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LATE CARNIVOROUS DINOSAURS: HAND MODIFICATIONS, EVOLUTION, AND ECOLOGY

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ABSTRACT Late theropods are distinguished by a variety of hand structures, divided into grasping and non-grasping types, easily identified and distinguished from each other. Both types were self-sufficient ecomorphological structures, and an ability to grasping-non-grasping is established without difficulty and unambiguously. The grasping hand is predetermined by predation, while functions of a non-grasping hand often remain undefined, retaining its evolutionary and ecological significance. A three-digited grasping hand is an exemplary grasping pattern in dromaeosaurids with a fixed pulley-like structure limiting dislocation and "late basal" oviraptorosaurs. The absence of a pulley-like joint in a non-grasping hand increased mobility and risk of dislocation. The fused pulley-like joint indicates its ultimate fixation. Two-and single-digited hands testify in favor of its non-grasping ability. Transformation of food preferences seems acceptable as a direction for interpreting the functions of giant hands that fall out of regularity in theropod evolution, suggesting the appearance and evolution of "terrible-handed" dinosaurs. Hand modifications reached different levels of completeness, perfection, and distribution in the late theropods of North America, China, and Mongolia; some examples of the latter were almost exemplary. Hand modifications were more likely the "last" innovations in the theropod evolution, and the non-predatory theropods probably opened the way to unpredictable relationships in the late dinosaur communities, but the "great extinction" ended their history as a whole.

KEYWORDS Late theropods, Hand modifications, Grasping, Non-grasping ability, Food preferences

INTRODUCTION

During the Cretaceous time, the carnivorous dinosaurs, so-called the late theropods, underwent various morphological changes, which reached a high level in the second half of the period. Here only the modifications of their hand (manus) are touched upon, which became more diverse, highly specialized, and therefore more narrowly functional. At first glance, the hand structures seem to be only a small part of their morphology, which had no special significance in the historical development of their bearers. However, the modifiable hand outlines some regularities in the morphological evolution of theropods. The regularities are formulated as follows: modifications signify an evolution and, with a high probability, reflect an ecology that is generally accepted, although, in reality, it is far from being known. Thus, hand modification and diversity are significant to a certain extent, as they were an indicator of both phenomena – evolution and ecology. The question seems inevitable – is it necessary to consider hand modification if it already indicates both of them? At the same time, it would be too simple if the ecology of the environment and organisms were revealed so easily. Modifications only generally indicate the probability of environmental differences without disclosing their content. These issues and related details are considered below.

The mentioned regularities reflect the following directions in the evolution of carnivorous dinosaurs: first, a mosaic combination of more generalized and more specialized characters; second, a transformation of food preferences. Regularities reached varying degrees of completeness, perfection, and distribution among the late theropods of North America, China, and Mongolia. Sometimes Mongolian samples were more indicative and often used here as the most illustrative examples (Barsbold, 2019). However, traditional understanding of functional morphology often remained limited due to a lack of knowledge.

DROMAEOSAURID HAND

The theropod hand was defined almost from the beginning,

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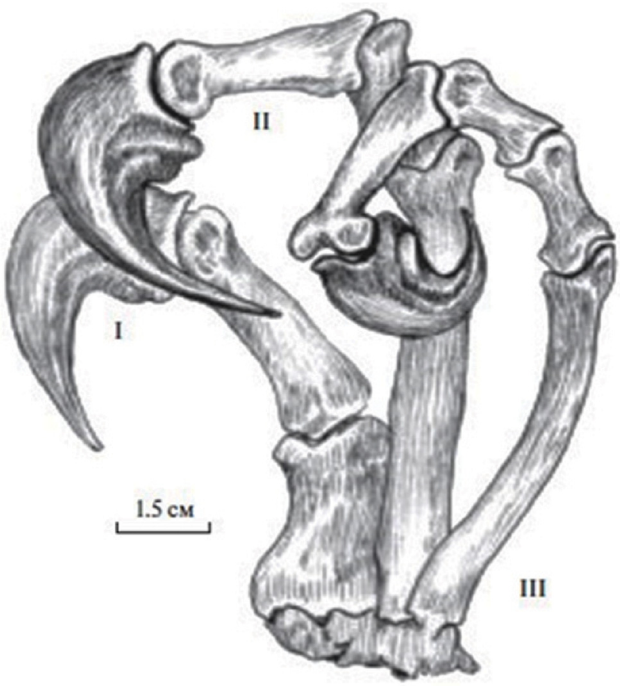

FIGURE 1. *Velociraptor*: left hand, exemplary-grasping type in flexor view. I-II-III - digits and metacarpals.

as grasping (Fig. 1), in contrast to the herbivore hand, whose actions are still little known. The ability of the hand to grasp objects is easily recognized by its structure. Morphological innovations of the theropod hands reaching their highest level by the second half of the Cretaceous were most likely the "last" in their evolution, representing samples of an even narrower specialization. The functional features of the late theropod hand became widely known, first of all, on an example of *Deinonychus* (Ostrom, 1969), the third in a row member of the dromaeosaurid family. Its first two species remained for almost half a century without movement and in full obscurity in the museum collections. Based on the first three co-family species, it was possible to identify and recreate the previously unknown structures and their functional capabilities across the whole family.

Most remarkably, interpretations of the possible functions of the hand (and foot) as a weapon of attack and defense were fully confirmed definitely by the uniquely interpreted location of these structures in dromaeosaurid *Velociraptor* Osborn 1923, one of the first theropods discovered in Mongolian Gobi, and one of two participants in the unique find of the "Fighting Dinosaurs" (Fig. 2). This happy confirmation is an almost impossible, unheard-of phenomenon in the history of vertebrate paleontology, as is the uniqueness of the "Fighting Dinosaurs" (Barsbold, 1974, 1988) so far. In this remarkable find, the hands of the carnivore *Velociraptor* (in addition to the highly specialized feet) demonstrated their functional role as effective organs for capturing a victim/enemy (Ostrom, 1969). The hand with an extremely high degree of grasping and pointed claws pierced the tissues, firmly holding the *Protoceratops* head from both sides, leaving the victim no hope of escaping from the deadly embrace of a predator. So, the weapon functions of dromaeosaurids were firstly determined in *Deinonychus* (Ostrom, 1969), but without the "Fighting Dinosaurs," these functional interpretations could turn out to be only rather successful conclusions, having remained largely speculative and divorced from a reality. Fortunately, this not happened.

Here there is no need to touch further on the various weaponry structures of the dromaeosaurids, which are beyond the scope of this consideration. Further, only the late theropod hand is touched upon, which, first, retained the "late basal" structure in more generalized groups and, second, in the specialized branches, was subject to significant shifts of changes. These more basal and equally advanced traits also fall under the two evolutionary lines outlined above (here briefly named) - a mosaic of features and transformation of food. The different mosaic features (previously known) and the transformation of food (known recently) are more concerned with the variability of the hand and its possible adaptations to the changeable environment. The established hand modifications are narrowly specialized, while other branches retain signs of more generalization, named further "late basal." This hand development is a natural consequence of morphological evolution and, more importantly, corresponds to changes in ecology in niches presented, which are not always accurately defined. Hand modifications are directly related to evolution, which is definitely and often obvious, and to the ecology of the environment, which is most indefinite and not obvious at all, considered below.

Thus, in the late theropods, thanking the example of the "Fighting Dinosaurs," a more generalized hand in a typical form represents a three-digited structure (I-II-III), which is capable of significant bending (providing a better "girth"), which created a powerful grasping effect, further enhanced by curved pointed claws. The ability of the hand to grasp objects is easily recognized by its structure. The hand has been specially adapted to perform the function of a strong

FIGURE 2. "Fighting Dinosaurs": *Velociraptor* (on the right) vs. *Protoceratops*. Predator uses its exemplary-grasping hands (along with the attacking means of the feet).

grip on the victim/enemy, thereby significantly limiting its possible counteraction. The further fate of the victim/enemy was indeed in the clutches of the predator, wonderfully demonstrated by the "Fighting Dinosaurs."

OVIRAPTOROSAURID HAND

The probable capacity for similar functions of the similarly built three-digited hand in other groups of carnivorous dinosaurs becomes high and is illustrated by the number of their branches. Among the late theropods, the hands of oviraptorosaurs (Oviraptorosauria) were the most illustrative, showing not only a typical three-digited grasping type in the "late basal" branch but also represented, in contrast to dromaeosaurids, a complete loss of the grasping ability in their advanced lines attributed to the family Ingeniidae (Barsbold, 1981, 1983). Hand modifications of the flight and swim-oriented dromaeosaurids (Lü and Brusatte, 2015; Cau et al., 2017), not considered here, were independent groups and represented, especially, in the first case, the most radical variability to conquer a special environment sphere. Perhaps, the swimming group needs more confirmation.

The grasping manus of dromaeosaurids (Ostrom, 1969) and more generalized "late basal" oviraptorosaurs (Clark et al., 2001) are practically indistinguishable from each other, being, perhaps, the highest expression of the grasping function and both representing an exemplary - grasping pattern. Dromaeosaurids and generalized oviraptorosaurs should probably be attributed to the niche of the typical attacking predators (remember "Fighting Dinosaurs," even if it was an accident).

The "late basal" oviraptorosaurs include relatively large and small forms, respectively, almost a third more (*Citipati*) and half less than dromaeosaurids (ingeniids). Small oviraptorosaurs were formerly assigned to Ingenia and Ingeniidae (Barsbold, 1981,1983), among which both more generalized (Fig. 3) and more specialized (Figs. 4, 5) forms are distinguished. Perhaps, the classification of ingeniids needs to be revised. The clear difference in the structure of an unmodified and modified hand indicates an equal difference in their functions: in the first case, the hand corresponds to the grasping, preserving

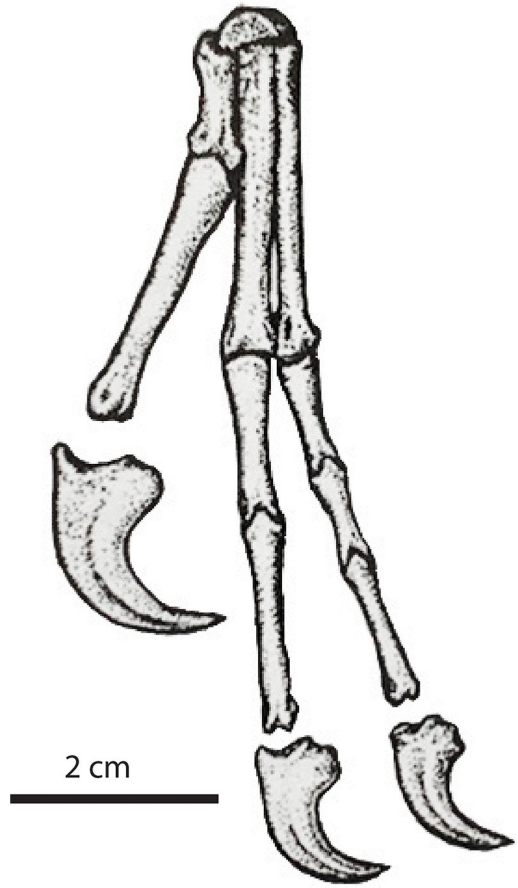

FIGURE 3. Unknown sp. of the small "late basal" Oviraptorosauria: right manus in dorsal view. Digits and their ungual phalanges are typical for a grasping hand. Assigned to Ingenia, most likely belongs to yet unidentified genus. The scale bar equals 2 cm (from Osmólska et al., 2004, fig. 8.4).

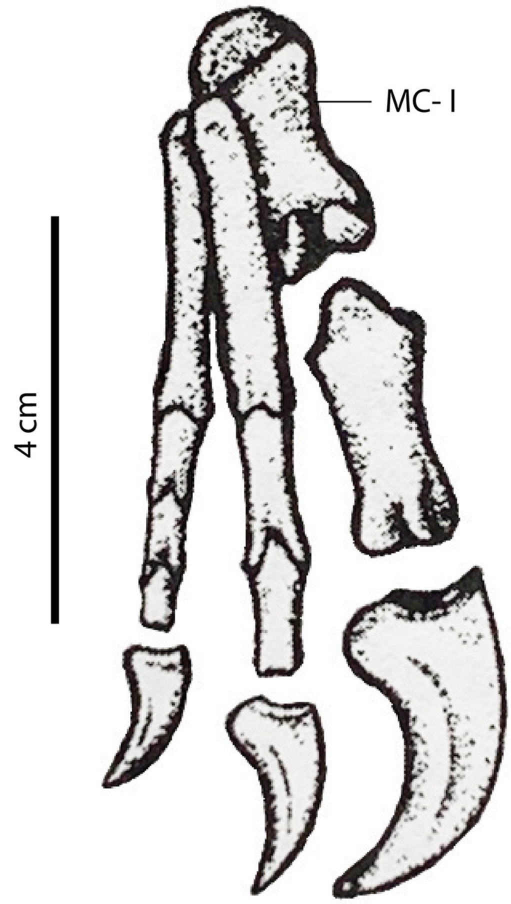

FIGURE 4. Ingeniid sp. (advanced Oviraptorosauria): right manus not grasping in dorsal view; mc I -metacarpal I. Lateral digits (II, III) are reduced (length almost equal to the first I), their ungual phalanges on straightening. The scale bar equals 4 cm (from Osmólska et al., 2004, fig. 8.3)

the main features of this type - inequality in the size of the first and two lateral digits, all with the certain signs of grasping ability. In the second, the hand is completely incapable of grasping: the hand is reduced, digit I is largest, the other two are almost equal in size, their ungual phalanges reduced and straightened. The clear difference in the structure of an unmodified and modified hand indicates an equal difference in their functions: in the first case, the hand probably possesses sufficient grasping ability, albeit inferior to larger oviraptorosaurs, like *Citipati*. In the second, the hand is completely incapable of grasping. Hence the first conclusion is: that there are at least two types of hand structure – grasping (Figs. 1, 3) and non-grasping (Figs. 4, 5). The functions of the grasping type are thoroughly defined above in dromaeosaurids (and "late basal" oviraptorosaurs, both large and small), including most clearly visible in the repeatedly mentioned "Fighting Dinosaurs."

FUNCTION OF NON-GRASPING HAND

An inevitable question - what are the functions of a non-grasping type? Various options are possible here, including those that depend to a certain extent on the imagination of researchers. There may be several acceptable real options, in case not so many. What follows are three main points regarding possible functions. First, in almost all variants, the functions of a non-grasping hand often remain indeterminate, and its actions are often not recognizable exactly. Although, for the interests of the case, an acceptable definition of the functions is certainly desirable. Second, the presence or

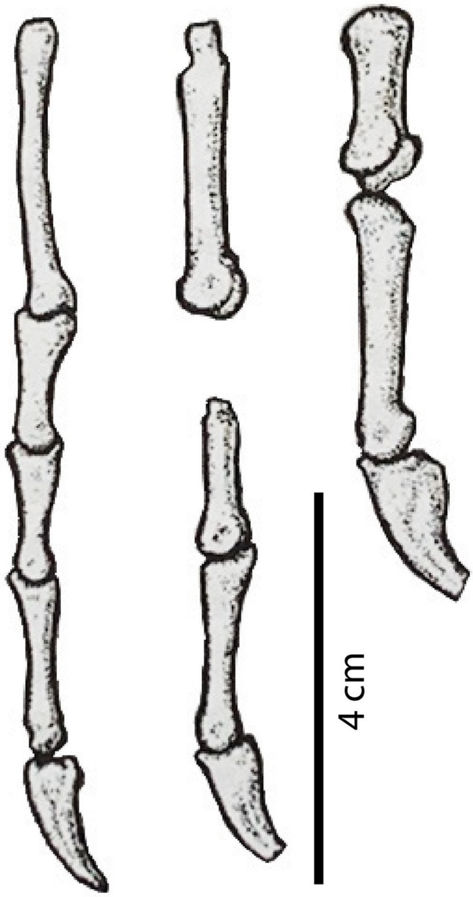

FIGURE 5. *Conchoraptor* (family Ingeniidae, advanced Oviraptorosauria): right hand not grasping, in medial view, metacarpals and digits reduced in size, thinned, ungual phalanges straightened. The scale bar equals 3 cm (from Osmólska et al., 2004, fig. 8.4).

absence of grasping ability in the vast majority is easily and accurately established: the size and shape of the hand, as a whole, then, digits and ungual phalanges, their mutual proportions make it possible to quickly and unambiguously determine whether the hand is grasping, or not. Third, for all the functional uncertainty of the non-grasping hand, its evolutionary and ecological significance does not underestimate. In ecology, much remains uncertain, although precisely this uncertainty serves (for researchers) as a warning sign of possible changes in the newly opened niches presented to the dinosaurs. Basal oviraptorosaurs with a well-pronounced grasping hand did not change the general type of feeding. The absence of teeth and the development of a horny beak may reflect the transformation of the food spectrum, but the methods of obtaining it can be variable. For example, modern flying theropods - birds of prey are equipped with a hook-shaped beak, being the predators. The "late basal" oviraptorosaurs had a massive beak, and usual grasping hands, that were probably adapted to the predation (Barsbold, 1983). The advanced branch (twice - three times smaller in size, as mentioned) with a less massive beak had a modified hand incapable of grasping. The structure of such a hand could suggest the development of a leathery (swimming) membrane. Of course, this is only one of the shaky assumptions, but consisting of the elongation of the spinal processes of the caudal vertebrae, which turns the tail into a swimming organ. Didn't specialized ingeniids feed on mollusks not capable of active resistance and living in abundance in the Late Cretaceous lakes (Martinson, 1982; Barsbold, 1983), thereby changing their habitat and preserving the predator lifestyle, but adapted to the new conditions? Basal oviraptorosaurs with a well-pronounced grasping hand did not change the general type of feeding. The hand modifications' examples of narrow specialization potentially contain supposed orientations in these conditions. In addition to the typical three-digited hand in theropods, another phenomenon of variability, as a reduction of the digit number took place-to two digits in tyrannosaurids and advanced oviraptorosaurs and, at least, in one alvarezsaurid (Bonaparte, 1991) species to one. Previously, these characters were known in tyrannosaurids at first, and later the examples of reduction gradually increased. The well-known two-digited hand in tyrannosaurids usually not raised any questions, although so far, the functions of their greatly reduced and shortened forelimbs have not found an acceptable explanation. The grasping ability of the two-digited hand was fully lost, being usually accepted even without taking into account its structure, which really hardly contained this ability with such a reduction in the forelimbs. Maybe, the loss of grasping and reduction of the forelimbs indicated a transition of the tyrannosaurids into the niche of scavenger predators (Edwin Colbert's remark that a tyrannosaurid was a mouth set on its hindlimbs). It is only about the main direction of their adaptation, but tyrannosaurid's food preferences could include dead animals and food objects caught by them, which is typical of the recent predators (Farlow & Holtz, 2002).

In the exemplary - grasping hand in dromaeosaurids, the numerically reduced carpal elements formed with metacarpals a "pulley"-like connection (Ostrom, 1969), which simplified and "modernized" this important joint allowing both mobility freedom of the hand and its strong fixation. This joint protected the predator's hand from dislocation due to sudden movements of the prey/enemy in order to free themselves from the deadly embrace of the predator. On the contrary, the extended participation of carpal elements (often up to 5, what's a typical "non-pulley" structure) in this joint forms a connection of the non-grasping hand with more freedom of mobility, more disorderly and much less fixation, and therefore more prone to dislocation (Barsbold, 1983). Such a joint is observed in Mongolian ornithomimids and tyrannosaurids (*Tarbosaurus*), which had a non-grasping ("non-pulley") hand, although in earlier works non-Mongolian ornithomimids, as a rule, were traditionally called grasping, and reconstructed, as grabbing their food objects, which now seems hardly acceptable. In extreme cases, their hand could occupy an intermediate position; however, this option has not yet been met; perhaps, they preserved (in vivo?) rarely, being probably maladaptive.

DISCUSSION

Approximately a dozen scattered remains of carpometacarpals found in a large area of Nemeget deposits in the Gobi, forming the completely fused pulley-like structure (Fig. 6), eliminating any mobility at this point of the hand. At first glance, such an unusually strong fusion, not seen before, suggested teratology in the hand of its bearers. However, the multitude of these remains testified with a greater probability that this fusion was not accidental and most likely represented the creation of a monolithic unity of metacarpal-carpal elements, which increased fixation to the complete exclusion of any mobility in the former joint. In this way, the possibility of any dislocations in the grasping hand was excluded since the articular connection was no longer in reality. With the resistance of the victim/enemy, the bones of the hands and forelimbs would be more likely to be broken than these monolithic joints dislocated.

It can be assumed that in a lifetime, this small but important region of the hand joint was often subjected to dislocations, which could serve as a challenge to strengthen this weak point, which would be a significant win for the predator. Doesn't this testify in favor of the fact that the grasping hand, as a weapon of attack and defense, often came into action, and the victim/enemy captured by it in the category of size and weight was at least not inferior to the predator, capable of active resistance and in attempts to free

FIGURE 6. Unidentified small "late basal" oviraptorosaur: metacarpals and carpals (medial-dorsal view) were completely fused, greatly restricting mobility freedom and protecting against dislocation in the joint. MC I - metacarpal I; pulley-like joint shown by arrow.

itself had a strong impact on the grasping hands up to dislocating or breaking off its weak point? An increase in the fixation of this point towards solidity and hardening was noted above in the pulley structures of dromaeosaurids. However, the structures of the hand considered here are more similar to those of specialized oviraptorosaurs (Ingenia) mentioned above, which could suggest that the hand was oriented towards a very strong, immovable connection in some of them (Barsbold, 1981). Unfortunately, the digits and ungual phalanges have not been preserved, so the question of the grasping - non-grasping in this curious case remains open. It seems unlikely this is a mass disease within one species over such a wide area. In any case, with or without grasping ability, this phenomenon could be a clear sign of a probable radical modification of the hand in one of the still-unknown late theropods.

Other apparently radical modifications include unusual

FIGURE 7. *Therizinosaurus*: ungual phalange probably of digit I, medial view about 0.7 m long (Maleev, 1954).

hand structures (and forelimbs) in *Therizinosaurus* and *Deinocheirus* (Rozhdestvenskiy, 1970; Barsbold, 1974; Lee et al., 2014), from the very beginning, separately assigned to independent families of therizinosaurids and deinocheirids correspondingly (Maleev, 1954; Osmólska and Roniewicz, 1970). Their hands were distinguished by gigantism, which was not previously found in theropods but differed sharply from each other (Figs. 7, 8). The former had laterally flattened ungual phalanges up to 0.7 m long, while the latter was half as large and very massive. One glance is enough that these hands are completely outside the grasping ability: their general structure, dimensions, shape, and proportions of the digits and ungual phalanges, in particular, clearly indicate an impossibility of any form of grasping or, holding a food object with the help of digits and claws, and even more so actively counteracting enemy.

For many decades these unusual giants remained the most mysterious Mongolian dinosaurs, although *Deinocheirus* (but not *Therizinosaurus*), now represented by almost complete skeletal material (Lee et al., 2014), went through its second discovery and its long-distinguished position was assigned to ornithomimosaurs. The first discoverers (H. Osmólska, personal communication) also suggested a possible assignment of *Deinocheirus* to ornithomimosaurs, the most numerous part of which (actually ornithomimids) are probable herbivores (Kobayashi et al., 1999; Chinzorig et al., 2017), in any case reflecting changes in the environment, and likely related approaches to the consumption of its resources. Stomach stones have been found in ornithomimids, and deinocheirids were not bypassed by this, being related to ornithomimosaurs. This adaptation is considered an indicator of herbivory, even though the recent crocodiles, which can hardly be classified as vegetarians, and some birds of prey are found to have stomach stones (according to Y.-N. Lee, stomach stones are also found in Mongolian *Tarbosaurus*). Perhaps, the presence of stomach stones is not so simple a phenomenon unequivocally deciding the food preferences, which seem to have led some late theropods into vegetarian niches. The reasons are unknown; one can name the increased competition for consumption (old-fashioned fight for food), an abundance and variety of plant foods, and the emergence of new resources (for example, angiosperms). Whatever the reasons

FIGURE 8. *Deinocheirus*: both forelimbs and right manus (front left) with the massive ungual phalanges. The first ungual phalange (shown by arrow) is about 35 cm long.

for the appearance of these strange reptiles, such an unusual developmental path only emphasizes the evolutionary and ecological potential of the late theropods and is an indicative sign of hand modifications in general. The gigantic size and theropod appearance of these "terrible-handed" theropods probably served as self-defense for them. Consumption of plant foods, if it was in reality, should have led to considerable changes in their digestive system (almost imperceptible in the fossil state) and other, taphonomically more accessible parts of their morphology (Xu et al., 2002; Zhou & Zhang, 2002; Barrett, 2005; Barrett & Rayfield, 2006; Chinzorig et al., 2017). However, the hand functions of both giants remain unshakably undefined, especially in *Therizinosaurus* ("Lizard mowing the grass," Maleev, 1954).

More than a decade ago, the classification, possible family ties, and ecological features of these dinosaurs were raised based on incoming new material in search of a way out of established ideas led to the most successful path - to a new approach in the evolutionary orientation of "terrible-handed" dinosaurs, exemplified the transformation of food preferences (Paul, 1984; Kirkland & Wolfe, 2001; Zhang et al., 2001; Li et al., 2007; Zanno, 2010) – mainly from carnivore to herbivore (Russel & Russel, 1993; Zanno et al., 2009; Zanno, Makovicky, 2011). The variety of vegetation could also suggest its differences, as food for "terrible-handed." But the most important is the transformation of food (Lautenschlager et al. 2013; Lautenschlager 2014), which serves as an acceptable explanation for the appearance of such unusual modifications of the hand (and how this food is consumed): it completely loses its no longer necessary grasping and acquires non-grasping function in probable accordance with the class of vegetable food and possible ways of its consumption. Some Mongolian examples (advanced oviraptorosaurs, as mentioned) may suggest a food change within predation (eating mollusks). Hand modifications demonstrate a simple and revealing approach to some peculiarities of the late ecosystems, whose dinosaur communities are now well known in contrast to many features of their ecology, consumption of the food resources, and environment as a whole.

Such a radical change outlines a way out of a hopeless situation for decades. Although the hand functions are not really defined, this uncertainty indicates the presence of a non-grasping hand, as established in all the above examples, and appears to be equally significant and self-sufficient in an evolutionary and ecological sense (Weishampel & Norman, 1989; Russell & Russell 1993; Kirkland et al., 2005), of course, being not free from the inherent problems of the non-grasping hand.

CONCLUSION

Late theropods are distinguished by a variety of hand structures, divided into grasping and non-grasping types, easily identified and distinguished from each other. Both types appear to be self-sufficient ecomorphological structures, the first fully adapted for grasping, the second for non-grasping. The ability to grasping-non-grasping is established without difficulty and unambiguously. The functions of the grasping hand are predetermined by predation, while those of the non-grasping hand most often remain completely undefined, nevertheless retaining its evolutionary and ecological significance. Like most other modifications, these reflect the movement of evolution, which is certain and obvious, and the ecology, which is often indefinite, indefinable, and therefore not obvious. The three-digited grasping hand is an exemplary-grasping pattern (as in dromaeosaurids and "later basal" oviraptorosaurs). In the exemplary-grasping hand, the carpal elements are reduced to two, constituting the pulley-like structure of the fixed connection, limiting the risk of dislocation. An increase in the number of carpal elements expands the freedom of movement in the joint, thereby increasing the risk of dislocation. The complete fusion of the metacarpal-carpal elements in the pulley joint indicates its ultimate fixation. The two- and single-digited hand correspondingly with a change in the remaining digits also testifies to its non-grasping ability. The transformation of food preferences seems acceptable as a general direction for interpreting the functions of giant and unusual hands, presumably indicating an infrequent and rather strange orientation that falls out of regularity in the late theropod evolution. This orientation suggests the possible consequences of the appearance and evolution of "terrible-handed" dinosaurs in the communities by the end of the Cretaceous. Perhaps, an intensification of the food competition and an abundance of diverse vegetation (including angiosperms) created favorable conditions for entry into the new consumer's spheres, formerly predatory groups, but capable of radical changes, which developed relationships never existed before in the late organic communities.

Manual structures and their significant and varied modifiability (in balance with all other features) outlined two established directions of the theropod evolution: a mosaic of more generalized and specialized features and a transformation of food preferences. All these features reached different levels of completeness, perfection, and distribution among the late theropods of North America, China, and Mongolia, some of which were almost exemplary. Much later, the evolutionary hand transformations are determined by their ecomorphology, primarily indicating a change in ecology and clearly stated in the evolution of the late theropods. Much later, it was discovered that hand modifications are the simple way of an attempt to define the late ecosystems, the dinosaur communities of which became now well known (like other organic groups), being more refined over time, but unlike many specific conditions of the environment.

The hand structure reached its development to a modifiable ecomorphological pattern, evolutionarily fixed in the late theropods, the functions of which were determined initially. Freedom from locomotion opened the way to diversity in structure, among which the non-grasping modifications were developed in various ways, leading to deviations in the evolution and ecology of their bearers. These modifications showed significant innovations, probably almost the "last" in the evolution of the late theropods. The appearance of probable non-predatory theropods of various, especially gigantic sizes, and generally retaining a theropod appearance could open the way to unpredictable relationships in the late dinosaur communities if not for the "great extinction" that ended the Cretaceous period and an entire Mesozoic history of the dinosaur evolution.

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