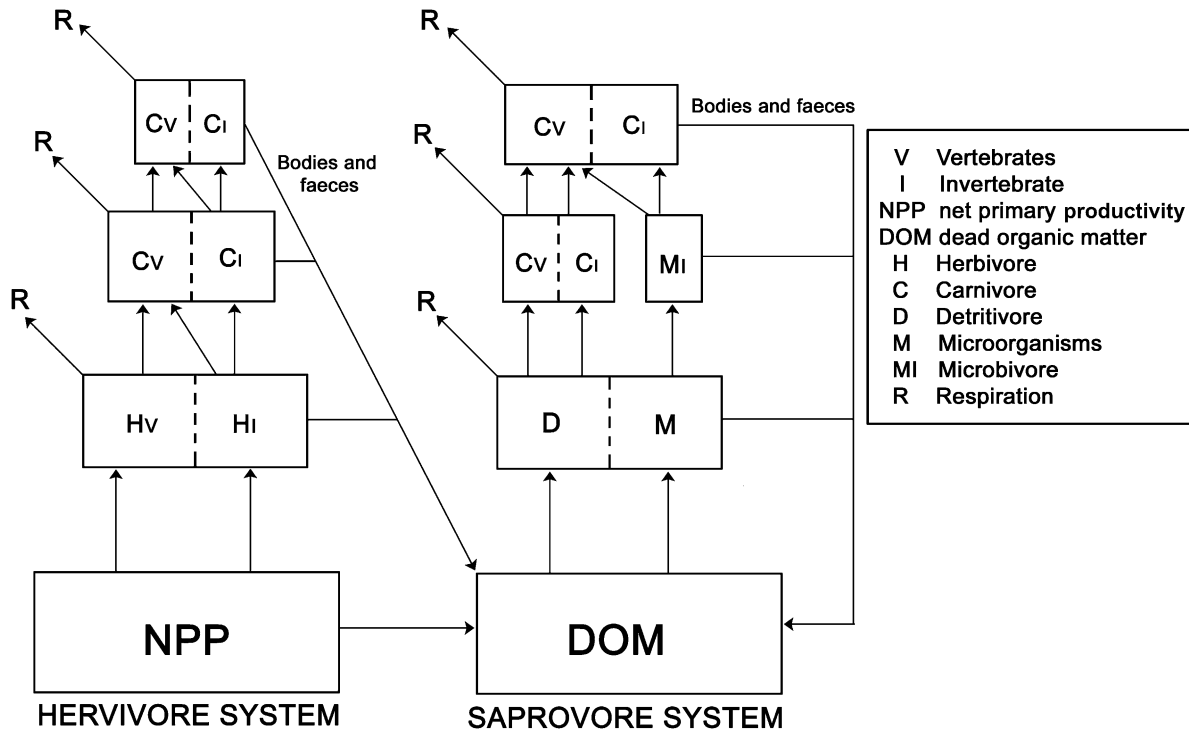


Fig. 2. A generalized model of trophic structure and energy flow for terrestrial ecosystems. Modified from Heal and MacLean (1975).

(Fig. 2). Heal and MacLean (1975) estimated secondary productivity by making an ecosystem reconstruction model that is controlled by the energy flow, and they attempted validation by comparing estimated data with confirmed data from 10 tundra, grassland, and forest ecosystems. There is good agreement in their results. Because their model is given specified values for components that control energy flow to various environments and animals, it can reduce many assumptions in ecosystem reconstruction processes. Therefore, in this paper we use an ecosystem reconstruction method that can estimate numbers of animals at each trophic level based on the Heal and MacLean model. Although their model includes the herbivore system and the saprovores system, our model takes only the herbivore system because it is very difficult to estimate the ancient saprovores system from the fossil record.

As only plants can convert the solar energy into carbohydrates that can be used by other living organisms, ecosystems are controlled by the Net Primary Productivity (NPP) of plants. Therefore, it is important to know the NPP of any ecosystem in order to reconstruct it. This is determined by the type of vegetation. The NPP estimates go to primary consumers and to higher trophic levels with three transform efficiencies: consumption efficiency, assimilation efficiency, and production efficiency (Fig. 3). These efficiencies vary by type of environment, food habits and metabolism, types of animals, trophic level, and so on. We can estimate energy quantities that flow to the next trophic level and multiply these efficiencies by NPP or by distributed energy. These energy quantities are distributed to each animal species of one trophic level according to ratios of numbers and energy intake of each species.

We estimate the NPP value and its subsequent consumption in the food web of the fossil biota and calculate the past population of each taxon based on its energy flow. The past productive and consumptive energy quantities for each species

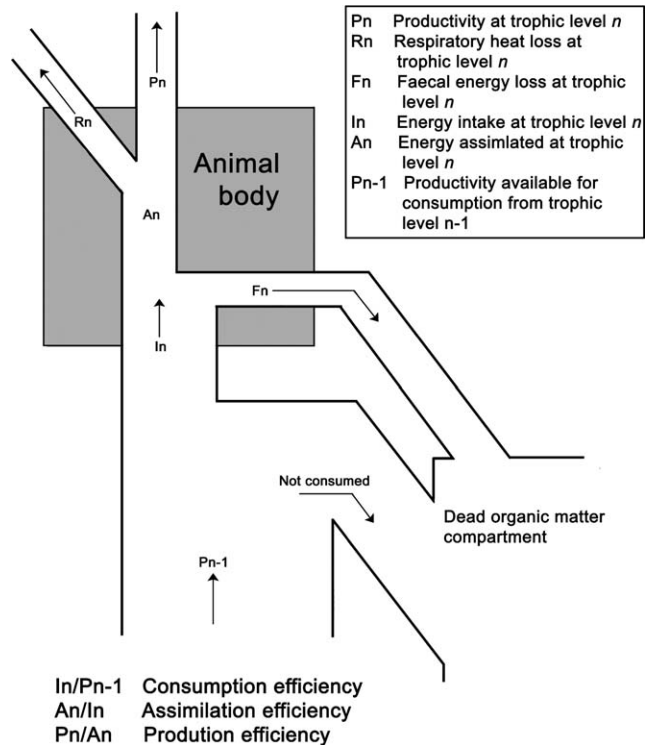


Fig. 3. An energy-flow pattern in one trophic level organism. Modified from Heal and MacLean (1975).

and each trophic level can be estimated using energy quantities that apply to extant plants, invertebrates, ectothermal and endothermal herbivores, and carnivorous vertebrates.

4. Community structure, food web, ecological pyramid, and ecosystem energy flow

4.1. Choyr Basin

4.1.1. Biota. Rich zoo- and phyto-assemblages occur in the Cretaceous Khuren Dukh and Khalzan Uul formations (Matsukawa et al., 1997b; Ito et al., 2006) (Fig. 4). Well-preserved vertebrate fossils are found from ten horizons in mud and sand beds of the Khuren Dukh Formation, 30 m in thickness, at the Khuren Dukh locality in western part of the Cretaceous Basin. Terrestrial plant fossils were found in the upper part of sandstone bed of the Khalzan Uul Formation in the southern part of the basin. Pollen and spores come from 30 horizons in the lower to upper part of the Khuren Dukh Formation.

Hitherto, some dinosaur research groups, the Soviet-Mongolia Joint Expedition (1969–1972), the joint Japan-Mongolia dinosaur project (1993–1995), the Japan-Mongolia Joint Paleontological Expedition to the Gobi Desert (1992–2000), the support team for the dinosaur excavation from the

Nakasato Dinosaur Center (1995–2000), and the Dinosaur Track Project in Mongolia (1999–2001), excavated many dinosaur remains including skeletons, teeth, and footprints from this Cretaceous basin. Although they are almost fragments, the occurrence of whole skeletons is also reported. They are housed at the laboratory in Ulan Bator. Their classification and systematic studies have been advanced by Barsbold and Perle (1984), Kobayashi and Barsbold (2003), but systematic studies are not yet completed. We collected 441 fragments of bones, teeth, shells, and fish scales at Khuren Dukh in 2000. Although fishes, turtles, and pterosaurs can be highly ranked occurrences among them, it is difficult to count their individuals from fish scales, ramified bones, and teeth. Based on articulated specimens and possible countable individuals, we list taxa and individuals (Tables 1, 2). Six dinosaur species, one champsosaur, one crocodile, one pterosaur, one turtle, several small lizard and fish species, four molluscan species, one insect species, six ostracode species, and one conchostracan have been recorded (Table 1). Among the vertebrates, the following individuals as articulated specimens could be counted: 16 dinosaurs, 4 champsosaurs, 1 crocodile, 2 pterosaurs, 10 turtles, 1 small lizard, and 80 fishes (Table 2). We show the census as an occurrence ratio of individuals in three habitats: aquatic, terrestrial, and aerial. The aquatic habitat group yields 95 individuals including

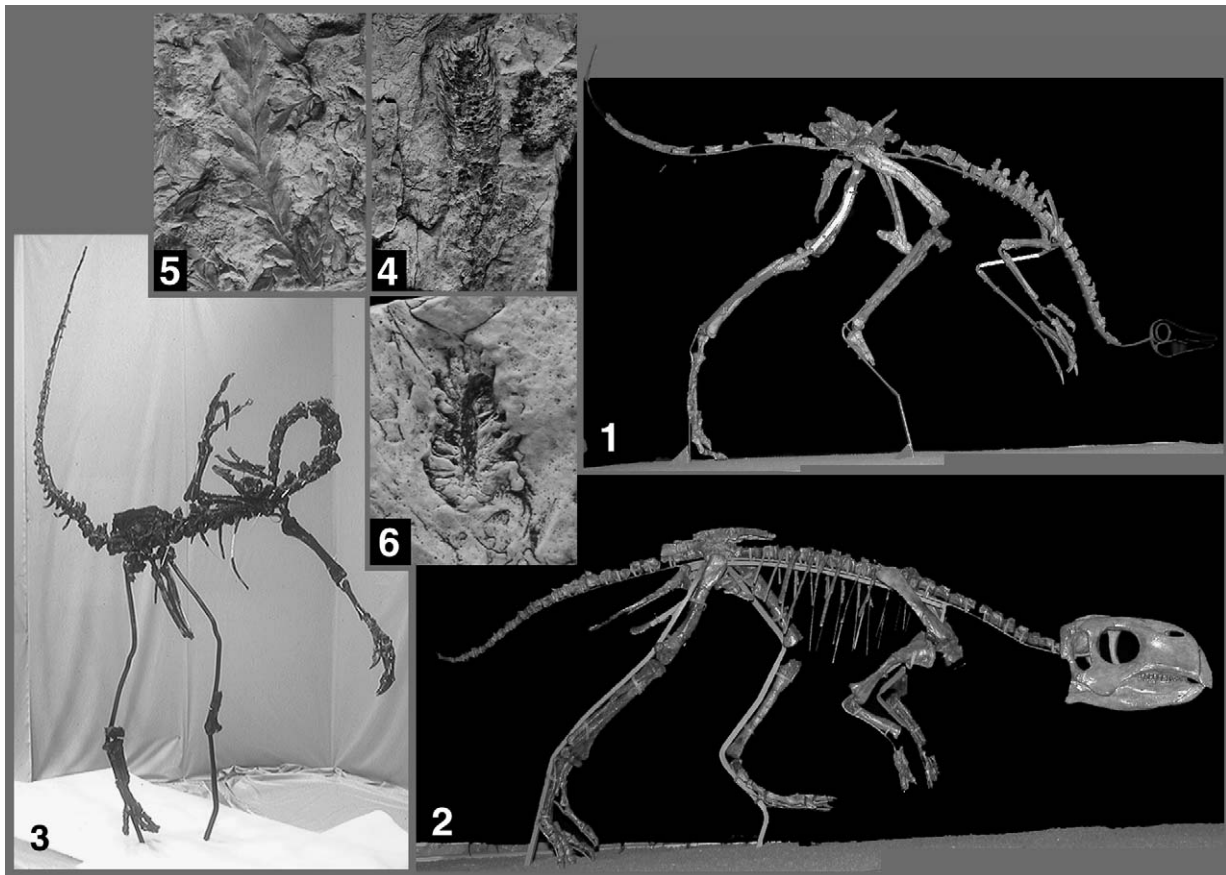


Fig. 4. Main vertebrate and plant fossils from the Lower Cretaceous deposits in the Choyr Basin, Mongolia. 1, *Ornithomimosauria* gen. et sp. indet. 2, *Psittacosaurus mongoliensis*. 3, *Harpyimimus okladnikovi*. 4, *Lycopodites* sp. A. 5, *Coniopteris burejensis* (Zalessky) Seward. 6, *Conites* sp. A.

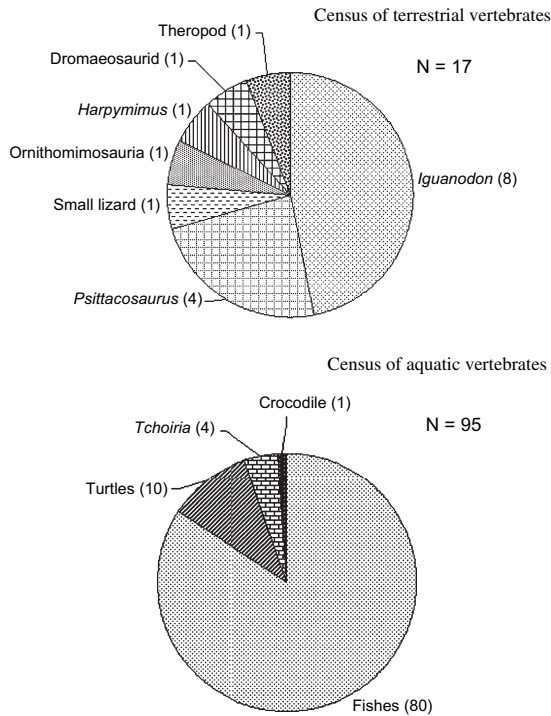


Fig. 5. Early Cretaceous vertebrate census of the Choyr Basin, Mongolia, based on taxa occurrences.

Kitazawa (1969, 1977) produced a food-web model for the main species in the Mt. Shigayama area, Nagano Prefecture, Japan, based on analysis of population data, productive structure of the community, and their connection with the environment. This ecosystem is typical modern deciduous broad-leaved forests in the Temperate Zone of Japan. The model includes photosynthetic plants as producers, and consumer trophic levels and soil decomposers. Based on Kitazawa (1969, 1977), we can infer trophic levels in food webs by using food habits of the main zoo-species in a paleoecosystem. Food habits of fossil species in the zoo-assemblage of the Choyr Basin are inferred from their allied living species. There are two energy-flow models: (1) the ratio of divided energy can be equally divided into all individuals on the same trophic level (this model is called the equality model); (2) the ratio of energy is not equally divided because zoo-species as consumers have a differential intake (Fig. 6). Here we use the equality model for simplicity, although Foster (2003a,b) showed relative abundances in carnivores to be reflected to some degree based on *Allosaurus* in the Morrison Formation paleoecosystem. In the equality model, the ratios of distributed energy are calculated from the required energy for an individual per day and the number of individuals. For example, we assume that there are some taxa that consume the same food resource (the number of taxa is n). The ratio of distributed energy for j th taxon R_j is estimated as follows:

$$R_j = \frac{a_j N_j}{\sum_{i=1}^n a_i N_i} \quad (1)$$

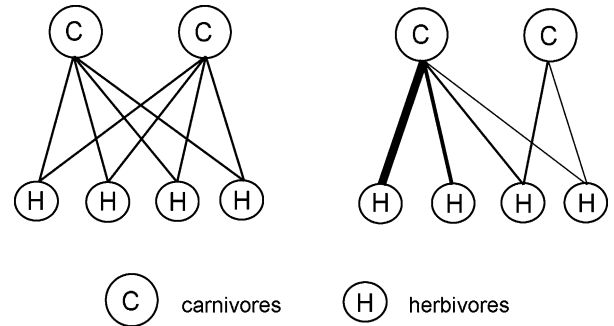


Fig. 6. Relation between carnivores and herbivores. Broader lines show stronger relationship than narrower lines. Left, equality model. Right, selection model.

where a_i is required energy for an individual per day and N_i is the number of individuals of i th taxon.

The equality model is based on the occurrence of individual numbers, which assumes no differential bias in fossil preservation. The equality model is not applicable if differential bias exists. If similar energy patterns had been studied in the present ecosystem, we could use the patterns to model the paleoecosystem. However, the examples of such studies are few. In such a case, all we can do is to infer working ratios and accept that they are uncertain.

However, small lizards (about 1 kg) could not prey on *Iguanodon orientalis* (901 kg). Thus, we infer that small carnivorous animals did not prey on large herbivores, because there is such a great weight differential between prey and predator. To be sure, scavengers consume carcasses that died for some reason, and *Iguanodon* young might have been taken by small theropods and crocodiles, etc.

Table 3 shows the inferred food habits of zoo-species in the Cretaceous Choyr Basin. We follow Kobayashi et al. (1999) in interpreting that *Harpymimus okladnikovi* and *Ornithomimosauria* gen. et sp. indet. had herbivorous food habits, although omnivorous or carnivorous interpretations were also proposed (Osmolska et al., 1972; Russell, 1972; Ostom et al., 1993). Wellnhofer (1991) inferred that pterosaurs took fish and that *Dsungaripterus weii* ate bivalves, gastropods, and crabs. Based on zoo- and phyto-fossil species and their presumed eating habits, the food web and trophic levels for Choyr Basin deposits are modeled (Fig. 7).

4.1.3. Ecological pyramid and energy-flow models. The relationship between food web, body size, and metabolism reveals ecosystem trophic levels (Odum, 1983). An ecological pyramid is made by accumulating biomass in successively higher trophic levels.

To quantify possible energy and population size for zoo-species and vegetation type, we have to assume the size of the area for reconstruction of the ecosystem. One method of establishing area size is to calculate that of the exposed strata or sedimentary basins. However, living-animal communities have certain areas of activity. For example, Serengeti National Park in Tanzania covers an area of 25,000 km² framing one ecosystem (Kruuk, 1972; McNaughton, 1985).

Table 3
List of Lower Cretaceous fossil organisms from the Choyr Basin and their presumed food sources

Taxa	Species	Presumed food	Feeding habit
Fishes	Osteichthyes gen. et sp. indet.	plankton, organic matter, plants, fishes	omnivore
Turtles	<i>Hangaemys hoburensis</i>	fishes and others	omnivore
Champsosaurs	<i>Tchoiria nomsarai</i>	fishes and others	carnivore
Crocodyles	Gen. indet.	fishes, turtles, and others	carnivore
Dinosaurs	Dromaeosaurid gen. et sp. indet.	small lizards, small dinosaurs, and herbivore dinosaurs	carnivore
	Theropod gen. et sp. indet.	small lizards, small dinosaurs, and herbivore dinosaurs	carnivore
	<i>Harpyimimus okladnikovii</i>	plants	herbivore
	Ornithomimosauria gen. et sp. indet.	plants	herbivore
	<i>Iguanodon orientalis</i>	plants	herbivore
	<i>Psittacosaurus mongoliensis</i>	plants	herbivore
Pterosaurs	<i>Dsungaripterus</i> sp.	clams and fishes	carnivore
Small lizards	Gen. indet.	insects	carnivore
Mollusks	<i>Unio heilongjiangensis</i>	detritus and plankton	detritus feeder
	<i>Sphaerium</i> (S.) <i>yanbianense</i>	detritus and plankton	detritus feeder
	gastropods gen. et sp. indet.	detritus and small animals	carnivore
Insects	dragonfly gen. et sp. indet.	ostracodes and others	carnivore
Ostracodes	<i>Darwinula ovata</i>	decomposing meat of fishes and turtles, plankton, etc.	scavenger
	<i>Cypridea zagustaica</i>	decomposing meat of fishes and turtles, plankton, etc.	scavenger
	<i>C. spinigera</i>	decomposing meat of fishes and turtles, plankton, etc.	scavenger
	<i>C. kosculensis</i>	decomposing meat of fishes and turtles, plankton, etc.	scavenger
	<i>C. grandicula</i>	decomposing meat of fishes and turtles, plankton, etc.	scavenger
	<i>Lycopteroocypris intantilis</i>	decomposing meat of fishes and turtles, plankton, etc.	scavenger
Conchostracans	Conchostracan gen. et sp. indet.	decomposing meat of fishes and turtles, plankton, etc.	scavenger

The Cretaceous area of the Choyr Basin is 512 km² (i.e., 16 km in width, east to west, and 32 km in length, south and north) (Matsukawa et al., 1997b). For comparison purposes, we use 100 times the Cretaceous exposures for our ecosystem area reconstruction. Thus, we calculate an area of 51.2×10^9 m². This is almost twice the size of the Serengeti National Park in Tanzania, but the estimate represents the nearest order of magnitude calculated from the actual figures.

Net primary productivity. The Net Primary Productivity (NPP) represents the actual rate of production of new biomass by plants. The NPP was inferred in each present ecosystem type (Whittaker, 1975) and the values can be applied to the reconstruction of paleoecosystems. The NPP is usually expressed in units of dry organic matter per unit area and time (e.g. g/m²/year). We can estimate total actual rate of production in the assumed area by multiplying NPP and the area size. To express values in units of energy, energy per dry organic matter of plants can be used (Whittaker, 1975).

In the Cretaceous Choyr Basin, ferns make up the waterside vegetation in fluvio-lacustrine habitats and those of the surrounding plain (Saiki and Okubo, 2006). Although fern savanna is not common in the modern vegetation, *Pteridium aquilinum*-type fern meadow occurs in Japan. The standing crop of *Pteridium aquilinum*-type fern meadow is measured as 883 g/m² for the aboveground part and 1185 g/m² for the underground part (Shimada, 1968). These values are almost same as those of monocot grassland of the same area. In the *Miscanthus sinensis*-type grassland of this area, the standing crop is measured as about 709 g/m² for the aboveground part and 1126 g/m² for the underground part (Shimada et al.,

1968). The ecology of *Pteridium aquilinum* is similar to *Miscanthus sinensis* in its perennial nature, presence of rhizomes, and in dying down of aboveground parts during the winter. These ecological similarities and similar values of standing crops of two types of meadow lead us to conclude that the NPP of the *Pteridium*-type fern meadow is almost same as that of *Miscanthus*-type grassland. Because no other information available for the productivity of fern meadows, we apply this information to estimate the NPP of the vegetation of Choyr Basin. Namely, the NPP of the vegetation of Choyr Basin can be compared with those of living temperate grasslands estimated at 600 g/m²/year (Whittaker, 1975). Thus energy intake of herbivore vertebrates in the meadow of Choyr Basin can be estimate as 150 g/m²/year. Although the presence of conifer forest in the highlands around the Choyr Basin is estimated (Saiki and Okubo, 2006), we focused only on meadow ecosystem for taphonomic reasons.

Unfortunately, we have almost no information about the fauna of the highlands around the Choyr Basin. As discussed above, the NPP of the vegetation of Choyr Basin can be compared with those of living temperate grasslands estimated at 600 g/m²/year (Whittaker, 1975). Thus, the NPP of the assumed area is calculated at 30.72×10^{12} g/year by multiplying 600 g/m²/year times the size of the area. This gives an estimate of consumers for the Cretaceous Choyr ecosystem. As the energy content of plant dry matter is 17.79 kJ/g (Odum, 1983), the NPP of the Cretaceous Choyr ecosystem is calculated as 546.63×10^{12} kJ/year by multiplying 17.79 kJ/g times 30.72×10^{12} g/year.

Three transform efficiencies in energy-flow systems. Three transform efficiencies' Consumption Efficiency (CE),

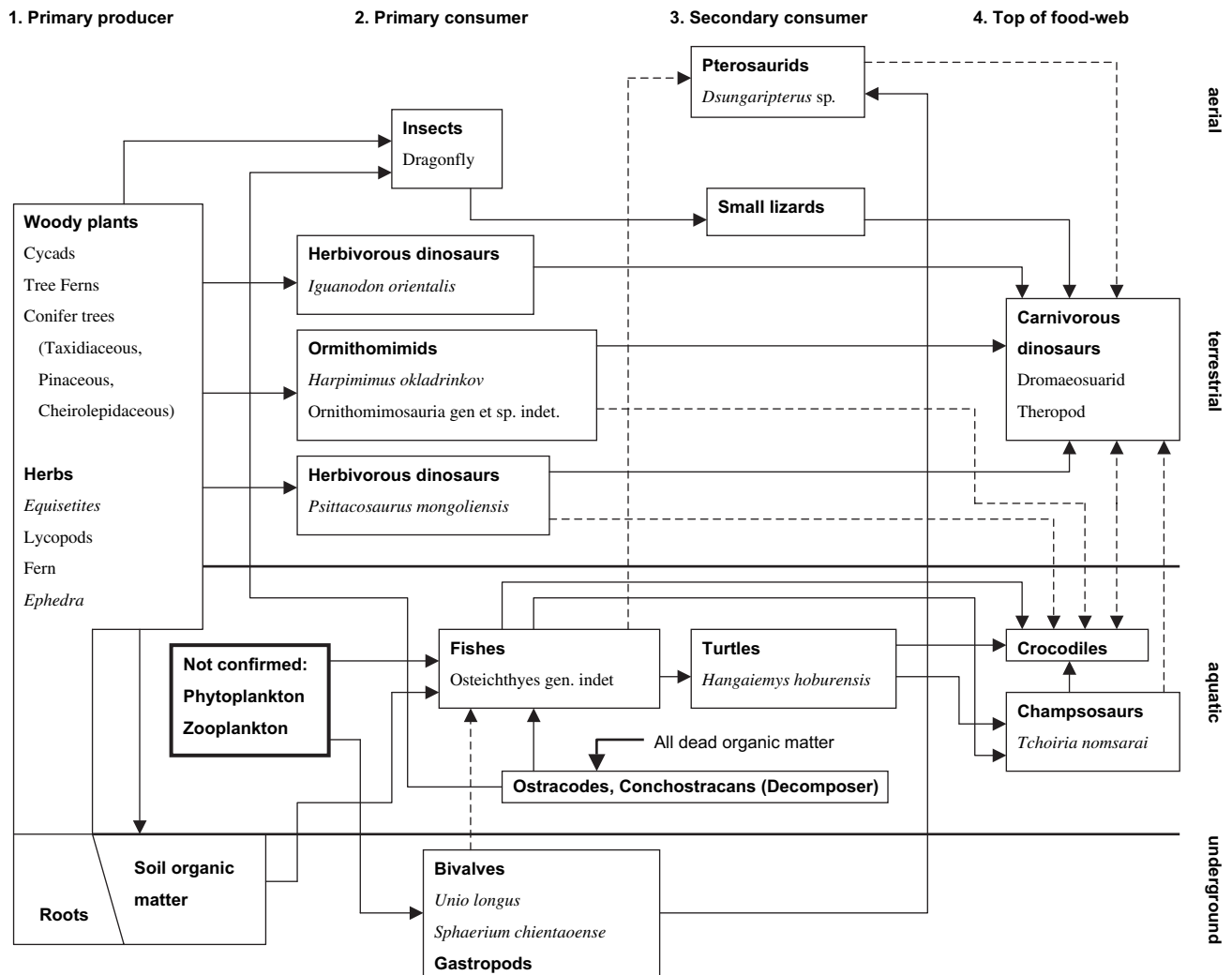


Fig. 7. Early Cretaceous food-web model of the Choyr ecosystem, Mongolia, based on occurrences of taxa.

Assimilation Efficiency (AE), and Production Efficiency (PE), are used in NPP estimates.

Consumption Efficiency (CE), $CE = (I_n/P_n - 1) \times 100$. The consumption efficiency is the percentage of total productivity available at one trophic level ($P_n - 1$) that is actually consumed (ingested) by a trophic compartment one level up (I_n) (Begon et al., 1996). The first consumers in the Cretaceous Choyr ecosystem consists of insects and the herbivorous dinosaurs *Iguanodon orientalis*, *Psittacosaurus mongoliensis*, *Ornithomimosauria* gen. et sp. indet., and *Harpymimus okladnikovi*. Heal and MacLean (1975) estimated CE of invertebrate herbivores as less than 5%, and of vertebrate herbivores as 25% in grasslands. Although Weigert and Evans (1967) estimated vertebrate herbivore efficiencies as 50%, and Golley (1960) evaluated herbivorous insects at 10 to 20% and herbivorous rodents as 2% in grasslands, they did not give estimates for plants above the land surface or other herbivorous mammals. Thus, we use the CE of Heal and MacLean (1975). Therefore, insect intake from plants can be calculated 2.733×10^{13} kJ/year by multiplying 546.63×10^{12} kJ/year (the NPP of the Cretaceous Choyr ecosystem) times 5% CE. Intake of herbivorous dinosaurs *Iguanodon orientalis*,

Psittacosaurus mongoliensis, *Ornithomimosauria* gen. et sp. indet., and *Harpymimus okladnikovi* can be calculated as 13.67×10^{13} kJ/year. This distributes each species by individual numbers based on fossil occurrences and required energy per year for an individual animal.

Assimilation Efficiency (AE), $AE = (A_n/I_n) \times 100$. Assimilation efficiency is the percentage of food energy taken into the guts of consumers in a trophic compartment (I_n) that is assimilated across the gut wall (A_n) and becomes available for incorporation into growth or is used to do work (Begon et al., 1996). Begon et al. (1996) estimated AE of invertebrate herbivores as 40%, and vertebrate herbivores as 50%, and carnivores as 80%. Thus, 40% of insect intake from the NPP of the Cretaceous Choyr ecosystem, 50% of the herbivorous dinosaur intake (*Iguanodon orientalis*, *Psittacosaurus mongoliensis*, *Ornithomimosauria* gen. et sp., indet. and *Harpymimus okladnikovi*) and 80% of the carnivorous dinosaur intake (*Dromaeosauridae* gen. et sp. indet. and *Theropoda* gen. et sp. indet.) is used to estimate growth, and activities.

Production Efficiency (PE), $PE = (P_n/A_n) \times 100$. Production efficiency is the percentage of assimilation energy (A_n) that is incorporated into new biomass (P_n) (Begon

et al., 1996). Begon et al. (1996) estimated PE as 40% for invertebrate herbivores, as 30% for invertebrate carnivores, as 10% for ectothermal vertebrates, and as 2% for endothermic vertebrates. In the Cretaceous Choyr ecosystem, productivity (kJ/year) of herbivore insects is calculated as 40% assimilation energy of insects. Productivity (kJ/year) of herbivorous the dinosaurs *Iguanodon orientalis* and *Psittacosaurus mongoliensis* is calculated as 10% assimilation energy of them.

Required energy per year of an individual animal. Farlow (1976, 1990) devised formulas for energy intake of endothermic herbivores, endothermic carnivores, ectothermic herbivores, and ectothermic carnivores based on data that are taken from the literature on caged and free-living animals and applied them to dinosaurs. However, dinosaurs are not necessarily represented in these four categories. Thus, if dinosaurs are included in another new category of metabolic rates, Farlow's formulas cannot be applied to them.

Energy intake is controlled by not only by metabolic types but also by activity levels. Therefore, we devised new formulas that can be varied according to characteristics of animals by including the variable that reflects the activity level of animals. They enable us to estimate the energy intake of various animals more specifically in reference to the type.

It is necessary to know metabolic types and rates to estimate number of animals. The Standard Metabolic Rate (SMR) is the metabolic rate of inactive animals and is defined by the minimum level of oxygen consumption required to sustain life at a standard temperature and pressure. The SMR of mammals can be calculated by the formula:

$$\text{SMR (kJ/day)} = 293.01 \times \text{weight (kg)}^{0.75} \quad (2)$$

This formula is effective for all mammals from small mice to big elephants (Fowler, 1978). The SMR formula of birds except for Passeriformes is:

$$\text{SMR (kJ/day)} = 327.83 \times W^{0.723} \quad (3)$$

and for Passeriformes is:

$$\text{SMR (kJ/day)} = 540.01 \times W^{0.724} \quad (4)$$

The SMR of reptiles is 10–20% that of mammals that are of the same size and body temperature (Fowler, 1978). When animals become active, their metabolic rate will increase. This addition to the SMR is called the Activity Metabolic Rate (AMR). The AMR can be twice or three times SMR. These doublings or triplings give us activity level variables. In this paper, we assume that the SMR of ectotherms is set at 15% of mammals (Fowler, 1978), and the AMR is twice SMR on average for mammals. As animals cannot assimilate all consumed energy, to calculate energy intake AMR should be multiplied by the reciprocal of Assimilation Efficiency (AE), making allowances for loss. Heal and MacLean (1975) showed that the assimilation efficiencies of endothermic herbivorous and ectothermic carnivorous are 50% and 80%, respectively.

Naggy et al. (1999) and Naggy (2001) also devised formulas for food intake rates based on field metabolic rates of wild terrestrial small vertebrates. The concept of metabolic rates of inactive animals for estimation of energy intake is not included in their formulas, however. This means we cannot have intermediate models for dinosaurs between endothermic and ectothermic animals. Therefore, their equations are formulized on the basis of small vertebrates (less than 100 kg). This suggests that their formulas are inapplicable large animals like elephants. Fowler (1978)'s formulas are applicable small to large animals including mouse to elephant sizes.

In the Choyr Basin, Ornithomimosauria gen. et sp. indet., *Harpymimus okladnikovi*, Dromaeosauridae gen. et sp. indet., and Theropoda gen. et sp. indet. can have Eq. (3) applied, because dromaeosaurids and so-called gracile dinosaurs are allied to birds (Ostrom, 1973, 1980). For *Iguanodon orientalis*, *Psittacosaurus mongoliensis* and small lizards, the SMR of reptiles is applied, because these herbivorous dinosaurs are considered as ectothermic reptiles.

It is necessary to know weights and diets of dinosaurs for calculating dinosaur energy intake. There are two types of methods for estimating weights of dinosaurs. The first method is using volumes of scale models of dinosaurs (Colbert, 1962; Alexander, 1985). The second method is using circumferences of limb bones (Anderson et al., 1985). Because there are model maker biases in using scale models, the second method can be considered reliable. We estimated 12.2 kg for a specimen of *Psittacosaurus mongoliensis* from the Cretaceous Choyr Basin. In regard to the taxa whose specimens we could not measure, we inferred the compatible weight with the body size based on the literature (e.g., Lambert, 1983; Norman, 1985) (Table 4).

Energy intake (kJ/day) per day can be calculated from Standard Metabolic Rate (SMR), Activity Metabolic Rate (AMR), and Assimilation Efficiency (AE) (Begon et al., 1996). Thus, we can use the following formula for each type of animal:

Herbivorous dinosaurs:

$$I = 293.01 \times W^{0.75} \times 0.15 \times 2 \times (1/0.5) \quad (5)$$

Carnivorous dinosaurs:

$$I = 327.83 \times W^{0.723} \times 2 \times (1/0.8) \quad (6)$$

Lizards:

$$I = 293.01 \times W^{0.75} \times 0.15 \times 2 \times (1/0.8) \quad (7)$$

in which I = energy intake (kJ/day) and W = weight (kg).

Table 4 shows energy intake per day and year for each species in the Cretaceous Choyr ecosystem.

A previous study to estimate energy intake for dinosaurs (Farlow, 1976, 1990) showed the empirical relationship between weight and daily energy intake based on modern living animals and applied it to dinosaurs. He used a formula for endothermic or ectothermic dinosaurs. Our estimates are almost the same as the results obtained using Farlow's formula. Reid

Table 4

Estimated weight, occurrence of individuals, basal metabolism, required energy per day, and total required energy per year of vertebrate taxa in the Early Cretaceous Choyr ecosystem

Taxa	Estimated weight (adult, kg)	Occurrence of individuals	Basal metabolism (kJ/day)	Required energy per day for an individual (kJ/day)	Required energy per year for an individual (kJ/year)
<i>Iguanodon orientalis</i>	901.00	8	7229.61	28,918.42	10,555,223.39
<i>Psittacosaurus mongoliensis</i>	12.20	4	286.97	1147.89	418,980.40
Ornithomimosauria gen. et sp. indet.	25.10	1	3369.83	8424.57	3,074,966.70
<i>Harpymimus okladnikovii</i>	139.60	1	11,651.87	29,129.67	10,632,330.64
Small lizards	5.00	1	146.99	367.48	134,131.68
Dromaeosaurid gen. et sp. indet.	30.00	1	3833.56	9583.90	3,498,122.25
Theropod gen. et sp. indet.	30.00	1	3833.56	9583.90	3,498,122.25
Insects	0.01	2		0.50	182.50

(1997) suggested that dinosaurs had more efficient circulation than any modern reptile possesses because of thermodynamics and fast growth to large size. He also inferred dinosaur aerobic activity on the grounds of the evidence of air sacs in saurischians. Reid’s dinosaur image reveals animals that have low SMR close to ectotherms and higher activity levels close to endotherms. Though it cannot be proved conclusively, we think it is reasonable, given current evidence. Therefore, we use the term “ectothermic dinosaurs” for dinosaurs whose SMR are at an ectothermic level but whose activity level is the same as endotherms. This means we do not use Farlow’s formula, because dinosaurs may have had intermediate metabolic systems (Reid, 1997). However, the formula by Fowler (1978) has an advantage of estimating intermediate animal metabolisms using easily changeable coefficients in the formulas.

Required energy per year for each species. Intake energy for vertebrate herbivores as primary consumers in the Cretaceous Choyr ecosystem can be calculated from the Net Primary Productivity (NPP) multiplied by the Consumption Efficiency (CE), 0.25. Thus, the Primary Consumption is estimated at 13.67×10^{13} kJ/year. This value is distributed between each species according to the ratio of each species’ intake. For example, the ratio of *Iguanodon orientalis* is 0.846, which is calculated from the required energy per year for an individual *I. orientalis* times the number of individuals, divided into the total amount of other species. Thus, *Iguanodon orientalis* requires 11.56×10^{13} kJ/year. This is also used for carnivorous dinosaurs at higher trophic levels in the food-web model. The energy for carnivorous dinosaurs can

be calculated from productivity of *I. orientalis* by multiplying the CE of carnivorous dinosaurs, 0.75. The productivity of *I. orientalis* is calculated from 11.56×10^{13} kJ/year multiplied by the assimilation efficiency (0.50) and production efficiency (0.10) of *I. orientalis*.

Intake energy of insects as primary consumers can be calculated at 2.733×10^{13} kJ/year by using the NPP multiplied by the CE (0.05). Then, the productivity of insects is calculated from 2.733×10^{13} multiplied by the AE (0.40) and the PE (0.40) of insects. This is based on small lizard consumers from higher trophic levels in the food-web model. By similar calculations, we can use estimated intake energy for each species, and can understand energy flow in the ecosystem. Hence, biomass and individual flows for the Cretaceous Choyr ecosystem can be estimated as an ecological pyramid (Fig. 8).

Estimation of individual numbers of vertebrates at the Cretaceous Choyr ecosystem. Based on the food-web model, productivity of plants and animals at various trophic levels and intake energy of animals, we can estimate individual numbers of animals in the Cretaceous Choyr ecosystem.

Estimated individual numbers of *Iguanodon orientalis* in the ecosystem can be calculated by dividing energy intake per year into intake energy of one individual of *Iguanodon orientalis*. Table 5 shows estimated individual numbers of seven species in the ecosystem. Individual numbers of each species are estimated as follows: *Iguanodon orientalis* is 10,951,724; *Psittacosaurus mongoliensis* is 5,475,862; Ornithomimosauria gen. et sp. indet. and *Harpymimus okladnikovii* are 1,368,965 each; small lizards are 5,450,647; and Dromaeosauridae gen.

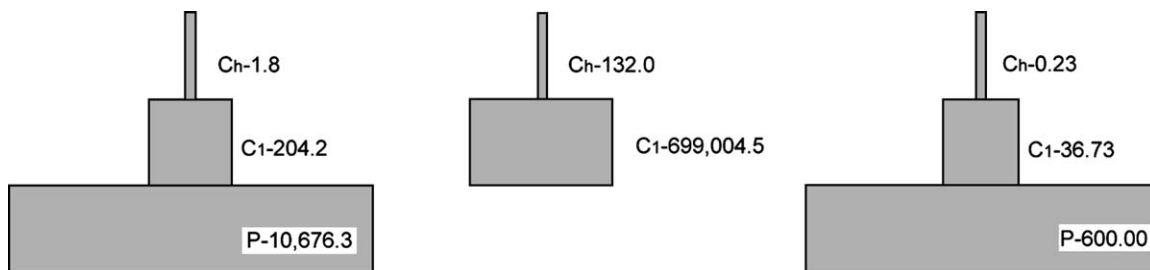


Fig. 8. Early Cretaceous energy pyramids of the Choyr ecosystem, Mongolia. Left, energy flows are given in kJ/square meter/year. Center, energy flows are given in population numbers in a square km of consumers on the food web. Right, flows are given in dry weight grams in a square m of consumers up the food web. P, primary producer, C₁, primary consumer, C_n, high-order consumer.

Table 5
Estimated individual numbers, head count ratio based on eight head of *Iguanodon orientalis*, occurrence of individual numbers and population density of vertebrate taxa in 1 km² in the Early Cretaceous Choyr ecosystem, Mongolia

Taxa	Estimated number of individuals	Head count ratio based on 8 head of <i>Iguanodon</i>	Occurrence of individuals	Population density of vertebrate taxa per 1 km ²
<i>Iguanodon orientalis</i>	10,951,724	8.0	8	213.9
<i>Psittacosaurus mongoliensis</i>	5,475,862	4.0	4	107.0
Ornithomimosauria gen. et sp. indet.	1,368,965	1.0	1	26.7
<i>Harpymimus okladnikovii</i>	1,368,965	1.0	1	26.7
Small lizards	1,630,124	1.2	1	31.8
Dromaeosaurid gen. et sp. indet.	653,896	0.5	1	12.8
Theropod gen. et sp. indet.	653,896	0.5	1	12.8
Total	22,103,433			

Area of activity: 51,200 km² is extrapolated from 100 times the area of the sedimentary basin (32 × 16 km).

Estimated individual numbers = required energy in year/intake of an individual animal.

Head count ratio = (Estimated individual numbers × 8)/estimated numbers of individuals of *Iguanodon*.

et sp. indet. and Theropoda gen. et sp. indet. are 653,896 each. The population density per 1 km² of these species are calculated as follows: *Iguanodon orientalis* is 213.9, *Psittacosaurus mongoliensis* is 107.0, Ornithomimosauria gen. et sp. indet. and *Harpymimus okladnikovii* 26.7 are each, small lizards is 106.5, and Dromaeosauridae gen. et sp. indet. and Theropoda gen. et sp. indet. are 12.8 each. These individual numbers derive from head-count ratios based on eight head of *Iguanodon orientalis*, four of *Psittacosaurus mongoliensis*, one each of Ornithomimosauria gen. et sp. indet. and *Harpymimus okladnikovii*, 4.0 for small lizards, and 0.5 each for Dromaeosauridae gen. et sp. indet. and Theropoda gen. et sp. indet. Although the size-biasing against small species is probably presumed, the estimated individual numbers of *Iguanodon orientalis* and small lizards are not influenced by this biasing. The sequence of calculation is started from the NPP.

These individual numbers reveal a predator to prey ratio of 5% carnivore to 95% herbivore (Fig. 9). This can be transferred to a predator/prey weight ratio of 0.4% (total weights of predator and prey are 38,121,269 kg and 10,167,927,670 kg each). This concurs with less than 1% of predator/prey weight ratios of Cretaceous desert system in Mongolia (Bakker, 1986). Bakker (1972, 1974, 1980) claimed that ectothermic predators eat only a seventh to a tenth as much as endothermic predators of similar sizes, and thought that the

metabolic rates of extinct animals can be measured by predator/prey biomass. He surveyed a wide array of fossil communities and compared predator/prey biomass ratios of modern mammals, fossil mammals, dinosaurs, thecodonts, therapsids, and early reptiles (Bakker, 1980, fig. 27). His data showed that ratios for dinosaurs clustered around a scant 5%, much the same as fossil mammals, but different when compared with ratios of about 25–65% for early reptiles. He also showed that ectothermic spider-insect communities have predator/prey ratios of 40% or more and concluded that dinosaurs are endothermic. In our analysis using the Standard Metabolic Rate (SMR) for each species, Dromaeosauridae gen. et sp. indet. and Theropoda gen. et sp. indet. are treated as endothermic, and *Iguanodon orientalis*, *Psittacosaurus mongoliensis*, and small lizards as ectothermic herbivorous. Thus, individual numbers of each species can be estimated. As the SMR of ectothermic animals is greater than endothermic animals, estimates of individual numbers of herbivorous *Iguanodon orientalis* and *Psittacosaurus mongoliensis* decrease under the ectotherm model. This means predator/prey weight ratios also diminish. On the other hand, if we look at endothermic animals from the Cretaceous Choyr ecosystem, predator/prey weight ratio is 0.4%. This is less than 4% estimated by Bakker (1986). Therefore, we cannot infer dinosaur metabolism as either endothermic or ectothermic, based on predator/prey weight ratios. This supports Farlow's (1990) discussion of dinosaur metabolism based on predator/prey ratio by Bakker (1980).

4.2. Tetori Basin (inner zone of southwest Japan)

4.2.1. Biota. Rich phyto- and zoo-assemblages are known from the Kuwajima, Okurodani, and Izuki formations of the Tetori Group (Matsukawa et al., 2003a,b, 2006). Many specimens belonging to vertebrate, invertebrate, and terrestrial plant species are reported from the fluvio-lacustrine Kuwajima Formation at Kaseki-kabe (Fossil bluff) in Shiramine Village, Ishikawa Prefecture (Matsuoka et al., 2000). These fossils occur in three different types of lithology, and three distinct vertebrate assemblages can be

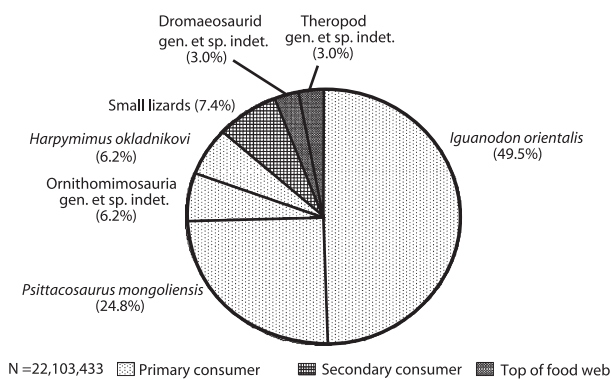


Fig. 9. Early Cretaceous vertebrate census of the Choyr ecosystem, Mongolia, based on estimated individual numbers.

identified. Although these assemblages show allochthonous-thanatocoenosis occurrences, the fossil species contained in all three lithotypes represent floodplain environments (Isaji, 2000).

Hitherto, over 1277 specimens including vertebrate bones, teeth, scales, and footprints have been reported from the Kaseki-kabe (Fossil bluff); see catalog of Matsuoka et al. (2000). They include fishes, amphibians, reptiles, mammal-like reptiles, birds, pterosaur, dinosaurs and mammals. For example, six teeth identified as the Family Iguanodontidae occur from the same horizon, suggesting up to 33 individual animals. One multituberculate lower jaw and tooth and another tooth from the same horizon suggest one or two individual animals. By similar methods, we estimated individuals for all fossil species from Kaseki-kabe (Fossil bluff). Table 6 shows the estimated maximum individual numbers (423) belonging to 21 species. The numbers are ten less than the estimation of Isaji (2000).

Ferns, bennettitaleans, ginkgoes, cycads including *Nilssonia*, and broad-leaved conifers occur at Kaseki-kabe (Fossil bluff)

(Kimura et al., 1978; Matsuo and Sekido, 2000). All of these plants are believed to be mesophytic, and no xerophytic plants like cheirolepidiaceus conifers or ephedrales have been described from the Tetori area. The floral composition of the Tetori area is very similar to that of the Siberian type flora. The paleoclimate of the Siberian paleofloristic area was inferred as moderately warm and humid for the following reasons (Vakhrameev, 1971): (1) intercalation of rich coal layers; (2) wide distribution of pycnoxylic wood remains with well-developed annual rings; (3) no manoxylic wood remains or arborescent ferns; and (4) abundant occurrence of deciduous ginkgoalean and *Podozamites* leaves, which would fall in a certain season similar to living *Ginkgo* leaves. Kimura (1975) inferred that the climatic condition of the Tetori area was basically the same as that of the Siberian paleofloristic area because of the close similarity of these floras.

Based on the taphonomical interpretation of living plants (Okubo, 1998), plant assemblages of Kaseki-kabe (Fossil bluff) reveal river and lake margin vegetation. Thus, the

Table 6

List of Early Cretaceous vertebrate taxa from the Kaseki-kabe (Fossil bluff) in the Tetori Basin, Japan (MIN and MAX show minimum and maximum numbers of individuals)

Group	Taxa	MIN	MAX	Ratio of taxa (%)	Ratio of group (%)
Amphibia	Anura gen. et sp. indet.	1	1	0.23	0.23
Theropod	Oviraptorosaurid gen. et sp. indet.	1	1	0.23	2.75
	Theropod gen. et sp. indet.	3	11	2.52	
Sauropod	Nemegtosaurid gen. et sp. indet.	1	2	0.46	2.52
	Sauropod gen. et sp. indet.	1	9	2.06	
Ornithopod	Hypsilophodontid gen. et sp. indet.	1	5	1.15	0.089
	Iguanodontid gen. et sp. indet.	1	33	7.57	
	Ornithopod gen. et sp. indet.	1	1	0.23	8.95
Dinosaurid	Dinosaurs gen. et sp. indet.	1	3	0.69	0.69
Lizard	Paramacellodidae gen. et sp. indet.	1	133	30.50	
	<i>Sakurasaurus</i> sp.	5	5	1.15	
	Lizard gen. et sp. indet.	3	26	5.96	
	Anguimorpha gen. et sp. indet.	1	14	3.21	40.83
Pterosaurid	Ornithocheiridae gen. et sp. indet.	1	1	0.23	
	Gnathosaurinae gen. et sp. indet.	1	6	1.38	
	Dsungaripteroidea? gen. et sp. indet.	1	2	0.46	
	Pterosaurid gen. et sp. indet.	1	1	0.23	2.29
Aves	Enantiornithes gen. et sp. indet.	1	2	0.46	0.46
Synapsid	Tritylodontidae gen. et sp. indet.	4	166	38.07	38.07
Mammalia	Triconodont gen. et sp. indet.	2	12	2.75	3.21
	Multituberculate gen. et sp. indet.	1	2	0.46	
	Total	33	436		

abundant occurrence of large fern leaves (*Gleichenites*, *Eboracia*, *Onychiopsis*), ginkgoaleans, nilssonians, taeniopterids, and *Podozamites* indicates the riparian nature of these plants. Numerous occurrences of in situ stumps of *Xenoxylon* trunks also indicate the growth of conifer forest around the river. The rare occurrence of cycads and bennettitaleans may suggest scarcity of these plants or that they had an inland habitat. The recent discovery of a cyathean tree fern trunk (Terada, 2002) from the Tetori area indicates the possibility of rare tree ferns scattered within the forest.

Paleovegetation of Kaseki-kabe (Fossil bluff) indicates a forest consisting mainly of broad-leaved conifers and ginkgoaleans. Forest clearings and river and lake margins were probably filled with herbaceous ferns. Cycads and bennettitaleans were scattered within the forest or at the riverside.

4.2.2. Food-web model, ecological pyramid, energy flow, and estimation of individual vertebrate numbers. Table 7 shows inferred food habits of zoo-species in the Cretaceous Tetori ecosystem based on comparison with their allied living taxa and interpretation of papers and references in Matsuoka et al. (2000). Based on their inferred eating habits, we presumed a food-web model consisting of five trophic levels (Fig. 10).

Distribution of the Cretaceous Tetori Group exposures can be measured as 90 km (distance from east to west) times 75 km (distance from south and north): total 6750 km² (Matsukawa et al., 2003a,b, 2006). For easy calculation, we use 100 times the Cretaceous exposures for ecosystem reconstruction. Thus, we calculate an area of 675×10^9 m². This is almost 27 times the size of the Serengeti National Park in Tanzania and 13 times that of the Cretaceous Choyr ecosystem in southern Mongolia.

Cretaceous vegetation from the Tetori area can be compared with living vegetation of temperate evergreen forest or temperate deciduous forest, because plant fossil assemblages from Kaseki-kabe (Fossil bluff) consist mainly of broad-leaved conifers and ginkgoaleans inferred to have grown on plains near rivers and lakes. NPP of the modern temperate conifer forest in Great Smoky Mountains, Tennessee, at about 500 m above sea level was estimated as about 1300 g/m²/yr in Whittaker (1966, 1975). Thus, the NPP of the Cretaceous Tetori ecosystem can be calculated 877.5×10^{12} g/yr by multiplying 1300 g/m²/yr and range area together. Then, regarding animal weights, we use weight estimates of Matsuoka et al. (2000) and we infer the matching weight for body size based on literature (e.g., Lambert, 1983; Norman, 1985). Thus, we can calculate the SMR of required energy per day and required energy per year (Table 8). Then, individual numbers of each species for each trophic level can be estimated (Table 9). Fig. 11 shows a census of the population in the Tetori ecosystem. Furthermore, based on estimated individual numbers of the species, energy pyramids and population density per 1 km² in the Cretaceous Tetori ecosystem are shown in Fig. 12 and Table 9.

Table 7

List of Early Cretaceous fossils from the Kaseki-kabe (Fossil bluff) in the Tetori Basin, Japan, and their presumed foods

Group	Taxa	Presumed food
Amphibia	Anura gen. et sp. indet.	insects
Theropods	Oviraptorosaurid gen. et sp. indet.	insects, small dinosaurs, herbivorous dinosaurs, small lizards, mammal-like reptiles, mammals
	Theropod gen. et sp. indet.	small dinosaurs, herbivorous dinosaurs, small lizards, mammal-like reptiles, mammals
Sauropods	Nemegtosaurid gen. et sp. indet.	plants
	Sauropod gen. et sp. indet.	plants
Ornithopods	Hypsilophodontid gen. et sp. indet.	plants
	Iguanodontid gen. et sp. indet.	plants
	Ornithopod gen. et sp. indet.	plants
Dinosaurids	Dinosaurs gen. et sp. indet.	(unknown)
Lizards	Paramacelodidae gen. et sp. indet.	insects
	<i>Sakurasaurus</i> sp.	insects
	Lizard gen. et sp. indet.	insects
	Anguimorpha gen. et sp. indet.	insects, amphibians, small herbivorous dinosaurs, small lizards, mammal-like reptiles, mammals
Pterosaurids	Ornithocheiridae gen. et sp. indet.	fishes, bivalves
	Gnathosaurinae gen. et sp. indet.	fishes, bivalves
	Dsungaripteroidea? gen. et sp. indet.	fishes, bivalves
	Pterosaurid gen. et sp. indet.	fishes, bivalves
Aves	Enantiornithes gen. et sp. indet.	insects, woody plant seeds
Synapsids	Tritylodontidae gen. et sp. indet.	plants
Mammalia	Triconodont gen. et sp. indet.	insects
	Multituberculate gen. et sp. indet.	plants

5. Characteristics of Early Cretaceous terrestrial ecosystems in East Asia

We made two energy-flow models in two types of Cretaceous fluvio-lacustrine basins characterized by features typical of modern steppe and forest vegetations in East Asia, and we estimated individual numbers of vertebrates in the basins. These ecosystems consist of four or five trophic levels and form wide-base ecological pyramids. Regarding ecological pyramids, Odum (1983) suggested three types of pyramids rendered in population per unit area, in biomass by dry weight per 1 m², and in biomass by energy flow. We followed his methods and

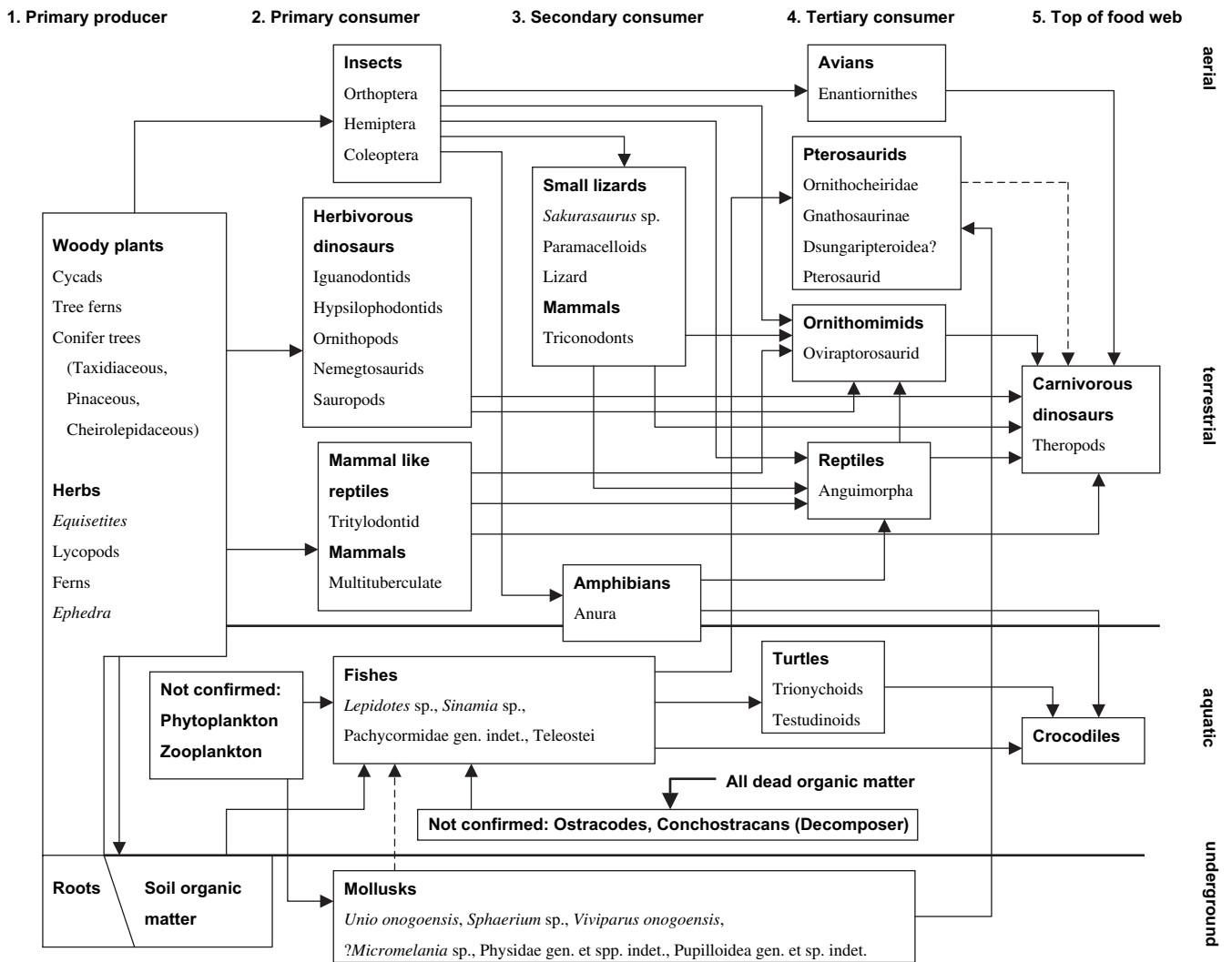


Fig. 10. Early Cretaceous food-web model of the Tetori ecosystem, Japan, based on occurrences of taxa.

use three types of pyramid rendered in biomass (productive energy) per 1 m² per year, in population per 1 km², and in biomass by dry weight per 1 m² for both the Choyr and Tetori ecosystems (see Figs. 8, 12). They reveal typical ecosystems consisting of very large producer and small consumer components. This means these ecosystem models are probably justified for both ecosystems. To confirm the reliability of the model, we have to compare it with that of recent ecosystem analysis.

The Serengeti ecosystem lies east of Lake Victoria in Tanzania and Kenya. The ecosystem includes various reserves such as the Serengeti National Park, which is kept in an almost natural condition so species and individual numbers of animals can be examined (Grimsdell, 1979; Houston, 1979; Sinclair and Norton-Griffiths, 1982; Sneron, 1986). Therefore, this ecosystem is useful for verifying the reconstruction model. We estimated individual numbers of vertebrates in the Serengeti ecosystem by using the same method as used for the Cretaceous ecosystems. Tables 10 and 11 show the estimated individual numbers, ratio of estimated individual numbers and confirmed individual numbers, population density of

estimated vertebrate species per km² etc. based on 13 herbivorous species and two carnivorous species reported by Sneron (1986) and 15 herbivorous species and five carnivorous species reported by Houston (1979). In both cases (Houston, 1979; Sneron, 1986), estimated numbers exceed confirmed number by a factor of 2.8 for primary consumers, and 7.0 and 7.8 for secondary consumers. Thus, it must be noted that reconstructed paleoecosystem population and biomass estimates are too high and represent theoretical idealized maxima.

In the Serengeti National Park actual per km² densities range from 52.00 wildebeest (*Connochaetes taurinus*) to 0.03 elephant (*Loxodonta africana*) and 39.24 Thomson's gazelle (*Gazella granti*) to 0.04 rhinoceros (*Ceratotherium simum*) for large herbivores as estimated by Sneron (1986) and Houston (1979), respectively. Likewise, per km² densities of 0.36 for hyena (*Hyena hyena*) and 0.06 for lion (*Panthera leo*), and 0.12 for hyena (*Hyena hyena*) to 0.01 for cheetah (*Acinonyx jubatus*) are also estimated by Sneron (1986) and Houston (1979), respectively, for the carnivore component. This indicates herbivorous dinosaurs in the Cretaceous Choyr

Table 8
Estimated weight, occurrence of individual numbers, basal metabolism, required energy per day and per year of vertebrate taxa in the Early Cretaceous Tetori Basin, Japan (dinosaurid category listed in Table 6 is omitted from this table because the taxonomy is uncertain)

Group	Taxa	Estimated weight (adult, kg)	Occurrence of individuals	Basal metabolism (kJ/day)	Required energy per day for an individual (kJ/day)	Required energy per year for an individual (kJ/year)
Amphibia	Anura gen. et sp. indet.	0.004	1	0.70	1.75	638.04
Theropod	Oviraptorosaurid gen. et sp. indet.	33.000	1	4107.04	10,267.60	3,747,674.77
	Theropod gen. et sp. indet.	30.000	11	3833.56	9583.90	3,498,122.25
Sauropod	Nemegtosaurid gen. et sp. indet.	6000.000	2	29,969.84	119,879.36	43,755,965.73
	Sauropod gen. et sp. indet.	6000.000	9	29,969.84	119,879.36	43,755,965.73
Ornithopod	Hypsilophodontid gen. et sp. indet.	20.000	5	415.76	1663.04	607,010.68
	Iguanodontid gen. et sp. indet.	901.000	33	7229.61	28,918.42	10,555,223.39
	Ornithopod gen. et sp. indet.	901.000	1	7229.61	28,918.42	10,555,223.39
Lizard	Paramacellodidae gen. et sp. indet.	0.020	133	2.34	5.84	2133.42
	<i>Sakurasaurus</i> sp.	0.020	5	2.34	5.84	2133.42
	Lizard gen. et sp. indet.	0.020	26	2.34	5.84	2133.42
	Anguimorpha gen. et sp. indet.	1.000	14	43.96	109.90	40114.73
Pterosaurid	Ornithocheiridae gen. et sp. indet.	22.000	1	3063.48	7658.70	2,795,425.45
	Gnathosaurinae gen. et sp. indet.	22.000	6	3063.48	7658.70	2,795,425.45
	Dsungaripteroidea? gen. et sp. indet.	22.000	2	3063.48	7658.70	2,795,425.45
	Pterosaurid gen. et sp. indet.	22.000	1	3063.48	7658.70	2,795,425.45
Aves	Enantiornithes gen. et sp. indet.	0.150	2	137.02	342.55	125,031.16
Synapsid	Tritylodontidae gen. et sp. indet.	8.000	166	1394.11	5576.44	2,035,401.39
Mammalia	Triconodont gen. et sp. indet.	0.500	12	174.26	435.66	159,015.73
	Multituberculata gen. et sp. indet.	0.500	2	174.26	697.06	254,425.17
Total			433			

Basin are 4.8 and 4.0 times of herbivorous mammals in the Serengeti National Park by [Snerson \(1986\)](#) and [Houstoen \(1979\)](#), respectively. Likewise, that in the Cretaceous Tetori Basin are 2.7 and 2.3 times of herbivores in the Serengeti. However, carnivorous dinosaurs in the Choyr are 60.8 and 105.5 times of carnivorous mammals in the Serengeti. Then, those in the Tetori are 26.0 and 45.1 times of carnivores in the Serengeti. This is probably caused by different metabolisms and time-averaging in paleoecosystems. Furthermore, in general, comparing vertebrate carnivores with vertebrate herbivores, we find that populations of carnivores are very much smaller than those of herbivores. Therefore, once vertebrate carnivores reduce their population, it is harder for them to recover than it is for herbivores. These causes may keep populations of vertebrate carnivores lower than estimated. To sum up, we can understand similarities and differences between living and Cretaceous ecosystems by comparing results of our reconstructions, based on energy flow and food-web models, with actual numbers and proportions from modern ecosystems.

6. Biodiversity of Early Cretaceous ecosystems in East Asia

Diversity refers to the taxonomic richness of a community. The simplest technique is simply to count the number of species present ([Raup and Stanley, 1978](#)). However, an important aspect of the numerical structure of communities is completely ignored when the composition of the community is described simply in terms of the number of species present. The simplest measure of the character of a community that takes into account both abundance (or biomass) patterns and species richness is Simpson's diversity index ([Simpson, 1949](#); [Begon et al., 1996](#)). This can be calculated by determining, for each species, the proportion of individuals or biomass that it contributes to the total sample. The value of the index depends on both the species richness and the evenness (equitability) with which individuals are distributed amongst the species. For a given richness, Simpson's index increases with equitability, and for a given equitability, Simpson's index increases

Table 9

Estimated individual numbers, ratio, head count ratio based on 33 head of *Iguanodontid*, occurrence of individual numbers, and population density of vertebrate taxa in 1 km² in the Early Cretaceous Tetori Basin, Japan (dinosaurid category listed in Table 6 is omitted from this table because the taxonomy is uncertain)

Group	Taxa	Estimated numbers of individuals	Census (%)	Head count ratio based on 33 head of <i>Iguanodon</i>	Occurrence of individuals	Population density of vertebrate taxa per 1 km ²
Amphibia	Anura gen. et sp. indet.	916,047	0.28	1.4	1	1.36
Theropod	Oviraptorosaurid gen. et sp. indet.	1,451,702	0.44	2.2	1	2.15
	Theropod gen. et sp. indet.	5,911,656	1.81	8.9	11	8.76
Sauropod	Nemegtosaurid gen. et sp. indet.	1,321,424	0.40	2.0	2	1.96
	Sauropod gen. et sp. indet.	5,946,408	1.81	9.0	9	8.81
Ornithopod	Hypsilophodontid gen. et sp. indet.	3,303,561	1.00	5.0	5	4.89
	Iguanodontid gen. et sp. indet.	21,803,497	6.63	33.0	33	32.30
	Ornithopod gen. et sp. indet.	660,713	0.20	1.0	1	0.98
Lizard	Paramacellodidae gen. et sp. indet.	121,834,174	37.06	184.4	133	180.50
	<i>Sakurasaurus</i> sp.	4,580,232	1.39	6.9	5	6.79
	Lizard gen. et sp. indet.	23,817,208	7.24	36.0	26	35.28
	Anguimorpha gen. et sp. indet.	13,387,316	4.07	20.3	14	19.83
Aves	Enantiornithes gen. et sp. indet.	1,832,093	0.56	2.8	2	2.71
Synapsid	Tritylodontidae gen. et sp. indet.	109,678,195	33.36	166.0	166	162.49
Mammalia	Triconodont gen. et sp. indet.	10,992,557	3.34	16.6	12	16.29
	Multituberculate gen. et sp. indet.	1,321,424	0.40	2.0	2	1.96
Totals		328,758,208			423	

with richness. Table 12 shows Simpson’s diversity index for the Choyr and Tetori ecosystems calculated based on estimated population size, biomass, and occurrence of individual numbers. The diversity indices based on estimated population size and the occurrence of individual numbers are almost same, but those estimated from the biomass of the Tetori ecosystem is twice or three times that of the Choyr ecosystem. This means that the Tetori ecosystem is higher diversity than is the Choyr ecosystem. In the Early Cretaceous of East Asia, the temperate evergreen forest or temperate deciduous forest is revealed to be a richer ecosystem than the temperate steppe. The high diversity inferred for the Tetori ecosystem gives us a new perspective on the Early Cretaceous terrestrial ecosystems in Asia from the viewpoint of energy-flow modeling. It also suggests a new perspective and point of comparison with the continental Choyr ecosystem which is representative of the Jehol Biota (Chen, 1988, 1999).

7. Significance and problems of paleoecosystem reconstruction using energy flow

The greatest significance of paleoecosystem reconstruction using energy flow is that it can reconstruct any world ecosystem past or present using the same method. This enables us to compare every paleoecosystem regardless of fossil preservation, sedimentary geology, age, etc., and to assess, in detail,

changing paleoecosystems, species composition, and processes of evolution. Besides, it may be possible to predict unknown species groups and “empty” niches not discovered in the fossil record. We should be able to learn more about

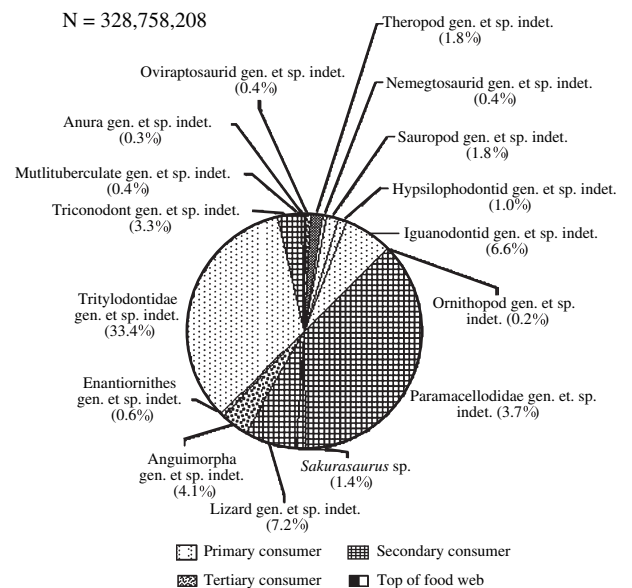


Fig. 11. Early Cretaceous vertebrate census of the Tetori ecosystem, Japan, based on estimated numbers of individuals.

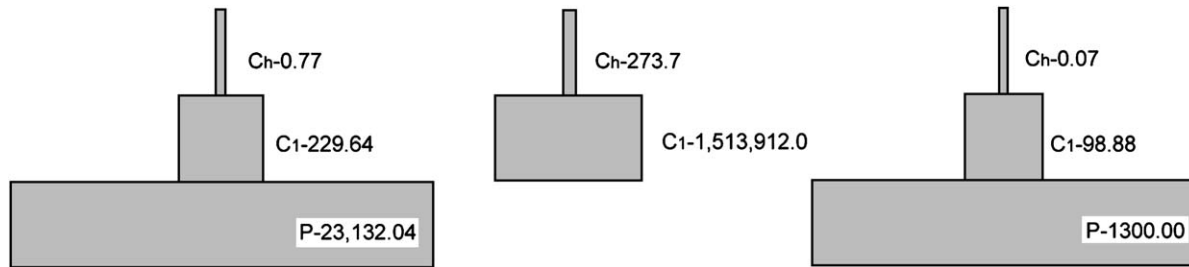


Fig. 12. Early Cretaceous energy pyramids of the Tetori ecosystem, Japan. Left, energy flows are given in kJ/square meter/year. Center, energy flows are given in population numbers in 1 km² of consumers on the food web. Right, energy flows are given in dry weight grams in 1 km² of consumers up the food web. P, primary producer, C₁, primary consumer, C_n, high-order consumer.

current environments and ecosystems by understanding the transition of paleoecosystem from deep time to the present.

However, this paleoecosystem reconstruction model also raises many problems. In the first place, fossil data do not provide all animal data for the paleoecosystem. Preservation of fossils is not uniform: it is controlled by biologic structure in relation to biologic, mechanical, and chemical destruction processes, sedimentary environments, and life habits. Fossils are also transported in many different ways. Furthermore, similar organisms are transported in different ways and so have differing relationships to their original habitats (Raup and Stanley, 1978).

We estimated the Net Primary Productivities, and the type of ecosystem was determined based on fossil plant occurrences and paleoenvironments. However, plant fossil assemblages lack some information about ancient vegetation owing to geographical features of plant habitats, life histories of plants, and physical and chemical strength of leaves. Therefore, plant fossil assemblages strongly reflect and over-represent vegetation near rivers and lakes (Okubo, 1998). Therefore, it is

important to reconstruct vegetation considering these factors and to reconstruct paleoenvironments in detail by sedimentological techniques. It is also important to consider productivity of plants even if the types of ecosystem are similar. For example, modern grasslands are composed of poaceous plants. However, the oldest fossil record of such grassland was reported from the Eocene (McNaughton, 1991) and grasslands do not extend back to the Cretaceous.

The inferences of energy-flow pattern or division of energy were mainly based on the equality model. However, animals have food preferences (Farlow, 1980, 1990; Begon et al., 1996) and the equality model assumes that the population restriction factor for animals is only energy. Actually, animal populations are restricted by other resource factors such as water and lifestyle strategy factors including comfortable nesting sites, territory, and habitat preferences. A large number of factors and processes influence the population, such as intraspecific and interspecific competition, density dependent effects, and human activity effects (Begon et al., 1996). In the Serengeti ecosystem, estimated population exceeds confirmed

Table 10

Confirmed individual numbers, weights, required energy of individuals per year, required energy of total individual numbers of species per year, energy distribution for each species, estimated individual numbers, error rate, and population density of vertebrate taxa in 1 km² in the present-day Serengeti ecosystem (H, herbivore, C, carnivore; data from Snerston, 1986)

Taxa		Feeding habitats	Body weights (kg)	Confirmed data		Estimated data		Errors
Common name	Scientific name			Individual numbers	Population density per 1 km ²	Individual numbers	Population density per 1 km ²	
Wildebeest	<i>Connochaetes taurinus</i>	H	123	1,300,000	52.00	3,590,943	143.64	2.8
Zebra	<i>Equus zebra</i>	H	200	200,000	8.00	552,453	22.10	2.8
Thomson's gazelle	<i>Gazella thomsoni</i>	H	15	250,000	10.00	690,566	27.62	2.8
Grant's gazelle	<i>Gazella granti</i>	H	40	30,000	1.20	82,868	3.31	2.8
Impala	<i>Aepyceros melampus</i>	H	40	70,000	2.80	193,358	7.73	2.8
Topi	<i>Damaliscus korrigum</i>	H	100	50,000	2.00	138,113	5.52	2.8
Kongoni	<i>Alcelaphus buselaphus</i>	H	125	15,000	0.60	41,434	1.66	2.8
Warthog	<i>Phacochoerus aethiopicus</i>	H	45	10,000	0.40	27,623	1.10	2.8
Eland	<i>Tragelaphus oryx</i>	H	340	9000	0.36	24,860	0.99	2.8
Giraffe	<i>Giraffa camelopardali</i>	H	750	8000	0.32	22,098	0.88	2.8
Buffalo	<i>Synceros caffer</i>	H	450	20,000	0.80	55,245	2.21	2.8
Elephant	<i>Loxodonta africana</i>	H	1725	800	0.03	2210	0.09	2.8
Ostrich	<i>Struthio camelus</i>	H	115	2000	0.08	5525	0.22	2.8
Lion	<i>Panthera leo</i>	C	347	1500	0.06	10,436	0.42	7.0
Hyena	<i>Hyaena hyaena</i>	C	65	9000	0.36	62,619	2.50	7.0
Totals				1,975,300	79.01	5,500,351	220.01	

Table 11
Data from the present-day Serengeti ecosystem as in Table 10 (from Houston, 1979)

Taxa		Feeding habitats	Body weights (kg)	Confirmed data		Estimated data		Errors
Common name	Scientific name			Individual numbers	Population density per 1 km ²	Individual numbers	Population density per 1 km ²	
Wildebeest	<i>Connochaetes taurinus</i>	H	123	720,000	28.80	1,981,979	79.28	2.8
Zebra	<i>Equus zebra</i>	H	200	240,000	9.60	660,660	26.43	2.8
Thomson's gazelle	<i>Gazella thomsoni</i>	H	15	981,000	39.24	2,700,446	108.02	2.8
Grant's gazelle	<i>Gazella granti</i>	H	40	6000	0.24	16,516	0.66	2.8
Impala	<i>Aepyceros melampus</i>	H	40	119,100	4.76	327,852	13.11	2.8
Topi	<i>Damaliscus korrigum</i>	H	100	55,500	2.22	152,778	6.11	2.8
Kongoni	<i>Alcelaphus buselaphus</i>	H	125	20,700	0.83	56,982	2.28	2.8
Warthog	<i>Phacochoerus aethiopicus</i>	H	45	34,200	1.37	94,144	3.77	2.8
Eland	<i>Tragelaphus oryx</i>	H	340	24,000	0.96	66,066	2.64	2.8
Giraffe	<i>Giraffa camelopardali</i>	H	750	17,400	0.70	47,898	1.92	2.8
Buffalo	<i>Synceros caffer</i>	H	450	108,000	4.32	297,297	11.89	2.8
Elephant	<i>Loxodonta africana</i>	H	1725	4500	0.18	12,387	0.50	2.8
Hippo	<i>Hippopotamus amphibius</i>	H	1000	2400	0.10	6607	0.26	2.8
Waterbuck	<i>Kobus ellipsiprymnus</i>	H	160	3000	0.12	8258	0.33	2.8
Rhino	<i>Ceratotherium simum</i>	H	816	900	0.04	2477	0.10	2.8
Lion	<i>Panthera leo</i>	C	347	2400	0.10	18,657	0.75	7.8
Hyena	<i>Hyaena hyaena</i>	C	65	3000	0.12	23,321	0.93	7.8
Cheetah	<i>Acinonyx jubatus</i>	C	48	250	0.01	1943	0.08	7.8
Wild dog	<i>Lycan pictus</i>	C	24	300	0.01	2332	0.09	7.8
Leopard	<i>Panthera pardus</i>	C	65	1000	0.04	7774	0.31	7.8
Total				2,343,650	93.75	6,486,374	259.45	

population (see Tables 10, 11). This suggests that there are other real-life restricting factors overlooked by the model. However, it is almost impossible to incorporate these restricting factors in the model by evaluation. Therefore, it is necessary to remember that estimated populations of this reconstruction model represent the maximum level. Thus, the actual population should probably be smaller.

When comparing reconstructed paleoecosystems, we must be careful to compare them at the same level. Vertebrate herbivores should be compared with vertebrate herbivores, invertebrates should be compared with invertebrates, and aquatic animals should be compared with aquatic animals. Comparing animals of different lifestyle levels may not so much reveal

differences in ecosystem structure as different life histories and life history strategies.

Ecosystem analysis compares communities based on species and individuals in well-defined units of time and space, but paleoecosystem analysis uses fossil communities consisting of time-averaged assemblages. Thus, we cannot guarantee that fossil community component species existed in the same time and space. This is a limiting factor in our analyses. Zoo-species and individuals inhabiting certain areas have their own range or radius. Thus, they overlap with the range of other species and affect fossil record and these ranges may change through time (Fig. 13).

8. Conclusions

Using fossils we can make an estimation of the past population density as an ecosystem index based on food-web and energy-flow models. There are many Lower Cretaceous fluvio-lacustrine deposits in East Asia. Using food-web and energy-flow models, terrestrial ecosystems can be reconstructed to give quantitative estimates. We chose Early Cretaceous fluvio-lacustrine basins (the Choyr, southeastern Mongolia, and the Tetori, Japan) for these analyses and as a model for reconstruction of similar basins in East Asia. We derive the following conclusions:

1. Food-web models of the two ecosystems could be reconstructed based on fossil species and inferred eating habits. We adjusted our models to models of modern reality by using a so-called "black box" for missing species.

Table 12

Simpson's diversity index (Simpson, 1949; Begon et al., 1996) of all animal taxa and vertebrate taxa only from the Choyr and Tetori ecosystems based on estimated population size, biomass, and occurrence of individual numbers (see text for explanation), Simpson's diversity index (D) = $1/\sum P_i^2$ where P_i is the proportional abundance of the species i

	Species richness	Simpson's diversity index		
		Estimated population size	Biomass	Occurrence of individual numbers
Choyr ecosystem (all animal taxa)	8	1.00	1.14	4.06
Tetori ecosystem (all animal taxa)	19	1.36	3.15	4.10
Choyr ecosystem (vertebrate taxa)	7	3.11	1.07	3.40
Tetori ecosystem (vertebrate taxa)	16	3.82	2.46	3.76

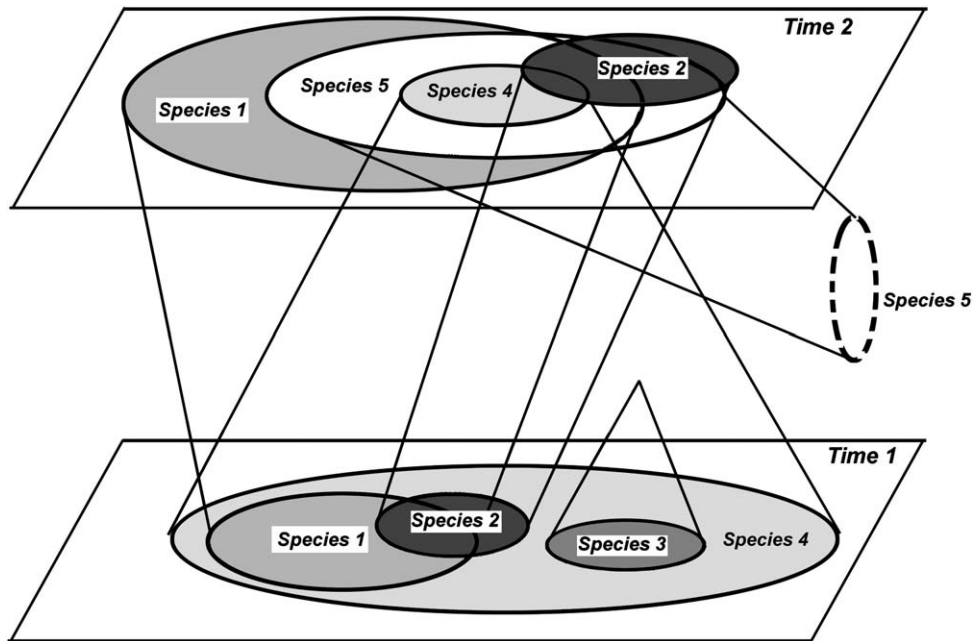


Fig. 13. Dynamic model shows animals moving within an ecosystem at different times.

- Individual numbers of zoo-species in these two ecosystems were estimated on the basis of food-web and energy-flow models. Those ecosystems consist of four or five trophic levels and form wide-base ecological pyramids.
- It is recognized that the estimated population density of herbivores and carnivores in living ecosystems is respectively 2.3–4.8 and 26.0–105.5 times less than in Cretaceous ecosystems. These differences are useful for the evaluation of estimates of past population densities of vertebrate taxa, because these differences are probably caused by the different metabolism of different taxa. Preservation and time-averaging may also be a factor.
- The temperate evergreen forest or temperate deciduous forest of the Tetori ecosystem is a richer ecosystem than the temperate steppe Choyr ecosystem. The high diversity of the Tetori ecosystem presents the Early Cretaceous terrestrial ecosystem in Asia from new perspective of energy-flow modeling.

We should be able to reconstruct paleoecosystems based on energy-flow models more rigorously using taphonomic analysis of plant fossils, consideration of plant productivities, sedimentological reconstruction of paleoenvironments, detailed inferences of energy-flow pattern, and the considerations of all factors that influence the population. Although it is relatively simple to apply the common method of present ecosystem analysis, we recognize that problems occur in the past ecosystem reconstructions.

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