“DEATH BEHAVIOUR” – THANATOETHOLOGY, NEW TERM AND CONCEPT: A TAPHONOMIC ANALYSIS PROVIDING POSSIBLE PALEOETHOLOGIC INFERENCES. SPECIAL CASES FROM ARTHROPODS OF THE SANTANA FORMATION (LOWER CRETACEOUS, NORTHEAST BRAZIL)

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ABSTRACT – A new concept, thanatoethology, is proposed and several peculiarities of the Santana Formation (Lower Cretaceous, Northeast Brazil) taphocenosis are analysed. Thanatoethology refers to the identification, interpretation and study of a specific behaviour performed by an organism moments before its definitive death, and also before the beginning of the fossilization process. This behaviour expresses agony, often due to asphyxia in land, air or water, and can be expressed in fossils as well as ichnofossils. The death behaviour in several cases can be associated with a mass mortality event and can be an extremely useful tool for paleoecological and paleoethological analysis. The identification of this paleobehaviour can be extracted from morphological traits preserved in the fossils, and some examples are furnished here.

Keywords: Thanathoethology, paleoethology, taphonomy, Santana Formation, Lower Cretaceous.

RESUMO – *R.G. Martins-Neto & O.F. Gallego – “Comportamento da morte” – Tanatoetologia, novo termo e conceito: uma análise tafonômica e possíveis inferências paleoetológicas. Casos especiais dos artrópodos da Formação Santana (Cretáceo Inferior, Nordeste do Brasil).* Propõe-se um novo conceito, Tanatoetologia, e várias particularidades de tafocenose são analisadas na Formação Santana (Cretáceo Inferior, Nordeste do Brasil). A Tanatoetologia diz respeito à identificação, interpretação e estudo de um comportamento específico de um organismo momentos antes de sua morte definitiva e também antes do começo do processo de fossilização. O comportamento expressa agonia, freqüentemente devida a asfixia em terra, ar ou água, e pode estar expresso em fósseis e também em icnofósseis. O comportamento da morte em vários casos pode ser associado com evento de morte em massa e constituir uma ferramenta muito útil nas análises paleoecológicas e paleoetológicas. A identificação do paleocomportamento pode ser feita em tratos morfológicos preservados de fósseis e são apresentados alguns exemplos.

Palavras-chave: Tanatoetologia, paleoetologia, tafonomia, Formação Santana, Cretáceo Inferior.

INTRODUCTION

Taphonomy (*taphos*, death, *nomos*, laws) is a term originally proposed by Efremov (1940), and literally could mean “the laws that drive death”, from the organism existence in the biosphere, either living (biocenosis) or dead (thanatocenosis), until it is incorporated into the lithosphere, when is buried and transported (taphocenosis), and it is at last fossilized, when it becomes part of a site (orictocenosis). Thanatoethology could be interpreted as the intermediate stage between biocenosis and an orictocenosis. Today taphonomy deals with the causes and processes involved before fossilization.

Traditionally, most of taphonomy is based on shelled molluscs and studies of such cases are available in many textbooks of paleontology. Much of the proposed nomenclature, examples and definitions are based on that group (*e.g.*, Kidwell et al., 1986). Not all concepts appropriate for molluscs, however, are applicable to arthropods, the main focus here.

Another important term is *lagerstätten*, which is a german term defining a paleontological site formed under very special geological conditions. Classic examples include the Solenhofen limestone from the german Jurassic, the Messel shale from the german Eocene, and the Santana Formation limestone (Araripe Basin, Lower Cretaceous of Northeast Brazil). All are famous for the preservational excellence of their fossils.

THE MULTIVARIATE PREMISES RESPONSIBLE FOR THE SANTANA FORMATION *LAGERSTÄTTEN*

Several chemical and physical factors are responsible for a well-preserved and intact fossil specimen. The main ones are: transport distance (*td*), floatation time (*ft*), decay rate (*dr*), mineralisation rate (*mr*), and sedimentation rate (*sr*).

The transport distance (*td*) depends on several possible variations of the water flux (if terrestrial) and wind velocity (if aerial), as well as the charge of the flux, terrain topography, inclination, barriers, vegetation, and precipitation rate. Simplifying to the minimal variable, the transport distance may be simplified in terms of long (*a*), middle (*b*), and short (*c*).

The floatation time (*ft*) depends on several characteristics of the water body: salt concentration, O_2 quantity, surface resistance, density, pH, temperature, depth, size, presence of minerals, and presence of debris. The floatation time also depends on the organism: if it is hard, slight, pointed, flat, delicate, big, small, and especially if it arrived alive or dead (if alive, for example, the organism will fight against asphyxia and try to get out of the water body by swimming, jumping or flying). Simplifying, we can reduce the floatation time to long (*d*), middle (*e*) and short (*f*).

The decay rate (*dr*) depends on several characteristics of the water body: microorganism quantity, presence or absence of anoxia in the bottom, presence, absence and quantity of specific minerals in the water body, and so on. Simplifying, we can reduce the decay rate to: high (*h*), middle (*m*) and low (*l*). The same can be applied to the mineralisation rate (*mr*), as well as the sedimentation rate (*sr*).

The floatation time (*ft*) combined with the transport distance (*td*) produces a final product (the collected fossil), which can be reduced and simplified to six variables: totally articulated (*ftd*), semi-articulated (*fte*), totally unarticulated (*ftf*), totally fragmented (*tda*), semi-fragmented (*tdb*) and unfragmented (*tdc*). Attributing hypothetical values to the variables it may be considered that $ftd = 0$, $fte = 0.5$, $ftf = 1$, $tda = 0$, $tdb = 0.5$, and $tdc = 1$. It seems to be coherent, because an unfragmented specimen (*ft* value 0) implies that flotation time is minimal to prevent or begin the fragmentation process.

On the other hand, a totally articulated specimen ($td = 0$) implies that the transport distance is minimal (if terrestrial) or fast (if aerial) to prevent or begin the abrasion process by transport. So, the flotation time and transport distance can be hypothetically closely related, and the possible relations may be expressed as follows (remembering that *tda* implies that the specimen was totally destroyed by the transport): $tdc + ftd = 0$ (unfragmented and articulated – Figure 1CA); $tdb + fte = 1$ (semi-fragmented and semi-articulated – Figure 1CI); $tdc + fte = 0.5$ (unfragmented and semi-articulated – Figure 1CB); $tdb + ftd = 0.5$ (semi-fragmented and articulated, Figure 1CJ); $tdc + ftf = 1$ (unfragmented and unarticulated, Figure 1CD); $tdb + ftf = 1.5$ (semi fragmented and unarticulated, Figure 1CE). The schematic diagram of these combined data is furnished in the Figure 1A.

The decay rate (*dr*) combined with the mineralisation rate (*mr*) produces a final product (the collected fossil), which can be reduced and simplified to six variables, as follow: undecomposed (*drg*), semi-decomposed (*drh*), totally decomposed (*dri*), unmineralised (*mrj*), semi-mineralised (*mrk*), and totally mineralised (*mrl*). Attributing hypothetical values to the variables it may be consider that $drg = 0$, $drh = 0.5$, $dri = 1$, $mrj = 1$, $mrk = 0.5$, and $mrl = 0$. Admitting that, if either $dri = 1$ or $mrj = 1$, it implies that simply the specimen no more exist (the specimen was totally destroyed by decaying and/or the specimen was not fossilized). On the other hand, if $dr > mr$ the chances of a good preservation are minimal; so the variables can be restricted to $drh + mrk = 1$ (semi-decomposed and semi-mineralised), $drg + mrl = 0$ (undecomposed and totally mineralised), $drh + mrl = 0.5$ (semi-decomposed and totally mineralised), $drg + mrk = 0.5$ (undecomposed and semi-mineralised).

Note that all figured specimens (Figure 1C) virtually exhibit no signal of decomposition and they are also totally mineralised. The fragmentation as well as the articulation degree does not necessarily imply poor mineralisation or high organic decay levels. Sometimes, a poorly preserved specimen is merely a collecting problem (part of the specimen in the counterpart of the slab, for example).

As traditionally has been pointed out in the literature, rapid burial could be responsible for exceptional preservation. Bate (1972) noted the excellent state of preservation of ostracods from the Santana Formation, believing that they probably had

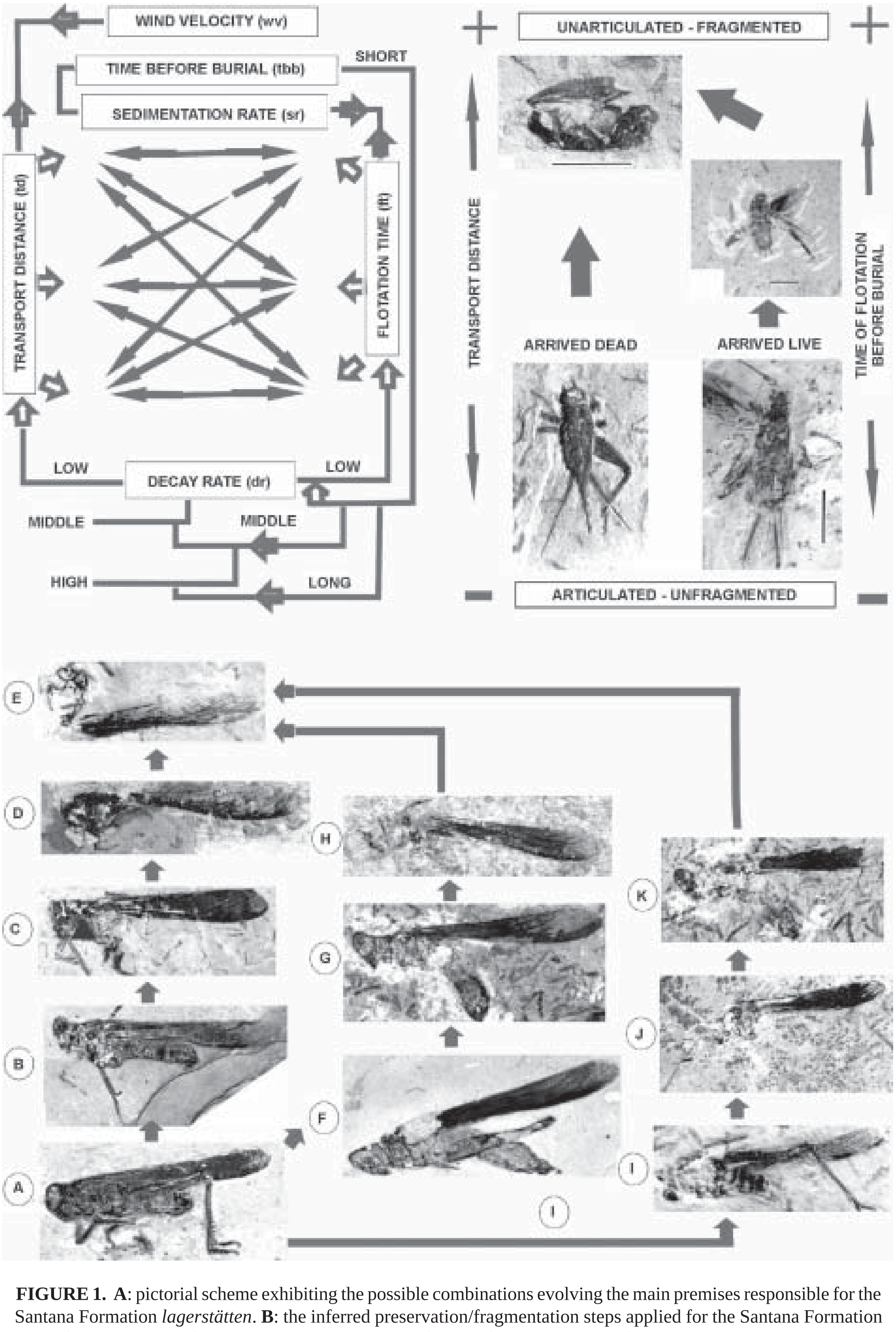


FIGURE 1. **A**: pictorial scheme exhibiting the possible combinations evolving the main premises responsible for the Santana Formation *lagerstätten*. **B**: the inferred preservation/fragmentation steps applied for the Santana Formation Ensifera. **C**: the same for the Santana Formation Caelifera. All figured specimens from Martins-Neto (1991, 2003).

been suddenly buried, suffered rapid asphyxia and the phosphate salts derived from the decaying fish could enable the rapid substitution of calcium carbonate and chitin by apatite.

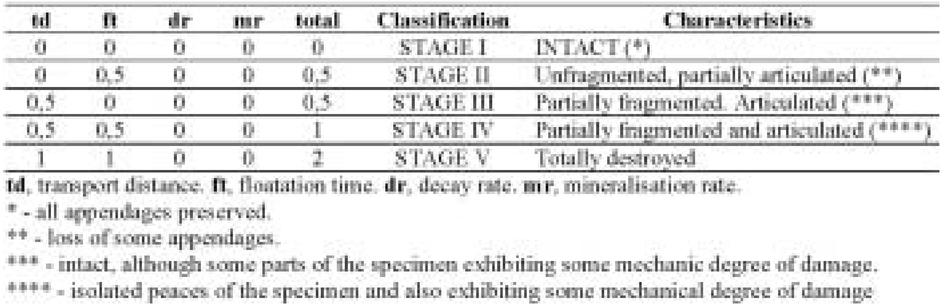
It is perfectly plausible to admit that exceptional physical and chemical conditions are requested for equally exceptional preservations, as pointed by Seilacher (1970). Another traditional inferred prerequisite for these cases refers to anoxia. Allison (1988), through experiences with extant invertebrates, had demonstrated that rapid burial, as well as anoxia, effectively diminishes the decay rate, but surely not stop it. In his opinion, the unique way stopping the decay is through the mineralisation, and some diagenetic reactions, as the formation of the pyrite and calcium carbonate, may occur within of weeks or months after the burial, and before the occurrence of the conspicuous decay of the organism.

In the case of the insects from the Santana Formation, the rapid burial hypothesis could be probable as well as a possible anoxia existence, what is plausible and could contribute for a slow decaying of the specimens, at the same time of diagenetic reactions (substitution of the chitin by apatite, for example), definitively interrupting the decaying process and furnishing an exceptional preservation, somewhat similar to the Eocenic preserved fauna from Messel, Germany (Franzen, 1985).

THE SELECTED PRESERVED ARTHROPOD GROUPS AND ITS TAPHONOMIC PECULIARITIES

Grasshoppers (Locustopsidae), crickets (Grylloidea) and hopes (Elcanidae) are the dominant insects from the Santana Formation (in number of named species, as well as number of collected specimens). This specific fauna, except Grylloidea, contrary to the other represented groups, are very peculiar, because quite all analysed specimens are preserved in natural *post-mortem* position (wings in a rest position, overlapped), well preserved (several intact ones) and totally articulated, three-dimensional. A little parcel exists with some part of the body lacking (generally the head and the legs), and other equivalent part just with the wings alone or some body fragment (summarised in Table 1). Indeed in the former case, the wings are still in rest position, sometimes slightly dislocated, which is perfectly compatible with a short transport.

TABLE 1. Santana fossil stages of detected fragmentation and articulation degree.



td	ft	dr	mr	total	Classification	Characteristics
0	0	0	0	0	STAGE I	INTACT (*)
0	0,5	0	0	0,5	STAGE II	Unfragmented, partially articulated (**)
0,5	0	0	0	0,5	STAGE III	Partially fragmented. Articulated (***)
0,5	0,5	0	0	1	STAGE IV	Partially fragmented and articulated (****)
1	1	0	0	2	STAGE V	Totally destroyed

td, transport distance. **ft**, floatation time. **dr**, decay rate. **mr**, mineralisation rate.

* - all appendages preserved.

** - loss of some appendages.

*** - intact, although some parts of the specimen exhibiting some mechanic degree of damage.

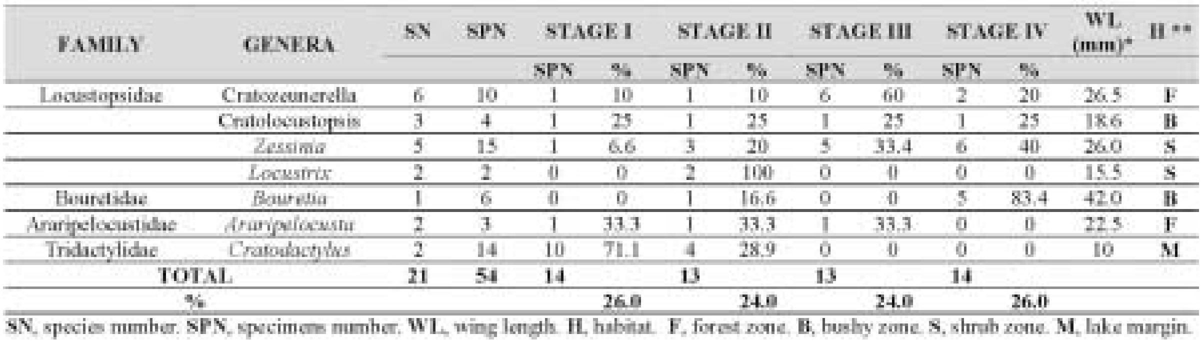
**** - isolated peaces of the specimen and also exhibiting some mechanical degree of damage

When an insect die debating in the water, the fossilization position is totally distinct, with the wings expanded and legs far from the body. The other elements of the paleoentomofauna are preserved in a more common way, with open wings (asphyxia signal), including the crickets, which had occupied – and occupies today – the same niches of the grasshoppers, implicate that, more than a simple asphyxia, the mass mortality of these grasshoppers (and also hopes) was conditioned by a situation of environmental stress.

So, the final product from Santana Formation may be reduced as showed in Table 2 (fixing *dr* = 0 and *mr* = 0, *i.e.*, well preserved: *dr* low, *mr* high).

The fossil grasshopper from the Araripe exhibits at least four of the proposed stages of detected fragmentation and articulation degree (of five possible), exampled in Figure 1C. The preservation of the Stage I (Figure 1CA) is possible when the specimen is intact, totally articulated and, in the case of the Santana Formation, also in a natural *post-mortem* position (wings in a rest position). From this stage derives two sub-stages: (a) predation, when another organism destroys part of the specimen, before or during the deposition, and (b) collecting problems, when part of the specimen is destroyed merely by inaccurate collecting. In Figure 1CC, the specimen could be stated in the Stage II, but

TABLE 2. Distributional pattern of fragmentation and preservation degree of collected Caelifera from Santana Formation. Data from Martins-Neto (1990a, b, 1995b, 1998b, 2001, 2003).



FAMILY	GENERA	SN	SPN	STAGE I		STAGE II		STAGE III		STAGE IV		WL (mm)*	H **
				SPN	%	SPN	%	SPN	%	SPN	%		
Locustopsidae	Cratozeunerella	6	10	1	10	1	10	6	60	2	20	26.5	F
	Cratolocustopsis	3	4	1	25	1	25	1	25	1	25	18.6	B
	Zessinia	5	15	1	6.6	3	20	5	33.4	6	40	26.0	S
	Locustrix	2	2	0	0	2	100	0	0	0	0	15.5	S
Bouretidae	*Bouretia*	1	6	0	0	1	16.6	0	0	5	83.4	42.0	B
Araripelocustidae	*Araripelocusta*	2	3	1	33.3	1	33.3	1	33.3	0	0	22.5	F
Tridactylidae	*Cratodactylus*	2	14	10	71.1	4	28.9	0	0	0	0	10	M
TOTAL		**21**	**54**	**14**		**13**		**13**		**14**			
%					**26.0**		**24.0**		**24.0**		**26.0**		

SN, species number. **SPN**, specimens number. **WL**, wing length. **H**, habitat. **F**, forest zone. **B**, bushy zone. **S**, shrub zone. **M**, lake margin.

seemly its abdomen was lost by predation. On the other hand, in Figure 1CJ the specimen could be stated in the Stage I, including the antenna preserved. The missing, apparently damaged parts could be preserved in the counterpart, characterising a mere collecting problem. The Stage II (Figure 1CB) is characterized by the partial loss of the appendages (*e.g.*, antenna and legs), what happen in few hours in extant grasshoppers before the death. In the Stage III (Figure 1CD), all the appendages are lost, the head fall and the body begin the decay process, culminating in the Stage IV (Figure 1CE), when just isolated wings are preserved or other isolated parts (as, for example, isolated fore legs). The next stage (V) could be characterised by the total fragmentation of the wings.

The exemplified stages in the Figure 1C could reflect variable periods of floatability of the specimens, before their final deposition and/or rapid transport by winds (passive or active). Quite all specimens arrived dead to the depositional site, with a minimal transport (very probably by the wind action).

Not only the grasshoppers and hopes (Elcanidae) exhibits these taphonomic peculiarities, but also several Neuroptera groups (Martins-Neto, 2002).

The named grasshopper and the state of preservation and fragmentation, based on the analysis discussed above, are exhibited in Table 2. The total collected grasshopper specimens reveal a uniform distribution for all stages (*ca.* 25 % in each stage). However, each genus has a particular degree of fragmentation/preservation, according with its inferred habitat and size (Martins-Neto, 2002). *Cratodactylus*, for example, a small type of grasshopper, which inhabits today the lakes boundaries, exhibits a distribution pattern concentrated at the Stage I (71.1 % of the collected specimens). On the other hand, *Bouretia*, a big sized grasshopper, which probably inhabited the forest zone, have 83.4% of the collected specimens concentrated at the Stage IV (isolated legs), as exemplified in Figure 3A.

Cratozeunerella have collected specimens concentrated at the Stage II (60%) and Stage III (20%), having an also inferred niche at a possible forestal zone (Martins-Neto, 2002). *Zessinia*, which inferred niche could be a shrub zone (Martins-Neto, 2002), have concentrated collected specimens also at the stages III (33.4%) and IV (40%), and also similarly sized as *Cratozeunerella* specimens. *Cratolocustopsis* have virtually the same distributional pattern of the whole Caelifera (25% of the collected specimens in each stage) and, perhaps for the *Araripelocusta* specimens could be identical, despite the low number of collected specimens (just three). As result the following distributional pattern (for Caelifera) is envisaged: Stages I and II – *Cratodactylus* specimens (100%); Stages III and IV – *Bouretia* (83.5%), *Cratozeunerella* (80%) and *Zessinia* (73.5%) specimens. The distributional pattern of *Cratolocustopsis*, *Araripelocusta* and *Locustrix* specimens (which are poorly sampled) remains indefinite.

This is implying that the grasshopper assemblage, notably diverse, came from also diverse niches and habitats and the distance transport rather than floatation time is the main responsible by the fragmentation degree. All collected specimens exhibits characteristics, which allow to conclude that arrived dead to the depositional site (wings in a rest position, a natural *post-mortem* display). All collected specimens exhibits a high degree of preservation, indicating that the mineralisation rate is high, as well as the decay rate is low. So, groups which live closest to the depositional site (*e.g.*, *Cratodactylus*) are rather concentrated in the stages I and II, and groups which live far from the positional site (*e.g.*, *Cratozeunerella* and *Zessinia*) are rather concentrated into the stages III and IV. The most plausible taphonomic process for the Santana Formation grasshoppers is schematised in Figures 2D, E.

For the crickets from the Santana Formation the taphonomic history is quite distinct. The collected number of specimens is very greater and, contrary to

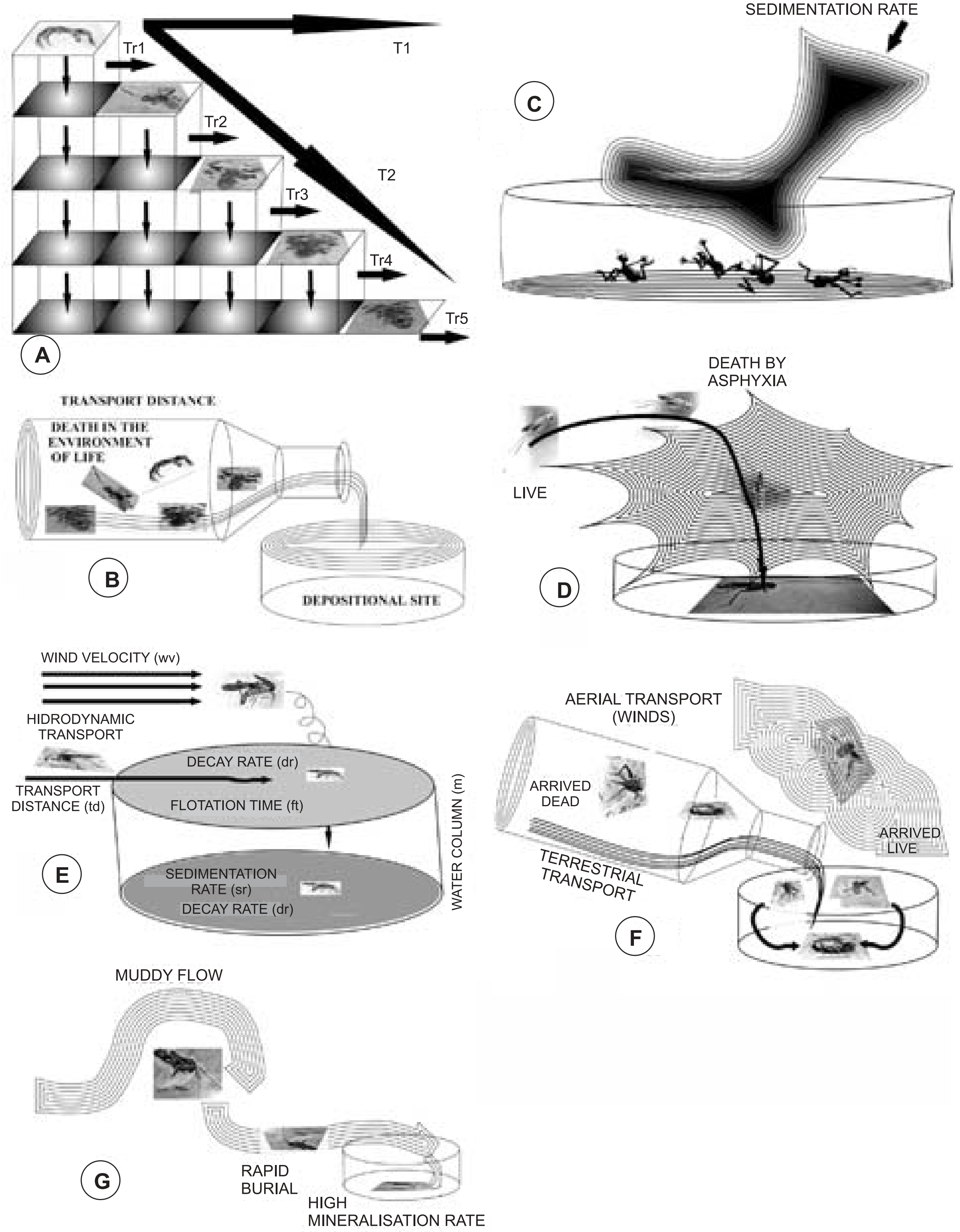


FIGURE 2. A, B: The “movies effect”. **C-G**: the possible explanation for the exceptional preservation of the Santana Formation arthropods – rapid burial at land (**B**) and at water (**C**), toxic gases inhalation (**D**), transport distance (**E**), aerial and terrestrial transport combined (**F**), muddy flow (**G**). All figured insect specimens from Martins-Neto (1991, 2003); spider specimens from SBPr collection; stage in life of grasshopper (**D**) modified and adapted from Blackenburry (2003), just for illustration.

the former analysed case, quite all specimens arrived live to the depositional site (wings not in a rest position, except Elcanidae). Contrary to the Caelifera preservation/fragmentation pattern, which is equally distributed to the stages, the Ensifera exhibits a conspicuous concentration at the stages III (50%) and II (34%). Genus by genus this tendency is the same (see Table 3). Note that all of the rare species (less than three collected specimens) are represented quite exclusively by isolated wings (Stage IV).

TABLE 3. Distributional pattern of fragmentation and preservation degree of collected Ensifera from Santana Formation. Data from Martins-Neto (1987, 1991a, b, 1992, 1995a, 1998a).

FAMILY	GENERA	SN	SPN	STAGE I		STAGE II		STAGE III		STAGE IV	
				SPN	%	SPN	%	SPN	%	SPN	%
Grylloidea	Araripegryllus	7	342	12	3.5	98	28.5	224	65.5	28	8.2
	Brontogryllus	1	1	0	0	0	0	0	0	1	100
	Caririgryllus	6	87	0	0	26	30.0	43	50	18	20
	Castillogryllus	1	1	0	0	0	0	0	0	1	100
	Olindagryllus	2	2	0	0	0	0	0	0	2	100
	Cearagryllus	9	39	2	6.0	9	23.0	16	40	12	30
	Notocearagryllus	2	2	0	0	0	0	0	0	2	100
	Santanagryllus	1	1	0	0	0	0	0	0	1	100
	Nanocearagryllus	1	1	0	0	0	0	0	0	1	100
Myrmecophilidae	*Araripemyrmecophilops*	1	1	0	0	0	0	1	100	0	0
Gryllotalpidae	*Archaeogryllotalpoides*	1	1	0	0	0	0	0	0	1	100
	Palaeoscapteriscops	1	1	0	0	0	0	0	0	1	100
	Cratotetraspinus	1	1	0	0	0	0	1	100	0	0
Stenopelmatoidea	*Kevania*	1	1	0	0	0	0	1	100	0	0
	Cratohaglopsis	1	1	0	0	0	0	0	0	1	100
	Phasmomimella	1	1	0	0	0	0	0	0	1	100
Elcanidae	*Cratoelcana*	2	151	26	17	87	57.5	32	21	6	4.5
	TOTAL	**39**	**634**	**40**		**220**		**318**		**76**	
	%				**5.0**		**34**		**49.5**		**11.5**

Abbreviations: as for the Table 2.

With respect to the Elcanidae (hopes) the general tendency is quite distinct: the specimens are concentrated at the Stage II (57.5%), and with a greater number of collected specimens at the Stage I (17%), as exemplified in Figure 3B. Contrary to the other Ensifera groups, virtually all collected specimens arrived died at the depositional site (wings in a rest position – a natural *post-mortem* display), so similar to the grasshopper specimens pattern. The same chemical and physical factors, which had affected the grasshopper fauna, probably were also responsible by the death of the hopes before its burial, as exemplified in the Figures 2D, E, G. The possibility of a high sedimentation rate while live in the depositional site (Figure 2C) is quite null, at least for the Elcanidae (hopes).

Specifically for the crickets, Figure 1B and Figure 2F exemplify the most coherent taphonomic process. In these cases, the floatation time seems be more significant than the transport distance.

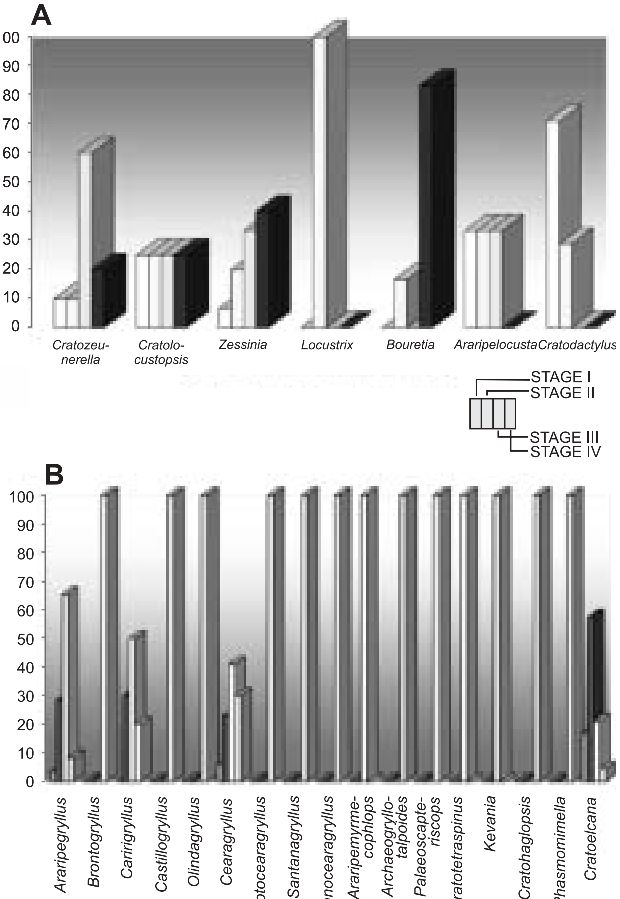


FIGURE 3. Distributional stages (from left to right), for each genus, respectively stage I to IV, of the Caelifera (**A**) and Ensifera (**B**), from the Santana Formation.

WHAT IS THE PALEOECOLOGICAL IMPORTANCE IN KNOW IF THE SPECIMEN ARRIVED LIVE OR DEATH IN THE DEPOSITIONAL SITE?

In the case of the alochtonous or parautochtonous specimens founded in the depositional site to know how the specimen arrived is really an important data. Obviously all collected fossil are dead! However, the taphonomic interest consist in know the exact moment before the definitive death. As stressed above, a specimen can arrive live or dead in the depositional site. If dead, something happened in its environments. For example, the arthropods where poisoned before their arrive (fire, volcanic eruptions, etc.) and so transported for the depositional site either by land (torrential waters, streams, rivers, rainfalls, etc.) or air (winds), being so a passive transport. If live, the arrive was due to winds or trough the same terrestrial hydrodynamic water flows pointed above, but in this case the transport was active. A terrestrial specimen found in the depositional site indicates nothing about the paleoecology of the local where was found, but much about the paleoenvironment which it was living.

In exceptional cases, it is possible that the water column itself was the responsible for the death of the organisms, which eventually overflow it. Several extant cases indicate that some algae species may have an explosive multiplication and cause mass mortality in the inhabitants of a lake and exhales toxic gases, killing the aerial life surrounding. This also may be happened in the geological past, and can be a coherent explanation for the grasshoppers and hopes from the Santana Formation, which arrived died in the depositional site, in a cyclic way along the geological column, but not for all other specimens founded.

After Martins-Neto (2002), at least three insect groups were demonstrated be experienced a mass mortality at Santana Formation: Elcanidae (hopes), Locustopsidae (grasshoppers), and Hexagenitidae nymphs (Ephemeroptera), the former two being alochtonous to the depositional site (terrestrials, not lived in the lake) and the last one being autochthonous (probably lived in the proper depositional site). The problems, which caused the death of the terrestrial arthropods, may be not the same for the aquatic ones. The hopes constitutes a peculiar group of the Santana Formation with thousands of collected specimens, but with just two recognized species characterizing a group that visibly reflects an environmental stress problem (thousands of specimens of the same species). This is not the same case for the grasshoppers, which are very diverse (at least 30 recognized species), and also quite all specimens arrived died to the depositional site. On the other hand, the Ephemeroptera nymphs was passing by a paleoecological problem (Martins-Neto, 1996, 2002) not restricted to them – the problem has affected probably also all other groups autochthonous to the paleolake: Odonata nymphs, aquatic heteropterans and coleopterans, fishes, anurans, and so on. This seasonal problem may be due simply to a salt concentration change, evaporation of the entire lake (coherent with the sedimentology and paleoclimatology – evaporation rate high, climates hot tending to aridity), poisoning (the algae cycle; Martins-Neto, 2002), acid rain, and so on. More than 90% of the other arthropod groups arrived probably live at the final depositional site.

THE “MOVIES EFFECT”: THE DEATH STEP BY STEP

Another interesting taphonomic peculiarity of the Santana Formation paleoarthropodofauna is the “movie effect”, *i.e.*, all steps of the death process of an organism preserved at the same depositional site. Figure 2A exhibits several steps of the death of a spider, as a movie or screen play: a spider specimen seeming walking in life (Tr1), beginning to die (some legs becoming retracted to the body: Tr2), retracting more (Tr3), totally retracted (Tr4), and finally a definitive death, at its natural ventral position (Tr5). Each of these steps evidently implies distinct relative times (Tr1 to Tr5) within a global time (the depositional site horizon: T1 and T2). Some of the possible explanations for this effect could be several distinct specimens falling live at distinct relative times and with distinct floatation time before the final burial, or several distinct specimens dieing in its terrestrial habitat at distinct times, and so transported altogether to the depositional site (Figure 2B). It is interesting to observe that each specific death stage was “frozen” and the normal process was interrupted. The unique way of occurs this is a “trap”. This is common, for example, in amber peaces. Thousands of arthropods trapped in amber peaces are virtually frozen in the time: insects in copula, ants at work, insects laying its eggs, parasites and its hosts, and so on. The former hypothesis seems to be not defensible because, for example, a death process by asphyxia of a spider in water implies in a “total” death, *i.e.*, the spider fall live, if this is the case, and die or not. If dies, it will attain rapidly the step Tr5, when could be or not be buried at the bottom, but the intermediate steps will be impossible to preserve in these conditions. So, the instantaneous death on land by trapping is more plausible, a “freezing effect” by rapid burial (Figure 2C). This can explain exceptionally preserved species as the hope of Figure 4A (in the exact instance of laying its eggs), that of Figure 4B (in the exact instance of its jump), or that of Figure 4C (apparently in copula). All these examples are extremely improbable to have occurred in water, and are better explained by the scheme of Figure 2G being instantaneously "trapped" probably by a muddy flow, producing the "movies effect".

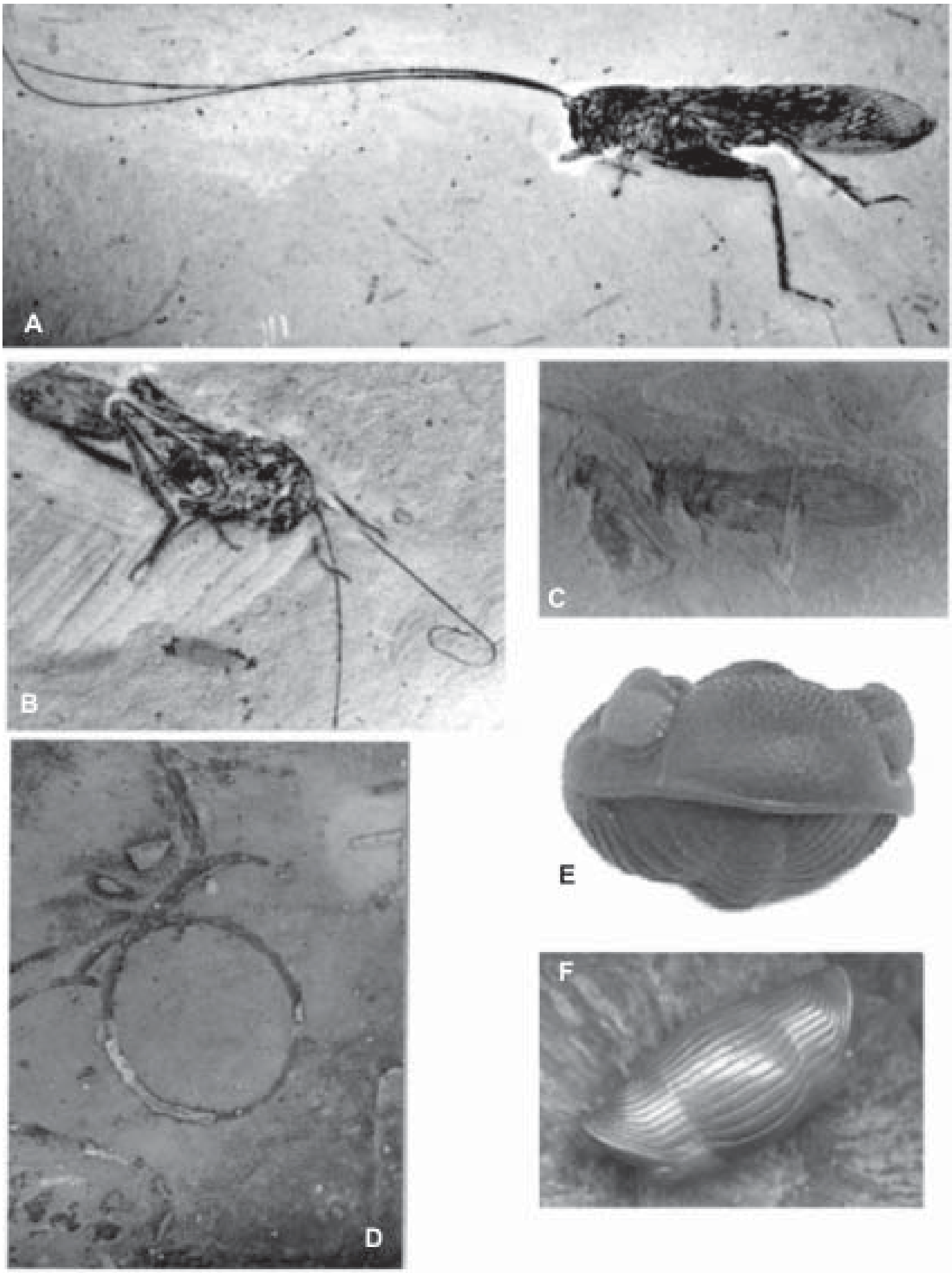


FIGURE 4. A-C: exceptionally preserved Elcanidae (*Cratoelcana* Martins-Neto) from the Santana Formation –in jump position (**A**); oviposition and a possible copula (**B**). **D**:"death behaviour" of the ichnogenus *Diplichnite*s sp. from the Varvite Park (Itu municipality, São Paulo State, Brazil – Paraná Basin, Carboniferous). **E-F**: enrolment in trilobites. **A**, from Kevin Mc Kevan, a gift in life to the senior author; **B**, from Martins-Neto (1991); **C**, from Martins-Neto (1995); **D**, photo by Martins-Neto; **E** and **F,** reproduced and adapted with permission from Gon III (2004).

PALEOETHOLOGY: THE DISTINCT FACES OF THE ANIMAL BEHAVIOUR

The behaviour consists of acts that the animal exhibits, non restrict just to the locomotion types (running, jumping, flying, and crawling) or to other activities which are in general derived from moving, as copula, burrowing or feeding (Del-Claro & Prezoto, 2003), but producing sounds, pheromones, twisting of the antenna, colour pattern, predation strategies and until the absence of movement (simulating death, enrolling, as well as others).

The facial muscles are studied today to understand distinct types of expressed behaviours. Due to the complexity of the facial muscles of the human being, a great account of associated behaviour can be expected and immediately understood, as for example when the individuals are hungry, timid, smiling, thinking, exhibit a surprise or terror expression, and so on (see some of them in Figure 5A). Several times, all their facial expressions are related with other adding movements, as for example of the eyelid, mouth, eyes, hands, arms, and sometimes altogether. On the other hand, a mouth movement may express behaviour completely different of the face one, at the same time. The same may occur for closely related animals (other primates for example), although a little less complex conjunct of facial muscles. Going back to the phylogenetic tree (vertebrates, for example), the complexity degree diminishes or not: basic behaviours, as mating, territoriality, defence and attack, and so on, are expected. All these behaviours are also expected to have occurred in animals of the geological past. Why not dinosaurs expressing a huge face, a hungry face, a surprise face, and all other probable ways to express behaviour? (In the Figure 5B, C, some probable ones).

So, ethology is the study of these observed acts and the paleoethology is the study of these same acts since be expressed or inferred in the external morphology of the fossils. Several of these paleobehaviour are extracted from the combination of the paleobiomechanic, paleophysiology, and from the paleoichnology (disciplines or sub disciplines which have experiencing notorious advances) data.

Apart vertebrates, the fossil invertebrates also furnishes good elements for inferences on paleobehaviour, as is the case of the insects. Many professionals, especially entomologists, have dedicated to behavioural studies, specially of so called social insects. Ants, bees, and termites, for example, have a really extraordinary spectrum of behaviours, documented and widely studied. The same could be occurred with fossil insects and it is possible to make inferences on the behaviour throughout the external morphology, as pointed below.

TANATOSIS (DEATH SIMULATION – TO FAKE OF DEAD)

Tanatosis is one of the more interesting invertebrate behaviours, due the fact that they may rapidly be observed in the nature and intuited with a relatively precision in fossils. From protozoan to molluscs, several species have special “sensors” acting in eminent dangerous situations: the nervous system of the organism temporarily stops all movements. This may occurs through the cilia with nervous termination, indeed rudimentary, retractile proboscis of echiuran and of several others platymorphs, or more specialized organs as the mollusc tentacles, which retracts to the first unexpected stimulus. Planarian, for example, paralyses itself under intense light. Several terrestrial gastropods totally retract itself, compacting (in the case of absence of a shell) or totally contracting inside the shell when they have one. Under danger, the traditional way could be simply run or fly, but is impossible to imagine snails trying this! For insects the antenna has high sensibility and some species are specialists in tanatosis. Really, the great majority when feeling itself in danger simply jump or go away flying; some are fast in the soil and run (*e.g.*, cockroaches), but there is extremely theatrical cases: some coleopteran species exaggerates so much in the scenic exhibition which includes from errant movements, simulating agony, to standing back for the substrate, with the legs close to the body, typical of a real *post-mortem* situation and stay paralysed by “unfinished seconds” (sometimes for hours; *e.g.*, Barreto & Anjos, 2002) until the potential predator go away (generally the predator insects uses visual stimulus for catch the prey and hate “dead lunch” – if it does not move, surely is not a good lunch). Apart insects with theatrical Shakespearean tendencies, others simply push back their more vital and important body parts (head and members) until their security is again established. This strategic behaviour generally can save several coleopterans specimens when captured in a web spider, which also hate dead prey (if the prey was not killed by itself, the spider rejects the meal and remove it from its web). Some spiders also simulate death depending on the situation, pushing back the legs, remaining paralysed until having the opportunity for a fugue or attack. Some crustaceans, when their movements are restricted of any way, without conditions

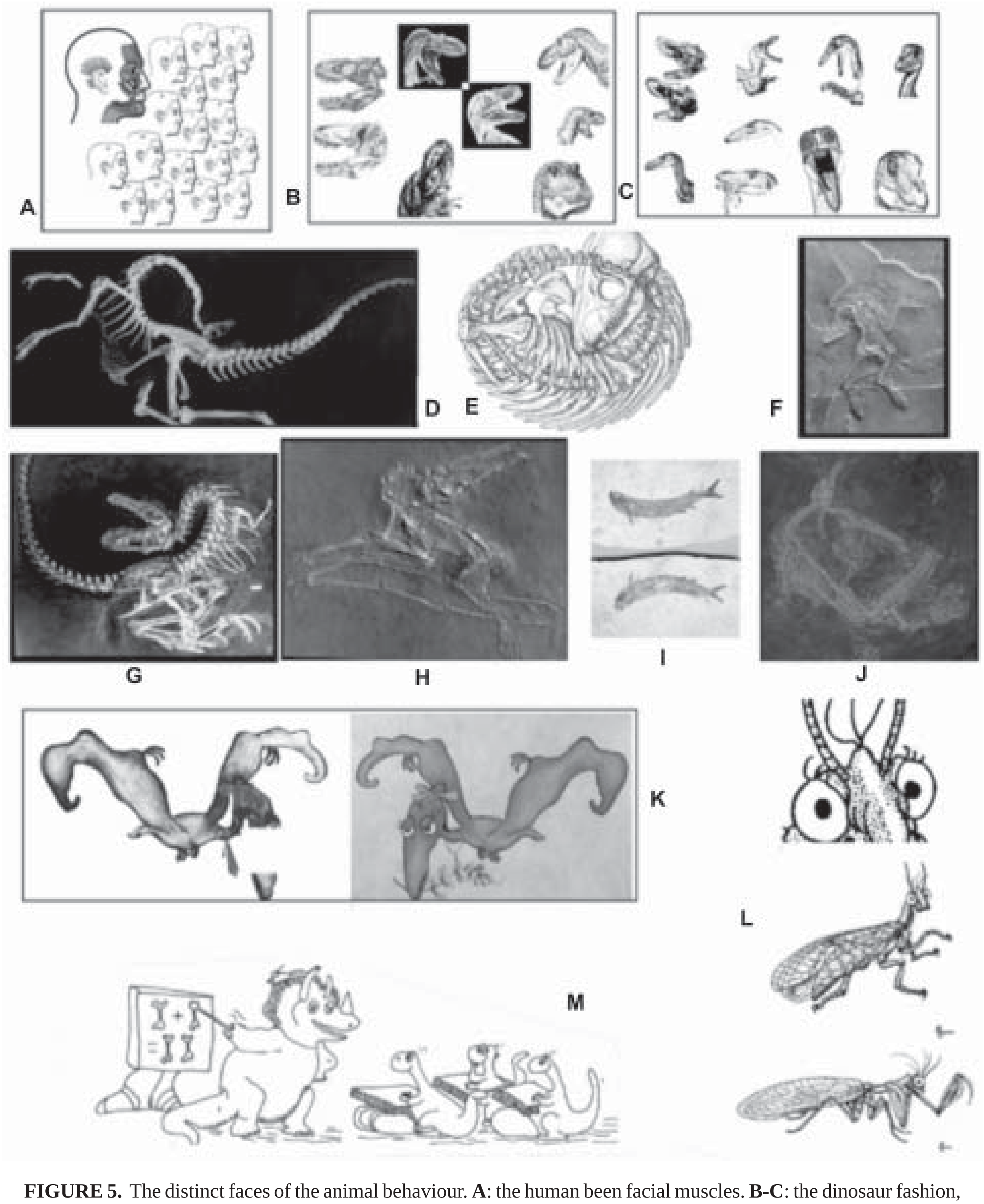


FIGURE 5. The distinct faces of the animal behaviour. **A**: the human been facial muscles. **B-C**: the dinosaur fashion, modified and adapted from several sources (specially Bakker, 1986). **D-J**: the death behaviour in dinosaurs (**D, G**) and pterosaurs (**H**), adapted from Wellnhoffer (1996); Cretaceous mammals (**E**), adapted from Czerkas & Czerkas (1990); *Archaeopteryx* (theropod dinosaur? Avis?), adapted from Wellnhoffer (1996); fishes from Santana Formation (photo by Martins-Neto); mesosaurid from Brazilian Permian (photo by Martins-Neto). **L**: "crazy" neuropterids insects (a special gift from Elke Gröning – Clausthal Institute, Germany); pterosaurs "facial behaviour" (drawn by Martins-Neto). **M**: "dinosaur teacher and students", from Martins-Neto (1993).

of a fugue or a possible attack, contract their bodies inside the carapaces until a more favourable situation.

All these cases however are not precisely detected in the fossil record because it is not possible to affirm if the founded fossil was really dead or if it was just simulating death in the moment that was preserved. But there are incontestable cases of derivation of tanatosis preserved in fossils, as the case of the enrolment (not properly tanatosis but a derivation of it: a defensive behaviour). Several arthropods, such as myriapods, diplopods, isopods and trilobites, have this faculty, a variation of the true tanatosis, so protecting their vital and important body parts, remaining immobile until the total disappearance of the situation that generates this behaviour. Several trilobites have the enrolment ability, forming a defensive ball or capsule, effectively protecting the vital body parts of the organism, including the ventral ones (Figure 4F), at the same time that exhibits a pseudo-aggressive posture (Figure 4E) to impress predators of any way. So, are the spiders of the Figure 2A simulating death at the moment which were "trapped"? It is probable; although just speculative, but perfectly possible, the specimens probably were "trapped" at distinct moments of several stages of a tanatosis, and the "trap" may represent the initial stimulus to this.

THE DEATH BEHAVIOUR: THANATOETHOLOGY, A NEW CONCEPT

Thanatoethology (*tanatos*, death; *ethology*, study of the behaviour), literally " the study of the death behaviour", cannot be confused with other classical concepts as Taphonomy ("laws which drives the death"), Tanatosis ("simulating death"), Taphocenosis ("a death assemblage"), or others closely related paleontological and biological terms.

Thanatoethology refers to the identification, interpretation and study of a specific behaviour realised by the organism, moments before its definitive death, and also before of the beginning of the fossilization process. This behaviour express agony, several times due to asphyxia (in land, air and water), and can be preserved in fossils as well as ichnofossils (see below).

The death behaviour in several cases can be associated to a mass mortality event (and constitutes a Taphocenosis), and may be an useful tool for paleoecological and paleoethological analysis. The identification of this paleobehaviour can be extracted from morphological traits preserved in the fossils, as for example fishes (mouth open, body contorted, typical of extant specimens dieing by asphyxia), dinosaurs and several other fossil vertebrates (head pushed back in a typical *rigor post-mortem* position; Figures 5D-J), and also in fossil invertebrates (virtually all which arrived live at the depositional site).

APPLICATION TO THE PALEOICHNOLOGY

The ethologic classification is very important for the paleoichonologic analyses and is based on the behavioural patterns inferred from the morphologic traits of the ichnofossils. Twelve categories or ethological groups are known (Buatois et al., 2002):

1. *Repichnia*: ichnogenera attributed to the arthropods displacement; it is related to the locomotion mechanisms, including marks of fish swimming traces;
2. *Cubichnia*: attributed to rest activities, several times confused with the *post-mortem* impression of the animal;
3. *Pascichnia*: attributed to the displacement and alimentation at the same time, related to the forrageceous activity on microbial beds or algalic beds or in strata rich in organic matter;
4. *Fodinichnia*: attributed to temporary subscavations of sedimentophagous organisms;
5. *Domichnia*: attributed to perforations or galleries, which serves as permanent or temporary home to infaunal organisms;
6. *Equilibrichnia*: reflects the variation rate of the sedimentation and/or erosion, and frequent reconstruction of the openings and reposition of the digging in the substrate;
7. *Fugichnia*: escape structures made by organisms in fugue;
8. *Agrichnia*: gallery systems, intrastratal swallow, horizontal, of high complexity degree, made by colonial or social organisms;
9. *Chemichnia*: multibranched galleries and meandrant excavations filled by decaying organic matter due to chemical symbionts organisms in anaerobic/disaerobic substrates;
10. *Calichnia*: simply or branched tubes with wide extremities (cell type), which are nidification structures, commonly of bees and coleopterans;
11. *Aedifichnia*: domic structures built over the

substrate (social insects as isopterans);

12. *Praedichnia*: perforation structures restricted to hard substrates, characterized by circular holes in shells and invertebrates carapaces, especially aquatics.

None of the briefly commented ethological groups is specific for the "death behaviour", although several good examples are available in the fossil record. "Death behaviour" is very different of, for example, a rest behaviour (*Cubichnia*) or a typical locomotion behaviour (*Repichnia* and *Pascichnia*). It is also different of a simple died organism, resting in the substrate. "Death behaviour" is also dynamic in essence, reflecting an activity of the organism when in life, or little before its definitive death. Several tracks founded at the Varvito Park (São Paulo State, Itu municipality – Upper Carboniferous, Paraná Basin) are attributed to myriapod locomotion (*Diplichnites*: tracks, trials and footprints epi- or intra-strata, linear or sinuous, sometimes branched, and continuous sulcus). A myriapod in life produces a linear track or little sinuous. The Itu tracks exhibit a conspicuous sigmoid or helicoidal tracks (Figure 4D), typical of animals in agony ("death behaviour"). Asphyxiated fish produces 8-shaped tracks (common examples are available from the Lower Cretaceous of Northeast Brazil), and, so, "death behaviour".

For all these specific cases, it is proposed here a new ethological group: *Thanatoichnia* n. nom., reflecting specifically tracks, trails or footprints produced by animal in agony (frequently caused by absence of oxygen, or inhalation of toxic gases, as ammonia, volcanic gases and other poisonous fluids and gases). "Death behaviour", now *Thanatoichnia*, is frequently associated to a local or regional mass mortality event being so very important to paleoecological inferences.

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