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OF CONFUCIUSORNIS AND PHAETHON

Birds are one of the most attractive classes of vertebrates, which have been studied for centuries. During the last two decades of the 20th century, a true explosion occurred in the discovery of fossil birds (for reviews see **[2]**, **[10]**, **[11]**). Early Cretaceous birds from Liaoning Province of China are of special interest in this respect. Chinese researchers have published a number of reviews, which provide an understanding of the history, taphonomy, and diversity of these animals **[6]**, **[7]**, **[9]**, **[17]**, **[18]**, **[21]**, **[22]**. Hundreds of well-preserved specimens of confuciusornithids were found near the villages of Sihetun and Jianshangou in Liaoning Province of northeastern China **[3]**. While skeleton and plumage of confuciusornithids have been described in detail (for the review see **[26]**) their possible mode of life is still debatable.

At present, the family Confuciusornithidae comprises three genera with six species **[22]**. Our ecological reconstruction is applicable to at least four species of two confuciusornithid genera, *Confuciusornis sanctus*, *C. dui*, *C. suniae*, and *Changchengornis hengdaoziensis*.

The skull of *Confuciusornis* (*C. sanctus*) displays a mosaic of primitive and derived characters (Fig. 1). Imprints of other horn structures (claws, feathers) and absence those of the ramphotheca in the same specimens strongly suggest that *Confuciusornis* had a relatively soft horn sheath of the beak, which is in agreement with the presence of sensory bodies. This character, noticed by Peters and Ji **[13]**, casts doubt on the herbivorous diet of *Confuciusornis*, as it was proposed by Hou et al. **[8]**. It is unlikely that powerful but sensitive beak of confuciusornithids, covered by delicate ramphotheca, could have crushed plant objects. The sensitive beak with a soft ramphotheca suggests that it was used for searching and grasping food objects (predominantly soft animal food) in the places inaccessible to eyesight. Strong jaws indicate a great load on them during prey capture; extremely powerful lower jaws must have undergone the major loading. The short beak of *Confuciusornis* suggests that it was most probably used for capturing prey in the upper layer of water and/or in other soft substrates. This feeding pattern is supported by upturned bony beak, which once was equipped with even more upturned ramphotheca. Its imprints were recorded in a specimen of *Confuciusornis dui* **[8]** (Fig. 1).

Like Archaeopteryx, *Confuciusornis* had digital claws. The better developed third digit combined with the reduction of its claw almost certainly shows its key for support of the extraordinary long primary feathers and the loss of the initial prehensile function. This is not true for the other two digits. Both have massive ungual phalanges, with well-developed flexor tubercles and strong (and, therefore, preserved in fossil state) horny sheaths, which are curved and sharp at the ends — indication of their active use **[24]**. Among extant birds, this use is observed in hoatzin nestlings, which climb in tree branches. Although certain extant birds retain one or more digital claws (for the review see **[14]**), latter are always covered with feathers and resemble weak third digital claw of *Confuciusornis*.

Location of antitrochanter indicates an almost horizontal position of the femur of *Confuciusornis*, similar to that of extant birds and different from the position in primate-like posture, proposed in some works **[12]**. Relatively short tibiotarsus and tarsometatarsus suggest that *Confuciusornis* was neither a good runner nor capable of walking along the shoreline. Curved pedal claws of *C. sanctus*, with laterally compressed and pointed horn sheaths are in contradiction with terrestrial habits (Fig. 1). Even in terrestrial passerines (Motacillidae, Alaudidae), many of which retain connection with trees, the curvature of claws is decreased

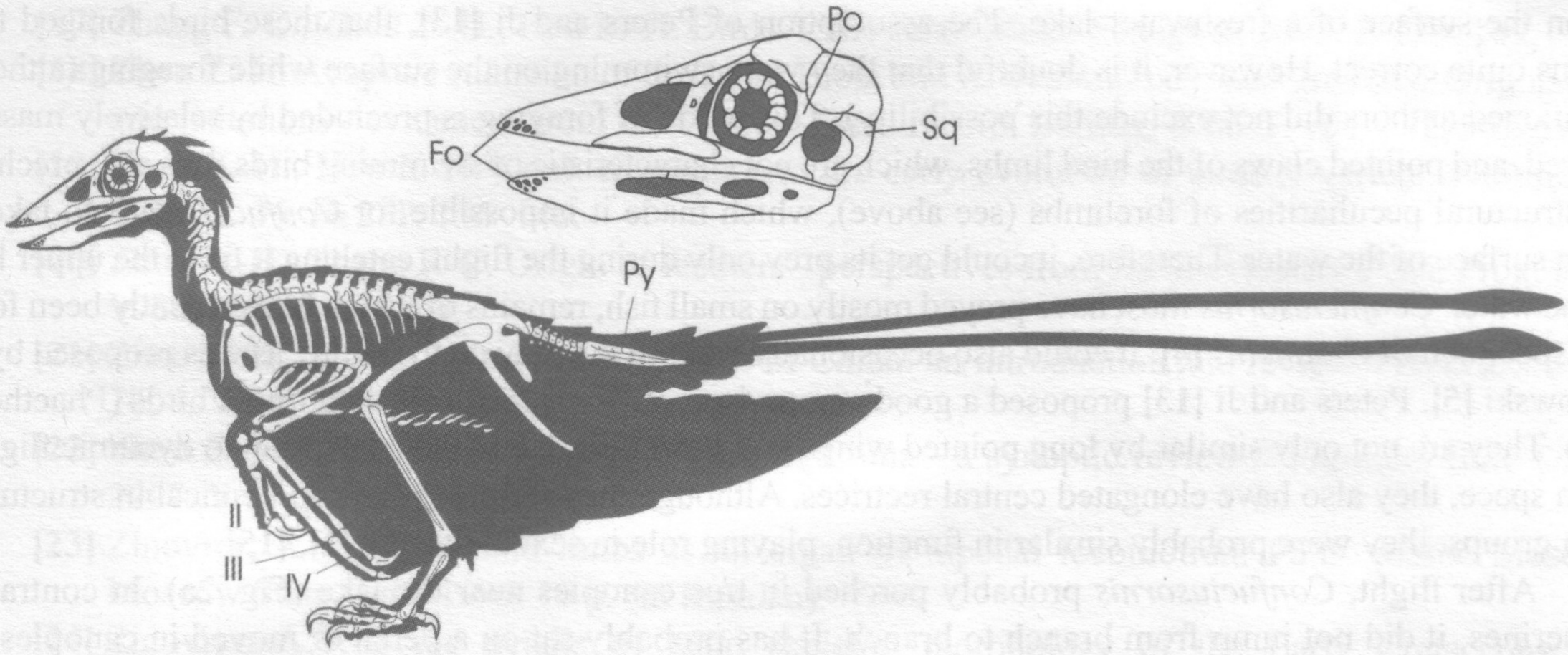

Fig. 1. Reconstructed skeleton of *Confuciusornis sanctus*, with signs of the plumage, horn sheaths, and magnified skull (after **[3]** modified); added elements include the ramphotheca (after **[24]**), horn sheaths of the claws, and elongated feathers of the tail; the second digit is relatively autonomous, the third digit is completely enclosed in the wing plumage (after **[24]**); the uncinate processes are removed. Designations: **(Fo)** pits on the maxilla and dentary, **(Po)** postorbital, **(Py)** pygostyle, **(Sq)** squamosal, and **(II-IV)** serial numbers of forelimb digits.

and the posterior claw is straightened becoming similar to a spur **[23]**. Short and somewhat raised posterior digit of *Confuciusornis* indicates that it could not move actively in canopies with the use of hind limbs for transverse grasping of a tree branch; however, it could have moved along thick branches as it is observed, for example, in modern Tetraonidae. At least second wing digit, free of alula, might have helped *Confuciusornis* to move in canopies.

The entire body of *Confuciusornis*, except for the tarsometatarsus, foot, and, probably, an area at the base of the beak, was covered with contour feathers, which appear similar to those in the extant birds **[19]** (Fig. 1). Extraordinary long primaries are pointed and have asymmetrical vanes. The plumage of *Confuciusornis* corresponds to that of an actively flying creature. Rectrices are extremely short (**[3]** compare with **[9]**). In approximately 10% of specimens, two central rectrices are elongated **[12]**, exceeding the body length (Fig. 2). They differ in structure from the feathers of extant birds in the absence of a distinct shaft and barbs over most of the feather extent, up to the distal quarter (to the apical lancelet expansion). Similar feathers are observed in some living birds (for example, Paradisaeidae), although they have a uniform structure over the entire length **[3]**. However, the situation observed in *Confuciusornis* is not unique. Feathers of similar structure are present in the enantiornithine *Protopteryx* **[16]**, **[20]**, **[21]**.

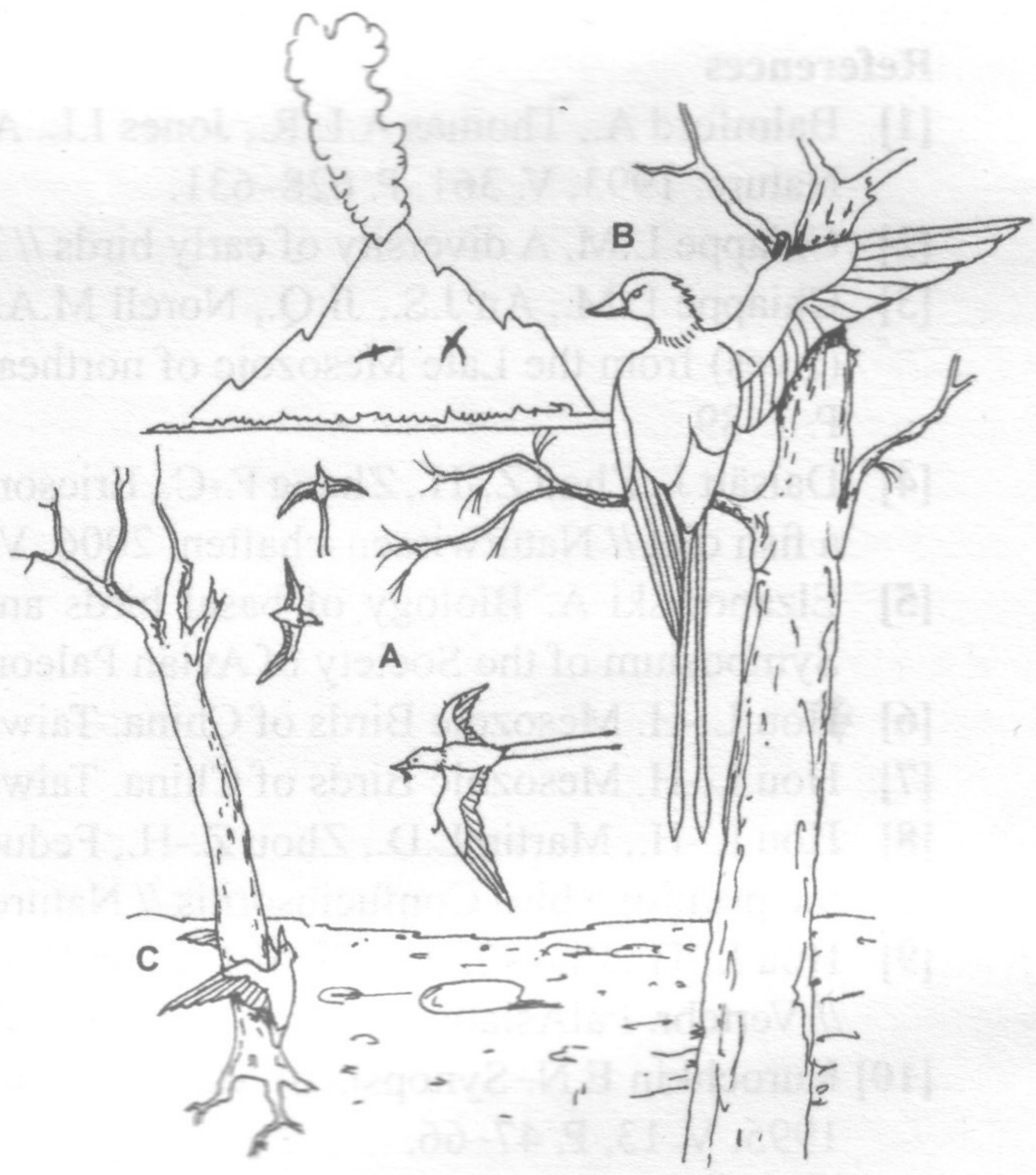

Fig. 2. Reconstruction of an Early Cretaceous landscape of Liaoning Province, with *Confuciusornis*: **(a)** hunting individuals; **(b)** resting individual; and **(c)** individual climbing a tree.

Simultaneous burial of many specimens of *Confuciusornis* (up to 40 per 100 m^2: **[3]**) within a limited area indicates, that they were probably gregarious birds; this point of view is shared by the majority of researchers [7], **[12]**, **[13]**. Taphonomic data and preservation of specimens suggest that a flock of birds just died above

or on the surface of a freshwater lake. The assumption of Peters and Ji **[13]**, that these birds foraged there seems quite correct. However, it is doubtful that they were swimming on the surface while foraging (although mentioned authors did not exclude this possibility). This mode of foraging is precluded by relatively massive, curved, and pointed claws of the hind limbs, which are not characteristic of swimming birds. It is also precluded by structural peculiarities of forelimbs (see above), which made it impossible for *Confuciusornis* to take off from surface of the water. Therefore, it could get its prey only during the flight, catching it from the upper layer of the water. *Confuciusornis* must have preyed mostly on small fish, remains of which have recently been found in a specimen of *C. sanctus* **[4]**. It could also occasionally capture the prey on the shore, as was proposed by Elzanowski **[5]**. Peters and Ji **[13]** proposed a good comparison of *Confuciusornis* with tropic birds (Phaethontidae). They are not only similar by long pointed wings and short tails due to the adaptation to dynamic flight in open space, they also have elongated central rectrices. Although these feathers are not identical in structure in both groups, they were probably similar in function, playing role in sexual display **[1]**, **[15]**.

After flight, *Confuciusornis* probably perched in tree canopies near the lake (Fig. 2a). In contrast to passerines, it did not jump from branch to branch. It has probably sat on a perch or moved in canopies like hoatzin nestling, helping itself with the claw of the second digit (Fig. 2b). The nest of *Confuciusornis* was probably located on the tree. It is quite likely that *Confuciusornis* was not as active tree-trunk climber, as *Archaeopteryx* **[25]**. Nevertheless, the large claw of the fourth digit suggests that it was still able to climb tree trunks. This was necessary when birds occasionally landed on the ground and could not take off from the surface. In this case, it climbed up the trunk to fly from an elevation.

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