

Archosaurian respiration and the pelvic girdle aspiration breathing of crocodyliforms

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Birds and crocodylians, the only living archosaurs, are generally believed to employ pelvic girdle movements as a component of their respiratory mechanism. This in turn provides a phylogenetic basis for inferring that extinct archosaurs, including dinosaurs, also used pelvic girdle breathing. I examined lung ventilation through cineradiography (high-speed X-ray filming) and observed that alligators indeed rotate the pubis to increase tidal volume, but did not observe pelvic girdle movement contributing to lung ventilation in guinea fowl, emus or tinamous, despite extensive soft-tissue motion. Re-examination of fossil archosaurs reveals that pubic rotation evolved in basal crocodyliforms and that pelvic girdle breathing is not a general archosaurian mechanism. The appearance of pelvic aspiration in crocodyliforms is a striking example of the ability of amniotes to increase gas exchange or circumvent constraints on respiration through the evolution of novel accessory breathing mechanisms.

Keywords: Archosauria; Crocodylia; Aves; pelvic aspiration; accessory breathing mechanisms

1. INTRODUCTION

Accessory mechanisms for lung ventilation may increase tidal volume or alleviate constraints on breathing under certain environmental or behavioural conditions (Baumel *et al.* 1990; Brainerd 1999; Owerkowicz *et al.* 1999; Farmer & Carrier 2000; Boggs 2002). Based on the reported involvement of the pelvis in breathing in birds (Baumel *et al.* 1990; Ruben *et al.* 1997, 2003) and crocodylians (Rathke 1866; Farmer & Carrier 2000), pelvic aspiration has been hypothesized to be a primitive breathing mechanism for the Archosauria (Carrier & Farmer 2000), despite the fact that the proposed pelvic breathing mechanisms of birds and crocodylians are very different. However, respiratory pelvic girdle movement has never been demonstrated in either taxon by direct quantitative evidence, but has been inferred from anatomy, electromyography or observed body wall movement (Rathke 1866; Baumel *et al.* 1990; Ruben *et al.* 1997, 2003; Carrier & Farmer 2000; Farmer & Carrier 2000).

Extant crocodylians and birds possess highly derived and seemingly unique respiratory mechanisms. Birds have fixed parabronchial lungs with unidirectional airflow in the palaeopulmo (the parallel series of parabronchi where gas exchange takes place), as a result of the interaction of bellows-like air sacs and fine-tuned valving of the respiratory tract (Scheid & Piiper 1989; Wang *et al.* 1992; Powell 2000). Cross-current bloodflow through the lungs combined with a near constant supply of oxygenated air through the parabronchi, both during inspiration and during expiration, provide for a high degree of efficiency in pulmonary gas exchange (Powell 2000). Crocodylians, in contrast, possess bidirectional pulmonary airflow and have the most complex multichambered lung structure of any reptile, with tubular monopodial branching chambers and intercameral and interedicular perforations (Duncker 1978; Perry 1989). In addition to costosternal movement, crocodylians ventilate their lungs through the contraction of a unique muscle, the diaphragmaticus, which originates

from the pelvis and the posterior row of gastralia and inserts on a fascia surrounding the liver. Upon contraction, the diaphragmaticus pulls the viscera caudad, thus expanding the thoracic cavity and inflating the lungs (Gans & Clark 1976; Farmer & Carrier 2000; Claessens 2002). The crocodylian diaphragmaticus muscle is not homologous to the mammalian diaphragm or the chelonian diaphragmaticus. Although the crocodylian lung appears to be capable of very efficient gas exchange, extant crocodylians seem to use only a fraction of the gas exchange potential of their respiratory system (Carrier 1987; Perry 1990).

The structure of the pelvis in extant crocodylians is highly derived. The pubic bones, rather than articulating with both the ilium and ischium and forming part of the acetabulum, articulate only with the proximal anterior margin of the ischium via a slightly concavo-convex joint. This structural configuration renders the pubic bones highly mobile, and through the actions of pelvic and hypaxial muscles the pubic bones can be rotated cranio-dorsally or caudoventrally (Farmer & Carrier 2000; Claessens 2002). Although considered to be a newly discovered accessory breathing mechanism (Farmer & Carrier 2000), rotation of the pubic bones has been hypothesized to function as a component of the crocodylian aspiration pump as early as 1866 (Rathke 1866). Electromyographic studies indicate that muscles attaching to the pubic bones contract during respiration (Farmer & Carrier 2000). However, direct observations of pubic rotation during lung ventilation have not been published previously, and pubic rotation has never been quantified.

Based on anatomical and electromyographic investigations, movements of the uropygium have been proposed to contribute to lung ventilation in birds by depressing the caudal vertebrae and pygostyle during expiration and elevating the postsacral vertebral column during inspiration (Baumel *et al.* 1990). Pelvic girdle-assisted lung ventilation has been hypothesized to be most important in resting birds in which the sternum is relatively fixed

Table 1. Average rotation of the pubic bones during lung ventilation under various conditions in five American alligators (*Alligator mississippiensis*), measured in degrees.

(The lower values recorded for pubic rotation in water are probably caused by skewing of the data towards low rest values, as a result of technical limitations associated with filming alligators breathing at the water surface in a fixed location after exercise.)

alligator	average pubic rotation at rest and recovery (deg)	range and s.d. (deg)	average pubic rotation during locomotion (deg)	range and s.d. (deg)	average pubic rotation in water (deg)	range and s.d. (deg)
1 L	11.6 ($n = 14$)	5.1–16.2 (s.d. = 2.9)	12.6 ($n = 5$)	7.4–15.5 (s.d. = 3.3)	6.6 ($n = 5$)	5.0–7.8 (s.d. = 1.2)
2 D	11.2 ($n = 19$)	4.3–18.9 (s.d. = 4.7)	—	—	6.0 ($n = 5$)	4.4–7.9 (s.d. = 1.4)
3 E	11.0 ($n = 15$)	3.2–17.7 (s.d. = 4.6)	13.0 ($n = 5$)	9.8–15.0 (s.d. = 2.5)	5.2 ($n = 5$)	3.5–7.8 (s.d. = 1.8)
4 H	9.1 ($n = 5$)	7.6–11.2 (s.d. = 1.4)	10.7 ($n = 5$)	7.6–12.9 (s.d. = 2.1)	—	—
5 C	8.0 ($n = 5$)	6.7–11.0 (s.d. = 1.7)	—	—	—	—

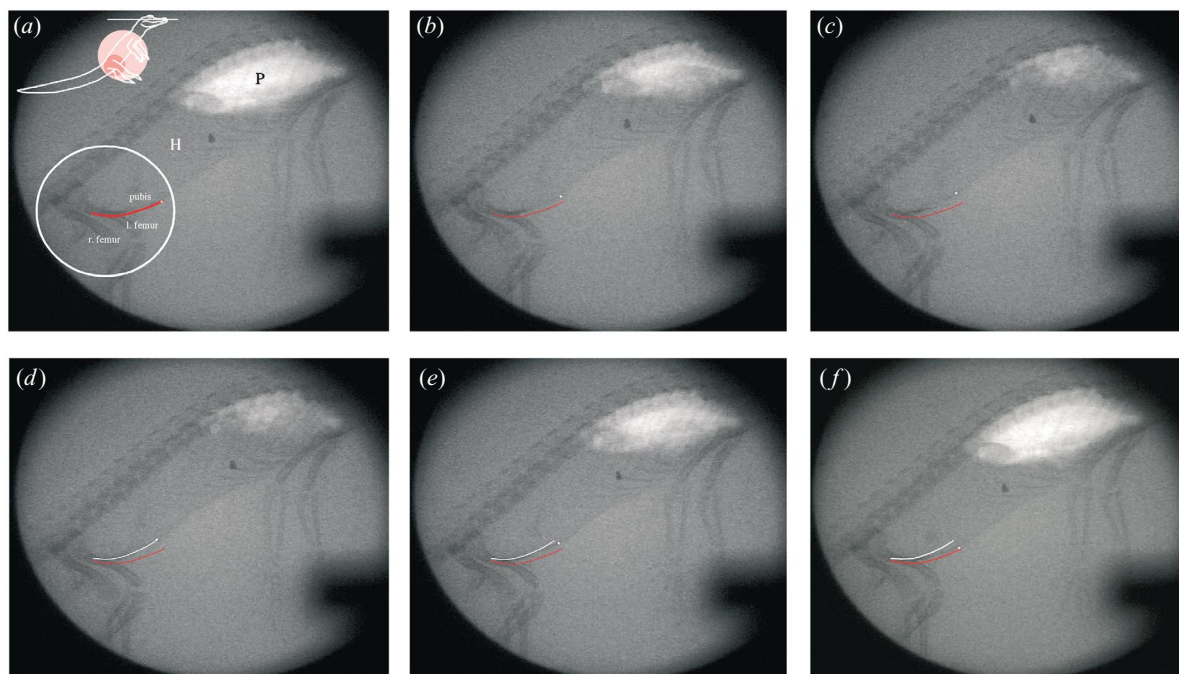


Figure 1. Pubic rotation and visceral movement in a male alligator, 82 cm, 1.62 kg, freely suspended in 25 cm of water. Lateral projection radiographs, X-ray positive. (a) Peak inspiration (breath hold): the position of the lower border of the pubis and the pubic cartilage (extending from the distal pubic extremity to the posterior gastralia) during breath hold is indicated in red. A white dot marks the contact between the distal pubic cartilage and the last row of gastralia. The air-filled lungs (P) are seen as an area of low density; the liver and other viscera (H) are not clearly visible because their density is equal to that of the surrounding water. (b,c) Expiration: the pubis and pubic cartilage (white dot) are displaced dorsally. (d) Peak expiration: a white reference line indicates the end-expiratory position of the pubis and pubic cartilage. (e,f) Inspiration: the pubis returns ventrally to its original position at peak inspiration.

(Baumel *et al.* 1990). Large dorsoventral excursions of the postsacral vertebral column have been inferred on the basis of an extreme dorsal curvature of the tail that is known from desiccated skeletal specimens (Ruben *et al.* 1997, 2003), but have not been demonstrated through direct observation.

2. METHODS

Cineradiography was undertaken with a Siemens system employing 16 mm Kodak Eastman Plus-X reversal film and Mini Digital Video. Still images were recorded on Kodak

Industrec M-2 film. Kinematic data were recorded at 220 mA, 38 kV, 100 frames per second (f.p.s.), using a Photosonics series 2000 high-speed cine camera. Digital video was recorded with a Sony DCR VX 1000 camera at 60 f.p.s. and 1/250 shutter speed at 220 mA and 50–90 kV.

The animals examined included the following: five American alligators (*Alligator mississippiensis*), ranging in length from 55 cm to 115 cm, and ranging in weight from 0.72 kg to 5.70 kg; four emus (*Dromaius novaehollandiae*), ranging in weight from 2.36 kg to 4.70 kg; two tinamous (*Nothoprocta perdicaria*), weighing 0.48 kg and 0.49 kg; and four guinea fowl (*Numida meleagris*), ranging from 2.60 kg to 2.90 kg. Respiratory kinematics

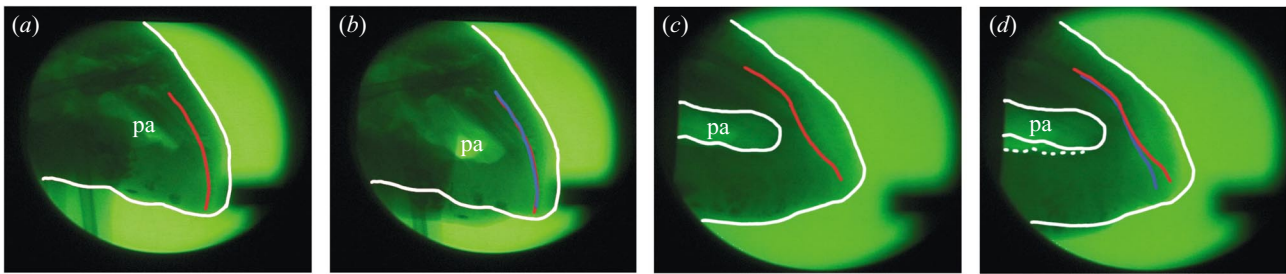


Figure 2. Position of the postsacral vertebral column and pygostyle in the emu during lung ventilation. Lateral projection radiographs, X-ray positive. The position of the lower border of the posterior synsacral vertebrae, postsacral vertebrae and pygostyle is indicated in red at end expiration (a) and in blue at end inspiration (b). The postsacral vertebral column is shown not to move during the respiratory cycle. The posterior air sacs (pa) are clearly visible owing to their low radiodensity. (c,d) 'Paradoxical' movement of the postsacral vertebral column during lung ventilation. During expiration, 'paradoxical' caudad expansion of the posterior air sacs and soft tissues of the tail results in an elevated position of the vertebral column and pygostyle (c). Ventral recoil of the postsacral vertebrae (d) occurs at the onset of inspiration. The dotted white line in (d) shows the limits of the expansion of the posterior air sacs upon inspiration.

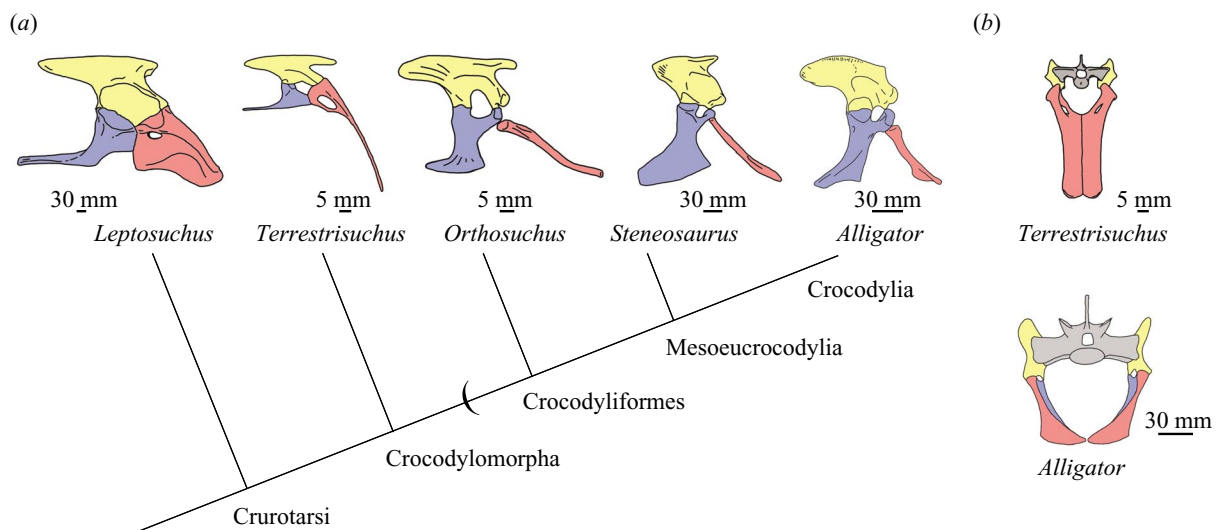


Figure 3. (a) Crurotarsan phylogeny showing the transition from fixed to mobile pubic bones (right pelvis, lateral view). In the phytosaur *Leptosuchus* UCMP 26699 and the basal crocodylomorph *Terrestrisuchus* BMNH R7562 the pubis still articulates with both ilium and ischium. However, in basal crocodyliforms, the pubis articulates only with the anterior proximal margin of the ischium, as in *Orthosuchus stormbergi* SAM K409. Within crocodyliforms, there is a trend towards reduction in length of the pubis, and increased expansion of the distal pubis into a blade-like structure, as shown by the basal mesoeucrocodylian *Steneosaurus* BMNH R3806, and the extant crocodylian *Alligator mississippiensis* MCZ 81457. (b) Anterior view of the pelvises of *Terrestrisuchus* and *Alligator*, showing the extensive midline contact of the elongated pubes in *Terrestrisuchus* and the expanded distal pubis of *Alligator*. Ilium coded in yellow, ischium in blue and pubis in red. *Leptosuchus* redrawn from Camp (1930), anterior view of *Terrestrisuchus* after Crush (1984). Phylogeny after Brochu (2001).

were recorded during treadmill locomotion at speeds of ca. 1 m s^{-1} to 2.5 m s^{-1} for the alligators and 2.5 m s^{-1} to 10 m s^{-1} for the birds. In addition, breathing was filmed during rest, recovery after exercise, standing upright and sitting (resting on the sternum). Alligators were also filmed breathing while suspended freely in 5 cm to 25 cm of water. Alligator peak inspiration and peak expiration were determined based on intrapulmonary pressure recordings in one individual, which were then aligned with the cineradiographic records from the other four individuals. Bird inspiratory and expiratory movements were determined based on the cineradiographic record of sternal excursion linked with the timing of air-sac inflation and deflation. The total number of breaths analysed was 88 for alligators, 60 for emus, 52 for tinamous and 60 for guinea fowl. All animal experiments were conducted in accordance with state and institutional guidelines (Massachusetts Division of Fisheries and Wildlife import permit 114.99IMP and propagation permits

194.00CL4, 200.01CL4, 076.02CCL4 and 027.03CL4; Harvard University Assurance of Compliance 99/06).

3. CROCODYLIAN PELVIC ASPIRATION

Cineradiography allowed direct visualization and quantification of pubic movement in a breathing crocodylian, as opposed to inferring movement from indirect evidence. In American alligators (*A. mississippiensis*) the pubic bones rotate during lung ventilation with every breath under a variety of conditions (table 1). Upon inspiration, the pubic bones rotate caudoventrally, and upon expiration, the pubic bones rotate craniodorsally (figure 1). The range of rotational movement of the pubic bones varies from as little as 3.2° , to as much as 18.9° , with an average of 10.2° measured over a total of 88 breaths in five individuals (table 1). The amount of pubic rotation

per breath generally increases during and immediately after exercise, and decreases during recovery. However, the amount of pubic rotation is relatively plastic. The degree of pubic rotation as well as visceral retraction appears to be adjusted with relative ease by the alligators, and may increase or decrease between sequential breaths. Also, the degree of pubic rotation varies between individuals, some alligators registering larger excursions than others (table 1).

4. AVIAN ASPIRATION BREATHING

Cineradiographic investigation of three different basal bird taxa, namely the emu and the tinamou (Palaeognathae) and the basal galliform guinea fowl (Neognathae), failed to show a contribution of the postsacral vertebral column to aspiration breathing (figure 2*a,b*). No significant movement of the caudal vertebrae and pygostyle during lung ventilation was detected in more than 50 breaths in guinea fowl and tinamous. In emus, however, postsacral vertebral movement was often observed in concert with respiration (figure 2*c,d*), but in these cases the movement did not contribute to lung ventilation. When movement was observed, the postsacral vertebral column was elevated during expiration, and depressed during inspiration (figure 2*c,d*), which is opposite to the movement that would be expected if the postsacral vertebral column were assisting in lung ventilation. The observed 'paradoxical' movement of the caudal vertebrae and pygostyle seems to occur when the posterior air sacs are abruptly compressed by the body wall, often during vocalization (although it does not occur in every instance of vocalization). The simultaneous occurrence of abrupt air-sac compression and paradoxical postsacral vertebral movement suggests that the vertebral movement may be passively induced by movement of the air sacs. I hypothesize that postsacral vertebral movement occurs when air-sac compression is so intense that in addition to air being forced out of the air sac toward the bronchi, a portion of the air is actually forced caudad towards the 'dead-end' of the air sac, thus lifting the postsacral vertebral column dorsally during expiration (figure 2*c*). Recoil of the postsacral vertebral column occurs during inspiration, when the muscles compressing the posterior air sacs relax and allow the air to redistribute itself within the posterior air sacs (figure 2*d*).

Movements of the pelvis as a whole about the notarial and synsacral joints, which are intervertebral joints in the extensively fused vertebral column of birds, have also been suggested as a mechanism of pelvic respiration in birds (Baumel *et al.* 1990; Ruben *et al.* 1997, 2003). However, no significant flexion and extension of the vertebral column at the notarial or synsacral joints was observed in the X-ray film of emus, tinamous or guinea fowl. Cineradiographic footage of flying black-billed magpies (*Pica pica*) has indicated notarial or synsacral movement in some individuals (Boggs *et al.* 1997). I agree with the authors of this study that the observed movements may be passive effects of the lift and recovery phases of the wingbeat cycle (Boggs *et al.* 1997). However, even if respiratory movement occurs along the notarial or synsacral joints, these movements should be equated with the thoracolumbar vertebral flexion and extension observed during lung

ventilation in living crocodylians, and not with pubic movement. Because of the extensive fusion of the thoracic vertebrae in living birds, it is to be expected that vertebral flexion and extension would be limited largely to the notarium and synsacrum. The absence of postsacral vertebral movement working in concert with lung ventilation in extant birds underscores the importance of verification of skeletal movements hypothesized on the basis of anatomy, external observation or electromyography alone.

5. THE EVOLUTION OF PELVIC ASPIRATION BREATHING

Because the cineradiographic data reveal that the only existing involvement of the pelvic girdle in aspiration breathing in living archosaurs is pubic rotation in crocodylians, the hypothesis that pelvic girdle aspiration is primitive for Archosauria (Carrier & Farmer 2000) is no longer supported by the extant phylogenetic bracket (Witmer 1995). Thus there is no unequivocal phylogenetic support for the inferred pelvic aspiration in dinosaurs and other non-crocodylian archosaurs.

A re-examination of fossil pelvic remains shows that a potentially mobile pubis is present in basal crocodyliforms and basal mesoeucrocodylians, but absent in basal crocodylomorphs (figure 3*a*). The basal mesoeucrocodylian *Steneosaurus* has been reconstructed with the pubis articulating with the anterior margin of both the ilium and ischium (Andrews 1913). However, re-examination of the original material shows that the pubic bone was previously reconstructed in the wrong orientation and in fact articulates with a single slightly concave facet to a proximal tuberosity on the anterior margin of the ischium alone (figure 3*a*). The pubo-ischial morphology of *Steneosaurus* resembles that of living crocodylians. Similarly, re-examination of the type material of the basal crocodyliform *Orthosuchus stormbergi* from the Early Jurassic of South Africa indicates that the pubic bone articulates with a single facet to a proximal tuberosity on the anterior rim of the ischium only (figure 3*a*). There is no connection between the pubis and the ilium, as previously reported (Nash 1968, 1975). The basal crocodyliform *Protosuchus* also appears to have a pubis that articulates only with the ischium, contrary to the published reconstruction by Colbert & Mook (1951), and the basal crocodyliform *Sichuanosuchus* also has a pubis that is separate from the ilium (Wu *et al.* 1997).

Re-examination of *in situ* articulated postcrania of the Upper Triassic basal crocodylomorph *Terrestriisuchus* confirms that the detailed reconstruction published by Crush (1984) is accurate, and that the pubes are broad, thin plate-like bones which are oriented cranioventrally and articulate with both the ischium and ilium (figure 3*a,b*). The pubis of the basal crocodylomorph *Hesperosuchus* also appears to have proximal articular facets for both the ilium and ischium (Parrish 1991). The articulation of the pubis with both the ilium and ischium renders the proximal pubis immobile, and therefore it does not appear likely that pubic movement was an important component of the aspiration pump in basal crocodylomorphs. The pubic bones of more basal crurotarsans, such as phytosaurs and aetosaurs, are also solidly incorporated into the pelvis and

are even more robust than those of basal crocodylomorphs (figure 3a).

Fossil evidence thus supports a basal crocodyliform origin of a separate, mobile pubic bone and the accessory breathing mechanism of pubic rotation. Although it is not impossible that a form of pelvic breathing may have evolved independently in another archosaur group (considering, for instance, the peculiar prepubic element unique to pterosaurs), I conclude that pubic rotation is a crocodyliform adaptation and that pelvic girdle breathing is not a general archosaurian character.

Extant crocodylians are unique in that they tend to significantly increase tidal volume instead of breathing frequency during hypercapnia, when the carbon dioxide level in the blood is elevated (Wang & Warburton 1995). Pubic rotation allows for even greater increases in tidal volume than can be achieved by diaphragmatic and costosternal breathing alone. It is possible that the evolution of pubic rotation in basal crocodyliforms reflects a trend towards a more aquatic mode of life, where increased tidal volume could prove beneficial for prolonged submergence below water level, although increased tidal volume could equally provide a selective advantage in a terrestrial environment. Together with the recent recognition of other accessory components of the amniote aspiration pump (Brainerd 1999; Owerkowicz *et al.* 1999; Farmer & Carrier 2000; Boggs 2002; Claessens 2004), the identification of the autapomorphic crocodyliform pubic rotation mechanism suggests that amniote respiration may be more complex than previously recognized and that other yet unidentified accessory breathing mechanisms may have evolved in other groups.

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