

Structural Variations in Feather Morphology and its Predicted Function in Indian Peacock *Pavo Cristatus*

Monalisa Mishra¹

Asst Professor, NIT Rourkela, Rourkela, Orissa, India

Abstract: Peacock exhibit a greate diversity in the morphology of their feather pattern. The diversity of feather changes with age and affect the appearance of peacock significantly. The causes of variations are not known and opens a wide field for scientific research under developmental biology, ecology, ethology and behavioral studies. The current study describes the complete documentation of feathers present in different body parts of peacock (*Pavo cristatus*) not reported in earlier studies.

Keywords: *Pavo cristatus*, Plumage pattern, Crown feather, Saddle feather, Contour feather, Eye spot, Tail covert.

I. INTRODUCTION

Feathers produced by birds are extraordinarily diverse and complex in nature¹. The diversification of feathers arises to congregate numerous physiological and functional requirements of the bird²⁻⁵. The various functions include flight, swimming, thermoregulation, physical protection, visual and tactile communication, sound production, foraging and water repellency^{2,6}. To execute a specific function, feather structures undergo certain changes in size, shape, color, and texture^{1,7-9}. In an individual bird various layers of feathers are found in different parts of the body and altogether it forms the complete plumage pattern.

Birds develop the most colourful plumage patterns. Each species has its own identifying plumage blueprint¹⁰⁻¹³. As a consequence plumage pattern offers an ideal topic for understanding the process of evolution among birds^{14,15}. Intraspecific variation of plumage pattern is observed in many species and such variation is associated with age and sex¹⁶⁻¹⁹. Sex-linked plumage variation (or sexual dimorphism) is a prominent phenomena among birds, which play a foremost role in avian communication such as mate selection. Earlier sexual dimorphism was focused only on the feather coloration, but later studies have found also its impact on the structural variation among feathers^{16,20}. In females, sexual dimorphism arises due to camouflage and instead male develop ornamental feathers.

Plumage patterns of male birds are often brightly and diversely coloured although evolutionary cause of this sexual dichromatism is not exactly deciphered^{21,22}. The ornamented feathers of male is an indicator of quality, condition, and parental effort which is associated with reproductive success²³. Plumage colouration in birds can broadly be classified into two types: (1) pigmentary colour (2) structural colour. The first one is the result of chemical properties of pigments^{24, 25} and their concentration in feathers, whereas the second one is due to the presence of nanostructures present in it^{26, 27}. The most common materials in these nanostructures are keratin, melanin and air²⁸. Colours like blue, green, violet and ultraviolet are usually the result of such structural coloration.

Plumage colouration, produced by birds covers a wide range of electromagnetic spectrum. Most plumage coloration includes the violet (VS), and ultraviolet sensitive (UVS). To perceive the wide spectral variation of plumage colorations diurnal birds evolve the most advanced color vision²⁹. Four different types of cone evolved during eye evolution in birds. Birds use UV cues for mate choice and foraging. The UVS help to discriminate between colours in the natural surroundings. The colour perception of an object/feather depends on three principles³⁰: (1) the physics of light reflection and transmission to the surface of the eye; (2) light transmission, reflection and photoreception within the eye; (3) the neural processes in the retina and brain. The second and the third phenomena are associated with the structure of the eye whereas the first one is allied with the structure of the feather.

The mechanism involved in the process of plumage colouration helps to understand the evolution of colourful plumage, as various mechanisms have their own impact on the cost of production and maintainance of feather^{31,32}. Analyses of feather structure, present in different parts of the body, offer a promising approach to specify how feather structure may mediate life history of an animal³³. Different types of feather texture indicates that the body plumage has undergone several changes over a period of time independently, making the plumage pattern different

¹ Corresponding Author :mishramo@nit-rkl.ac.in

and distinct and which may help for further study and analysis in this field. Although the feather structure remains uniform at the earlier period of life it undergoes a typical change at the later part of life^{1,34}. However, remarkably little is known about the functions and trade-offs responsible for variations in the body structure of the feather.

The male Indian Peafowl (*Pavo cristatus*) is one of the iridescently colored bird belonging to the family of Pheasant. Members of this family possess sexual dimorphism in their plumage pattern. Besides sexual dimorphism strikingly diverse plumage patterns are observed over different parts of the peacock body. So far most of the studies focuses only on the eye spot of the tail feather or its structural colorations and its role in mate selection process³⁵⁻³⁷. A study describing the structure and colour variation of various feathers present in different body parts is lacking from the literature. Feather coloration is a complex phenomena and how various plumage coloration develop just from a single melanocyte is receiving attention in these days³⁸. The current study is an attempt to analyse the variations of plumage pattern in Indian Peacock *Pavo cristatus* as no such studies are conducted earlier. The study will help stem cell biologist, morphologist, physiologist and comparative anatomist in various ways.

II. MATERIALS AND METHODS

Peacocks generally molts once in a year during the period of July-October in India. Feathers of peacock were collected from BITS Pilani, Rajasthan Campus during these months. The feathers were brushed to remove the dust and twigs to make them clean and kept in a separate plastic zipped lock bags to preserve them for future observation. At least 5 feathers were used for the measurement and Butler et al.³³ were followed for measuring various parameters.

III. RESULT AND DISCUSSION

Peacock plumage can be classified into the following categories such as (1) Crown feather (2) Neck feather (3) Dorsal/Back feather (4) Contour feather (5) Tinge feather (6 and 7) Flight feather (8) Tail feather (9) Abdominal feather (Fig 1).



Fig1. Plumage pattern of the peacock. (A) Various feathers are numbered sequentially in different figures. Feathers highlighted in this figure are Crown feather (1), Neck feather (2), Saddle feather (3) and Contour feather (4). (B) Tinge feather (5) along with other feathers of figure A are shown in this figure (C) Flight feather (6 and 7) and various Tail feathers (8) demarkated in this figure.

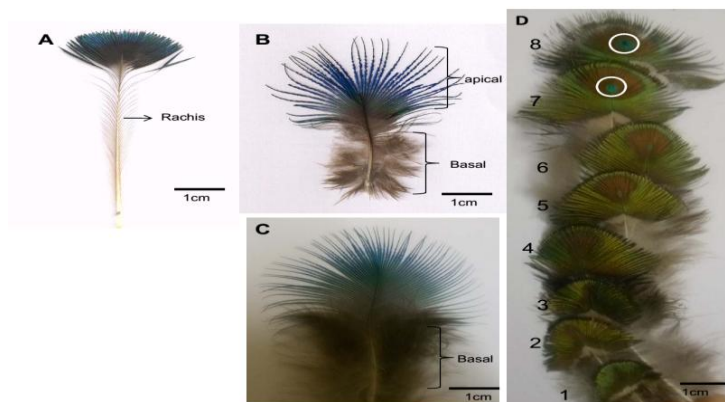


Fig2. Individual Feathers labelled in Fig.2 (A) Crown feather with a long rachis at the centre and palmately arranged barbs at the tip. (B) Neck feather differentiated into basal and apical region. (C) Nape feather. In neck

and nape feather the proximal part is plumaceous and the distal part is pennaceous in nature. In the apical part of the barbs are arranged in palmate pattern of a leaf and barbules present in it give an iridescent colour to the feather (**D**) Saddle feather. The progression of pattern development in saddle feather is shown in this figure. Eight different stages of feathers are shown here and the lower number depict the early developmental stage. Circle demarcates the appearance of colour in the feather.

3.1. Crown Feather

Crown feathers are group of feather present at the top of the head. They are often called as crest feather. The crest is formed by 12-15 spatula tipped feather present in a fan shaped manner along the central axis at the top of the head. The length of the feather varies from 6.5-8 cm. The rachis terminates in a flat fan shaped triangular structure with a blackish dome at the centre which is surrounded by royal blue colour (Fig.1A, 2A). The fan is 0.3-0.5 cm in length with a width of 0.3cm (Fig. 2A).

3.2. Neck Feather

The Indian male peafowl has an elegant long, slender neck with royal blue colour. The blue colour comes from the neck feathers which are overlaid over one another. The length of the feathers present in the neck varies from 2-6 cm. The basal part of the feather is plumaceous in nature and the rachis is covered with fluffy brownish barbs. The apical region terminates in vibrant blue barbs which are widely spaced (Fig. 2B). The end of rachis is marked by a semi circular green band of barbules which progressively become more widely spaced and blue in colour at its end. As the neck region terminates into breast, the diameter of green tinge increases which give rise to blackish green barbules which are comparatively closely spaced than the apical ones (Fig. 2C). The nape culminating onto the dorsal side has feathers that progressively form the back feathers. The length of the barb varies from 1.5-2.5 cm. Each barb contains numerous barbules of 0.2-0.5 mm in size.

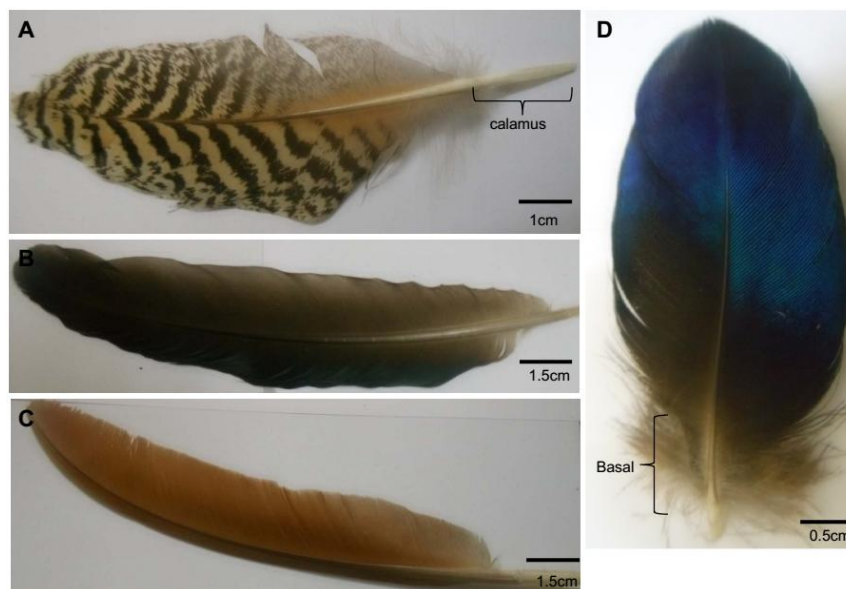


Fig3. Description of feathers in peacock (A) Contour feather. The calamus is thick and the rachis is present at the centre of the feather. Both outer and inner vane are of equal in size. Alternate dark/light bands are present throughout the feather. (B) The calamus of primary feather is very thick and flat in shape. The outer vane is wider in shape than the inner vane. Feathers are rigid in its texture. (C) Secondaries have a thick rachis and flat calamus in it. Both outer and inner vane are of equally shaped. This is pennaceous in nature. (D) Tinge feather: The basal part is plumaceous and the apical part is pennaceous in nature. The rachis is present at the center. These feathers are iridescent in nature.

3.3. Dorsal/ Back/ Saddle Feather

The dorsal or the back feathers are commonly known as saddle feathers (Fig. 2C). The length varies from 5-8cm in length. The basal part of one feather is overlaid over the apical part of the other. In a dorsal feather the rachis is covered with brownish white barb during development which progressively form a brownish dome shaped structure

at its end (Fig. 2d Stage 1). The apical part of the rachis is green. The barbs are arranged in dome shaped structure with gap among each other. At the tip the barb has a rusty brown coloured structure which surrounds the vibrant green barbules (Fig. 2D). The diameter of the dome increases as it reaches the posterior end (Fig. 2D). With the progression of brownish dome a tint of light green colour appears at the centre of the brownish dome. The green colour increases its size with the increase of dome and changes to dark green at the posterior end. The peak of brown expands into spear head shape with a turquoise tint in the centre, gently leading like an eye spot (Fig. 2D). The diameter of brown increases with the appearance of turquoise diamond in the centre as the Saddle feather progresses into tail feathers. The length of the barb and eye spot size varies according to the length of the feather. The barbs present at the central region are smallest in size where as the ones present at the periphery are longest in size.

3.4. Contour Feather

These feathers are localised above the wings. It is penneaceous in nature. The length of the feather varies from 2-15 cm. (Fig. 4A). It consists of a feather shaft and an evenly shaped flat vane extending from it 1.5. Counter feather has a nice pattern in it which includes an alternative arrangement of creamy orangish brown and black latitudinal stripes. The width of the stripe is more in smaller feather. In long feather the number of stripes are more but the band width is small. The vane is composed of numerous barbs which in turn, have small barbules branching from them. The distal barbules bear hooklets, which makes the feather rigid in structure. The distal barbules of one barb overlap and hook onto the ridged proximal barbules of the preceding barb, thereby forming a strong interlinking structure. The calamus is roundish and hard in nature.

3.5. Tinge Feather

Tinge feathers are present at the trunk and they border the starting of the wings (Fig. 1B). The length varies from 10-15 cm. These feathers are differentiated into pinaceous and plumaceous region (Fig. 3D). The proximal part of the feather is plumaceous and the distal part is pennaceous in nature. Their coloration changes with the angle from which they are seen. They appear black which reflect greenish blue hues when seen from different angles of the light. The rachis is black in colour and is invisible at the distal region within the closely and evenly spaced barbs present on either side of the rachis. The length of the barbs varies from 1.3-1.7 cm.

3.6. Flight Feather

Collectively flight feathers are known as remiges. They can be classified as primary and secondary on the basis of body weight shared by the feather during the flight. The primaries are black in colour (Fig. 1C, 4B) and are 9-10 in number. The length of these feathers are 30-45 cm. Barbs are arranged evenly on either of the rachis and hooked with each other. The calamus is flat, thick and hard in both primary and secondary flight feather. The secondaries are orangish brown in colour and 6 in number (Fig. 1C). The length of the feather varies from 30-45 cm. A rachis is present at the center. Surrounding the rachis, on either side, barbs are arranged and hooked with each other. The barbs of the outer vane is broader than the barbs of the inner vane. Length of the outer barb varies from 3.6-3.8cm (Fig 4C) and number of barbs is 16/cm in the outer vane. Tergential packing is 13 for this feather.

3.7. Tail Feathers

The tail feathers can be classified into two types: 1) The main tail feather 2) Tail covert/ Decorative tail feather

The main tail feathers: These are grayish brown in colour and are overlaid by the decorative extended upper covert feathers and T-feathers. The length of these feathers varies from 50-75cm. The decorative tail feather is borne by this feather. The rachis of this feather is very strong. The barbs are evenly branched. Throughout the length the feather is pennaceous in nature. The length of the barb varies from 4-4.5cm. Number of barbs is 11/cm. Each barb contains numerous barbules (Fig. 3A).

Decorative tail feather: Tail feathers are observed next to the saddle feathers and are involved in fan formation. Around 200 decorative tail feathers are present in Indian peacock. The length of the feather varies from 1-6 feet. It can be classified as: Eye feather, T-feather and Sword feather on the basis of their structure and location in a fan. Eye feather is present at the centre and bordered by T-feather in the fan. Sword feather forms the lateral margin for the entire fan. All the tail feathers are arranged in such a way, so that all the eyespot of eye feathers should be displayed when the fan is open. In a peacock the number of eye and T feather is 170 and 30 respectively.

Eye feather These are named so due to the presence of eyespot in it. The barbs are widely spaced though the shaft and the rachis terminates into closely spaced barbs forming an oblong shape. A developed eyespot includes several adjacent iridescent colors, including a dark purple-black center surrounded by 2 large concentric regions of blue-

green and bronze-gold, as well as a few narrower outer bands of additional colors. Purple colour appear at the centre and form the pupil for the eyespot. Blue colour outline the iris for the eyespot. The eyespot size increases with the length of feather. The development of eye spot in an eye feather follows the same pattern as described for the saddle feather (Fig. 3B). The barb and barbule length is directly proportional to the length of the feather.

T feather The eye feathers are ornately surrounded by T-feathers which border the eye feathers. These are the longest feather (upto 6feet) found in peacock. The barbs are widely spaced though the shaft and the rachis terminates into closely spaced barbs forming a semicircular T shaped structure at the end (Fig. 3C). It includes green, and dark brown colour. These feathers lack the eye and forms the semicircle when the tail feathers are fanned.

Sword feathers In the marginal region of the tail feather some curved feather appears. We named them as Sword feathers since the feather appears like a sword. The sword feathers borders the fan parallel to the ground. They form the diameter of the semi circle fan. Sword feathers are 35-45 cm in length. The rachis of this feather is curved and barbs are present unevenly on either side of the rachis. The length and density of the barb present on one side of the rachis is more than the other. The length of the barb and barbule varies with the length of the feather. The length of the barb is more at the proximal region which decreases towards the tip. The barbs have metallic green tinge near the rachis and terminates into turquoise blue. Often sword feathers develop eyespot in it which progresses in a similar manner as an eye feather (Fig. 3D).

3.8. Abdominal Feathers

They are over layered over down feathers. They are semiplumes and both pennaceous and plumaceous in nature. The length of the feather varies from 5-8 cm (Fig. 5). They are white, fluffy and very light in weight. A white rachis is present at the centre which is surrounded by barbs of equal length. The rachis is thin and flexible in nature. The length of the barb is 3cm and are not hooked.

IV. DISCUSSION

Feathers, being a complicated structures allow a multitude of possible morphological alterations to give the animal best condition to live in that environment. Across species, textural differences in feather of the same region are obvious and often extreme for some species³³. For example, the contour feathers of chickadees (*Parus spp.*) have long and loosely arranged barbs and in swallows (e.g., *Hirundo spp.*) the barbs are short and tightly arranged. Variation of feather is also observed within the same animal, albeit the originally appearing feathers are of single type^{1,34}. Feather structure change with its length, and to maintain the mechanical properties³⁹ structural and mechanical component changes⁴⁰. Peacock develop a complex plumage pattern among birds. Complex plumage patterns are considered as a honest social signal^{41,42} and structural variations described in diverse parts of the body is a functional adaptation made by the animal. All the structural variations are discussed with the light of known function for feathers in various birds.

4.1. Crest Feather

Crest feather of peacock share similar structural features with other bird species. Crest plumage is often used for signalling and display purpose. In *Callipepla californica* female selects the male on the basis of crest length⁴³. In species like crested auklets *Aethia cristatella*⁴⁴ and European shags *Phalacrocorax aristotelis*⁴⁵ crest ornaments are used for mutual mate choice. Crest further function as a status signal during competition with the sexes⁴⁴. Besides crest length, the crest coloration is also involved in mate selection in *Cyanistes caeruleus*^{46,47}. In male blue tits, UV crown plumage cooperate in inter-sexual signalling during extra-pair mate choice^{48,49}, offspring sex allocation⁵⁰⁻⁵³ and allocation of maternal care⁵⁴. In peacock, crest is used for signalling purpose. The individual with wider crest possess agonistic behavior among the same species⁵⁵.

4.2. Neck Feather

Neck contains the densest area of feather than any other parts of the body. Neck feather possess highest visual saliency in an open habitat bird⁵⁶. In peacocks the neck is blue in color. Blue-ultraviolet plumage ornamentation is an honest advertisement of quality that can be assessed by conspecifics during mate choice or during male-male competition. Expression of blue plumage is an indicator of physical condition of a male during the fall when new feathers molted in many birds⁵⁷. The blue colour is further coupled with the body size, territory quality and past nutritional history in some bird species. Territory size and male blueness suggests an intrasexual function for male ornamentation because territory boundaries are established through direct male contests⁵⁷. According to sexual selection theory male with highly ornamented feather have greater reproductive success. In blue grosbeaks the blue ultraviolet colouration is an ornamental trait predicted by sexual selection theory⁵⁸. In peacock blue neck colour

changes to green as it move towards the nape. The barbules of the neck feathers become increasingly hooked as neck gives away to the back and also becomes increasingly dull green. Since a study dealing with peacock neck colour and reproductive success is missing from the literature it is difficult to conclude what the function of this blue signal is.

4.3. Contour Feather

Contour feathers are accessory structures and require a skeleto-muscular apparatus for moving and stabilizing them⁶. These feathers stack on one another and protect the animal from rain and keep the body insulated. Besides, the integrity and smoothness, it helps to maintain the streamline condition of the body⁶. The contour feather during its movement creates the stimuli that are received and transmitted by the various receptors and filiform feathers, and collected and processed in the spinal cord and cerebellum⁵⁹⁻⁶². In peacock contour feathers are localized above the wing and have a distinct pattern in it^{31, 63-65}. Such kind of pattern falls under the sub category of "barred pattern" as described by Prum & Williamson, 2002³¹. The function of this pattern is to camouflage and thus difficult to chase the animals movement in barred environment⁶⁶. Birds such as cuckoo used this pattern as an indicator of cryptic behavior⁶⁷. In birds like *Taeniopygia guttata*⁶⁸, *Alectoris rufa*⁴¹ used this for display purpose. The regularity of barred patterns signals plumage conditions and reflects individual quality.

4.4. Tail Feather

Tail is often associated with flight performance. Most birds develop two types of tail feather: (1) Main tail feather (2) Tail covert feather⁶⁹. The main tail feather is associated with flight where as the second one helps to protect the tail region. In most birds the covert feather is few cm where as in peacock these are elongated structures. These are often referred as ornamental /decorative feathers and are the primary source of mate selection^{36,69,70}. The structure of the tail feather changes along with feather length and it requires extra energy. The tail feathers are very flexible in nature and this probably help the peacock while dancing. The mechanical properties of feathers are associated with the functionality and are determined by various feather components, which may have evolved concomitantly with length and function of tail feather⁷¹. In peacocks the actual weight of tail feathers are borne by the main tail feather and hence it develops thick and flexible calamus. Tail feathers are involved in fan formation and the fan size increases with the age of the animal. The coloration of the eyespot feathers are key determinant than variation in the number and size of eyespots in mate attraction during courtship period^{36,37}. T feather present in the margin further give a nice ogee pattern to the fan⁶⁹.

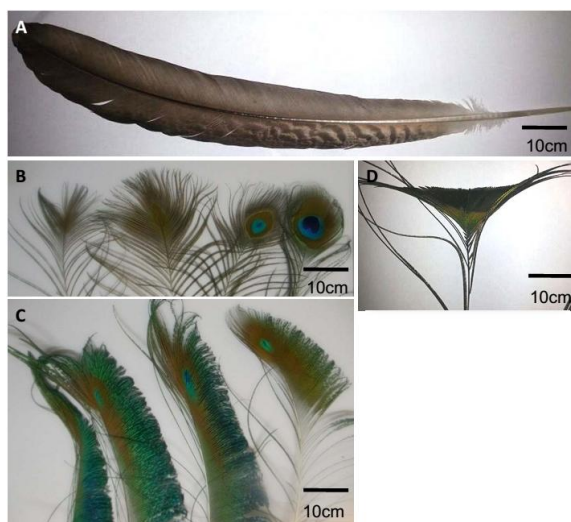


Fig4. Tail feathers (A) The main tail feather: These are long and pennaceous in nature. The rachis is present at the centre and the outer and inner vane are of equal in size. (B) The various stages of eye feather. The progression of the eye shown from left to right. (C) The T feather margin the fan formed by tail feather. Only tip of the T feather is shown in this figure. (D) Various types of sword feather present in the tail.

4.5. Flight Feather

These are lightly textured and associated with sustained flight. The feathers develop thicker calamus and thus enabling the bird to support the body weight during short flight. Flight feathers have the smallest pennaceous barb

angles and the most barbs per cm, and thus the highest tangential packing. Furthermore, barbules per mm of pennaceous ramus is also more in comparison to the other parts of the body (current study). All these structural adaptation help the bird for flight³³. A similar kind of adaptation is also reported from other species as well^{72,73}. Flight feathers are associated with the flight efficiency and in maintaining thermoregulation of the body⁷⁴. To survive in adverse condition birds molt their flight feathers regularly. Nevertheless, molting is a metabolically costly phenomena⁷⁵⁻⁷⁷, which requires large amounts of energy and time⁷⁸⁻⁸⁰. For this reason larger birds usually molt only a part of their flight feathers whereas smaller birds replace all of their flight feathers annually^{81,82}.



Fig5. Down feather In Peacock down feather is a semiplume. A white rachis is present at the centre. On either side of the rachis barbs are present.

V. CONCLUSION

Various feathers present in different parts of the body make peacock an ideal ornamental model to study plumage pattern. Feathers present in external parts of the body have a nice striking pattern in it. However, the feather which is involved in flight does not contain any specific pattern. Most of the feathers present in different parts of the body are blue and green in color. Ornamental feathers are metabolically costly organ. Why male has to spent so much energy to maintain this coloured feathers? What is sacrificed in male at the cost of this beautiful plumage pattern? What information the female peafowl gets from the various feathers present in different body parts? An eye ultrastructure and functional study of the male and female peafowl will answer the unsolved mysty of the evolution behind this colourful plumage pattern.

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