*Palaeontologia Electronica*
palaeo-electronica.org

# A complete passerine foot from the late Oligocene of Poland

**Zbigniew M. Bochenski, Teresa Tomek, and Ewa Swidnicka**

## ABSTRACT

The paper describes a nearly complete articulated specimen of a passerine foot imprinted on a slab and counter slab of the siliceous clayey shales belonging to the upper part of the Menilite Formation of the Outer Carpathians in southeastern Poland and dated to the late Oligocene (Chattian, ca. 25 m.y.a.). It is one of the very few Paleogene specimens of passerines and just the third with a complete foot preserved. Its passerine affinities were established on the basis of a combination of characteristic features but owing to the incompleteness of the specimen its more precise systematic position within Passeriformes cannot be resolved. For the same reason the specimen is not described as a new extinct species although it differs from all known Oligocene passerines. The proportions of phalanges, size of the tarsometatarsus and shape of claws point to an arboreal bird, which increases the known Paleogene diversity of this bird group.

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**Keywords:** Fossil birds; Passeriformes; Menilite shales; Carpathian flysch; Oligocene; Paleogene

## INTRODUCTION

The order Passeriformes includes more than half of all extant bird species but little is known about its early history because of the paucity of its fossil record from the Paleogene. The oldest two fossils of possible passerine affinities were found in Australia and are dated to the early Eocene (Boles, 1995, 1997), but unquestionable remains of passeriforms come from the Oligocene of Europe. So far only three species based on relatively complete specimens have been described from the Oligocene: *Wieslochia weissi* Mayr and Manegold, 2006 from Germany (Mayr and Manegold, 2004, 2006a) and two species from Poland – *Jamna szybiaki* Bochenski, Tomek, Bujoczek, and Wertz, 2011

PE Article Number: 17.1.6A

Submission: 17 September 2013. Acceptance: 27 January 2014

Bochenski, Zbigniew M., Tomek, Teresa, and Swidnicka, Ewa. 2014. A complete passerine foot from the late Oligocene of Poland. *Palaeontologia Electronica* Vol. 17, Issue 1;6A; 7p;
palaeo-electronica.org/content/2014/674-oligocene-passerine-foot

**FIGURE 1.** A map of Europe with Poland (orange) and the location of the village of Hłudno (asterisk) in southeastern Poland, where the specimen ZPALWr. A/4005 was found.

(Bochenski et al., 2011) and *Resoviaornis jamrozi* Bochenski, Tomek, Wertz, and Swidnicka, 2013 (Bochenski et al., 2013a). All three species are dated to the early Oligocene, and their systematic position within Passeriformes remains unresolved because they show a mosaic of characters typical for the Oscines or Suboscines. Another complete specimen of a passerine bird was found in the early Oligocene of Lubéron, France, but it has not been described yet (Mayr, 2009). The remaining Oligocene remains described in the literature include an articulated wing (Mayr and Manegold, 2006b) and a handful of isolated wing bones – those from the late Oligocene represent both Oscines and Suboscines (Manegold, 2008; Mourer-Chauviré et al., 1989). Leg bones and especially their distal elements are even rarer. Legs of *Wieslochia weissi*, *Jamna szybiaki* and *Resoviaornis jamrozi* are incomplete. Only one specimen of a complete articulated passerine leg is known from the Oligocene (Bochenski et al., in press). Apart from it, only two other fragments of the tarsometatarsus are known from the Oligocene of France (Mourer-Chauviré, 2006; Mourer-Chauviré et al., 1989, 2004).

In this paper, we describe a nearly complete articulated specimen of a passerine foot found in southeastern Poland (Figure 1) which is a large region, very abundant in fossil remains preserved in marine deposits of the former Paratethys Ocean (Bochenski et al., 2013b). Animal fossils other than fishes are found only sporadically there and birds are also extremely rare. The paper provides new details on the scanty record of the foot morphology of Paleogene passerines and increases the known diversity of this bird group.

## METHODS

Osteological terminology follows Baumel and Witmer (1993). Dimensions are given in millimeters and refer to the greatest length along the longitudinal axis of the bone. The fossil was compared with extant specimens from the osteological collection of the Institute of Systematics and Evolution of Animals, Krakow, Poland. The fossiliferous horizon in the village of Hłudno has been dated on the basis of the fish assemblage and correlated with the calcareous nannoplankton (Berggren et al., 1995; Kotlarczyk et al., 2006).

## SYSTEMATIC PALEONTOLOGY

Class AVES Linnaeus, 1758
Order PASSERIFORMES Linnaeus, 1758
Family, genus, and species indeterminate

**Material.** Two slabs (Figures 2, 3) with imprints of a complete right passerine foot, deposited at the Division of Palaeozoology, University of Wroclaw, Poland (ZPALWr. A/4005). Found in 1976, first mentioned in the literature in 1979 (Bochenski and Szymczyk, 1979).

**Locality and horizon.** The specimen was found at one of the 15 exposures of Oligocene marine deposits in the Menilite Formation of Skole Nappe of the Outer Carpathians, situated along a forest

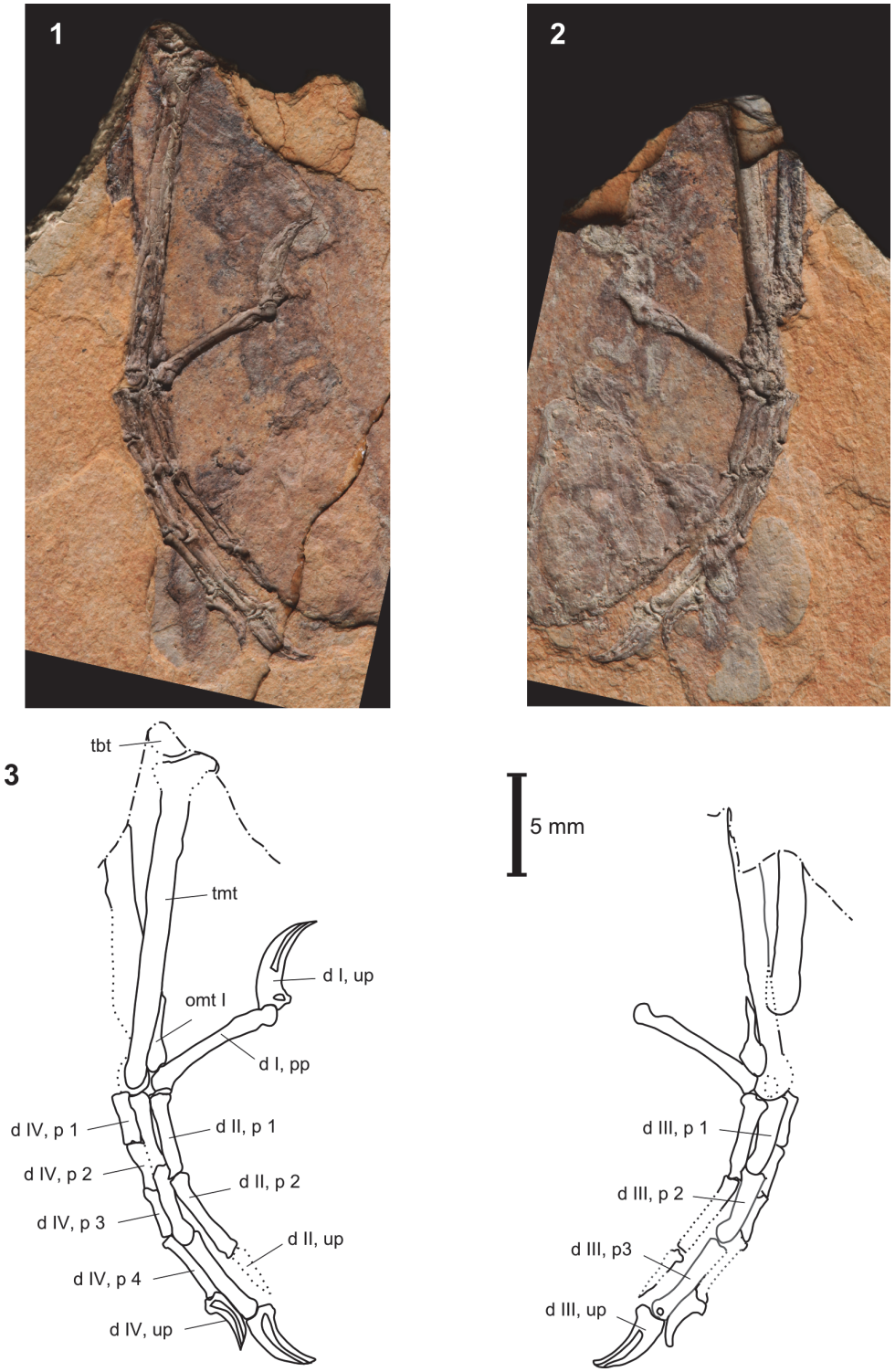


**FIGURE 2.** Specimen ZPALWr. A/4005 of a passerine bird foot from southeastern Poland, Hłudno, late Oligocene, ca. 25 m.y.a. **1,** Main slab; **2,** Counter slab; **3,** Interpretative drawings of the main slab and counter slab. Abbreviations: d I, pp – digit I, proximal phalanx; d I, up – digit I, ungual phalanx; d II, p1 – digit II, phalanx 1; d II, p2 – digit II, phalanx 2; d II, up – digit II, ungual phalanx; d III, p1 – digit III, phalanx 1; d III, p2 – digit III, phalanx 2; d III, p3 – digit III, phalanx 3; d III, up – digit III, ungual phalanx; d IV, p1 – digit IV, phalanx 1; d IV, p2 – digit IV, phalanx 2; d IV, p3 – digit IV, phalanx 3; d IV, p4 – digit IV, phalanx 4; d IV, up – digit IV, ungual phalanx; omt I – os metatarsale I; tmt – tarsometatarsus; tbt – tibiotarsus (fragment of the condylus lateralis).

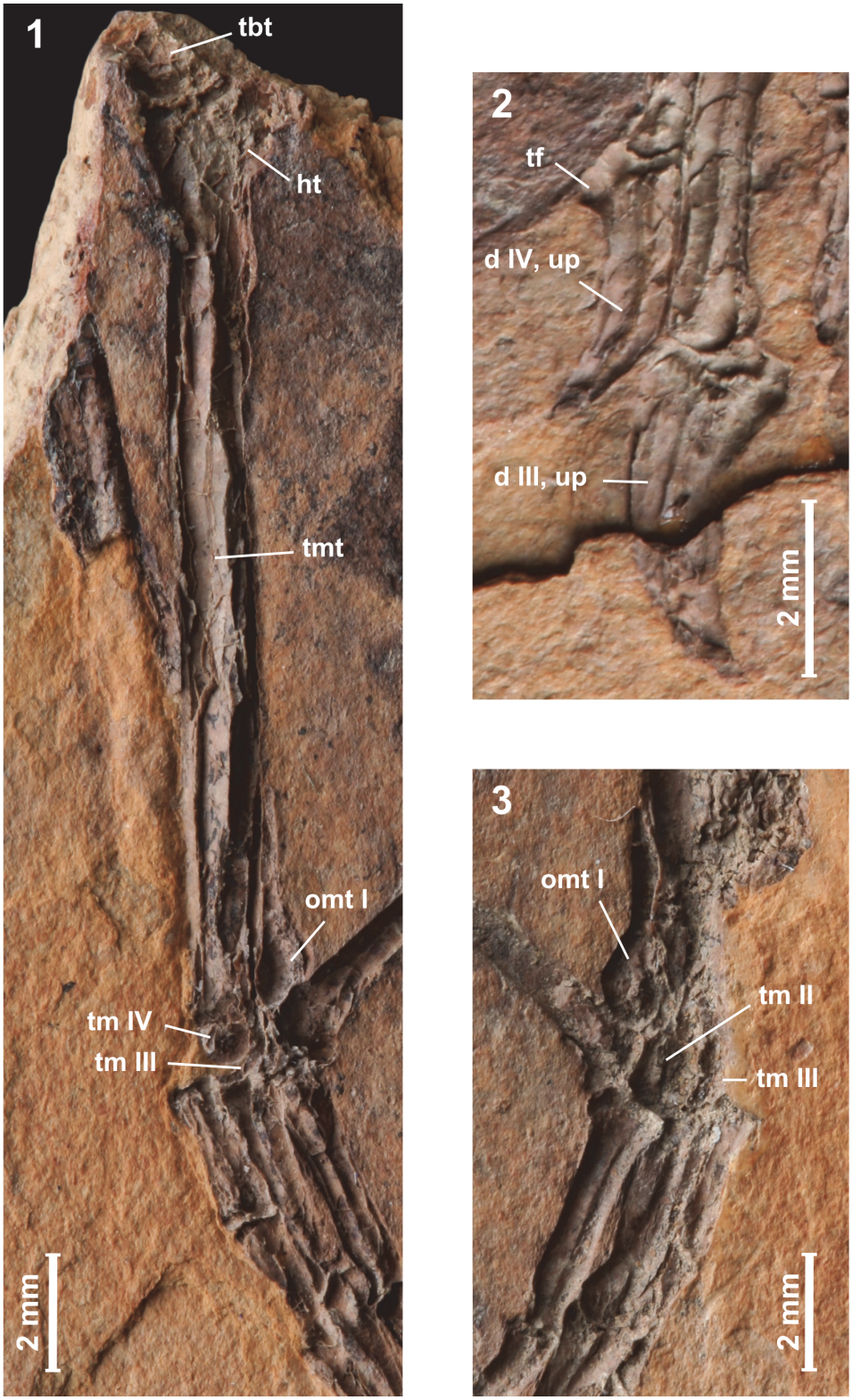


**FIGURE 3.** Specimen ZPALWr. A/4005 of a passerine bird foot from southeastern Poland, Hłudno, late Oligocene, ca. 25 m.y.a. **1,** Enlarged tarsometatarsus from main slab; **2,** Enlarged ungual phalanges (claws) of digits III and IV from main slab; **3,** Enlarged distal tarsometatarsus from counter slab; Abbreviations: d III, up – digit III, ungual phalanx; ht – hypotarsus; omt I – os metatarsale I; tf – tuberculum flexorium; tm II – trochlea metatarsi II; tm III – trochlea metatarsi III; tm IV – trochlea metatarsi IV; tmt – tarsometatarsus; tbt – tibiotarsus (fragment of the condylus lateralis).

road in the village of Hłudno, about 7 km southwest of Dynów and 30 km southeast of Rzeszów, Podkarpackie Voivodeship, southeastern Poland (Figure 1). Geographical coordinates of the site: 49°46.835′N, 022°08.122′E. ZPALWr. A/4005 was found in association with several articulated fish imprints including *Eovinciguerria obscura* (Danilt-shenko, 1946), *Eomyctophum koraense* Danilt-shenko, 1947, *Sardinella sardinites* (Heckel, 1850) and *Alosa* sp., Linck, 1790. The fish taxa composition is characteristic of the upper bathypelagic assemblage of IPM6 zone (Kotlarczyk et al., 2006) which correlates with the calcareous nannoplankton of the upper part of the NP25 zone *sensu* Berggren et al. (1995) and indicates a late Oligocene age (Chattian, ca. 25 m.y.a.) for the assemblage.

**Diagnosis.** Small passerine, approximately the size of a Great Tit *Parus major* or a Tree Sparrow *Passer montanus*, which is distinguished from all other non-passerine taxa by the combination of the following characters: (1) the tarsometatarsus bears a relatively short proximo-distally hypotarsus, (2) a marked crista plantaris lateralis, and (3) has the small trochleae of the second, third and fourth pedal digits arranged in a line (i.e., dorso-plantarly level in distal aspect) and reaching approximately equally far distally; (4) the specimen shows an anisodactyl foot; (5) the proximal phalanx of the hallux is greatly elongated; (6) on each digit the penultimate phalanx is the longest; (7) the claws show relatively little curvature and their tubercula flexoria are weakly developed.

## Description and Comparison

Similarly to other bird fossils from the Oligocene of Poland (Bochenski and Bochenski, 2008; Bochenski et al., 2010, 2011, in press), particular elements in ZPALWr.A/4005 are broken longitudinally and preserved as imprints partly lined with remnants of bone. Therefore, often a mixture of an imprint and the inner side of a bone rather than its external surface is visible, which sometimes makes it difficult to recognize the left and right sides or the anterior and posterior views at first glance, especially in the photographs.

**Measurements (maximum length in mm).** tarsometatarsus, 18.0; hallux: proximal phalanx, 7.4; hallux: claw, 4.9; first phalanx of digit II, 4.4; second phalanx of digit II, 5.1; claw of digit II, ~3.1; first phalanx of digit III, ~4.0; second phalanx of digit III, 4.2; third phalanx of digit III, 5.4; claw of digit III, 4.1; first phalanx of digit IV, 2.7; second phalanx of digit IV, 2.6; third phalanx of digit IV, 2.7; fourth phalanx of digit IV, 3.8; claw of digit IV, 3.3.

The percent lengths of the nonungual phalanges of digit III are as follows: Phalanx III-1, ~29.4%; Phalanx III-2, 30.9%; and Phalanx III-3, 39.7%.

**Tibiotarsus.** A small fragment of the condylus lateralis is visible on the main slab but it is too poorly preserved to allow meaningful comparisons.

**Tarsometatarsus.** An imprint of the lateral side with remnants of bone is seen in the main slab, and a partial imprint of the medial side is preserved on the counter slab. The tarsometatarsus is similar in length to that in the early Oligocene *Wieslochia weissi* and distinctly shorter than in ZPALWr. A/4004 from Przysietnica (Bochenski et al., in press); among extant species, its size corresponds to that in *Parus major* or *Passer montanus*. As in extant passeriforms, the lateral edge of the cotyla lateralis is slanting somewhat distally toward the dorsal side. The eminentia intercondylaris is not preserved. The exact outline of the hypotarsus is not preserved because fragments of its distal edge are hidden in the matrix. However, it is clear that the hypotarsus is relatively short proximo-distally as in all extant passeriforms and the early Oligocene ZPALWr. A/4004 from Przysietnica (Bochenski et al., in press). No details of hypotarsal canals and/or furrows are visible. The shaft bears a marked crista plantaris lateralis, which is hidden in Figures 2 and 3 under an overhanging edge of matrix but is visible when the main slab is tilted. The marked crista is present only in extant passerines and cuckoos (Manegold et al., 2004) and it was also present in the extinct early Oligocene passerine ZPALWr. A/4004 from Przysietnica (Bochenski et al., in press). The distal end with the small trochleae of the second, third and fourth pedal digits that are arranged in a line (i.e., dorso-plantarly level in distal aspect) is highly characteristic for all passeriforms. The well-imprinted trochlea metatarsi IV reaches only a little less distally than the shallower imprinted trochlea metatarsi III (seen in the main slab). Also, the trochlea metatarsi II is only a little shorter than the trochlea metatarsi III (seen in the counter slab).

**Toes.** As in all passeriforms, the foot has anisodactyl arrangement of toes, with three digits directed forward and one digit directed backwards. The phalangeal formula is 2-3-4-5. As in most extant passerines, all digits are thin and relatively long although on each digit the penultimate phalanx is clearly the longest. In the early Oligocene ZPALWr. A/4004 from Przysietnica the second and the third phalanges of digit III were approximately of the same length. As in all other passeriforms, the os metatarsale I bears a cylindrical trochlea metatarsi I. Also as in all extant passeriforms, the early Oligo-

cene *Wieslochia weissi* and ZPALWr. A/4004 from Przysietnica (Bochenski et al., in press), the proximal phalanx of the hallux is greatly elongated. The third digit is the longest; its length is approximately the same as that of the tarsometatarsus. The second digit is a little shorter than the fourth. The claws show relatively little curvature, their tubercula flexoria are weakly developed and they bear a groove along their length.

## DISCUSSION

While there is no doubt that ZPALWr. A/4005 belongs in Passeriformes, its more precise affinities remain unresolved due to the incompleteness of the specimen and large number of extant taxa. The fact that ZPALWr. A/4005 differs in absolute size and proportions from other Oligocene passerines described so far from Poland, and that it is younger from the early Oligocene *Wieslochia weissi*, *Jamna szybiaki*, *Resoviaornis jamrozi* and ZPALWr. A/4004 (Bochenski et al., in press) might mean that it represents a different taxon. However, the material available is too scanty to describe it as a new extinct species.

It is generally accepted that the proportions of the nonungual phalanges reflect the locomotor habits of birds. In modern birds with grasping feet, i.e., including many passerines, the penultimate phalanx of digits II, III and IV is typically longer than the more proximal phalanges (e.g., Hopson, 2001; Morschhauser et al., 2009; Stresemann, 1927-1934). The phalangeal proportions of ZPALWr. A/4005 correspond well with those of typical “arboreal” modern birds (Hopson, 2001). Living birds with grasping feet are distinguished in that the penultimate phalanx 3 of digit III is relatively longer than the other phalanges in the digit and, consequently, it constitutes a larger percentage of the total length of the digit (in our case 39.7% of the three nonungual phalanges). The higher the percent total length of phalanx III-3, the more specialized the foot appears to be for grasping (Morschhauser et al., 2009). Of the 39 passerine species studied by Hopson (2001), the most similar to ZPALWr. A/4005 in phalangeal proportions are two “arboreal” species *Catharus fuscescens* and *Cyanocitta cristata* whose penultimate phalanges of digit III make up 38.0% and 38.6% of the three nonungual phalanges, respectively, but they have much longer tarsometatarsus than our specimen. The two modern species with the absolute length of the tarsometatarsus similar to ZPALWr. A/4005 also have their phalangeal proportions similar to our fossil specimen – the penultimate phalanx of digit III makes up 41.4% in *Parus major* and 37.4% in *Passer montanus* (own data). However, the relative proportion of phalanx III-3 should be interpreted with caution because Hopson's (2001) measurements of the “terrestrial” *Menura novaehollandiae* (39.2%) are also similar to that of ZPALWr. A/4005.

Short legs are interpreted as adaptations to arboreal locomotion and indeed many species that forage in trees have their leg bones shorter than those foraging on the ground (e.g., Zeffer et al., 2003). Therefore, the short tarsometatarsus of ZPALWr. A/4005 would support the conclusions drawn from the proportions of phalanges but caution is advised because we do not know what the remaining leg bones looked like. Unfortunately, not much can be drawn from the relatively little curvature of the claws in ZPALWr. A/4005 because it does not preclude ground or arboreal foraging behaviour (Glen and Bennett, 2007).

The evidence discussed above strongly suggests that ZPALWr. A/4005 was an arboreal rather than terrestrial bird. In this respect it differed from the early Oligocene *Jamna szybiaki*, *Resoviaornis jamrozi* and ZPALWr. A/4004 (Bochenski et al., 2011, 2013a, in press, respectively) that spent much time on the ground, foraging among trees and shrubs.

## ACKNOWLEDGEMENTS

We thank K. Wertz for his help in editorial works that included the text and figures.

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