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Notostraca trackways in Permian playa environments of the Lodève basin (France)

Pistas de Notostráceos en ambientes de playa en la Cuenca de Lòdeve (Francia)

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Abstract

For nearly 20 years, Dr. Lapeyrie, surgeon at Lodève, has gathered many fossils coming from the Salagou Formation of the Lodève Permian basin. They are Insects, Notostraca, plants and ichnofossils. Among the latter, appears a multitude of Arthropoda trackways, finely preserved, which were collected in the top of sequences deposited in a playa environment.

The locomotion experiments undertaken with extant animals suggested allocation of the majority of these trackways to Notostraca which are also known by several hundreds of remains (carapace, appendages, body whole). From these different parts, it was described as *Triops cancriformis permiensis* and *Lepidurus occitaniacus*. All these trackways were made under water and correspond to various etho-morphotypes known in the literature under the name of *Acripes* for the walking prints, *Rusophycus* for resting traces (= stationary digging; horizontal, procline and opisthocline positions) and *Cruziana* for locomotion active and digging. Many fossiliferous slabs clearly allow to see the passage from one activity to another. A similar situation was also filmed with the modern *Lepidurus*.

The following ichnotaxa were distinguished: *Acripes multiformis* nov. isp, *Rusophycus eutendorfensis, R. carbonarius, R. versans, R. minutus, R. furcosus, Cruziana problematica, C. pascens* and *Scoyenia,* isp., less common. With also numerous footprints, this assemblage characterizes the *Scoyenia* facies restricted to overbank settings. For the Salagou Formation, they correspond to a floodplain/playa in which shallow and temporary pools were inhabited by Nostotraca, Insects, Arachnids and Conchostraca (= Spinicaudata + Laevicaudata), this last group only known by body-fossils. This distal playa environment under arid climate lasted during most of the Permian, possibly between Upper Cisuralian to lower Lopingian.

Keywords: Permian, France, Notostraca, *Scoyenia* ichnofacies (*Acripes, Rusophycus, Cruziana*), playa

Resumen

Durante casi veinte años, el Dr Lapeyrie, cirujano en Lodève, ha reunido numerosos fósiles provenientes de la Formación del Salagou de la cuenca pérmica de Lodève. Los mismos incluyen insectos, notostráceos, plantas e icnofósiles. Entre los últimos, hay una multitud de pistas de artrópodos, muy bien preservadas, las cuales fueron recogidas en el techo de secuencias depositadas en alrededores de lagos tipo playa.

Experimentos sobre locomoción de artrópodos efectuados con animales actuales sugieren que la mayoría de las pistas estudidas fueron producidas por Notostracos de los cuales se han encontrado algunos millares de restos (caparazónes, apéndices, cuerpos enteros) asignados a *Triops cancriformis permiensis* y *Lepidurus occitaniacus*. Todos estos rastros fueron producidos de forma subacuática y corresponden a diferentes eto-morfotipos conocidos en la literatura con el nombre de *Acripes* para las huellas de locomoción, de *Rusophycus* para las de descanso y excavación (posiciones horizontales, proclinales y opistoclinales) y de *Cruziana* para locomoción y excavación activa.

Numerosas planchas fósiliferas permiten ver claramente el paso de una actividad a la otra. Esta situación fue registrada en una película con *Lepidurus* actuales. Se reconocieron los icnotaxones *Acripes multiformis* nov. isp, *Rusophycus eutendorfensis, R. carbonarius, R. versans, R. minutus, R. furcosus, Cruziana problematica, C. pascens* y, menos abundantemente, *Scoyenia* isp. También fueron encontradas numerosas pisadas, destacando la icnofacies *Scoyenia,* encontrándose solamente en los «overbank settings». Para la Formación del Salagou, éstos corresponden a llanuras de inundación/playas donde las zonas inundadas eran temporales y de poca profundidad, y en las que vivían Notostracos, Insectos, Aracnidos y Concostracos (= Spinicaudata + Laevicaudata), este último grupo conocido solamente por cuerpos-fósiles. Este ambiente de playa distal, desarrollado en un clima árido, ha perdurado durante una gran parte del Pérmico, posiblemente entre el Cisuraliense superior y el Lopingiense inferior.

Palabras clave: Pérmico, Francia, Notostraca, icnofacies *Scoyenia* (*Acripes, Rusophycus, Cruziana*), playas.

1. Introduction

For a long time, the Red Permian formations of the Lodève basin were regarded as few fossiliferous. However, recent findings of traces and body fossils have changed that picture (Gand *et al.,* 1997; Nel *et al.,* 1999a-c; Béthoux 1999, 2003).

From numerous and beautifull Arthropod trackways observed on more than 150 slabs, a connection between various morphotypes was established. As some of them were defined several times, a complex and difficult nomenclatural correspondence problem took place which is discussed.

Research on the track-makers leads to do new locomotion experiments with present Arthropods. The results confirmed the classical suggested zoological attributions but only proven by Trusheim (1931). However new researches have allowed to explain the fossilization of these invertebrates traces.

The trace assemblage characterizes the *Scoyenia* ichnofacies redefined by Buatois and Mángano (1995). Its integration with sedimentological data indicates that these invertebrate tracks were mainly formed in playa environment pools.

2. Location and ages of ichnofossil sites (Fig. 1-2); stored collection places.

2.1. Location and ages

The trace fossils were observed in the Rabejac Formation (= Formation F4) and Salagou (= Formation F5) (Odin, 1986) which belong to the Saxonian Group (Gand *et al.,* 1997). In Formation F4, they were collected at the surface of sandstones and red siltstones and, in that of Salagou, in many centimetric levels of carbonated siltstones, commonly with desiccation marks, which overlay massive and metric mudstones. The vertical repetition of this binary sequence mudstone/siltstone is the characteristic of the Salagou Formatin (= F5) which was interpreted as a playa deposit (Odin, 1986).

According to different paleontological studies references, the age of these formations ranges from the upper Sakmarian or upper Artinskian to the lower Lopingian (Körner, 1999; Körner *et al.,* 2003; Legler *et al.,* 2004; Schneider *in* Gand *et al.,* 1997, 2004 a, b).

2.2. Collections

The samples collected in the Lodève basin are labelled in the following way: Ldg Gand, Ld LAP, Ldi GAR for respectively Gand, Lapeyrie and Garric collections. These letters are also preciced by a number for each specimen. The Lapeyrie collection is stored in the “Musée Fleury” of Lodève in Hérault (acronym = MFL). Those of Gand are in the “Centre des Sciences de la Terre”, University of Burgundy (CST-UB). For Garric, they are in the Palaeontologic Laboratory, Montpellier II University. By preoccupation with a simplification, in our paper work, the slabs will be only indicated by Ldg, Lap and Gar; for example Ld LAP 222 becoming Lap 222.

3. Locomotion trackways

Most of them were observed on many small slabs which result from a natural breaking of slend siltstones beds exposed under meteoric conditions. Many of them are up 5 to 17 cm long. Exceptionally, three exceed 40 cm and the largest reaches 60 cm (Lap 648). On the surface a sinuous trackway, 50 cm long, is preserved.

They are *Repichnia* (walking) (Seilacher, 1953) or *Movichnia / Natichnia / Cursichnia* (Müller, 1962), with/

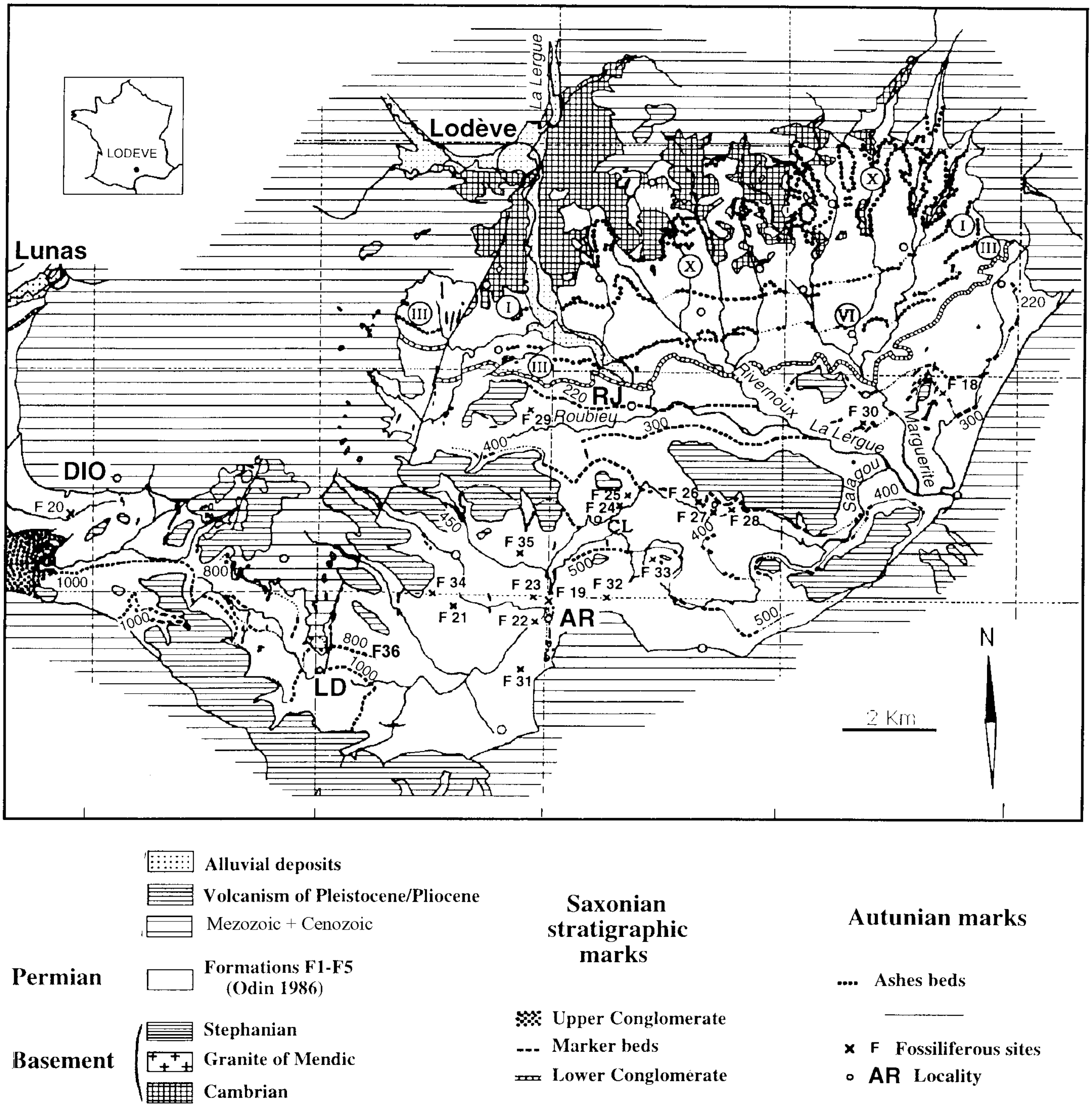

Fig. 1.- Geographic location of *Acripes*/ *Rusophycus/Cruziana* levels in the Lodève Permian basin; F20-F35 = main Fossiliferous sites located in the Rabejac Formation (F4) and Salagou (F5); 220-1000 are Marker beds in the Salagou Fm; RJ = Rabejac, AR = Arièges, CL: Celles, LD = la Lieude; Roman numbers = ashes beds in Autunian Group.

Fig. 1.- Localización geográfica y estratigráfica de los niveles con *Acripes/Rusophycus/Cruziana*) en el Pérmico de la cuenca de Lodève; F20-F35 = principales localizaciones fósiliferas situadas en las Fms. de Rabejac (F4) y del Salagou (F5); 220-1000 son cauces-marcas en la Formación del Salagou; RJ = Rabejac, AR = Arièges, CL = Celles, LD = la Lieude; números romanos = cauces volcánicos en el Grupo Autuniano.

without resting traces = *Cubichnia* (Seilacher, 1953) named also stationary traces (Bromley and Asgaard, 1972, Schlirf *et al*., 2001). We used Seilacher (1953) ethologic classification because it is based on fundamental characters: locomotion, resting, fooding and dwelling which it is often easy to distinguish from the ichnofossils. We will supplement it by that of Müller (1962) which was used by Walter (1983).

3.1. General characters and variability (Figs. 3. 1-14, 4. 1-15).

These trails are epichnia or hypichnia (Martisson, 1970). They are therefore observed as concave epireliefs

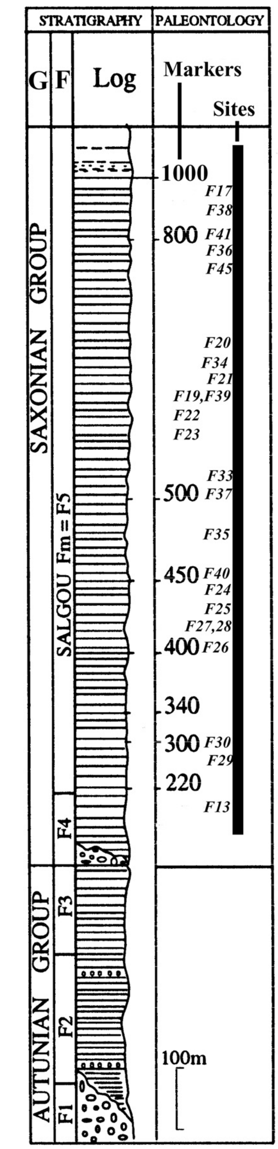

Fig. 2.- Ichno-fossiliferous sites in the Saxonian Group. Stratigraphy: G = Group, F = Formations (Fm) with F1 = "Usclas et St-Privat" Fm, F2 = "Tuilières-Loiras" Fm, F3 = "Viala" Fm, F4 = "Rabejac" Fm, F5 = "Salagou" Fm; Palaeontology, Markers = grey siltstone beds precised by arabic numbers (220-1000); the Fossiliferous sites range from F13 to F17.

Fig. 2.- Sitios icno-fosiliferos en el Grupo Saxoniano. Estratigrafía: G = Group, F = Formaciones (Fm) con F1 = Fm de «Usclas y de St-Privat», F2 = Fm de «Tuliières- Loiras», F3 = Fm de «Viala», F4 = Fm de «Rabejac», F5 = Fm del «Salagou»; Paleontología: marcas = cauces a arenas grises finas, precisados por numeros arábigos (220-1000); los sitios fósiliferos están repartidos desde F13 hasta F17.

(= EC) but more often they appear as hyporeliefs (= HC) which are their natural moulding. They consist of 2 band-prints made by distal end appendicular marks (= Figs. 3. 1 B; 4. 2, 9). They are either symmetrical or asymmetrical on both sides of a median axis. In several cases, the axis consists of two internal and parallel furrows (= Si), locally bordering a kind of gutter or channel (Figs. 3. 7, 8; 4. 10, 15). In other cases, the spacing between two furrows also parallel is larger. So that, they wrap up, more or less completely, the appendage traces (Figs. 3. 9, 10-12, 14). They are, herein, displayed as external furrows (= Se).

Each appendicular band, more or less broad, consists of fine series called as SL, SP and SD in this work. Those which are longitudinal or parallel to the direction of movement are called SL; perpendicular and oblique being successively SD and SP. The figure 5 a, b illustrate their origin. For example, if an arthropod has different long appendages such as A1<A2<A3, one can infer that the animal makes the trackway illustrated on the figure 5 b. If the gait is regular, one can expect to see that the A1-A3 end-tarsus tracks form 2 symmetrical B bands in which they are aligned according to 3 directions. They consist of 3 types of series.

It seems clearly that the SL number is also that of the thoracopods which printed the substrate. The SP series refers to the A1, A2, A3 distal appendicular end marks which were made successively in a step (= set). They are series *sensu* Osgood (1970) and Walter (1983). In the trackway, the prints draw a trapezoid or a V reversed shape. The SD or "differed series in time" gradually increases, from inside to outside and back-ahead, of a print, by each appendage moving. Thus, at the end of the second step, only the posterior series SD has all the appendicular marks preserved. The anterior ones will be complementary of a print by line during the animal moving; therefore up to 3 in the selected example.

This theoretical diagram helps to define the various parts of the different trackways and to infer their ethologic interpretation. However, because of variable gaits: walking to swimming passage, short stationary stages, quick direction changes, unequal fossilization or absence of the tarsian-end marks and irregular working of the two appendages rows, it will be often difficult, if not impossible, to interpret them with accuracy.

In trackways, the SD or SP series are formed by tarsian-end traces (= TA) more or less numerous. They are circular, oblong, "uni-polyfides", often prolongued by scratches, (Figs. 4. 14-17, 19; 8. 4, 10-12; 10. 1-3, 6; 11. 4-6, 8-11). In several cases, these series are formed by squeezed, right to curvilinear structures in which one distinguishes, more or less well, even not at all, the individual appendage marks (Figs. 4. 1-5, 7-11; 8. 1-2; 11. 1-3).

Pseudosymetric trackways have curvilinear appendages series in the double V (chevron) morphotypes. Where they are rather rectilinear, the trackways have ear shape if their orientation is oblique with the median axis and a scalar shape when they are perpendicular. But there is often passage from one to another form.

Asymmetrical trackways are particularly quite illustrated where they have distal end appendage imprints and external furrows. The strong asymmetry is due to a different orientation of the series from one to another row: e. g. perpendicular for one and oblique for the other; And also at the large lateral interval of the appendicular bands and the two external furrows (Figs. 3. 12; 11. 9-11; 9. 5, 7-8; 10. 1, 3-4). Large slabs, such as Lap 649 (Fig. 13. 1), in the case of the pseudosymmetrical and asymmetrical trackways TASe, shows that they were made by the same arthropod. Morphological differences in this case reflect behaviours.

3.1.1. Trackways having only distal end appendage traces (= TA).

Scalar or/and ear shape with or without cubichnia

These trackways are 1 to 12 mm wide. The smallest hardly exceeds one millimetre. They are many and commonly dense (slabs Lap 222, 229, 241, 242; 3 and 4). Their course is more or less sinuous with sometimes changes of directions becoming orthogonal. On the slabs Lap 222, 229 and 298, they are in the same direction turned.

These microtrackways consist of a bilateral SD and SP series, short and brought closer, commonly squeezed, having also a "keyhole". It is the fusion result, more or less complete of the circular to oblong appendage-end traces (Fig. 4. 1-5, 7-8). Trackways are often relayed or/and finished by a bilateral smooth structure, slightly striated, of which each part points out the shape of an open bean. It is the "coffee bean" of English authors. In this paper, they are precised by C on figures 4. 1-2; 6. 2, 4; 7; 8. 1-4; 11. 1-2; 12. 1-2.

Wider trackways have the same organisation as the preceding ones (Figs. 4. 6, 9-10, 14; 8. 5-9) but the appendage serie length tends to increase involving their distal curve. (Figs. 4. 9-10; 8. 5, 7). The appendicular end marks, quite separated of each other on the Gar 15 B 5 (Figs. 4. 6; 8. 12) and Lap 08 (Figs. 4. 14; 8. 10) slabs,

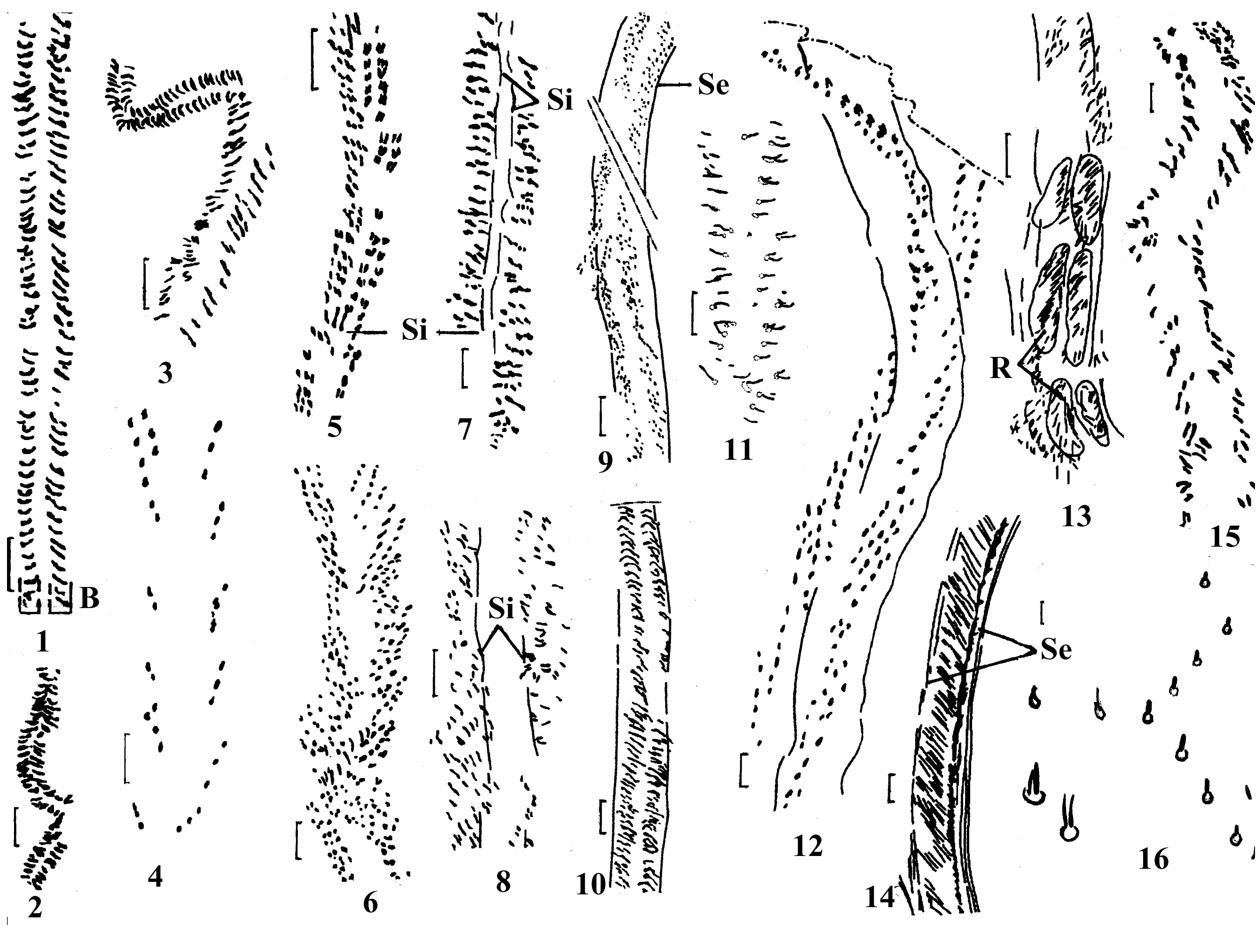

Fig. 3.- 1-12: Various *Acripes multiformis* repichnia morphotypes nov. isp.; 13: *Acripes multiformis* nov. isp. with *Rusophycus minutus,* cubichnia form (= R); 14: *Cruziana problematica,* paschichnia form; 15: *Permichnium*; 16: *Octopodichnus*; B = traces of appendicular serie bands, Se = external furrows, Si = internal furrows; scale-bar = 5 mm.

Fig. 3.- 1-12: Diferentes morfotipos de Repichnia *Acripes multiformis* nov. isp.; 13: *Acripes multiformis* nov. isp. y *Rusophycus minutus* forma Cubichnia (= R); 14: *Cruziana problematica* forma pascichnia; 15: *Permichnium*; 16: *Octopodichnus*; B = fajas de series de huellas apendicularias, Se = surcos externos, Si = surcos internos; escala = 5 mm

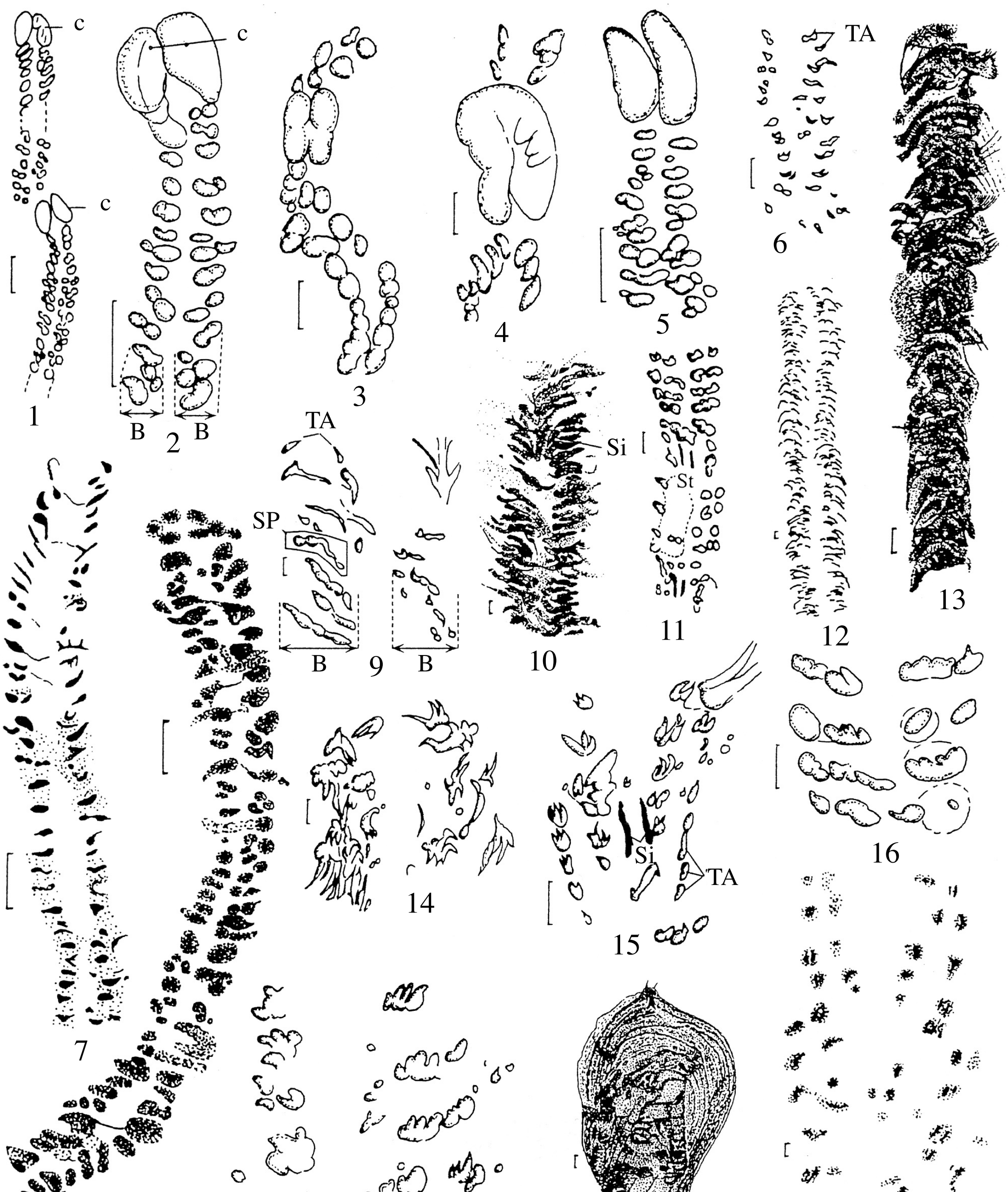

Fig. 4.- 1-17, 19: *Acripes multiformis* nov. isp.; **18**: digging holes**; 1-8**: TA forms without furrow with possible cubichnia presence (C = *Rusophycus*); **12**: double V shape TA form; **13:** left band detail of fig. 12; **10-11**: TA form with Si; **9**: detail of **10** with SP = serie produced from successive printed TA during the pace (= set); TA = appendage traces; **14-17, 19**: morphologic variability of TA = distal end appendicular traces; scale-bar = 1 mm.

Fig. 4.- 1-17, 19: *Acripes multiformis* nov. isp.; **18**: agujeros de perforación; **1-8**: formas TA sin surco con presencia o no de cubichnia (C = *Rusophycus*); **12**: forma TA en doble « cheurrón »; **13** = detalle de la faja izquierda de 12; **10-11**: forma TA con Si; **9**: detalle de **10** con SP = serie hecha de TA sucesivamente imprimidas en el paso, TA = huellas de las extremidades apendicularias; **14-17, 19**: variabilidad morfológica de las huellas de extremidades apendicularias TA; escala = 1 mm.

have a variable morphology. They are punctiform prints, more or less fine, prolonged by 1 to 4 parallel scratches, perpendicular to the trackway axis.

The figures 4. 19 and 8. 11 represent those on the Gar 11 C slab. Each series is laid out very obliquely with the axis of the trackway. The appendicular impressions are clear and quite separated there. Several of them are consisted by 2 short parallel features; others have a Y form.

Double V shape without cubichnia

This last morphotype is well represented on the Lap 282 slab (Figs. 4. 12-13; 8. 8) but also on Lap 222, 229 and 287. The series of impressions are much more arched there than in the preceding trackways but the appendicular ends are not detected. A band structure is detailed in Fig. 4. 13 in which certain series appear bordered of fine striations.

3.1.2. Trackways with distal end appendages and two furrow traces (= TAS)

Scalar to ear shapes with 2 internal, discontinuous/ continuous and median furrows (=TASi)

A first group of repichnia, 5 mm wide, is well documented on Lap 222, 226 and 242 slabs (Fig. 9). The short series there are perpendicular (Fig. 9. 1) or slightly oblique to the median axis (Fig. 9. 2-4). They consist of 2 to 5 "tetrafid" or polylobed appendicular impressions where they are isolated. According to the state and the nature of the sediment, these traces can be merged producing a squeezed aspect to the series (Figs. 4. 15-17; 10. 1-3, 5-6).

The trackways have regular discontinuities, better marked in the ear-shapes. This aspect results from of a longitudinal repetition of encased centimetric trapezoidal patterns (Fig. 9. 4 d1 d2). Each one of them is formed by the regular grid of distal appendicular impressions. It shows at the base or at the top, 2 short discontinuous furrows prints in median position (Si, Fig. 9. 1; 10. 3, 5).

In a more continuous way, these latter are also represented on the Lap 227 and Lap 09 slabs. On the trackway of this latter (Figs. 12. 9; 17. 1), the series of 6 appendages, few mm separated, are oblique there. But in a trackway part, the appendicular impressions of each series are connected, each one being prolonged by a curvilinear scratch which reaches the following series (Fig. 18. 1d). A kind of checkerboard with losangic pattern results which is seen on the Gar 15 B 5 trackway (Fig. 10. 8).

The double internal furrow is finally observed in trackways ranging from 1 mm (Lap 227/229) to 14 mm (Lap 09) in width.

Scalar to ear shapes having 2 furrows overflowing or crossing the appendicular series with or without cubichnia (=TASe).

The appendicular mark organization and characters are similar to the preceding trails (Fig. 11). On the Gar 15 B1 slab, poorly preserved punctiform impressions as well as oblong and arched series, are ornemented with small

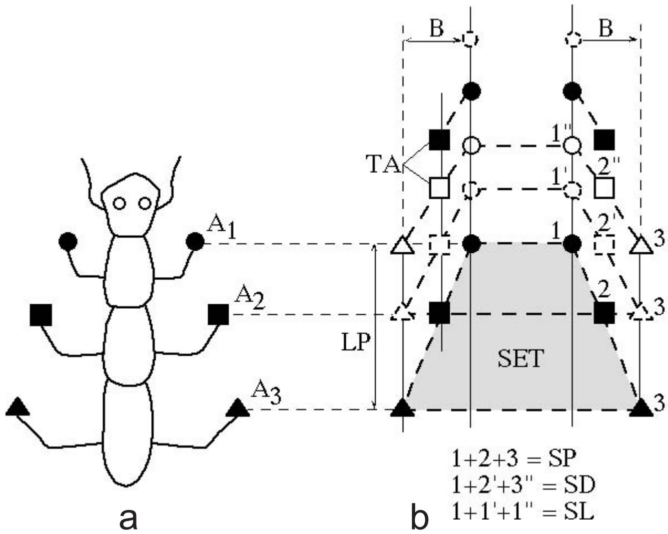

Fig. 5.- **a**: Theoretical terrestrial arthropod with 3 appendage (A1-A3); **b**: produced trackway during the walking. The diagram shows the thoracopod (TA) appendicular trace disposition; SP: trace series impressed in a step, SD: differed trace series, SL: longitudinal trace series, L: length of the step or set: distance covered after the movements of 3 A1-A3 appendages (explanation in text).

Fig. 5.- **a**: Artropódos terreros teoricos, con 2 apéndices (A1-A3); **b**: pista producida durante la locomoción. Esquema explicativo de la disposición de las huellas de las extremidades apendicularias de torácopodos (TA) en un paso, SP: serie de huellas en el paso, SD: serie de las huellas diferidas, SL: serie longitudinal, L: longitud del paso: distancia recorrida después del movimiento de los 3 apéndices A1-A3.

peaks notched on the margins (Fig. 11. 1-3). Locally the indentations are prolonged on the sediment surface by sparks. Lap 649 shows series with clearly preserved impressions (Figs. 11. 8; 13. 1-2), but on Ldg 148, those are reduced to scriptural forms (comma, accents…) (Figs. 11. 4-5).

The appendicular bands are locally bordered outside by 2 parallel furrows of which a part may be duplicated (Figs. 10. 10; 11. 3). But this arrangement is not constant because, generally, these two structures intersect (Figs. 11. 1-5, 8; 12. 1-5, 7-8).

The sinuous marks of the furrows, not very deep in epirelief, crested in hyporelief is, according to cases, continuous to discontinuous and locally better printed or not, on a side. In certain trackways of the Lap 649 slab, the orientation change is abrupt and accompanied by a short break. After a short interval, the 2 furrows are again marked with a light lateral interval in the hook shape (Figs. 13. 1-2).

3.1.3. Trackways without distal end appendage impressions having only the furrows (Se/Si).

Extremely rare, these hyporelief trackways were observed on Lap 1-3 slab. They are reduced to a central fur-

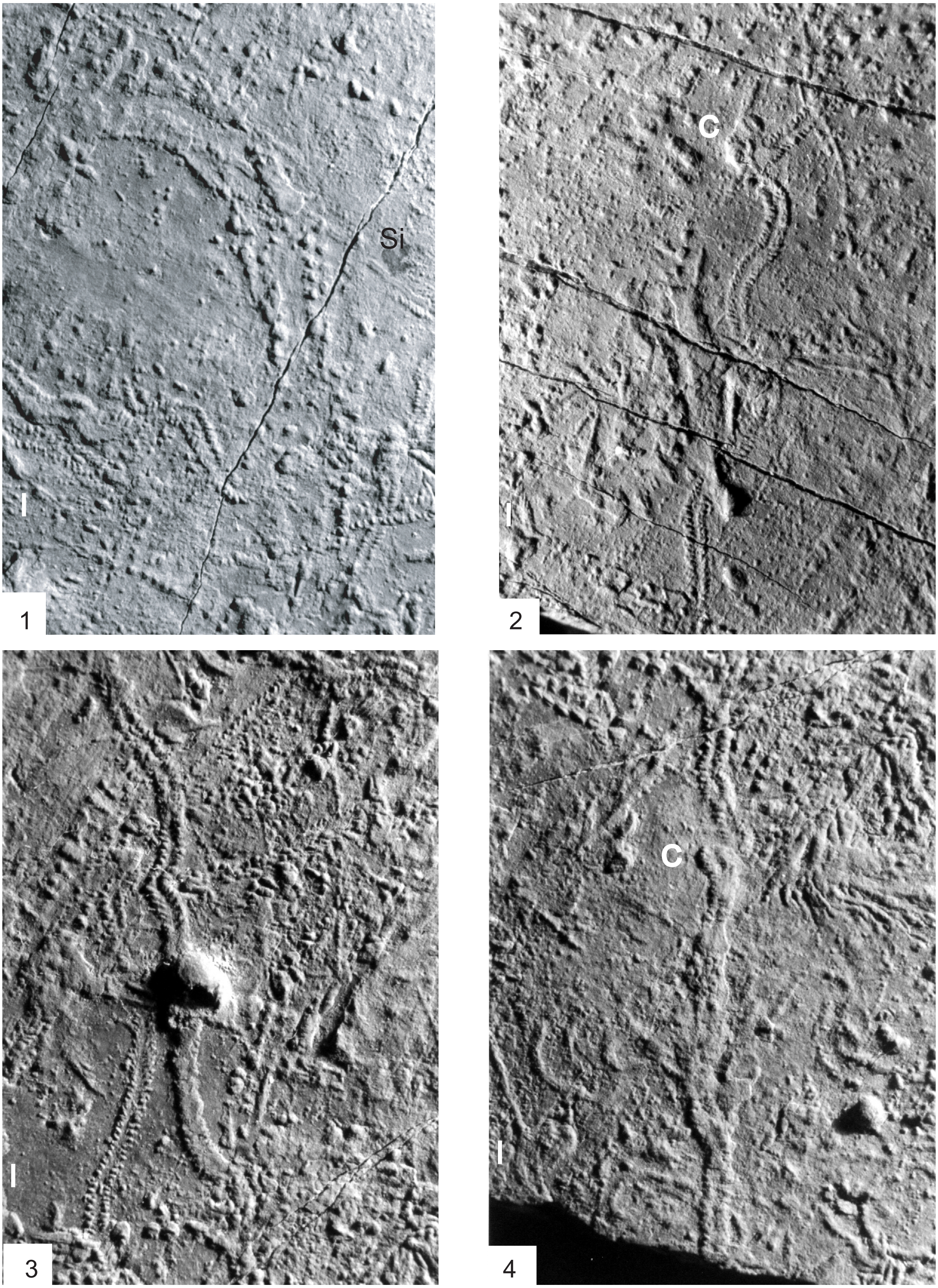

Fig. 6.- 1-4: *Acripes multiformis* nov. isp., C = «coffee bean» = Cubichnia = *Rusophycus minutus;* Si = internal furrows; 1-2: Lap 229 slab, 3-4: Lap 242 slab; scale-bar = 1 mm.

Fig. 6.- 1-4: *Acripes multiformis* nov. isp., C = «grano de café» = Cubichnia = *Rusophycus minutus*; Si = surcos internos; 1-2: losa Lap 229; 3-4: losa Lap 242; escala = 1 mm.

row (Si), partly duplicated on the Lap 02 slab (Fig. 10. 4). This last occupies the median part of a ribbon, 1 cm wide, bounded by 2 other furrows (Se). As in the preceding trackways, their impression is discontinuous.

The thread-like aspect of the furrows is changed, in a variable way, by V-shapes, laterally prolonged by sparks. These figures, similar to those which are noticed on the Lap 222 slab (Fig. 7. 1 Cy), are due to the cyanobacterian veil tearing by an animal body part (Demathieu and Durand 1975).

3.2. Systematic ichnology.

From the abundant material, represented by nearly 400 trackways observed on 200 slabs, the morphological variability can be assesed. That they are long or short, more or less wide, pseudosymetric to asymmetric, reduced to only appendicular traces or comprising, in more, the furrow marks, it is established that these various morphotypes, described above, are only the parts of a trackway specified on the synthetic figure 22.

3.2.1. Analysis of the current nomenclature for TA, TAS and Se/Si.

The trackway characters reduced to distal end appendage traces (= TA).

They are rather those of the successive *Acripes* Matthew (1910) and Walter (1983) diagnosis. This ichnogenus which comprises several isp, was discovered in the "Lower Cordaïtes" Formation (Carboniferous, USA). Then Walter (1983) revised and used it to name *A. sittichenbachensis* collected in Obere Hornburger Schichten Formation of Rotliegende (Saxony). He provided the following diagnosis "Thin, maximum 10-15 mm thick trackways, mostly graduated (in straight, fishbone-like following one another series) on one side; the series of impressions resulting from the individual situation mostly consists of 6-9 single impressions". However the existence of millimetric-wide trackways in the material of the Salagou Formation shows that this ichnogenus can include also smaller morphotypes and having also a lower number of appendicular-end imprints per series, than that indicated by Walter (1983).

In the Lower Autunian Group of the Lodève basin western part, Debriette and Gand (1990) described *Trachomatichnus* Miller, 1880, a morphotype similar to those of the trackways coming from the Salagou Formation. This one was preferred at *Acripes*. But *Trachomatichnus* was synonymized with the profit of *Diplichnites* Dawson, 1873 by Seilacher (1955). And this one, after having indicated, for Dawson, the pectoral spines prints of a fish, Seilacher thought that *Trachomatichnus* represented rather Cambrian Trilobites traces. But in its revision, Osgood (1970) wrote that *Diplichnites* was too poorly definited to be used. Although Häntzschel (1975: 61) validated it in its synthesis, we think that *Diplichnites* is not adapted to name the trackways of the Lodève basin made by arthropods having moving in a continental aquatic environment. More recently, this ichnogenus was used to define Arthropleuridae trackways from lacustrine facies of the French and German Upper Carboniferous/Lower Permian (Briggs and Almond 1984; Walter 1988, Schneider and Werneburg 1998) which are quite different from those that we described here.

In this "lodévoises" trackways entire, some of them show TA prints series, partly or mainly curvilinear. Based on a fragmentary material, these double V shaped footprints (cf supra) could be included in the monotypic ichnogenus *Multipodichnus* Walter, 1983. However the examination of abundant material showed that in many trackways there is a continuous passage between rectilinear and curvilinear series. Thus *Multipodichnus* makes double employment with *Acripes.*

Protichnites Owen, 1852, validated *in* Häntzschel (1975: 97) could be used to name trackways of appendages traces with 2 internal, discontinuous to continuous and median furrows (TASi). Originally, they were regarded as Xiphosura and Gastropods imprints. Seilacher (1955) used it to name those of Trilobites belonging to the Upper Cambrian whose trackways may be connected to the *Rusophycus* resting traces.

During our study, WH proposed to use *Acripes* to name the trackways having 2 furrows overflowing or crossing the appendicular series (with or without cubichnia) (= TASe). But on the basis of the diagnostic elements, *sensu* Walter (1983), GG thinks that it should be necessary to define again *Acripes* in order to include the furrows existence.

Euproopichnus Walter, 1983 could be appropriate but its definition is too precise, therefore too restrictive and does not include the "lodévoises" trackways characters. Moreover, Walter (1983) allocatted this ichnogenus to Limulids. By mutual agreement between HW and GG, it seems preferable not to use this taxon to indicate the repichnia of the Lodève basin.

The trackways without distal end appendages traces having only the furrows (Se/Si).

They remain still enigmatic. They share similarities with "*Cloephycus*" of the lower Permian of Podkrkonoší from Russia (Holub and Kozur 1981). Two double furrows, partly V shaped, are observed in figure 10. 4 (Lap

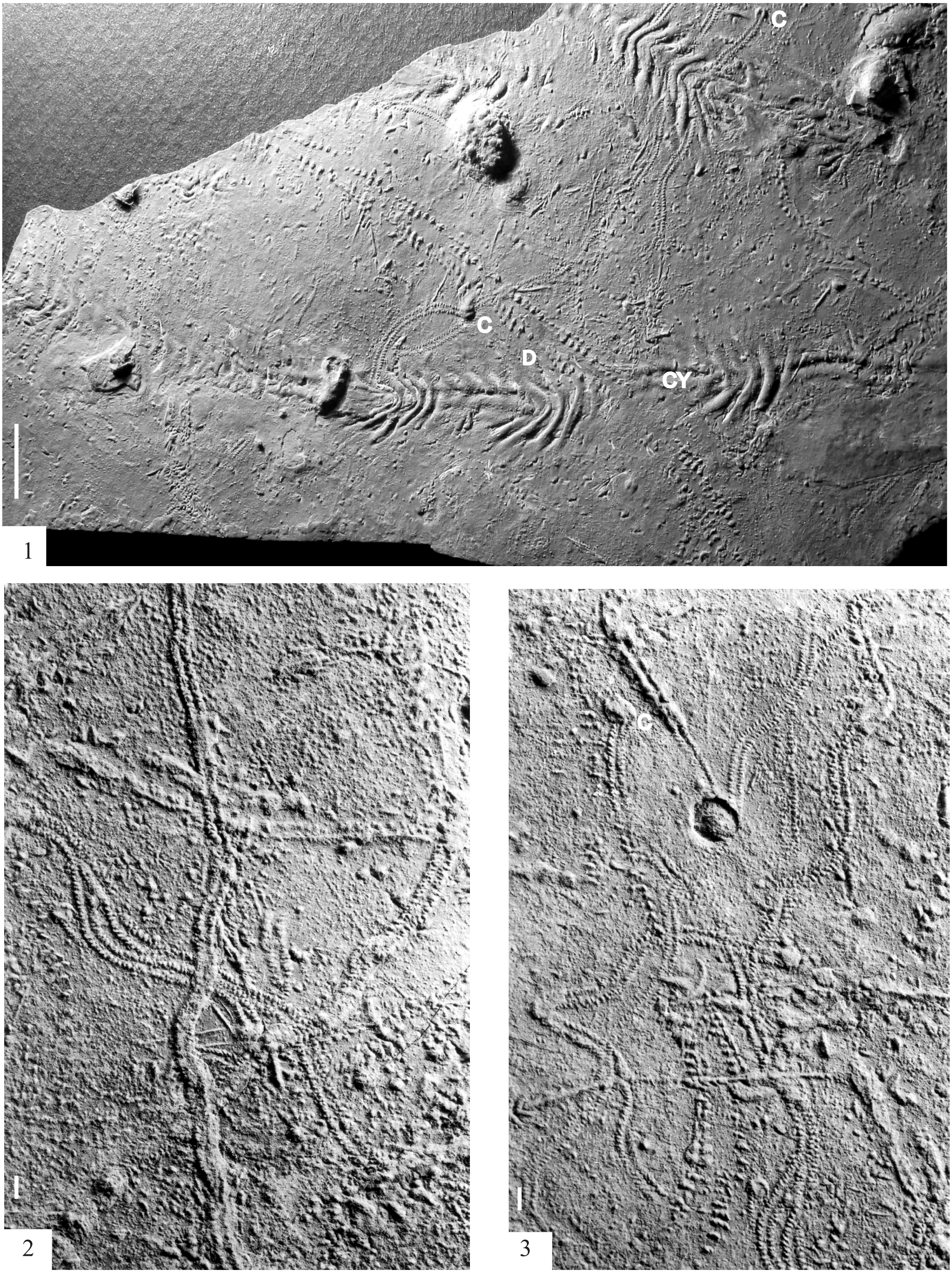

Fig. 7.- *Acripes multiformis* nov. isp., TA forms with/without cubichnia (= C); **1**: Lap 222; **2-3:** Lap 241;Cy = cyanobacterian crumpling veil; scale-bar = 1 cm for 1 and 1 mm for 2-3

Fig. 7.- *Acripes multiformis* nov. isp., formas TA con o sin cubichnia (= C); **1**: Lap 222; **2-3** = Lap 241; Cy = rugosidad del velo cianobacteriano; escala =1 cm para 1 y 1 mm para 2-3

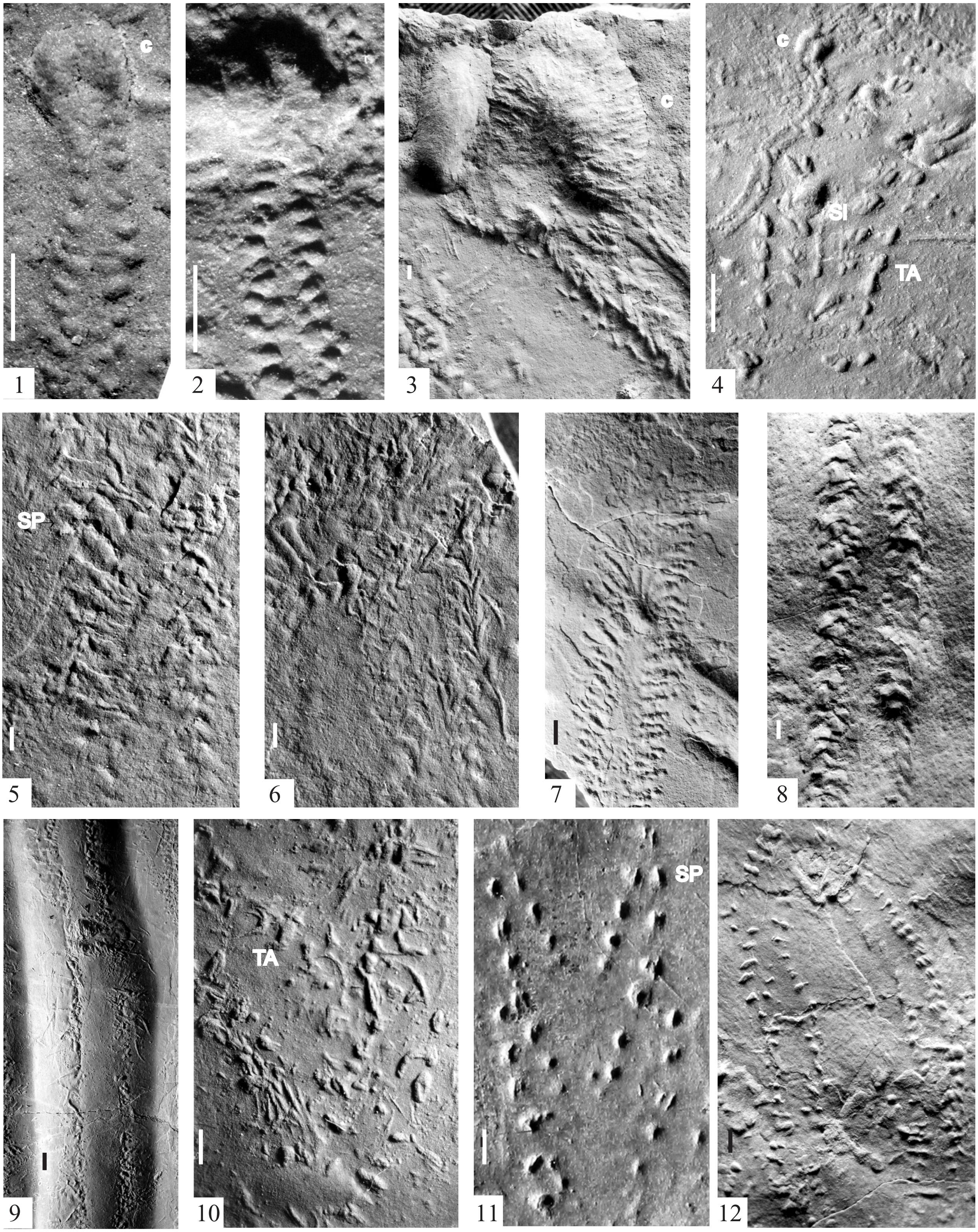

Fig. 8.- **1-12**: *Acripes multiformis* nov. isp.; **1-4**: TA forms with C = cubichnia = *Rusophycus*; **1-2, 4**: Lap 222 slab; **3:** Lap 196; **5-7**: TA forms with right to curved SP and indistinct TA; **5-6**: Lap 202 slab; **7**: TASi form, Lap 302; **8**: double V shape TA, Lap 282; **9-12**: TA forms variability; **10:** enlargement of **fig.** 9 = trackway produced in a ripple bottom, Lap 08; **11-12:** TA produced from possible SP or SP/SD series; Si = internal furrows; scale-bar = 1 mm for 1-2 and 2 mm for 3-12.

Fig. 8.- **1-12**: *Acripes multiformis* nov. isp.; **1-4**:formas TA con cubichnia C = *Rusophycus*; **1-2, 4**: losa Lap 222, **3**: Lap 196; **5-7**: formas TA con SP rectas a curvadas y TA indistintas; **5-6**: losa Lap 202, **7**: forma TASi, Lap 302; **8**: forma TA en doble cheurrón, Lap 282; **9-12**: formas TA mostrando la variabilidad; **10** aumento de la fig.9 = rastro producido en el fondo de una onda (Lap 08); **11-12:** TA hechas por posibles series SP o SP/SD; Si = surcos internos, C = cubichnia = *Rusophycus*; escala = 1 mm para 1-2 y = 2 mm para 3-12.

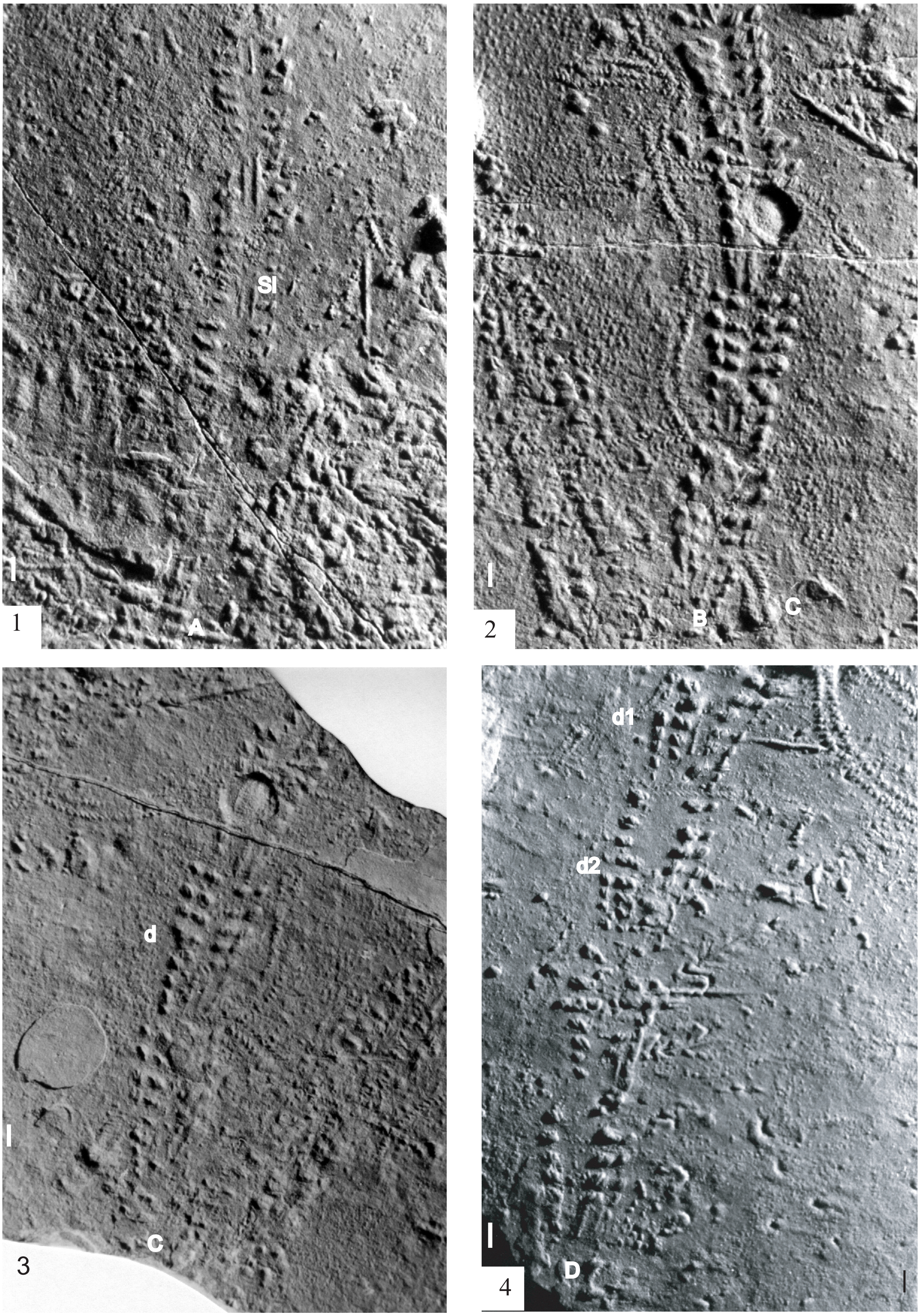

Fig. 9.- *Acripes multiformis* nov. isp., TASi forms (A-D trackways) with SP, SD and SL (SL = longitudinal serie); 1-2: Lap 242 slab; 3: Lap 226; 4: Lap 222; d, d1, d2 = trackway different parts; scale-bar = 1 mm

Fig. 9.- *Acripes multiformis* nov. isp., formas TASi (pistas A-D) con SP, SD y SL (SL= serie longitudinale); **1-2:** losa Lap 242; **3**: Lap 226; **4:** Lap 222; d, d1, d2 = diferentes partes de las pistas; escala = 1mm

02 slab).

If the preceding nomenclature were used, 5 ichnogena would encompass the lodévoises trackways. In addition, often, several of these ichnogenera should be choosed for the same trackway. This “imbroglio” is not new and is reflected by the creation of many ichnotaxa which were originally defined from fragmentary, incomplete and generally not sufficiently informative trackways. As underscored by Häntzschel (1975), the discovery of a more abundant, varied and preserved better material is necessarily the occasion for nomenclatural adjustments. This is the case of the trackways from the Salagou Formation and, after many discussions and hesitations, by preoccupation with a simplification, we chose to redefine *Acripes* by lumping Repichnia/Natichnia of the Formation of Salagou in the ichnospecies *multiformis* nov. isp.

3.2.2. New taxonomic proposition

*Ichnogenus *Acripes* (Matthew, 1910)

Emended diagnosis

Walter (1983): “Schmale, maximal 10 bis 15 mm breite multipode Fähtenzüge mit meist einseitiger Staffelung. Die daraus resultierenden Eindruckserrien setzen sich in der Regel aus 6 bis 9 Einzeleindrücken szusammen”; English translation: *cf.supra*.

Gand *et al*. (in this work): Symmetrical to assymmetrical repichnia/natichnia, millimetric to centimetric wide. The distal appendage series imprints are only present or connected with 2 parallel furrows. Along the trackways appear, from place to place, bilobate structures.

*Ichnoespèce-type. *Acripes multiformis nov. isp.*

Derivatio nominis. This epithet underlines the variable morphology and size of the trackways.

Holotype: Lap 649 B slab (hyporelief convex), Lapeyrie coll., “Musée Fleury”, Lodève (= MFL) (Fig. 11. 8-9; 13. 1-3).

Type-site (Locus typicus) and type-level = F 36 named Rieupeyre located 500 m nord-eastwards from la Lieude (= LD Fig. 1), level 800, Salagou Formation, Permian, Lodève basin (Fig. 2).

Paratypes, geographic and stratigraphic location. Lodève basin, Salagou Formation, Saxonian group; Lapeyrie coll.: about 200 trackways distributed in the following fossiliferous sites: Caunas, F6 (Lap 05, 09; Fig. 12. 4, 9; 17. 1); la Fourille, F29 (Lap 08; Fig. 8. 10); Gèbre, F18 (Lap 192-205; Figs. 8. 3, 5-6); Ceberou, F24-25 (Lap 212-218; Fig. 12. 6); les Clans, F26, F28 (Lap 206-211); Dio, F20 (Lap 01-03, Fig. 10. 4), (Lap 182; 219-304: Figs. 6; 7; 8. 1-2, 4, 7-8; 9. 1-4; 10. 1-3, 5-7, 10; 11.6, 16; 12. 7, 8); Rieupeyre, F36 (Lap 649 A; Fig. 11. 8-9; 13. 1-3), nearly observed on 100 slabs; Gand coll., Rieupeyre, 17 slabs with inventory numbers (Ldg 134-142; Figs. 10. 9; 12. 1), (Ldg 144-151; Figs. 11. 4-5); Ldg 156, 158, about 30 trackways, Earth Sciences Center, Burgundy University (= CST-UB); Garric coll., Rieupeyre, 7 slabs Ldi. Gar 11A-11G; (14 B1; Figs. 11. 1-3), (11C; Figs. 8. 11); (11D; Figs. 13. 4; 11. 10-11); (15B1; Figs. 11. 1-3; 12. 2, 3); (15B2; Figs. 12. 5; 17. 2); (15B5; Figs. 8. 12; 10. 8), 10 trackways, Paleontology Laboratory, Montpellier II University; Autunian group, Lower Tuilières-Loiras Formation, Gand coll., Ldg 123, 1 trackway, CST-UB, *in* Debriette and Gand (1990).

St-Affrique basin, “Grès du Dourdou” Formation, SAg 114 B, 1 trackway (Gand coll., CST-UB); le Luc basin (Provence), Pelitic Formation, Gonf G58, 1 trackway (Gand coll., CST-UMB).

Diagnosis. Repichnia having rectilinear, sinuous with sometimes angular course, infra millimetric to more than centimetric wide. The series consist of distal appendicular-ends quite separated or amalgamated. Where they are well marked, those are “uni to polyfid” (divided), circular or oblong, very few, not exceeding ten. These series form arched lines, more generally straight, which are then perpendicular or oblique to the median axis. Their succession forms 2 edge lines, symmetric or not, with respect to the median axis. Locally, on the same course of the trackways appear, in more, but irregularly, 2 parallel and internal furrows with the appendicular series or 2 external furrows, each one being seldom duplicated. In some rare cases, the trackway may be reduced to the only furrows.

Description: cf supra

3.3. Identity of the trace-makers

3.3.1. First possibility: Notostraca.

Experimental ichnology.

Morphology of the trackways suggests polypod and heteropod arthropods with different long appendages and a dorsaly/ventraly flattened body. Moreover, these animals are provided with body-organs like a carapace, a shell or/and a furca, able to trace two parallel furrows, more or less separated.

In the *Acripes* layers, the exclusive abundance of Triopsids body-fossils (= *Triops cancriformis permiensis* and *Lepidurus occitaniacus* Gand *et al.,* 1997) and Conchostraca lead us to ascribe these *Acripes* repichnia to Triopsids. But by assuming that the trackways could have been made only on an emerged ground, one of them, AT, specialist in Notostraca pointed out that this choice was not the good since the thoracopods are not enough strong

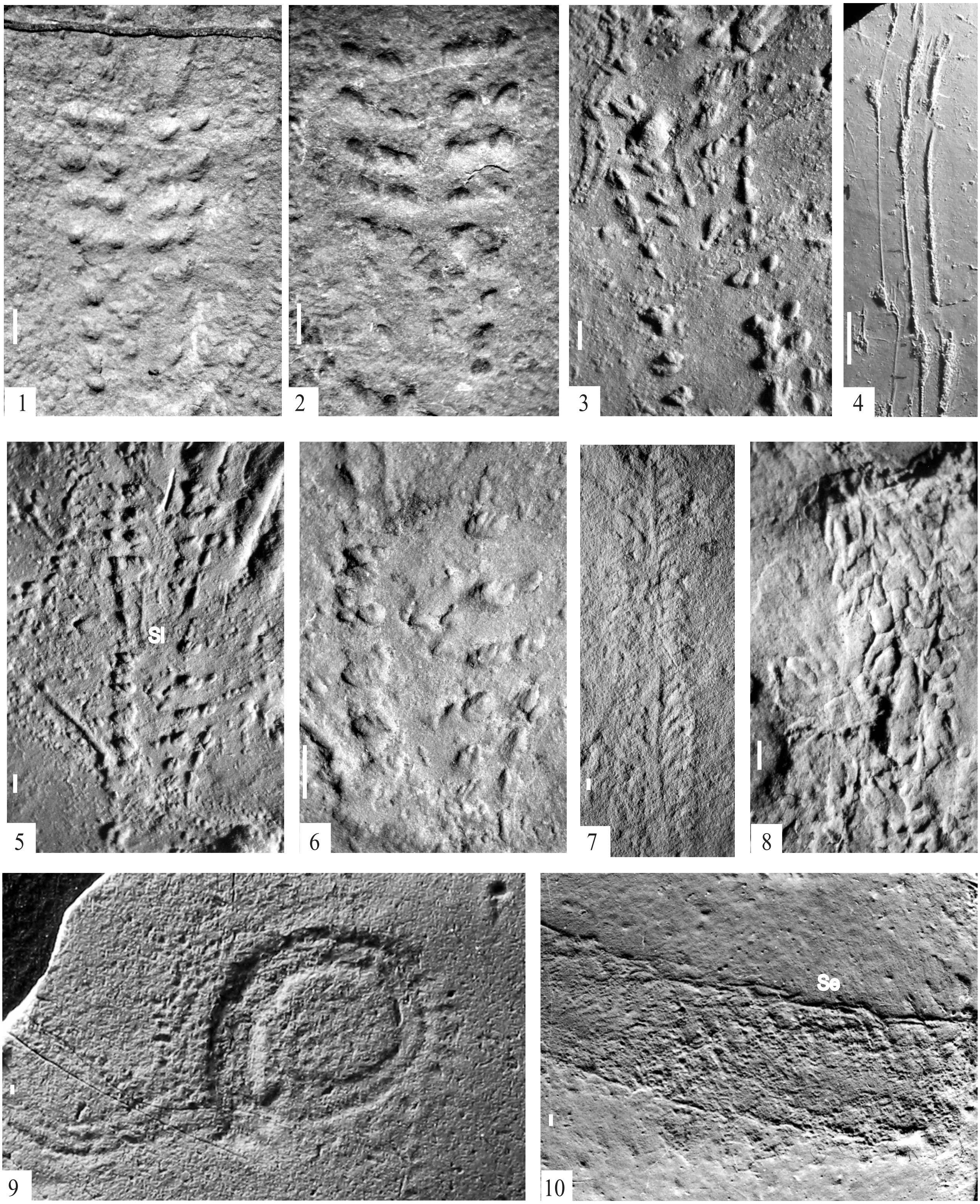

Fig. 10.- **1-10**: *Acripes multiformis* nov. isp.; **1-3** (Lap 226, 242, 222); **5-6** (Lap 222): TA serie enlargements with SP / SL / SD possible disposition; **1**: Lap 226, cf **fig.** 9. 3d; **2**: Lap 242; **3**: Lap 222, *cf* **fig.** 9. 4. d1-d2; **4:** Se-Si type, Lap 02, Dio; **5**: Lap 222, *cf* **fig.** 7. 1 D; **6**: enlargement of **fig.** 10. 5; **7**: double V shape TASi, Lap 220**; 8, 10:** TA Se forms, Se = duplicated external furrow on **fig.** 10. 10; successively from Gar 15 B 5 and Lap 244; **9**: atypical shape with wide Si (Ldg 139); scale-bar = 1 mm;

Fig. 10.- **1-10**: *Acripes multiformis* nov. isp.; **1-3** (Lap 226, 242, 222); **5-6** (Lap 222): aumento de las series de TA con disposición SP / SL / SD posible;**1**: Lap 226, cf **fig.** 9.3.d); **2**: Lap 242; **3**: Lap 222, **fig.** 9. 4. d1-d2); **4**: Se-Si tipo, Lap 02, Dio**; 5**: Lap 222, cf **fig.** 7. 1D); **6**: aumento de la figura 10. 5; **7**: forma TASi con doble V, Lap 220**; 8, 10:** formas TASe (Se = surco externo desdoblado sobre la fig. 10. 10), sucesivamente en Gar 15 B 5 y Lap 244; **9**: forma atípica con ancho Si (Ldg 139); escala = 1 mm

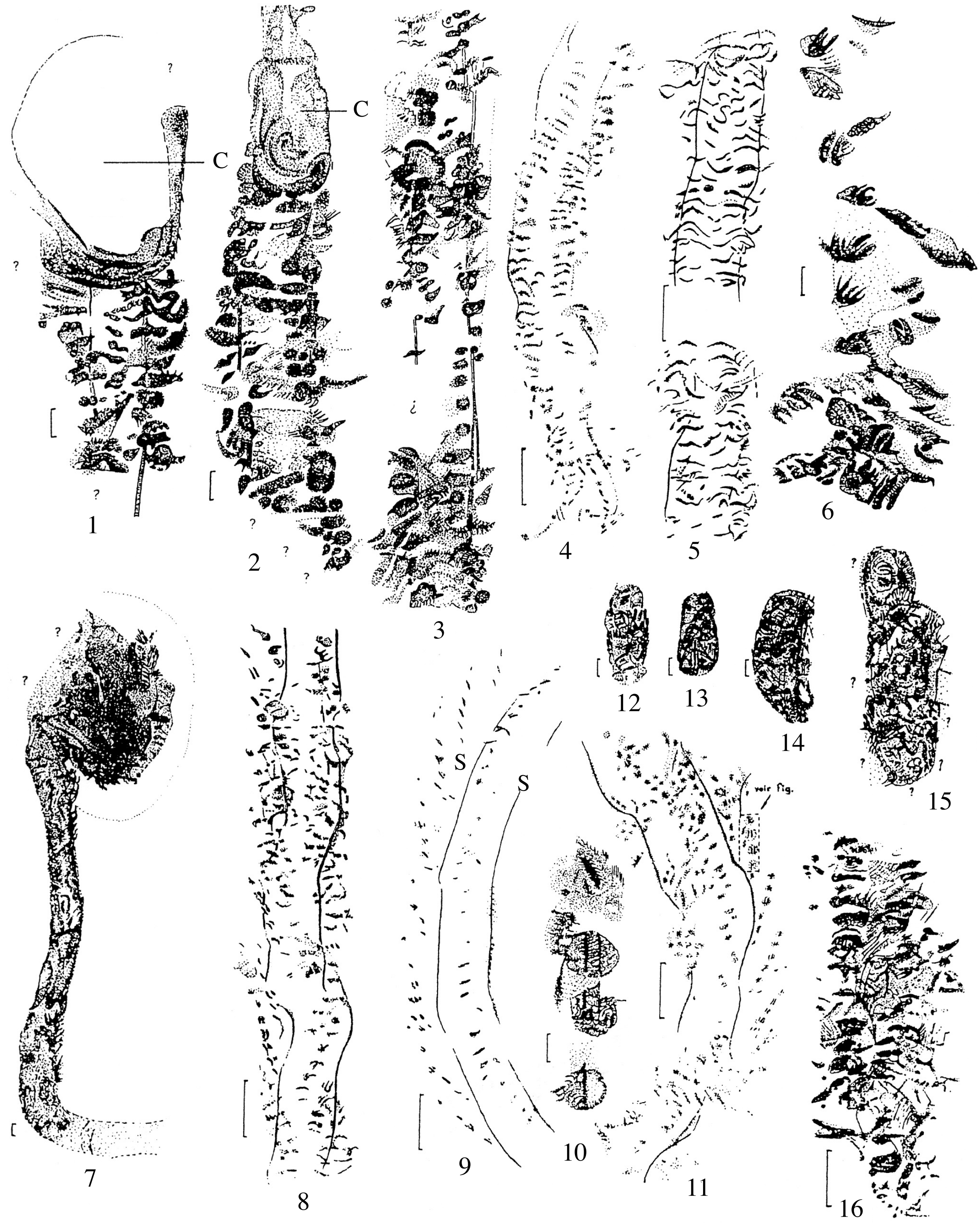

Fig. 11.- *Acripes multiformis* nov. isp. drawings. **1-5, 8-11:** TASe symmetrical and asymmetrical forms; **1-3**: Gar 15 B 1; **4-5**: Ldg 148; **8-9**: Lap 649; **10** detail of **11,** Gar 11 D; **6:** band TA details from Lap 286; **16**: detail of the trackway middle from Lap 279; **7, 12-15**: digging holes at the top of the trackway for fig. 11. 7 (Gar 15 B 2) and isolated for others; **12-14**: Gar 15 B 4; **15**: Gar 15 A1; scale-bar = 1 cm for 4, 5, 8, 9, 11, 16; 1 mm for others; C = cubichnia.

Fig. 11.- *Acripes multiformis* nov. isp., esquematisaciones. **1-5, 8-11:** formas TASe, simétricas y asimétricas; **1-3**: Gar 15B1; **4-5**: Ldg 148; **8-9**: Lap 649; **10** detalle de 11: Gar 11 D; **6:** faja de detalles deTA de Lap 286; **16**: detalle del medio de la pista de Lap 279; **7, 12-15**: perforaciones en la extremidad de la pista para fig. 11. 7 (Gar 15 B 2) y aislados para los otros; **12-14:** Gar 15 B4; **15:** Gar 15A1; escala = 1 cm para 4,5, 8, 9, 11, 16; 1 mm para los otros; C = cubichnia.

to ensure the walking out of water.

In fact, experiments carried out by Trusheim (1931) with *T. cancriformis* and recently by GG with *Lepidurus* on wet, emerged and varied substrates (plaster, clay, sand) showed that these Phyllopods were unable to move out of water. After some torsion movements of the abdomen, the animals stop moving and mark a fuzzy print of the cephalothorax. If the plaster is very wet, after stimula-

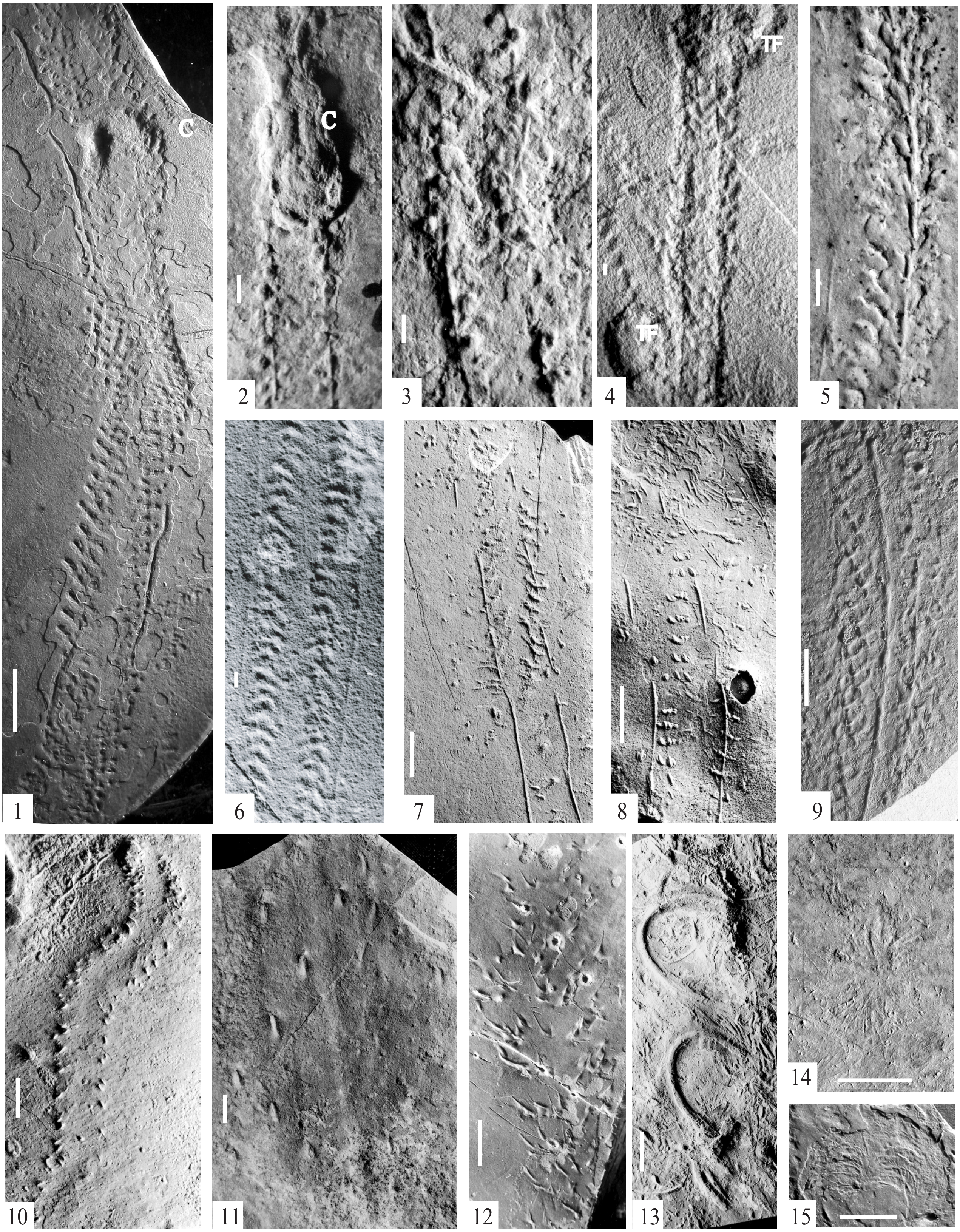

Fig. 12.- *Acripes multiformis* nov. isp.;**1-8**: symmetrical and asymmetrical TASe forms, successively on Ldg 141, Gar B 1 (2-3), Lap 05, Gar 15 B 2, Lap 212, 236, 225; **9**: TASi form (Lap 09); **10**: *Permichnium* sp. (Lap 273); **11**: *Octopodichnus* sp. (Lap 209 B), **12-15***: Incertae sedis* (Ldg 151, Lap 270, 251, 182); C = cubichnia (*Rusophycus*); TF = digging holes; scale-bar = 1 cm except for 2-6 = 1 mm.

Fig. 12.- *Acripes multiformis* nov. isp.; **1-8:** formas TASe simétricas y asimétricas, sucesivamente sobre Ldg 141, Gar B1 (2-3), Lap 05, Gar 15B2, Lap 212, 236, 225; **9**: forma TASi (Lap 09); **10**: *Permichnium* sp. (Lap 273); **11**:*Octopodichnus* sp. (Lap 209 B), **12-15***: Incertae sedis* (Ldg 151, Lap 270, 251, 182); C = cubichnia (*Rusophycus*); TF = hoyos de excavación; escala = 1 cm, fuera de 2-6, = 1 mm.

tion, GG observed that *Lepidurus* can still move for one or two cm by leaving only the carapace margins traces.

Unable to walk, on the other hand, Notostraca are excellent swimmers. Always moving during our filmed experiments, we also could see them excavating the substrate with the front thoracopods (except Pt1), the often tilted body forwards an approximately 45° angle; the front edge of the shield being used as a shovel. Put in a thickness of water which just makes it possible to submerge them, these arthropods are still very mobile and their appendages are in permanent contact with the substrate (Fig. 14)

Although we made them crawl on different nature substrates (plaster, clay, sand), no trackway was printed. At the end of several tests, we thus could not confirm the positive results of Trusheim (1931). It is true, that after several negative tests carried out with substrates like ours, Trusheim (1931: 236) had finally obtained *Triops cancriformis* trackways by using "a natural calcareous mud Tubifex" with better results when he added "a fine algae and diatoms layer".

Thus, several morphotypes were obtained by animals "crawling" on the bottom (Fig. 15 a-e). They are characterised by the presence of "short, aligned, concave and wedge-shaped" distal appendage imprints. They are laid out in perpendicular series to the trackway axis, on both sides of a double furrow due to the furca mark. These furrows are outlaid in the turns. Trusheim (1931) stated that a "third element appears from time to time: traces left by the antennas". Fines and undulated, they largely overflow the appendicular series marks. But this last Trusheim's interpretation poses an anatomy problem because the antennas are very short at Notostraca and absent in the adult *Lepidurus*. It is, therefore, possible that these antenna imprints are due to one of the 3 long endites of the n° 1 thoracopod; probably number 5 (Fig. 16. 4).

By modifying the water depth in order that *Triops* have the possibility of carrying out small swimming ways, Trusheim obtained trackways without the furca trace and in which there is an orientation change of the "legs prints" from perpendicular to oblique with the median axis (Fig. 15 e-d).

The ichnomorphotypes obtained by Trusheim were confirmed recently by one of us (JS), except that which comprises the "antenna traces". By using a mixture of clay and fine sand, JS succeeded in obtaining remarkable *Triops cancriformis* trackways. Some of them are represented on figures 16. 1-2 due to J-S. The first was schematised by HW (Fig. 17. 1). The 3 trackways (A-B) show appendicular end series having, more or less, a double internal and discontinuous furrow due to the furca. The carapace marks are not observed.

Comparison with the Lodève Permian trackways.

The experimental morphotypes obtained by Trusheim (1931) and JS are similar to the scalar / earforms trackways with 2 internal discontinuous / continuous furrows, named as TASi in this work. On refering to this analogy, it is, thus, probable that Notostraca were the trackmakers of *Acripes* trails. Thus, by integrating the theoretical locomotion way of a polypod arthropod (cf *supra* and Fig. 5), one can suggest, for example, that the trackways of Lap 222, 226 and 242 slabs (Fig. 9. 1, Si), were produced by animals which marked the substrate, only by distal parts of 2 thoracopods because there are only two longitudinal SL series. The longest, the external one, left a succession of prints made of 2 short parallel features or in V shape open in the walk direction. The second thoracopod printed more complex traces, commonly trifids. By comparing the shape of these marks with that of the Notostraca distal end thoracopods (Fig. 16. 4-7), it is possible that they were made by the silky teeth n°5 and 6 endites of the Pt2 and Pt3.

In addition to the appendages marks, these TASi trackways show the furca evidence. This one would be produced 2 continuous median furrows on the Lap 227 and Lap 09 slabs and discontinuous on the Lap 222, 226, 242 slabs (Fig. 9). In this last case, their periodic discontinuity may indicate the fast passage of walking to brief swimming moments; the telson motions helping to excavate the sediment.

Some TASi trackways, Lap 09 in particular, show a squaring which is due to the gathering of the SL appendicular serie marks and a fine rectilinear structure, the whole drawing kind of small lozengic cells (Fig. 12. 9; 18. 1D). From a detailed study made by JG, these last structures would be the combined work result of gnathobases and thoracopods others parts. The first make back-ahead water current while the second function in the opposite direction by a shifted way.

Trusheim (1931)'s results do not exhaust all the "Lodévois" fossil morphotypes. It misses the TASe and SeSi trackways, i.e. those comprising the appendicular prints having two external furrows (Se) and those which are reduced only to the external and internal furrows (SeSi). For the first, if the Se external furrows are well made to the the carapace edge, Trusheim did not observe them in experiments. Besides, he noted (1931: 236): "(that) the dorsal shield and the abdomen, generaly, don't' touch the ground and consequently they can't make any traces". This observation is confirmed by GG who experimented with ten *Lepidurus* evolving in a filled with water crystalliser. Triopsids always move there from the full water towards the bottom with fast ascents.

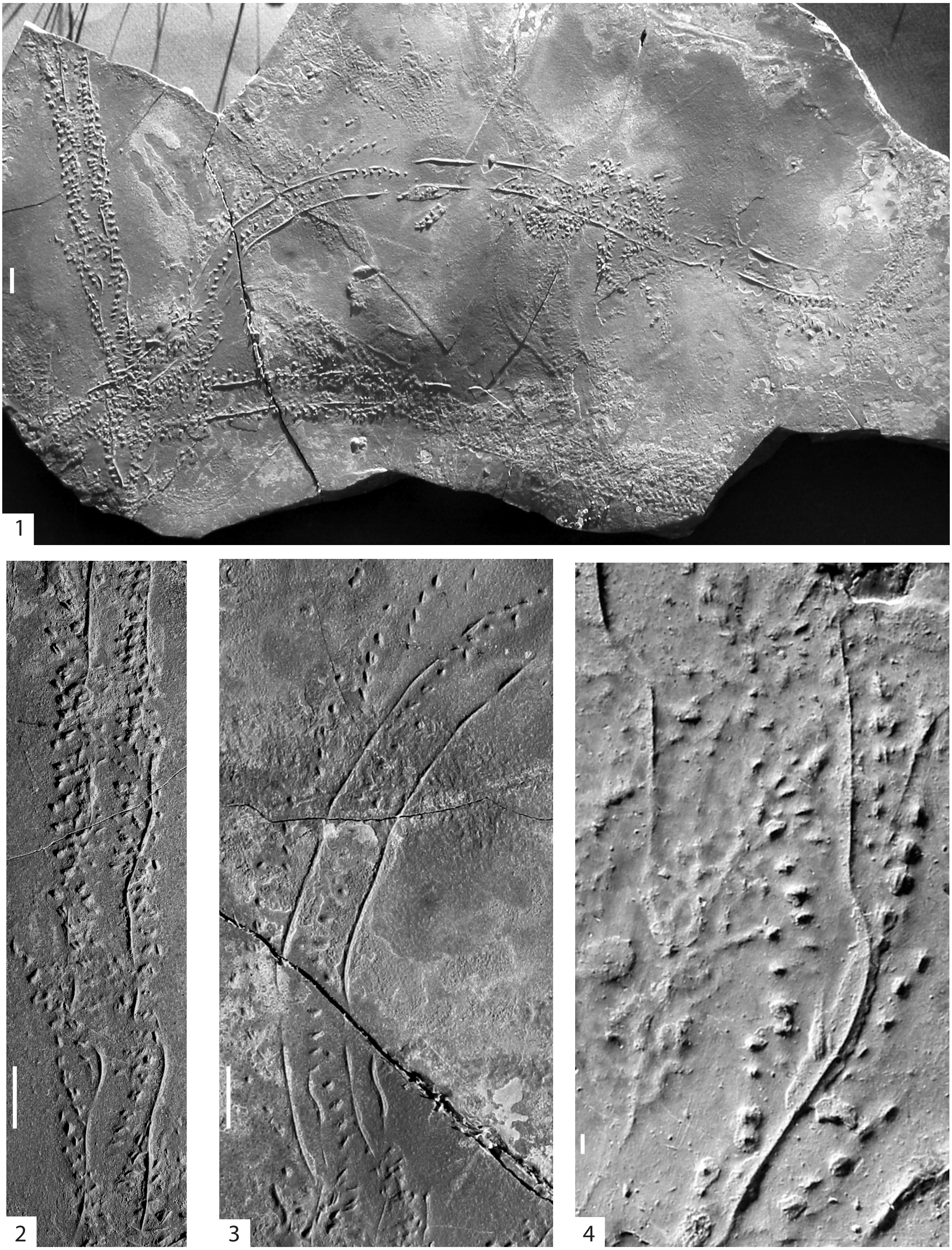

Fig. 13.- *Acripes multiformis* nov. isp., symmetrical and asymmetrical TASe; **1**: holotype, slab 649, hyporelief; **2-3**: details; **4**: Gar 11 D slab showing SP/SD/SL series of TA (cf. fig. 5) and 2 external furrows produced by the carapace; scale-bar = 1 cm except for 4 = 1 mm

Fig. 13.- *Acripes multiformis* nov. isp., formas TASe simétricas y asimétricas; **1**: holotipo, losa 649: hiporelieve; **2-3**: detalles; **4**: Gar 11 D mostrando series de rastros apendicularios SP/SD/SL (cf. fig. 5) y los 2 surcos externos producidos por el caparazón; escala = 1 cm, excepto 4 = 1 mm

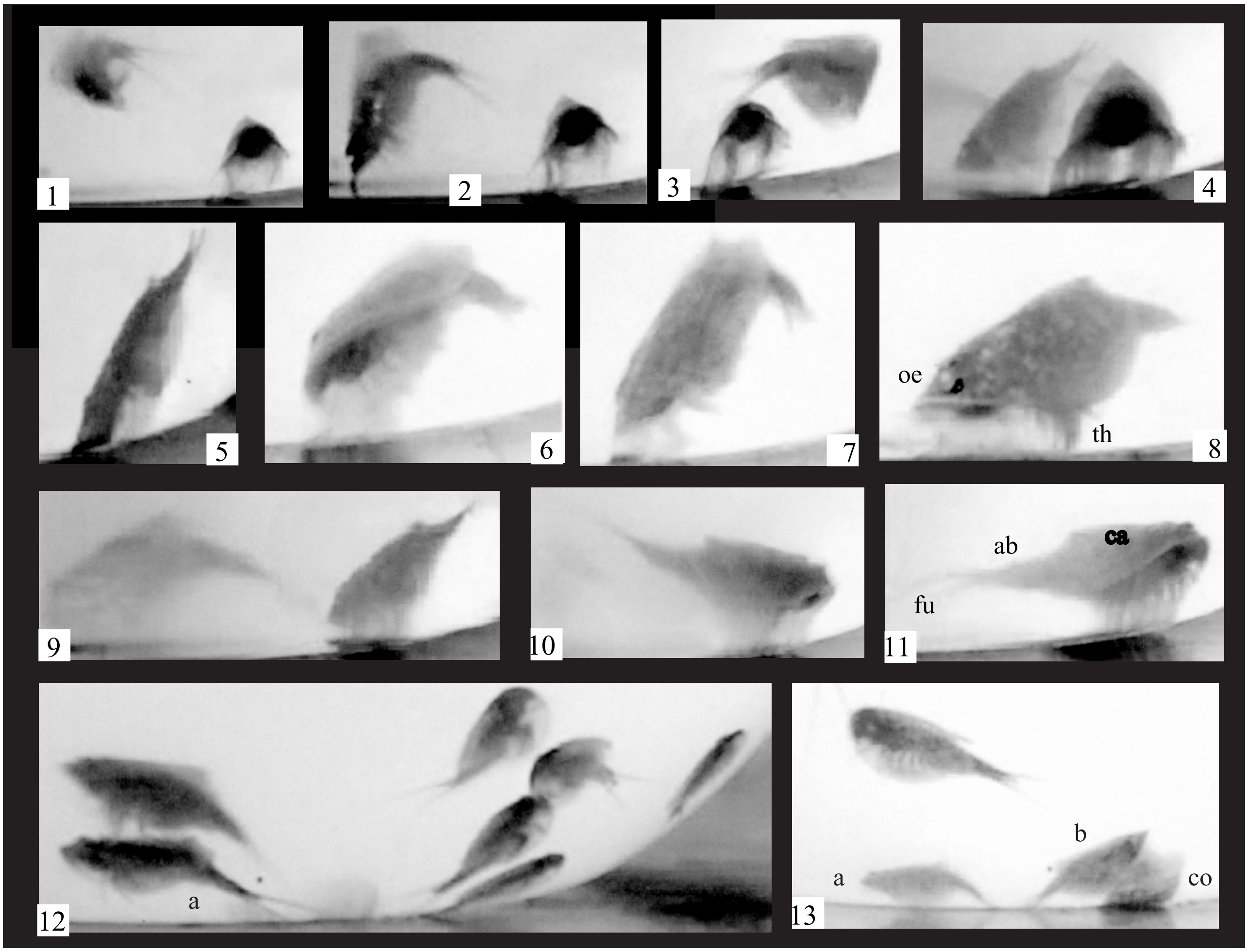

Fig. 14.- **1-13**: Photos from Gand and Vavon' video showing different *Lepidurus apus* behaviours moving in a water glass-tank; **1-11: "**resting"/stationary position with thoracopod lateral outside-inside movements contacting the bottom, explaining fine furrows seen on *Cruziana*/*Rusophycus*; **1-4**: head face views; **5-7, 9**: procline positions could explain *Rusophycus furcosus*; **8, 10-11**: horizontal stationary position could produce *R. eutendorfensis / R. carbonarius;* **12-13**: swimming in full water and **a** animals walking on the bottom, this last position may make *Acripes* with the furca trace (= TASi trackways, cf fig. 16. 1-2); oe = eyes, th = thoracic appendages, fu = furca caudal ramus, ab = abdomen, ca = carapace, co = *Lepidurus* corpse; a, b = *Lepidurus apus*.

Fig. 14.- **1-13**: Fotos del video de Gand y Vavon mostrando diferentes comportamientos de *Lepidurus apus* moviendose en un acuario; **1-11**: posición de "descanso"/estacionaria con movimientos laterales exterior/interior de torácopodos tocando el fondo, explicando los finos surcos de *Cruziana/Rusophycus* **1-4** vistas de frente de la cabeza: **5-7-9**: posición inclinada hacia la parte delantera que pudiera explicar *Rusophycus furcosus* **8-10-11** posición horizontal estacionaria que pudiera producir *R. eutendorfensis/R. carbonarius;* **12/13** nadando en el agua, y, fig.a = animales andando sobre el fondo, este última posición que pudiera producir Acripes con el rastro de la furca (pistas TASi, cf. fig.16 1-2); oe = ojos, th = apéndices torácicos, fu = látigo caudal de la furca, ab = abdomen, ca = caparazón, co = cuerpo.de *Lepidurus*, a,b = *Lepidurus apus*.

On the substrate, they move slowly, using the Pt2-Pt13 thoracopods which touch the bottom by their distal end. It is also, thus, for the furca. In this attitude, the animal in frontal sight has a "Chinese hat" aspect, worn by two crutches which represent the appendages. According to the distal spacing, more or less large of the two furca whips, such a step could explain the TASe trackways or TASi with continuous furrows. But this regular locomotor phase often makes place with a "jumps" moving during which the animal briefly leaves the substrate. This behaviour involves an break recording trace like it was written for the trails seen on many slabs of which Lap 222, 226 and 242.

More rarely, animals move on the bottom, with bent thoracopods and one carapace border trailing on the mud. This posture seems, obviously, favorable to the side margins marking of the shield. We ascribe to them the duplicated prints observed on the Lap 2444 slab which seem due to the external and internal layers prints of this organ (Fig. 10. 10)

The few Se-Si trackways remain enigmatic. If they are Notostraca trails, it should be admitted that the furca and carapace traces are not accompanied by those of the appendages. It is possible that the latter did not print the

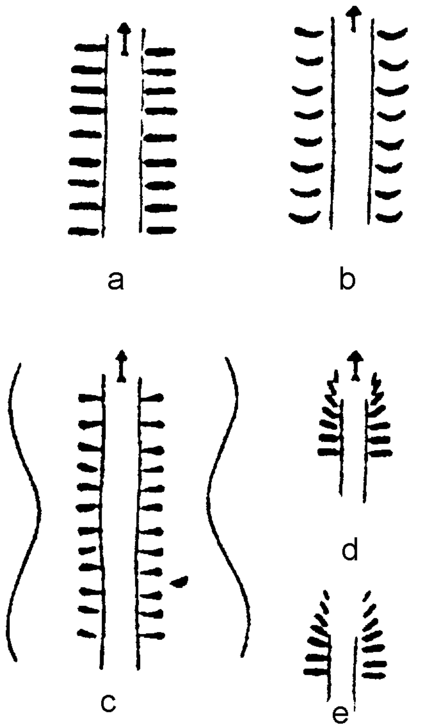

Fig. 15.- *Triops cancriformis* trackways *in* Trusheim (1931); **a-e**: "more important trackways", arrow = moving direction; horizontal (**a, c**), curved (**b**), horizontal to oblique (**e,d**) black strokes mean thoraco appendage end traces (= TA series in our work); parallel inside straight lines are furca traces (= Si in our paper); the outside undulated line in fig. **c** was produced by antenna after Trusheim. Present authors think it is due to the longest endit of the n° 1 thoracopod (see also in text); **e-d** = two successive trapezoidal parts of a trackway separated by a gap due to a swimming phase. These Permian *Acripes* trapezoidal parts are also clearly present in trackways of the Lodève basin (Fig. 9 d, d1, d2). The strong similarities with the Trusheim's results prove that Notostraca are trackmakers of these *Acripes*.

Fig. 15.- Pistas de *Triops cancriformis* representadas e*n* Trusheim (1931); **a-e**: «las pistas más significativas» según este autor; la flecha indica la dirección del desalojamiento, los trazos negros horizontales (**a, c**), curvados (**b**), horizontales hacia oblicuos (**e, d**) son rastros de torácopodos (= TA en este trabajo). Los dos surcos internos y paralelos son rastros de la « furca » bífida (= Si en nuestro trabajo); las dos lineas onduladas externas de la fig. **c** corresponden a los rastros de las antenas según Trusheim. Los autores piensan que será más bien a longitud de exopoditas de los torácopodos n° 1; **e-d** son dos partes trapezoidales de una misma pista, hechas durante la locomoción sobre el fondo. Están separadas por una laguna que corresponde a una fase de natación durante la cual el animal deja el sustrato. Estas dos morfologías trapezoidales fueron reconocidas en algunas pistas *Acripes* del Pérmico de la cuenca de Lodève (Fig. 9 d, d1, d2). Estas similitudes refuerzan la asignación de estas pistas fósiles á Triopsideos.

ground or that their prints were not recorded.

3.3.2. Other hypothesis.

In the Salagou Formation, Triopsids are locally associated with many and varied up to 1 cm long Conchostraca. Thus, it is legitimate to wonder whether these arthropods could be the authors of certain *Acripes* trackways described previously.

Conchostraca (= Spinicaudata + Laevicaudata), Thiery (1996)

Based of Trusheim (1931)'s experiments, Tasch (1964) used Conchostraca to observe their behaviour. He used *Cyzicus mexicanus* and was the first to obtain trackways made, under water, on a mud-silt sediment mixture for the substrate. During 7-months experiment period, observations were done every day without result except for a full day during which, animals made trackways only kept for 2 days. Then, it nothing else happens!

The serpentiform trackways consist of 2 side ribbons separated by a median wrinkle. The trails reflect the animal width and are the result of digging by using its "paired appendages"; undoubtedly the antennules which are long and bifid at Conchostraca. The morphology of these digging trackways can't be confused with Repichnia/Natichnia which are described in this work, excluding Conchostraca like possible trackmakers.

Bromley and Aasgard (1972, 1979) also referred to the coexistence of *Cruziana* and Conchostraca in the Upper Triassic of Jameson Land (Greenland). Based on several observations, these authors specified that the *Cruziana* attribution to these arthropods is not possible because only their antennules can print the substrate. This is done in the longitudinal direction because the 2 valves of the carapace are not very separated of each other during the moving. Moreover, it is clear that *Acripes* were left by flattened dorso-ventraly animals, which is not the case of Conchostraca.

In the Greenland Triassic, Bromley and Aasgard (1972) observed that "the conchostracans are associated in several cases with the trace fossil *Lockeia"* (= *Pelecypodichnus*).

Crustacean, Chelicerata, Myriapoda.

In the Salagou Formation, no other Arthropod have been recorded, except for insects, Notostraca and Conchostraca. On the other hand, in the German Lower continental Permian, Arthropleuridea, the Diplopoda *Pleurojulus steuri* Schneider and Werneburg, 1998 (Schneider and Barthel, 1997; Schneider and Werneburg, 1998) and Euthycarcinoidea (Schneider, 1983) have been documented. Arthropleurids are known to produce *Diplichnites* (Walter and Gaitzsch, 1988) and *Striatichnus* Walter 1983 are, maybe, due to Euthycarcinoids. In other regions, although rare, Chelicerata were also found in the Permian (Størmer *et al.,* 1973) like Myriapoda (Hoffman, 1969). However, analysis of their anatomy compared with their trackways (Häntzschel, 1975) precludes a connection with *Acripes*.

Having noticed the arrival of Chilopoda in current desiccated ponds rich in Triopsids bodies, one of us (AT), had suggested that Chilopoda could have produced *Acripes*; the two furrows being the gonopode traces. The experiments made with *Lithobius* by Guy Barnay (Société d'Histoire Naturelle d'Autun) and GG lead us to exclude this possibility.

Contrary to waited results, it was initially impossible to observe the moving imprints of these animals walking on a wet substrate, in particular, clay coming from a bor-

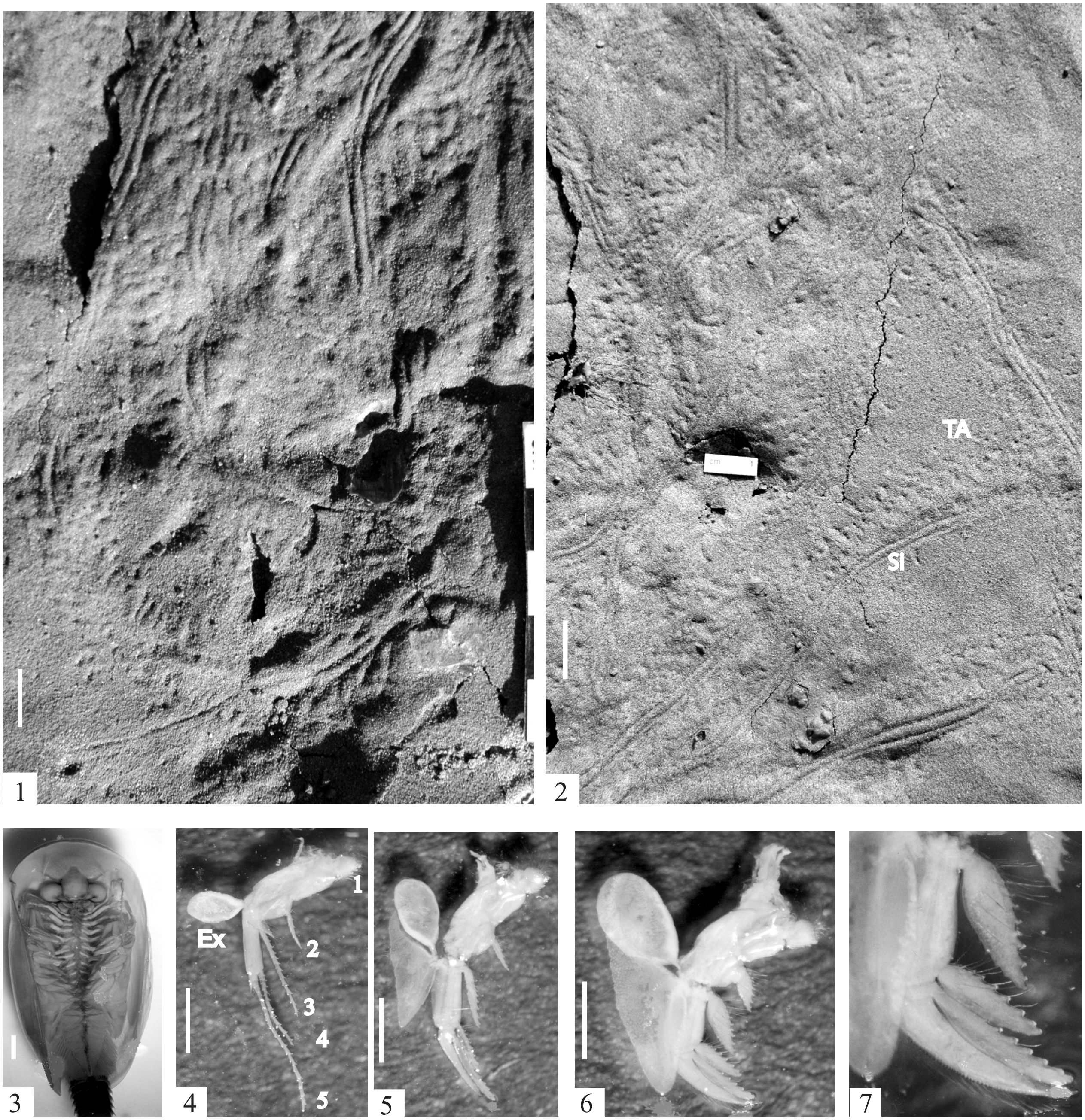

Fig. 16.- Experimental results. **1-2**: *Acripes* = current trackways of *Triops cancriformis* produced on a silt-clay mixture from Pr. Schneider's experiment; **3**: *Lepidurus apus* ventral view; **4-6:** successively Pt1, Pt2 and Pt3 thoracopods of *L. apus*; **7**: Pt3 enlarging; Ex = exopodite; **1-5**: endites of endopodite with 1 = gnathobase; TA= appendage (thoracopod) traces, Si = internal furrows due to furca traces; scale-bar = 1 cm for 1-2 and = 1 mm for 3-6.

Fig. 16.- Resultados experimentales **1-2** pistas tipo *Acripes* actuales obtenidas por el Prof. Schneider; con *Triops cancriformis* sobre un sedimento arcilloso-limoso **3**: *Lepidurus apus* frente ventral; **4-6:** sucesivamente torácopodos Pt1, Pt2 et Pt3 de *L. apus*; **7**: aumento de Pt3; Ex = exopodita; **1-5**: endiduras de la endopodita con 1 = gnatobase; TA= rastros de apéndice, Si = surcos internos producidos por rastros de « furca »; escala = 1 cm para 1-2 y = 1 mm para 3-6.

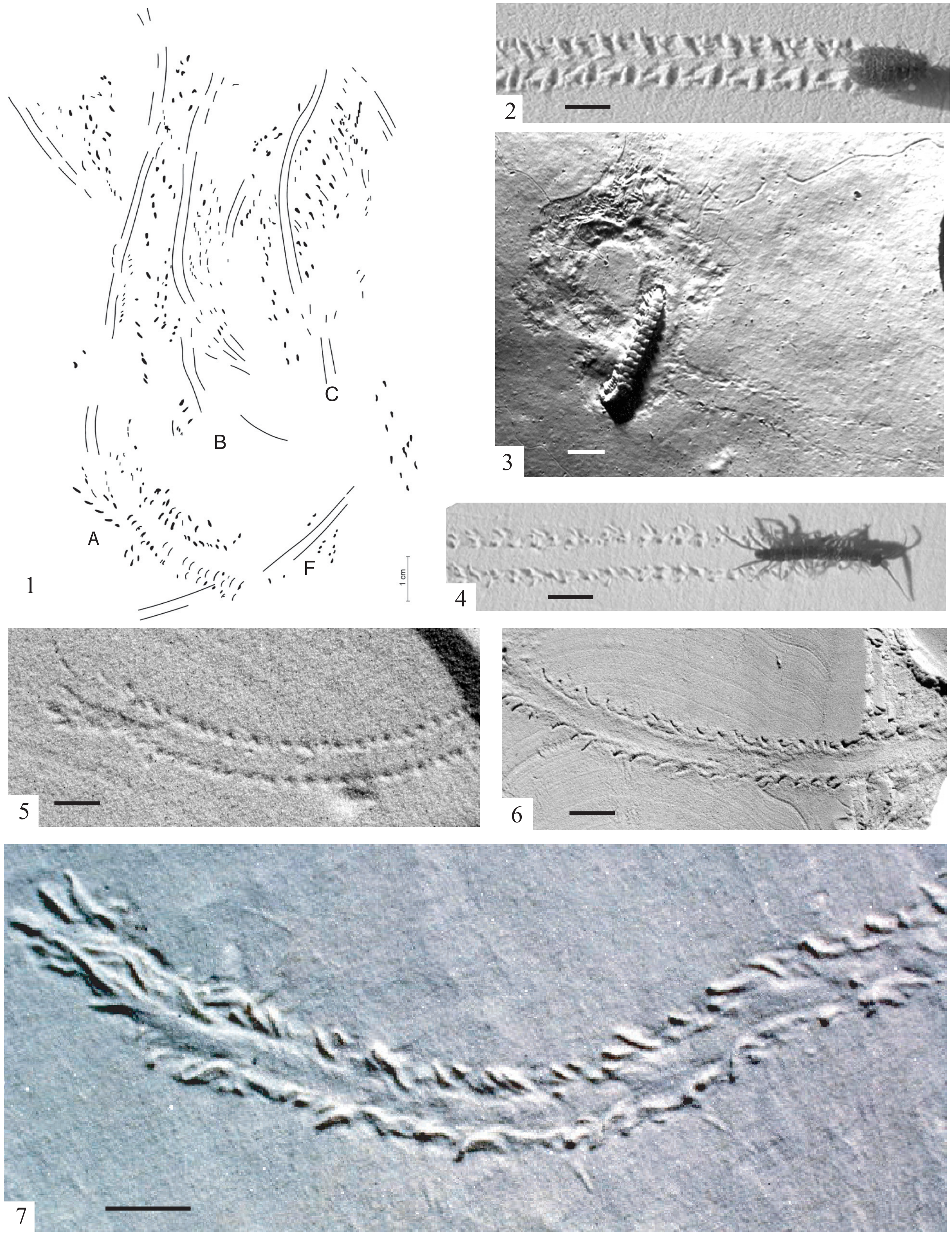

Fig. 17.- **1**: Diagram of the fig. 16. 1, A-C trackways of *Triops cancriformis*; **2**: Cloporte *(Porcellio)* trackway; **3**: a dead *Polydesmus* observed at its trackway head; **4:** *Lithobius* walking on a dry sand; **5-7**: *Lithobius forficatus* current trackways produced on dry sand; diameter respectively of 120, 40 and 80 microns; scale-bar = 1 cm

Fig. 17.- **1**: Esquema de la foto 16. 1, A-C pistas de *Triops cancriformis*; **2**: pista de Cochinilla *(Porcellio);* **3**: *Polydesmus* observado muerto en la extremidad de su pista; **4:** *Lithobius* andando sobre una arena seca; **5-7**: pistas de *Lithobius forficatus* actuales hechos sobre una arena seca de 120, 40 y 80 micrones respectivamente de diámetro; escala = 1 cm

der pond. However, by using a dry argillaceous powder and a 40 microns sand mixture or only 80 to 120 microns sandy, the animal marked trackways easily; the clearest being obtained with an average granulometry, e. g = 80 microns (Fig. 17. 5-7).

Fleeing the light, the arthropod moves, rather quickly, in a rather rectilinear way and without stopping; gonopods being always raised (Fig. 17. 4). The trackway is symmetrical, one cm wide for an animal whose dimensions length/width are respectively of 3 cm and 3 mm. Its belly trails and leaves a succession of punctiform holes aligned in the walk direction, each one of them being prolonged by a coma shaped scratch. In the curves appear SD differed series made from 2 or 3 appendicular marks. In summary, after experiments or current observations, Chilopoda and Diplopoda trackways don't suite with *Acripes multiformis*.

Definitively, in the "lodévoises" trackways, the character which basically discriminates *Acripes* Reptichnia/Natichnia of the Salagou Formation of the other arthropods trackways is the coexistence of *Isopodichnus-Rusophycus* bilobates which correspond to stationary but active traces (= cubichnia).

4. Feeding traces = Pascichnia (furrowing/ploughing) and resting/stationary trails = Cubichnia (Seilacher, 1953; Müller, 1962).

Originaly, these trails are concave epichnia. But one finds also their natural casts which are convex hyporeliefs.

The pascichnia correspond to isolated or dense, discontinuous, rectilinear or sinuous trails whose width lies between 1 and 17 mm. They basically consist of two, more or less finely striated ribbons, with appreciably equal width, generally separated by a thin ridge.

On many specimens, these ribbons are relayed in the length direction by smooth or/and striated bilobate structures, a little longer than wide, in the V shape or "coffee-bean". These trails which resemble more the bovidae or cervidae footprints were arranged in Cubichnia. They can be also numerous and isolated.

4.1. Pascichnia = ribbon structures (Fig. 18, 20)

The smallest trails, millimetric wide, were observed close to Caunas, in siltstones of the Salagou Formation (F7 C). On the slabs Gar 14B, they are very few and associated with bilobate structures there (Figs. 18. 3, 10-11; 20. 1 n° 3) or present only by 2 small contiguous and discontinuous ribbons, above all striated in the transversal direction (Fig. 20. 1 n° 4).

With appreciably the same size, these pascichnia were also collected in relative abundance in the Rabejac quarry (F13 site, Rabejac Formation). On the slabs Gar 5A-C, the trails are more abondante than in the site F7C. Their course is long, rectilinear to sinuous and locally abruptly angular. The trackways can cross, to stop and begin again after a side shift. They are often relieved by bilobate structures, isolated or overlapping. In several cases, at the pascichnia end, the ribbons fray and deviate; the whole drawing a V shape, directed in the same direction of the bilobate structures (Figs. 18. 5, 10; 20. 11-12).

Trails, 0, 5 cm wide, were observed in the Groupe Autunien top ("Permian red infraconglomeratic" (Debriette and Gand 1990). They are also abundant in the F13 site (Rabejac), close to Ricazouls (F35, Salagou Formation). At this place, the slabs are covered with short pascichnia being next to bilobate structures (*I. furcosus* Gand, 1993). The ribbons consist of rather thick transversal scratches commonly bifid. (Figs. 18 7-9; 20. 4-5).

These trails are better visible on number 177 slab coming from the Gèbre site (F 18) where they are longer, dense and all directed in the same direction. The ribbon scratches are smooth to strong and marked well, tranversaly or obliquely oriented (Figs. 18. 4; 20. 3).

A discontinuous to sinuous pascichnia with an angular course and a V shape end occurs on the Gar 3 B slabs (epireliefs) and Gar 3 C (hyporeliefs) from the F13 site of Rabejac. In contrast to the others trails, the ribbons are finely striated and separated by a band (Figs. 18. 6; 20. 6). One of them (Gar 3 B) contains a fine, narrow and discontinuous ridge.

Several others centimetric wide pascichnia coming from the same level of the Dio site (F20, Salagou Formation) show two other structures which were not observed in the preceding material. On slabs collected by JL, one can observe there two fine furrows, parallel between them, directed like the two ribbons. Those are prolonged on the slab Lap 265 by a beginning of repichnia. The whole is associated with bilobate structures (*I. furcosus* more *I. minutus*) and Notostraca carapaces and Conchostraca (Lap 87, 262, 265, 272, 274).

The two ribbons are of equal width and made from transverse, fine, tightened, rectilinear to arched scratches. On Lap 264, 280 epichnia, the ribbons are bordered by the two furrows. (Fig. 18. 9). But because their side shift, one of both develops its course in a ribbon. This disposition is quite visible from the hyporeliefs pascichnia (slabs Lap 263, 270, 272 B; Fig. 20. 10). On Lap 272 B slab, the external furrow appears duplicated on part of its way with the marked better internal part. The other, related to the ribbon is deformed by the appendicular scratches. The making of these two furrows, thus, seems former to

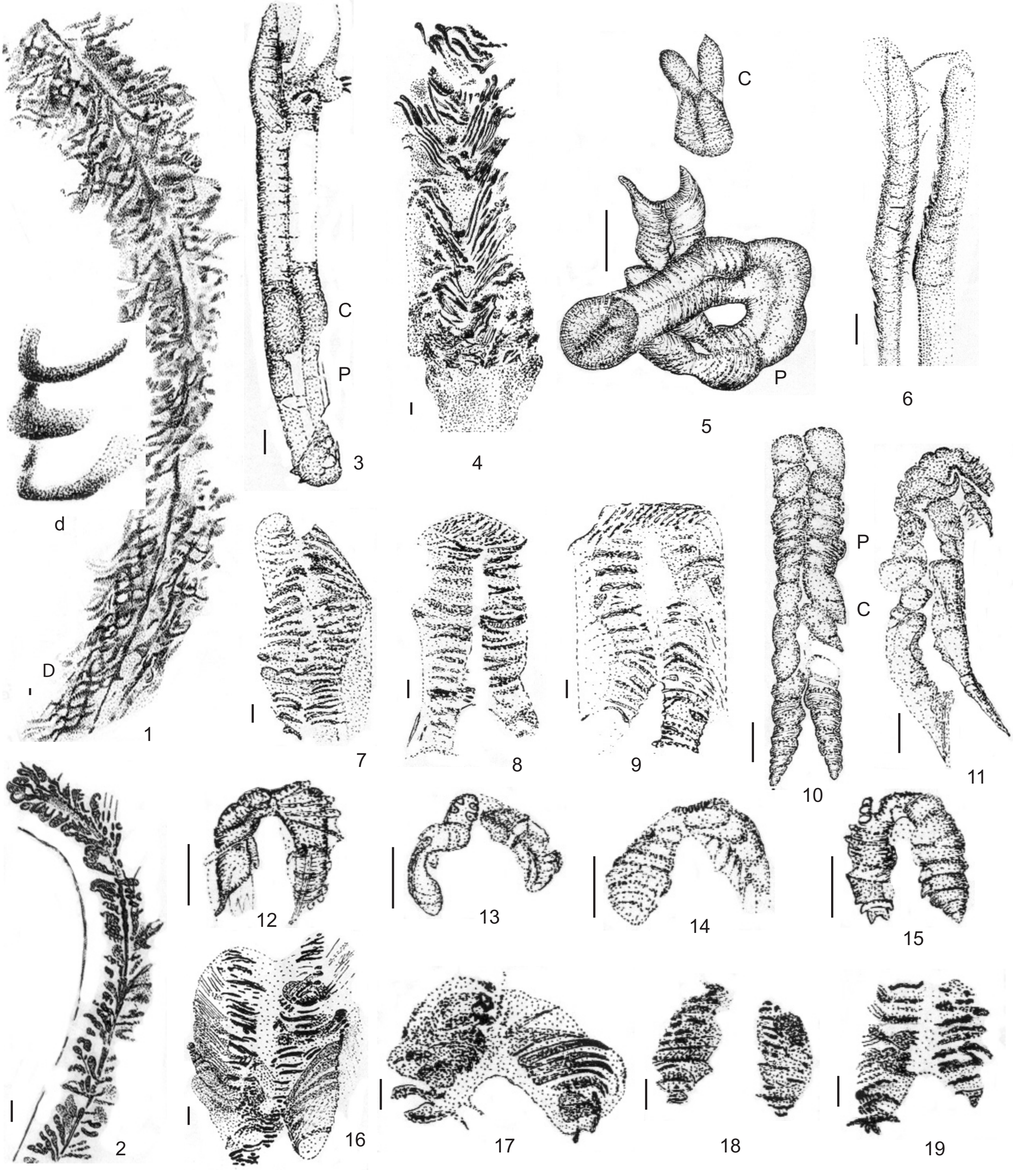

Fig. 18.- *Acripes multiformis* nov. isp. Repichnia*;* **1** = TASi form, Lap 09; **2** = TA Se form, Gar 15 B 2 (d = D detail); **3-11:** pascichnia (= P) + cubichnia (= C); **6:** *Cruziana* sp.), Gar 3 C; **4, 7-9:** *Cruziana problematica;* **4**: Lap 177; **7-9**: Gar 7; **12-19**: cubichnia, **12-15**: *Rusophycus minutus*; **12**: Gar 14 B 2. 3; **13**: Gar 14 B 5.1; **14**: Gar 14 B 6. 1; **15:** Gar B 2 n° 4; **16-19**: *Rusophycus*; **16**: *R. eutendorfensis* / *R. carbonarius*, Lap X (A) 2; **17- 19**: *R. carbonarius*; **17**: Lap X (A) 1; **18**: Lap XXYY; **19**: Lap Z; **3, 5, 10-11**: Cubichnia C = *Rusophycus minutus* and pascichnia (= P) = *Cruziana problematica* alternating; **3, 11**: Gar 14 B 1, 5 and **10**: Gar 05; scale-bar = 1 mm

Fig. 18.- Repichnia *Acripes multiformis* nov. isp.*;* **1** = forma TASi, Lap 09; **2** = forma TASe, Gar 15 B 2 (d =detalle de D); **3-11:** pascichnia (= P) + cubichnia (= C); **6:** *Cruziana*)., Gar 3C; **4, 7-9:** *Cruziana problematica;* **4**: Lap 177; **7-9**: Gar 7; **12-19**: cubichnia, **12-15**: *Rusophycus minutus*; **12**: Gar 14 B 2. 3; **13**: Gar 14 B 5. 1; **14**: Gar 14 B 6. 1; **15:** Gar B 2 n°4; **16-19**: *Rusophycus*; **16**: *R. eutendorfensis* / *R. carbonarius*, Lap X (A) 2; **17- 19**: *R. carbonarius*; **17**: Lap X (A) 1; **18**: Lap XXYY; **19**: LapZ; **3, 5, 10-11**: Cubichnia C = *Rusophycus minutus* y pascichnia (= P) = *Cruziana problematica* alternante; **3** y **11**: Gar 14 B 1, 5 y 10: Gar 05; escala= 1 mm

that of the ribbons.

The Lap 265 hyporelief trackway of Dio shows the passage from the pascichnia to the repichnia with two fine furrows which only extend the trackway before disappearing (Fig. 18. 8).

4.2. Cubichnia = bilobate structures = bilobates (Fig. 18-21).

4.2.1. Small striated and ringed bilobates: Isopodichnus minutus Debriette and Gand, 1990.

These ichnospecies correspond to elongate bilobates, a little longer than wide. They have a bilateral symmetry and the bovidae or cervidae footprints shape (Debriette and Gand 1990) or/and that of a coffee-bean (Häntzschel, 1975; Pollard, 1985). Their width is currently between 0, 5 to 2, 5 mm.

They are abundant in the F7C Caunas site where Debriette discovered them in the Salagou Formation on the surface of small yellowish siltstone slabs. The trails are presented as isolated or associated hyporeliefs, more or less overlapping and imbricated, in rather rectilinear, V shaped, outlined and discontinuous trackways.

JG collected new samples which were redrawn and studied (Gar 14 B1 to B 13) (Fig. 20. 1). These new observations confirm that the two oblong lobes are generally smooth but that they are also rather annulated. (Figs. 18. 12-15; 19. 1-3; 21. 1). In one case, two short furrows,

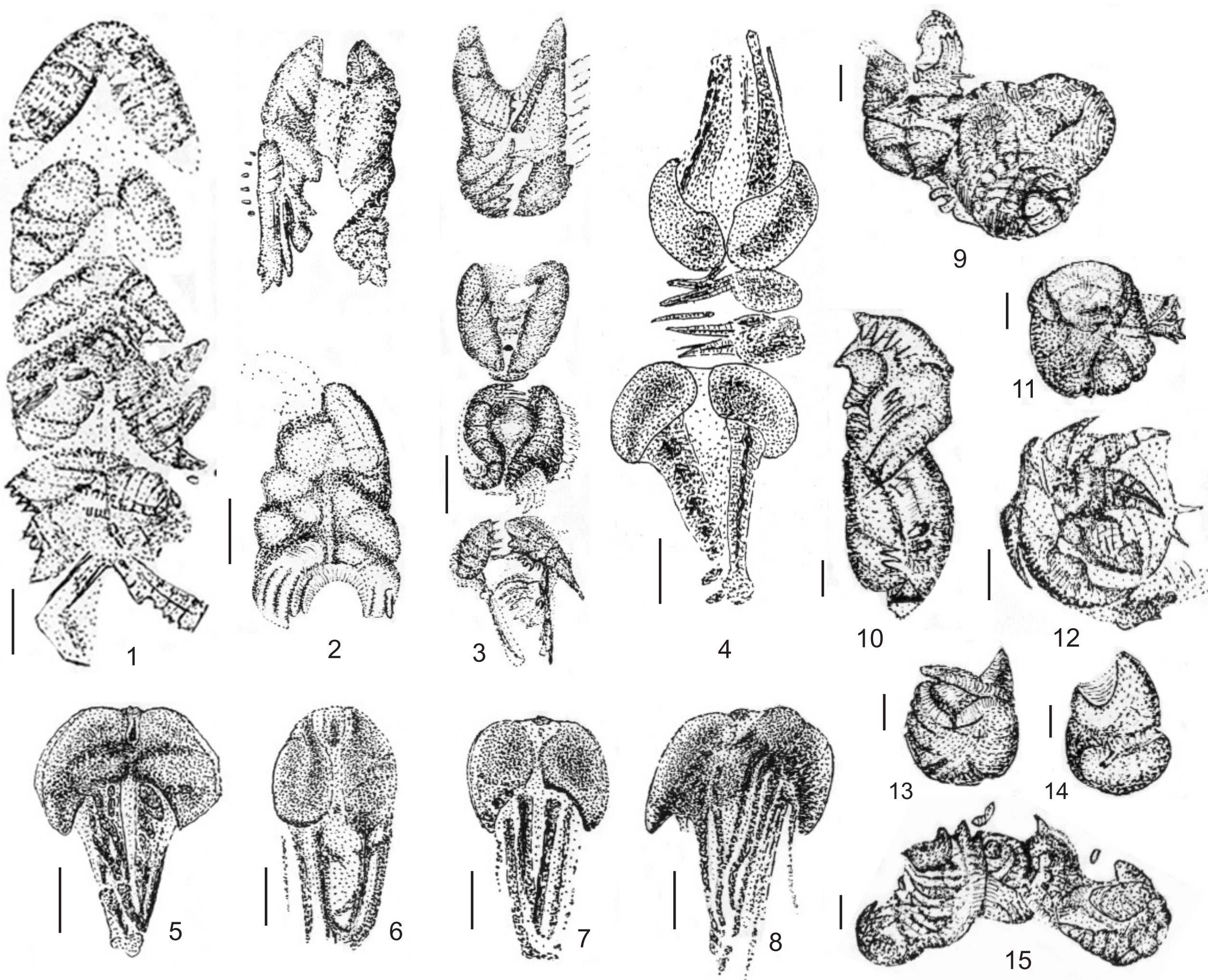

Fig. 19.- **1-8:** Cubichnia; **1-3**: *Rusophycus minutus;* **1**: Gar 14 B 2. 1; **2**: Gar 14 B 8. 1; **3**: Gar 14 B 1. 5 with also *Rusophycus furcosus*; **4, 5-8**: *R. furcosus,* Gar 6, successively 6c, 6f, 6c1, 6c2, 6g1; **9-15**: isolated digging holes, **9**: Gar B 1. 9; **10**: Gar 14 B 1. 8; **11:** Gar 14 B 1. 11; **12**: Gar 14 B 2. 5; **13**: Gar 14 B 1; **14**: Gar 14 B 1; **15**: Gar 17 B 1. 10; scale-bar = 1 mm;

Fig. 19.- **1-8:** Cubichnia; **1-3**: *Rusophycus minutus;* **1**: Gar 14 B 2. 1; **2**: Gar 14 B 8. 1; **3**: Gar 14 B 1. 5 con también *Rusophycus furcosus*; **4, 5-8**: *R. furcosus,* Gar 6, sucesivamente 6c, 6f, 6c1, 6c2, 6g1; **9-15**: agujeros aislados, **9**: Gar B 1. 9; **10**: Gar 14 B 1.8; **11:** Gar 14 B 1. 11;**12**: Gar 14 B 2. 5; **13**: Gar 14 B 1; **14**: Gar 14 B 1; **15**: Gar 17 B 1. 10; escala= 1 mm.

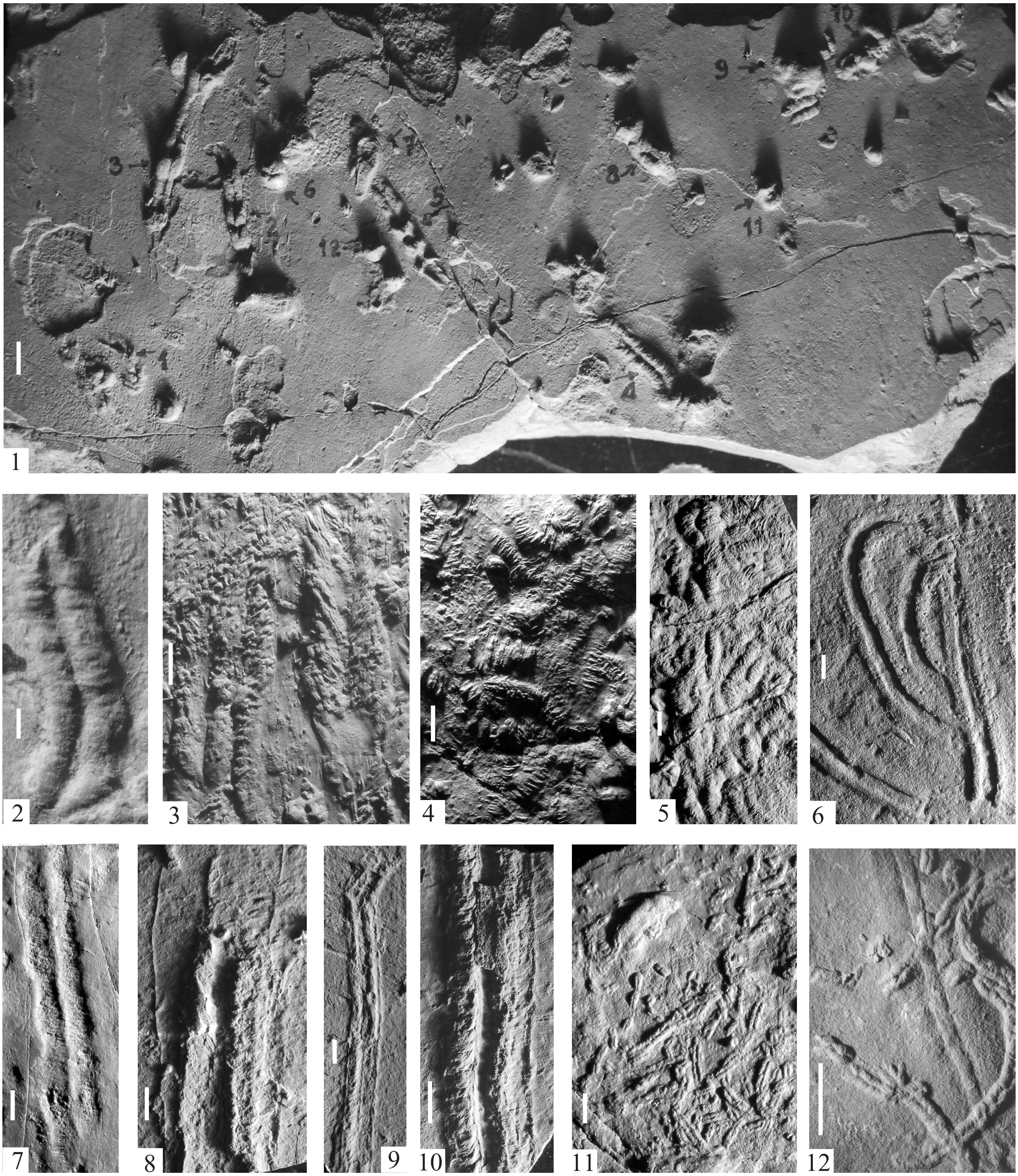

Fig. 20.- **1, 11-12**: Cubichnia and pascichnia; **1:** *R. minutus* + *R. furcosus* (Gar B 1); **11-12**: *Cruziana problematica* + *R. minutus* (Gar 5 and 5C); **2-10**: pascichnia *Cruziana problematica*; **2**: Gar 14 B 1. 4; **3-5**, **7-10**: successively Lap 177, Gar 7 H 2, Gar x, Gar 12 A, Lap 265, 280, 270, Gar 05; **7-10**: *C. problematica* with the carapace trail; scale-bar = 5 mm except for 2 = 1 mm

Fig. 20.- **1, 11-12**: Cubichnia y pascichnia; **1:** *R. minutus* + *R.. furcosus* (Gar B 1); **11-12**: *Cruziana problematica* + *R. minutus* (Gar 5 y 5C); **2-10**: pasichnia *Cruziana problematica*; **2**: Gar 14 B 1. 4; **3-5**, **7-10**: sucesivamente Lap 177, Gar 7 H 2, Gar x, Gar 12 A, Lap 265, 280, 270, Gar 05; **7-10**: *C. problematica* con la huella probable del caparazón; escala = 5 mm, fuera de 2 = 1 mm

0, 5 mm apart, occur in the median plane of a bilobate. They are present in *I. furcosus* of the Gar 14 B11 (n° 2) slab (Fig. 21. 5) and in another incomplete specimen of Gar B11 (n° 1) slab (Fig. 21. 6); but they are more spaced there and connected to the lobes

Several *I. minutus* trackways are also geometrically associated with two external, parallels furrows, spaced as the bilobates. One observe them on Gar B7 n°4 (Fig. 21.

16) and Gar B7 n° 3 (Fig. 21. 15) slabs where *I. minutus* is relayed by the appendage traces of a repichnia. This transition is visible on Lap 277 as well (Fig. 21. 14). These three trackways indicate that repichnia/natichnia/cubichnia and pascichnia were left by the same animal. On Gar B10 slab, the n° 2 trackway show that the two external furrows are duplicated (Fig. 21. 18). This duplication was already made in the preceding repichnia (cf *supra*). It is also visible on *Cruziana problematica* described *in* Bromley and Asgaard (1979: 67).

4.2.2. Smooth or slightly striated bilobates with forked prints: Isopodichnus furcosus Gand, 1993.

On the small slabs of Caunas, there are also cubichnia whose lobes are prolonged by two elongate generally bifid structures. They are laid out symmetrically compared to the bilateral plan and are transversely segmented (Fig. 21. 8-10). These trails are known from several levels of the Salagou Formation (F7 C of Caunas, F18 of Gèbre sites) but are also abundant in the Rabejac Formation (F13 site). The Rabejac trails are 2-10 mm long and may locally occur in great density (Lap 6P slab). One always recognizes there the presence of thread-like structures often pasted, emergent from 2 smooth lobes between which a small oblong trace appears (Fig. 19. 4-8). This one was already noticed on some epirelief paratypes (Gand, 1993: 81).

Isopodichnus furcosus is always isolated except on two slabs from Caunas where this cubichnia belongs to a trackway with *I. minutus* (Gar 14 B1 n° 5, Fig. 19. 3; 20. 1; Gar 14 B4 n° 2, Fig. 21. 7). In both cases, the two lobes orientation is 180° reversed compared to those of *I. minutus*.

4. 2. 3. Striated bilobates

Beautiful bilobates in epirelief and hyporelief are scattered on Lap YY (A) and X (A) slabs. They were produced in the ripple-marks and are represented by two unequal lobes, separated and drawn aside from an angle which can reach 55°. These wide cubichnia (L x l = 5, 8 x 6, 6 mm) are transversely striated. The scratches are rather strong and forked (Fig. 18. 17-19). One of these bilobates with the partially broken lobes, shows, on a few mm, the appendage imprints in Y form (Fig. 21. 3).

The second morphotype is represented by elongate bilobates definitely longer than wide (L x l = 11, 5 x 7, 5 mm) with the oblong and little drawn aside lobes at 6° angle. Each one of them consists of two parts. The internal, of rectangular form, is traversed by strong bifid scratches. The external part is rather triangular and cuts the preceding one. It is smooth to finely striated. On Lap X (A) sample, occur polyfid and oblique scratches, discordant on the internal part (Fig. 18. 16; 21. 2). Such a morphology is known in *Rusophycus* from the Upper Triassic of Greenland (Bromley and Aasgard, 1972, 1979).

This last circumvented morphotype and rolled up partially is also seen on YYA Lap (Fig. 21.4). It corresponds to *Rusophycus versans* Schlirf *et al.,* 2001 of the Franconie Triassic (Germany).

As *I. minutus*, all these striated bilobates are not always isolated but may join to form trackways connected to pascichnia (Fig. 21. 13-14).

4.3. Digging excavations ?

Based on the *Rusophycus versans* form, we have interpreted as digging excavations, may be produced by Notostraca, a great number of circumvented structures seen on slabs with repichnia/cubichnia/pascichnia (Fig. 11. 7, 13-15; 19. 9-15).

4.4. Systematic ichnology

4.4.1. Analysis and discussion.

After having compared the preceeding trails with those of various ichnogena, several of them are possible to name the cubichnia/pascichnia of the Lodève basin. They are *Rusophycus* Hall, 1852, *Cruziana* d'Orbigny, 1842 and *Isopodichnus* Bornemann, 1889 whose nomenclatural problem have been addressed by Glaessner (1957), Osgood (1970: 303), Bromley and Asgaard (1979), Pollard (1985: 283) and Pemberton and Frey (1991).

As stated by Pollard (1985), "one considerable confusion exists in literature concerning the synonymy of *Isopodichnu*s with the ichnogenera *Cruziana* and *Rusophycus"*. Thus, *Isopodichnus* was successively used to name, at the same time, cubichnia and pascichnia (Schindewolf, 1921, 1928; Linck, 1942, 1949; Glaessner, 1957, Seilacher, 1963, Häntzschel, 1975, Walter, 1983, Debriette and Gand, 1990) or to indicate only cubichnia (Osgood, 1970, Schlirf *et al.*, 2001). Each of the three preceding ichnogenera will be selected also successively to announce the same morphotype by Seilacher: *Cruziana* (Seilacher 1953)*, Rusophycus* (Seilacher, 1954) and *Isopodichnus* (Seilacher, 1960).

Based on the nomenclatural rule of priority, several authors abandonned *Isopodichnus* in favor of *Cruziana* and *Rusophycus,* although their use varied over time according to authors. Thus, Bromley and Asgaard (1972) used only *Cruziana* to name cubichnia and pascichia from the Upper Triassic of east Greenland (Jameson Land). Subsequently, Bromley and Asgaard (1979) prefered to indicate by *Rusophycus* the bilobates (cubichnia) and by *Cruziana*

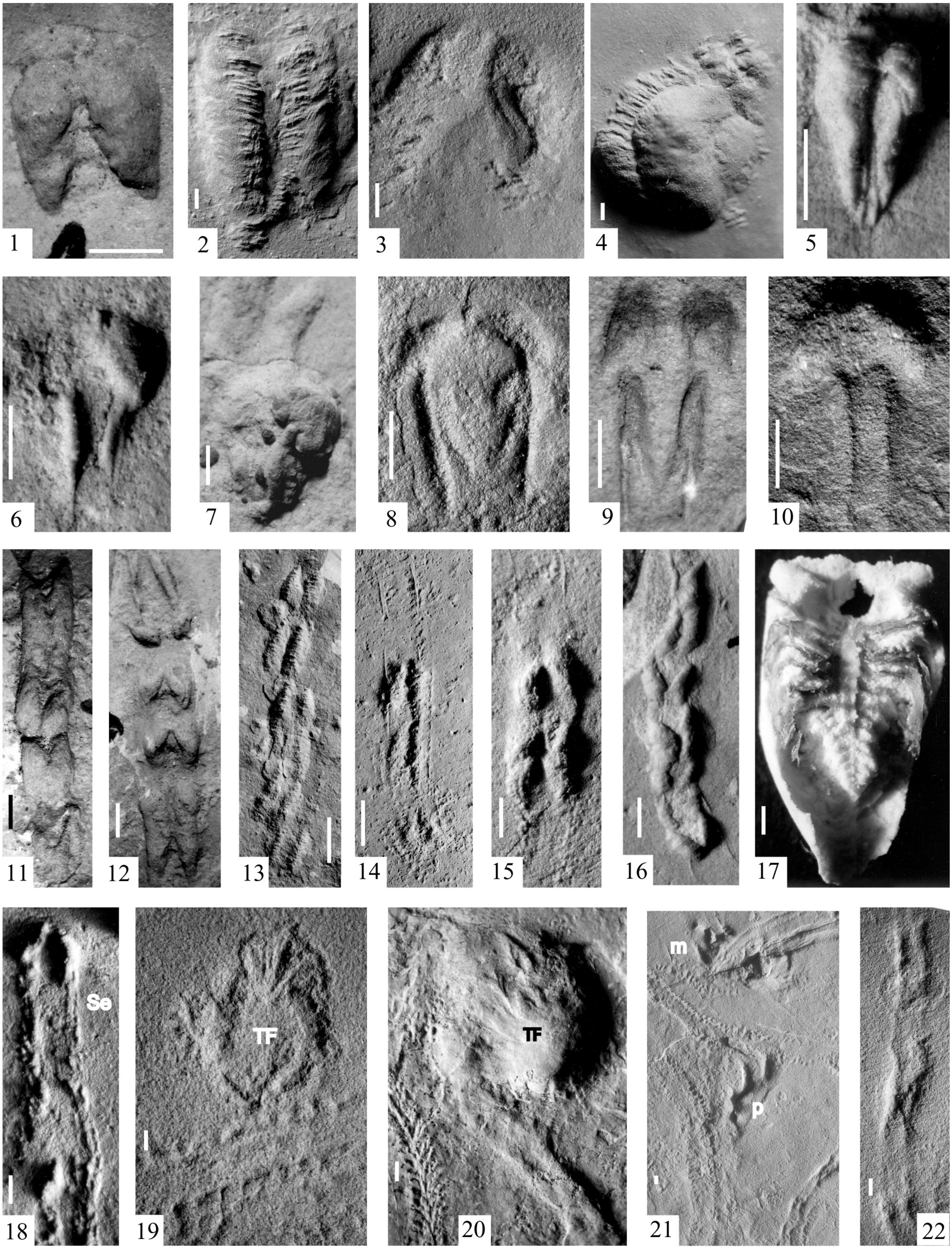

Fig. 21.- **1-16, 18, 22:** Cubichnia; **1**: *R. minutus* (Gar B 10), **2 =** *R. eutendorfensis / R. carbonarius,* **3**: *Rusophycus* sp. [(Lap X (A) n° 2, Lap YYA]; **4**: *Rusophycus versans* Schlirf *et al.*, 2001, (Lap YYA); **5-10**: *R. furcosus;* **5**: Gar B 11-2; **6**: Gar 14 B 11-1; **7**: Gar 14 B 4. 2; **8** and **10**: Ldg66; **9**: Gar 14 B 1, **11** and **16**: *R. minutus*, Gar 14 B 1 et 14 B 7-4; **12**: *R. minutus* + *R. furcosus* (Gar 14 B 1); **13**: *R. carbonarius* (Lap 648); **14** and **15**: *Rusophycus* + *A. multiformis* nov. isp. (Lap 277, Gar B 7-3); **18:** *R. minutus* with Se (Gar 14 B 10-2); **22**: *Rusophycus* sp. (Lap 220); **17**: *Lepidurus apus* ventral face moulding; **19-20:** digging holes (= T F) (Lap 05, Gar 15 B 2); **21**: pes (p) and hand (m) couple traces of Amphibian connected with *Acripes multiformis* nov. isp. (Lap 220); scale-bar = 1 mm except for 13 and 14 = 1 cm

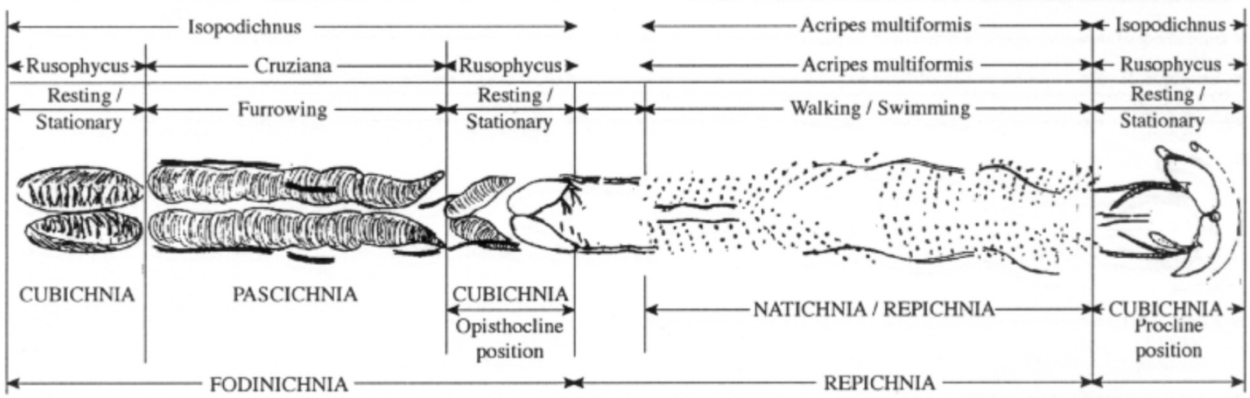

Fig. 22.- Geometric relationships between the different Permian *Acripes/Rusophycus/Cruziana* ichno-ethomorphotypes observed in the Saxonian Group of the Lodève Basin. They were due to Triopsids.

Fig. 22.- Relaciones geométricas entre los diferentes icno-morfotipos *Acripes/Rusophycus/Cruziana,* considerados en el Grupo Saxoniano de la cuenca de Lodève. Fueron hechos por triopsideos.

the pascichnia, redefining the ichnospecies *R. eutendorfensis* (Linck, 1942) and *C. problematica* (Schindewolf, 1921). Schlirf *et al.* (2001), later, emended their diagnosis.

In front of such difficulties, how to decide? Undoubtedly, by pointing out the advantages and the disadvantages that there is to use each of the three *Isopodichnus*, *Cruziana* and *Rusophycus* ichnogenera.

Isopodichnus Bornemann, 1889, was created after the first ichnologists have discussed a long time about interpretations and synonymies of *Rusophycus* (Pemberton and Frey, 1991). *Isopodichnus* is an ichnogenus which gathers cubichnia/pascichnia distributed from Cambrian to Tertiary but which was especially used to describe ichnospecies discovered in the Germanic continental Triassic (Buntsandstein), lagoon deposits (Keuper) and Carboniferous-Permian. In a unanimous way, these trails are ascribed to Phyllopoda (Seilacher, 1960; Osgood, 1979; Pollard 1985; Glaessner 1957; Häntzschel, 1975; Bromley and Asgaard 1979; Debriette and Gand, 1990; Schlirf *et al.*, 2001; Gand *et al.*, this work). What is not the case of *Rusophycus* and *Cruziana* which were used to indicate Trilobite traces. Besides D'Orbigny (1842) mentions clearly this attribution in its diagnosis, used again by Seilacher (1970). Osgood (1970) announces also these last arthropoda trackmakers for the *Rusophycus* and *Cruziana* ichnoespecies reviewed in its work.

The stratigraphic range of these ichnoespecies led Seilacher (1970) and Crimes (1970, 1975) to establish a biostratigraphy of the Cambrian and Silurian. However, for this time, such a ichnostratigraphy seems difficult by using different *Isopodichnus* species from Triassic (Schindewolf, 1928; Linck, 1942; Pollard, 1985; Bromley and Asgaard, 1972, 1979), Carboniferous (Glaessner, 1957) and Permian (Debriette and Gand 1990; Gand *et al.*, this work) because their characters are closed, even the same ones. We, thus, consider them without stratigraphic value.

Although the cubichnia can be separated from the pascichnia, in the Lodève basin, it should not be forgotten that they are met often joined together in the same trackway where there can be a continuous passage from one to another form. Which is, then, the interest to distinguish these 2 forms by using two ichnogenus in a trackway which was made by the same animal? Crimes (1970), Keighley and Pickerill (1996) *in* Schlirf *et al*. (2001) recommend to do it on referring to the limit-value of the length /width ratio concerning the cubichnia. But the first author fixes it at 1.5 and the second at 2!

Ultimately, after many hesitations and discussions, by retaining the argument that the ichno-name is necessarily independent of the trackmaker which created it and facing the need to distinguish the resting (cubichnia), and the digging/feeding (pascichnia) traces, it appeared to us more adapted to use the *Rusophycus* and *Cruziana* ichnogenera in the place of *Isopodichnus* which has the disadvantage to be too general. Thus, we follow the general tendancy already explained in Trewin (1994), Bertling *et al*. (2006)

Fig. 21 (página opuesta).- **1-16, 18, 22:** Cubichnia; **1**: = *R. minutus* (Gar B10), **2 =** *R. eutendorfensis/R. carbonarius,* **3**: *Rusophycus* sp. [(LapX (A) n° 2, Lap YYA]; **4**: *Rusophycus versans* Schlirf y *al.*2001, (Lap YYA); **5-10**: = *R. furcosus;* **5**: Gar B 11-2; **6**: Gar 14 B 11-1; **7**: Gar 14 B 4. 2; **8** y **10**: Ldg 66; **9**: Gar 14 B 1; **11** y **16**: = *R. minutus,* Gar 14 B 1 et 14 B 7-4; **12**: = *R. minutus* + *R. furcosus* (Gar 14 B 1); **13**: *R. carbonarius* (Lap 648); **14** et **15**: *Rusophycus* + *A. multiformis* nov. isp. (Lap 277, Gar B 7-3); **18:** *R. minutus* con Se (Gar 14 B 10-2); **22**: *Rusophycus* sp. (Lap 220); **17**: amoldamiento de la frente ventral de *Lepidurus apus*; **19-20:** agujeros TF (Lap 05, Gar 15 B 2); **21**: huellas de pié (p) y de mano (m) de anfibio asociadas a *Acripes multiformis* nov. isp. (Lap 220); escala = 1 mm, fuera de 13 y 14 = 1 cm

4. 4. 2. Adopted taxonomy

Rusophycus Hall, 1852.

Emended diagnosis *sensu* Schlirf *et al.* (2001): " Short, bilobate, rarely multilobate traces. Lobes predominantly bilaterally symmetrical. Convex forms (hypichnia) with a distinct median furrow; concave forms (epichnia) with median ridge. Outline ovate to coffee-bean shape; sculptured with oblique to transverse or longitudinal striae in various arrangements, or almost smooth".

Rusophycus eutendorfensis (Linck, 1942).

This ichospecies was created by Linck (1942, Fig. 5 and 7) based on transversely and obliquely striated resting traces. Also is more a short pascichnia with transverse scratches (1942, Fig. 8). The whole was included in the *Isopodichnus* ichnogenus. The *eutendorfensis* ichospecies will be defined later in the following way:

- emended diagnosis from Bromley and Asgaard (1979): "small *Rusophycus* having variable morphology. The two lobes can be separated or in contact. Commonly the fore end is splayed to varying degrees. Lobes finely to coarsely striated. In very short specimens the striations are transverse. More typical forms have two areas of striations. The forward two-third is covered with a set of oblique striae making rearward-closing chevrons. The latero-posterior area may be smooth, but normally bears a set of sublongitudinal striations. Observed range of width [including Linck's (1942) material] is 0.8-14 mm".
- emended diagnosis from Schlirf *et al.* (2001): "Small, predominantly smooth, coffee bean shaped forms with longitudinal striation along lobes; lobes either parallel or diverging at one end. Occasionnaly with perpendicular to transverse striation".

Rusophycus carbonarius Dawson 1864.

On referring to the Linck's description which specifies the only existence of longitudinal scratches, Schlirf and Uchman (2001) included in *R. carbonarius*, all other resting traces presenting transverse scratches. They proposed the following emended diagnosis: "Small, coffee-bean-shaped form with transverse to oblique, generally fine striation. Lobes parallel or sligtly gaping".

It will be noticed that in their *R. eutendorfensis* diagnosis, Schlirf *et al.* (2001) (cf *supra*) mentioned the possibility of meeting transverse to oblique scratches. What attenuates much the ichnospecific differences existing between *R. carbonarius* and *R. eutendorfensis*.

Rusophycus versans Schlirf and Uchman, 2001.

It occurs on Lap YYA slab (Fig. 21. 4) with *R. carbonarius* and *R. eutendorfensis sensu* Schlirf *et al.,* 2001.

Rusophycus minutus (Debriette and Gand, 1990).

1990 *Isopodichnus minutus* Debriette and Gand, 1990; p. 23, Fig. 4 E-G, pl. I. C.

We maintain these small ichnospecies, millimetric long, very abundant in the Rabejac Formation where they are observed with pascichnia and some *Isopodichnus furcosus*, at the base of the Salagou Formation.

Rusophycus furcosus (Gand, 1993).

Isopodichnus furcosus Gand, 1993; p. 77, Fig. 6-7.

It is a trail which is isolated on the substrate but, by twice, it was noted associated with *R. minutus* in a short V shaped trackway (Fig. 20. 1 n° 5, 12 et 16).

Cruziana D'Orbigny, 1842

Several ichnospecies of *Isopodichnus* were gathered in *Cruziana* by Bromley and Asgaard (1979) and Schlirf *et al.* (2001). The latter proposed the following diagnosis, modified from Fillion and Pickerill (1990): "Elongated, band like, bilobate or, rarely, unilobate furrows or burrows covered by herringbone-shaped or transverse ridges; with or without two outer smooth or longitudinally striated zones outside the V-markings; with or without lateral ridges and/or wisp-like markings soles".

Cruziana problematica (Schindewolf, 1921)

- emended diagnosis from Bromley and Asgaard (1979): "Small *Cruziana* having transverse to nearly transverse striae. Slight tendency for grouping of striae in pairs in some specimens. Observed range of widh 1-11 mm"
- emended diagnosis from Schlirf *et al.* (2001): "straight to curved, relatively small *Cruziana* showing faint, transverse striae which can reach the margin of the trace in shallow specimens or terminate before reaching the margin in deep specimens (modified after Fillion and Pickerill, 1990)".

These diagnoses are close of each other; that of Bromley and Asgaard (1979) being most precise. The presence of scratches pairs was observed, indeed, in several Lodève basin samples, in particular on Lap 177 slab from the Gèbre site. 25 cm long and 13 cm wide, this slab is entirely covered with parallel *Cruziana problematica*. The figures 20. 3 shows a small part of it.

Cruziana pascens Schlirf and Uchman, 2001

"Straight to meandering, sometimes rotating, undulose double rows of fine striae, perpendicular or sligthly oblique with respect to main axis of each double row; rows tend to be parallel." The authors' diagnosis shows that there is very little difference with *C. problematica*. They specified that: "there is a transition of *Cruziana pascens* to *Cruziana problematica* and to *Rusophycus eutendorfensis*, and the three taxa can be referred to the same tracemaker, such as notostracan crustaceans".

4. 5. Interpretation

The progressive passage between the *Acripes* and *Isopodichnus* = *Rusophycus* + *Cruziana* morphotypes leads us to ascribe them to Notostraca, supporting the view of previous authors (Seilacher 1963; Bromley and Asgaard 1972; Häntszchel 1975; Walter 1983, 1984; Pollard 1985; Gand 1993; Schlirf *et al.,* 2001). It remains to know the animal body parts which marked the cubichnia and pascichnia morphotypes.

By comparing the structure of the Germanic Triassic bilobates in "coffee bean" form with that made by the trilobites, many authors interpreted these Phyllopodes/ Branchiopodes trails like resting traces. It was in the same way for the Permian samples (Walter 1983, 1984; Debriette and Gand 1990; Gand 1993).

In the Lodève basin material, three cubichnia morphotypes occurs now referred to *Rusophycus.* There are bilobates with subparallel and striated lobes (*R. eutendorfensis*) and others in which, they are spaced and smooth (*R. minutus*) or transversely striated (*R. carbonarius*), asymmetrical (*R. versans*) and *R. furcosus* with divergent lobes associated with forked structures.

The first morphotype, *R. eutendorfensis,* of "coffee bean" type (Fig. 21. 2) is completely in conformity with that which was observed by Bromley and Asgaard (1972: 8) in the Triassic of Greenland. For these authors, these cubichnia are "deeply dug down stationnary" of *Lepidurus* which were made by the ventral face thorax. The comparison between the Lodève basin bilobates and the various body parts of the Permian Notostraca, in particular, those of the *Lepidurus* ventral face (*in* Gand *et al.,* 1997: 688) and current (Figs. 16. 3, 16. 2) confirm this interpretation and allow to suggest that the internal, strong and often bifids scratches are probably due to the thoracopode endopodites. The fine and discrete external scratches were made by the lamellate exopodites (noted Ex on the Fig. 16. 4-6). We agree with Bromley and Asgaard (1972: 10) that the endopodites leave their marks during stationary digging and the exopodites, which have a propellant role, make it when the animal leaves the substrate.

After comparing a current *Lepidurus* ventral face moulding (Fig. 21. 17) with the second *R. minutus* morphotype, it seems that this latter represents the posterior part. The absence or scarcity of the thoracopod imprints can be explained by the abrupt departure of the animal from its resting position which creates a water current that erases their prints. Such a behaviour was observed by Bromley and Asgaard (1972) for *Lepidurus arcticus*. They specify that in this case, Notostraca leave behind them only a "shapeless exogen depression".

From the zoological interpretation of Gand (1993), *R. furcosus* would correspond to the print of the Notostraca anterior zone joined together with the n° 5 and 6 endites, possibly more n° 3, of the thoracopod endopodite n° 1. Thus in the rare trackways where *R. minutus* and *R. furcosus* coexist (Figs. 19. 3; 20. 1; 21. 12), the first cubichnia would represent the discontinuous, stationary but active V shaped marks of the posterior thoracopods whose opening indicates the moving direction. The orientation of the second cubichnia suggests clearly that the animal passed from a frequent opistocline to procline position which is much rarer in the trackways. Seilacher (1970) noted this ahead-back swing in the trilobites digging ("ploughing tail down to head down").

R. minutus and *R. eutendorfensis/carbonarius* cubichia are locally associated with two parallel furrows (Fig. 21. 14-16). It seems logical to interpret them as the carapace edge traces.

The double furrow trackway *I. problematica* = *Cruziana problematica sensu* Bromley and Asgaard (1972) and Schlirf *et al.,* 2001) represent a longitudinal activity of Notostraca digging (= Pascichnia). The transverse striation is due to the endopodite movements which are made, above all, perpendicularly to the animal displacement, as one can see it from our video film. The scratches orientation compared to the trackway axis, in our opinion, depends of the animal speed which is higher when the scratches are oblique. But from the Seilacher (1970: 453) interpretations concerning the trilobites trails, it is possible also that the scratches direction should be connected with the animal orientation during the digging. In a procline position, only the anterior thoracopods excavate and transversely mark the substrate; obliqueness being obtained with the opisthocline position. As for the cubichnia, the two associated furrows can correspond to the edge carapace marks (Fig. 20. 7-10).

5. Stratigraphical and palaeoenvironnemental significance.

5. 1. Chronostratigraphic aspects

Acripes multiformis, various ichnospecies of *Rusophycus* and *Cruziana problematica*, were observed in many siltstone levels distributed from the base to the top of the 1500 m thick Saxonien group. Because these deposits accumulated between the Upper Sakmarian or Upper Artinskian and Tatarian (lower Lopingian), these ichnofossiles have no biostratigraphic interest. However, on the other hand, their frequency and abundance mean numerous biotopes with Notostraca in a large playa environment.

5.2. Invertebrates biotas of the playa environment

For the first time, the branchiopod crustacean presence was revealed in the Lodève basin Permian by some *Scoyenia*, *Acripes*, *Isopodichnus* (Debriette and Gand, 1990; Gand, 1994) then by body remains hundreds found with Conchostraca, insect wings in metric silstones channels of the Salagou Formation. Aside on large surfaces, in cm thick yellow-gray carbonaceous siltstone horizons with desiccation cracks, water ripples, *Scoyenia, Acripes, Rusophycus, Cruziana,* invertebrate traces were observed in many sites distributed in the Saxonian Group (Fig. 2).

From actual *Lepidurus* and *Triops* which live only during a few months of the year in temporary pools of flood plain or playa environments, we may suggest that it was also thus during the Saxonian Group deposition (Upper part of the Rabejac and totality of Salagou Formations).

In these Permian pools or biotas, from the trace fossils, one can imagine these crustaceans, swimming or walking on the bottom, marking it with the distal parts of endites, then leaving up it abruptly to swim, return there to excavate sediment in the energetic or more peacefully. According to the body part used and their behaviour, the animals produced *Acripes* trackways, *Rusophycus* resting traces whose the morphology depends of the animal body orientation (Fig. 14) and *Cruziana* pascichnia. Although none of their trails was identified, we known from body fossils remains that Conchostraca also lived in these biotas.

Unable to move out of water, it is clear that Notostraca produced traces in a submerged substrate. Trusheim (1931) and JS (this work) proved in experiments that it was possible to observe their trails under such conditions and that their fossilization was accelerated in the presence of cyanobacterians (this mechanism is explained *in* Freytet 2003 and Freytet *et al.* 2003). The subaqueous making of the trails is also suggested by the quasi-absence of the sediment repression mark around the distal appendicular ends (= withdrawal marking), noticed on the fossiliferous slabs. With that mechanism in mind, one understands better why, in our fossiliferous material, Triopsid bodies were never found connected with their trackways.

Once, on Lap 220 slab were observed an amphibian pes footprint (= p) covering an *Acripes* trackway and the hand footprint (= m) of the same animal cut by another *Acripes* (Fig. 21. 21). These results suggest that these footprints were made under water like the swimming vertebrates traces mentioned by Gand (1987) for the Autunian Group of the Lodève basin.

The trail density locally very high on certain slab surfaces may be completely bioturbed as seen on Lap 177 slab (Fig. 20. 3). Pascichnia or cubichnia can show preferential orientation. It was observed by Bromley and Asgaard (1972) and Gand (1993) for cubichnia and interpreted as a rheotropism of Notostraca as a result of currents.

Although *Acripes, Rusophycus, Cruziana* were dominant in Notostraca biotas, a few *Scoyenia,* insect, possible arachnids and some *incertae sedis* trackways/burrows (cf. *infra*) have been a little found in these *Scoyenia* facies. Insect traces are represented by two parallel lines of bi to tridactyl prints, clearly separated of each other. They belong to the Lap 273 and 283 slabs of Dio and are included in the ichnogenus *Permichnium* (Guthörl, 1934) Walter, 1983; (Figs. 3. 13; 12. 10). The second is a trackway part represented in figures 3. 16 and 12. 11, ascribed to *Octopodichnus* Gilmore, 1927 (209 A and B slabs from les Clans). This ichnogenus, discovered in the "Coconino sandstone Formation" (Permian, USA), was defined as "Apparently eight footed with tracks arranged in groups of four, alternating, two anterior impressions didactyle, two posterior unidactyle" (Gilmore 1927: 30-32). It was attributed successively to Crustaceans, Arachnida and Scorpions (Häntschell, 1975); all of them present during the Permian (Størmer *et al.,* 1973).

Also others animals produced traces *incertae sedis*. The trail seen on the Ldg 151 slab of la Tour (Fig. 12. 12) looks like to *Allocotichnus* Miller, 1880 *in* Osgood (1970, pl. 74). The "buckled" trace noticed on the Lap 270 slab of Dio (Fig. 12. 13) still remains enigmatic, as the other two which are represented in the photos 12. 14-15. The Lap 251 slab of Salasc shows small centimetric round structures, finely radiated (Fig. 12. 14), resembling *Asterichnus* Bandel, 1967, of animal origin. The discovered samples at Dio (Lap 182, Fig. 12. 15) and close to la Lieude (Ldi Gar 10 A-E) allow to observe epirelief trails with a rather bilateral symmetry. They are made of two fine curvilinear, parallel scratchs lines which meet, roughly, in the median plane, reaching up to 5 cm length. They seem close to *Laminites* Ghent and Henderson, 1966 (*in* Häntschell, 1975), a preservational variant of *Scolicia* (Uchman, 1995). This ichnogenus gathers burrows which expand parallel to the "bedding plane" stratification.

*5.3. The subenvironments of the playa: channel and overbank settings***.**

In a more general way, the *Acripes/Rusophycus/Cruziana* biotas of the Rabejac and Salagou Formations belong to the *Scoyenia* ichnofacies which were defined at the first time by Seilacher (1967). As redefined by Frey *et al*. (1984) and Buatois and Mángano (1995, 2004) it is characterized by "horizontal meniscate backfilled traces *Scoyenia, Beaconites, Taenidium*, produced by feeders, Arthropod trackways such as *Umfolozia, Merostomichnites, Diplichnites, Hexapodichnus, Permichnium and Acripes*, horizontal trails: *Cruziana* and *Rusophycus* with also "simple forms (*Planolites* and *Palaeophycus*) sinuous crawling traces (*Cochlichnus*) and banana-shaped traces (*Fuersichnus*); vertical burrows are *Skolithos*, *Cylindricum* and *Macanopsis. footprints* may be abundant".

The *Scoyenia* facies occurs in "low energy deposits between… aquatic and non aquatic environments" and may be produced mainly in lacustrine environments (Buatois and Mángano 1998) and in fluvial systems (Frey and Pemberton 1984; Frey *et al*., 1984, Buatois and Mángano; 1995, 2002, 2004).

5.3.1. The Salagou Formation

From the sedimentological and paleontological characters of beds bearing ichnofossils (desiccation marks, ripple-marks, root traces, *Acripes/Cruziana/Rusophycus*, few *Scoyenia*, *Permichnium* and *Octopodichnus*, numerous footprints), it seems that this *Scoyenia* assemblage was rather produced in a fluvial system during the overbank deposition (Buatois *et al*., 1997; Buatois and Mángano, 2002). The "…deposits correspond to floodplain waterbodies that experienced progressive drying (Buatois and Mángano, 2004). Based on ichnofossil mark characters, they infer the chronological bioturbation of the overbank deposits (Buatois and Mángano, 2002: 316) with the following steps. After the "establishement of floodplain waterbodies", they are two possibilities: 1 with a: "poorly defined traces in water-satured substrates" becoming b1: "Meniscate burrows in emergent sofgrounds" then c1: "Striated burrows in subaerally exposed firmgrounds" (b1 + c1 = *Scoyenia* ichnofacies) or 2 with a becoming b2: "well definided traces in submerged sofground" (*Mermia* ichnofacies) becoming b1, directly c1 or c2: "obliteration of animal traces by root traces".

However, from experiments with Notostraca, it is clear that *Acripes/Cruziana/Rusophycus* were not produced during emergent sofground (b1 phase) but while a and b2 phases. Except for aquatic insect larvas of Odonata, nevertheless unknown now and a few footprints (*cf supra*), it was not the same process for most footprints which were made during the b1 phase because they are surrounded by the driving back trace.

Insect wings are abundant and varied in the Salagou Formation. (Béthoux, 2003; Nel *et al.,* 1999 a-c). So that the scarcity of *Permichnium* and, more generally, the absence of terrestrial invertebrate trackway is surprising in *Scoyenia* facies; besides also, noticed in similar playa environment of other Permian basins such as Saint-Afrique (Gand, 1987) and the Luc, in Provence (Walter unpublished). However, experiments carried out with some terrestrial arthropods (Fig. 17) show us that it is not enough that the sediment is fine, wet and emerged to record the walking traces. Thus, we noticed that they were made on the substrate but disappeared quickly because of the surperficial tension of the sediment or a thyxotropical phenomenon. On the other hand, the trackways are easily made on dry sediment but probably under natural conditions, they were fastly deformed or destroyed by wind, water actions or oblitered by root traces (c2 phase). Finally they could be recorded if they are protected by a cyanobacterian film. Thus, Pierre Freytet (unpublished) explains the Fennec fox footprints preserved on dune slopes.

5. 3. 2. The Rabejac Formation.

It consists of coarse alluvial fan deposits in the basin western border passing east and upwards to two Members forming the deltaic Rabejac faciès. The lower Member contains red sandstones deposited in channels progressively replaced by the upper mud-siltstones Member (Odin, 1986). The first occurs near the Rabejac village where it contains various ripple marks, desiccation cracks, rain-drops, footprints due to Reptiles (*Hyloïdichnus major*, *Varanopus curvidactylus* / *Microsauripus acutipes, Dimetropus leisnerianus* and *Dromopus didactylus*) and Amphibians (*Batrachichnus salamandroides, Limnopus zeilleri*, *Amphisauropus latus),* roots, macroflora and invertebrates trails: *Acripes, Rusophycus, Cruziana* and burrows: *Scoyenia, Beaconites* (Gand *et al*., 2004a,b; Lopez *et al*., 2005).

These two last ichnogenera of this *Scoyenia* assemblage, specify a fluvial system with "abandoned or inactive channel deposits" in which feeders produce meniscate traces. However *Acripes, Rusophycus, Cruziana* mean the environmental change with a flood plain setting inhabited by a lot of various vertebrates, invertebrates and plants.

6. Conclusions

Acripes, Rusophycus and *Cruziana* are the three main ichnomorphotypes related with Notostraca activities. The first ichnogenus indicates walking/swimming trackways (repichnia/natichnia), the second and the third, respectively, those of stationary digging (cubichnia) and burrowing (pascichnia).

The examination of numerous fossiliferous slabs showed that there were transitions (geometrical continuity) between the three ethomorphotypes repichnia/cubichnia and pascichnia (Fig. 22). Based on experiments undertaken with current *Lepidurus*, it was shown that *Acripes, Rusophycus* and *Cruziana* could be attributed to Notostraca. They also prove that these trails were made under water and that their fossilization could be accelerated by cyanobacterians.

With the horizontal meniscate traces *Scoyenia* and the *Permichnium* trackways, both due to insects and *Octopodichnus,* may be produced by arachnids, the previous traces constitute an assemblage that define the *Scoyenia* facies. It characterizes overbank deposits which established in an inunded and dessicated periodically flood plain.

In Rabejac and Salagou Red Formations of the Lodève Permian basin, the *Acripes, Rusophycus* and *Cruziana* abundance testifies to the existence of temporary pools inhabited by crustacans and numerous Conchostraca (= Spinicaudata + Laevicaudata), these last only known from body-fossils. From sedimentological and paleontological data, it is therefore possible to imagine a playa environment under arid climate which lasted during most of the Permian period, possibly between the Sakmarian/ Artinskian (Cisuralien) and the Lower Lopingian.

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