Middle Triassic archosaur population structure: interpretation based on *Isochirotherium delicatum* fossil footprints (Southern Alps, Italy)

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Abstract

Well-preserved archosaur footprints have recently been found on a single bedding plane in the Italian Alps. The tracks are referable to *Isochirotherium delicatum* Courel and Demathieu 1976, a form that was identified for the first time at the Anisian–Ladinian boundary in the area of Argentières (Ardèche, France). The *Isochirotherium delicatum* footprints and trackways from Gampenpass represent a possible social group or ‘herd’. Estimating the age of the trackmakers from the examination of the footprints is difficult and complicated by the fact that the sample can be divided into two groups of tracks (distinguishable by the L/W, cross axis and interdigital angle). The diversity of the tracks is here interpreted as an indication of sexual dimorphism. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Middle Triassic; archosaur; footprint; social group; sexual dimorphism

1. Introduction


Well-preserved footprints have been recently found in western Trentino near Bolzano (northern Italy). The ichnosite was exposed by road works (S.S. 238, km 11.7) at an altitude of nearly 1600 m near the Gampenpass (Fig. 1) and the village Unsere Liebe Frau im Walde (ULF). The trampled layers consist of red, grey, and yellow sandy to marly dolomites and marly sandstones probably deposited in a relatively arid transitional continental to marine environment characterised by coastal delta mouth bars (Avanzini and Neri, 1998).

The most abundant footprint association oc-
curs on a dark red siltstone layer coated by a submillimetre-thick veil of yellow shale close to the transition from the Voltaggo to the Richthofen Conglomerate (upper Pelsonian—lower Illirian in age). All the footprints (46) described in this paper occur on a single bedding plane, and on a surface that is smaller than 2 m². The specimens are stored at the Museo Tridentino di Scienze Naturali (Trento, Italy).

The footprints are well defined. The feet of the trackmakers crossed a surface of firm or stiff mud and sank to depths of no more than a few millimetres, leaving distinct and sharply defined footprints that lack collapsed shaft walls, significant marginal ridges and ejecta (Fig. 2). Marginal ridges were weakly developed in some cases, and were limited to only one side of the shaft. The footprints preserve fine anatomical details, and in some cases an impression of the skin can be recognised (Fig. 2B).

The trampled layers reveal desiccation fractures at an early stage of growth (Fig. 2A). The absence of trampling by later trackmakers, and lack of erosion features, suggest that the duration and severity of the modifying events that took place after the impression of the footprints, and before final burial was very short. A relatively large group of archosaurs (at least 16 individuals), therefore, shared the same habitat, and left their traces in a very small area over a brief period of time.

2. Systematic ichnology

The tracks are referable to Isochirotherium delicatum Courel and Demathieu, 1976. This form was identified for the first time at the Anisian—Ladinian boundary near Argentière (Ardèche, France) (Courel and Demathieu, 1976; Courel et al., 1979; Demathieu, 1984; Gand, 1978). Their morphology is distinctive. The footprints are longer than they are wide, with an average length to width ratio \((L/W)\) of around 2.4 (Courel and Demathieu, 1976). Digit impressions II and III are almost equal in length, and are decidedly the longest. The digit I impression is very small and thin, and parallel to digit II, from which it is almost indistinguishable. The impression of digit IV is shorter than I and separate from III.

Digit V is characterised by the presence of a large metatarsal—phalangeal pad impression. Phalangeal pad impressions can be observed on all the digits that end with robust claws. The claw impressions of digits II and III are robust and triangular. Those of the fingers I and IV are thinner and arched. The handprints are very small (about 1/5 of the length of the footprints) with short, small and variable digit traces (Fig. 2C,D).

3. Possible palaeontological attribution of the trackmakers

In the ichnogenus Isochirotherium the dominant pes digit impressions are II and III. Digit IV is reduced and is separated from the group of I–III.
Normally, the tendency towards tridactylism is concentrated in the first three digits (Haubold, 1971; Haubold, 1983), but in Isochirotherium delicatum, the crocodile-like functional prevalence of digits II and III is particularly marked, as is the reduction of digit IV and I. The configuration of the impression of digit V, and its relationship with the metatarsal–phalangeal articulation is also characteristic, suggesting the relatively elevated position of the metatarsal bones with respect to the ground (Courel and Demathieu, 1976). The very small hands and the extremely narrow track-

Fig. 3. The Isochirotherium delicatum samples from the Gampenpass site shows a wide dimensional range, with length values that vary from 27 to 90 mm. The most remarkable features are the division into two clusters and the presence of both slender and robust forms. (A) ULFMA2. (B) ULF30/1. (C) ULF1/1. (D) ULF4/1. (E) ULF9/1. (F) ULF2/1. (G) ULF53 (scale: 5 cm; ULF = Unsere Liebe Frau, the name of the village near the site).
way seem to indicate specialised locomotion in which the hind limbs played the dominant role.

Among Middle Triassic archosaurs, some small-bodied proterochampsid forms of the South America Ladinian (i.e. *Chanareasuchus*) show a much-reduced digit V with a general foot morphology that is very similar to the crocodilians (Romer, 1972; Sereno, 1991). Therefore, we believe, that *Isochirotherium delicatum* tracks could represent archosaurs, which were possibly related to proterochampsids.

4. The Gampenpass sample

The tracks (a total of 46, representing 16 individuals) have lengths (*L*) ranging from 27 to 90 mm. The width (*W*) of the footprints varies from 9 to 48 mm. The measured shoulder–hip length (gleno–acetabular distance: sensu Leonardi, 1987) of the trackmakers varies from 102 to 308 mm, and allows an estimation of a possible total length of the individuals that varied from 400 to 1500 mm. The *L/W* ratio (from 3 to 1.4) is relatively constant up to a *L* equal to 58 mm (Table 1). Above *L* = 58 mm, there are two groups characterised by a different length/width ratio, a different divarication angle of the digits I–V, and a different position of the metatarsal–phalangeal articulations that would suggest a slightly different functional anatomy. The generally good preservation of the ichnites would indicate that the diverse morphology of the footprints corresponded to real differences in the anatomy of the trackmakers’ feet (Figs. 3 and 4).

The footprints belonging to the largest of the two groups indicate a slender foot (slender form) with a *L/W* ratio that is always greater than 1.8. In these prints the value of the cross axis exceeds 86°, and the divergence angle of digits I–V is <56° (Fig. 4A). In the second group the tracks are shorter and stouter with greater interdigital angles (robust form). The *L/W* ratio is smaller than 1.8, the cross axis is always <78° and the I–V divergence is greater than 56° (Fig. 4B). The posterior pad (V) is shorter (i.e. less slender or elongate) in the robust form.

Cross axis, interdigital angle I–V and *L/W* ratio

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Differences are also confirmed by Landmark analysis (Karl and Haubold, 1998), which indicates differences in symmetry between the slender and robust varieties. For example, the slender toed forms have a pes axis (digit III axis) that is oriented more towards the anterior (i.e. close to the trackway axis), and the axis defined by the metatarsal–phalangeal pads is almost perpendicular to this long axis. Thus the geometry is in the form of a symmetric cross (Fig. 4). By contrast, when placed in the same orientation, the pes long axis of the robust form is directed slightly more out-
wards, and the metatarsal–phalangeal pads make a more oblique angle. Thus the foot of the robust form appears to be more asymmetric.

5. Archosaur ontogeny and population structure

It is very difficult to correlate tracks with specific kinds of archosaurs at low taxonomic levels (ichnogenus and ichnospecies), or prove that an ichnoassociation represents a truly monospecific association. Lockley (1994) affirms that the tracks that most probably represent monospecific assemblages are those obtained for a single ichnotaxon, and from a single bedding plane. But this is uncommon, and often an association derived from the same ichnofacies is considered monospecific when spread over several relatively closely spaced stratigraphic levels within a given facies (Lockley, 1994; Matsukawa et al., 1999).

Despite unanswerable questions, footprints undoubtedly offer various advantages. It is possible to obtain more abundant information on size–frequency from an ichnoassociation than from a thanatocoenosis of bones, because the fossil ichnoassociations register live populations and their activity over very short time periods. Recent studies have demonstrated that, in modern vertebrate associations, the tracks were made over a period of a few days or weeks and that they were made by individuals that formed part of the same local population (Cohen et al., 1993).

The use of footprint data in the study of vertebrate ontogeny and population structure must take account of the fact that within a particular ichnotaxon the track size is a reflection of vertebrate body sizes and, therefore, their relative age. Studies of modern elephant tracks, living archosaurs or lepidosauromorpha footprints (i.e. *Varanus, Tupinambis*), and bird tracks (ostrich) show that this positive correlation holds true for several large mammals, birds and reptiles (Farlow and Britton, 2000; Farlow and Pianka, 2000; Leonardi, 1975, 1984; Western et al., 1983).

Matsukawa et al. (1999, p. 39) affirm that “Estimation of the age of dinosaur and other extinct reptiles is an intriguing but [difficult] problem.” We know that the age is related to size, but the exact relationship is unknown. Only a few studies have mentioned relative age estimates based on dinosaur tracks (Lockley, 1994; Matsukawa et al., 1999), and no studies have mentioned growth curves based on other fossil archosaurian (nondinosaurian) tracks.

Among dinosaurs, ornithopod population structure was inferred from a large sample of footprints (*Caririchnium leonardii*) from the mid-Cretaceous Dakota Group of Colorado, New Mexico and Oklahoma (Matsukawa et al., 1999). Allometric analysis suggests a growth curve that can be subdivided into three segments: juvenile (possibly yearlings), sub-adults and adults.

6. *Isochirotherium delicatum* population structure

The Gampenpass sample was subdivided into seven size classes based on the average length of the tracks where animals of the same size class have roughly the same pes length (from 25 to 95 mm). By assuming that footprint dimensions are related to age, footprint size classes should correspond to age classes. Size distribution of the Gampenpass sample shows that the large tracks are more abundant than small ones and that there are only a few very large individuals (Fig. 5). If size classes are not the products of taphonomic or ecological phenomena, then we can infer that our
sample represents a population where the adults were predominant. The lack of small tracks in dinosaur and archosaur footprint assemblages has been attributed to the poor preservation potential of small tracks as well as to rapid early growth rates (Leonardi, 1981).

Little is known about the growth rates and longevity of fossil reptiles. However, the life history and longevity of some fossil reptiles compares well to that of many modern reptiles of similar body size (Leonardi, 1984; Sander, 1990). It is also possible that the average-sized adults of Isochirotherium delicatum trackmakers were five to seven years old and did not get much older. This age estimate is derived from a comparison with estimated ages at which various small theropod dinosaurs reached sexual maturity and died (Chinsamy, 1990; Reid, 1993; Varicchio, 1993).

From the studied sample it is also evident that, with increasing size, pes length decreases relative to the gleno-acetabular distance (shoulder–hip length) – a pattern similar to that observed by Farlow and Britton (2000) in Alligator mississippiensis.

The most remarkable features of these footprint groups is the division into two clusters and the presence of both slender and robust forms on the same trampled layer.

From a theoretical point of view it would seem almost impossible that two similar species could exist simultaneously and optimally in space and time if they occupied identical ecological niches (Huxley, 1974). So the tracks could belong to the same ichnotaxon, and the different clusters identified by dimensional analyses could represent intraspecific dimorphism, i.e. sexual dimorphism.

The footprint cross axes and the footprint lengths were plotted against their divergence angles and widths, and yielded two scattergrams (Fig. 6). The portion of the graphs that includes slender forms also includes all the small individuals (Fig. 6A), whereas robust individuals appear only once footprint length is about 60 mm or more, suggesting that footprint robustness was attained only when a particular size was reached (i.e. an advanced age) (Fig. 6B). Such mid- or late-life ontogenetic development of secondary characteristics is not uncommon in vertebrates. The graph also suggests that slender specimens might have grown to a larger absolute length than stout specimens (Fig. 6B).

The size–frequency distribution of the two main footprint variants in the studied samples supports the contention that robustness develops at, or near, sexual maturity: no juveniles (size class 1–2) are robust. Among sub-adults (size class 4), slender forms are predominant. The number of slender and stouter forms is similar. A bimodal variation has also been observed in the skeletal remains of Plateosaurus (Weishampel and Chapman, 1990) and Syntarsus (Raath, 1990), and was interpreted as sexual dimorphism.

7. Discussion

Though it has been suggested that some of the variety seen in chirotheroid tracks may be due to sexual dimorphism (Treasise, 1996; Lockley and Meyer, 2000), no studies have postulated sexual dimorphism based on quantitative studies of fossil footprints. Lockley (1999a,b) has also suggested that there is a lawfulness to the polarity between slender (narrow) and robust (wide) archosaur tracks that is coherently related to the morphodynamics of whole body growth, and thus to the relative size of pes and manus, which in the case of chirotheres varies between what Peabody (1948) calls large manus and small manus forms.

Fig. 6. (A) Relationship between Isochirotherium delicatum footprint cross axis and digit group I–V divergence angle. The division into two clusters is evident. Black circles represent robust forms, open circles represent slender forms. The portion of the graphs that include slender forms also includes all small individuals. (B) Relationship between footprint length and width. Robust individuals (black circles) appear only once footprint length is about 60 mm or more (sexual maturity?). The graph also suggests that slender specimens (open circles) might grow to a larger absolute size than stout specimens.
Treasise (1996) observed that Chirotherium tracks at certain sites often fall into two distinct categories, slender and stout. Slender tracks are tentatively attributed to females, whereas the stouter tracks are attributed to males. Although such an interpretation is largely conjectural, in several modern reptiles sexual dimorphism is well represented in footprint dimension (i.e. Iguana and Alligator).

It is therefore possible that the Isochirotherium delicatum variation in slender and stouter forms might reflect sexual dimorphism, and not taxonomic diversity.

If the morphological variation is sexual, however, which morph represents which sex?

Sexual dimorphism in living animals is typically associated with body size and/or secondary characteristics. In living reptiles such as Iguana and Alligator the male may grow as fast and as large as the female, and late development, especially in male secondary sexual characteristics, has been demonstrated for several extant animals, and usually in association with social hierarchies (Sampson and Ryan, 1997; Farlow and Britton, 2000). The classic explanation for one sex being larger than the other is competition within the larger sex for mating with the smaller. Generally, this means big males. The possible reasons for sexual dimorphism in size include the exploitation of different niches, and energy considerations connected with rearing the young. Whilst the reasons for males being bigger than females are well understood, reasons for the opposite condition are less so. However, with the exception of mammals, examples of larger females are to be found in all vertebrate groups. Incidentally, sexual dimorphism is marked in many invertebrate groups where the females may be gigantic in comparison with the males.

Only a few studies have documented sexual dimorphism in non-dinosaurian reptiles (Sander, 1989, 1990), but the identification of each sex could not be unequivocally determined. Among dinosaurs, sexual dimorphism in the ceratopsian subfamily Chasmosaurinae shows that the largest individuals may represent the male morph (Farlow and Dodson, 1975; Lehman, 1990). Raath (1990) suggests that in the small theropod Syntarsus the robust morph might represent females. The case of two skeletons of Coelophysis bauri from Ghost Ranch quarry (AMNH 7223 and AMNH 7224; Colbert, 1989), one showing a long skull, long neck, and small forelimbs, the other showing a shorter skull, shorter neck but larger forelimb, is cited as another example of sexual difference. Colbert (1990) suggested that the skeleton with the larger skull, the longer neck, but the smaller limbs is a male, on the basis of the inference that a large skull and a long neck were advantageous in predation and intraspecific combat.

8. Conclusion

The Isochirotherium delicatum footprints and trackways from Gampenpass represent a sample from a single bedding plane, and indicate a possible social group, such a sample of the same local population.

Using footprint length as an arbitrary measure of age, seven relative age intervals have been identified, allowing the construction of an age pyramid, from which one can infer the age structure.

Based on length measurements alone, the adult specimens seem to have been predominant. The footprints of the inferred adult trackmakers may be divided into two groups, distinguishable by \( L/W \) ratio, interdigital divarication angles, and cross axis angles. Both groups are represented by a similar number of individuals, perhaps indicating a balanced population structure (i.e. similar numbers of males and females). Although it is not possible to affirm with certainty the reason for the differentiation into two groups, it seems reasonable to suggest sexual dimorphism, possibly with the females being long and slender and the males being short and stout.

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