Parental care in *Stenotaenia rhodopensis* (Kaczmarek, 1970) (Chilopoda: Geophilomorpha)

Родительская забота у *Stenotaenia rhodopensis* (Kaczmarek, 1970) (Chilopoda: Geophilomorpha)

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ABSTRACT. The females of the geophilomorph centipede *Stenotaenia rhodopensis* (Kaczmarek, 1970) guard the eggs and young by wrapping their bodies around the brood so that the ventral side is exposed to the outside. This observation confirms the basal division of the Geophilomorpha into Placodesmata (comprising only the family Mecistocephalidae) and Adesmata, which corresponds to the anatomical differences between these groups, especially with regard to the absence or presence of ventral pores, the openings of the ventral glands. We have provided comparative data for some external morphological characters between young and their mothers to clarify changes in taxonomic characters during early post-embryonic development. In addition, we have explained some of the key terms used in the study of the evolution of parental care and identified ecological factors such as harsh environments and predation pressure as possible evolutionary drivers of parental care in centipedes.

РЕЗЮМЕ. Самки геофиломорфной многоножки *Stenotaenia rhodopensis* (Качмарек, 1970) охраняют яйца и детенышей, обхватывая выводок своим телом так, что брюшная сторона оказывается наружу. Это наблюдение подтверждает базальное деление Geophilomorpha на Placodesmata (семья Mecistocephalidae) и Adesmata, что соответствует анатомическим различиям между этими группами, особенно в отношении отсутствия или наличия вентральных пор, отверстий вентральных желез. Для выяснения изменений таксономических признаков в период раннего постэмбрионального развития мы предоставили сравнительные данные по некоторым внешним морфологическим признакам детенышей и их матерей. Кроме того, мы объяснили некоторые ключевые термины, используемые при изучении эволюции родительской заботы, и определили экологические факторы, такие как суровые условия окружающей среды и давление хищников, как возможные эволюционные движущие силы родительской заботы у многоножек.

Introduction

Parental care is a character that shows enormous diversity both within and between different animal taxa and is an important topic in evolutionary biology and behavioural ecology. It can be defined as any parental trait that enhances the fitness of a parent's offspring and that seems likely to have originated and/or to be currently maintained for this function [Clutton-Brock, 1991; Smiseth *et al.*, 2012]. The simplest and probably most widespread form of care consists of the females supplying the eggs with additional nutrients over and above those required for successful fertilisation. For example, the females of the seed

beetle *Stator limbatus* (Horn, 1873) adjust the egg size to the environmental conditions in order to enhance the survival of the larvae after hatching. At the other extreme end, the parents of some mammals continue to care for their offspring even after they have reached adulthood. This form of care is extremely rare, but occurs in bonobos, where females support their adult male offspring in competition with rival males, thus enhancing their son's social status and mating success. Between these two extremes, there are many other ways in which parents can enhance the fitness of their offspring [Smiseth, 2018].

The terminology used to describe the diversity of parental care can sometimes be confusing, as alternative schemes are used for different taxa and the same form of care may go by different names in different taxonomic groups [Blumer, 1979; Crump, 1995]. Smiseth *et al.* [2012] have provided a general description of the basic forms of care observed in all animals in chronological order during the development of the offspring. The most common and phylogenetically most widespread form of post-fertilisation parental care in invertebrates, fish and amphibians is egg attendance, which takes place in species where the parents remain with the eggs at a fixed location, usually the oviposition site. This form of care is often associated with behaviours directed towards specific threats, such as egg guarding (directed at predators or oophagic conspecifics), egg fanning (to prevent hypoxia) and egg cleaning (directed at fungal pathogens). On the other hand, egg brooding is a non-behavioural form of parental care in which the parents carry the eggs after laying either externally (e.g. parent's back) or internally (e.g. specialized pouches or parent's mouth). Similarly, offspring attendance occurs in species where the parents stay with the young after hatching at a fixed location or escorting the offspring as they move around, whereas offspring brooding implies the carrying of young after hatching or birth, either externally or internally. Egg/offspring brooding could offer some advantages over egg/offspring attendance to parents breeding in variable environments, as brooding allows parents to move more freely while caring for the eggs [Smiseth *et al.*, 2012; Smiseth, 2018].

Relatively little is known about why different taxa or species have evolved specific forms of care. This may reflect differences in the ecological conditions of a particular species and the specific hazards for the offspring. For example, selection might favor different forms of parental care when offspring are exposed to a high risk of predation as opposed to a high risk of starvation. In addition, the evolution of different forms of care in different species may also reflect differences in life histories and the presence of pre-existing characters that can be modified by selection into parental care. Thus, the risk of predation may favour parental care only if the parents are able to defend their offspring against predators, and it may be due to behaviours that males or females use to guard a territory or a partner [Clutton-Brock, 1991; Smiseth *et al.*, 2012; Smiseth, 2018].

In centipedes (Chilopoda) — one of the two main lineages of extant myriapods — parental care includes relatively simple forms of care, especially in the basal groups. After fertilisation, the females of Scutigeromorpha and Lithobiomorpha (i.e., the centipedes with the most obvious anamorphic post-embryonic development) lay a number of eggs, one by one, without additional care for eggs after covering them with a secretion that cements the soil particles together. In the absence of guarding mother to protect them, the newly hatched Scutigeromorpha and Lithobiomorpha must be active and able to feed and breathe through their tracheae, although the number of articulated trunk segments and appendages is still incomplete [Minelli, 2011]. Evolutionary transitions to more complex behaviours include attendance of eggs and offspring in *Craterostigmus* Pocock, 1902 (which hatches from the egg as a 12-legged stadium and acquires the adult number of 15 pairs of legs in the subsequent stadium), Scolopendromorpha and Geophilomorpha, with the latter two orders almost universally united in a group named Epimorpha due to their strictly epimorphic mode of development, i.e., having a fixed number of segments during the post-embryonic development [Fernández *et al.*, 2014]. These centipedes lay all their eggs in a single clutch, inside a brood cavity in soil, decaying logs or under bark. The females then spend weeks in guarding, grooming and moistening clutches of eggs, hatchlings (which are still embryoid and rely on residual yolk from the anterior part of the body) and juveniles until they reach a sufficiently advanced stadium of development to fend for themselves [Minelli, 2011]. The females of these groups are sensitive to disturbance while caring for the eggs and hatchlings, and they always react either by abandoning the brood, which then invariably perishes from desiccation or fungal infestation, or by devouring the eggs and hatchlings (filial cannibalism) [Brunhuber, 1970]. Two alternative postures are observed here: in *Craterostigmus* and all Scolopendromorpha in which guarding females have been observed, the mother rolls her body around the mass of eggs, hatchlings or young and presents her ventral surface to them [Manton, 1965; Brunhuber, 1970; Mitić *et al.*, 2012, 2016, 2023; Siriwut *et al.*, 2014; Vega Román *et al.*, 2018], whereas in Geophilomorpha the opposite posture is generally observed [Bonato, Minelli, 2002; Chipman *et al.*, 2004; Edgecombe *et al.*, 2010; Mitić *et al.*, 2010; Stojanović *et al.*, 2020]. Significantly, such behaviour is a valuable character for the phylogenetics and systematics of centipedes [Dohle, 1985; Bonato, Minelli, 2002; Edgecombe, Giribet, 2004; Fernández *et al.*, 2014].

In this study, we describe multiple observations of parental care in the geophilomorph centipede *Stenotaenia rhodopensis* (Kaczmarek, 1970), a previously unknown species from Serbia [Mitić, 2001, 2002; Mitić, Tomić, 2002]. We also provide comparative data for some external morphological characters between young and their mothers to clarify changes in taxonomic characters during early post-embryonic development, and discuss factors that have favoured the evolution of parental care in centipedes. The geophilid genus *Stenotaenia* Koch, 1847 shows an unusual diversity in body size and contains several minute species, one of which is *S. rhodopensis*.
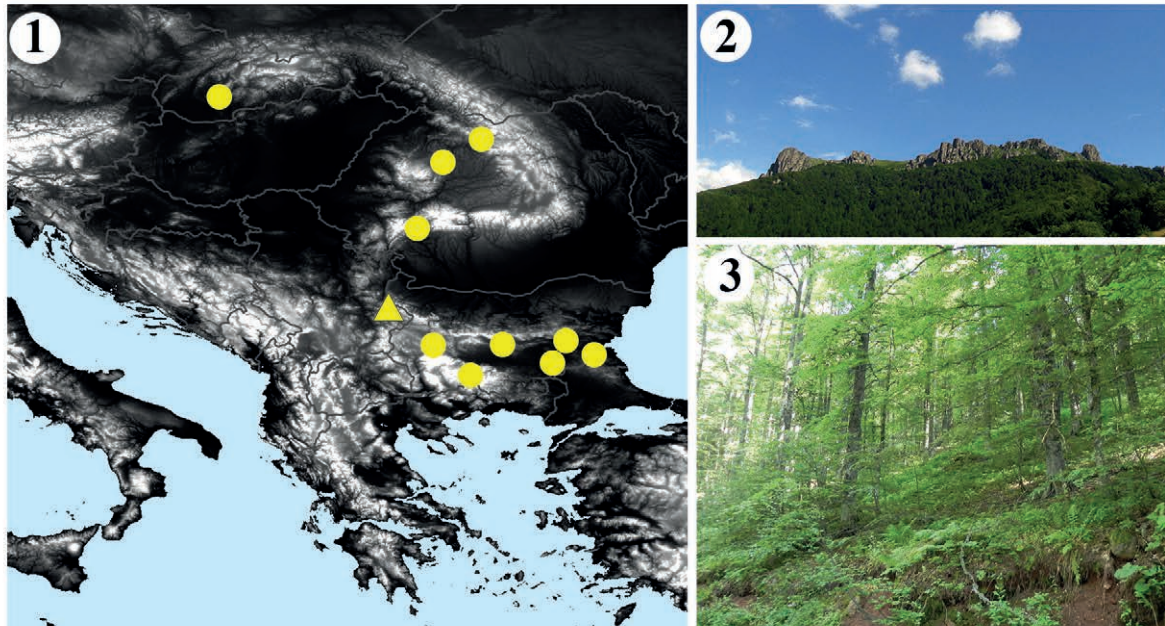
Figs 1–3. Geography and ecology of *Stenotaenia rhodopensis* (Kaczmarek, 1970). 1 — distribution in Slovakia, Romania, Bulgaria (dots) and Serbia (triangle); 2 — mountain peak Babin Zub on the Stara Planina Mountains; 3 — the sampling site, old mountain beech forests (*Fagetum moesiacae montanum*). Photographs by D. Stojanović.

Рис. 1–3. География и экология вида *Stenotaenia rhodopensis* (Kaczmarek, 1970). 1 — распространение в Словакии, Румынии, Болгарии (кружки) и Сербии (треугольник); 2 — горная вершина Бабин Зуб на горном массиве Стара Планина; 3 — место отбора проб — старые горные буковые леса (*Fagetum moesiacae montanum*). Фотографии Д. Стояновича.

This species has been reported from Bulgaria, Romania and Slovakia [Kaczmarek, 1970; Dányi, 2010].

Material and methods

Broods of *S. rhodopensis* with adult females, eggs (embryos) and young were sampled in Babin Zub (Mt. Stara Planina) in eastern Serbia (43°22.262′N; 22°36.532′E), at an altitude of about 1580 m (Figs 1–3), in a phase of the breeding season (from mid-June to mid-August, 2013–2016; collected by D. Stojanović and D. Antić), which was chosen to maximise the probability of collecting broods. In the field and before conservation, the females and offspring were photographed and some of their behavioural characters (such as the position of the female's body in relation to the offspring, the conditions under which the females leave their brood and the type and frequency of the hatchlings' movements) were recorded. The collected specimens were analysed using light microscopy and standard methods for clearing, temporary mounting and dissecting the mouthparts of geophilomorph centipedes [Foddai *et al.*, 2002]. Identification was based on the diagnostic characters given by Kaczmarek [1970], Dányi [2010] and Bonato *et al.* [2014] (see Fig. 4). For the separation of the developmental stadia, we follow the same characters previously used to distinguish the embryonic and post-embryonic stadia of *Geophilus serbicus* Stojanović, Mitić et Antić, 2019 [Stojanović *et al.*, 2020] and *Strigamia maritima* (Leach, 1817) [Brena, Akam, 2012; Brena, 2014]. Fecundity was calculated on the basis of the number of eggs or young found in the broods. The photographs of the egg and foetus stadium and the sterna were taken using a Nikon DS-Fi2 camera with a Nikon DS-L3 camera controller attached to a Nikon SMZ 1270 binocular stereomicroscope, and with a Canon PowerShot A80 digital camera connected to an Axioscope 40 microscope.

Individual broods were preserved in labelled plastic vials with 70% ethanol. The material is deposited in the collection of the Institute of Zoology of the University of Belgrade – Faculty of Biology.

Results

The aim of this study was to analyse parental care in the geophilomorph *S. rhodopensis*, to better identify stadia that are guarded by the females and to discuss how ecological factors shape the evolution of parental care in centipedes. Adult females of *S. rhodopensis*, body length 12.99–17.18 mm (mean, 15.30 mm; n = 9), with a mass of eggs or young, were observed under stones. All females had their ventral surface facing outwards and their dorsal surface in contact with the broods (Fig. 5). When disturbed, the female moved slightly away from the original position, but the terga remained in contact with the brood and the sterna were exposed outwards while the head waved with open forcipules. If the disturbance persisted, the female abandoned her brood. Clutch sizes vary from 2 to 4 (mean, 3.33; n = 9). The eggs are spherical and have a diameter of 0.79–1.22 mm (mean, 1.05 mm; n = 26). The shell (chorion) is yellow in colour, translucent and elastic (Fig. 6). The foetus stadium is capable of "writhing" movements and begins to be slightly compressed dorso-ventrally; it is yellowish-cream in color and 6.35–8.40 mm long (mean, 7.52 mm; n = 4). The antennae are fully segmented and directed forwards. This stadium tends to contract and bring the head close to the posterior end of the animal; all legs are developed

Fig. 4. The subtriangular ventral pore fields 6 and 7 of *Stenotaenia rhodopensis* (Kaczmarek, 1970). Scale bar: 2 mm.
Рис. 4. Почти треугольные вентральные поровые поля 6 и 7 вида *Stenotaenia rhodopensis* (Kaczmarek, 1970). Масштабная линейка: 2 мм.

Figs 5–7. *Stenotaenia rhodopensis* (Kaczmarek, 1970). 5 — ♀ guarding the mass of eggs *in situ*; 6 — embryonic stadium; 7 — foetus stadium. Scale bars: 1 mm. Photograph by D. Stojanović.
Рис. 5–7. *Stenotaenia rhodopensis* (Kaczmarek, 1970). 5 — ♀ охрана массы яиц на месте; 6 — эмбриональная стадия; 7 — стадия плода. Масштабные линейки: 1 мм. Фотография Д. Стояновича.

and the forcipules are stretched forwards (Fig. 7). The first small setae appear, although they are only clearly visible on appendages (antennae and legs). The last leg-bearing and genital segments are clearly separated, but not yet fully developed. Therefore, sex determination is not possible at this post-embryonic stadium.

Discussion

A basal split of the Geophilomorpha into Placodesmata (= Mecistocephalidae) and Adesmata (all other geophilomorphs), which has been recognised in many studies [Verhoeff, 1902–25; Foddai, Minelli, 2000; Edgecombe, Giribet, 2004], corresponds to the anatomical differences between these groups, especially with regard to the absence or presence of the ventral pores – openings of the ventral glands. Ventral pores are observed in members of all Adesmata families with the exception of the small tropical American family Neogeophilidae, although there are repeated apparent secondary losses within different families. In contrast, ventral pores are absent in the Mecistocephalidae, apart from doubtfully homologous structures present only in the males of most species of the genus *Tygarrup* Chamberlin, 1914 [Turcato *et al.*, 1995]. The observation that egg and offspring attendance in the geophilid *S. rhodopensis* follow the pattern of all Adesmata (the female guards the brood with the sterna facing outwards) [Chipman *et al.*, 2004; Mitić *et al.*, 2010, 2016; Stojanović *et al.*, 2020] and not that of the mecistocephalid *Dicellophilus carniolensis* (C.L. Koch, 1847), Scolopendromorpha and *Craterostigmus* (guarding with the terga facing outwards) [Manton, 1965; Bonato, Minelli, 2002; Mitić *et al.*, 2012, 2016, 2023; Siriwut *et al.*, 2014; Vega Román *et al.*, 2018] is behavioural evidence for the hypothesis of the Placodesmata-Adesmata division. However, the guarding behaviour documented in another mecistocephalid species, *Mecistocephalus togensis* (Cook, 1896) [Edgecombe *et al.*, 2010), shows that at least some mecistocephalids guard their brood with the ventral side facing outwards, as in Adesmata. This variability between different mecistocephalids suggests that guarding posture may be more subject to homoplasy (convergence or reversal) than previously thought. Within the clade of centipedes with prolonged parental care (= Phylactometria), the female position with outward-facing terga is plesiomorphic, while the position with outward-facing sterna is an apomorphy that appeared early within the Adesmata [Bonato, Minelli, 2002; Edgecombe *et al.*, 2010]. According to the alternative Amalpighiata hypothesis, in which Lithobiomorpha and not *Craterostigmus* is the sister group of Epimorpha, it is assumed that maternal care is homoplastic. It is either a general feature of Pleurostigmophora (which includes all living centipede orders except Scutigeromorpha) that was secondarily modified (lost, reversed or otherwise altered) in Lithobiomorpha, or it was convergently shared by *Craterostigmus* and Epimorpha [Fernández *et al.*, 2014].

We have confirmed here that in all geophilomorphs from temperate regions for which adequate data are available [Verhoeff, 1902–25; Palmén, Rantala, 1954; Weil 1958; Bonato, Minelli, 2002; Mitić *et al.*, 2010, 2016, 2023; Stojanović *et al.*, 2020], egg-laying and attending the eggs and offspring usually take place in the summer months. Weil [1958] has reported that the time of egg and offspring attendance in *Geophilus flavus* (De Geer, 1778) and *Stenotaenia linearis* (C.L. Koch, 1835) lasts until October and November, respectively, but these data were based on laboratory observations. The egg-laying and attending period is much shorter in the littoral species *S. maritima*, and Lewis [1961] has suggested that this may be necessary to prevent the eggs and young from being exposed to immersion by the high autumn tides. In large parts of Europe, most centipedes are perennial. They are characterised by a low reproductive potential, a long life span and a high intraspecific variability in terms of duration and number of developmental stadia. Almost all European centipedes are such equilibrium species or k-strategists [Voigtländer, 2011]. Considering that the average clutch sizes of Geophilomorpha vary between ten (*G. serbicus*) [Stojanović *et al.*, 2020] and 39 (*Geophilus rubens* Say, 1821) [Lewis, 1981], the fecundity of the studied species is very low, probably due to the small body size of the females, as is the case for most insects [Honěk, 1993]. Our results are also in line with previous studies [Brena, 2014; Stojanović *et al.*, 2020], according to which there is a developmental gradient along the antero-posterior axis during this phase of post-embryonic development, with the last segments being less developed. The adult structures/organs in *S. rhodopensis* are not yet fully developed and foetus relies exclusively on the yolk.

What factors have promoted parental care in centipedes? Parental care is considered a prime example of an altruistic character that has evolved to enhance the fitness of the recipients of care (offspring) at the expense of the donor of care (parents). The costs of decreased parental reproductive success associated with parental care must be outweighed by the indirect benefits of the parents in the form of increased fitness of the offspring [Clutton-Brock, 1991; Smiseth *et al.*, 2012; Wong *et al.*, 2013; Smiseth, 2018]. Although the few empirical studies on parental care in epimorphic centipedes provide good evidence for its current benefits, almost nothing is known about the evolutionary origins of care [Mitić *et al.*, 2017]. Ecological factors such as harsh environments, ephemeral food sources or predation pressure in combination with life history or social interactions are generally accepted as evolutionary drivers of parental care [Wong *et al.*, 2013]. In agreement with previous studies [Manton, 1965; Brunhuber, 1970; Bonato, Minelli, 2002; Chipman *et al.*, 2004; Edgecombe *et al.*, 2010; Mitić *et al.*, 2010, 2012, 2016; Siriwut *et al.*, 2014; Vega Román *et al.*, 2018; Stojanović *et al.*, 2020], we have demonstrated that in Epimorpha not only the egg clutch is cared for until hatching, but also the early post-embryonic stadia, which are very incomplete and show only restricted movements (if any), remain under the protection of the mother. Several studies have shown that if the attending mothers are disturbed or irritated beyond a certain level, they react by either devouring the eggs or abandoning the brood to their fate. In the latter case, the eggs or young soon die due to natural enemies (preda-

tors, cannibalistic conspecifics and pathogens) or harsh environmental conditions (desiccation) [Lawrence, 1947; Auerbach, 1951; Palmén, Rantala, 1954; Brunhuber, 1970; Radl, 1992; Cabanillas *et al.*, 2019]. Such forms of care probably emerge from relatively simple ancestral forms of care — once egg attendance has evolved, it could evolve into offspring attendance by simply delaying the time of parental desertion [Smiseth, 2018].

To understand why parental care is or is not present in centipedes require a thorough understanding of phylogeny and ontogeny. The morphologically supported tree recognises a fundamental division of the Chilopoda into Notostigmophora (composed of the single order Scutigeromorpha) and Pleurostigmophora, which groups the other four living orders [Pocock, 1902; Verhoeff, 1902–25]. Pleurostigmophora is further divided into Lithobiomorpha and a putative clade that groups the remaining three orders; this group is called Phylactometria and is based on the common behavior of maternal care for the eggs and hatchlings. Phylactometria consists of the relictual *Craterostigmus*, Scolopendromorpha and Geophilomorpha, whereby the latter two orders are almost universally united in a group called Epimorpha [Edgecombe, Giribet, 2004]. The genus *Craterostigmus* has a single anamorphic stadium in its life cycle; it hatches from the egg as a 12-legged stadium and acquires the adult number of 15 leg-pairs — the plesiomorphic number of legs in Chilopoda — in the following stadium. This is in contrast to numerous anamorphic stadia in the orders Scutigeromorpha and Lithobiomorpha, which hatch with 4 or 6–8 leg pairs respectively and add more and more segments until they reach the definitive 15 leg pairs. The Phylactometria hypothesis has generally regarded the "reduced hemianamorphosis" of *Craterostigmus* as a transitional stadium in the evolution of complete epimorphosis in Epimorpha [Fernández *et al.*, 2014], where the evolutionary change in developmental timing (i.e. the acceleration of segment formation) has led to the "embryonalisation" of the originally post-embryonic stadia which would risk an early death without parental care [Arthur, 2011]. The ancestral state of Chilopoda is to have no parental care, which has evolved later in evolutionary history in the stem-group of Phylactometria. According to the alternative Amalpighiata hypothesis, in which Lithobiomorpha and not *Craterostigmus* is the sister group of Epimorpha, parental care is considered homoplastic. It is either general feature of Pleurostigmophora as a whole that was secondarily modified (lost, reversed or otherwise transformed) in Lithobiomorpha, or it was convergently acquired by *Craterostigmus* and Epimorpha [Fernández *et al.*, 2014].

Last but not least, the geophilomorph centipede analysed in this study was previously unknown in Serbia. *Stenotaenia rhodopensis* is closely related to *S. antecribellata* (Verhoeff, 1898) and *S. cribelliger* (Verhoeff, 1898), from which it differs by the first maxillary lappets (present in *S. rhodopensis*, absent in the other two species) and by the shape of the ventral pore fields (sub-triangular in *S. rhodopensis*, trapezoidal-oval in *S. antecribellata* and oval-elongated in *S. cribelliger*) [Kaczmarek, 1970;

Dányi, 2010]. Our results confirm that *S. rhodopensis* is a montane species distributed in the Carpathians and the Balkans. Significantly, the centipede fauna of Serbia, based on critically revised literature data, is represented by a total of 69 species (one Scutigeromorpha, 35 Lithobiomorpha, five Scolopendromorpha and 28 Geophilomorpha).

In summary, the enormous diversity of parental care among invertebrates is an advantage and a challenge. There is richness in both the number of groups that have evolved extended parental care and the forms of care provided by parents. In centipedes, maternal care is a derived (apomorphic) character restricted to *Craterostigmus* (with the suppressed anamorphosis) and Epimorpha, in which heterochronic change has led to embryonalisation of early post-embryonic stadia that would risk early death without offspring attendance. Such form of care is likely to have emerged from relatively simple ancestral form of care — once egg attendance has evolved, it could evolve into offspring attendance by simply delaying the time of parental desertion. Natural enemies and harsh environmental conditions have driven the evolution of centipede parental care.

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